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TOPICAL REVIEW

Controlling legs for locomotion—insights from robotics and neurobiology

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Abstract

Walking is the most common terrestrial form of locomotion in animals. Its great versatility and flexibility has led to many attempts at building walking machines with similar capabilities. The control of walking is an active research area both in neurobiology and robotics, with a large and growing body of work. This paper gives an overview of the current knowledge on the control of legged locomotion in animals and machines and attempts to give walking control researchers from biology and robotics an overview of the current knowledge in both fields. We try to summarize the knowledge on the neurobiological basis of walking control in animals, emphasizing common principles seen in different species. In a section on walking robots, we review common approaches to walking controller design with a slight emphasis on biped walking control. We show where parallels between robotic and neurobiological walking controllers exist and how robotics and biology may benefit from each other. Finally, we discuss where research in the two fields diverges and suggest ways to bridge these gaps.

1. Introduction

Walking, the most common terrestrial locomotor form in animals, is a cyclic motor behavior. When walking, the legs alternate between two main phases: stance serves as power stroke and propels the organism relative to its environment and swing serves as return stroke and re-establishes the starting position for the next stance phase. These two phases are generated by the cooperative action of a number of leg segments, for example femur, tibia and foot in mammals or coxa, trochanter, femur, tibia and tarsal segments in insects. To generate steps, the motion of the leg segments is finely coordinated by one to several dozen muscles (see section 2.1.1). Each muscle individually contributes to the generated leg movement through its specific biomechanical properties (e.g. Ahn and Full (2002), Ting *et al* (2000), for review see Chiel *et al* (2009), Ting and McKay (2008)). The number of legs animals use for walking varies widely: humanoids use two, tetrapods four, insects six, arachnids eight, crustaceans ten and myriapods up to several dozen. This leads to great versatility and flexibility of

locomotion with a broad range of speeds from less than one body length per second to 32 in ants (Hughes 1952, Wilson 1965, Alexander 1989, Zollikofer 1994, Wosnitza *et al* 2013). Animals with four legs cover the range of velocity by choosing speed dependent gaits that allow for energetically optimal propulsion across the range of speeds (Hoyt and Taylor 1981, Alexander 1989). A larger number of legs is favorable to ensure stability in unpredictable environments, e.g. when not all legs can contact the ground. Finally, legged animals can negotiate complex environments by climbing stairs and stepping or climbing over obstacles, etc (e.g. Bläsing and Cruse (2004), Ritzmann *et al* (2012)). Thus, even though wheels allow for faster top speeds on flat ground, walking has the advantage of enabling efficient locomotion in a large variety of environments.

The versatility and flexibility of walking also makes it a highly attractive form of locomotion for robots. First attempts at building human or animal-like mechanisms date back as far as ancient Greece and China. Development of modern walking robots was enabled by advances in computer, sensor and actuator

technology and started in the 1960s, but early work goes back to the 1940s. Refer to Raibert (1986) and Song and Waldron (1989) for overviews of the early stages in the development. A more recent overview is given by González de Santos *et al* (2006). Bekey (2005) gives a comprehensive overview of historic and current walking machines, their hardware and control systems.

For decades, the performance of walking machines was severely limited, but much progress has been made in recent years. Still, the performance is limited when compared to animals. For example, even though top speeds of robots have been increasing steadily (see section 3), they are still only a fraction of those seen in animals⁵ and variations of (or unpredictable incidences in) the environment can be dealt with, but not yet to the degree of perfection displayed by animals (see section 3, especially section 3.4.1).

The goal of this review is threefold: (1) to give walking control researchers from biology and robotics an overview of the current knowledge in both fields without a restriction on per se biorobotic approaches (cp. e.g. Beer *et al* (1998)). We personally have found the lack of such an overview to be an obstacle for collaboration in a joint research project involving neurobiologists and roboticists. Furthermore, ‘biologically motivated’ controllers in robotics often appear to be based on a limited understanding of the current knowledge on the neural control of walking, indicating a lack of readily accessible reviews of the two fields. Since the goals and available techniques in robotics and biology only partly overlap, the detail of what is known about the different aspects of walking control in both fields differs substantially. We therefore chose to structure this review into two main parts, section 2 on the neural control of animal walking and section 3 on walking robots. In section 2 we will summarize today’s knowledge on the neurobiological basis of walking pattern generation in animals emphasizing overarching common principles across the animal kingdom. This review tries, like (Büschges *et al* 2011), to bridge between various model animals to a broader extent than other recent accounts, e.g. (Zehr and Dusen 2004, Yang and Gorassini 2006, Pearson 2008). Mainly the neurobiology of human, cat and stick insect walking is presented—for other animals only where important additional data is available. Since the details of the neurobiology of human locomotion are, as of yet, unknown, the reader will notice that the corresponding description is rather incomplete. For all animals a focus is put on the organization and

operation of the individual leg controllers for locomotion since the knowledge on this aspect is the most complete. In section 3 we will review the technology of walking robots. Due to the very large body of work on the design and control of walking machines, we cannot attempt to cover all research. Instead, we will review the basic approaches to walking controller design and try to point out similarities and differences with biological counterparts whenever applicable. Overall, we put a stronger emphasis on biped robots than on quadrupeds and hexapods, since there is a larger body of work in this area. (2) To show where parallels exist and how robotics and biology may benefit from each other and (3) to point out where research in the two fields diverges and to suggest ways to bridge these gaps. For example, the neural basis of intersegmental coordination in animals is largely unknown (Borgmann *et al* 2009, von Twickel *et al* 2011, Schilling *et al* 2013), whereas this intersegmental coordination is a prerequisite for any successfully operating robot. Goals (2) and (3), which constitute the critical discussion, are mainly addressed by giving cross references between the two main parts ‘Animal walking’ (section 2) and ‘Robot walking’ (section 3). Section 4 (‘conclusion’) concludes the paper and tries to indicate promising areas in which walking control researchers from robotics and neurobiology might learn from each other.

2. Animal walking

In this section we summarize the knowledge on the control of walking behavior in insects and vertebrates, focusing on the neural control of the single limb. The step cycle is characterized by four phases, which play an important role in the neural control of walking: (1) when the leg touches the substrate, the muscles move the animal into an intended direction relative to the walking surface. (2) Stance ends when the leg reaches a posterior extreme position and is then lifted off the ground, initiating swing. (3) During swing, the leg moves relative to the body toward the next foothold. (4) The swing phase ends when the leg touches the ground, completing the cycle.

In the following, we describe the organization (section 2.1) and operation (section 2.2) of the leg muscle control system and give examples of higher order neural control during locomotion (section 2.3). Finally the importance of simulations in biological walking control research and as a link to robotics is explained (section 2.4).

2.1. Organization of the leg muscle control system

2.1.1. Biomechanics

The legs of animals are complex appendages that allow flexible movements under all kinds of varying conditions, e.g. walking on level ground, walking on inclines, stepping across gaps or obstacles, climbing up

⁵ The Cheetah robot developed by Boston Dynamics www.bostondynamics.com/robot_cheetah.html is currently (by far) the fastest legged robot at approximately 10 body lengths s⁻¹ (45.5 kmh, estimated length 1.3 m), while the cheetah animal can run at approximately 20 body lengths s⁻¹ (93 kmh, Wilson *et al* (2013)) and ants up to 32 body lengths s⁻¹ (Zollinger 1994). The fastest (freely running) biped reaches 10 kmh (Takenaka *et al* 2009c), while humans reach approximately 36 kmh.

stairs or even walls. Feet can be placed in three dimensional space and their contact forces with the environment can be modified in a large range, depending on context. Furthermore, their passive properties provide them with robustness to perturbations. These effects are called *preflexes* (Loeb *et al* 1999) or *self-stability* (Blickhan *et al* 2007). Legs can do so, because they are multi-segmented with the segments being connected by joints. Compliance of the joint actuators, i.e., muscles, leads to compliance of the leg which is in contrast to the majority of walking machines (Blickhan *et al* 2007).

All legs show virtually the same phases of activity and functions during the step cycle and the morphology of different leg pairs is similar for hexapod and quadruped animals. However, there are notable specializations of leg pairs in multi-legged animals. Hind legs are usually responsible for propelling the animal forward, with little lateral variability and limited descending control. Forelegs have higher variability, which is under greater control of higher centers and is used for braking forward locomotion. This is in contrast to multi-legged robots, which usually use identical leg pairs.

Although the general organization scheme and further biomechanical features are shared between vertebrates and insects the segment-joint configurations differ in detail (cf figures 2(a) and (c) respectively)

The vertebrate hind limb, for example, has three main leg joints, the hip-joint connecting thorax and femur, the knee-joint located between femur and tibia and the ankle joint moving the foot relative to the tibia, figures 2(a), (c); for review see (Rossignol 1996). These three joints are operated by multiple sets of muscles, which can be organized in pairs of antagonists. For example, the anterior biceps and iliopsoas at the hip joint of the hind leg respectively extend and flex the thigh. Due to their antagonistic arrangement, their nonlinearities and their low impedance, biological actuators (muscles), may act as motors, brakes, springs and struts (Ahn and Full 2002). Importantly, some of the muscles span two joints. These so-called bi-articulate muscles serve important biomechanical functions when the leg is in rather stretched positions (Rossignol 1996). One example is the posterior biceps spanning from the hip to the shank in the hind leg. Finally, the foot together with the toes allow for highly adaptive contact of the foot with the environment, for general overview see (Rossignol 1996). Amongst others, this led to the formulation of the principle of ‘proximal actuation and distal compliance’ of biological legs (Lee *et al* 2008). The vertebrate leg is operated by almost three dozen muscles. In mammals the three main leg segments are aligned in a vertical plane, parallel to the animals’ body-axis. The legs of lower vertebrates, e.g. anurans and salamanders, are composed of only two main segments and also aligned in a common plane. Here, however, the leg-plane is perpendicular to

the body-axis, for further description see (Ritzmann *et al* 2004).

Insect legs share design features of the leg organization of lower vertebrates. The legs are often arranged almost orthogonally to the body-axis and are moved laterally to the thorax, as well as forward and backward, to generate stance and swing phases (review in Ritzmann *et al* 2004). The insect limb is also multi-segmented (figure 2(b)): the basal joint, i.e., the thoraco-coxa joint, moves the coxa forward and backward, the coxa-trochanteral joint serves levation and depression of the leg, as does the trochanter-femur joint in those species, in which two adjacent segments are not fused. The femur-tibia joint serves flexion and extension of the tibia. Finally the multi-partite tarsus is connected to the tibia via the tibia-tarsus joint. In some insects the parallel orientation of the distal leg joint axis from the coxa-trochanter joint to the tibia-tarsus joint creates a single leg plane that is moved by the thoraco-coxal joint relative to the insect thorax. Such a situation exists for example in the stick insect middle leg (Cruse and Bartling 1995, Zill *et al* 2012). The individual segments of an insect leg are operated by antagonistic muscles at each joint (e.g. Snodgrass (1935), Marquardt (1940)). For example, levation of the trochanter is mediated by the levator trochanteris and depression of the trochanter is mediated by the depressor trochanteris. The muscle that moves the segments of the tarsus, the retractor unguis, is an exception. Upon contraction this tripartite muscle flexes the tarsal joints, while extension of these joints is operated by passive elastic properties of the joint membranes (Radnikow and Bässler 1991). Altogether there are more than a dozen muscles in charge of operating the insect leg.

In vertebrate as well as in insect limbs the activity of the antagonistic muscles controlling the main leg joints shows a fine grained pattern of activity with much more complexity than the two phases of a step might lead the observer to expect (figures 2(c) and (d)). Further information on the setup of the muscle skeleton system can be found in various review articles (e.g. (Rossignol 1996; section 12, 173–216), (Graham 1985a; 31–140), Bässler (1983)).

2.1.2. Sense organs

It is common knowledge today that the generation of a functional walking motor output crucially depends on sensory signals reporting the actual movements from the periphery (Clarac *et al* 2000, Pearson 2000a, 2000b, Grillner and Wallen 2002, Büschges and Gruhn 2008, Büschges *et al* 2011, Fouad *et al* 2011). These sensory feedback signals control the magnitude and the timing of motor activity during stepping (figure 3). In doing so they assist the generation of ongoing stance or swing or initiate transitions between them and serve interleg coordination. At the same time sensory feedback promotes both robustness and

adaptivity of the motor program for walking (Cruse 1990, Büschges and Gruhn 2008).

The relevant sense organs are located on and/or in an animals' leg. They report specific information about the actual movements generated, for review see (Büschges and El Manira 1998, Büschges *et al* 2011), as well about forces generated or load encountered, for review see e.g. (Duysens *et al* 2000, Zill *et al* 2004, Büschges *et al* 2011). Prominent evidence for the importance of sensory feedback in generation and control of animal stepping derives from experiments in which individual legs of an animal are forced to step on a motor driven treadmill. For example in the stick insect walking with five legs on a passive treadmill, the sixth leg stepping on a separate motor driven treadmill will adapt to the speed of this (Foth and Bässler 1985a, 1985b), the sensory signals from the leg moved by the belt will *entrain* the neural networks generating the motor activity for stepping (Foth and Bässler 1985a, 1985b). Similarly, spinal and decerebrate cats will adapt their stepping rate to the speed of a motor driven treadmill over a wide range of speeds. Thereby, stance duration is modified according to the change in speed, while swing duration is kept fairly constant (Pearson 2008).

The legs of animals are equipped with a large number of sense organs, which can simultaneously code for multiple sensory qualities, e.g. for position, velocity and acceleration in proprioceptors, e.g. Burrows (1996), Zill *et al* (2004, 2012). They provide (1) proprioceptive information about movement and position of the legs' segments, (2) the forces generated in the muscles as well as the load on the muscles and (3) they report touch of the skin or exoskeleton or ground contact. Robots have fewer sensors which encode exactly one physical property (such as position or force) at a fixed sensitivity over the whole range of measurements. Today's knowledge on the role and processing of sensory feedback contributing to the control of leg stepping in animals mostly concerns sensory signals about force and load and sensory signals about movements and position of a leg segment, while similar information is only sparsely available with respect to sensory feedback about ground contact.

Force and load perception In vertebrates the golgi-tendon organs (GTOs), the sensitive structures which are situated in the tendons of all skeletal muscles (Eccles *et al* 1957, Houk and Henneman 1967, Duysens and Pearson 1980), report tension and changes in tension in the muscle tendon to the nervous system. Such tension can either arise from forces generated by muscle contractions against a resistance or from load arising from the pure weight of an animal. In anthropods the analogue sense organs reporting force and load are located in the outer skeleton of the animal. Those are the campaniform sensilla (Thurm 1964, Moran *et al* 1976, Zill *et al* 2012). They are activated when the cuticle is distorted by force or

load. Thus, both sensory systems report similar information to the CNS.

Movement and position perception In vertebrates muscle spindles (MSs) are the sensory organs sensitive to movement of the leg segments by reporting position and stretch velocity in the skeletal muscles to the CNS (Merton 1953, Lennerstrand 1972, Prochazka and Gorassini 1998a, 1998b). MSs reside inside skeletal muscles as intrafusal muscle fibers which do not contribute to muscle force production. By adjusting the activity of γ -motoneurons that innervate them their sensitivity to length changes can be modified (cf Hoffer and Loeb (1980), Prochazka *et al* (1985)), e.g. to maintain their high resolution over the full working range of the muscle. This is in contrast to robots, where the sensitivity and point of operation usually is fixed. The MSs are attached in parallel to the force producing extrafusal muscle fibers which are innervated by α -motoneurons. Based on structural specializations MSs are categorized in dynamic and static types. Their respective sensitivity can be independently regulated by dynamic and static γ -motoneurons. Furthermore, they are innervated by two types of afferent fibers: afferent fibers of the MSs signal dynamic and static aspects of muscle activity: type Ia fibers report muscle length and velocity of stretch, type II fibers predominantly report muscle length. The individual contributions of position and stretch velocity components to the Ia signal are variable, depending on the specific muscle (fiber) and the relative activation of the dynamic and static γ -motoneurons (Brown and Matthews 1966).

In anthropods three different types of sense organs report movements of the leg segment, see also (Graham 1985a, 1985b, Burrows and Hedwig 1996, Büschges and Gruhn 2008). (1) Close to a leg joint hair plates consisting of 20–30 tactile hairs can be located on the cuticle in such way that the joint membrane that connects the segments across a joint will deflect the hair sensilla when the joint is flexed (Wong and Pearson (1976), Schmitz (1986); for review see (Bässler and Büschges 1998)). (2) Internal chordotonal organs (CO) report position and movement signals of leg segments. COs reside at the base of one segment, e.g. in case of the femoral CO (fCO) at the base of the femur and are connected to the next segment, e.g. the tibia, via an apodeme (Füller and Ernst (1973); review in Field *et al* (1998)). Sensory neurons of fCOs report information about position, velocity and acceleration of the tibia (Hofmann and Koch 1985, Hofmann *et al* 1985, Matheson 1990). (3) The third type of sensor that can provide information about movement and position of leg segments are muscle receptor organs. These sensors span along muscles and are excited by changes in muscle length (Hustert 1983).

2.1.3. Neural control

Neural networks control the biomechanical motor system and are, in doing so, heavily influenced by

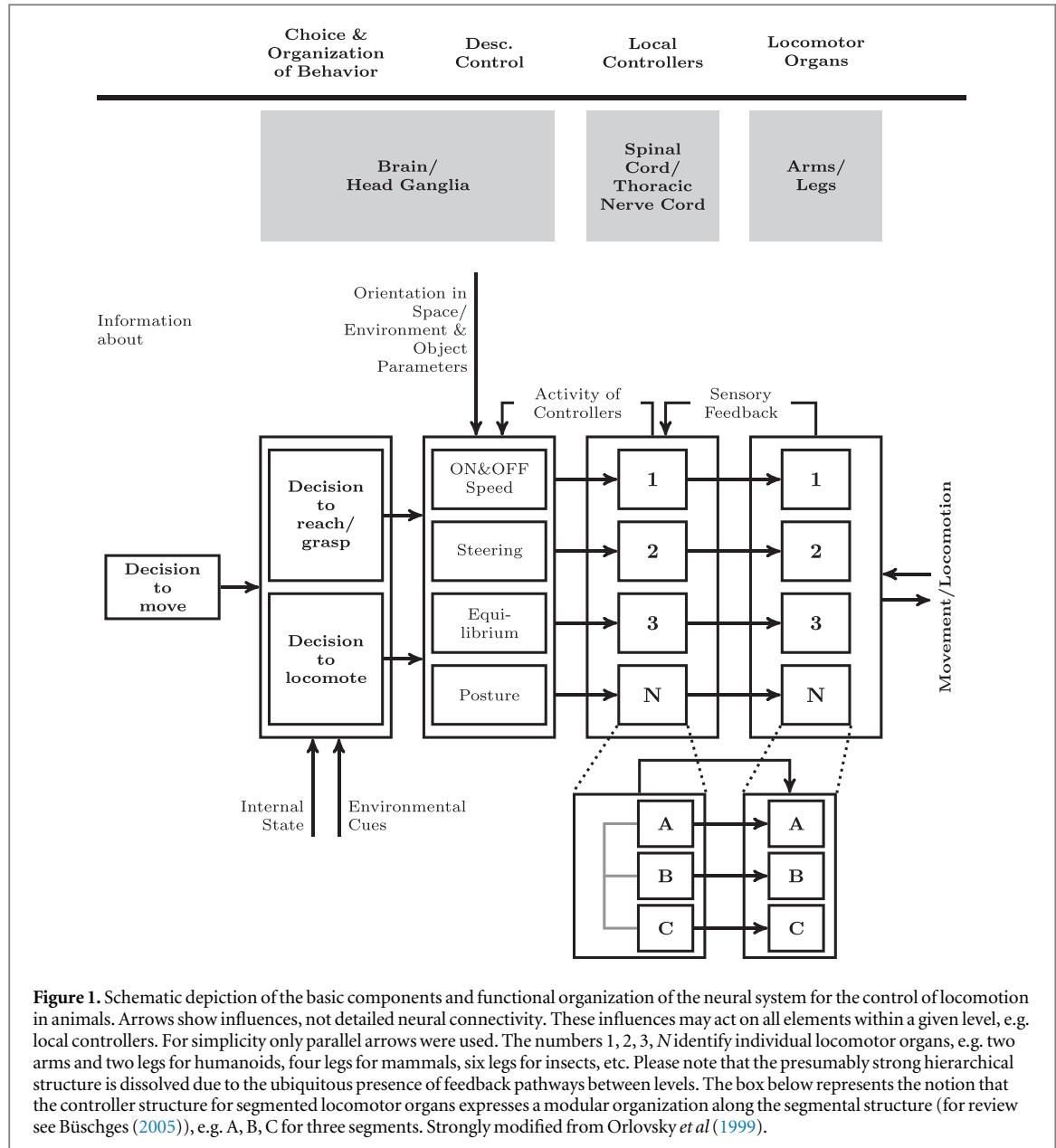


Figure 1. Schematic depiction of the basic components and functional organization of the neural system for the control of locomotion in animals. Arrows show influences, not detailed neural connectivity. These influences may act on all elements within a given level, e.g. local controllers. For simplicity only parallel arrows were used. The numbers 1, 2, 3, N identify individual locomotor organs, e.g. two arms and two legs for humanoids, four legs for mammals, six legs for insects, etc. Please note that the presumably strong hierarchical structure is dissolved due to the ubiquitous presence of feedback pathways between levels. The box below represents the notion that the controller structure for segmented locomotor organs expresses a modular organization along the segmental structure (for review see Büschges (2005)), e.g. A, B, C for three segments. Strongly modified from Orlovsky *et al* (1999).

sensory information. Therefore, the sensori-motor control interface, including all sensor inputs and motor outputs, is crucial for the operation of the neural network (for a discussion see e.g. von Twickel (2011)). Compared to robotics (cf section 3.1.2), the large number of sensor inputs and motor outputs per degree of freedom (DoF) stand out (see sections 2.1.1 and 2.1.2). Across the animal kingdom, the contribution of the nervous system to the generation and control of locomotion shares substantial similarities (figure 1; reviews in Orlovsky *et al* (1999), Büschges *et al* (2011), Grillner (2006)). The most prominent similarity is the existence of a division of function for the generation of individual aspects in the control of motor behavior among specialized areas of identifiable neural networks, each serving different contributing tasks of neural processing. In general, in the anterior parts of the nervous system, i.e., so-called higher brain

areas of all animals with segmented CNS (from mollusk to man) environmental signals, such as visual, chemosensory or tactile cues, as well as information about the internal state, e.g. hunger, fear or circadian activity, are processed (figure 1). The output of these networks drives downstream neural networks in which the decision towards the generation of a specific motor behavior to be generated is filed. Once the decision is filed, command systems are activated. The three most prominent ones control initiation and maintenance, speed and steering of locomotion. A fourth system serves maintenance of posture and equilibrium during locomotion. These systems drive the networks downstream in the CNS that represent the controllers of the locomotor organs. For each locomotor organ individual controllers, i.e., neural networks, exist. Those networks generate the rhythmic locomotor activity upon activation by descending

commands (see section 2.2.1). Coordination of locomotor organs is generated by interaction between these controllers, i.e., for the two arms and two legs for humanoids, the four legs for mammals and the six legs for insects. For most forms of locomotion the locomotor organs are segmented, e.g. the trunk in fish or the legs of animals. This is reflected by the fact that the relevant controllers are subdivided in neural networks for each segment (see below). The output of the controllers, finally, drives the muscles and thereby generates the locomotor movements. It is important to note that the impression of the neural structures underlying the generation of locomotion to be exclusively hierarchical is misleading: all levels of processing receive marked feedback from the subsequent levels (figure 1). The contribution of downstream neural control becomes particularly apparent in view of new findings on the neural mechanisms for gaze-stabilization in vertebrate locomotion: in the anuran tadpole during locomotion the extra-ocular nuclei are under the control of ascending rhythmic neural activity, which originates from the locomotor CPGs (see section 2.2.1) in the spinal cord (Lambert *et al* 2012).

Today ample information is available on the location of the neural networks in the CNS of animals that contribute to the functions mentioned above. In vertebrates, for example, the sequence of levels involved from decision making to the generation of movements of the legs, spans from cortical inputs to the basal ganglia, their disinhibition of particular neurons in the di- and mesencephalic locomotor regions, the activation of the reticulospinal system to the activation of the CPGs in the spinal cord at the level of the locomotor organs. Detailed information on the state of knowledge can be found in various review articles and text books (Grillner 2006, Orlovsky *et al* 1999, Kalaska and Drew 1993). Even though the gross anatomical organization of the neural networks involved is well-understood, knowledge is fairly limited on the detailed topology and operation of the contributing neural networks in the control of legged locomotion, for example, with respect to the explicit mechanisms in charge of mediating the above named functions. Among others, three issues are open as of today: how does the nervous system selectively control movement and posture in locomotion simultaneously? Which neural components in the local controller networks are targeted by the command systems? How do primates differ from other mammals on the mechanistic level by the cortical contribution to locomotor function?

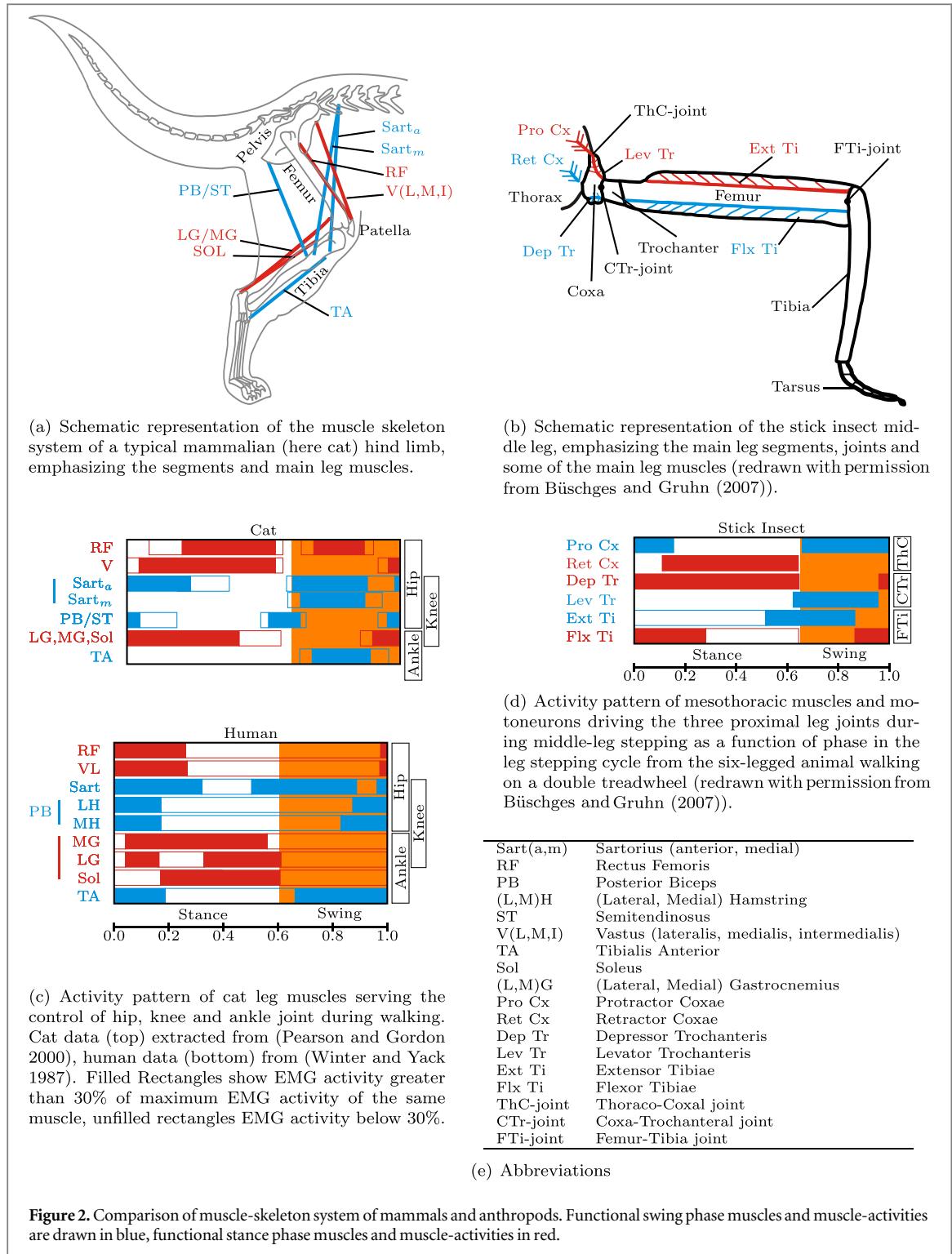
2.2. Organization of the controller architecture for stepping

In the following sections the role of sensory feedback will be reviewed for all four phases forming a stepping cycle for well-studied two, four and six legged animals. It will become clear that general principles underlie the generation of the functional stepping motor

output of an animal leg and that sensory feedback constitutes a major contribution.

2.2.1. Intrinsic factors: CPGs

It has been known for more than a century that there are neural networks in the CNS of walking animals, so called central pattern generators (CPGs, see figure 3), which can generate a basic rhythm in the motoneurons innervating leg muscles. It is characterized by alternating activity between the antagonistic sets of neurons associated with the stance and the swing phase (Brown (1911); for reviews see Delcomyn *et al* (1981), Grillner (1981), Pearson *et al* (2000), Büschges *et al* (2011); most recent comprehensive summary in Orlovsky *et al* (1999)). Today information on the topological organization of the neural networks underlying walking pattern generation is still not complete, but fundamental organizational features of those networks are known. The most comprehensive knowledge for locomotor networks in general are available for lamprey swimming (figure 4(a)) and locust flight (summary in Orlovsky *et al* 1999, Büschges *et al* 2011): many well studied CPGs for locomotion share (1) a topology that ensures via mutual inhibition the alternating activity between networks of neurons in charge of driving the pools of motoneurons, the so-called ‘half-center’ organization (figures 3, 4(a)). They also share (2) their location close to the innervated appendage, i.e., networks controlling stepping in vertebrate hind legs reside in the lumbar spinal cord whereas networks controlling front leg movement reside in the cervical spinal cord (for review see Grillner (1981)). Networks controlling an insect middle leg reside in the mesothoracic ganglion (for review see Ritzmann and Büschges (2007a)). *In vivo* the CPGs can be brought to generate rhythmic motor activity by descending pathways from brain centers, like the mesencephalic locomotor region in vertebrate walking (for review see Orlovsky *et al* (1999)). *In vitro* the CPGs can be activated by pharmacological treatment with neurotransmitter agonists. In mammals, e.g. in cat walking, this rhythmic activity has been called *fictive locomotion* (Grillner 1981), because the coordination of the various sets of motoneuron pools supplying the leg joints bears similarities to their coordination during *in vivo* stepping (Rybäk *et al* 2005, Pearson 2008). Interestingly, the neural networks generating a basic motor output for stepping in vertebrates are distributed across at least five segments in the lumbar spinal cord, see also (Yakovenko *et al* 2002). The notion of one single CPG controlling all motoneurons and muscles supplying a limb of a mammal in locomotion has been challenged for a long time: 30 years ago evidence from *in vivo* motor activity of various cat preparations, e.g. (Grillner and Zanger 1979) prompted (Grillner 1981) to question the notion that there is one CPG for hind leg movements in the cat lumbar spinal cord. In the light of the varying coordination in muscle activity across leg joints the



notion arose that the neural networks for hind leg stepping may be composed of multiple modules, each acting as a unit CPG. These unit-CPGs are thought to generate rhythmic activity in the antagonistic motoneuron pools of the main leg joints each. The activity of these multiple CPGs would be coordinated and modified to form the functional motor output to be generated by descending signals from the brain and sensory feedback. Grillner (1981) termed this the *unit-burst-generator* (UBG-) hypothesis.

In vertebrate swimming, i.e., in the lamprey, a very basal swimming vertebrate, for summary see (Grillner 2003), such organization of the neural networks generating a locomotor output has been found: multiple unit CPGs along the lamprey spinal cord each driving the motoneuron pools of one hemisegment have been identified (Cangiano and Grillner 2003). Evidence for a modular organization of the neural networks underlying pattern generation for stepping in vertebrates has been presented for the neural control

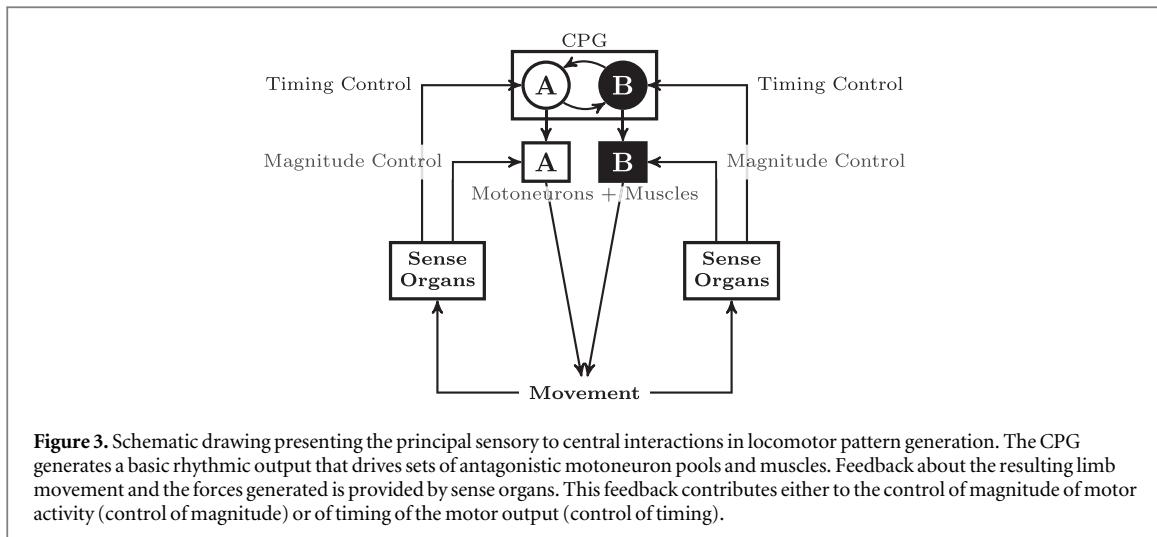


Figure 3. Schematic drawing presenting the principal sensory to central interactions in locomotor pattern generation. The CPG generates a basic rhythmic output that drives sets of antagonistic motoneuron pools and muscles. Feedback about the resulting limb movement and the forces generated is provided by sense organs. This feedback contributes either to the control of magnitude of motor activity (control of magnitude) or of timing of the motor output (control of timing).

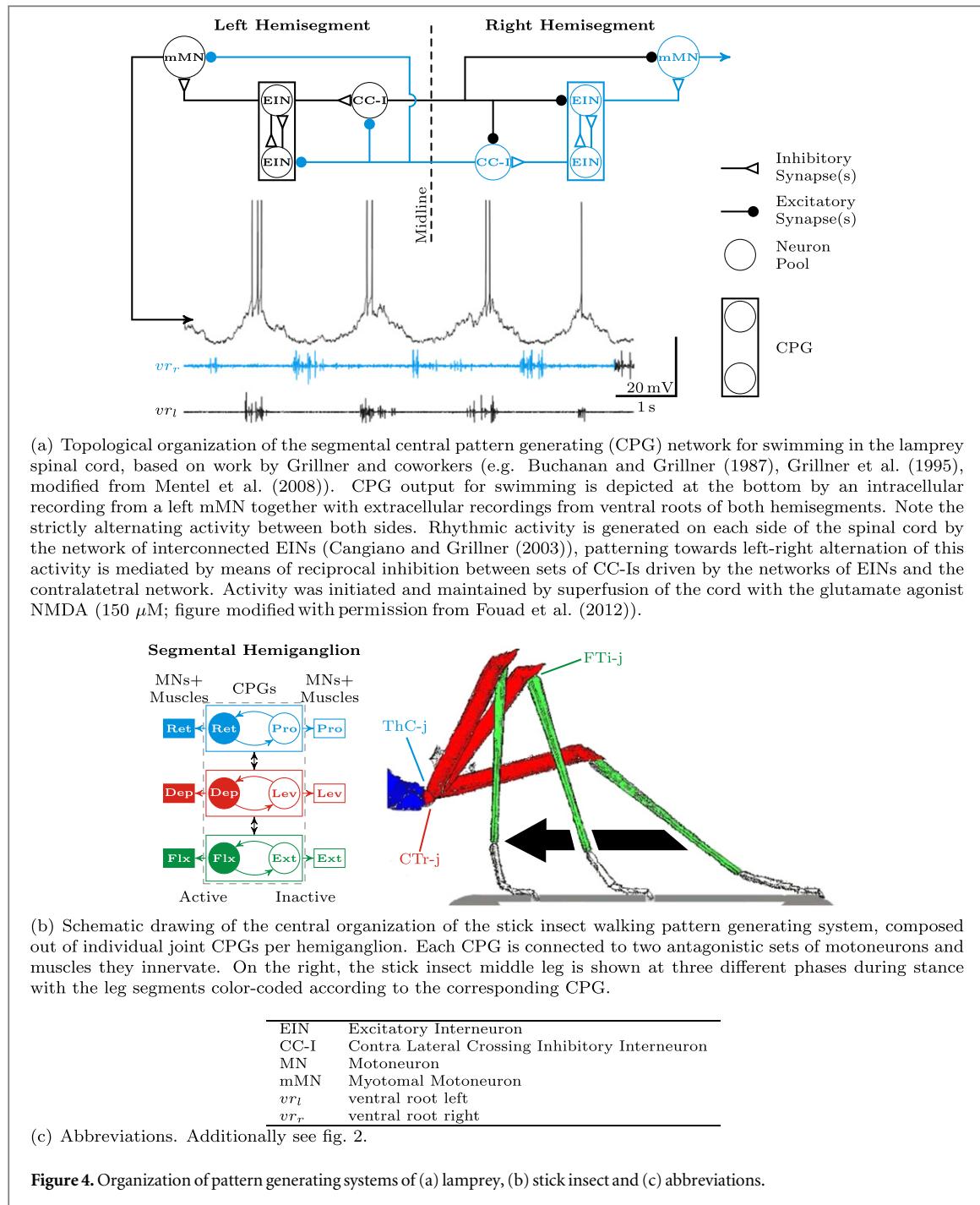
of the turtle hind limb (Field and Stein 1997) and the neural control of the mudpuppy forelimb (Cheng *et al* 1998). Recently, such a modular organization of CPGs in the spinal cord has been confirmed for the mammalian walking system as well (Hägglund *et al* 2013). Conclusive evidence for such modular organization of the neural control architecture for walking in line with the UBG-concept comes also from invertebrate walking, i.e., from the stick insect (figure 4(b)). Individual neural networks, i.e., CPGs, that control each leg joint are located in the corresponding segmental ganglia (Büsches *et al* (1995), Borgmann *et al* (2012), von Uckermann and Büschges (2009); for review see Bässler and Büschges (1998), Daun-Gruhn and Büschges (2011)).

The neural networks that control the individual leg joints of the most studied leg in this animal, the middle leg, are located in the mesothoracic ganglion. Four lines of evidence have given rise to the notion that individual joint CPGs operate rather independently from each other in the mesothoracic segment (for details see Bässler and Büschges (1998), Daun-Gruhn and Büschges (2011)): (i) rhythmic alternating activity in antagonistic motoneuron pools of individual leg joints, which is not coordinated across joints, can be initiated upon tactile stimulation of head or abdomen in an otherwise deafferented mesothoracic ganglion (Bässler 1983, Büschges *et al* 2004). (ii) Motoneuron pools of individual leg joints can be activated to generate rhythmic alternating activity between antagonistic motoneuron pools in the isolated mesothoracic ganglion by application of neurotransmitter agonists (Büsches *et al* 1995) without a fixed cycle-to-cycle coupling between motoneuron pools of different leg joints. In another insect, the locust, some stronger central neural cycle-to-cycle coupling appears to be present between the motoneuron pools of the main leg joints (Ryckebusch and Laurent 1993), however, only when the most regular sequences are selected. (iii) Rhythmic activity in

antagonistic motoneuron pools of individual leg joints in the mesothoracic segment arising from local CPG activity can be initiated and entrained by front leg stepping (Borgmann *et al* 2009). (iv) Today individual premotor interneurons are known to be kernel elements of these networks both in the generation of the intact locomotor output for leg stepping (stick insect: Schmitz *et al* (1991), Büschges (1994), von Uckermann and Büschges (2009); locust: Wolf and Büschges (1995)), as well in the operation of CPGs generating rhythmic locomotor activity in leg motoneuron pools (Büsches 1994, Büschges *et al* 1995, Bässler and Büschges 1998, von Uckermann and Büschges 2009).

In summary, the above results have given rise to the notion that the CNS provides a modular neural architecture for the generation of rhythmic motor activity for walking. Importantly, this architecture includes neural networks, the CPGs that support the generation of rhythmic and alternating activity between functionally antagonistic sets of motoneuron pools. However, additional neural signals, e.g. feedback signals from sensors on the leg (figure 3), coordinating signals from adjacent appendages and descending commands from the brain are needed to sculpt the functional motor output for stepping. This feature is similar across all locomotor systems. In animals that walk, crawl, swim and fly, all available evidence suggests that some basic cyclic motor pattern is generated in neural networks situated in the CNS, the CPGs (Grillner 1985, Pearson 1993, Marder and Bucher 2001, Grillner 2003, Pearson 2004), which is then turned into a functional locomotor pattern by specific extrinsic inputs (figure 4(a)). Even though explicit information about neural components is much sparser for human walking, evidence suggests a similar organization of the neural control for human walking (Dimitrijevic *et al* 1998, Cheron *et al* 2012).

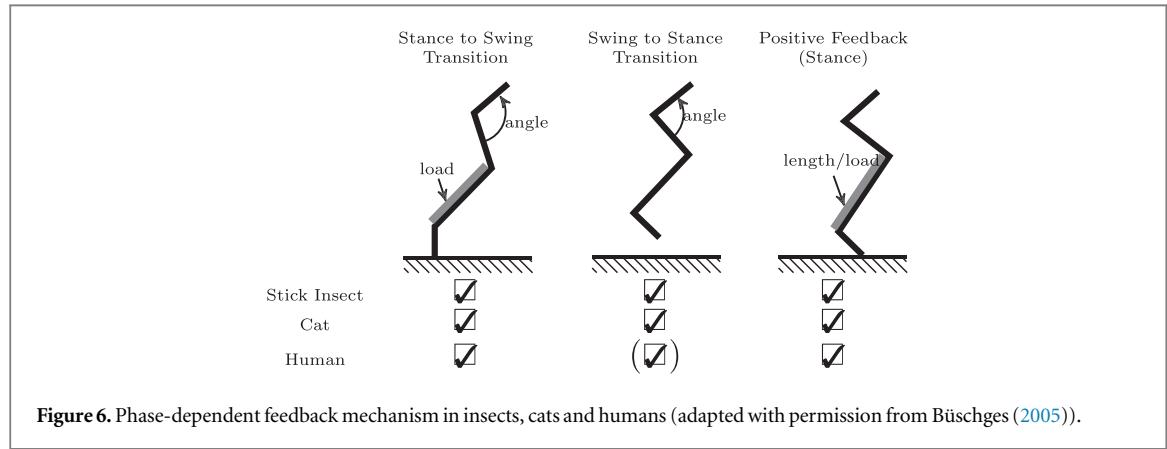
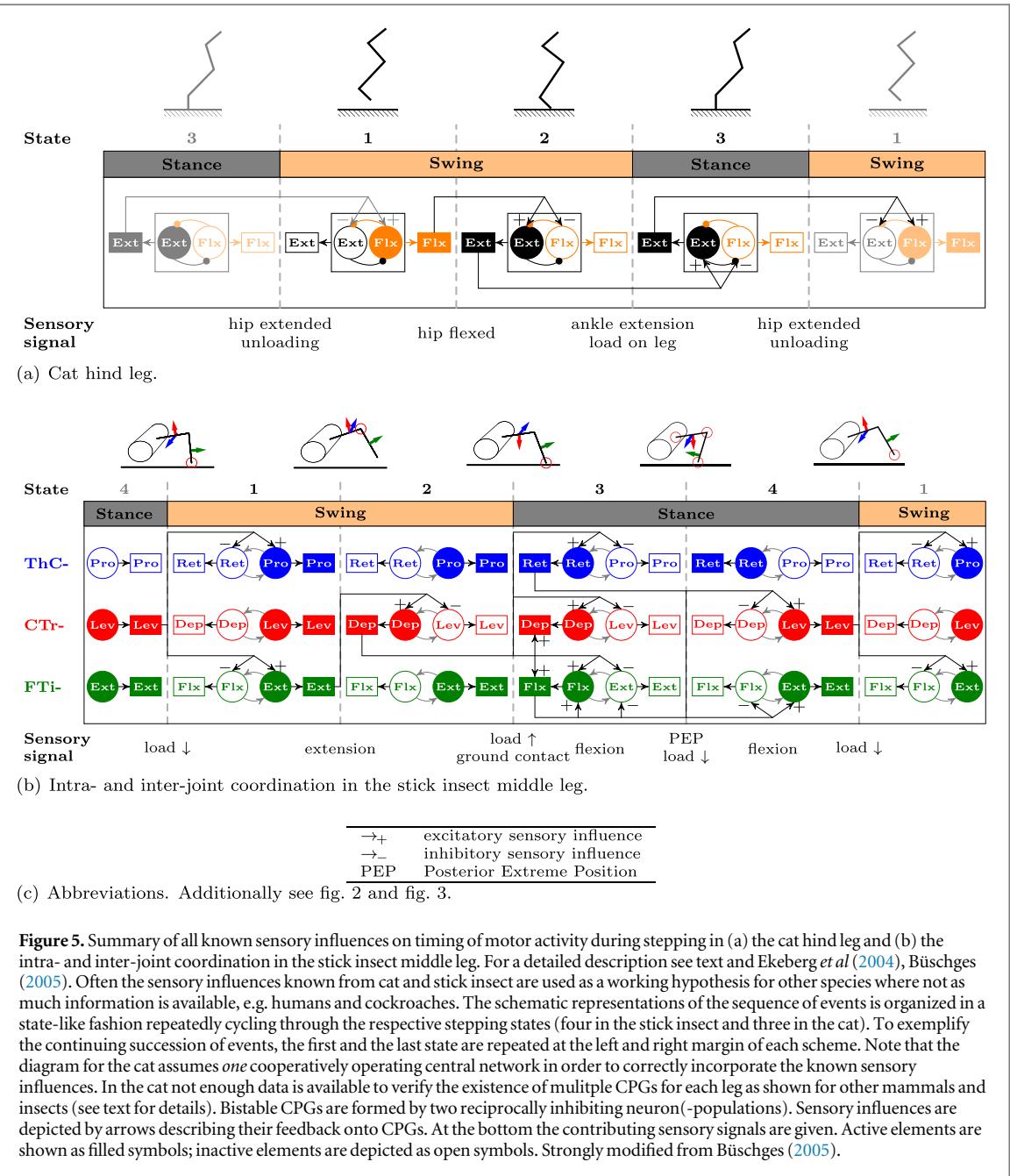
There has been a repetitive debate in the field of motor control during the past century, whether the



rhythmic activities recorded *in vitro* conditions are based on neural mechanisms active during *in vivo* locomotion as well (Pearson *et al* 1985, Bässler 1986a, 1986b, Cruse 2002). For example, theoretical approaches based on behavioral studies have pushed forward the notion that stepping of legs can be generated without implementation of CPGs (e.g. Cruse (2002), Dürr *et al* (2004)). Today this issue can be considered to be resolved to a large extent: for some animals it is known that individual interneurons or groups of these serve similar function during rhythmic motor activity generated *in vivo* and *in vitro* (e.g. insect walking Büschges *et al* (1994), Daun-Gruhn and Büschges (2011)).

2.2.2. Sensory feedback in the control of a step-cycle

Leg stance During the contact phase in level ground walking the motor activity driving the leg muscles serves two functions: it contributes to equilibrium and posture control of the animal in order to keep the animal in a desired posture above the substrate and it generates the force necessary to move the animals' body towards an intended direction. In generation and control of stance motor output *movement* as well as *force and load feedback* from sense organs (see above for details) determine magnitude as well as timing of stance motor activity (see figures 5–7; for summary see Grillner (1981), Büschges (2005), Pearson (2008)).



The sensory signals coding for loads and forces assist the generation of stance motor output and thus reinforce the ongoing stance phase motor activity.

They do so on the one hand by directly affecting the timing of activity of the leg CPGs to hold them in stance phase activity. In addition these sensory signals

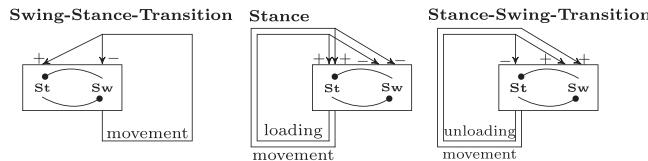


Figure 7. Schematic representation of the role of sensory feedback in generating the stepping motor output and the respective transitions (swing-stance-transition; stance; stance-swing-transition) so far known from all walking animals. In these schemes, central neural networks generating stance and swing phase motor activity are simplified and lumped together to form two states, i.e., stance St and swing Sw. Strongly modified from Büschges (2005).

modify motor activity via direct or indirect pathways onto the leg motoneurons (see figure 2; Pearson (2000a, 2000b), Büschges (2005)). Apparently this holds for all animals regardless of the number of legs: In the hind limb of the cat sensory feedback from GTOs reporting force generated by the stance muscles as well as load on the leg has an excitatory action on the activity of extensor motoneurons and assists the generation of the stance phase motor activity in ankle extensor motoneurons and muscles (see figure 5(a), Grillner and Rossignol (1978b, 1978b), Duysens and Pearson (1980), Pearson and Collins (1993), Gossard *et al* (1994b, 1994a), McCrea *et al* (1995), Hiebert and Pearson (1999), Donelan and Pearson (2004a, 2004b)). Interestingly, not only in large and heavy, but also in rather small and light animals, such as the stick insect and the cockroach, load feedback from the leg has been shown to contribute to the generation of stance motor output. Stimulation of the leg campaniform sensillae (CS) can initiate and reinforce stance motor output (cf figure 5(b), Bässler (1977), Akay *et al* (2001, 2004), Borgmann *et al* (2012)). Similarly, movement signals from the leg contribute to the generation of stance motor output. In the cat hind limb such sensory information is provided by Ia-afferent fibers from the MSs in the extensor muscles (see figure 5(a)). Their activation is thought to cooperatively assist the generation of stance motor output together with load signals from GTOs (Whelan *et al* 1995), (Pearson 1995, Ekeberg and Pearson 2005). Also in the stick insect, movement feedback, i.e., flexion signals from the femur-tibia joint provided by the fCO, assist ongoing motor activity during stance of the leg by reinforcing stance motor activity (figure 5(b); Bässler (1976, 1986a, 1986b, 1988); for review see Bässler and Büschges (1998)). This influence of movement feedback has been found to be assisted by load signals (Akay and Büschges 2006).

From humans evidence suggests a similar sensory control regime: force signals from the leg in stance assist the generation of stance motor activity (Grey *et al* 2007). Movement signals from the hip influence stance generation, again in interaction with sensory signals reporting load on the leg (figure 6; Pang and Yang (2000); for review see Zehr and Duysens (2004), Yang and Gorassini (2006)).

In summary, the current picture shows that sensory feedback from movement and force sensors during stance assists and reinforces—partly in an interactive fashion—activation of those central neural networks that are in charge of activating stance motor neurons, while they provide inhibition to those that drive swing motoneurons (cf figure 7, Büschges (2005), Pearson (2008)). This type of feedback is usually missing in robots, where adequate actuator forces are typically achieved via high-gain position feedback or feed-forward control.

Stance termination and stance-to-swing transition Sensory information about load and movement signals also contributes to the termination of stance and the transition of the leg into swing, again in a cooperative fashion: sensory signals reporting progression of the leg towards a posterior extreme position during stance and simultaneous signals reporting unloading of the leg as occurring towards the end of stance initiate the termination of stance and the initiation of swing during stepping (see figures 5, 7).

In the cat hind limb persisting load signals from the GTOs inhibit and postpone the initiation of activation of leg swing motoneurons and muscles in the ankle joint (Duysens and Pearson 1980, Pearson *et al* 1992). However, a decrease in load assists the transition from stance to swing, provided the leg has reached a posterior position. This influence is so strong that experimental modulation of force feedback signals in a rhythmic fashion is capable of entraining the locomotor rhythmicity in the cat hind limb motor system with stance phase motor activity being generated with high load and swing phase activity being initiated upon load decreases, for review see (Pearson *et al* (2006), figure 5(a)). The underlying sensory information appears to be provided by GTOs of the extensor muscles signaling load decrease and MS-signals from the hip flexors reporting a caudal position of the cat hind limb (figure 5(a), for review see Pearson (2008)).

Similarly in insects, evidence suggests that unloading signals from the CS on the proximal leg segments can initiate leg swing, provided that the leg has reached some posterior position during stance (Cruse (1985), figure 5(b)). Position and movement signals most likely arise from the ventral coxal hairplate monitoring movement and position of the coxa relative to the

thorax (Büsches and Schmitz 1990) and from the fCO reporting these parameters for the femur-tibia joint (Bässler (1988), Bucher *et al* (2003), for summary see figure 5(b) and Büschges *et al* (2008)). Load signals arise from the CS on the trochanter and femur, summary in (Zill *et al* 2004, 2012). Activity of the coxal and trochanteral motoneurons is primarily under control of the trochanteral CS (Schmitz 1993, Borgmann *et al* 2012), while activity of the tibial motoneurons is under control of the femoral and tibial CS (Akay *et al* 2001, Zill *et al* 2011).

The origin of a load decrease at the end of stance is most likely induced by other legs of the animal entering stance and thereby contributing both to posture control of the animal as well as to its propulsion. This has been nicely exemplified by a recent study of Zill and collaborators: Zill *et al* (2009) reported a close correlation between an unloading response of CS in the middle leg and touchdown of the ipsilateral hind leg prior to the stance-to-swing transition of the middle leg in cockroach walking. This finding indicates that unloading of the leg results from the mechanical coupling between the legs of an animal via its body. Similar sensory influences appear to play a role for stance-to-swing control in human walking (Yang and Gorassini (2006), figure 6).

It is important to note that we currently only have a rather qualitative understanding of the interaction of movement and force signals. Also, only little information exists on the topology of the neural pathways mediating the known sensory influences by movement and force sensors (cf Stein and Schmitz (1999), Akay and Büschges (2006)) and their interaction underlying the transition from stance to swing (for summaries see Pearson (1995), Pearson *et al* (2006), Pearson (2008), figures 5, 7). Therefore, control models incorporating the sensory feedback pathways might at the current stage be well represented by finite state machines (FSM).

The importance of inducing gait phase switching by sensory signals has been recognized in robotics and applied to various systems (cf section 3.6.2), but purely clock-driven systems still dominate.

Swing Motor activity during leg swing appears to be under control of movement signals. Lam and Pearson (2001) have shown that movement signals from the hip assist hip flexor activity in the control of the cat hind leg, which is supported by the finding of excitatory inputs onto hip flexor motoneurons upon stimulation of muscle spindle afferents (groupI) during swing activity in fictive locomotion (figure 5(a), Quevedo *et al* (2000)). Similar evidence has been collected for human walking: in stepping babies Musselman and Yang (2005) found that swing phase activity is prolonged when weights are added to the ankle, resisting flexor activity during leg swing. Two further lines of evidence suggest that movement signals play a role in the control of leg swing (figure 5(a)): (i) in the cat and the stick insect it has been shown that kinematics of leg

swing can be modified in a task dependent fashion during its execution: in the cat hind leg fast corrections during leg swing have been reported by (McVea and Pearson 2007a) during obstacle avoidance. Similarly, (Schütz and Dürr 2011) reported changes in front leg swing kinematics upon touch of an obstacle by the animal's antennae. (ii) Cats can be trained to generate different swing kinematics in the hind limb (McVea and Pearson 2007a, 2007b,). For example, when leg swing of a cat hind leg is repeatedly disturbed with a hook at a fixed height above ground, the cat will modify its swing kinematics of that hind leg towards higher passages in order to avoid the obstacle permanently. Such modifications can only be executed when sensory control of leg swing motor activity is possible.

Even so, the notion that leg swing is under continuous *online* sensory control from movement sensors must be handled with care: Dean (1984) disturbed ongoing swing of a hind leg in a stepping stick insect by means of a small weight fixed to the leg with a rope becoming effective during ongoing swing. The occurring changes in swing kinematics that became apparent within 20 ms were interpreted to represent changes in the neural drive to the leg muscles. Recent analysis of the biomechanical properties of the leg muscles in stick insects question this conclusion, because the neuromuscular system of the stick insect is too slow, e.g. having a dead time of at least 30 ms, to counteract disturbances during leg swing that quickly (Guschlbauer *et al* 2007, Hooper *et al* 2009). Recent analysis indicate that the fast reactions reported by Dean (1984) upon loading a leg during swing that occur within 20 ms reflect almost exclusively muscle properties and not neural control.

Swing-to-stance transition For the control of the transition from swing to stance, movement and position signals from the leg appear to play an important role (figures 5–7). Movement signals from the leg in swing initiate activation of motoneurons and muscles that induce touchdown of the leg on the ground. For the cat hind leg this information appears to be provided by movement signals from the hip joint (Pearson 2004). The detailed sensory origin, however, is not clear yet. In the cat walking system it is also known that this transition is facilitated by the contribution of the CPG activity. Even before leg touchdown, CPG activity provides a basic activation to stance motoneurons (for details see Pearson (2008), figures 5(a), 6, 7). This activity at the end of leg swing activity is called *E1* phase and is thought to support stance initiation by pre-activating stance phase muscles prior to leg touchdown in order to help to support body weight of the animal at the time of leg touchdown (figure 2(c)). For the stick insect, movement signals reporting extension of the tibia, arising from the fCO, were found to activate depressor motoneurons, resulting in touchdown of the leg (Hess and Büschges (1999), figures 5(b), 6, 7). This in turn results in an increase in load on that leg which then reinforces the activation of stance motor

activity (figure 2(d)). A similar situation appears to exist in human walking (Yang and Gorassini (2006), figure 6). After the transition from swing-to-stance the cycle of leg stepping is closed with the generation of the next stance phase and the stepping cycle resumes. Activation of the stance phase based on sensor signals has also been used in many robots and is usually based either on contact switches or contact force sensors (cf sections 3.6.2, 3.5).

2.3. Examples of higher order neural control during locomotion

2.3.1. Posture and balance

Maintaining posture and balance in walking animals is a complex neural task, because they have to be generated and controlled while the animal is locomoting. Controlling posture concerns the generation of motor activity to produce an orientation of the animal relative to the vector of gravitation. Controlling balance comprises the actions of the body skeleton-muscle system to prevent the body from falling out of any position taken during (quasi-) static motion and to prevent falling during dynamic locomotion (e.g. Winter (1995), Orlovsky *et al* (1999), Deliagina *et al* (2012)). Legged animals differ in the control of posture and balance depending on the number of legs. In six legged insects, for example, the control of posture and balance is realized in a distributed fashion among the muscle control systems of the joints between the segments of the body and appendages, for summary see (Bässler 1983, Dettner and Peters 1999). The relevant sense organs known, as of today, reside either on the cuticle at the boundaries between the segments, as in the case of hair plates (see above and e.g. Schmitz and Habfeld (1989), Büschges and Schmitz (1990); for review see Bässler (1983), Burrows and Hedwig (1996)) or within the segments, as is the case for COs (Bässler 1977). The signals of these sensors control the motoneurons supplying the muscles of the individual segments. It is important to note that the same sense organs and local, segmental neural networks contribute to the control of posture and balance that were reported to control motoneuron activity during the execution of locomotion. The overall posture of the animal results from the mechanical interaction between the body and leg segments under the presence of gravity. For orientation under gravity and to keep balance insects either use the distributed postural control system or in some cases specialized sense organs have evolved that can monitor the relative position of the animal with respect to the vector of gravity. For example, cockroaches and crickets possess club-shaped hair sensillae on their cerci at the abdomen, which are deflected differently depending on the position of the animal with respect to gravity, since their mass is concentrated at their tip (Dettner and Peters 1999). A particularly significant issue arises from the fact that during the generation of

movements posture control tasks should not conflict with movement control tasks—postural reflexes can counteract movement generation (Pearson 1993, Büschges and Manira 1998). Various studies, the earliest dating from almost 40 years ago, found that during the generation of leg movements the corresponding postural reflexes are strongly modulated, e.g. show a decrease in gain or are even reversed in sign (e.g. Bässler (1976), DiCaprio and Clarac (1981); summary in Büschges and Manira (1998)). For example, while flexion signals from the tibia in a stick insect induce a postural reflex in tibial muscles of a standing insect, the same flexion signals will be processed as to assist ongoing flexion of the tibia when the animal is in the locomotor state. Both kinds of neural control regime are generated by shifting weights between neural pathways of the same distributedly operating premotor network (e.g. Driesang and Büschges (1996)). In the insect leg muscle control system such modifications concern the neural control for two out of three of the leg joints (figure 2(c), Bässler (1976, 1988); Schmitz, unpublished observations). Still at present there is no complete picture of how the nervous system controls the overall animal posture during the generation of the motor output for locomotion, e.g. Hooper *et al* (2009).

In four legged animals, as well as in two legged humans, the neural basis for balance and posture control differ in some important aspects, because the neural control is partly centralized. There are two neural mechanisms contributing in these animals (for review see Orlovsky *et al* (1999), Deliagina *et al* (2012)): one of them resides in the spinal cord at the level of the appendages, e.g. hind legs. It receives input from limb mechanoreceptors about force, load and position. It counteracts disturbances by generating corrective motor responses. The second system resides in the motor cortex and the brain stem. It also receives signals from limb mechanoreceptors, and in addition vestibular and visual signals (figure 8). These three sensory qualities contribute to balance control in a redundant fashion. This second system mediates its influence on the muscle-skeleton system by acting on those local networks in the spinal cord that generate motor activity controlling posture and movements (summary see Winter (1995), Deliagina *et al* (2012)). The relative contribution of both systems is not clear yet.

The details of neural control of human balance are not well-understood, but basic postural reflexes and some fundamentals of the dynamics of locomotion are known from biomechanical studies. In stance, humans respond to external disturbances with a limited set of motor primitives (Horak and Nashner 1986). The dominant reaction is the *ankle-strategy*, when anterior and posterior disturbances are effectively counteracted by reflex activation of ankle plantarflexors and dorsiflexors to maintain balance. An alternative response is the *hip-strategy*, i.e., flexion or

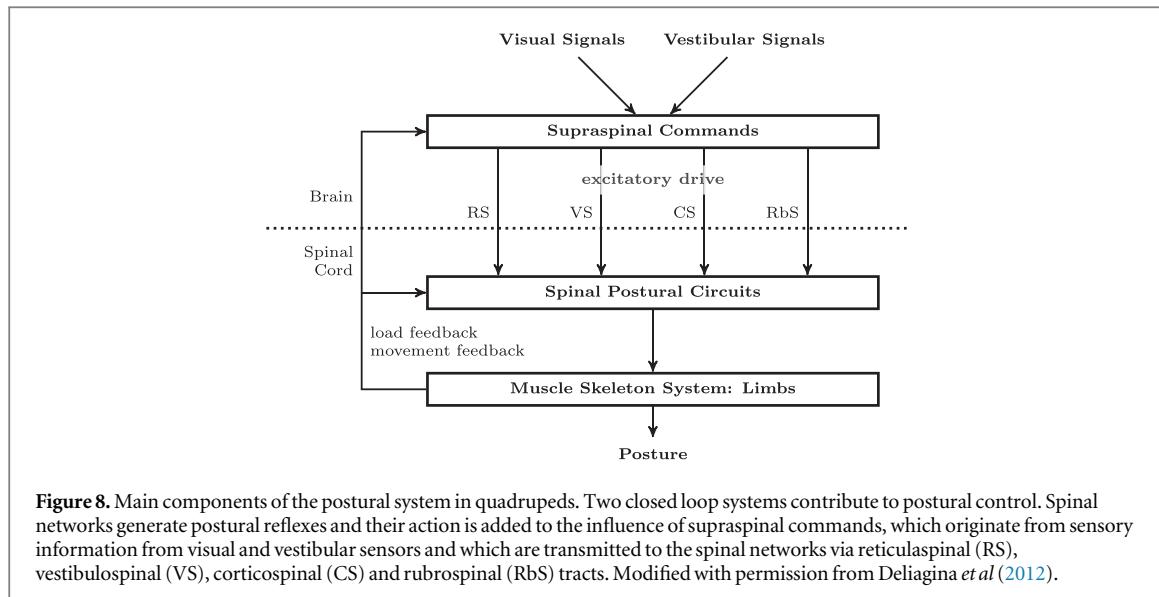


Figure 8. Main components of the postural system in quadrupeds. Two closed loop systems contribute to postural control. Spinal networks generate postural reflexes and their action is added to the influence of supraspinal commands, which originate from sensory information from visual and vestibular sensors and which are transmitted to the spinal networks via reticulospinal (RS), vestibulospinal (VS), corticospinal (CS) and rubrospinal (RbS) tracts. Modified with permission from Deliagina *et al* (2012).

extension of the hip. There also are mixed reactions containing ankle and hip activation, suggesting that these strategies are really *muscle synergies* underlying the neural control of balance (Torres-Oviedo and Ting 2007, Horak and Nashner 1986). Larger disturbances are compensated by a *stepping-strategy*, i.e., by modifying the base of support (BoS), or even by hopping or stumbling motions (Horak 1987). It has been suggested that ankle-, hip- and stepping-strategy constitute a hierarchy of possible responses (Horak 1987), but more recent work indicates that all strategies are activated in parallel and that the stepping strategy is aborted if deemed unnecessary (Maki and McIlroy 1997). It has also been shown that prior knowledge of and repeated exposure to perturbations significantly changes the response (Marigold and Patla 2002, Horak and Nashner 1986). These three basic control strategies are also applied in many biped walking control algorithms (see section 3.4.1).

There have been some attempts to model and reproduce the overall behavior of human balance control during stance using methods from control theory. Fujisawa *et al* (2005) analyzed the hip and ankle strategies in humans by studying responses to small disturbances during stance⁶. Using system identification techniques and modeling the human as a double pendulum, linear transfer functions from upper and lower body inclination to ankle and hip moment were determined. The study found proportional and derivative contributions in the response, but distinguishing the contributions of neural control and the muscle-skeleton system is not possible. A different model of stance control based on sensor fusion, disturbance estimation and linear control theory is discussed in (Tahboub and Mergner 2007, Mergner *et al* 2009).

In biomechanical studies balance in humans is mostly studied based on simple models such as the

(linear) inverted pendulum model (IPM/LIPM) and the concept of balance is usually not clearly connected to the mathematical theory of the stability of dynamical systems. In this field, balance is classically equated with keeping the center of mass (CoM) over the BoS (Winter 1995). Hof *et al* (2005) proposed an extended *stability measure* based on an IPM, requiring that the *extrapolated CoM* (XCoM) remain within the BoS (cf section 3.4.1) and proposed hypothetical walking control laws based on this concept (Hof 2008). Note that this analysis is based on a transformation of the pendulum equations previously proposed in the context of biped robots (see section 3.4.1). Aftab *et al* (2012) proposed another hypothetical control law for stepping based on an optimal predictive controller for the LIPM and found similar responses to perturbations during stance also found in humans.

It should be noted that current state of the art robots are not only capable of maintaining balance during stance, but also during dynamic locomotion and even in somewhat uneven terrain (cf section 3)—behaviors that are difficult to analyze experimentally in animals and humans (cf section 4).

2.3.2. Motor flexibility as a prerequisite for goal directed locomotor behavior

When animals move through their environment, be it by flying, swimming, crawling or walking, they need to generate a motor output suitable for both propulsion as well as directing the animal towards goals that have been identified by means of visual, chemosensory, auditory or tactile cues or internal drives. Therefore, locomotor activity needs to be modifiable in order to allow for curvatures in the locomotor path or to surpass or climb over obstacles. Modification of locomotor activity constitutes an even more complex control task for the nervous system when compared to generating a default, basic locomotor output. In higher order animals, such as mammals and arthropods, the

⁶ Knee bending was prevented by wooden splints.

sensory systems providing the information about goals to reach in the environment are mostly localized at the front end, i.e., the animals head. The neural networks in charge of generating the motor output for locomotion, however, are localized much more caudally in the segmented CNS at the level of the locomotor organs: in insects, for example, these networks reside in the thoracic nerve cord and in legged vertebrates in the cervical and lumbar spinal cord (cf, section 2.2.1, see also Büschges *et al* (2011)). To generate goal directed locomotor behavior, these networks are under continuous, specific descending control from brain regions. The descending information allows for continuous modification and adjustment of the actual locomotor output to serve the behavioral needs. In contrast to knowledge on the organization and operation of the locomotor networks in the thoracic nerve cord and spinal cord, today's understanding of the nature and specific action of the descending signals from the brain and rostral segments of the nervous system in the generation of goal directed locomotor behavior is very limited. By now, it is mostly neuroanatomical data on descending neural pathways together with some physiological aspects, which is available (e.g. Bender *et al* (2010), Mu and Ritzmann (2008a, 2008b), Orger *et al* (2008), Portugues and Engert (2009), Zelenin *et al* (2007)). There are at least two ways of possible action: descending signals could directly control the motor activity generated or they could modify the action of sensory feedback in order to modify ongoing motor activity (e.g. Mu and Ritzmann (2008a, 2008b)). The nervous system might employ these mechanisms individually or complementary.

Curve walking as an example of motor flexibility

Curve walking of insects is a well-suited example of motor flexibility for studying goal directed behavior: walking sequences can be reliably elicited in animals as optomotor responses by projecting moving stripes onto two screens left and right in front of the experimental animal (see e.g. Gruhn *et al* (2006)). The stripe movements determine curve walking direction, i.e., when the stripes move outwards the animals walk straight forward, when the stripes move left or right on both screens, curve walking can be induced.

Turning is generated by explicit changes in the leg movements on both sides of the animal as compared to straight walking (e.g. Mu and Ritzmann (2005), Dürr and Ebeling (2005), Gruhn *et al* (2009); for summary see Büschges (2012)). To generate a turn, the legs outside of the turn generate stance movements that direct the animal forward, while leg movements on the inside of the turn pull the animal towards the side of the curve (Jander 1982, Dürr and Ebeling 2005). In free walking animals the different kinematics in leg movement arise from both mechanical coupling between the legs via the ground and neural control of each individual leg. The contribution of the neural control to the generation of turning is particularly obvious when an insect is walking on a slippery surface

with reduced mechanical coupling through the ground (Gruhn *et al* 2006, 2009). When animals generate stepping movements on the slippery surface that would move them straight, the kinematics of contralateral legs are similar and based on the same neural control regime. In contrast, when curve walking is induced by optomotor stimulation, kinematics of contralateral legs are quite different: for example, leg stance of a stick insect middle leg on the inside of a curve is generated mostly by flexion of the femur-tibia joint with little contribution of coxal displacement, while leg stance of the middle leg on the outside of a curve is generated by retraction of the coxa (Mu and Ritzmann 2005, Gruhn *et al* 2006, 2009).

Recent evidence has indicated that task-specific modifications in sensory-motor processing in the thoracic motor networks play a role in generating the motor output for curve walking (Hellekes *et al* 2012). On the inside of a stationary curve walking animal flexion signals from the fCO of a middle leg reinforced flexor activity in tibial MNs. In contrast, flexion signals from the fCO did not systematically assist flexor activity in the outside leg. This observation suggests that the processing of movement signals from the leg in the premotor network of the FTi-joint differs between both sides of a curve stepping insect. This observation indicates a task specific change in premotor signal processing that complements previous evidence for task specific processing of sensory feedback signals in the stick insect (Akay *et al* 2007). A recent modeling study showed that leg movements during turning in the cockroach can be explained by reversing certain leg joint reflexes, supporting the view that sensory signal processing contributes markedly to the action of local controllers (Szczechinski *et al* 2014). In summary, high-level behaviors such as curve walking are apparently generated by the combined effect of modifications in low-level control loops and descending control signals. The latter point is emphasized by recent work linking turning behavior of the cockroach to activity in specific areas of the brain (Guo and Ritzmann 2013). Note that the currently predominant approach to generating high-level behaviors such as curve walking is markedly different in robotics. Here, control of high-level behaviors such as turning is usually based on explicit kinematic models in combination with task-space planning (cf section 3).

2.4. Simulation as a tool for biologists and as a link to robotics

The extent to which an understanding of the operation of animal walking systems has been reached today would not have been possible without employing simulations. Using simulations in the research on biological walking systems has a long standing tradition: already in the early 19th century the Weber brothers demonstrated the power of combining detailed biological data and numerical simulations by

visualizing human walking sequences and stated that general control principles of human walking could be derived from simulation (Weber and Weber 1836). This was even before experimental methods like high speed photography became available.

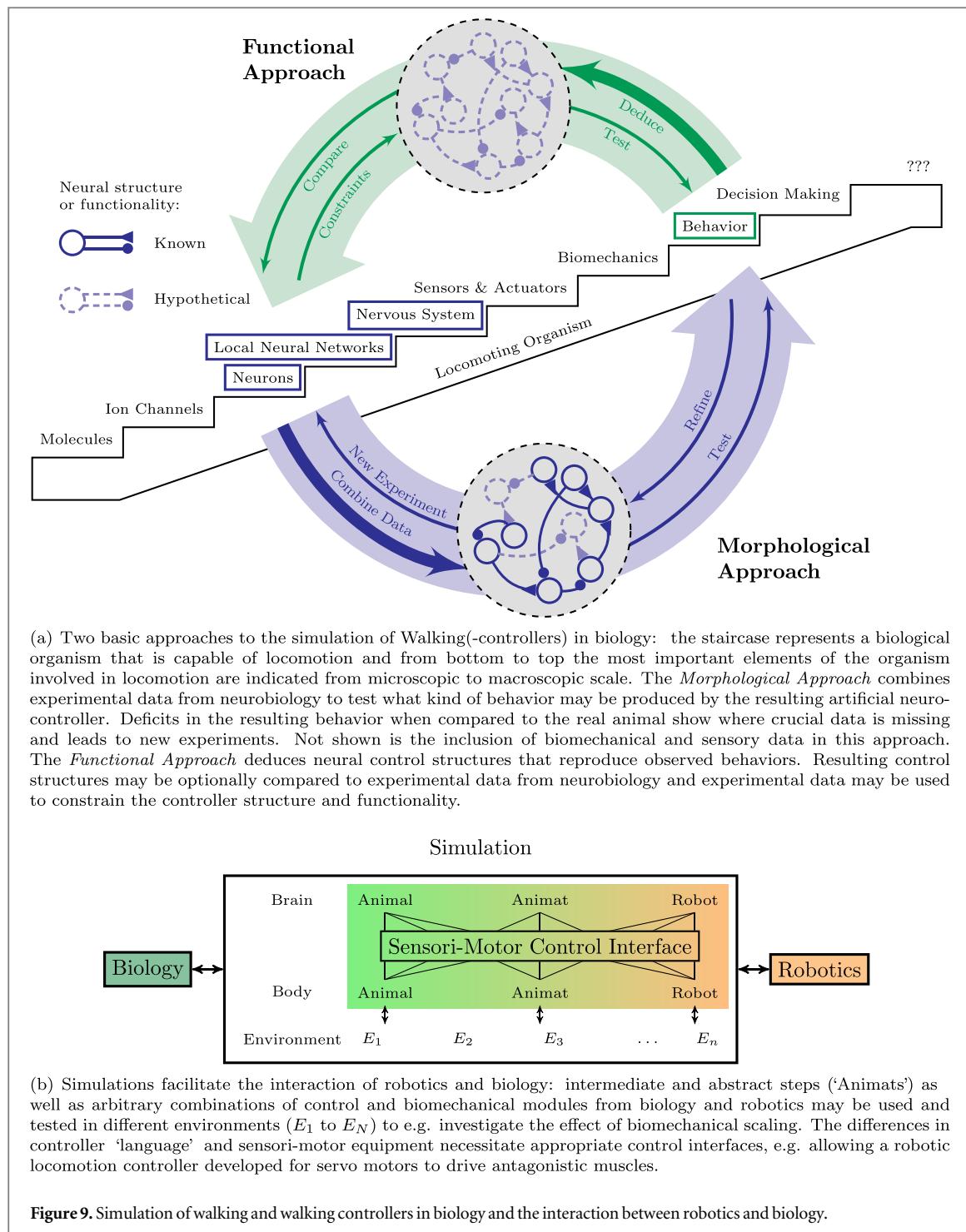
Simulation as an answer to complexity and limited experimental techniques The importance of simulations in walking research stems from the complexity of neural walking control systems on the one hand and limited experimental techniques to cope with this complexity on the other hand. Even seemingly simple walking control systems like that of a single leg in insects possess a huge number of parameters: it is estimated that 120 motoneurons and 270 local inter-neurons per hemi-ganglion locally control a single leg (for data on stick insects and locusts see e.g. Burrows (1996), Goldammer *et al* (2012)). The number of sense organs for e.g. the locust middle leg amounts to 37 and additionally many single cell exteroceptors with altogether more than 2400 sensory neurons exist. These code for proprioceptive signals, e.g. position, velocity, acceleration, for strains and forces on the cuticle and muscles and for sensory touch of the cuticle or chemosensory cues. Furthermore, multiple nonlinear closed feedback loops interact and lead to emergent phenomena. This renders reductionist approaches insufficient. When considering the interplay of neural, biomechanical and environmental systems (concepts of embodiment and situatedness, cf Pfeifer and Gómez (2009), Beer (2009), also termed neuromechanics, cf Nishikawa (2007)) the problem becomes even more complex. Available experimental approaches only allow to record a small subset of parameters at once (Ritzmann and Büschges 2007b), mostly under simplified conditions.

Simulation studies that combine physical simulators for biomechanics and environment interactions with artificial neural networks promise to complement experimental techniques in several ways: (1) they have the power to describe available biological data in a unified ‘language’. (2) They allow to access and to change all simulation parameters, as a prerequisite for a thorough analysis of the walking control system and for generating novel hypotheses by ‘playing around’. (3) They provide a holistic view by allowing to investigate the interplay between neural controller (modules), biomechanics and environment. (4) They allow to use different levels of detail from the simulation of reduced sub-systems or simplified animals to detailed simulations of walking animals. (5) They allow to test the explanatory power of existing hypotheses and to visualize them. Alternative control mechanisms may be compared on the same plant and alternative hypotheses developed. (6) They are fast and cost-effective, when compared with ‘wet’ biological or robotic experiments. This is essential for performing a large number of evaluations as required by machine learning techniques or evolutionary robotics (see below).

Neuro-mechanical simulations of locomotion have been performed for multiple animal species, amongst others humans (Taga 1995, Anderson *et al* 2006), cats (Pearson *et al* 2006, Yakovenko *et al* 2004, Frigon and Rossignol 2006, Maufroy *et al* 2008), salamanders (Ijspeert *et al* 2007), lampreys (Grillner 2006), cockroaches (Pearson and Iles 1973, Beer *et al* 1997, Szczecinski *et al* 2014) and stick insects (Schumm and Cruse 2006, Ekeberg *et al* 2004, Beer *et al* 1997). In many cases derived control mechanisms have been implemented and tested on robots (e.g. Beer *et al* (1997), Maufroy *et al* (2008), Ijspeert *et al* (2007), von Twickel *et al* (2012) also cf. section 3.5).

Basic simulation approaches in biology In biology two basic approaches to the simulation of walking control are taken (cf figure 9(a), see also Cruse *et al* (2007)): the *functional approach* asks the question of what kind of control systems reproduce observed behaviors. A prominent example is the WALKNET controller, a distributed neural network, developed by Holk Cruse and co-workers (e.g. Dürr (2001), Schumm and Cruse (2006), Kindermann (2002), Cruse *et al* (2004, 2007)) which reproduces six-legged stick insect walking behavior unmatched by other simulation approaches. As an inherent limitation of this approach, the correlation of artificial and real neural structures is difficult because from a theoretical point of view an unlimited number of neural structures may produce identical behavior (Negrello *et al* 2008). Conversely, the *morphological approach* asks the question of what kind of behavior may be produced by known neural and biomechanical structures and of how to complement these structures to achieve desired behaviors. This approach was e.g. applied to the control of single (Ekeberg *et al* 2004, von Twickel *et al* 2011, Toth *et al* 2012) or coupled (Knops *et al* 2012) stick insect legs. A direct extension of this approach to unrestricted six-legged walking or to more complex behaviors is demanding due to the huge number of parameters in the system.

Future simulation studies that strive to correlate artificial and real neural structures controlling more complex behaviors need to combine functional and morphological approaches (von Twickel 2011). Behavioral, biomechanical and neural data may then be used to constrain the parameter space. In most cases it will be difficult or impossible to reduce the parameter space to allow hand-tuning, but even then parameter hand-tuning introduces a subjective bias in form of the experimenter. Therefore, additional tools from computer science that help to efficiently explore the parameter space will be useful. In addition to other machine learning techniques a promising approach is the artifical life approach to evolutionary robotics (Nolfi and Floreano 2000, Beer 2009, von Twickel and Pasemann 2007, Bongard 2011), which allows to explore structure in addition to parameter space taking into account biological constraints (Izquierdo and Beer 2013, Rempis and Pasemann 2011).



Simulations accelerate bi-directional interactions between biology and robotics Traditionally, biological and robotics research on the control of locomotion have fundamentally different goals: biologists strive to understand basic principles of locomotion control in animals whereas roboticists want to find a control mechanism that allows a given robot to locomote sufficiently well. As a consequence, biologists have used robotics mostly to visualize biological data and to demonstrate that control mechanism derived via simulation 'maintain an essence of reality' (Brooks 1989). In contrast, roboticists have used

biology to draw inspiration for new control mechanisms for machine locomotion. A close interaction between the two disciplines promises to lead to deeper insights into general control mechanisms (Beer *et al* 1998, Webb 2002, Azevedo *et al* 2007, Ijspeert *et al* 2007). Here simulations may bridge the gap caused by different 'languages' to describe control mechanisms, different control interfaces to motor and sensor systems and different scales (figure 9(b), cf also von Twickel (2011), von Twickel *et al* (2012)). As a result the transferability of controllers between robotic and biological simulations would improve, allowing to

compare different robotic and biologically derived controllers on the same simulated robot, simulated animal or even a more abstract animat. As a result new hypotheses about the control mechanisms in animals and new control techniques for walking machines could be developed.

3. Robot walking

There are some parallels in the design and control of legged robots and animals, since they share the same basic principle of locomotion and are governed by the same physical laws. However, there are significant differences, mainly due to three reasons. (1) The mechanical properties of robots and animals are not fully alike, especially with regard to sensing and actuation. (2) Since any robot must function as a whole, the focus in robot walking control is often on global coordination, postural control and balance, especially for biped and quadruped robots. In neuroscience, on the other hand, the complexities of the organisms and available experimental techniques lead to a focus on low-level aspects of neural control. (3) Because there is no thorough understanding of the neural control of posture and balance in the CNS, robotic controllers cannot refer to a biological template and are mostly based on first principles and control theory⁷.

The remainder of this section is organized as follows. In section 3.1 we review typical hardware designs, since they determine the dynamics, the sensing capabilities and applicable forces. Section 3.2 covers basic concepts in the mechanics of legged locomotion, while the remaining sections review widely used walking control approaches, which we have classified into model-based control of underactuated robots (section 3.3), model-based control of fully actuated robots (section 3.4), CPG-based control (section 3.5) and gait cycle-centered control (section 3.6).

3.1. Hardware design

3.1.1. Robot structure

Walking robots have been built with one, two, three, four and more legs, according to their biological counterparts⁸. A large range of mechanical designs has been proposed. The leg mechanisms of walking robots are often designed as rigid links connected by rotary joints. The rigidity of the links is especially important for model-based control approaches: measuring link deformations is difficult even with additional sensors such as strain gauges on structural components. Also,

⁷ This does not indicate an inherent superiority of neural control over model-based approaches. However, if details of neural control of posture and balance were known, they would be a natural starting point for robotic controllers.

⁸ One-legged robots may be seen as an abstraction of hopping animals like kangaroos.

structural elasticity can lead to undesirable vibrations and link deformations can cause early or late ground contact, disturbing the gait. A notable exception is the RHex robot, which uses elastic legs, making the robot underactuated (Saranli *et al* 2001). However, the entire design strongly deviates from typical walking systems. Instead of segmented legs moving back and forth to achieve locomotion, curved elastic appendages perform rapid full rotations. A more common use of elastic components is either in the drives (see below), or in telescopic legs of hopping and running robots, e.g. Scout II described by Poulakakis *et al* (2005).

To overcome the inefficiency of walking machines due to energy consumption of joints even during the *negative work mode*, i.e., joint moments opposing joint motion, Hirose (1984) proposes the concept of *gravitationally decoupled actuation* (GDA). A robot design following GDA leads to energy consumption only during positive work mode (Hirose 1984). GDA can be achieved by choosing kinematic leg structures such as pantograph mechanisms (e.g. for the quadruped robot Titan III (Hirose and Kunieda 1991)) or by locking joints to avoid power consumption during the negative work mode (Hirose 1984).

Examples of the use of complex leg mechanisms are the eight-legged robot Dante II (Bares and Wettergreen 1999) and the quadruped robot TITAN III (Hirose *et al* 2009): they are equipped with electric linear actuators and the walking motion is generated by pantograph mechanisms. Some robots are also equipped with additional springs in the legs, such as the quadruped robot Cheetah (Rutishauser *et al* 2008) where the knee joint is equipped with a mechanical spring, the modular (four to eight legged) robot Octavio (von Twickel *et al* 2012) where the shoulder-joint is equipped with a pre-loaded mechanical spring or the quadruped robot KOLT where the knee joint is equipped with a pneumatic spring (Estremera and Waldron 2008). These features are intended to mimic biomechanical properties of the muscle skeleton systems of walking animals (cf section 2.1.1).

For fully actuated bipeds, the most common design includes six actuated joints per leg and feet enabling surface contact (Hirose and Ogawa 2006, Pfeiffer 2006, Nelson *et al* 2012, Pratt 2009, Ogura *et al* 2006). Planar bipeds and some three dimensional systems use point feet and as few as two DoFs (Chevallereau *et al* 2003, Miura and Shimoyama 1984). Point feet are the predominant design in quadrupeds and hexapods. A notable exception are some early quadrupeds with flat feet and complex leg mechanisms (Hirose 1984). Overall, the variety of leg configurations and actuation methods is arguably higher for machines with more than two legs than it is for biped robots.

3.1.2. Actuation

Differences in robot hardware in comparison to biology are to a large extent due to available actuator

technologies (see section 2.1.1, cf also Pons (2005)). For many years, the prevalent choice of actuators for bipedal robots were geared brushed DC motors (Hirai *et al* 1998, Nishiwaki *et al* 2000, Pfeiffer *et al* 2002). More recently, permanent magnet synchronous motors have been used for highly loaded joints (Lohmeier *et al* 2009, Hirose and Ogawa 2006, Tsagarakis *et al* 2011). Hydraulics (Nelson *et al* 2012, Cheng *et al* 2006, Raibert *et al* 2008) and pneumatics (Vanderborght *et al* 2005b, 2005a) are also used, but less often.

One motivation for using pneumatic actuators is their inherent compliance, which is also apparent in biological muscle-tendon systems where it has a significant impact on the dynamics of walking (cf, section 2.1). An early attempt towards designing a human-like actuation system is described by Yamaguchi and Takanishi (1997). The humanoid Wabian has antagonistically driven joints incorporating non-linear spring mechanisms, which enables the robot to control both the effective torque and stiffness of the joint, similar to animals and humans. Another machine employing biomimetic actuation is the lobster robot described in (Ayers and Witting 2007). This underwater robot uses shape memory alloys, which are especially well-suited for this application. Elongation of the actuators after a contraction caused by resistive heating is significantly faster than usual due to the inherent water cooling.

In a different approach to actuation involving compliance, one position controlled, geared electrical motor is connected to the output side by mechanical springs, a concept known as *series elastic actuation* (SEA) (Pratt and Williamson 1995). The goal is to provide high-fidelity force control by measuring and controlling the spring deflection, which is proportional to the applied force, but also adds an unactuated DoF to the system and lowers the position control bandwidth. Robots using these devices include the 2D-biped Spring Flamingo (Pratt and Pratt 1998b), the 3D-bipeds M2⁹, its more recent redesign M2V2 (Pratt and Krupp 2008) and the quadruped StarLETH (Hutter *et al* 2012). Remy *et al* (2012), Hutter *et al* (2012) also cite high fidelity torque control as an advantage of SEA¹⁰. SEAs are similar to the muscle-skeleton system in animals, which also includes elastic components (see section 2.1.1). The primary intent of SEAs to enable high-fidelity force control, however, is different.

As an extension to the SEA approach several servo motors are connected to a single mechanical spring in the biped Myon (Hild *et al* 2012), resembling the high number of actuators per DoF in biological walking

systems (cf sections 2.1 and 2.4). Several humanoid robots with compliant, antagonistic and bi-articular actuation were developed at the University of Tokyo¹¹ (e.g., Shirai *et al* (2011)).

In multi-legged robot, DC motors are widely used, but hydraulics and pneumatics are also common. The six-legged AirBot is an example of a pneumatically driven robot (Kerscher *et al* 2002), while HyQ is driven both by DC motors and hydraulic cylinders (Semini 2010)¹².

Multi-legged machines typically have one to four actuated DoFs per leg. Examples for robots with only one actuator for each leg are the planar quadruped robot KUMO-I (Hirose *et al* 2009), the quadruped robot Scout (Buehler *et al* 1998) and the hexapod robot RHex (see section 3.1.1 and Saranli *et al* (2001)). The quadruped robot Scout II has two DoFs per leg (Poulakakis *et al* 2005). In many cases, the legs are fully actuated, such as those of the quadruped ALoF with three DoFs per leg driven by DC motors (Hoepflinger *et al* 2010), the quadruped TITAN VIII with three active DoFs per leg, each actuated via cables driven by DC motors (Arikawa and Hirose 1996) or the Genghis robot which has two active DoFs driven by servo motors (Brooks 1989).

In a significant number of cases, multi-legged robots have passive DoFs such as the quadruped robot BigDog¹³ which has four active DoFs that are actuated hydraulically and one passive DoF (Raibert *et al* 2008) or a modification of the quadruped robot Scout II with unactuated knees with a locking mechanism (Hawker and Buehler 2000).

Elasticity is widely used in the actuation systems of one-legged and multi-legged hopping robots. Hyon and Mita (2002) and others use mechanical springs, Raibert (1983) uses pneumatic cylinders and Brown and Zeglin (1998) bow-shaped legs. For an overview of the hardware design (and control principles) of one-legged hopping machines, refer to Sayyad *et al* (2007). Most notably, Raibert (1983) built a one-legged hopping machine to conduct experiments on balancing in three dimensions during continuous hopping. The leg is a pneumatic cylinder that is connected to the body by a gimbal joint. The lateral DoFs of the leg are actuated by hydraulic actuators. For details on the hardware design, refer to (Raibert 1983, Raibert *et al* 1984, Raibert 1986).

Sensing In contrast to animals, walking machines generally have a much lower number of sensors (cf sections 2.1.2 and 2.4). Most robots are equipped with motor encoders for position sensing, a smaller percentage also has torque sensing in the joints and/or link

¹¹ <http://www.jsk.t.u-tokyo.ac.jp/research.html>

¹² The hip abduction/adduction DoFs are actuated electrically, the flexion/extension DoFs at hip and knee are actuated hydraulically (Boaventura *et al* (2012)).

¹³ Note that there are several robots developed by Boston Dynamics that carry the name BigDog. The passive DoF is only present in the model referred to in Raibert *et al* (2008).

side encoders. Superficially, these sensors share similarities with muscle spindle afferents and GTOs in vertebrates (cf section 2.1.2). Due to the importance of contact forces for balance, force/torque sensors (FTSs) in the feet are a standard component in biped robots. FTSs are sometimes combined with or substituted by contact switches for detecting ground contact. Multi-legged systems often have only contact switches used for gait coordination. Many robots, especially bipeds, also have inertial measurement units (IMUs) in the upper body or pelvis which are used for balance control (Lohmeier *et al* 2009, Tajima *et al* 2009, Hirose and Ogawa 2006, Kaneko *et al* 2004, Nelson *et al* 2012). The quadruped robots StarlETH (Hutter *et al* 2012) and LittleDog (Murphy *et al* 2011) and the hexapod robot X-RHex (Galloway *et al* 2010) are examples for multilegged robots that are equipped with IMUs.

Some robotic sensors are significantly more precise than the biological counterparts, while others are inferior. Examples of superior technological sensors are high-quality fiber-optic gyroscopes for IMUs, which can provide ≤ 0.003 bias stability (Barbour and Schmidt 2001). In contrast the mammalian vestibular system has an angular velocity detection threshold of $\approx 4^\circ \text{ s}^{-1}$ on the afferent (Sadeghi *et al* 2007) and $0.06\text{--}0.4^\circ \text{ s}^{-1}$ on the perceptual level (Grabherr *et al* 2008, Fitzpatrick and McCloskey 1994). In some cases, superior technology is available, but typically not used in walking robots. High quality angular encoders achieve better than one arc second accuracy, but most devices in legged robots have closer to 0.1° accuracy¹⁴. In comparison the human joint angle sense detects changes of 0.04° in the hip, 0.17° in the knee, 0.16° in the ankle and 2.4° in the toe for angular velocities of $12.5^\circ \text{ s}^{-1}$. For decreasing angular velocities the corresponding angular detection thresholds increase considerably (Refshauge *et al* 1995). An example of inferior technological sensors are cameras. Robots typically use systems with less than 10^6 pixels¹⁵, while the resolution of the human eye is orders of magnitude larger: the human retina has approx. 100×10^6 photoreceptors which are 60 times more densely packed in the center (the *fovea*) than in the periphery (Curcio *et al* 1990), allowing for a high resolution in the center and a wide viewing angle in the periphery. Using additional mechanisms humans exhibit hyperacuity, a phenomenon where the maximum visual acuity reaches a value of $1\text{--}5$ arc sec ($\approx 2.8^\circ$), six times smaller than the diameter of the smallest photoreceptor (Klein and Levi 1985, Wilson 1986).

In walking robots joint position, joint velocity and force sensing are usually assumed to be provided by dedicated sensors at an adequate accuracy. The

specific role of each of the many redundant sensory inputs in biology, by contrast, remains unclear and highly debated in many cases, as e.g. in case of the human hand angle sense (Johnson 2004, Panarese and Edin 2011). Multi-sensor fusion is also used in robotics, but mostly for tasks related to environmental perception, mapping and inertial navigation, not for direct control of walking (Durrant-Whyte and Henderson 2008).

Despite the superior precision of many technical sensors biological systems still outperform walking machines (cp. introduction). One possible explanation is already suggested by some of the examples given above: biological systems efficiently integrate the available multisensory information (Stein and Stanford 2008, cp. also section 2.2.2) resulting in more precise and more task specific sensory information when compared to the output of a single sensor.

3.2. Basic dynamics of legged locomotion

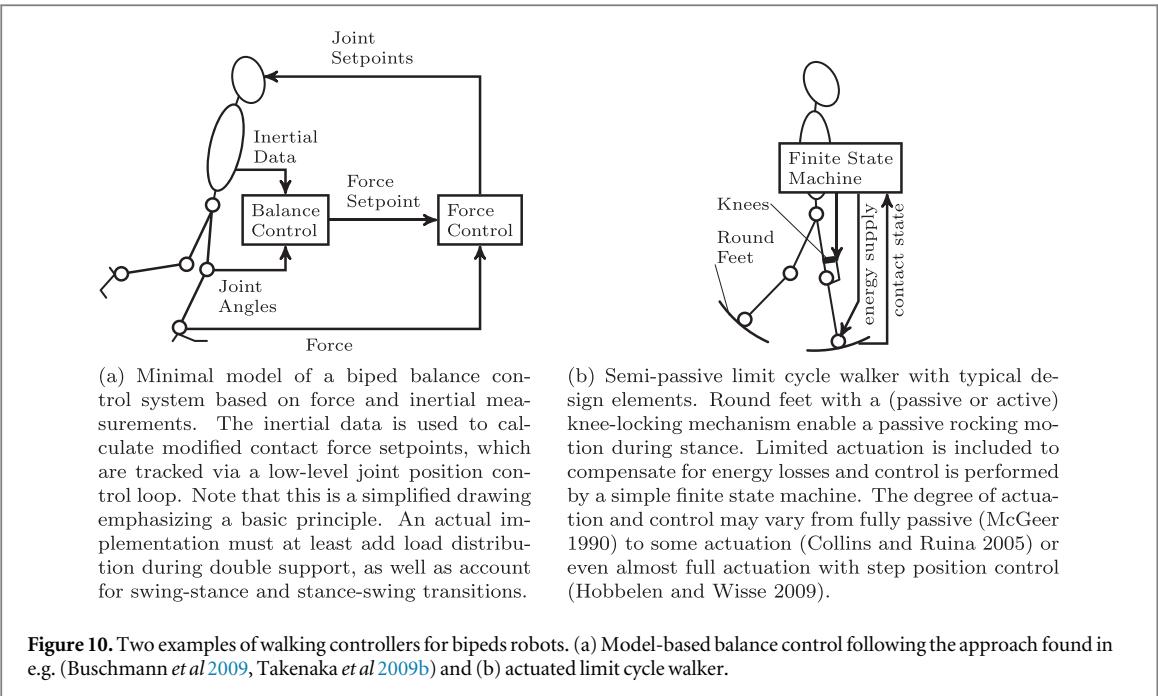
Machine locomotion can be categorized either as statically or as dynamically stable (cf, Berns *et al* (1999), Bekey (2005), Full *et al* (2002)). The first formulation of a condition for static stability of a walking system is given by McGhee and Frank (1968), where the authors define static stability for walking on a horizontal plane as a configuration where the projected center of gravity lies within the current BoS. This criterion, however, is only suitable in the idealized quasi-static case, when inertial forces are negligible. In cases with significant accelerations, dynamic stability has to be investigated. See Raibert (1983) and Full *et al* (2002) for a discussion of dynamic stability. Note that stability is not to be confused with feasibility, which is related to set of possible contact forces compatible with the unilateral foot ground contact. See also section 3.4 and Wieber (2002). No information about neural control mechanisms using such concepts is available.

Walking machines are hybrid systems, since the foot-ground contact is unilateral: the contact states of the feet take on discrete values such as opened, closed, slipping or sticking, while at the same time the pose of the robot varies continuously. This hybrid nature is also found in the dynamics of walking systems: trajectories of joint angles or joint torques are continuous functions of time, but landing positions of feet and stride lengths have discrete values for each step.

As with any controlled system, the resulting motion of the robot will depend both on the dynamics of the uncontrolled system, composed of the robot and its environment, and the walking controller. In the large body of work on walking control, the emphasis put on the design of either (passive) mechanics or control varies greatly, as does the emphasis put on either the discrete (step-to-step) or continuous aspects of walking. Figure 10 illustrates two different approaches towards stable bipedal walking described in more

¹⁴ For example the ECI-type encoders by Heidenhain used in the Lola robot. For data see, e.g., <http://www.heidenhain.com>

¹⁵ Many robots still use VGA-resolution cameras ($640 \times 480 \approx 3 \times 10^5$), few more than XGA ($1024 \times 768 \approx 8 \times 10^5$).



detail below: stabilization through contact force control (figure 10(b)) and (almost) passively stable walking, augmented by some control and energy supply (figure 10(a)).

Strictly speaking, every legged robot is underactuated, since the foot-ground contact always has finite stiffness and there is no input corresponding to the elastic deformation of the contact. Nevertheless, robots with one actuator per joint will be termed *fully actuated* in this paper, if the remaining underactuation is only due to the deformation in the ground contact. This is to distinguish them from robots with point feet, with unactuated joints or additional elastic DoFs.

3.3. Model-based control of underactuated robots

In this section, we give an overview of model-based control methods for underactuated hopping machines (section 3.3.1), biped robots (section 3.3.2) and multi-legged machines (section 3.3.3).

3.3.1. Hopping machines

Raibert's experiments with one-legged hopping machines (cf section 3.1) and the general control strategy developed for them is a milestone in legged robot research. The control system is model-based and the control task is decomposed into the three parts *forward running velocity*, *body attitude* and *hopping height* (Raibert 1983). The employed control principle is often referred to as *Raibert's three-part control* (Semini 2010). By introducing the *virtual leg* concept originally introduced by Sutherland and Ullner (1984), where multiple legs are considered to behave as one *virtual leg*, the *three part control* principle can be used to control walking machines with more than one leg (Raibert 1986).

3.3.2. Biped robots

An interesting theoretical framework for walking control that emphasizes the problem of underactuation was developed for the five-link planar robot Rabbit (Chevallereau et al 2003, Westervelt et al 2003). This robot uses four electric motors for actuation. The actuated joints, as well as the passive joints connecting the robot to the central boom enforcing the planar motion, are equipped with position sensors and the feet with contact force sensors. The robot has point feet, leaving one degree of underactuation at the foot-ground contact.

The controller enforces the same number of position-dependent *virtual constraints* as can be directly controlled via the actuators, i.e., four in this case. The constraints are not given as a function of time, but parameterized by some monotonic state variable, e.g. the stance leg inclination. Since the chosen outputs (or virtual constraints) can easily be tracked by a position controller, stability is determined by the remaining internal dynamics of the system (the zero dynamics) that are not visible in the outputs. Since the robot is a hybrid dynamical system, the internal dynamics are called *hybrid zero dynamics*. A stable control system is designed by calculating virtual constraints using off-line optimization methods that can enforce stable zero dynamics via inequality constraints in the optimization problem. The essence of the approach is to control only as many outputs as can be directly controlled and to choose these in such a way as to assure stability of the uncontrolled DoFs.

This approach has more recently been applied to the planar five-link biped Mabel (Sreenath et al 2011). The basic structure is similar to Rabbit's, but forces are applied by compliant, antagonistic actuators, increasing the degree of underactuation and adding a

mechanical energy storage and shock absorption mechanisms. Very recently, Park *et al* (2013) expanded the system to include a component based on an FSM for reacting to large changes in ground height. According to the detected system state (step-down, step-up, tripping,...), modified virtual constraints are controlled. Additionally, active force control is added to stabilize the system and attenuate shocks when stepping off high platforms.

While a number of robots with elastic actuation mechanisms have been developed (see section 3.1), the question of how to utilize the compliance in walking machines remains an open problem. In the controller proposed by Vanderborght *et al* (2005b) for the pneumatically actuated robot Lucy (cf section 3.1), joint position references are tracked at a lower control level, compensating joint elasticity.

Robots with *series elastic actuators* are also underactuated (see section 3.1.2). However, since a low-level controller tracks the desired joint torque, the upper control levels can view the system as a torque controlled robot. Pratt *et al* (2001) proposed using *virtual model control* for such robots. In this approach, virtual forces acting on the robot are generated using intuitive, heuristic rules and then mapped to actuator forces.

3.3.3. Multi-legged robots

The hexapod robot RHex (cf, section 3.1) is not equipped with external sensors. It uses an open-loop gait generated by clock-driven reference trajectories in joint space (Saranli *et al* 2001). The motivation for this setup is a hypothetical running animal that would generate locomotion by restricting the control architecture to a CPG and biomechanics, removing sensory feedback which might be too delayed due to limited neural transmission speeds (see sections 2.2.1 and 2.2.2). According to Clark *et al* (2001), the elastic system of RHex has self-stabilizing properties and together with the biologically inspired functional morphology of the legs provides a *zero-order* response to perturbations which means that it does not depend on neural processes and therefore exhibits no time delay. According to Bekey (2005), each of the legs of RHex and the quadruped robot Scout II (Poulakakis *et al* 2005) can be modeled as a *Spring-Loaded IPM* (SLIP). It should be noted, that the large body of research on animal locomotion emphasizes the importance of sensory feedback and that the existence of locomotion in animals that does not make use of proprioception for stabilization is controversial. It appears, however, that the role of sensory feedback in the online control of the motor output decreases along with the cycle period. This is due to the substantial dead time the biological muscle-skeleton system exhibits before generating forces, e.g., between 30 ms and 40 ms in walking insects (see e.g. Wosnitza *et al* 2013).

The robot KOLT (cf section 3.1) is able to perform pronk and trot gaits in a plane by controlling the liftoff speed of the legs from the ground. The thrusting force between the feet and the ground is generated by the pneumatic springs in the knee. As soon as the desired liftoff speed is reached, the foot is lifted off the ground using the electric motor in the knee (Estremera and Waldron 2008).

Poulakakis *et al* (2005) present a control system for realizing a bounding gait with the quadruped robot Scout II. In this control system, running is achieved by regulating the touchdown angle of the virtual legs¹⁶ during the swing phase and the motor torque during stance. Each of the two virtual legs can be in one of four states (Poulakakis *et al* 2005) and the transitions between these states are initiated by touchdown and lift-off events (Buehler 2002). For comparison with the situation in animal stepping, see section 2.2.2.

3.4. Model-based control of fully actuated robots

Many successful approaches to walking controller design for fully actuated robots are based on physical models and classical control system design. In section 3.4.1 we review model-based control of fully actuated bipeds. Methods for multi-legged robots are reviewed in section 3.4.2.

3.4.1. Biped walking control

From a control systems perspective, the major differences between the control of a (rigid) robot manipulator and walking control are the hybrid nature of the walking system, the underactuation and the inequality constraints imposed by the unilateral ground contact. While questions such as low-level control of the joints can be efficiently handled with well-known methods from manipulator control, the additional tasks of (1) satisfying all constraints and (2) stabilizing the unactuated DoFs, while (3) exhibiting the desired walking behavior remain challenging.

Due to the highly nonlinear dynamics and the inequality constraints, a straightforward solution of the control problem, using e.g. optimal control methods, is currently impossible due to the computational costs. Nevertheless, a number of promising results from simulation studies using detailed models and optimization have been reported: Azevedo used nonlinear model predictive control (MPC)¹⁷ for a planar bipedal robot (Azevedo *et al* 2002), Schultz presented optimal trajectories for a 3D model of a human (Schultz and Mombaur 2010) and Tassa reported a fast but non yet real-time MPC method for generating and stabilizing various motions of a humanoid robot

¹⁶ The front and hind leg pairs are considered as virtual legs each represented by a linear spring-damper system during stance (Poulakakis *et al* 2005).

¹⁷ That is, solving an optimal control problem, using the result for the next time step and then repeating the procedure at every time step.

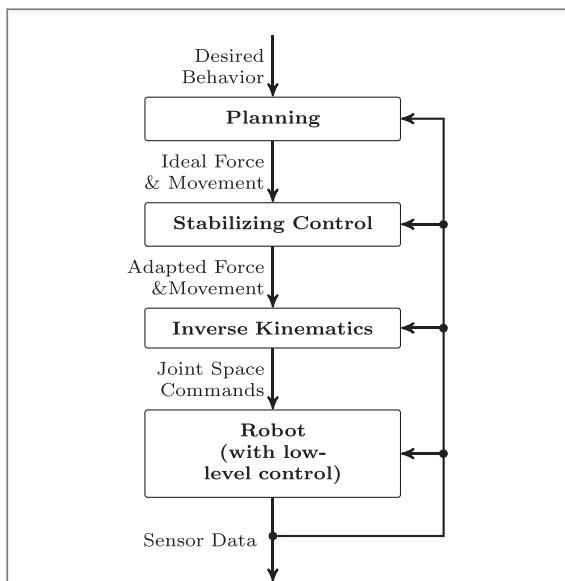


Figure 11. Example of a hierarchical control architecture with real-time planning and balance control for fully actuated robots, as it is used in many state of the art walking machines (e.g. Buschmann *et al* (2009)). Each level can have multiple sub-levels, e.g. step-cycle and trajectory planning within the ‘Planning’ level. Planning and control are typically formulated in terms of foot and CoG positions and contact forces. Joint space variables for low-level control are then obtained from inverse kinematics. Most early and some current implementations use offline planning, but online methods now dominate since they facilitate more reactive behavior.

(Tassa *et al* 2012). Therefore most control systems use a hierarchical design with higher levels responsible for overall behavior, intermediate levels for the discrete gait sequences and lower levels for task-space and joint-space motion (see Buschmann *et al* (2009), Nishiwaki *et al* (2002) and figure 11), thereby expressing organizational similarities to walking animals (cf section 2.1.3). The control problem is often separated into planning ideal reference trajectories and modifying the references using feedback control. However, more recently there has been a trend towards incorporating sensor feedback into planning to improve long term stability, thereby blurring the distinction between planning and feedback control (Tajima *et al* 2009, Nishiwaki and Kagami 2006). In animals the local neural circuitry for stepping pattern generation, residing e.g. in vertebrates in the spinal cord segments, appears to operate rather independently in the generation of a basic motor output (e.g. Orlovsky *et al* (1999)). Evidence suggest that trajectory planning is mediated in higher order control centers, e.g. when modification of stepping trajectories is necessary to overcome obstacles (e.g. Pearson and Gramlich 2010, Lajoie *et al* 2010, McVea *et al* 2009).

Planning reference trajectories Since real-time planning using complex multibody robot models is currently computationally intractable, there are two dominating approaches to planning reference trajectories: (1) off-line planning using comprehensive models and (2) on-line planning using simplified

models. Due to the importance of real-time gait generation for adapting to changes in the environment or the desired behavior, most systems today use real-time methods. For examples of offline planning methods see (Denk and Schmidt 2003, Buschmann *et al* 2005, Bessonnet *et al* 2004, Cho and Oh 2008). Most work on real-time planning is based on simplified lumped mass models, usually the LIPM (Kajita and Tani 1995). This model describes the linear dynamics of the CoM in the lateral and sagittal planes when the CoM height remains constant (see Buschmann (2010) for a discussion). Occasionally, additional terms for approximating the influence of leg motion and torso rotation are added (Pratt *et al* 2006, Takenaka 2004b, Park and Kim 1998, Buschmann *et al* 2007).

The simplified robot model is given as an ordinary differential equation (ODE) relating the CoM to the contact moment at the foot. The planning system must determine contact force and CoM trajectories that satisfy the ODE and for which the forces satisfy the inequality constraints imposed by the unilateral ground contact. In biped walking control the zero moment point (ZMP, the point where the resulting contact force acts) is often used instead of the contact moment, since it leads to a simple criterion for feasible contact forces when walking on flat ground: the ZMP must remain within the convex hull of the BoS (Vukobratović and Borovac 2004). This feasibility criterion is often mistakenly used as a *stability criterion*, even though satisfying it does not assure that the robot will not fall¹⁸. General feasibility criteria are discussed in (Hirukawa *et al* 2006, Takao *et al* 2003). Most planners first calculate an admissible force trajectory that can then be used to determine a CoM trajectory by solving the ODE. To assure a stable solution to the planning problem, this approach requires either a deviation from the ideal force trajectory by actively modifying the reference (Takenaka *et al* 2009a, Buschmann *et al* 2007), by only approximately satisfying it (Kajita *et al* 2003, Diedam *et al* 2008), or by violating the desired boundary values for the CoM-trajectory (Sugihara and Nakamura 2005). Proposed planning

¹⁸ The relationship between ZMP and stability is controversial (Vukobratović *et al* 2006, Sardain and Bessonnet 2004). We will only try to briefly describe the controversy, since the details of the discussion are beyond the scope of this paper. A central issue is the fact that Vukobratović distinguishes between the case when the ZMP is strictly within the BoS and the case when it is on the edge (Vukobratović *et al* 2006), a fine point that is often overlooked. Vukobratović only refers to the first case as stable, since the ZMP may be moved towards the edge to stabilize the system. If the resulting contact force lies on the edge of the BoS, this point is no longer called the ZMP. This distinction separates the center of pressure from the ZMP according to Vukobratović. Nevertheless, it is easy to design cases when the ZMP is at the center of the BoS and no feasible control can prevent the robot from falling. This is possible, since the state of the system is not uniquely defined by the ZMP. The simplest examples are statically stable configurations for which a very high CoM velocity is chosen (Buschmann 2010). Regardless of the relationship of the ZMP to stability, the concept has been instrumental in the development of biped walking controllers.

algorithms using this approach include analytical solutions (Harada *et al* 2004, Morisawa *et al* 2006, Löffler *et al* 2004), numerical solutions by finite difference approximation (Kagami *et al* 2002), a kind of shooting method (Takenaka 2004b, Takenaka *et al* 2009a), methods based on MPC (Kajita *et al* 2003) and a method based on spline collocation (Buschmann *et al* 2007). Diedam *et al* (2008) proposed using linear MPC for solving the planning problem. The implementation is based on quadratic programming, enabling a simple extension of CoM-planning to footstep adaptation (see above for the situation in animals).

Stabilizing control A large and growing number of control methods for stabilizing fully actuated bipeds has been proposed and successfully implemented. The task of balance control (also called stabilizing control) is to assure a given reference motion while simultaneously preventing the robot from falling. Most methods build on the basic stabilizing mechanisms of (1) modifying the contact forces, (2) horizontally accelerating the CoM and (3) foot step control. These mechanisms are roughly equivalent with the (1) ankle-strategy, (2) hip-strategy and (3) stepping-strategy observed in animals (see section 2.3.1). Figure 10(a) illustrates the basic idea of balance control through contact force modification.

If the robot becomes unstable, it will diverge from the ideal, stable reference motion. A deviation of individual joint angles from the reference gait pattern is not critical, but the robot must avoid falling. Since a computationally tractable, practical and correct stability criterion for walking systems remains to be found (cf Wieber (2002)), the divergence of the total linear and angular momentum of the system may be taken as a practical measure of instability. The total linear and angular momentum of a system can only be changed by external forces acting on the system boundary. Modifying contact forces therefore is the only possible way of stabilizing the system. In fact, the hip-strategy changes contact forces by accelerating the CoM (or vice-versa) and the stepping-strategy modifies the whole range of feasible forces by changing the support polygon.

The dominant method of stabilization via contact force control consists of modifying the contact moment in order to stabilize the upper body orientation or CoM position (Kajita *et al* 2005, Löffler *et al* 2004, Takenaka 2004a, Takenaka *et al* 2009b, Buschmann *et al* 2009). Usually, the contact moment is measured by the FTS in the foot and controlled via an underlying joint position controller. The landing impact may be reduced by an additional vertical impedance or force control (Löffler *et al* 2004, Kajita *et al* 2005, Nishiwaki and Kagami 2009, Buschmann *et al* 2009), or an indirect force control via reduced joint position control gains (Tajima *et al* 2009, Nishiwaki 2001, Hashimoto *et al* 2009).

Accelerating the upper body or CoM for balance control is also widespread (Tajima *et al* 2009, Nishiwaki and Kagami 2006). Takenaka *et al* propose activating this strategy when the maximum admissible contact moment is reached (Takenaka *et al* 2009b).

An interesting approach addressing the issue of underactuation was proposed by Chevallereau *et al* (2008). Instead of tracking trajectories, only a reference path is tracked. This adds the path parameter as an additional control input, making planer bipeds fully actuated. This method is related to ideas from robot manipulator control (Pfeiffer and Johanni 1986).

Modifying the next foothold leads to a strong deviation from the originally intended motion, but at the same time is the most powerful method of stabilization. For the stepping-strategy the range for modifying the forces is limited by the maximum step length and stepping speed, while contact force control and upper body acceleration are limited by the size of the feet and the friction coefficient between the feet and the ground.

The stepping-strategy was also used by the one, two and four legged hopping machines developed by Raibert and colleagues (Raibert 1986, Hodgins and Raibert 1991). In this work the control of speed and balance is achieved by modifying the stepping position relative to a neutral point defined by the foothold corresponding to a periodic hopping motion (Raibert 1986, Raibert and Brown 1984). This strategy could be used very effectively for the hopping machines due to the very low leg mass and inertia.

Takenaka *et al* (2009b) proposes modifying the step positions in case modifications of the upper body trajectory induced by the hip-strategy cannot be compensated during the next step without changing the step length. Urata *et al* (2011) proposes calculating footstep positions using singular preview control and on-line parameter optimization. The strategy requires fast stepping, which is enabled by high-speed actuation and high structural stiffness (Urata *et al* 2010). Tajima *et al* (2009) proposed a controller for a running biped based on frequently replanning the CoM trajectories, as proposed by Nishiwaki and Kagami (2006). The system uses the initial velocity of a periodic gait pattern as final velocity for calculating the CoM trajectory of the current step. The resulting final CoM position for the current step and the initial distance of the CoM from the stance leg for the periodic gait are then used to determine the next stance leg position.

Pratt *et al* (2006) coined the term *capture point* for positions where the robot can step in order to come to a complete stop. The set of all capture points is called the *capture region*. To facilitate the calculation of capture points, the robot is modeled as a LIPM, augmented by a fly wheel. Based on this concept, strategies for push-recovery and walking control are formulated. Nelson *et al* (2012) propose positioning the foot relative to the capture point according both to the desired

gait and the balancing requirements in the walking control of the Petman robot.

For the LIPM, the *capture point* is equivalent to the XCoM introduced by Hof *et al* (see section 2.3.1). It is also equivalent to the *divergent component* introduced even earlier in a patent by Honda Motor Co. Ltd. (Takenaka *et al* 2004). The essence of Honda's method is a diagonalization of a first-order representation of the LIPM ODE, which leads to two decoupled systems, of which one is stable (the *convergent component*) and one is unstable (the *divergent component*). The divergent component is then used to assure convergence of the CoM-trajectory to a desired periodic gait¹⁹. The concept has since been extended to running gaits with non-constant CoM-heights (Takenaka *et al* 2009c).

Uneven terrain Walking in unknown and uneven terrain is especially challenging for biped robots and has been addressed using both control and hardware design. Kang *et al* (2010) developed a special foot mechanism with distance sensors that can mechanically adapt to uneven terrain for the robot Wabian-IIR. Similar mechanisms were previously developed at the same institute for biped walking chairs (Yamaguchi *et al* 1995, 1994). Impedance or force control have been proposed for reducing the landing impact during walking (Buschmann *et al* 2009, Nishiwaki and Kagami 2010, Lim *et al* 2001). Other researchers have proposed implicit force control for reducing landing impacts, implemented by reducing joint position control gains during the expected impact phase (Tajima *et al* 2009, Nishiwaki 2001, Hashimoto *et al* 2009). Very recently, the robot ATLAS developed by Boston Dynamics for the DARPA Robotics Challenge²⁰ based on Petman, was shown to walk over loose rocks held in a wooden frame. To our knowledge, the only publication is a video²¹ released on the internet and details on the controller design are unknown. Animals appear to be using simple dynamical systems exhibiting 'self-stability' as templates for neural control (cf section 2.1). Similar to the simple template models, animals are remarkably stable on uneven ground see (e.g. Full *et al* (2002)). Humans actively adapt to visible changes in ground height both during contact and one step before a change in ground level is encountered. When stepping on hidden changes in the ground level, kinematic and kinetic adaptation are more pronounced, since no predictive control is possible. Both for visible and invisible drops, adjustments of step length and torso angle are apparently central to balance control (Müller *et al* 2014). The details of neural control while walking on uneven terrain are unknown.

¹⁹ Note that coming to a complete stop is a special case of a periodic orbit.

²⁰ <http://www.theroboticschallenge.org>

²¹ <http://youtu.be/SD6Okylclb8>, accessed 2013/18/10.

3.4.2. Multi-legged robots

For quadruped locomotion, McGhee and Frank (1968) derived a sequence of leg movements for statically stable quadrupedal locomotion that maximizes a static stability measure under idealizing assumptions:

$$\begin{array}{l} \text{right hind leg} \rightarrow \text{right front leg} \\ \rightarrow \text{left hind leg} \rightarrow \text{left front leg} \end{array}$$

This step sequence often serves as a basis to realize static a quasi-gait for quadruped robots, e.g. Kolter and Ng (2011), Kalakrishnan *et al* (2011), Hutter (2013).

In 2005, DARPA started the *Learning Locomotion* program to forward autonomous legged robot technology using machine learning techniques (Pippine *et al* 2011). The participating teams developed control systems for the quadruped robot LittleDog²² that is able to perform locomotion tasks in uneven terrain. For an overview of the tasks and the results, see Pippine *et al* (2011). Kolter and Ng (2011) realize a statically stable gait to walk over uneven terrain where footstep locations are generated within a machine learning framework²³. Kalakrishnan *et al* (2011) use a greedy search algorithm to calculate the footstep positions for a statically stable gait in uneven terrain.

The trajectories of the robot HyQ (cf section 3.1) for trotting motion are generated by prescribing trajectories in work space where the foot trajectories are sinusoidal during the swing phase and constant during the stance phase. Desired joint torques are determined using inverse dynamics and controlled using a low-level force control based on feedback linearization (Boaventura *et al* 2012).

For low locomotion velocities StarlETH (cf section 3.1) uses statically stable walking with an optimization of the ground contact forces (Hutter *et al* 2013). Trajectories for dynamic gaits are generated using gait patterns prescribing the timing of stance and swing phase for each leg, determining appropriate footstep locations and using a modified LIPM (Gehring *et al* 2013).

The quadruped robots LS3 and Cheetah developed by Boston Dynamics show impressive capabilities on video²⁴. LS3 is designed as a transportation robot suited for rough terrain²⁵. Cheetah is a planar quadruped with a reported top speed of 45.5 km h⁻¹ while running on a treadmill²⁶. The three dimensional untethered quadruped WildCat was shown to run at 26 km

²² Developed by Boston Dynamics, see Murphy *et al* (2011) for specifications.

²³ Kolter and Ng (2011) call their approach *hierarchical apprenticeship learning*.

²⁴ LS3: <http://youtu.be/R7ezXBEBE6U>, accessed 2013/18/10; Cheetah: <http://youtu.be/chPanW0QWhA>, accessed 2013/18/10.

²⁵ http://www.bostondynamics.com/robot_ls3.html

²⁶ http://www.bostondynamics.com/robot_cheetah.html

h^{-1} ²⁷. To the best of our knowledge, there are no scientific publications about these machines yet.

3.5. Biologically-based pattern generation

Most robot control systems are model-based and adopt the basic architecture of planning ideal reference trajectories and modifying these based on sensor feedback (cf figure 11). In contrast to this, many biologically inspired concepts use CPG models for creating the default motor output, i.e. muscular contractions, for generating walking trajectories (cf section 2.2.1). The goal of these concepts is to replicate the generation of rhythmic patterns for walking generation as observed in animals and humans (cf, section 2.2.1) in the walking machine control systems. As a CPG model, a neural oscillator proposed by Matsuoka (1985) is often used (e.g. Endo *et al* (2008), Fukuoka and Kimura (2009)). Matsuoka's CPG is a model of two mutually inhibiting neurons described by coupled differential equations. This model represents the half-center oscillator concept which is the most important element of neural networks for creating alternating left-right locomotion activity in vertebrates (cf section 2.2.1). One feature of CPGs is their ability to synchronize their intrinsic oscillations with input signals (entrainment, see section 2.1.2), thus allowing adaptability to changing environments. This integration of internal and reflex loops is seen as one of the key features of biological walking control (see sections 1, 2.1.2, 2.1.3, 2.2 and 2.4). Note that single CPGs are often used in robotics, especially for bipedal systems. This is different from animals, where multiple CPGs, at least one per leg, contribute to stepping (cf UBG-hypothesis, section 2.2.1). It should be noted that recent evidence suggests that multiple CPGs also exist in mammals (Häggblund *et al* 2013). However, for human walking no insights exist about the detailed organization, and a potential modularity of the spinal networks for walking (e.g. Dimitrijevic *et al* 1998).

A drawback of CPG-based methods is the necessity of costly parameter tuning to realize even basic walking in bipeds. Many optimization methods have been proposed for creating a set of suitable parameters, such as a gradient method with reinforcement learning (Matsubara *et al* 2006, Sugimoto and Morimoto 2011). Extended CPG models that allow the definition of arbitrary waveforms (Tran *et al* 2014) might bridge the gap to model based controllers.

One important approach in CPG-based control is the concept of resetting the phase of a neural oscillator as soon as ground contact of the swing leg is detected. It has been shown in theory (e.g. Shinya and Tsuchiya (2006)) and experiment (e.g. Nakanishi *et al* (2004)) that this phase reset can improve the stability of a CPG-controlled walking machine. Fukuoka and Kimura (2003) propose a CPG-based control system

for a quadruped robot in which the walking pattern for each leg is generated by defining desired joint positions depending on the current state of the leg. The criteria for state transition initiation depend on CPG model variables and position feedback.

3.5.1. Biped robots

Sugihara (2009) proposes a CPG based on a controlled LIPM of the robot. While the pendulum is inherently unstable when generating the pendulum position by integrating the equation of motion based on a given ZMP trajectory, a stable limit cycle can be generated by calculating the input ZMP using a nonlinear feedback law.

Geng *et al* (2006) proposed a biologically inspired control method for the small biped robot RunBot with four active joints, based on previous work with the similar WalkBot robot. The robots are laterally stabilized by a suspension system, allowing the controller to ignore lateral dynamics. Walking is based solely on reflexive control implemented in a network of non-spiking neurons consisting of one extensor and one flexor neuron per joint (cf, section 2.2.1; Büschges *et al* 2011). The motoneuron output is directly converted to an armature voltage for the driving DC motors. The mechanical design of WalkBot has typical features of passive walkers such as mechanical end-stops in the knees and rounded feet. Sensory feedback is provided by potentiometers in the joints and contact sensors in the feet. The authors have also used on-line learning based on policy searching to tune controller parameters (Geng *et al* 2006).

3.5.2. Multi-legged robots

The findings from neurobiology suggesting that rhythm generators in the CNS (CPGs) are central to generating walking motions in animals (cf, section 2.2.1) have also been used for controlling multi-legged robots. CPG-based control can be interpreted as biomimetic controller design (Kalakrishnan *et al* 2011) and is often believed to be particularly beneficial for walking machines with compliance (e.g. Kolter and Ng (2011), p 152). This belief is based on the fact that all animals have a certain amount of compliance in the muscle-tendon system and make use of CPGs for walking control. Examples for CPG-controlled quadruped robots are the robots of the Tekken series²⁸, LittleDog (cf, section 3.4.2) with the control environment developed by Kolter and Ng (2011) and BISAM (Ilg *et al* 1999). All of these walking systems are capable of maintaining stability while walking over uneven terrain.

In general, CPG-based walking controllers utilize a CPG model such as the one proposed by Matsuoka (1985) (cf, section 3.5) to generate trajectories and

²⁸ Tekken1 (Fukuoka *et al* 2003), Tekken2 (Kimura and Fukuoka 2004), Tekken3 and Tekken4 (Fukuoka *et al* 2010).

²⁷ <http://youtu.be/wE3fmFTtP9g>, accessed on 2013/18/10.

feedback mechanisms to modify these trajectories directly or indirectly by acting on the behavior of the CPG. According to Ilg *et al* (1999), a framework of CPG and reflex mechanisms enables robust walking and allows the use of online learning methods.

If sensory signals are available, they can be used to implement responses of the walking system to external stimuli, often called *reflexes* (e.g. Kimura and Fukuoka (2000), Espenschied *et al* (1996), Pearson and Franklin (1984)). In many cases, responses known from biological walking systems are implemented in walking robots. Fukuoka *et al* (2010) distinguish a total of seven different types of reflexes that are implemented in the walking system of Tekken3 and Tekken4. Three examples of reflexes are²⁹:

- The vestibulospinal response: Fukuoka *et al* (2003) call the reflex caused by the inclination of a robot in the pitch direction³⁰ vestibulospinal response. In the implementation of this reflex on the robot Tekken, the hip moment of the robot is modified during stance (Fukuoka *et al* 2003). The same principle is employed in the robots Tekken2, Tekken3 and Tekken4³¹ (Fukuoka *et al* 2010). The robot Patrush uses a similar principle (Kimura and Fukuoka 2000).
- Reinforcement of force/load (Tendon response): As shown in section 2.2.2, leg loads cause excitatory signals on the activity of extensor motoneurons during the stance phase, thereby assisting the ongoing stance phase. Kimura and Fukuoka (2000) use the term *tendon response* and present an implementation on the quadruped robot Patrush where the angular velocity of the hip joint is used as a sensor signal instead of a load signal to generate the excitatory feedback signal to the CPG.
- Reinforcement of movement (extensor and flexor responses): Joint movements are reinforced by positive movement feedback (for summary of the neurobiological findings cf section 2.2.2), e.g. causing assistance to leg extension when extensor muscles are active and to leg flexion when flexor muscles are active (Kimura and Fukuoka 2000). In the control system of Tekken3 and Tekken4, a flexor reflex (Kimura and Fukuoka 2000) is triggered when a collision with an obstacle is detected (Fukuoka *et al* 2010).

An example of a biologically-based walking machine that closely follows its animal model, also employing a combination of CPGs and reflexes, is the robotic lobster developed by Ayers *et al* (cf e.g. Ayers

and Witting (2007)). It uses an FSM-based controller resembling the connectivity and dynamics of the lobster CPGs and outputs amplitude and timing for the actuators (Ayers and Witting 2007, Ayers *et al* 2010). The internal state is encoded in quantized state variables and low-level reactive control is achieved by feedback to these variables (exteroceptive reflexes). Higher-level control is possible through a library of motion primitives (action patterns) that can be used in a sequencer. Current work is directed towards mimicking the neural control even more closely (Ayers *et al* 2010): CPGs will be implemented as analogue very large scale integrated electronic neural networks and higher levels for commands and coordination as discrete time maps, i.e., discrete time models of neurons.

Some biologically-based robotic approaches focus on the integral role of sensory feedback influences in generating the basic alternating swing and stance rhythm for walking. Instead of exploiting auto-rhythmic CPG properties, controller components are merely employed to ensure alternating activity of swing and stance components, e.g. by mutual inhibitory coupling influences in between them or by a bistable element driving both components with opposite sign. Examples are walking controllers derived from the stick insect (cf section 2.4) that have been implemented on robots (Pfeiffer *et al* 1995, Beer *et al* 1997, Lewinger *et al* 2006, Schneider *et al* 2011, von Twickel *et al* 2012).

3.5.3. Applicability and potential

For high-performance walking robots the dominant control methods are based on physical models and classical control theory. We can hypothesize that biologically-based pattern generation approaches have been less successful so far, because they have mostly focused on low-level aspects, such as the structure of the neural oscillators instead of the performance of the system as a whole. However, it is known from neurobiology that the relevant aspect of the pattern generators is not necessarily the periodic output they are capable of generating, since this will always be modified by task-dependent intra-joint-, intra-leg- and inter-leg- sensor feedback and coupling influences of other CPGs as well as by higher brain areas (cf sections 2.2.1, 2.2.2, 2.3 and 2.4). The more important aspect is the structure of possible feedback paths they define, e.g., positive force feedback during stance or position feedback during swing (see sections 2.2.1, 2.2 and figure 6). Therefore, simulation studies and also some robotic studies started to focus on these feedback paths (cf section 2.4, Schneider *et al* (2006)). Additionally, the nonlinear dynamical interaction between multiple feedback pathways is of high interest.

²⁹ The same enumeration as below can be found in Kimura and Fukuoka (2000).

³⁰ As opposed to the roll direction.

³¹ Tekken4 is a lightweight version of Tekken3 (Fukuoka *et al* 2010).

3.6. Gait cycle-centered control

3.6.1. Limit cycle walkers

It is known from biomechanics that the physical properties of the musculoskeletal system are important for human and animal walking. In fact, simple mechanical models of walking and running have been developed that exhibit force patterns in simulations that are also observed in experiments. The simplest models are the IPM and the SLIP model (Blickhan 1989). Interestingly, it has been observed that such very simple spring-mass models are stable without active control, a property also called *self stability* or *open-loop stability* (cf, section 2.1.1).

This has motivated the design of a number of mechanisms and robots that emphasize the *natural dynamics* of walking over active control. At the extreme end are passive dynamic walkers with no active control pioneered by McGeer (1990), which go back to simple mechanical toys that can walk down an inclined slope by rocking from one foot to the other. The gait is fully determined by the kinematics and mass distribution of the mechanism and the incline of the slope. In a sense, the walking control is embedded into the mechanical design of these machines. The passively swinging legs are stabilized by mechanical stops during stance, the landing impact acts as a physical resetting mechanism and the inclined ground provides energy. While mostly explored in the context of bipedal robots, the underlying principles of passive dynamic walking have also been applied to multi-legged mechanisms (Sugimoto *et al* 2011).

More recent work has focused on exploiting passive dynamics while adding some actuation and control (cf figure 10(b)). Collins and Ruina (2005) presented a mechanism incorporating actuators and springs connected in series to the ankle joints. This mechanism provides energy via a push-off motion after initial contact of the contralateral leg. The actuator is controlled by a simple FSM. Sensing is provided by ground contact and foot extension switches.

In general, limit cycle walkers emphasize step-to-step control, not continuous stabilization or tracking control (Hobbelin *et al* 2008). An example of a more recent limit cycle walker is the robot Flame. It combines some classical design elements seen in passive dynamic walkers, such as hyperextension stops in the knees, but still is capable of level ground walking thanks to the addition of joint actuation (Hobbelin *et al* 2008). The robot uses lateral foot placement for stabilization. The heuristic linear control law is based on the CoM position and velocity in combination with foot contact switches for step-phase control (Hobbelin and Wisse 2009).

3.6.2. Step-phase control

In the majority of robot walking control systems there is no real step-phase control in the sense of a feedback control system, since timing and duration of stance and swing phases are predetermined by a planning

module, contrary to the situation found in animals (see section 2.2.2). Note that this is not the case for CPG-based controllers, which often include step-phase control via a phase-resetting mechanism for the neural oscillators (see section 3.5). This section focuses on step-phase control for non-CPG-based systems.

Event-based phase switching mechanisms that incorporate sensory feedback into step-phase control have been developed for a variety of walking systems such as a hopping robot (Sato 2007), quadruped robots (Fukuoka and Kimura 2003, Hawker and Buehler 2000), planar biped robots (Pratt and Pratt 1998a, 1998b, Pratt *et al* 2001, Sreenath *et al* 2011) and 3D biped robots (Furusho and Sano 1990, Pratt and Pratt 1999, Morisawa *et al* 2011, Buschmann *et al* 2012). Sato (2007) presents a switching controller for a hopping robot where the same controller is used during the flight and the ground contact phases. Phase change events cause a switching of desired variables and gains.

The control framework for biped robots developed by Pratt *et al* incorporates a state machine for each leg. The rules for state transitions are formulated intuitively based on the position of the body relative to the feet and ground contact force information (Pratt and Pratt 1998a, 1999, 1998b, Pratt *et al* 2001). In simulation, the contact forces acting on the feet are used to realize a phase reset mechanism for the transition to the double support phase. The transition to the single support phase is initiated once the ground contact force on the designated swing leg falls below a given threshold (Pratt and Pratt 1998b, 1999). In experiments with a planar robot, these contact force conditions are replaced with geometric conditions (Pratt and Pratt 1998a). The phase reset mechanism is also used by Furusho and Sano (1990), who developed a walking control system for a 3D robot and realized stable walking at a speed of 0.18 m s^{-1} . The condition for the transition to the single support phase is that the center of gravity passes above the toe. A phase reset mechanism is also used in the walking control of the planar robot MABLE (Sreenath *et al* 2011) and in a simulation of the robot HRP-2 (Morisawa *et al* 2011).

Currently, many realizations of event-based walking control systems incorporate intuitive rules for phase transition, especially for the transition to the single support phase (Furusho and Sano 1990, Pratt and Pratt 1998a, 1998b, Pratt *et al* 2001, Sreenath *et al* 2011). Most of the event-based control strategies mentioned above are tested in simulation (Pratt *et al* 2001, Pratt and Pratt 1998a, 1999) or experiments with planar robots with few degrees-of-freedom (Pratt and Pratt 1998a, 1998b, Sreenath *et al* 2011) and not in experiments with 3D robots. The authors have proposed step-phase control laws for biped walking based on stability considerations, which has enabled the robot Lola to walk over unexpected and unmodelled obstacles (Buschmann *et al* 2009).

4. Conclusion

In this section we highlight areas in which we believe that neurobiology can help improve walking machine control and vice-versa. In section 4.1 we discuss known facts from neurobiology that could be exploited today and areas in which we believe that future neurobiological research could further advance robot walking control. Section 4.2 discusses future directions for robotics research that could advance neuroscience.

4.1. Learning from animal walking

4.1.1. What we can learn today

We believe that robot walking controllers should ideally take both the discrete and continuous aspects of walking dynamics into account (cf, section 3) by implementing adequate continuous and phase-dependent control components. This conclusion is intuitively plausible and supported by neurobiological research revealing both phase-dependent and continuous neural control in animal and human walking (cf figure 5, section 2.2.2). Theoretically, MPC methods should be the tool of choice for walking control since they provide a systematic approach to optimally exploiting the known dynamics in feedback controllers for complex systems. However, we believe that the direct implementation of walking control using real-time MPC for realistic robot models is still many years away due to the prohibitive computational cost. More importantly, no control method can tell us how to choose the inputs, the outputs and the control objectives. Neurobiological findings indicating which physical quantities are controlled during a certain task in animals (positions, velocities, forces, etc) and which coordinates are chosen for the control (joint velocities, foot velocities, etc) can help us derive promising control approaches for walking machines. Here neurobiology can be valuable for constraining the search space. Even though many details of the neural control of walking are still unclear, some structural information concerning the feedback paths and control objectives is known (cf figure 6). This structure can be used as a starting point for improving current robotic walking controllers (Buschmann *et al* 2012). We believe that the basic structure, i.e. the feedback pathways of neural walking control, is more important than details of the implementation. That is, control could be implemented in several ways such as FSM, neural networks, or any number of programming paradigms. We cannot conclude that the CPGs dominate the entire step cycle in vertebrates (cf section 2.2.1). However, they do define a certain structure for the possible (local) feedback paths (see figures 6, 5). This structure, however, could also be represented by an FSM (cf section 2.2.2, page 14).

4.1.2. What is missing

There are at least two important issues to be resolved: (1) for bipeds and quadrupeds the issue of balance and stability and their interaction with motor control is especially important and challenging. On the network level, this is one of the least well-understood aspects in the neural control of these animals (cf Orlovsky *et al* 1999 with Deliagina *et al* (2006) and Horak and Macpherson 2010). Most research on balance and posture control is from the fields of biomechanics and movement science (e.g. Blickhan 1989, Hof *et al* 2005). While this research has been quite valuable for robotics, it gives no direct evidence of the actual mechanisms of neural walking control. We therefore believe that more detailed findings in the areas of posture and balance control during standing, walking and running of bipeds and quadrupeds would currently be the most valuable results from neurobiology the technology of walking robots could hope for. (2) In general there is no conceptual framework available that explains the mode of action and the targets of descending control in the generation of walking behavior. This is especially true for adaptive behaviors (Ritzmann *et al* 2012, Deliagina *et al* 2012, Büschges 2012).

4.2. Learning from robotics

The ultimate goal in biological walking control research is to answer the question of what enables an animal to exhibit its versatile and flexible locomotion behavior (cf section 1). The large and growing amount of data from diverse subdisciplines such as biomechanics, neurophysiology and genetics in combination with the complexity of the animal systems under study and the limited available techniques (cf section 2.4) more than ever necessitates a whole systems view that combines the available data in a meaningful way. The interplay with robotics is beneficial for biologists for several reasons: (1) biologists are forced to describe findings and combine available data in such a way that they are formalized and can be implemented on a robot. (2) Robotics demonstrates how well available biological data explain the control of locomotion. (3) The whole systems approach inherent to walking machines allows to test the functional importance and interplay of biomechanical and neural components, including the multitude of coupled feedback loops. (4) Robotics suggests what might be missing in a control structure derived from neurobiological experiments to make a walking system walk and thus leads to new experiments. Diverse robotic subdisciplines such as control theory and machine learning offer powerful techniques to propose new and alternative controller hypotheses.

How could robotics be more helpful for biologists? Since robotics has the top priority to make a system work, predominantly those biological control principles are implemented and tested that promise to

(quickly) lead to an improved robot performance. In contrast biologists would also profit from the implementation and test of control structures and details thereof that do not initially promise to be valuable to robotics or are too time consuming to implement and to see under which conditions and with what kind of modifications they could contribute to walking control. In this regard the different control interfaces in consequence of available controller ‘languages’, actuators, sensors and materials as well as scaling effects often impede a straightforward transfer and test of controller components (cf also section 2.4 and figure 9(b)). Therefore, a task for the future is to improve the compatibility and transferability of control structures between robotics and biology by providing robotic control interfaces that speed up the test of biological control structures.

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