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# The functional sense of central oscillations in walking

**H. Cruse**

Faculty of Biology, University of Bielefeld, Postfach 100131, 33501 Bielefeld, Germany

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**Abstract.** Rhythmic motor output is generally assumed to be produced by central pattern generators or, more specific, central oscillators, the rhythmic output of which can be entrained and modulated by sensory input and descending control. In the case of locomotor systems, the output of the central system, i.e., the output obtained after deafferentation of sensory feedback, shows many of the temporal characteristics of real movements. Therefore the term fictive locomotion has been coined. This article concentrates on a specific locomotor behavior, namely walking; in particular walking in invertebrates. In contrast to the traditional view, an alternative hypothesis is formulated to interpret the functional sense of these central oscillations which have been found in many cases. It is argued that the basic function of the underlying circuit is to avoid cocontraction of antagonistic muscles. Such a system operates best with an inherent period just above the maximum period observed in real walking. The circuit discussed in this article (Fig. 2) shows several properties in common with results described as "fictive walking". It furthermore could explain a number of properties observed in animals walking in different situations. According to this hypothesis, the oscillations found after deafferentation are side effects occurring in specific artificial situations. If, however, a parameter called central excitation is large enough, the system can act as a central oscillator that overrides the sensory input completely.

## 1 Fictive locomotion

Many behaviors are based on rhythmic motor output. Well-studied examples are swimming, flying, and walking in both vertebrates and invertebrates. Other thoroughly studied rhythmic systems are responsible for breathing, swallowing, or chewing. It is usually assumed that in such cases the rhythmic motor output is basically produced by a system called a central pattern generator or central oscillator, and that sensory feedback does nothing but modulate this central rhythm (e.g., Delcomyn 1980). The essential argument supporting this view is that a number of experiments have shown a rhythmic motor output after deafferentation which appears to correspond to the rhythms found in normally behaving animals (e.g., flying in locusts: Wilson 1961; swimming in lamprey: Grillner et al. 1991; walking in cat: Rossignol et al. 1993). This observation lead to the hypothesis that the underlying central systems are responsible for the motor output in the normally behaving animal, or, in other words, that central pattern generators control the normal movement. In the case of locomotor systems, the output of the central system, i.e., the output obtained after deafferentation of sensory feedback, is therefore often called fictive locomotion (Grillner 1981).

In walking, on which we will concentrate in the following, such experiments have been performed with cat (Grillner 1981), crayfish (Chrachri and Clarac 1990), and insects (cockroach: Pearson and Iles 1970; locust: Ryckebusch and Laurent 1993, 1994; stick insects: Bässler and Wegner 1983, Büschges et al. 1995). An excellent review comparing vertebrates and invertebrates has been given by Pearson (1993). In the more recent studies concerning invertebrates on which we will concentrate in this text, deafferentation was accompanied by activation of the neuronal system using the muscarinic agonist pilocarpine, for example. This is usually interpreted as mimicking increased sensory excitation. In crayfish, the partly deafferented ganglion produces rhythmic and coordinated motor output in the muscles of the two basal joints, with the promotor–remotor system and the levator–depressor system resembling the situation of backward walking or forward walking. The rhythm was 10–30 times slower than normal walking. The rhythm was more irregular when the connectives to the neighboring ganglia were cut (Chrachri and Clarac 1990). In the locust hind leg, a coordination between three joints has been found which has been described as a walking-like pattern by (Ryckebusch and Laurent 1993). In addition, antiphase interleg coordination was found between contralateral and ispilateral neighboring legs (Ryckebusch and Laurent 1994). In both locust and crayfish, bursts of motoneurons innervating muscles which control swing movement in walking were of approximately constant duration, whereas units which in freely walking animals drive stance muscles show variable duration and an approximately linear relation between stance duration and period (see also Fig. 4c). This has already been found for cockroaches in the seminal paper of Pearson and Iles (1970). As these findings agree with observations on walking animals, the results support the hypothesis of central pattern generators controlling walking movements.

This interpretation, however, leads to several problems. In general, the rhythms found in the deafferented situation are much slower than in the intact animal (for mammals, see Grillner 1981). This has often been explained as an effect resulting from the decreased level of sensory excitation. Another more general argument challenges the biological sense of this hypothesis (Cruse et al. 2000; Pearson 1985, 1987; Zill 1985): a centrally produced rhythm may be advantageous in a predictable world. When, however, the physical situation changes, a central system can lead to problems (as anyone suffering from jet lag can attest). In swimming and flying, the environment is mainly predictable and therefore a central oscillator may be advantageous. However, even for locust flight Pearson (1985) challenges the view of whether it is sensible to speak of a central pattern generator, because in the intact animal the central system is considerably reorganized by sensory input. Even more so when walking on an uneven, irregular surface, the situation may vary dramatically from one moment to the next and, if a central oscillator is in charge, the system has the additional problem of mediating between the possibly divergent actions commanded by the central oscillator and by the signals from the periphery. Such a central oscillator thus may have a negative effect on the behavior of the system.

Furthermore, central oscillators have been proposed as a basis to solve an important problem occurring during leg control in walking, namely the coordination of the different joints of a leg: in a walking leg there is not one oscillation but, due to the different leg joints, several ones. Often, the oscillatory movements driving the antagonistic muscles in the different leg joints show a phase shift relative to each other. Furthermore, the swing–stance rhythm may not be identical to the movement of different joints. Therefore, the oscillators driving the different joints of a leg and the swing–stance rhythm have to be coordinated somehow. To cope with the problem of joint coordination, Grillner already in 1981 proposed a system of oscillators, one for each joint. Those oscillators, which he called unit-burst generators, were assumed to be coupled in a way to explain this coordination. In the following, data are reviewed which show that it is difficult to imagine how coordination of walking movements may be achieved only by coupling these local oscillators. The coordination might be an easy task for the above-mentioned case of the locust hind leg, for the cockroach hind leg, or for the front leg of a stick insect walking straight forward, because the situation is mechanically similar in these cases. All three leg joints – the thoracic–coxal joint, the coxa–trochanter joint, and the femur–tibia joint – switch from agonist to antagonist during the swing–stance transition. This is also true for the stick insect middle leg (Fig. 1) walking sideways. Similarly, for the simple case of a two-joint, planar leg as it is typical for some mammals (e.g., humans), there is an obvious geometrical constraint to couple the joints. But even in this simple case, extensor and flexor muscle activations are not exactly identical with stance and swing (Grillner 1981). The problem is, however, more complicated for a typical insect leg as, for example, a locust or a stick-insect middle leg in forward walking. In this case the femur–tibia joint shows two transitions during a step cycle and neither transition occurs together with the swing–stance transitions. Double frequency in a joint during one step occurs also in the femur-tibia joint in cockroach front leg. When negotiating tight curves or when walking sideways (also for front and hind legs) the situations get more complex, and even more so when any leg walks on a soft substrate. In these situations swing and stance may be very different from the rhythms of the different leg joints.

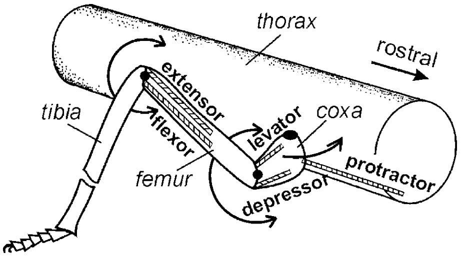

**Fig. 1.** Schematic drawing showing the arrangement of joints and major leg muscles of a typical insect leg. Retractor muscle is omitted for clarity

As already mentioned above, Büschges et al. (1995) performed experiments with stick insects using deafferentation and superfusing the ganglia with the muscarinic agonist pilocarpine. The authors found oscillations in all joints. There was, however, no coordination between the joint of a leg and very weak (and if so, in-phase) coordination between joints of different legs. The oscillations were relatively irregular in period length. The main feature was, in accordance with the other findings mentioned, that either one or the other antagonist was active. Therefore, these systems are described as bistable ones. This has been interpreted by the authors as supporting the idea of the existence of local joint oscillators – an idea already put forward by Grillner (1981). On the other hand, Büschges et al. (1995, p. 453) state that the motor output does not correspond to any coordinated motor rhythm found in freely behaving animals, and that therefore the term of fictive locomotion should not be used in this case.

In order to maintain the idea that joint coordination is performed on the basis of coupled oscillators, the authors speculate that in real walking these oscillators require some coupling which is provided by sensory feedback. Based on experiments showing sensory coupling between oscillations of neighboring joints, Bässler and Büschges (1998) furthermore assume that there is no strict hierarchy, but that (via sensory coupling) the actually "leading oscillator" determines the other oscillators to switch state. According to this hypothesis, which oscillator is leading depends on the actual walking situation. This is a simple and therefore appealing assumption based on central unit oscillators coupled by sensory signals to gain better adaptivity. However, the problems of how to coordinate these oscillators can be solved easily only for the above-mentioned simple cases in which all oscillators move in-phase. As in more complex walking situations, the different oscillations of the joints and that of the general state (swing–stance) can show varying relations, a separate control system seems to be necessary. It is responsible for the actual control of the phase relations of the individual oscillators and depends on the actual walking situation (see also Pearson 1987 for a detailed discussion).

It is therefore not immediately clear how control of a multijointed leg could be solved on the basis of the actually known influences that coordinate the movement of different joints of a leg. This is even more true given that seemingly contradictory interjoint coactivations have been observed in different experiments: In fixed animals (stick insects), Hess and Büschges (1997) found an influence from the femur–tibia joint to the coxa–trochanter joint, suggesting a coactivation of extensor muscle of the femur–tibia joint and levator muscle of the coxa–trochanter joint. Bartling and Schmitz (2000) found corresponding results in freely walking animals (*Carausius morosus*) as did Delcomyn (1971) for cockroaches. However, for the "active" stick insect, Bässler (1993) found a cooperation between extensor and depressor. This has also been described by Cruse et al. (1992) for the passively moved leg. Reflexes that coordinate motor output in different joints of a leg have also been shown for crustaceans (Clarac 1977). However, there is no obvious picture explaining the functional cooperation between joints during walking, let alone during other possible behaviors.

There are further results which appear not to be in accordance with the idea that the cooperation of local joint oscillators is sufficient to explain leg movement. The coactivation between depressor and flexor described by Bartling and Schmitz (2000) may support a sensible reaction to avoid the foot from slipping sideways when walking on soft ground. A change of activation in this system is however not necessarily coupled with a change in swing–stance mode. Bartling and Schmitz showed – by pulling the substrate, on which the leg of a freely walking insect rests sideways – that, depending on the direction of the disturbance, the torque developed in the femur–tibia joint may switch sign from flexor to extensor activation or vice versa, with the leg continuing nevertheless its stance until the posterior extreme position is reached. Comparison of forward walking and backward walking provides a similar argument. In forward walking the functional stance muscle is the retractor, whereas in backward walking the functional stance muscle is the protractor. Swing movement in forward walking begins with a protractor–levator coactivation; in backward walking it begins with retractor-levator coactivation (Graham and Epstein 1985). This suggests that a superior system must determine the different connections for swing and stance movements for forward and backward walking. As for crustaceans, Ayers and Davis (1977) proposed a simple explanation for such a system.

The results of Schmitz and Hassfeld (1989) further strongly suggest that the swing–stance level is controlled independently of the control systems switching between agonistic and antagonistic muscles on the joint level. They investigated a specific reflex called treading on tarsus (Graham 1979). When a middle leg at the end of its swing movement accidentally treads on the tarsus of its anterior neighbor (the ipsilateral front leg), the middle leg performs a brief backward step to free the front-leg tarsus. This backstep of the middle leg can also be elicited when mechanically stimulating the tarsus of the front leg with a brush. In forward walking, the backstep is driven by an activation of the retractor muscle of the middle leg, i.e., the functional stance muscle. In a backward-walking animal, a corresponding backstep of the middle leg can be elicited when the front-leg tarsus is touched. However, in this case the movement is driven by the protractor muscle of the middle-leg, thus moving the leg rostrally. Note that in backward walking this reflex is completely senseless because the middle leg, when the reflex is elicited, is at its posterior extreme position and therefore far from the front leg. Furthermore, the middle leg does not step away from the stimulated front leg but moves nearer to it. What might be the underlying circuit? Apparently, the treading on tarsus reflex is connected to the functional swing–stance muscle, which is the retractor muscle during forward walking and the protractor muscle during backward walking. This indicates that there is a system that controls swing–stance movements independent of the muscles that are actually used. The latter are determined by another lower-level system which decides between backward and forward walking and which, as mentioned above, is assumed to be arranged above the joint controllers. Therefore it appears difficult to imagine how the decision between swing and stance could be made at the level of local joint oscillators.

Taken together, there are several arguments that illustrate that, at least for more complex, i.e., realistic walking situation the hypothesis of local, coupled unit-burst generators appears to bear at least two unsolved problems. The first concerns the question of how such oscillators may be coupled to control realistic walking movements. A separate control system appears to be necessary to coordinate the joints of a leg in different walking situations. The second point of interest mentioned earlier is more general, as it questions the functional sense of oscillators as such (see however Sect. 4). This attitude is further supported by the fact that it has been shown (Brooks 1989; Cruse 1980; Cruse et al. 1998; Espenschied et al. 1993) that control of walking situations, even complex ones, is possible without the application of central oscillators. This raises the question whether the interpretation that concerns the functional sense of the oscillators found in fictive locomotion situations is appropriate with respect to control of walking.

## 2 Why bistable systems?

In order to stimulate discussion I would like to oppose the traditional hypothesis which assumes that the neuronal oscillators underlying the oscillation found in the different preparations are responsible for driving the rhythmic motor output found in a walking animal to control the movement of the leg joints. To propose an alternative hypothesis I assume that the oscillators described in the experiments studying different locomotor, in particular walking systems, have no functional meaning with respect to the control of the timing of the rhythmic motor output in walking. What else could then be the reason for the evolutionary invention of these bistable systems found in all these investigations? The following might offer an answer to this question.

Given the antagonistic structure of biological motor systems, a serious problem of this architecture is that uncontrolled coactivation of antagonistic muscles should be avoided: (1) in order to avoid unnecessary energy consumption and (2) to avoid production of injuries. A simple solution to this problem is to introduce a winner-take-all (WTA) system. This is a network in which each of the competing units influences all other units by recurrent inhibition. In such a circuit, after some iterations only one member is excited and all its partners are completely inhibited even if the excitatory input to the units differs only by a small degree (for a brief review see Möller et al. 1998). There is only one "winner", and all the other units are "losers". In the case of a simple antagonistic structure as considered here, there are only two units: one winner and one loser. Therefore, if one applied a WTA system, this circuit could effectively avoid coactivation of antagonistic muscles. (There are WTA systems with and without self excitation of each unit. For a continuous input and for strong enough inhibitory connections, self excitation is not necessary. The latter case will be considered in the following).

What are the properties of such a WTA system? Figure 2 shows a simple circuit containing two antagonistic output units which might be interpreted as representing a simplified motor system controlling a single-joint leg, with a protractor muscle controlling swing and a retractor muscle controlling stance. Both output units show low-pass properties (time constant = 25 ms) and are connected by mutual inhibition. A central excitation drives both units. This circuit essentially corresponds to Brown's classical half-center model (Brown 1911). Finally, a sensory input is applied which alternatively excites each unit. One sensory input signals stance (e.g., via leg contact), the other signals swing, and the influences are applied in such a way that the sensory input drives the appropriate motor output. For example, position sensors may be activated when a given threshold is reached (e.g. the posterior extreme position) which can inhibit the agonist and/or activate the antagonistic muscle (Bässler 1986; for reviews see Bässler and Büschges 1998; Pearson 1993).

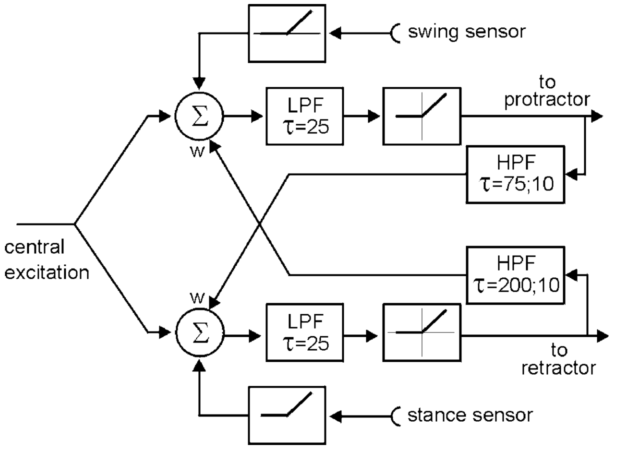

**Fig. 2.** A simple circuit containing two output units, and a protractor and a retractor unit. The units are driven by a central excitation and receive inhibitory influences from each other. $w$ describes the strength of this inhibitory influence. Furthermore, they receive input from sensors signaling stance or swing. *LPF*, low-pass filter, *HPF*, high-pass filter. Time constants are given in milliseconds

What are the necessary prerequisites and properties of the recurrent inhibitory connections? First of all, in order to guarantee the WTA property, the weights of these connections which are called $w$ in Fig. 2 have to be large enough. Second to make the transition from one state – swing or stance – to the other faster, the inhibitory connections are provided with high-pass filters. This transition is sharper with a smaller time constant of the high-pass filter and a larger weight $w$. However, the time constant must not become too small and $w$ not to too large, because otherwise the system may show transitions between states which occur independent of the actual sensory input. To avoid such unintended state transitions, the time constants of the high-pass filters have to be adapted to the longest state duration occurring during normal walking.

To adapt the time constants to the usually short swing duration and possibly long stance duration, I have choosen a value of $\tau = 200$ ms for the retractor branch to inhibit the protractor, and a value of $\tau = 75$ ms for the protractor branch to inhibit the retractor. In this simulation, these values allow for a maximum stance duration of about 650 ms and a maximum swing duration of about 220 ms. If longer periods are to be simulated, the time constants have to be enlarged correspondingly. Weight $w$ should not be smaller that 4 – I have decided to choose a value of $w = 10$, since values larger than 10 decrease the maximum duration of the half cycle. A side effect of the inhibitory influence via a high-pass filter is that the ending of the excitation of one unit does not only end the inhibition of the other, antagonist unit, but, due to the properties of the high-pass filter, releases an excitation of this antagonist which may be called a rebound effect. If the time constant of this "rebound" effect was too long, it would dominate the behavior of the antagonist compared to the influence of its sensory input. To avoid this effect, the time constant, in this case, must be smaller. Therefore, in the simulation I applied non-linear high-pass filters with a small time constant in the case of negative output values. As the time constant should be within an order of magnitude smaller than the shortest excitation, I used a value of $\tau = 10$ ms for the reaction to decreasing input values; i.e., negative output values. An alternative solution would be to reduce the gain factor $w$ for negative values, or to opt for a combination of both: a decrease of $w$ by a factor of 0.5 with an increase of the time constant by a factor of 2 leads to approximately the same results. As mentioned above, the output units are provided with a low-pass property using a time constant of $\tau = 25$ ms. Larger values produce significant delays between the change in sensory input and the subsequent switch between the output units.

Figures 3 and 4 give some examples of the behavior of this system. After “walking” is switched on by application of a positive central excitation (Fig. 3a), the system shows quasirhythmic oscillations. The switch between states is determined by sensory signals. These sensory influences control the switch between antagonistic muscles (see also Bässler 1986, Brown 1911; Land 1972), leading to varying swing and stance durations. During “normal walking”, the system shows the mentioned property of a clear-cut distinction of excitation of either agonist or antagonist. This is particularly obvious for the transitions between states. Figure 3a further illustrates that if the sensory input is constantly active for too long, the system switches state by itself (Fig. 3a, during the last activation of stance sensors and during the last activation of swing sensors). In the simulation this occurs when the induced period of one state exceeds the corresponding time constant by about three times. The WTA property of the system becomes obvious in Fig. 3b, c. Clear-cut transitions between agonist and antagonist activation is found even when the input values are very small (Fig. 3b) or when the input shows soft transitions as in the case of a sinusoidal wave (Fig. 3c). The phasic–tonic time course can be seen in all examples. Interestingly, the strength of initial activation of the agonist depends on the strength of activation of the antagonist in the preceeding half cycle (Fig. 3d). This “rebound” effect can also be observed in Fig. 3b (last but one activation of protraction). I will return to this result below.

How does the system shown in Fig. 2 behave when the sensory input is switched off? With sensory input set to zero, but with a positive central excitation, due to the high-pass properties of the inhibitory connections, the system can show oscillations the rhythm of which depends on the time constants of the inhibitory

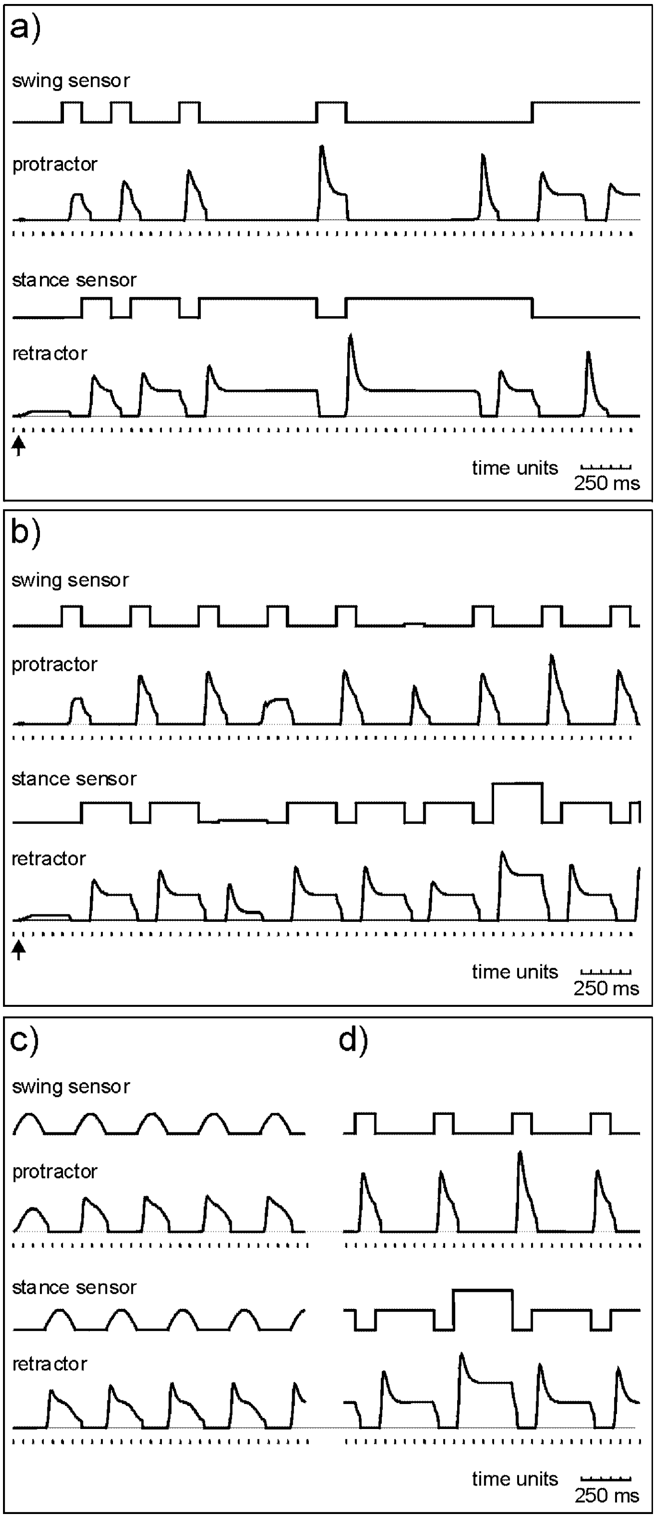

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**Fig. 3a–c.** The behavior of the system shown in Fig. 2. Walking is switched on by changing the central excitation from 0 to 5 (*arrow*). **a** Sensory input is applied with increasing duration of periods. In the rightmost part these periods are longer than the inherent period determined by the time constants of the inhibitory connections. Therefore the system switches from stance to swing independent of the sensory input. **b** Clear-cut transitions can be seen even when the sensory input is small (see third activation of retractor and sixth activation of protractor). **c** Clear-cut transition between states can also be seen when the input changes gradually. **d** The phasic activation of a unit increases when the activation of the preceding half cycle was high (compare second and third activation of protractor). *Arrow*, central activation is switched on

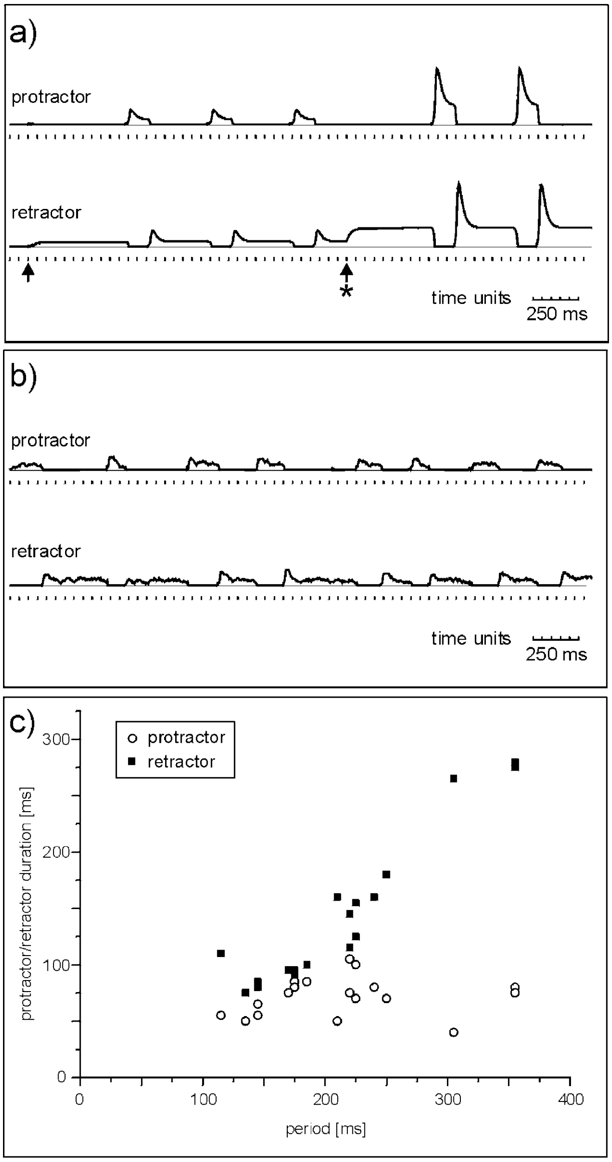

**Fig. 4a–c.** The behavior of the system shown in Fig. 2 when the sensory input is switched off. **a** The output shows oscillations, the amplitude of which depends on the central excitation: time 1ms to 100 ms: central excitation = 0; time 21 ms (*arrow*) to 1850 ms: central excitation = 5 units; after time 1850 ms (*arrow* and *asterisk*): central excitation = 25 units. **b** The duration of swing and stance varies when both units are subject to additive noise (amplitude = ±8 units). **c** A graphical evaluation of runs as shown in **b**. Duration of stance (*closed circles*) and of swing (*open circles*) are plotted vs. period ( = swing duration + stance duration)

connections (Fig. 4a). The amplitude of the oscillation increases when the central excitation of the system is increased (Fig. 4a). As mentioned above, different time constants for the inhibitory connections lead to different durations of activation. In the case of large time constants, stochastic effects may lead to considerable variation in duration of the half periods: if the threshold to switch from one stable state to the other is approached slowly, the duration of this state depends dramatically on these stochastic influences; an example is shown in Fig. 4b. A plot of stance duration and swing duration versus period (Fig. 4c) looks very similar to those published in the above-mentioned investigations (e.g., Pearson and Iles 1970; Chrachri and Clarac 1990). Swing duration is approximately constant, whereas stance duration depends linearly on period.

Interestingly, the system can be made to act as a central oscillator that completely overrides the sensory input (not shown): if the value of the central excitation is large enough, the system oscillates with a period that depends on the value of the central excitation, but is independent of the sensory input. When, for instance, a central excitation of 30 units is applied, the system oscillates with a constant period of about 600 ms, even if a varying sensory input is given as has been applied in the examples of Fig. 3. The duration of that period decreases with increasing central excitation.

Before discussing these results, three points should be mentioned regarding the possible biological realization of the circuit shown in Fig. 2. First this circuit may be realized at the level of the motor neurons or at a premotor level. The latter is more probable because as far as I know no direct inhibitory connections between motor neurons have been described, whereas the existence of mutual inhibitory influences at the level of premotor neurons is generally accepted knowledge. Cohen (2000) speculates that these mutual inhibitory connections may indeed form the essential part of the central pattern generator. The real neuronal system is, however, more complex, as the excellent studies of Grillner and coworkers (1995) have shown for the lamprey swimming system. The same goes for the detailed investigations of the locust flight system by Pearson and collaborators (e.g., Pearson and Ramirez 1992). Secondly what kind of sensory influences might be involved has been left open. Critical influences of position, velocity, and acceleration sensors have been described (for reviews see Bässler and Büschges 1998; Pearson 1995). But force (load) sensors (for review see Duysens et al. 2000) are also of importance. All of them are good candidates to serve for signals used in the way described here, alone or in combination. Furthermore, sensory input might also arise from sensors of other joints as described above (e.g., influences from the chordotonal organ of the femur–tibia joint to the coxa–trochanter joint, Hess and Büschges 1999). Thirdly, Harris and Wolpert (1998) recently proposed an elegant solution for motor control tasks like multijoint reaching based on the assumption that the movement trajectory is selected to minimize the variance of the final position. Qualitatively their control function shows a time course similar to the output functions presented in Fig. 3, insofar as it starts with a high excitation and then monotonously decreases until the antagonist is briefly activated. However, their function does not correspond to a decreasing exponential function, the slope of which decreases continuously as is the case in Fig. 3, but to a function which starts with a small slope that continuously increases. This means that a simple high-pass filter is not sufficient for a quantitative simulation of the control function of Harris and Wolpert (1998).

## 3 Fictive walking in insects – a fiction?

The circuit shown in Fig. 2 provides a possible explanation for the findings that after deafferentation and central excitation: (1) oscillations are observed; (2) the periods of the oscillations are usually longer than those occurring in normal walking; (3) the oscillation show the typical dependency of swing and stance duration on period; in the walking animal it has been observed that (4) cocontraction of antagonistic muscles is rare or of only short duration; and that (5) the phasic–tonic time course of the activation values corresponds to the one found in deafferented preparations (Pearson 1987). In free-walking animals the spike frequency within bursts often shows a similar temporal behavior (cockroach: Pearson and Iles 1970; locust: Burns and Usherwood 1979; stick insect: Graham and Epstein 1985), but may be modulated by sensory feedback.

In the light of these results I would like to argue that rhythmic motor output in the case of deafferented neuronal systems set under chemical excitation may be regarded as an artifact in the sense that it has nothing to do with the control of rhythmic output in walking as such (see also Pearson 1987). According to this proposal, its basic function is to avoid cocontraction of antagonistic muscles and to lead to a clear-cut transition between excitation of antagonistic muscles. The oscillations are side effects that only occur in specific artificial situations.

Nevertheless, the structure of Fig. 2 has several impacts with respect to motor control. The first and basic one has already been mentioned, namely the avoidance of unwanted cocontraction, in particular during transients of activation from an agonist to an antagonist. Cocontraction, however, is not only avoided, but the dynamic of the transition is even sharpened. At the end of the excitation of one agonist the inhibitory connection leads to an (automatic) ‘‘rebound’’ excitation of the antagonist (Cruse 1983; Pearson 1985). The amplitude of the rebound excitation depends on the excitation of the antagonist in the preceding half cycle (Fig. 3d). Figure 3b shows an example where small protractor activity (sixth activation) leads to a small rebound effect in the following retractor activation, and another one where a high retractor activity leads to a high rebound excitation in the directly following protractor burst (last but one protractor activation). Figure 3d shows a further example for this case.

This rebound effect could explain in a simple way a number of findings described in the literature. Pearson (1972) showed that when cockroaches have to drag a load, excitation of retractor muscles is increased. Furthermore, protractor excitation increases and, probably as a kinematic consequence of increased protraction velocity, swing duration decreases. Similarly, increasing the load in crayfish during stance leads to decreased swing duration (Cruse and Müller 1984). It can easily be imagined that loading the animal excites stance muscles via direct sensory feedback mechanisms (positive and negative feedback have been discussed), whereas swing muscles cannot receive such direct input because the legs are lifted off the ground during swing. However, increased excitation during swing could be explained by the rebound effect discussed here, which excites swing muscles more when their antagonists showed a higher excitation during the preceding stance.

J. Schmitz, S. Ernst, A. von Kamp (unpubl. work, 2002) have found that the average velocity of swing movement increases when stick insects walk uphill and decreases when they walk downhill. Again this phenomenon could be qualitatively explained by the assumption proposed here. Walking uphill requires a higher excitation of stance muscles compared to walking on a horizontal plane. This should lead to a rebound effect on swing muscles. The effect was most obvious in hind legs which indeed produce the greatest downward and rearward directed forces during uphill walking (Cruse 1976). Walking downhill requires small propulsive forces during stance if not forces acting against the walking direction. Therefore, the rebound effect should be small or even negative, which should lead to a decrease of swing muscle excitation as has been shown by Schmitz and coworkers.

Furthermore, in stick insects a specific behavior has been found which may simply be explained by such local inhibitory connections at the level of the antagonists of one joint. Stick insects show different types of swing movement depending on the substrate they walk on. Generally the form of the swing movement can be approximated by a section of a circle. Walking on a flat horizontal plane leads to a swing movement with an extreme point of this circle being about 6 mm above the substrate. In this situation, the transversal distance between contralateral legs is somewhat larger than 30 mm. When walking on a treadmill of 30 mm breadth or less the extreme point of the leg is lowered by about 4 mm or more (Cruse and Bartling 1995). This was not possible when walking on a flat plane because then the tarsus would slip along the substrate. This behavior appears to be adaptive because when walking on a small path it is not necessary to lift the legs, which might save energy. These results show that during swing the time course of the functions controlling the movement of the different leg joints depends on the form of the substrate. How are these control functions determined? The circuit shown in Fig. 2 may yield a simple, low-level explanation. When the legs are placed on a horizontal surface the distribution of torques in the joints during stance is different to the situation when walking on a treadwheel or – which is mechanically similar – walking up a vertical path of the same breadth (Cruse 1976). The average force vector during stance in the former case is oriented downward and away from the body, whereas in the latter case it is upward and to the body. Application of the above-mentioned rebound effect to the control of swing movement would predict that in the former case the legs are lifted upwards and in the latter case they are moved more to the side or downwards, as has been found for walking on the horizontal plane and the treadmill. In other words, the circuit shown in Fig. 2 should lead to swing trajectories that are directed opposite to the direction of the ground force developed during stance. This would mean that no special calculation is necessary to change the swing trajectory accordingly. Therefore, this circuit allows for a simple local adaptation mechanism: the muscle which is strongly excited during stance automatically excites its antagonist during the subsequent swing. This adaptation, which might be regarded as some kind of simple short-term memory, works on a step-to-step basis.

Recent results from animals walking along an inclined surface support this interpretation. Diederich et al. (2002) found different shapes of swing trajectories for the legs walking uphill compared to the legs walking downhill: in the downhill case the relative contribution of the levator–depressor system to swing movement in the legs is stronger than that of the extensor–flexor system. The opposite is true for the uphill case. Due to the different mechanical situation during stance, different torques are necessary in the corresponding joints of uphill and downhill-moving legs. If these torques are used to predict the swing trajectories on the basis of the rebound effect described here, qualitative properties can be expected that correspond to those found in the experiments.

In conclusion, according to the hypothesis proposed here, the basis of the centrally driven rhythm found in many experiments following deafferentation is a WTA system which avoids cocontractions (it might be mentioned that if such cocontractions are intended, additional control systems are able to override this structure). This bistable system serves to transform possible ambiguous input situation into a unique output situation. The rebound effect does not as such produce a continuous oscillation, but only influences the next half cycle. This is advantageous because its "predictive" property is based on actual, local knowledge and therefore avoids the possible misprediction of a central oscillatory system having an inherent rhythm. According to this idea, the quasirhythmic motor output observed in walking is not based on a central rhythm generator – an internal "world model" in the form of a central oscillator – but rather is based on "reality", i.e., on direct sensory information. This means that a central question is still open which was hoped to be solved when using coupled joint oscillators: how are the single joints of a leg and the legs coordinated during walking? This question could be answered in part by using the "half-cycle" principle. It can serve to simplify the adaptation of the swing movement to differently shaped substrate and different load situations. However, other questions are still open. For example, there exist only hypotheses concerning the control of the switch from levator activation to depressor activation during swing. Therefore, other coupling mechanisms wait for investigation. However, it should be mentioned here that not all the details have to be explicitly computed by the neuronal system. Simulation results and experimental investigations have shown that simple, local rules exploiting feedback loops and the mechanical properties of the body can produce the basic rhythm and can sufficiently explain a considerable part of the coordination (Brooks 1989; Espenschied et al. 1993; Full and Koditschek 1999, Schmitt and Holmes 2000a,b). In particular during stance, positive feedback at the level of the individual joints has been proposed to coordinate different joints within a leg and between legs exploiting the existing mechanical connections (Cruse et al. 1998).

## 4 Why central oscillators?

In this article I have argued that the centrally driven rhythmic motor output may not be based on a system responsible to produce the quasirhythmic motor output during walking. Such central "world models" may be helpful in a predictable world, but such central pattern generators are not only unnecessary but could even cause the behavior to deteriorate in unpredictable situations. Nevertheless, I do not wish to argue that central oscillators are completely senseless for the control of rhythmic motor output in general. Apart from predictable situations, central systems may also be successfully applied when the mechanical device possesses a low number of degrees of freedom, for example only one joint (possibly a wing or a fin) or a simple planar two-joint leg, because in these cases the critical problem mentioned above, namely the coordination of the joints with the swing–stance rhythm, can be solved easily. There are, however, other situations where a central pattern generator may also be sensible. In emergency situations the central system may be used to replace the "peripheral oscillator". As explained earlier, the system shown in Fig. 2 can be used directly to act as a central oscillator if the value of the central excitation is chosen large enough. A dramatic case of such an emergency could be the loss of one or several sensors. A less dramatic case, but for biological systems probably equally important, occurs when fast rhythms are to be produced as is the case in a cockroach walking at high speed. Fast, here, is meant to be relative to the time delays resulting from the slow neuronal transduction: if sensory feedback is too slow, it may not be able to contribute to the production of the rhythmic output. Although, as has been argued above, such a central system might be inaccurate in the case of external disturbances, it may be better to use this approximate information than wait for an exact information that comes too late. (Note that this argument is usually not relevant for an artificial electronic system, because there the transmission of signals is usually fast enough.)

However, instead of using central oscillators as active devices to control motor output, they may be used in a more passive way, that is for predictive purposes. One way is to change sensory thresholds in a given time window (Degtyarenko et al. 1998). Moreover, central oscillators may be used on a longer time scale to detect long-term deviations (e.g., in case of sensory drift) by providing expectation values that could be compared with the sensory input. If a long-term deviation is detected, this information can be used to readjust the system via backpropagation mechanisms for example (Kawato and Gomi 1992). Such central systems may have evolved from such simple inhibitory systems as discussed in this article.

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