Load-Regulating Mechanisms in Gait and Posture: Comparative Aspects

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Duysens, J., F. Clarac, and H. Cruse. Load-Regulating Mechanisms in Gait and Posture: Comparative Aspects. *Physiol. Rev.* 80: 83–133, 2000.—How is load sensed by receptors, and how is this sensory information used to guide locomotion? Many insights in this domain have evolved from comparative studies since it has been realized that basic principles concerning load sensing and regulation can be found in a wide variety of animals, both vertebrate and invertebrate. Feedback about load is not only derived from specific load receptors but also from other types of receptors that previously were thought to have other functions. In the central nervous system of many species, a convergence is found between specific and nonspecific load receptors. Furthermore, feedback from load receptors onto central circuits involved in the generation of rhythmic locomotor output is commonly found. During the stance phase, afferent activity from various load detectors can activate the extensor part in such circuits, thereby providing reinforcing force feedback. At the same time, the flexion is suppressed. The functional role of this arrangement is that activity in antigravity muscles is promoted while the onset of the next flexion is delayed as long as the limb is loaded. This type of reinforcing force feedback is present during gait but absent in the immoble resting animal.

I. INTRODUCTION

A. General Description

Control of posture and locomotion is closely linked to control of gravitational load. All animals, which have to deal with this problem, rely on a variety of more or less specialized receptors. Activation of these receptors is essential for some human postural reactions (162, 163) and for the control of the intensity and duration of extensor activity bursts (stance phase) during walking in different groups of animals (97, 260, 471). This is possible because during movement the input from load receptors interacts with command signals and rhythm-generating circuitry. In fact, activation of these receptors can even determine the choice of the appropriate coordinated pattern.

One spectacular example of the effect of frictional load has been given by Wendler et al. (530) when studying the hemipterus *Nepa rubra*. This insect walks in a classical alternating tripod coordination (at least 3 legs on the ground at any time), with alternation of the legs of the same segment. In this case, the stance phase is normally longer than the swing phase. When swimming, all legs are in phase and the swing phase is significantly longer than the stance phase. It has been possible to design experimental situations in which the frictional load is intermediate between the ground and the water condition (walking on mercury or on a slippery surface). In this latter case, swing and stance are equal in duration, and both in-phase and out-of-phase locomotor patterns were used in alternation. This demonstrates that load, which is important during stance, is crucial in controlling the interleg pattern. Similar load-dependent switches in interlimb coordination have been described in the fishing spider *Dolomedes*, which rows on the water surface and walks on land (19).

There are several reasons why this review is needed. First, the definition of load receptors should be reevaluated. In mammalian physiology, the question of load receptors is often reduced to a discussion of a single type of receptor, namely, the Golgi tendon organ (GTO) of extensors. However, when a limb is loaded during stance, a wide variety of receptors are activated, including cutaneous receptors of the foot, higher threshold force receptors, and spindles from stretched muscles (105, 106, 460). To what extent, and by what means, are these diverse sensory inputs combined at the spinal cord level to inform the animal about load? Should one make a distinction between receptors involved in the detection of gravitational versus inertial versus frictional load? In arthropod physiology, a large amount of data are now available on load receptors and load-compensating reflexes. Previously most attention has been given to position and move-ment detectors [such as the hairplates, the muscle receptor organ (MRO), or the chordotonal organs (CO)], but more recently, there has been an increasing interest in the cuticular receptors, such as the campaniform sensilla, which may act as typical load receptors. Moreover, the role of passive load-compensating mechanisms should be considered.

Second, a review on the mechanisms of load regulation is timely. In the cat, the discussion of load compensation in leg muscles has long been dominated by the concept of autogenic inhibition (negative force feedback) from Ib afferents of GTO from leg extensors. However, the view on Ib feedback is rapidly changing because recent experiments have shown that this inhibition is very short-lasting; therefore, its functional importance is in doubt (343, 344). On the other hand, support is growing for alternative ideas based on experiments testing the function of load feedback under conditions related to locomotion (412, 416, 534). In particular, the proposal has been made that, under such conditions, the Ib input from extensors inhibits flexors and facilitates extensor activity in the cat (191). The evidence in favor of this proposal has rapidly accumulated over the last few years (111, 246, 415). Moreover, additional new data are presented to show that these flexor suppressive effects are due to Ib rather than Ia input from extensors. On the basis of these findings, it is concluded that activity from Ib afferents from extensors reinforces the ongoing extensor activity during the stance phase and can block the initiation of swing. Cutaneous afferents from the foot can have a similar effect. Hence, different types of load receptors can signal unloading, and this might be essential for the termination of stance. In addition, other afferent input (presumably primarily related to limb position) can facilitate the transition to swing (260). Recently, these findings have attracted the interest of researchers working with patients with spinal cord injury, because it has become possible through intense training to regain some locomotor activity in these patients, and this rhythmic efferent output can effectively be manipulated by changing the load level (168, 277, 388). These new training schemes are based on the knowledge that the above-described load-compensating reflexes to extensor muscles (111, 191, 246, 415) can be effective not only in spinal cat (274, 277, 364) but also in spinal human.

As in the cat, it has been found that afferent activity from load receptors in arthropods feeds into pathways that were described as substrates for negative and positive force feedback. These feedback mechanisms play a crucial role in phase-switching during locomotion. Moreover, both in arthropods and in cats, the direct influence of this input on the central sites involved in the generation of locomotor output has been demonstrated by experiments involving rhythm entrainment or resetting (20, 412). The crucial question is how the activity in these

different load feedback pathways is regulated. Does it depend on the task (locomotion)? During such a task, is the modulation of activity a function of the phase of the movement? To what extent is positive force feedback a sensible interpretation?

Although some reviews are available that describe specific load receptors and their reflexes (e.g., Refs. 20, 314, 442, 513), there have been few attempts to incorporate this knowledge with respect to behavior (283, 436, 457, 534). Moreover, a thorough comparison with human neurophysiological data is seldom made. In comparison with other species, bipeds such as humans face the problem of a reduction in the number of supporting limbs. For our review, we have considered three animal groups where load is a crucial control parameter: the arthropods, which include hexapods, octopods, and even multipods; the mammalian quadrupeds like the cat or the rat; and the bipedal human. In the past, the application of a similar comparative approach has proven to be fruitful in detecting some striking similarities in basic principles used to handle gravitational load during walking (93, 128, 412, 416, 556). The different load-compensating mechanisms are then discussed, along with their role in postural reactions and in regulating the phases in walking. The data are considered within a theoretical framework of feedback regulation of position, force, and stiffness.

B. System Theory Definitions

At the onset, it is necessary to define load and force. Force is the mechanical interaction between an object (body) and its surroundings. Its SI unit of measurement is the Newton (N). A force is applied to a mechanical structure by a mass independent of velocity and acceleration (e.g., weight, gravitational load), by an accelerated inert mass (inertial load), or by frictional forces (frictional load). This force changes the form of the mechanical stucture. It imposes stress (i.e., force applied per unit area) on the mechanical structure which may then experience strain (the change in length ratio to the initial length, expressed as a percentage). Sense organs are sensitive to such changes, and their inputs to the central nervous system (CNS) provide information about the force applied, be it via a gravitational, inertial, or frictional load. Therefore, load is always measured as a change in position in one way or another.

Another point that sometimes leads to misunderstanding is the definition of positive and negative feedback. For example, a classical closed-loop controller works with negative feedback, i.e., the actual value x_{act} to be controlled is measured by sensory systems, and this value is then compared with the desired value to determine the error signal (Fig. 1A).

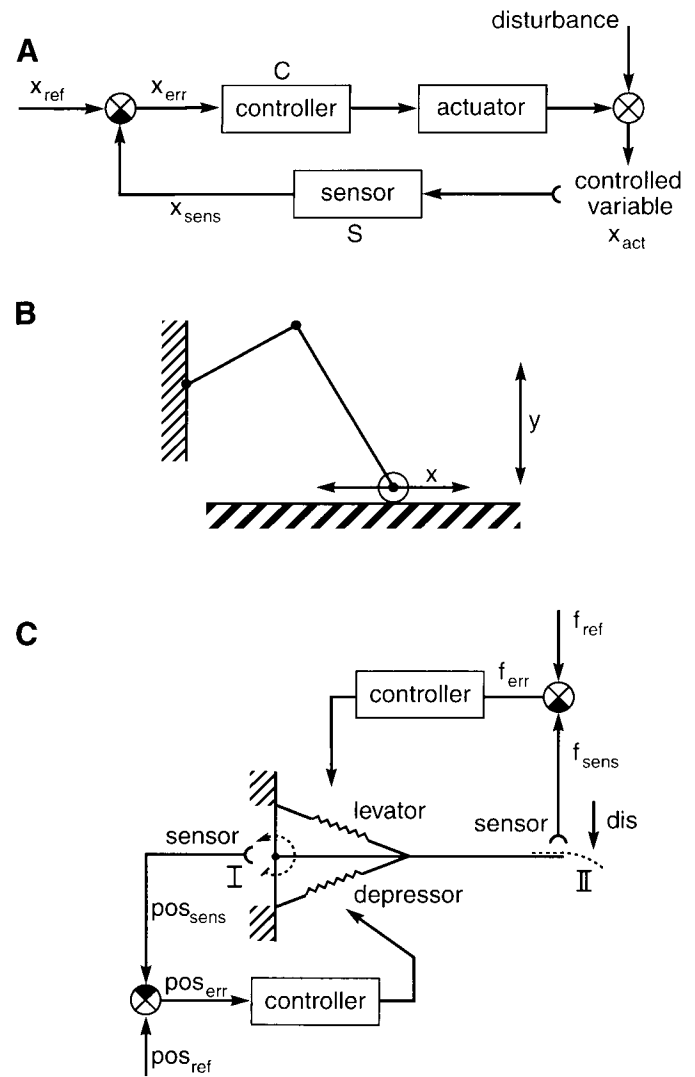This comparison is done by subtracting the actual

FIG. 1. *A*: scheme showing a negative-feedback controller. X_{ref}, reference input, desired value; X_{err}, error signal; X_{sens}, actual value as measured by sense organ. *B*: 2-joint arm tip of which should be moved along x-axis on horizontal surface. *C*: 2 negative-feedback systems controlling position (pos; I) or force (f; II). For explanations, see text.

sensed value x_{sens} from the desired value x_{ref}. For this subtraction, the sign of the sensed value has to be inverted, giving rise to a description in terms of negative feedback. Depending on the sign of the deviation, such a feedback control system can, however, provide actions with different, i.e., positive or negative sign, depending on the sign of the error signal x_{err}. The overall gain G of the feedback system is $C/(1 - C \times S)$, where C is the gain of the forward part of the loop (controller plus actuator, Fig. 1A) and S is the gain of the recurrent part (sensor, feedback transducer). As long as the disturbance is zero, the reference value determines the actual value according to $x_{act} = G \times x_{ref}$. If the desired value of such a closed-loop controller is fixed, this system provides the basis for the so-called resisting reflexes. As an example, take a simple

joint moved by two antagonistic muscles, a levator and a depressor muscle. Assume that the joint is in a resting position such that both muscle forces (plus gravity) balance each other. If by an external disturbance the limb is lifted, for example, the depressor muscle will be activated to resist this disturbance. Such a system could also be used as a servocontroller, i.e., a feedback controller, the set point (reference input, desired value) of which is not fixed but can be changed by higher centers. The servocontroller might, for example, be used to activate the depressor to move the limb downward. If the limb is loaded such that it does move only slowly or not at all, the error signal increases as the set point is moved to values corresponding to more lower positions. This increases the strength of the motor output, and therefore, the load of the leg is further increased. This observation might lead to the interpretation of an "assisting" reflex or positive feedback, because increase of load leads to higher muscle activation that further increases the load. However, this assisting effect is based on a system with negative feedback.

1. Control of compliant motion

In addition to position, or its higher derivatives velocity or acceleration, the controlled variable might, for example, be force. To simplify the discussion, the nature of force versus position control requires consideration. When a leg or an arm has to be moved through free space, the movement of the hand or the leg tip need not necessarily be specified in fine detail. Therefore, different control principles like velocity control, or soft or rigid position control, are applicable. The situation is different when the arm or the leg has to be moved under some mechanical constraints. Assume, as an example, that the tip of a two-joint arm should be moved along a horizontal line while gliding on a horizontal surface (Fig. 1*B*). Assume that the tip of the arm is controlled by means of a rigid position controller, for example, an "integral" controller (i.e., *controller C* in Fig. 1*A*, having the property of an integrator; see also Ref. 130). Then a small deviation of the horizontal line, be this caused by an uneven surface or only by inexact sensor data, would cause the tip to either lose contact with the surface or the controller would produce maximum force to push the tip hard against the surface to reach the ideal horizontal line (assuming the above-mentioned I-controller or a position P-controller of high gain). To avoid these problems, a control system permitting compliant motion is required. Compliant motion means that the movement trajectory is modified by contact forces or tactile stimuli occurring during the motion.

Compliant motion can be obtained in two ways that are called passive and active compliance. For passive compliance, elastic elements are used which in biological systems are in the form of elastic muscles. Tendons and skeletal structures may also contribute to passive elasticity of the limb. Using an elastic element, the problems mentioned above could be solved. However, the force cannot be controlled properly. It rather depends on the size of the disturbance. In active compliant systems, the degree of compliance can be adjusted according to variable requirements. Two different principles will be discussed, namely, "soft" position control (using a proportional controller) and force control. Both will be explained using a single joint system. Figure 1*C* shows a limb that can be moved by two muscles, here symbolized by two springs (with adjustable stiffnesses). A position measuring sense organ (I) is attached to the joint to measure the actual position of the limb. This value is compared with a reference value, the desired position pos_{ref}, by means of a subtraction (negative feedback). The resulting error signal pos_{err} is given to the controller, which in this case represents a proportional element (P controller). The output of this controller determines the activation of the two muscles. A disturbance, for example, an external weight attached to the limb, moves the limb downward, thereby increasing the error signal. This in turn increases the activation of the muscles, in this case the upper "levator" muscle to compensate for this disturbance effect. Because the controller is a proportional element, the compensation is not complete, but proportional to the size of the disturbance. Therefore, the whole feedback system acts like an elastic element, whose stiffness can, however, be adjusted by changing the gain of the feedback loop (this form of active compliance is sometimes called impedance control, Ref. 47). This system represents a negative-feedback system controller for the position of the joint. In arthropods, joint position may be measured by hair plates or chordotonal organs, for example. Correspondingly, muscle spindles or joint receptors could alternatively be used to measure joint position in vertebrates.

Figure 1*C*, *top*, shows another control system, namely, a force feedback controller. A small elastic element (II) is attached to the end of the arm. This is bent when the limb is loaded by, for example, a weight as symbolized by the arrow "dis" in Figure 1*C*. This element can be interpreted as a sensor of the force or the load. In arthropods this could be realized by campaniform sensillae, cuticular stress detectors, or other organs. In vertebrates, Golgi organs are the main sensors. This sensor signal can be compared with a value representing the desired force f_{ref} to determine the error signal f_{err}. Via a controller, this signal influences the muscles. When in this case the same disturbance force (limb pushed downward; see arrow "dis") is provided as has been considered in the case of the position controller, the levator muscle activation now decreases to move the limb downward, i.e., away from the disturbance input, because this controller

tries to maintain a constant force value as measured by the sensor. Therefore, although we again have a negative-feedback system, in this case of force feedback, the reaction to the same disturbance input has a different sign.

Therefore, if one is not aware of the modality of the relevant sense organs, one may interpret this effect as to result from a positive position feedback. An ideal position sensor is compliant (Fig. 1*C*, I), whereas an ideal force sensor is stiff (Fig. 1*C*, II). Correspondingly, an ideal position tranducer is in series, an ideal force transducer in parallel with the moving element. However, there are also somewhat compliant systems like impedance-controlled muscles, whose muscle spindles could be used to transmit information about force. Therefore, the distinction is not always immediately clear.

At first sight, one might assume that a given joint could not at the same time be under force and position control because, as in the example explained here, both controllers act in opposite directions. However, both controllers may cooperate sensibly. When, for example, the force controller of the levator-depressor system shown in Fig. 1*C* is used to carry a given weight (represented by the arrow "dis" in Fig. 1*C*) against gravity and therefore develops an upward directed (levator) force, and, at the same time, the position controller is used to lift the limb upward, then both controllers cooperate to excite the levator muscle.

There are of course also true positive-feedback systems, but these can show different behavior. Let us consider a position controller. In the case of negative feedback, the movement stops when the desired value, or set point, is reached. In the case of positive feedback, the overall gain is $C/(1 - C \times S)$. For $C \times S < 1$, the system behaves in principle like a negative-feedback system but has a higher overall gain for given values of C and S. For $C \times S \geq 1$, the system is instable, i.e., the movement continues infinitely and possibly with increasing velocity and stops only if an external reason is provided or a saturation level is reached. (Correspondingly, in the case of positive force feedback, the force should continuously increase.) A critical test for positive feedback is to experimentally change the direction of the movement of the actuator output by application of a disturbance, in our example by moving the leg. For positive displacement feedback, the actuator should now augment this new movement, whereas for negative feedback it should continue to follow the old direction (e.g., Ref. 467).

The theoretical basis of positive feedback has not been studied in great detail because positive-feedback systems are generally considered to show problems concerning stability. However, very recently it was shown that proportional systems with positive feedback cannot only be stable but can show interesting properties (for positive force feedback, see Refs. 437, 438; for positive displacement feedback, see Refs. 133, 467). Particularly

elegant solutions that can explain puzzling experimental results are provided by concomitant positive force feedback and negative displacement feedback (Refs. 437, 438; see sect. VII). Application of a positive displacement feedback with a loop gain of ~1 ($C \times S \geq 1$) can be used to solve several problems occurring when mechanically coupled joints have to be coordinated. This is possible when the instability is "tamed" by the introduction of a high-pass filter into the loop (133, 467).

2. Resistance and assistance

The importance of this point on terminology can be judged by inspection of the current literature on Ia and Ib effects in the mammalian system. As will be described further in section VI*B*, it is often argued that Ia afferents cause reflex effects consistent with negative feedback and Ib afferents provide effects in line with positive feedback, at least during the stance phase of gait. It is important to realize that in fact, both types of feedback can assist each other during the stance phase, since they both only provide basically for facilitation of extensor activity assuming the extensors actively lengthen. Hence, they both can be seen as assisting reflexes from the point of view of extensor contractions and load compensation, because the sign of the action depends on the sign of the error signal. In this way, particularly elegant solutions that can explain puzzling experimental results are provided by concomitant positive force feedback and negative displacement feedback (437, 438; see sect. VII).

3. Open-loop control

Another possible misunderstanding refers to the term *open-loop control*. This is meant to describe a system that does not rely on feedback signals, for example, a targeting movement with dorsal roots cut, and is sometimes also called feed-forward control. In reality, however, this control signal is usually influenced by sensory signals, for example, visual input, which provides feedback of target position. Therefore, a so-called feed-forward control might, on a higher level and maybe on a different time scale, also correspond to a feedback controller (136).

4. Hybrid control

The above-mentioned problem of control of compliant motion could be solved by a force controller or by a soft position controller, or in some cases as mentioned, by a combination of both. A problem not addressed up to now is that, in a realistic situation, the movements of several joints have to be controlled. Thus the system has several degrees of freedom. The control task might then be complicated in such a way that the task differs for the different degrees of freedom. For example, the task de-

scribed in Figure 1*B* has two degrees of freedom: one along the *y*-axis and the other along the *x*-axis. This task requires a compliant control in the direction of the vertical (*y*) axis as mentioned above. However, along the horizontal axis, a rigid position control might be advantageous because a rigid position control helps to minimize errors. How can both goals be achieved? The classical engineer's solution to this problem is the so-called hybrid control; movement in the horizontal direction is under position control, whereas movement in the vertical direction is under force control. In the case of a leg in stance, we have just the opposite situation. Movement in the vertical direction (control of body height) is under position control, but for movement along a horizontal axis, the leg might be under force control (133). It is, however, not always possible to attribute these two tasks to separate joints. Usually all joints can contribute to both tasks making a hybrid controller a possible, but complicated system (47).

II. LOCOMOTOR BEHAVIOR AND LOAD

Walking is a repetition of successive steps. Each step is composed of two phases. In forward walking during the swing phase, the leg is lifted from the ground and is moved by its muscles against its inertial load. At the end of this phase, the leg reaches an anterior extreme position (AEP). During the stance phase, the leg is on the ground supporting the gravitational load of the body and propelling the animal, i.e., acting against inertial and frictional load. At the end of this phase, the leg reaches the posterior extreme position (PEP). In invertebrates, but also in vertebrates which use other modes of locomotion with a specific locomotor apparatus (like a paddle for swimming or a wing for flight), the two phases are also present and often named power stroke for the corresponding stance phase and return stroke for the corresponding swing phase. The movement during the stance phase has often been compared with a slow ramp, whereas the movement during the swing phase to a ballistic action (152). Because body weight depends on the surrounding medium, the importance of load is very different in these various motor activities. Gravitational load is especially crucial in terrestrial walking, whereas it is relatively less important during locomotion under water, where frictional load is an important element.

A. Invertebrates

The role of load is particularly well illustrated in animals that locomote in various media. For example, amphibious animals can move equally well in and out of water. The crab, *Carcinus maenas*, walks laterally most of the time with four pairs of legs. The legs in the direc-

tion of walking are the leading legs; those pushing the body behind the cephalothorax are considered trailing legs. In seawater, the crab's weight is about seven times less than on land. In general, the cadence under water is faster than on land. The basic motor pattern, however, is somewhat similar in both cases with respect to muscular synchronization and opposition. A careful study of motoneuronal discharge demonstrates significant differences in the two media (101). On land, power stroke muscle discharges lasted longer and involved the activation of additional motor neurons in muscles that are innervated by several motor neurons. Under these conditions, maximal discharges occurred at the beginning of the burst and reached frequencies as high as 200–350 Hz. Such discharge rates are sufficient to increase significantly the muscle contractions needed to support the animal on the ground.

In walking stick insects, load influences were produced experimentally in various ways. The direction of gravity changed by letting the animals locomote under different conditions (e.g., walking on a horizontal plane or on a vertical plane and hanging upside down from a horizontal beam, Ref. 120). The latter situation was recently also studied with cockroaches and the locust (183, 346). The frictional force was changed by letting the animal walk on mercury (255) or on a slippery oil plate (138, 213), or applying friction to the treadwheels (227). Furthermore, the inertia of the wheel was changed (252), or different external torques were applied to the wheel (153, 227, 228). Because the mass of the body has to be carried during stance, load influences are to be expected to affect leg movement during stance, but tests with loads applied specifically during the swing show that it, too, compensates well for experimental changes. Generally, these load influences affect the position of the AEP and the PEP as well as the duration of the swing.

For example, in the rock lobster, the removal of load receptors by autotomy of the legs is assumed to cause the activity in the remaining stump to switch from an alternating pattern, such as seen during walking, to an activity profile in phase with the other legs, as is seen in a behavior in which load receptors are minimally activated, namely, during swimming. The direction of walking can also be determined by load. The grain weevil, *Sitophilus granarius*, which in complete darkness has a circling behavior on a horizontal surface, is able to go straight when the animal walks on inclined surface (529). In that case, it has a preferred direction (downward) due to the activation of the receptors of the leg which indirectly measure the direction of gravity. Another example of the effect of frictional load has already been given in section I, namely, the change in coordination of *Nepa rubra* legs from swimming to walking, dependent on frictional load (530).

Load afferent input can be decisive in triggering spe-

cific types of locomotor behavior. In the cockroach it has been demonstrated that there are some interneurons (IN) that can induce flight if load-related tarsus information is absent and walking if it is present (447). Similarly in the crab, the combined activity of four groups of equilibrium IN is necessary to ensure bilaterally organized movement, and the input to these IN determines the type of motor output. Fraser et al. (231) suggested that these IN can trigger both swimming and walking. The crab has some specific load receptors in the dactyl (distal part of the leg), the stimulation of which induces walking activity. In the absence of this sensory activity, swimming is the default motor output (41).

B. Vertebrates

Comparing different motor behavior in the ontogenesis of birds, Bekoff (36) has shown that in patterns where forces are exerted, return stroke and power stroke durations in the step cycle are very different, while they differ only slightly when the load is limited.

In mammals, comparable differences can be found between walking and swimming. Both types of locomotion use similar motor programs, but the relative timing of the main phases depends on the load. In rat, for example, the flexion phase of swimming and walking has many elements in common, including similar electromyogram (EMG) activation patterns. In contrast, the extension phase is extremely short in swimming as compared with walking and followed by an intermediate period of knee flexion and selective activation of semitendinosus muscle activity (401). If one assumes that the muscles are driven to their maximum contraction rate, swing bursts have similar durations and timing in walking and swimming, whereas the extensor bursts are totally different (269) because of the presence or absence of ground reaction forces.

Iles and Coles (311) have extended these experiments, studying decerebrate rats. Locomotion was induced at controlled step rates by electrical stimulation of the mesencephalic locomotor region. Animals were running on a freely moving wheel to which frictional loads could be added, which caused an increase in the extensor burst duration. This increase was 10% for semimembranosus and vastus lateralis and 40% for the other extensors. For muscles with double bursts, such as the semitendinosus, the extensor phase activity is prolonged. In contrast, when gravitational load was reduced by performing similar experiments in a tank of water, the duration of the extensor bursts was reduced by 35% while flexor bursts increased by 60%.

Hence, various muscles can react very differently to loading. Probably the best studied example is the difference between various muscles belonging to triceps surae.

In the guinea pig, Gardiner et al. (237) found that loading the animal (through a halter-pulley apparatus) led to a much more dramatic increase in the EMG activity of lateral gastrocnemius (LG) than of soleus. Varying speeds give the same type of results in cats (426), with a higher contribution of gastrocnemius than soleus under conditions where more force is required. In humans, the same basic difference between LG and soleus is seen with changes in speed (199).

In cats, the role of gravity on walking has been studied extensively using locomotion on inclined surfaces (292, 426, 503). As expected, the activity in extensor muscles greatly increases during uphill walking. Interestingly, however, during downhill walking, Smith and Carlson-Kuhta (503) found that it was the flexors and not the extensors that dominated the stance phase. In this respect, it is worthwhile mentioning that some animals use flexors as antigravity muscles. The slow loris is a primate that uses arboreal locomotion. It climbs in trees and can progress along the branches either in an upright or in an inverted position. A combined kinematic and EMG study (183, 326) demonstrated that the upside down sagittal pattern is a mirror image of a pronograde upright pattern. The flexors acted as antigravity muscles when the animal was in an inverted position. Propulsion was still achieved through activity in extensor muscles. This is a necessary consequence of the physical situation and is therefore more or less also found in climbing insects (120, 183).

Humans can commonly bear loads of up to 70% of their body mass during walking (297, 369). In the case of African women of some tribes, the task of load-bearing on the head has resulted in some remarkable adjustments (369). These women can carry loads of up to 20% of their body weight without increasing their rate of energy consumption. For other humans, as well as for horses, dogs, or rats, a similar increase in load results in an increase of ~20% in rate of energy consumption. When humans bear loads or walk uphill there is an increase in activation of extensor muscles (410). Inversely, when weight is reduced by body immersion, the EMG and postural reflex responses are reduced in ankle extensors (166). Similar gravity dependence is absent for ankle flexors, implying that proprioceptive input has a more dominant role in extensors than in flexors. The same conclusion was reached following a study on split belt gait, in which it was shown that the amplitude of the ankle extensor activity increased with speed despite constancy of step cycle duration, whereas this was less so for the ankle dorsiflexors (175). A similar asymmetry is apparent in an extreme form in the masticatory system, where stretch reflexes are present in the antigravity closers but not in openers.

In conclusion, load information is important in regulating different types of motor behavior. To understand this regulation, it is necessary to consider first how load is

sensed in animals and humans and how this information is used to control the behavior. However, effects of load are not only counteracted by sensorineuronal mechanisms that use skeleton and muscles as mere executing organs. The physical properties of skeleton, tendons, and muscles by themselves already play an important role.

III. PASSIVE LOAD COMPENSATION: BIOMECHANICAL FACTORS NOT RELATED TO LOAD FEEDBACK

Even in the absence of reflexes, it is possible to resist changes in load. The stiffness of muscles is partly due to passive viscoelastic properties and partly to active contractions. Movement against a load (or "constraint") can follow either of two strategies. In the feedback strategy, information about load is used in real time to adapt the motor command. In the feed-forward strategy, an internal model of the constraint is used to adjust the compliance of the limb in anticipation of the contact force. The latter type of feed-forward control is undoubtedly very important, especially for fast movements [see, e.g., control of movements both of arms (378) and legs (504)], but this is not the main topic of the present review. In this section we limit ourselves to the discussion of some biomechanical elements that are important in load compensation in the absence of load feedback.

A. Invertebrates

Some arthropods can maintain postural positions in the absence of muscle electrical activity (EMG) (548). This is due to the combination of passive elastic muscle tension and of particular biomechanical arrangements of the fibers. When measuring the length tension characteristics of muscles in various insects and crustaceans, Wilson and Larimer (538), Burns and Usherwood (64), and Hawkins and Bruner (284) demonstrated that there is a residual tension when the joints are at their extreme positions so that muscle develops force without energy consumption. It has been suggested that this resting tension could be sufficient to support the weight of the animals (548).

Another important feature for tonic postural activity is the catch property, as described by Wilson and Larimer (538) in the locust (*Schistocerca gregaria*). The extensor tibiae muscle is innervated by two excitatory motoneurons (MN), a slow (SETI) and a fast (FETI) extensor tibiae, respectively. The catch effect can occur when a high-frequency activation of the SETI axon is superimposed on a continuous low-frequency train. The response, which is only present in some of the fibers, takes the form of a tension plateau following the burst. This additional tension is maintained as long as the low-frequency acti-

vation is present. This is thought to be especially useful for the maintenance of posture and when the animal is climbing, in which case the SETI is continuously active at high frequency (64). During fast movements, the FETI MN are activated along with inhibitory MN that selectively speed up the relaxation after a contraction of the slow muscles. This is an elegant method of avoiding the slowing of the fast movement due to the long time constant of the slow fibers (see also Ref. 539).

Similarly, during crab walking, Ballantyne and Rathmayer (16) have shown that the tonic discharge of such an inhibitory MN (the common inhibitor, CI) plays a role in reducing the interburst tension of the rhythmically activated fibers. Bevengut and Clarac (40) confirmed this result in crab swimming. The frequency of such CI can increase with increasing activity. This can be due to the increase in sensory inputs, which are monosynaptically connected to the CI (85). This adaptive mechanism ensures that any increment in burst intensity due to increased load is compensated for by an increase in the burst relaxation mechanism.

In addition, it has been found that certain neuromodulators could play a crucial role in augmenting the muscular tension. For example, in the abdomen of the crayfish, 5-hydroxytryptamine (5-HT) increases the tension of flexors while octopamine has the same effect on extensors. Both substances, 5-HT and octopamine, act at two levels. As hormonal substances, distributed in the hemolymph, they facilitate the muscular contraction, whereas within the CNS, specific 5-HT or octopaminergic neuromodulatory neurons are involved in the control of flexor or extensor motor commands, respectively (336).

B. Vertebrates

By analogy with arthropods, humans and other mammals require relatively little muscular contraction to achieve weight bearing during standing because of biomechanical factors (arrangements of ligaments and bones, intrinsic muscle properties such as its force-length and force-velocity relationships, and intrinsically stabilizing mechanisms in the musculoskeletal architecture; see Ref. 547). Small postural disturbances do not always induce active corrective reactions. Instead, these perturbations are compensated through passive viscoelastic properties of muscles and joints. When muscles are actively contracting, their stiffness increases, and they are even better suited to resist load changes. In fact, it has been argued that, under these circumstances, the muscle properties are more important for load compensation than stretch reflexes (257). Furthermore, for humans it has been shown that muscles can store and release mechanical energy (10), and this property can account for the high efficiency of muscles during gait (87).

On the other hand, it is clear that there are limits to the potential for load compensation by muscle on its own. For example, Nichols and Houk (398) showed that the stretch reflex in the decerebrate cat is well-suited to compensate for nonlinear properties of muscles and can complement these properties for the regulation of muscle stiffness. Muscles differ in their ability to resist loads either phasically or tonically. For vertebrates, as for arthropods, there are specialized slow muscles and/or muscle fibers that are resistant to fatigue (61, 327). There is some evidence that the MN supplying slow muscles can be inhibited actively during fast movements, such as during paw shaking in the cat (502). During postural tasks these slow fibers are essential, since they are specialized for providing high short-range stiffness for immediate compensation for postural perturbations (in advance of the reflex stiffness; see Refs. 368, 398).

In the cat triceps surae, motor units of the slow type produce markedly more force when they are activated by patterned stimulation of high frequency. The presentation of only a single interval, which is much shorter than the others (doublets), is sufficient to elicit this "catch property" (61). During locomotion of intact cats, doublets were found to be quite rare in a variety of muscles (294), but it is possible that they are used selectively to activate only slow muscles.

As in invertebrates, a potentially even more important mechanism is provided by the voltage dependency of the synaptic activation of MN. In the cat, Brownstone et al. (54) have demonstrated a strong "boosting" of the synaptic excitation from locomotor drive networks as MN are nearing their firing threshold in immobilized spinal cats in which rhythmic locomotor neural activity was induced by injecting L-dopa. The motor output of the latter type of preparation is commonly referred to as "fictive locomotion" (267, 325, 422, 550). The Brownstone et al. (54) results may explain why MN are recruited directly to high efficient firing rates during real locomotion, although, under different conditions, they have the potential to fire at lower rates as well (54, 55, 294, 483, 549).

IV. RECEPTORS INVOLVED IN RECORDING LOAD

What are load detectors? Often the term is used specifically to indicate receptors that measure muscle force. However, this definition is too narrow. When a standing animal receives a sudden unexpected increase in gravitational load, this load is not only perceived by muscle receptors sensitive to muscle contractions. Cutaneous receptors of the sole of the foot will be activated as well, along with all receptors that can sense the reduction in the joint angle of knee, ankle, or hip resulting from the extra loading (162). This includes not only joint receptors but also skin receptors signaling skin stretch and muscle length receptors (spindle afferents from extensors in the mammalian system). Hence, it is misleading to focus only on one type of receptor when discussing load-compensating reflex pathways. In this review, a distinction is made between main receptors (true load receptors and body load receptors) and accessory receptors (neuromuscular and joint receptors).

As we will see, afferent input from several receptors that may play a role in the detection of loading of the limb converge onto common IN. This illustrates that, for the regulation of load compensatory reflexes, the nervous system is interested in the ensemble of the afferent input related to loading rather than in the separate "private lines." This does not exclude the possibility that such precise information could be sent separately to higher centers for further processing. Hence, the question is not whether a given sensor is a load receptor or a force, length, or position receptor, since the same sensor can serve several of these functions. Nevertheless, all of these receptors are not equally sensitive to load, and it thus still makes sense to describe some of these receptors as being primarily load receptors (true load receptors, Table 1).

One should keep in mind that even a strict force receptor always measures changes in position because force can only be detected by its effect on movable, usually elastic material. Thus the difference between position and force distorting receptors is a quantitative not qualitative one. If the compliance of the elastic part is high, and therefore the movement is small, it is considered a force sensor, and vice versa. Therefore, in principle, a position receptor could also carry information concerning force. This is even more the case for those "position" receptors that also monitor velocity and acceleration, as described for the femoral CO of the stick insect (296). However, information on load changes could also be obtained when a change in load is not accompanied by a change in position.

A. Invertebrates (Arthropods)

In many arthropod species, changes in motor output to walking leg muscles are found that are related to the gravitational load they encounter during stepping and to dragged weight that impedes forward walking (crayfish, Refs. 101, 268; cockroach, Ref. 411; stick insect, Refs. 27, 28). In arthropods, load can be monitored in terms of exoskeletal strain (23, 44). Sensory cells inserted in the cuticule are real biological strain gauges present in insects, arachnids, and crustaceans. Although they vary in their morphological details, their design and arrangement provides for deformation even by small forces (22, 23).

TABLE 1. *Types of load receptors*

	Main Receptors		Accessory Receptors	
	True load receptors	Body support receptors	Neuromuscular receptors	Joint receptors
Mammals	Golgi tendon organ	Cutaneous receptor on sole of feet	Muscle spindle	Ruffini endings; Pacinian corpuscles
Arthropods	Campaniform sensilla	Campaniform sensilla of walking leg tarsi	Muscle receptor organs	Chordotonal organs, hair plates, hair row
Insects and chelicerates (spiders, scorpions)	Lyriform organs (spiders)	Tactile hairs (spiders, insects)	Muscle receptor organs (insects)	Multipolar cells and strand receptor organs (insects)
	Cuticular stress detectors	Funnel canal organ of walking leg dactyl	Muscle receptor organ	Chordotonal organs
Crustaceans	Tendon receptor organs		Thoracocoxal muscle receptor and myochordotonal organ	Multipolar cells

Moreover, internal proprioceptors can also be stimulated by load.

1. External specific load receptors

The main receptors in insects are the campaniform sensilla (CS). They are usually disposed in groups close to a joint and are composed of a bipolar cell innervating a small hole within the cuticle with dendritic terminals terminating in a cap of the exoskeleton. In the cockroach, the tibial CS have been studied in great detail by Zill and Moran (552–554). They respond to strain in the cuticle, resulting from forces due to muscle contraction and loading of the leg by the animal's weight (434, 435). In the tibia, there are two groups with different orientations. The proximal group, oriented perpendicularly to the long axis of the leg, responds mainly to dorsal bending of the leg and also to isometric contraction of the tibial flexor. The distal group, where cap orientation is parallel to the tibial axis, is activated by ventral bending and cuticular strains produced by contraction of the extensor muscle. Recently, it could be shown that both groups respond to the rate of force (446). The proximal group, for example, fires not only when the tibia is bent dorsally, but also when a force bending the tibia ventrally is released.

Probably the most important CS are situated at the coxa and the trochanter. In general, there are five groups of CS arranged next to the coxa-trochanter joint (cockroach, Ref. 435; locust, Ref. 309; stick insect, Refs. 28, 466, 469). Delcomyn (158) and Hofmann and Bässler (295) found tonic and phasicotonic units, but no pure phasic units, when recording from the trochanteral CS.

In the crustacean decapod leg, at least two different structures are involved in recording load (true load receptors, Table 1). The proximal cuticular stress detectors (CSD) (103) are composed of two elements. The first is located anterior and dorsal (CSD1) and the second is ventral (CSD2). They correspond to a soft cuticular region, innervated internally by a group of bipolar cells in a structure comparable to a true chordotonal organ.

Klärner and Barth (331) have explained that the CSD2 is sensitive to deformation of the compliant cuticle. It is an accurate load receptor when the leg presses against the ground during standing or during the stance phase of the step cycle. These sensory cells are sensitive to local pressure of the cuticular soft patch (with either "on" or "off" responses or both). Most of the afferents give phasicotonic on responses.

The activity of on units increases with force, whereas it decreases with rising forces for the off units. The on units are also sensitive to low-frequency vibration, with an optimum around 10–30 Hz (331). The CSD1 has been studied only recently (370). Some of these sensory units have similar responses to those of CSD2, with on and off responses to pressure on the external patch, and they respond preferentially during the stance phase in walking. Another group of CSD1 afferents is sensitive to high-threshold stimulation. They are not likely to be involved in the routine perception of load, but they may be important in inducing autotomy (the loss of the whole limb, see Ref. 370). There are two advantages for these load receptors in insects and crustaceans to be located proximally in the leg. One is that neuronal conduction time is shortened when the sensors are near the base of the leg. The second is that for mechanical reasons the surface strain of a cantilever is strongest near its base.

In the crab, there are some very sensitive load detectors situated in the dactyl, which is the most distal segment (body support receptors; Table 1). These are the funnel canal organs (FCO) analogous to insect CS (22).

Two types are present with different positions within the dactyl. The most proximal ones are innervated by two sensory cells, grouped in one canal. They respond in a phasicotonic way to imposed load and encode vibrations at low frequency. One sensory cell is activated by dorsal stimulation, and the other by ventral stimulation. Hence, these proximal dactyl FCO receptors are directionally sensitive. During walking, these two units discharge more or less simultaneously during the stance phase. Neverthe-

less, the unit sensitive to dorsal bending always has a significantly higher discharge at the onset of stance (353, 354). The sensitivity of these units in response to applied force follows a sigmoid curve with the greatest change in firing occurring in the range of 25–70 mN (equivalent to the force produced by a mass of 3 to 8 g). A crab that weighs 60 g in air weighs only 8 g in water. Because the animal load is supported by six to eight legs, each leg exerts on the ground a range of force from around 10 mN when it is in water to up to 100 mN when it is in air. The FCO response curve demonstrates that the sensory units respond over the whole of this range.

The most distal FCO receptors are located at the tip of the dactyl. They are innervated by only one cell, and they only respond phasically. They encode vibrations at much higher frequencies than the proximal receptors (354). This difference in sensitivity may be related to topographical differences in the structure of the exoskeleton. Distally, the tissue is more flexible than proximally (lower calcium concentration). During walking, the distal phasic units are mainly active at the onset of ground contact. It is worth mentioning that these receptors are not only sensitive to externally applied load. Both CSD and FCO respond well to contraction of their surrounding muscles (levator and depressor for CSD, and opener and closer muscles for FCO).

In the arachnids, receptors that are comparable to those mentioned above have been described. For example, the lyriform organs and the CS of spiders (484, 485,486) have been described as true load detectors (Table 1).

2. Proprioceptors and indirect control of load

Some receptors in arthropods are primarily involved in the registration of position and movement. Under certain loading conditions these receptors are activated as well because of the related changes in joint angles (see Table 1, accessory receptors). For example, in crustaceans as in insects, chordotonal organs are present at most leg joints (24, 27, 28, 30, 49, 65, 78, 214). The afferents firing during stance can be implicated in load compensation, since their firing rate is a function of the joint changes, partly induced by gravitational forces.

In insects, leg joint angles are also measured by hairplates or hair rows, external sensory hairs which are bent by the soft joint membrane when the leg joint changes its position. Such hair plates can monitor the position of the head relative to the body, and as such, they can be exploited to provide information concerning the direction of gravity (e.g., honey bee, Ref. 355; dragon flies, Ref. 385). Sensory hairs cover the whole surface of the body and the legs. These can detect local contact and may also monitor acceleration which, for example, is provided by loading a leg at the end of the swing movement.

In the femurotibial joint of the insects, different types of sensory afferents have been characterized, and recently, Matheson and Field (373) have summarized the complexity of the innervation of that joint in the locust. The structures involved are the CO, CS, multipolar receptors (28, 109, 516), and muscle tension receptors (for the subcoxal joint, see Ref. 308). In the crustaceans, similar structures have been studied in great detail. In the abdomen of the crayfish, each segment possesses two pairs of muscle receptor organs (MRO), located on either side of the dorsal midline, one phasic and one tonic. The phasic MRO is associated with rapid movement, and the tonic MRO provides a reliable signal of either muscle length or tension. In the legs of crustaceans, other neuromuscular proprioceptors have been described [e.g., the thoracocoxal muscle receptor (TCMRO) (76) or the myochordotonal organ (MCO) (see Ref. 78)]. Similar sense organs have also been found in insects (50).

All these proprioceptors (MRO, TCMRO, MCO) are coupled in parallel to independent contractile elements. Both the proprioceptor and the parallel muscle fibers are controlled by the same MN. These receptors can serve as peripheral references for the determination of a stopping point or set position. When shortening of the muscular part of the MRO is driven simultaneously with contraction of a parallel working muscle, the sense organ is not activated unless a resistive load is encountered during a movement and stretching of the receptor occurs.

Perhaps the receptors that are the most likely candidates for being true load receptors are the tendon receptor organs (Table 1; true load detectors). They are present in a fairly large number of crustacean leg segments (78, 281). They are not very sensitive to passive stretch, but their location is such that increases in muscle tension transmitted via the apodeme (an invagination of the cuticle on which the muscle fibers are attached) bring about increases in sensory discharge. The sensory cells are bipolar and grouped in clusters along the apodeme. If we compare them with the vertebrates, they differ from the GTO of the mammals in that they are not intimately associated with the muscle fibers themselves. They resemble more the receptors of the lizard (442), which lie in the tendon at a distance from the muscle-tendon junction. In crustaceans, this means that the tendon receptor organ may be sensitive to whole muscle tension as well as to a localized tension produced by the contractions of individual muscle fibers. Sensory cells connected to the muscle tendons have also been described for insects (28, 373).

Large groups of afferents are thus able to record load, and we have tried to limit the description to some major types. We may add, however, that loading of the whole body can be detected by specialized statocyst organs or gravity receptors that correspond to the otolith component of the vertebrate nonacoustic labyrinth (42).

B. Vertebrates

1. Exteroceptors

In mammals, one can distinguish two main load receptor types, one of which consists of body support receptors (Table 1). Cutaneous receptors of the sole of the foot can sense the deformation of the foot and ankle due to loading. Just after footfall there is a sharp rise of activity in the nerve supplying the foot pads in intact cats (193). Recordings from single afferents during the stance phase in the cat have shown that activity is generated selectively during stance even from skin areas that are not directly in contact with the ground (360, 362). Presumably, this is due to skin stretch, which can activate low-threshold mechanoreceptors. Such stretch-sensitive skin receptors could thus have a proprioceptive function. This is not only true for the foot but also for other parts of the body. For example, in humans, Collins and Prochazka (110) reported movement illusions evoked by stretches of the skin of the dorsum of the hand. In the monkey, it was shown that tactile activity during arm movements, avoiding direct skin contact, reached the primary somatosensory cortex (108).

In humans, the activity from cutaneous afferents during movement has been recorded through microneurography (59, 206, 305, 332, 366). These studies have confirmed that activity from mechanoreceptors can signal changes in joint angles and thus indirectly also loading. However, in general, this technique can only be used for small movements. For walking, a different technique is needed. To record the afferent activity from the foot during human walking, an implanted cuff electrode has been used (498). Activity in the sural nerve, which innervates the lateral side of the ankle and foot, was largest just after the foot hit the floor, although the innervation area of the nerve did not touch the ground. Moreover, a series of small bursts was seen throughout stance, coinciding with fluctuations in heel contact, as measured by separate sensors.

The role of the skin in load-compensating mechanisms has been most extensively studied in some forms of fine motor control. For example, due to the elegant work of Johansson and Westling (321, 322), we now know a great deal about the role of mechanoreceptors in the finger tips for precision grip and load detection. During precision grip, one produces forces that are slightly larger than the minimum required to hold an object (322). Insufficient force leads to slip, which is very effectively detected by skin mechanoreceptors. Compensatory reactions to sudden, unpredicted increases in load force occur with a latency of 40–50 ms in adults and 20 ms in young children (207), and it is thought that mechanoreceptors on the fingers are important for such reflexes. In general, grasp reflexes in infants show all the characteristics of a force "positive-feedback" system (see also Ref. 438 for review).

2. Proprioceptors

In mammalian muscles, the main receptors are spindles and GTO. Both are abundant in muscles that compensate for load during gait, and the number of both tends to covary in a given muscle (236, cited in Ref. 481). These proprioceptors have been mostly studied with respect to the reflex actions in the parent muscles, but there are good indications that this homonymous control is not the most important function. Scott and Loeb (481), for example, have argued that the distribution of spindles among human muscles seems better related to the need for information about the position of joints spanned by those muscles than to the control of the muscles themselves. Overall, the distribution shows a proximodistal gradient that is consistent with the observation that humans are better in judging positions of proximal than of distal joints (104, 276). For cats, some detailed measurements of the distribution of spindles have been made for some muscles (see, e.g., Ref. 444), but unfortunately there is no systematic survey available yet. On the other hand, the cat has been very thoroughly studied with respect to reflex connections (for a recent review, see Ref. 397).

3. GTO

Ever since Sherrington's work on cats, extensors have been equated with antigravity muscles in quadrupeds. Consequently, the Ib afferents from extensors are usually considered as the most important gravitational load receptors (Table 1; true load receptors). Golgi tendon organs are force-sensitive receptors that respond to muscle contraction and that have been studied most extensively as potential detectors of load (for review, see Ref. 314). They consist of capsules containing collagenous fascicles and intertwined sensory endings. Most of the GTO are not found in the tendon but rather at the transition from tendons to muscle fibers and aponeurotic sheaths. In the cat, there are about 10 muscle fibers in series with a single tendon organ. A contraction of any one of these 10 fibers is sufficient to elicit a discharge in the Ib afferent arising from a GTO.

Basically, the GTO acts as a strain gauge measuring active and passive forces, especially those produced by the inserting muscle fibers (43, 302, 314, 320, and 514 for review). In some instances, it was possible to measure the discharges of all Ib afferent fibers of a single muscle (300). From this study, it appears that tendon organs are very good in following variations in force, and it was concluded that they code for dynamic and not for static muscle force. Initially, it was thought that strong muscle stretch was the optimum stimulus for Golgi tendon afferents (307). However, in the 1960s it was discovered that

small twitches of soleus (320) or tibialis anterior (3) were very effective in eliciting responses from Ib afferents from these muscles. The most convincing evidence for the very high sensitivity to muscle force came from experiments in which stimulation of ventral roots demonstrated that isolated Ib afferents had a very low threshold (1 mN) for their responses to muscle contraction (302). Only under some circumstances the Ib afferents can also effectively be activated by passive stretch. Stuart et al. (512), for example, showed that the firing threshold of tendon organs can be about equal for passive stretch and graded contraction. In most instances, however, passive stretch was clearly less effective than active contraction (440, 509). To validate the role of GTO in measuring muscle force in the intact cat or even in human subjects, one can measure the tendon force directly, using a "buckle" type of tendon transducer as introduced by Yager (540) and used by Walmsley et al. (524) and others (for review, see Ref. 363, 433).

In summary, both in invertebrates and vertebrates (including humans), load receptors can be divided into two groups, namely, main receptors and accessory ones (Table 1). In general, the latter are more sensitive to movement or position than to the load. However, in some particular circumstances, the accessory receptors are sensitive to the load supported. Considering the main receptors, it is also obvious that they are not only detecting load but also muscle tension. In both groups, it seems that the main factor for load recording is the particular location of the receptors in the animal or human. For this reason, the cutaneous afferents from the sole of the feet or the cuticular receptors of the insect leg tarsus or of the crustacean leg dactyl are of primary importance. Although load receptors show many similarities between invertebrates and vertebrates, some major differences exist as well. First, in the arthropods, the presence of an exoskeleton offers some interesting possibilities for recording load by receptors inserted on certain parts of cuticle. This particular material has itself some specific load-resisting properties that have been studied in detail (problem of compliance, see Ref. 23). Second, the ensemble of receptors is much more diverse in invertebrates, ranging from very simple forms (hairs, setae) to complex organizations (cuticular structures, tendon organs). In comparison, in mammals we have mostly rather complex structures (GTO, skin mechanoreceptors).

V. CONTROL MECHANISMS IN STATIC CONDITIONS

The aim of this section is to describe direct load feedback through reflexes under static postural conditions. It is realized that there is also an indirect role of load feedback, needed to update internal models used in feedforward control, but this type of feedback mechanism is beyond the scope of this review (see Ref. 136).

A. Invertebrates

1. Compensatory movements and righting responses

Load exerted on an animal is one major element to be controlled by equilibrium reactions. The latter can be divided into compensatory movements, when a constant position has to be maintained, and righting responses, in which the appendages actively restore the previous position. In crustaceans, such reactions involve the receptors described previously (cuticular receptors, CO, and the statocysts). The manner in which visual, gravitational, and proprioceptive cues interact in the control of compensatory eye movements has been investigated by Neil (394). Righting reactions are mostly dynamic and involve the generation of forces to oppose external disturbances. The ensuing reaction has then to be integrated in the animal's usual behavioral posture. For example, in *Homarus*, the elevation of the claw, unilateral swimmeret beating, and uropod opening and closing along with movements of antennae are all motor reactions that are aimed at restoring the upright position (42). Both the statocyst and some proprioceptors have been shown to be important for these reactions. For example, the role of the coxobasal CO has been demonstrated both for the righting reaction of the antennae (102) and for the control of swimmeret beating (84).

In normal stance, arthropods maintain a low center of gravity. As a result, the different leg joints are partially or totally held in a flexed position while head, thorax, and abdomen are held in suspension from the proximal leg joints. Resistance reflexes then ensure the appropriate maintenance of this posture. This includes equilibrium reactions and adjustment of body height.

In the hermit crab, the stabilization of the abdomen has been studied in detail by Chapple (88). A cocontraction reflex is described that is activated by both stretch and release of the central superficial muscles in the abdomen. The reflex has two components and is very sensitive to ramp stretch. It is primarily sensitive to stretch velocity. Mechanoreceptors that produce this response are activated by active force as well as stretch, suggesting closed loop control.

In general, posture is maintained actively by negative feedback produced continuously by sensory afferents controlling the different leg joints in *Crustacea* as in *Insecta* depending on the muscles involved in counteracting the gravitational forces. Skorupski et al. (501) demonstrated that a particular pool of MN is devoted to negative feedback, whereas another, more directly connected with central drive, is involved in positive feedback.

The extensor muscles develop the force required for

jumping. A special mechanical arrangement within the femur-tibia joint allows a high force to be developed by the extensor muscle, although the joint remains flexed as long as the jump is not yet elicited. During static conditions this flexor force is developed against a cuticular structure and can easily counteract the extensor contraction (while inhibition of this flexor force leads to a jump; see sect. v*A2*).

Many resistance reflexes are known in arthropods. These are based on position sensors (30, 69, 92, 217). In many cases, where whole joints rather than individual sense organs are stimulated, the participation of load sensors cannot be excluded. By specific stimulation of the CS at the cockroach tibia (551, 553, 554), different reflexes could be induced: proximal sensillae inhibit flexor MN and excite extensor MN, distal sensilla induce opposite responses with excitation of the flexor MN and inhibition of the extensor MN. Such reflexes thus provide negative feedback, since loading the upright standing animal stresses the proximal sensilla, which reflexly excite extensors. Inversely, lifting the animal produces strain in the distal sensilla, thereby causing flexor activation. Therefore, bending of the tibia in either direction is minimized. This corresponds to a load compensation system based on counteracting the bending forces produced by the animal's weight on the leg. In the stick insect, Schmitz (466) confirmed these previous data for a proximal joint that acts perpendicularly to the femur-tibia joint. He studied the role of the trochanteral CS in controlling the retractor and protractor coxal MN. These reflexes also represent a negative feedback system that continuously compensates cuticular stress in the legs of the standing animal. Moreover, he was able to show that these reflexes are also active in the walking animal. During the stance, depending on whether the femur is loaded (in posterior direction) or unloaded, either the retractor coxae or the protractor coxae is excited reflexively. This would lead to a prolongation of the ongoing stance or would facilitate the transition from stance to swing, respectively.

Similarly, in the crayfish, reflexes induced by the CSD receptors have been studied by intracellular recording of different MN. Monosynaptic connections have been found from CSD1 and CSD2 to the different levator and depressor MN, although responses are quite complex and are in the main polysynaptic (352). It may be concluded that during stance, these receptors elicit activity that reflexly induces cocontraction of opposite muscles, which should result in an overall stiffening of the leg. The outcome of the reflexes of CSD1 reflexes depends on the force level (351). Inhibitory responses in the anterior levator were correlated with the activation of low-threshold CSD1 units, and excitatory responses with the activation of high-threshold CSD1 units. For the FCO, the final outcome of the reflexes is totally different. In studies on the crab, rock lobster, and crayfish, stimulation of the FCO

dactyl nerve resulted in polysynaptic responses in proximal MN (levator, depressor, promotor, and remotor, Ref. 98). The main response is facilitatory for the levator MN and inhibitory for the depressor MN, thereby causing a limb swing movement.

In crabs, the great sensitivity of tendon receptors to centrally initiated increases in muscle tension suggests that these receptors are very well situated to evoke compensatory motor discharge that will overcome load encountered during leg movements. Stimulation of the tendon receptor nerve inhibits resistance reflex motoneuronal activity in the homonymous muscle and causes some inhibition in the opposing muscle (100). However, depending on the intensity of the stimulation of that nerve, some authors (408) have found some local facilitation, inducing an assisting effect. These receptors then influence the general control of leg joint position and movement (367).

A great variety of reflexes have been described in postural reactions, and all of them involved the load supported by the animal. They can be summarized as resistance reflexes that can be understood as representing negative-feedback controllers. These reflexes counteract the effects of external forces applied to the body. The most important natural case is gravity, which can act in different directions depending on the position of the body, e.g., standing on a vertical plane or hanging upside down from a horizontal beam (stick insect, Ref. 120; cockroach, Ref. 346).

These resistance reflexes and the sense organs responsible for them were investigated in detail for the stick insect (24, 463–465, 527). The whole leg was shown to act as a height controller, and the different legs act independently of each other (standing insect, Refs. 144, 527; walking insect, Refs. 121, 148). It could be shown that the reaction of the whole leg represents mostly, but not completely, the vectorial sum of the resistance reactions of the individual joints (135). Distributed reflexes that might be responsible for these differences were described for crustaceans (92). The resistance reflexes in the individual joints act together to give the leg a springlike behavior.

In the stick insect, the height controller has a dynamic component that adapts to long-term external loads. This results from the sensitivity of the reflexes to extremely slow movements, which is also responsible for the behavior of flexibilitas cerea (32), where a leg after a disturbance seems to remain in that new position. However, in effect, the leg moves back to its original position, but so slowly that is is often very difficult to recognize the movement by eye. As mentioned in section vɪɪ*A*, the dynamic behavior of the height controllers changes when the animal changes its state from standing to walking; the "spring" now shows a tonic behavior with a small time constant (148, 463).

2. Other types of reflexes

In spiders, stimulation of tactile hairs on the ventral, proximal part of the legs induced a contraction in some leg muscles that raised the body (204). Such a reaction, which involves coordination of more or less all eight legs, can be induced by stimulation of just one tactile hair with a latency to 100–160 ms. These "tactile hairs" appear to be mechanical touch receptors and are innervated by three bipolar sensory cells. Local IN could suffice to mediate local interleg reflexes, whereas plurisegmental IN may serve to generalize the reaction (380). Several parallel reports have been presented in insects (424, 492).

Some experiments on postural control before jumping in locusts by Burrows and Pflügers (70) have shown positive-feedback effects that could be important in increasing force (and load). The tibia of the hindlegs of the locust is of particular interest because these legs are used in walking, climbing, and providing propulsive force for jumping. The tibia is moved by a powerful extensor muscle and by a much weaker flexor muscle. They alternate during walking but cocontract to generate the high forces required for kicking and jumping. Such force can be measured by two CS disposed in the proximal part of the tibia, one anterior and one posterior; they are excited by strains set up when the tibiae try to extend against a resistance. The afferents excite both flexor and extensor muscles: they excite the fast axon to the extensor (FETI), certain flexor MN, and some nonspiking IN and then indirectly the slow axon to the extensor (SETI). This reflex may be useful during jumping. Before a jump can occur, both flexor and extensor muscles must cocontract, and it is the inhibition of the flexor MN that allows the stored force to be released explosively (286, 287). During the cocontraction, the CS produce afferent spikes so that they contribute to the facilitation of both muscles. Campaniform sensilla appear to make direct connections with the fast extensor; however, there is also an inhibitory influence onto the flexor, and as only the connectivity has been investigated, the functional contribution is still open. Femoral chordotonal afferents also synapse monosynaptically on such MN and on nonspiking IN, spiking local IN and intersegmental IN. Inhibition of flexion originates from the IN, which can be gradually depolarized and which inhibit the flexor directly (67).

B. Vertebrates

The role of sensory feedback in postural control has been the subject of several reviews (162, 272, 371, 372). Here we focus on the issue of load-compensating reflexes.

1. GTO reflexes in the cat

It has been difficult to assess the reflex effects from Ib afferents because few methods are available to activate these afferents in isolation reliably. Most of the early studies (202, 203, 345) used electrical stimulation of nerves to study the reflex responses in cats. The main problem, however, is that Ia and Ib fibers have about the same diameter, and it is usually impossible to selectively activate the Ib afferents. For a few nerves, such as the ones innervating knee flexors and extensors, one can activate Ia afferents before reaching the Ib threshold (46), and this feature was extensively used to separate Ia from Ib effects (see Ref. 374 for review).

On the basis of these studies, it was first concluded that Ib afferent activity induced inhibition in the MN of homonymous muscles, while providing excitation to antagonist MN ("the inverse myotatic reflex," Ref. 345). It soon became clear that this was a misleading term, since the projections were much more widespread, and there was no distinct inhibition favoring the parent muscle (202, 203). In fact, the effects were present even in muscles acting across different joints. Sometimes the effects were opposite: Ib afferent input from extensors causing inhibition of flexors (202, 203). The latter type of "exception" was found quite often when the Ib reflex effects were studied during facilitations from some descending tracts (rubrospinal tract, Ref. 298). Furthermore, studies using spike-triggered averaging showed that Ib effects were frequently excitatory to synergistic MN (525).

More recently, large changes in gain of Ib reflexes have been demonstrated by lesioning some of the descending pathways (312, 313). In the latter studies, an alternative method was used to obtain selective activation of Ib afferents. This method was proposed by Coppin et al. (114) and used extensively by Fetz et al. (216). High-frequency stimulation of the tendon of soleus is a selective stimulus for Ia afferents, and its prolonged application elevates the threshold for Ia activation above that of Ib afferents for periods ranging from 10 to 25 min. With this method it was possible to confirm that Ib stimulation causes autogenic inhibition.

A third method to activate GTO is based on the high sensitivity of these receptors to induced muscle contractions. The latter method has been used to study Ib reflex effects as well. In one of the first studies of this type (106), the responses of IN in laminae V to VII were recorded during induced muscle contractions. Most of these units did not respond to vibration, but many were responsive to stretch. Surprisingly, it was found that only about one of every four IN was responsive to electrically induced Ib input. In contrast, almost all of these units responded well to light stroking and tendon squeezing of more than one muscle. It was concluded in line with several other studies (39, 105, 208, 333, 379, 407) that presumably afferents with free endings provided the input to these cells. Muscle spindles may be accidentally activated as well (reviewed in Refs. 307 and 374). When γ-MN are coactivated, the

firing of spindle afferents may be increased, especially when tetanic stimuli are used (278, 282, 292, 315).

Given these restrictions, the method of contraction-induced Ib activations nevertheless yielded some important insights. For example, in many schemes based on the concept of autogenic inhibition, it is tacitly assumed that the time course of the inhibition parallels the time course of the contraction eliciting the Ib discharges. A series of studies from the laboratory of Jami (335, 342–344, 423, 557, 558) has undermined this notion and replaced it by a much more dynamic view of Ib autogenic inhibition. Lafleur et al. (343, 344) and Zytnicki and co-workers (557, 558) showed that sustained isometric contractions of gastrocnemius medialis elicited short-lasting inhibitions in homonymous and synergistic MN, whereas Ib afferent activity persisted throughout the contraction period. The decline in autogenic inhibition is presumably due to presynaptic inhibition of Ib terminals (342). Furthermore, the same group recently showed that even in the anesthetized cat there is evidence for contraction-induced excitation instead of inhibition in homonymous MN of the peroneal muscles (335, 423).

The method of contraction-induced Ib activation has also been successful in the study of the widespread distribution of the effects over various muscles. For example, Lafleur et al. (343, 344) activated gastrocnemius medialis Ib afferents through induced contractions of the parent muscle and found a rapidly declining inhibition in a wide variety of both antagonist and agonist MN. Nichols (397) has argued that force-dependent, inhibitory pathways among antigravity and stabilizing muscles link muscles crossing different joints and members of different synergistic groups that exert torques in different directions. It follows that each muscle receives a unique combination of reflex inputs. A reduction in degrees of freedom of the musculoskeletal system is achieved at high force levels because the cross-joint coordination resulting from actions of force-dependent pathways becomes stronger.

2. Convergence in the Ib pathway

Although the importance of descending input onto Ib pathways was being revealed, other studies have emphasized convergence from other types of afferents. Lundberg et al. (365) described convergence of cutaneous and Ib afferent input onto common IN. Fetz et al. (216) found that Ia afferent input from ankle and toe extensors could also cause autogenic inhibition, and they termed this "Ia nonreciprocal inhibition." Later, such inhibition was found to be present in all groups of MN for which autogenic inhibition was previously demonstrated following triceps surae and plantaris stimulation (319). Basically, the experiments were performed as previously, using electrical stimulation of nerves to activate Ib afferents,

but in addition muscle stretch, below threshold for Ib activation, was applied. The pure Ia stretches were as efficient at causing the "autogenic inhibition" as the electrical Ib stimulus. To emphasize the parallel effects of Ia and Ib afferents in this pathway, the term *Ia-like-Ib inhibition* was coined.

Interneurons, receiving mixed Ia-Ib input, are also activated by cutaneous input (317), as well as by afferents from joint receptors and by muscle afferents with free endings (for review, see Ref. 473). As mentioned above, cutaneous afferents can signal load-related changes during movement. It is not surprising then that these afferents have many features in common with Ib afferents. For example, it has long been known that such afferents have parallel excitatory and inhibitory pathways to extensor MN (60). Recently, it was found that, by analogy with autogenic Ib inhibition, the efficacy of the sural nerve induced inhibition decreases rapidly when repetitive stimulation is used while the excitation is maintained (285). Finally, the convergence of cutaneous input on group I muscle afferent pathways shows some functional specialization. Powers and Binder (430) found that presumed Ib input yielded preferentially excitatory postsynaptic potentials (EPSP) in gastrocnemius MN which also received excitatory (sural nerve) input. In contrast, Ib inhibitory effects generally appeared in MN receiving inhibition from the sural nerve.

3. Autogenic inhibition (inhibition of homonymous MN) and antagonist excitation

Like autogenic inhibition, the excitation of antagonists did prove to be a mixed Ia-Ib rather than a specific Ib effect (319). Moreover, many IN, which were excited by such mixed Ia-Ib input, were found to excite rather than to inhibit antagonist MN (317). Such antagonist excitation was even clearer when more selective Ib stimulation was used. Lafleur et al. (343, 344) activated gastrocnemius medialis Ib afferents through induced contractions of the parent muscle, and they found a rapidly declining inhibition in a wide variety of both antagonist and agonist MN.

One of the difficulties arising here is that the notion of antagonist is often difficult to define. A given muscle, e.g., the biceps femoris, may be a synergist of another muscle, e.g., semitendinosus, for one function (in this case hip extension), but they may be antagonists for another (exorotation of lower leg). Alternatively, the antagonism may lie in the speed of contraction. For example, gastrocnemius and soleus are certainly synergists with respect to ankle extension, yet these two muscles are often controlled differentially by the CNS. During fast scratching movements of the cat, gastrocnemius may be activated while soleus is being inhibited (502). Skin afferent input (sural nerve) activates fast gastrocnemius units but may inhibit slow soleus MN (60).

Nichols (396) found that stretches of gastrocnemius and soleus combined gave larger stretch responses than when only soleus was used, at least when the force in both muscles was low. However, at higher contraction levels, the combined effect was smaller. This implies that these muscles act as "synergists" at low force levels and as "antagonists" at high force levels (where Ib afferent firing may be expected to be important). Similarly, the ankle flexors and extensors are linked differently depending on the contraction level. Nichols and Koffler-Smulevitz (399) found that reciprocal excitation from antigravity extensor muscles onto pretibial flexors parallels reciprocal inhibition at high force levels only.

4. Functional significance of autogenic inhibition

A coherent proposal for the role of autogenic inhibition has been provided by Houk (301). He has suggested that this type of feedback is essential to regulate muscle stiffness. Earlier work from Nichols and Houk (398) had shown that the stretch reflex is essential for the control of muscle stiffness, and Houk proposed that Ib feedback helps to organize this feedback. However, it is still unclear how this could be achieved (397). The Ib inhibitory effects were found to be smaller in decerebrate than in spinal cats. This led Nichols and Houk (398) to propose that the increased stiffness in decerebrate rigidity was partly due to an absence of Ib autogenic inhibition. They hypothesized that in the intact animal, the Ib inhibitory feedback would balance the Ia-induced reflex stiffness during eccentric contractions (lengthening of contracting muscles).

Polymodal convergence improves the flexibility of reflex control (375) and is meaningful in the context of load compensation. It is hard to imagine, in daily life, a loading situation in which only Ib afferents are activated (see above). Extra loading or unloading is likely to be detected by a multitude of afferent signals, and the appropriate reflexes presumably require a sufficient amount of spatial summation of the different channels. This may include the simultaneous contraction of several muscles, as Harrison and Riddell (279) have shown that some Ib IN are not activated by contractions of single muscles but respond readily to the more synchronous activation of groups of muscles provided by electrical stimulation.

The general idea emerging is that Ib afferent input, along with other load-activated afferent input, feeds into alternative excitatory and inhibitory pathways to a variety of MN and that the gating of the activity in one pathway or the other depends on several factors, such as contraction strength and the context of the motor task in which the animal is involved and which determines the actual reference value. To understand the impact of the latter element better, it is essential to consider the results from studies of these pathways in the behaving animal (see further).

The simple view that autogenic inhibition is the primary type of force feedback has survived for a surprisingly long time, given the relative weakness of the evidence. It is now well-recognized that there is extensive convergence both from descending tracts and from different types of afferents onto IN receiving Ib input. The notion that Ib reflexes inhibit agonists and excite antagonists has to be replaced by the idea that Ib input, under static conditions, can give rise to short-lasting inhibitions in both agonists and antagonists throughout the limb. The question now arising is whether this inhibition survives under dynamic conditions and whether other, facilitatory pathways then become more prominent. Such a switch was already predicted in 1970 by Stuart et al. (514), but its experimental basis had to wait until experiments on behaving animals could be performed (see sect. VI).

5. Intensity dependency

In the previous section on invertebrates, some examples were given whereby either assisting or resisting reflexes were obtained depending on the stimulus intensity. Consequently, it may be too simple to relate a given type of receptor to either assisting or resisting reflexes, since sometimes both can be obtained depending on the range of the load applied. In vertebrates, a good example for this is mastication, where mechanoreceptors around the teeth can signal load. In humans, the afferent activity can induce either short-latency inhibition or long-latency excitation of jaw-closing muscles such as the masseter (51, 242). Fast loading, as provided by a tap on the teeth, preferentially induces masseter suppression, while slow pushes are optimal for masseter facilitation (521). The fast suppression can protect the teeth and soft tissues in the mouth in case one bites on an unexpectedly hard object. The slow facilitation could help to grip the food bolus between the teeth during chewing. Evidence for such reinforcing feedback has come from many sources (51, 406, 520). The general idea emerging is that such phenomenological so-called positive feedback from periodontal afferents is especially important at relatively low load levels.

At high tooth loads, the periodontal afferents saturate, and the response reverses to suppression of the MN of jaw-closing muscles (analogous to the withdrawal reflex of the limbs). Thus the switch between resisting and assisting reflexes might be either due to a negative-feedback system under the control of a changing reference input or, in other cases, to stimulus intensity.

Similarly, during locomotion, both assisting and resisting influences could be useful. When loading is fast and extreme so that muscles or ligaments could be damaged, feedback should be negative. The clasp-knife reflex,

which is especially prominent in humans with spasticity, results in a sudden release of tension in muscles that are loaded very fast and heavily (resulting in the limb bending as the blade of a jackknife). It is currently thought that this reflex is due to activation of group II and III afferents innervating the muscles through free nerve endings (105). When load is applied more progressively, such as during the stance phase, then the need for an assisting effect (or positive feedback in the phenomenological sense) is more prominent. Some yielding in early stance makes walking more elegant and has physiological advantages (pre-stretch facilitation and ensuing shortening of extensor muscles, see Ref. 83). On the other hand, the activity of the antigravity leg muscles should be scaled with the load provided by the body weight. Cutaneous receptors on the foot could signal this loading while GTO in extensors are properly positioned to measure the force exerted by these muscles. In this respect, it is worthwhile recalling that in the cat, Nichols (396) found that the reflex actions of contraction induced reflexes is indeed different at low and high force levels.

Recently, the effects of induced contractions have been studied not only in reduced preparations but also in intact standing cat (431). Pratt (431) found that intramuscular stimulation of hindlimb extensor muscles evoked short latency facilitatory responses (occurring some 21–22 ms after onset of vertical force) that were widely distributed among hindlimb extensor muscles. For the hip extensors, for example, the responses appeared exclusively in extensors at hip, knee, and ankle. In contrast, the hip, knee, and ankle extensors were not activated when the flexors at any of these joints were stimulated. The effects on extensor stimulation were taken as evidence for a Ib extensor reinforcing feedback and interpreted as positive force feedback.

One other central issue concerns the question of what exactly is controlled in load-compensating reflexes. One might think that changes in load primarily lead to regulation of the center of gravity. However, it was shown that in the standing cat it is body geometry rather than center of gravity that is controlled (for review, see Ref. 340). It was argued that one control system regulates limb length and axis with respect to the vertical (geometry) and the other regulates horizontal forces and stability (341).

6. Proprioceptive reflexes in humans

One major problem in humans is that it is even more difficult to selectively activate Ib afferents than in animals. Recently, a method, based on direct electrical stimulation of muscle tendons, was used to demonstrate autogenic inhibition in humans (62). However, most work on Ib reflexes was done using a different method, based on the relative scarcity of Ia excitatory projections from gastrocnemius medialis to soleus both in monkeys and humans (299, 428). Stimulation of the gastrocnemius nerve below motor threshold does not elicit H reflexes in soleus but instead produces short-latency suppression of soleus H reflexes. This short-latency inhibition is supposed to rely primarily on Ib activation, although a contribution of Ia afferents cannot be excluded completely (428). Reflex effects through activation of cutaneous afferents are very unlikely since separate activation of cutaneous afferents does not elicit the same effects.

The method of Pierrot-Deseilligny (stimulation of motor nerves at 0.95 motor threshold) was extended to other nerves and other groups of motor neurons (429) and used extensively to study presumed Ib reflex effects.

As for the cat, it was found that the presumed Ib autogenic inhibition in humans was very widespread, even including muscles spanning different joints, and that there was a considerable amount of convergence with other afferents and with descending tracts. The inhibitory pathway between extensors of the ankle (medial gastrocnemius) and knee (quadriceps) was inhibited by cutaneous input specifically from the sole of the foot (427, 429). The implication is that during standing, or during the stance phase, a coactivation of extensors throughout the limb is possible because Ib inhibitory interactions are suppressed by afferent input signaling that the limb is loaded (foot sole). This release of inhibition then could enable activity in other facilitatory paths to extensors to become more prominent. These extensor facilitations could be caused by activation of oligosynaptic Ia afferents, but recent data (215, 511) suggest that it is also possible that they are due to hitherto undiscovered Ib facilitatory paths, as was postulated on the basis of cat experiments (191, see sect. VI*B4*).

In general, it is difficult to extrapolate data from reflex studies on static reduced animal preparations to conditions in which normal subjects are tested during motor tasks. The comparison with studies on behaving subjects or animals is therefore essential. For example, it is quite possible that in humans the Ib autogenic inhibition is suppressed during posture and locomotion as in cats. Some indirect evidence in this direction has been obtained (215, 510, 511).

In humans, postural reflexes such as evoked by rapid displacement of both feet (393) are heavily influenced by gravitational load, but it is as yet unknown which receptors are involved. When postural reactions were tested under water, it was found that there was a linear relationship between the contact forces (actual body mass related to load on the subjects) and the amplitude of compensatory responses in leg muscles (173). It is thought that extensor load receptors are able to signal the changes in the projection of the body's center of mass with respect to the supporting feet. Using either rotation or translation stimuli, the same

group (171, 243) found further evidence for this idea. Rotation (toe up) induces primarily a reflex response in the ankle flexors to compensate for the backward sway of the body. Backward translation evokes a gastrocnemius response to compensate for the forward sway. The scaling of the responses with the degree of translation was taken as evidence for a role of extensor load receptors in the regulation of compensatory responses aimed at the stabilization of posture. Although the facilitatory paths from load receptors in ankle extensors may be important for postural support and compensatory reactions, the inhibitory paths could play a role in voluntary contractions of the antagonists. Yanagawa et al. (541) found that Ib inhibitory effects from gastrocnemius medialis onto soleus were enhanced at the onset of weak voluntary contractions of the antagonist, tibialis anterior.

C. Concluding Remarks

In standing arthropods, the detection of loading is achieved both through extero- and proprioceptors. Some of the exteroceptors are sensitive to muscle contractions, and the distinction with proprioceptors is artificial. The reflexes elicited by activation of the exteroceptors involve a wide variety of muscles throughout the limb. These reflexes are aimed either at stiffening the whole limb or, conversely, at inducing limb flexion or extension. The proprioceptors belong to two categories (Table 1). To the first group belong receptors that are primarily involved in the detection of position and movement (CO, muscle receptors). It is argued that they can also play a role in detecting load. A second group of proprioceptors is more specialized for the latter function (CS). Reflexes from these proprioceptors can provide either resisting or assisting influences with respect to loading, and they interact with the first group of proprioceptors.

In cats and humans, the registration of the loading of a limb by gravity is also achieved through several types of afferents, including those connected to exteroceptors from the skin. The latter type of afferents can give rise either to flexion or extension of the whole limb. Among the proprioceptors, the spindle afferents are well-suited to detect position and movement, but they could contribute to load compensation indirectly. Golgi tendon organs could provide autogenic inhibition under some conditions, but whether such feedback is functionally important is in doubt. Indeed, as described in section VI, during walking, this type of feedback may be suppressed. Instead, extensor force feedback suppresses flexor activity. The pathway for the latter effect is only apparent in the behaving animal, since it involves motor centers that are essential for the execution of a given motor task. In the case of locomotion, the center for the generation of flexion during swing plays a crucial role.

VI. CONTROL MECHANISMS IN WALKING ANIMALS

During locomotion, it is well known that there is a continuous interaction between central networks and sensory afferents (5, 30, 77, 94, 259, 260, 261). The pathways used for information about load during standing may not necessarily be the same as those used during walking. Moreover, it has been demonstrated that sensory input is particularly crucial at the transitions between both phases of the step cycle (27, 97, 122, 126, 127, 138, 140, 149, 228). The potency to interact with central rhythm-generating centers can be evaluated by investigating how well a given input is able to reset or entrain the rhythm produced by a central pattern fenerator (CPG) (11, 77, 205, 264, 265, 352, 528).

In the arthropods, a central rhythmical activity can be induced with muscarinic agonists such as oxotremorine or pilocarpine (75, 90, 209, 352, 459, 495). It is obvious that the rhythmical activity obtained in these conditions is much slower than the real locomotor rhythm and that the relationship between the motoneuronal bursts are often unstable or, alternatively, much more stereotyped than in free walking. However, some locomotor patterns are characteristic, and in the crustaceans, forward or backward walking can be well defined. In the crayfish, such central activity is obtained from thoracic ganglia totally isolated from the peripheral nerves. If we compare these activities with those described in the cat, it can be said that it corresponds to fictive locomotion. These preparations are interesting in presenting the activity of the locomotor central network without the influence of the different sensory inputs. In these cases of fictive locomotion, the selective mechanical or electrical activation of a given load receptor could reveal its role in the organization and regulation of these locomotor sequences.

A. Invertebrates

During the stance phase in terrestrial arthropods, load and antigravity forces are important at the onset of the stance and become maximum around the middle of the stance; they decrease steadily until the leg lifts at the end of stance. However, force measurements show that in free walking there is a considerable step-to-step variation even on a flat surface (120).

In insects and crustaceans, position, velocity, and force seem to be controlled parameters. First we describe sensory influences acting during stance or swing. Later we mention influences leading to the transition between these phases. To characterize the sense organs involved, several types of experiments have been performed in which animals are held above a treadmill and a given leg is held fixed on a separate platform. Both in the stick

insect and in the rock lobster it was found that if the platform was held in an anterior position (corresponding to early stance), the muscles propelling the body produced higher output than when it was in a more posterior position (99, 134, 145). Furthermore, for each leg position, the motor output was higher when the adjacent posterior leg was in the swing phase than when it was in the stance phase (145). Under normal conditions, it takes some time for the force to reach its maximum value in early stance. When the platform is moved backward by the experimenter, the retracting muscles are shortened so that the force produced by these muscles decreases. If the platform is then suddenly stopped, forces increase for a short time but then subside in the stick insect (126). In contrast, in the rock lobster, the forces are maintained depending on the position of the platform. The increase found during the stop indicates that velocity is perhaps a controlled variable as well. For the stick insect, this was verified for the swing phase (152, 154) and also at the level of MN for active movements of a fixed animal (526). This assumption is also supported for the lobster by using various imposed speeds on a treadmill belt. If the velocity of the leg deviated from a given "desired" value, then the negative feedback changed the motor output correspondingly. Cruse et al. (134) found that, at slow imposed speed, the force exerted on the treadmill was higher than at a fast speed. The main stance phase muscles (retractor and depressor) discharge at much higher frequency and with more motor units at a slow belt speed than at higher speed. The question arises whether this increased motor output at slow speed can be considered as an assistance reflex (positive feedback). Usually the latter terms are used to indicate that an ongoing movement is reinforced. However, in this case, the reinforcement is velocity dependent. If velocity is the controlled variable, then the increased motor output is due to a (negative feedback) servo-mechanism continuously relating the central command to the actual movement. A velocity error signal is then driving the muscle forces directed posteriorly.

Pearson (411), studying walking cockroaches dragging a weight, found that they increase their motor output to power stroke muscles. It was then supposed that a positive-feedback signal was elicited by an increasing load. In the stick insect, Schmitz (466) could show that experimental stimulation of the anterior trochanteral CS, which is naturally excited by bending the femur to the rear, led to an increase of the motor output of the retractor muscle, whereas stimulation of the posterior trochanteral CS decreased the excitation of this muscle in standing as well as in walking insects. This means that this reaction opposes too strong a bending of the femur in either direction. When during walking the leg is pulled by an external disturbance in the anterior direction, for example, the excitation of the protractor muscle is decreased. This corresponds to the negative force feedback

scheme depicted in Figure 1*C*. By adding a weight to be dragged as in Pearson's experiment, a force controller with a fixed set point would decrease the retractor output. However, increased motor output was found. This could be obtained by an additional velocity controller that changes the set point of the force controller. If the sensed walking speed is too slow, for example, as a result of the high friction of the weight, the desired force value would be increased, and thus the motor output would increase. Velocity feedback control has been shown several times (e.g., Ref. 526). Therefore, in the insects investigated, velocity feedback control is probably applied during both swing and stance. In addition, force control might be used during stance. Various types of experimentally induced load changes showed that the duration of the swing, which can depend on step period, is shorter for a given step period when the load increases (stick insect, Refs. 227, 252; crayfish, Ref. 141). This shows that load measured during stance can influence the movement during swing.

1. Transition stance to swing

Recently, it has been confirmed that strain acting on the exoskeleton of the locust leg, which is monitored by CS, can aid the transition from stance to swing. In parallel studies, one on forces operating during walking and the other on intracellular recording of the reflex pathway, Newland and Emptage (395) reached the conclusions that the tibial CS, mainly activated at the end of the stance phase, directly excites the flexor tibiae MN and inhibits the extensor tibia MN indirectly through an IN (see also Ref. 155).

For the transition from stance to swing it could be shown that both position and force are critical. Bässler (27) and Dean and Schmitz (155) showed that manipulation of the hair plates such that they incorrectly monitor the leg being moved anteriorly, prevented or delayed the stance-swing transition. The second part of the "active reaction" also indicates that position signals, in this case monitored by the femoral CO, can elicit the stance-swing transition (33). An influence of position of the anterior leg in the walking animal has already been shown by Cruse (122) and Dean and Wendler (157). General stimulation of all trochanteral CS of one leg or loading the whole animal by a weight also prevented the start of swing (27). Dean (153), however, showed that the situation is not simply that higher load shifts the PEP in posterior direction. Rather, this is only true for external forces smaller or equal to body weight. For larger forces, the opposite effect is found, indicating that not load per se but rather load in combination with movement velocity is the important parameter.

This agrees with earlier findings where stick insects were observed walking up a vertical wall (120). Cruse

(127) showed that a sudden unloading of a leg during stance could elicit swing only beyond a critical posterior leg position. Therefore, both load and position are important parameters for the stance-swing transition. However, during stance, position appears not to be a controlled variable.

Activities of tibial CS in freely walking cockroaches are correlated with the stance phase activity (553–555). Proximal sensilla are activated just before the burst from the slow extensor MN, whereas the distal sensilla burst near the end of stance. In this case, the afferents might be adequate to facilitate the onset and the end of the stance phase. In rapid walking (step frequency more than 5 Hz), however, activities of the CS shift in phase. The proximal sensilla burst occurs after the onset of the extensor activation and the distal sensilla after its termination. In that case, these receptors cannot participate in the initiation or termination of the stance phase. Further reviews on swing initiation in cockroaches have been provided by Pearson (411–413).

In the crustaceans, it has been demonstrated that CSD within the leg are mainly involved in reflexes increasing levator or depressor activity and in maintaining the leg activation (see Fig. 2). On the contrary, FCO seem to be involved (as the insect CS) in compensatory reactions that can facilitate the switch from stance to swing. The reflex elicited by FCO stimulation is similar at rest and during walking. It facilitates the levator and the promotor MN (normally active during swing), and it inhibits the depressor and the remotor (stance phase muscles) (see Fig. 3). Such electrical stimulation, imposed during free walking in a crab or during treadmill driven walking in the rock lobster (353, 389, 390), induces different responses depending on the phase of the step cycle. During the swing phase, the stimulation increases both the intensity and the duration of the levator bursts, while during stance it terminates the depressor burst and reinitiates a new swing phase. At the end of the stance phase, the effects are smallest. The interpretation of this result is that the artificial induction of the swing phase is least disturbing at this moment, since it coincides with the time this phase would have started anyway. The FCO activation not only increases the levator activity in the stimulated leg, but it also increases depressor activity in adjacent legs (Fig. 3). This pattern is exactly as expected if FCO reflexes assist the ongoing locomotor activity, since the swing phase of one leg is coupled to the stance phase of neighboring legs. During the stance of normal walking, the FCO reflexes presumably have little effect, although these receptors may be quite active during this period. However, other receptors are activated in parallel, and the resultant afferent input can interact with the signals from the FCO and reinforce the stance-generating mechanism.

2. Transition swing to stance

The end of the swing movement is determined by ground contact. This is most probably registered by the different load sensors mentioned. In insects, it is likely that different sensory hairs on the tarsus further contribute to this signal but are not essential because destruction of the tarsus does not prevent the swing-stance transition. The end of the swing can, however, also be determined by position sensors. In the stick insect, this position is given by the position of the next anterior leg (56, 122, 137, 155, 157). Influence of position was also shown by Bässlers classical experiment (25) of the crossed receptor apodeme. Here the tendon of the femoral CO was manipulated such that the CO recorded flexion when the joint extended, and vice versa. This change of sign did not influence leg movement during stance possibly because of mechanical coupling with the other intact legs but prevented the leg from finishing the swing movement. Force seems not to be controlled at touchdown (131) in contrast to findings from vertebrates described below.

If the leg strikes an obstruction during swing preventing it from moving forward, or touches the ground with a part of the leg other than the tip, different correction reflexes are described (34, 132, 152, 156, 417). A load higher than 0.5 g during swing may suffice (152). One can assume that these reactions require a detailed analysis of the signals from the different load and position sensors as well as probably the tactile hairs dispersed over the leg.

B. Vertebrates

For some rhythmic movements such as mastication, there is good evidence for the contribution of load-compensating reflexes (406). In contrast, such a contribution has been particularly difficult to prove for locomotion, presumably because it is very difficult to apply well-controlled load perturbations during gait. In principle, load-related feedback can reinforce stance activity either directly through spinal reflex pathways or indirectly through an excitatory effect on the part of the generator network involved in the production of extensor activity. Both pathways can produce effects on the extensor output amplitude, whereas effects on the duration and on the timing of the stance/swing transition can be attributed to actions on the generator.

1. Load and amplitude of extensor activity: proprioceptive reflexes not necessarily involving the CPG

How much of the activity in extensors during the stance phase of gait depends on load feedback? During walking, the contribution of passive and active muscle properties versus reflexes in cat and human remains a
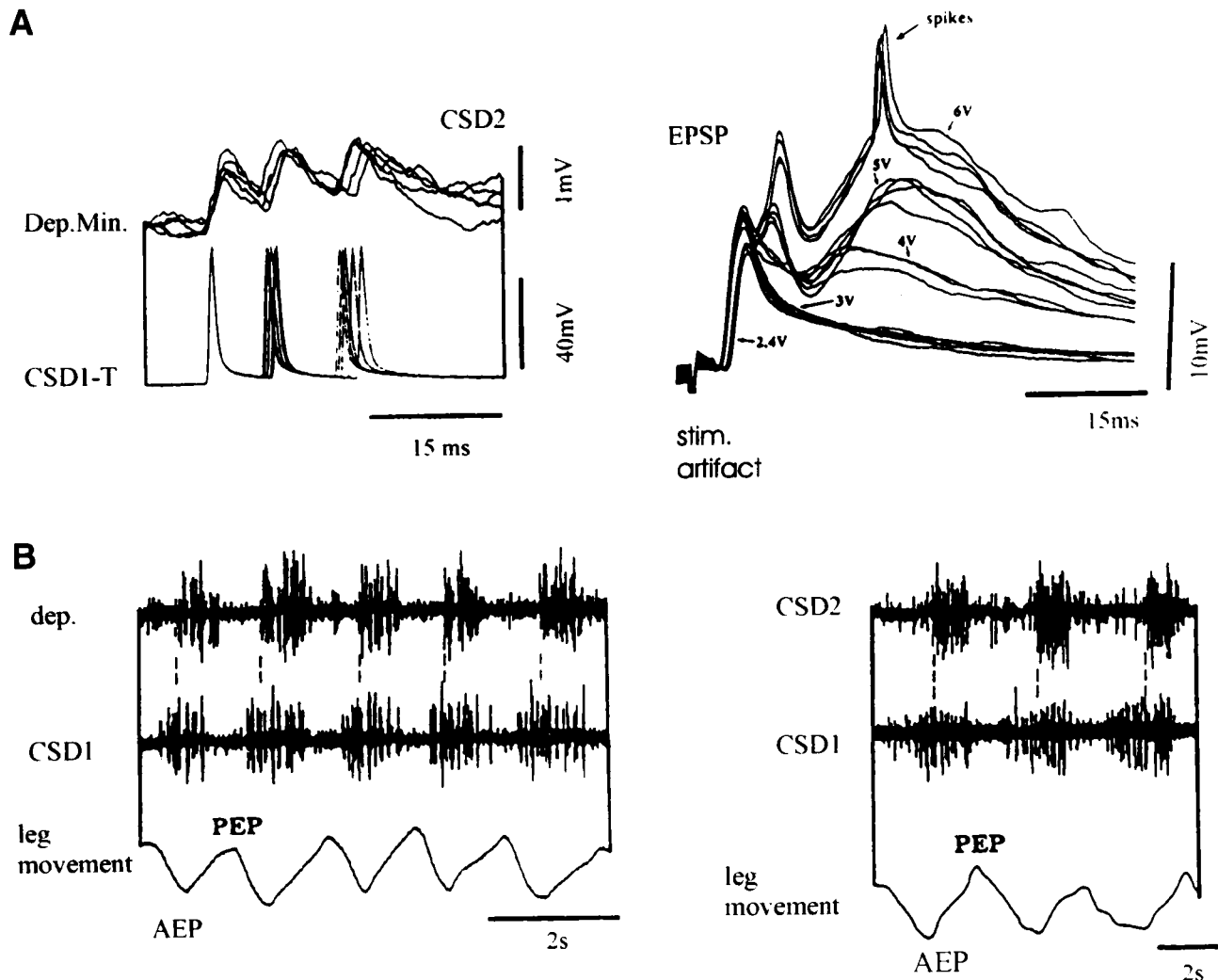
FIG. 2. Physiology of cuticular stress detector afferents in crayfish. Both receptor cuticular stress detectors CSD1 and CSD2 are disposed in a soft patch of cuticle in proximal part of walking legs. They have been studied both in an in vitro preparation (*A*) and chronically during walking (*B*). *A*: in an in vitro preparation, it has been demonstrated that some of afferents are monosynaptically connected to proximal leg muscle motoneurons (dep, depressor; lev, levator). For example, *left panel* shows a monosynaptic connection between a CSD1 terminal afferent and a depressor motoneuron (several sweeps have been superimposed). In *right panel*, electrical stimulation at different intensities of CSD2 afferent nerve shows complexity of connections with an anterior levator motoneuron. In this case, it has been possible to identify 2 early and 5 late excitatory postsynaptic potentials (EPSP) in same motoneuron. [From Leibrock et al. (352).] *B*: during locomotion on a treadmill, CSD1 and CSD2 have been recorded simultaneously (*right*) and with depressor muscles (*left*). Movement of fourth leg has been recorded at its tip (AEP, anterior extreme position of leg; PEP, posterior extreme position of leg). If CSD2 discharges exclusively during stance phase (with depressor muscle), CSD1 becomes active at end of swing phase and during stance phase (see dotted line). [Adapted from Marchand et al. (370).]

matter of debate. Just after touchdown a sharp rise in EMG activity is seen in ankle extensors in both species. In the intact cat, the EMG rise occurs some 10–25 ms after contact. Initially, this was attributed mainly to stretch reflexes (and not to cutaneous reflexes, since anesthesia of the foot pads did not affect the peak; Ref. 357). However, recently, it was found that the peak persisted when cats stepped on an actuator-controlled trap door, thereby withdrawing ground support just before foot contact (244). This suggests that the activity is mainly central in origin under these conditions. This conclusion is in line

with the finding that in monkeys trained to land either on a solid surface or on a tissue paper "false" floor, no difference was found in the peak extensor EMG just after touchdown (348). In cats during landing after a free fall, there was an increase in ankle extensor EMG just before landing, followed by a sequence of suppression and activation at touchdown (439). This sequence was unaffected by local anesthesia of the plantar cushion, but the authors argued that some of the observed effects may have been related to proprioceptive reflexes. For the comparison with insects, it is noteworthy that, as was mentioned
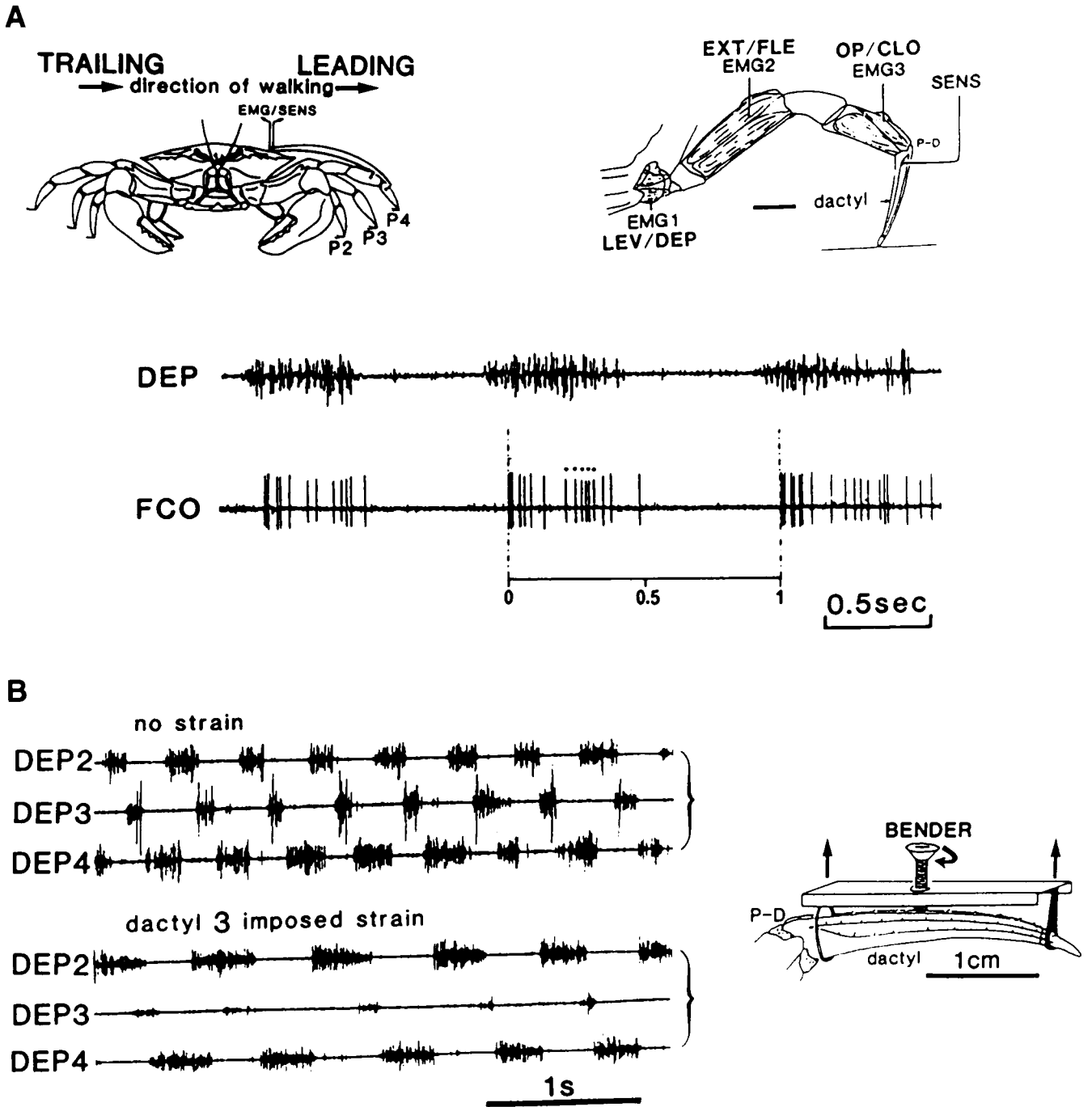
FIG. 3. Activity of funnel canal organ (FCO) mechanoreceptors in crab *Carcinus maenas* during lateral walking (*A*). Legs on side of direction of walking are termed leading legs, whereas those of opposite side are termed trailing legs (*top left*). In chronic animals, electrodes are positioned for recording simultaneously sensory and motor activities (*top right*). EXT, extensor; FLE, flexor; OP, opener; CLO, closer. In *bottom record*, sensory activity of 2 units (one large and one smaller with dots along spikes) are presented in relation to discharge of depressor (DEP) muscle. *B*: with a special device producing a continuous chronic bending of dactyl and inducing a continuous FCO mechanoreceptor activity it is possible to characterize the role of these receptor during walking. In comparison with normal walking, it appeared that bending of *leg 3* dactyl significantly diminishes activity of depressor of that leg (*leg 3*), enhancing discharge of 2 ipsilateral adjacent legs (*legs 2–4*). [Adapted from Libersat et al. (354).]

above, no centrally produced effect was found in the stick insect.

What happens with load feedback in the rest of the stance phase? There is a wealth of data available on the activity of single muscle afferents and γ-MN during cat gait (359, 361, 441, 482), but the question remains how

much of this activity is used in load-compensating re-flexes? Applications of brief stretches are difficult to perform in intact cats but can be achieved in reduced cat preparations. In the mesencephalic cat, the role of reflexes versus muscle properties of extensors has been evaluated by several authors (2, 37). In the cat, the intrinsic muscle stiffness of ankle extensors gradually decreases during stance, as does the gain of the stretch reflex pathways to these muscles (2). Hence, under these conditions, the goal is not to maintain total stiffness (as the sum of reflex and intrinsic sources) constant. According to the most recent study (37), reflexes could contribute 23% of the movement-related force of the triceps surae during locomotion. In all these cases, however, one has to take into account that the reflex gain in decerebrate preparations can differ considerably from the one found in normal cats (293). It is also still unclear as to which pathway is involved in these effects. Sometimes the amplitude increases are accompanied by prolongations of the stance phase duration. In such cases it is possible that a pathway involving the CPG is used. However, when the effects are purely related to amplitude, then oligosynaptic pathways outside the CPG are the most likely source (377).

In humans, Dietz et al. (174) found that there was a sudden increase in ankle extensor EMG just after footfall in human running, thereby providing evidence for a role of afferent feedback in the generation of this activity. This feedback was thought to be less important for these muscles during walking, but this remains a controversial point. Some used a pneumatic device to deliver brief ankle rotations during walking (542, 544) and estimated that the stretch reflex could contribute up to 30–60% of the activation of soleus during walking, especially during the early part of stance (162). This conclusion was confirmed by the study of Sinkjaer et al. (497), using a semiportable stretch device to study soleus stretches in various phases of the step cycle.

Other muscles were tested as well. Stretch reflexes elicited in quadriceps were largest at the moment of impact and then gradually decreased during stance (169). Stretch reflexes in biceps femoris, a knee flexor, are enhanced in the first extension phase of swing (119). This would be consistent with the idea that, during normal gait, the activity in this muscle during this period of the step cycle is partly generated through stretch reflexes, as was proposed earlier by others (421, 441, 502).

Nevertheless, during gait, the question of feedback is still controversial because it is quite difficult to produce the same mechanical stimulation during different phases of the step cycle reliably. Therefore, many authors have used electrical stimulation and H reflexes to study oligosynaptic pathways during walking (82, 117, 170, 238, 386; for review, see Ref. 52). By simultaneously monitoring the M response (elicited by stimulation of MN), it is possible

to control the stability of the stimulation during the movements. Several reviews of these studies are available (162, 198, 375, 507). Basically, it was found that the amplitude of H reflexes in soleus is generally lower during walking than while standing (82, 386; for review, see Refs. 52, 505). This reduction in H-reflex amplitude is especially prominent when walking is made more difficult, for example, in beam walking (358). During the step cycle, the soleus responses are suppressed during swing (546), small during early stance, and largest in late stance. In contrast, in quadriceps, the H responses are largest at the onset of the stance phase (170). This is functionally meaningful, since facilitation of quadriceps at the onset of stance may help in weight support.

For quadriceps, the behavior of H reflexes (170) largely agrees with that of reflexes elicited with tendon taps (169). For soleus, however, there is a clear difference because H reflexes are actively suppressed during swing (546), while stretch reflexes are not (497). Sinkjaer et al. (497) attribute this difference to more prominent presynaptic inhibition induced by the synchronous electrical volley. As pointed out by Sinkjaer et al. (497), the H-reflex responses are usually about 10 times larger than the stretch-induced responses. Hence, it may be that presynaptic influences differ in relation to the massive H-reflex volleys, as compared with the more modest and less synchronous Ia discharges related to stretch.

2. Load and amplitude of extensor activity: exteroceptive reflexes not necessarily involving the CPG

Because a lot of afferent activity is generated from the skin of the foot after touchdown (498), the question arises as to whether this activity could be used to support ongoing muscle activations during the stance phase of gait. The evidence pointing in this direction is derived from the observation that electrical stimulation of nerves that supply the skin of the foot can yield potent reflex activations in various leg muscles, especially during gait both in cats (190) and in humans (189, 543). Both in the premammillary (190) and in the intact (193) cat, stimulation of the sural nerve enhances the burst of activity in ankle extensors.

In humans, the reflex responses have a latency of ~80 ms, which is quite long but still well within the range of durations of the human stance phase during running or walking. Stimulation of the sural nerve, which supplies the lateral side of the foot and ankle, strongly activates the biceps femoris during the stance phase, while having little effect in semitendinosus (196, 515; for equivalent results in cat, see Ref. 432). Both muscles are hip extensors and knee flexors, but biceps femoris causes external rotation (exorotation) of the lower leg and foot, while semitendinosus does not. Similarly, during the stance

phase, sural nerve stimulation activates the medial gastrocnemius more than the lateral gastrocnemius, presumably producing ankle extension in combination with foot exorotation (201). These effects are quite specific, since biceps femoris reflexes are barely present after stimulation of nerves supplying other parts of the foot (533), and they are strikingly similar to results seen in the cat (1, 349, 400).

This specificity is the basis of a rotation assistance hypothesis (197) as adapted from Hugon (304). The basic idea is that, during the stance phase, the skin of the lateral side of the foot is activated, which reflexly induces foot exorotation. It is important to point out that in humans, a small part of the propulsion during the stance phase is provided by foot exorotation. Hence, the proposed feedback system can be viewed as a stance-reinforcing circuit (the activation of biceps femoris supporting both hip extension and foot exorotation in this part of the step cycle). In conclusion, in motor control in general, and in locomotion in particular, the relative importance of passive versus reflex-mediated stiffness depends on the type of muscle investigated (extensor vs. flexor), on the contraction level (499, 518), on the task (walking vs. running), on the type of preparation studied (intact vs. decerebrate), and on the type of afferents involved (proprioceptive vs. exteroceptive). There is now a growing body of evidence supporting the contention that part of the muscle activity during stance may be reflexly generated through pathways some of which do not involve the CPG. To demonstrate actions through the CPG, one has to find effects not only on burst amplitude but also on the duration of the phases.

3. Sensory influences on the CPG

Because spinal cats can adjust their walking pattern to the speed of a treadmill belt, it is evident that peripheral feedback signals can influence the timing of the phases as produced by the spinal CPG (221; for review, see Refs. 260, 450, 453, 534). At the end of the stance or swing phase, a sensory environment is created on which the locomotor system can rely to switch automatically to the subsequent phase. Is there evidence in mammals that some sensory triggers are specifically used for this purpose? In analogy with the invertebrate work, one could expect two elements to be of crucial importance, namely, limb position and loading. At end stance, the limb is extended and unloaded, whereas at end swing the limb is flexed and loading starts. To demonstrate that these sensory cues are indeed involved in phase switching and actions on the CPG, one should find that *1*) the particular phase switch is blocked when the appropriate sensory state is not reached, *2*) the imitation of these sensory states can induce phase switching, and *3*) rhythm entrainment and/or resetting can be achieved.

It is not always easy to distinguish between load and position-related feedback. Both in the premammillary (416) and spinal cat (261, 262), it was shown that stopping the movement of the leg in stance prevented the onset of swing [much as was observed in the stick insect (527) and the lobster (99)]. In the cat, the stepping rate on the contralateral side was increased during the period of block of the ipsilateral rhythm. If the ipsilateral leg was then brought backward, a flexion of the limb was initiated at hip angle that approximately corresponded to the angle at which the cat usually switched to flexion (equivalent results were described for the stick insect, Ref. 127). It was suggested that these results could best be explained by assuming that the proximal joint (the hip) of the ipsilateral leg failed to reach a threshold extended hip position (263). However, the same data can be explained by the prevention of hip extensor unloading (337), since holding the limb in stance is equivalent to resisting hip extension.

4. Load and proprioceptors

When gravitational loading is increased in cats, the extensor activity not only gets larger but also lasts longer (403). Conversely, unloading of extensors leads to induction of swing through unloading. In both intact (244) and spinal cats (288), an unexpected loss of ground contact during the stance phase induces a premature onset of the next swing phase and prolongs the ongoing contralateral stance phase (see scheme in Fig. 4).

Both reactions are compatible with an explanation that extensor unloading facilitates the onset of the swing phase, but the question remains which proprioceptors and which muscles are involved. Proprioceptors from two types of extensors have received considerable attention, namely, those from ankle and hip extensors.

To the group of ankle extensors afferents belong Ia and Ib afferents from muscles such as triceps surae and plantaris. To demonstrate the effects of this type of afferent in blocking stance-swing (ST-SW) switching, high decerebrate cats have been used ("premammillary or thalamic cats"; Ref. 190). These animals can walk on a treadmill while one hindlimb, which is partly denervated, is being held in a fixed position. The fixation allowed measurement or manipulation of both the force and the length of ankle extensors, while these muscles were rhythmically activated in the locomotory process. Because limb position was constant, these manipulations could be used to activate muscle or cutaneous load receptors selectively, independent of changes in hip position receptors that might play a role in regulating phase transitions. Applying a gradually increasing stretch to the Achilles tendon led to an increase both in amplitude and duration of the rhythmic bursts of the ankle extensors, while the ankle flexor bursts were reduced and eventually
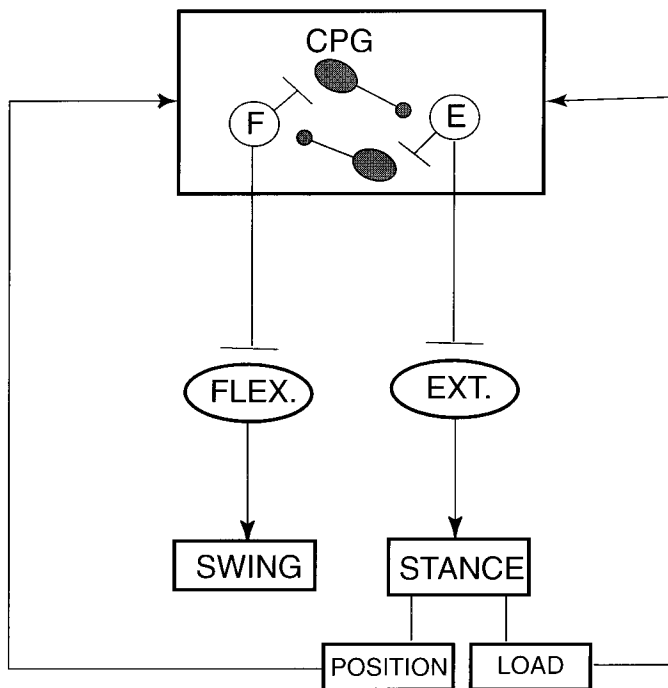
FIG. 4. Schematic representation of current hypothesis about reflex pathways of load-detecting afferents in cat. Central pattern generator (CPG) contains flexor (F) and extensor (E) half-centers, controlling flexors (Flex.) and extensors (Ext.), respectively. *Group II* cutaneous afferents are from foot sole, and *group I* muscle afferents are from extensors in leg. For further explanation, see text.

disappeared in an all-or-none fashion (191, 416). The flexor burst failures indicated that afferent input from the stretched extensors reached premotor centers involved in the generation of the bursts.

In principle, both GTO and spindles of the stretched muscles could be involved. To discriminate between these two possibilities, the same sort of experiments were made (fixed hindlimb) but now with ventral root stimulation to obtain a selective activation of Ib afferents. The latter method was used to induce contractions in the ankle extensors. When the ventral root stimulation strength was kept below the level for the activation of γ-MN, a contraction was induced that produced an increase in firing of the Ib afferents, while simultaneously reducing the firing rate of Ia afferents (Fig. 5, *top*). Continuous stimulation of the appropriate ventral roots led to activation of ankle extensors and suppression of rhythmic ankle flexor bursts (Fig. 5; see also Ref. 191).

It was concluded that, during walking, the Ib activity of extensors can reinforce the ongoing extensor activity and prevent the initiation of flexor activity (191). This would seem to be functionally meaningful because it provides a mechanism whereby the initiation of the swing phase can only occur when the limb is sufficiently unloaded and Ib extensor activity falls below a given threshold level. Such a mechanism implies that extensor Ib input can have direct access to the central sites involved in the generation of flexor and extensor activity during locomotion (Fig. 4).
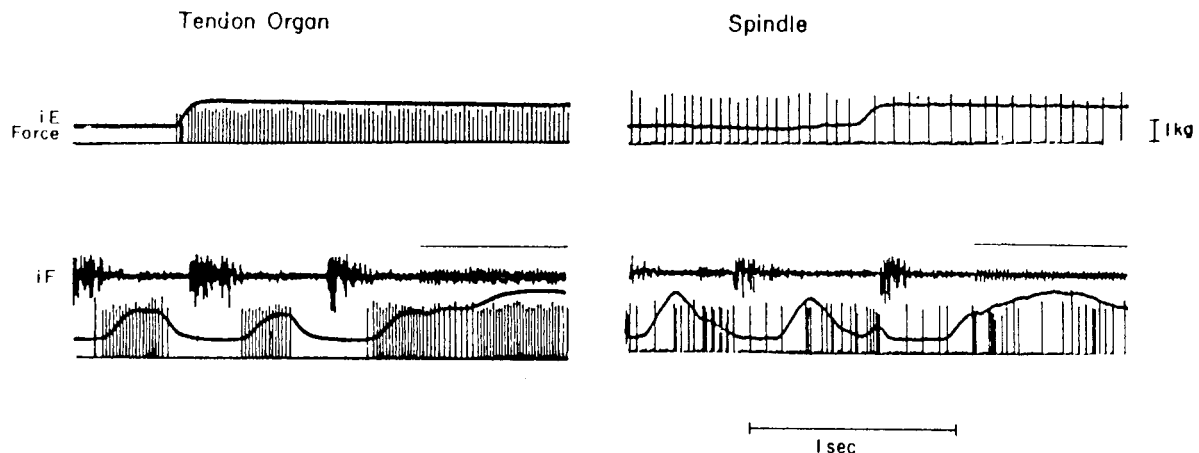

FIG. 5. Responses of single triceps surae (iE, ipsilateral extensor) afferents to stimulation of S1 ventral root, in a premammillary cat at rest (*top traces*) and during walking (*bottom traces*). *Top left*: Ib afferent firing from a Golgi tendon organ with superimposed trace of force produced by parent muscle (iE force). *Top right*: Ia afferent firing from a spindle from same muscle. At rest, electrical shocks to S1 ventral root (0.05-ms pulses at 60 Hz and at 1.5 times motor threshold and at 90 Hz) induced a tonic contraction, leading to increased firing of Ib afferent and decreased firing in Ia afferent (ventral root stimulation was below threshold for γ-axons). During walking (*bottom*), electromyogram activity in ipsilateral flexors (iF, in casu tibialis anterior) alternated with contractions in fixed triceps surae (force records on *bottom*). Application of same S1 ventral root stimuli (horizontal bar) similarly induced a contraction in ankle extensors (now superimposed on rhythmic contractions) and similarly affected firing of afferents (increase for Ib, decrease for Ia). However, in addition, stimulation suppressed generation of rhythmic flexor bursts (iF) in fixed hindlimb of a cat, which walked freely with remaining 3 limbs on a treadmill. (From J. Duysens and K. G. Pearson, unpublished observations.)

An alternative method for the selective activation of muscle afferents is to use graded electrical nerve stimulation. In the intact cat (193), little effect was found after lateral gastrocnemius soleus (LGS) stimulation at group I strength but, as was claimed later (535), this may have been due to the use of inappropriate stimulus parameters (low frequency) and timing of experiments (too early after surgery). However, it is also possible that such effects are simply not present in intact cats in which there is an abundance of sensory cues along with input from descending systems. Whelan and Pearson (537) compared the effects of stimulation of the LGS nerves in cats first in the intact state and later in the decerebrate state. They found that stance-prolonging effects could be evoked in both types of preparation, but the effects were clearly weaker in the intact animal. During swing, the same type of stimulation can reset the cycle to extension. For both the stance and the swing effects, stimulation of LGS was much more effective than of medial gastrocnemius. However, after cutting the LGS nerve, the stimulation of the medial gastrocnemius became much more potent, thereby illustrating the plasticity potential of these pathways (536). Whelan et al. (535) found that it was necessary to stimulate at a strength recruiting both Ia and Ib afferents to obtain extensor prolonging effects. For a selective study of Ib effects, the use of either medial gastrocnemius or LGS stimulation has limited value, since one cannot readily distinguish between Ia and Ib fiber effects. In decerebrate rats, a prolongation of extensor bursts can also occur after stimulation of gastrocnemius nerves, at least when adult rats are used (229). In neonatal rats with fictive locomotion, one observes similar effects only when high-intensity stimulation is used (310).

Another argument that can be used to show that Ib input from ankle extensors has access to the CPG is rhythm resetting or entrainment. For this purpose, brief periods of low-intensity stimulation of ventral roots (191) or of extensor nerves (111) have been used. These inputs were shown to cause rhythm resetting. Activity from low-threshold afferents from flexors never caused resetting (111). Entrainment of the rhythm was achieved in several ways. Both Conway et al. (111) and Pearson et al. (418) used periodic stretches of extensor muscles. They could only entrain the rhythm when the stretches were sufficiently large to recruit not only Ia but also Ib afferents. Ventral root stimulation, inducing contractions which were certainly strong enough (>10 N) to activate extensor Ib afferents, caused reliable entrainment (418). A similar result was achieved by Pearson and Collins (415) using direct application of shocks to the plantaris nerves. The Ia afferents in plantaris nerves make either no or weak connections with MN of gastrocnemius medialis, and therefore the medial gastrocnemius reflex responses following weak stimulation of the plantaris nerve can be reliably ascribed to Ib activation. Plantaris stimulation

proved particularly effective in entrainment of the locomotory rhythm. Neither the entrainment nor the burst-enhancing effect was present when plantaris was vibrated so as to optimally activate Ia afferents.

Although involvement of Ib afferents in the flexor delaying effects is well documented by many experiments, it should be mentioned that a limited set of data suggests that Ia afferents may participate as well. Guertin et al. (271) made some observations during mesencephalic locomotor region (MLR)-induced fictive locomotion, suggesting that Ia afferents have much the same effect as Ib afferents in prolonging the extensor activity in the stance phase. This would indicate that Ia-Ib convergence is not only present in pathways subserving autogenic inhibition (365; see sect. v*B2*) but also in those leading to global extensor activation. The Guertin et al. (271) study also showed that the latter effects are primarily induced by stimulation of afferents in ankle extensors and much less from other extensors (271).

Alternatively, extensor Ia afferent input may be important for yet another pathway that is selectively opened during locomotion. In decerebrate cats, McCrea et al. (377) showed that activation of these afferents evoke disynaptic EPSP in extensors in periods of fictive locomotion only. The short latency of these responses make it unlikely that they act on the CPG network (9).

5. *Load and exteroceptors: load-sensitive receptors in the skin of the foot*

As mentioned above, during the stance phase of the walking cat, gravitational loading of a single limb can be detected by cutaneous afferents from the foot. The potential for affecting the transition from stance to swing by cutaneous input from the foot strongly depends on the presence of other sensory input, which under normal circumstances helps stabilize the rhythm. In intact cats or humans, the application of brief nonpainful skin stimuli can increase the length of the swing phase slightly and has little effect on total cycle duration (179, 193, 199).

In the premammillary cat, the changes are more pronounced, especially if rhythmic output is studied in a fixed limb that is partly deafferented. Under such conditions, stimulation of nerves innervating the skin of the foot during stance can delay the onset of flexion (186, 190). The functional interpretation is similar to the one advanced for Ib input. Skin afferent input, related to limb loading during stance, is able to block the onset of the swing phase. Inversely, unloading signaled by the withdrawal of this type of input is a trigger for the onset of flexion. Hence, one would predict that such cutaneous input can inhibit the premotor center for the generation of flexion during swing (the "flexor half-center"). Using L-dopa-treated spinal cats, Jankowska et al. (318) showed that late flexor discharges, presumably originating from

the flexor half-center, always occurred after termination of a period of stimulation (for example, of cutaneous afferents). It has been argued therefore that the late flexor reflex discharges may be due to disinhibition ("rebound hypothesis," Ref. 187). More recent work on sural nerve stimulation during L-dopa-induced fictive locomotion further supports this idea (479). It was found that such stimulation could prolong extension when given during the extension phase, and terminate flexor activity and induce extensor activity when given during the late flexion phase. It is known that cutaneous afferents feed into "alternative pathways," which can activate extensors and inhibit flexors (for review, see Ref. 473). Hence functionally, these pathways resemble those described above for Ib afferents. Load-detecting cutaneous afferents prevent the generation of the swing phase in much the same way as load-detecting afferents from extensors. In view of this common role, it may not be surprising that extensive convergence occurs of Ib and cutaneous afferents onto common IN (365). The inhibitory effects of foot afferents on the flexor generating circuits are spinal, since they persist not only in MLR-evoked fictive locomotion (271) but also in decerebrate spinal cats injected with L-dopa (112). The latter authors (112) found that low-threshold stimulation of the deep or plantar nerves during late flexor reflexes abruptly terminated flexor activity. Medial plantar nerve stimulation did not produce this effect.

Because cutaneous afferent activity from the foot can cause shifts in phase transitions, one would expect such input to be effective in resetting and/or entrainment of the rhythm as well. First such input was shown to be potent enough to reset the contralateral CPG (186). Electrical stimulation of the pad of a freely moving hindlimb of a premammillary cat during the ipsilateral stance prolonged the contralateral flexor bursts. The same stimuli given during contralateral stance induced a prolongation of the contralateral extensor bursts. Hence, a reversal occurred from crossed flexor to crossed extensor facilitation. This type of reversal was also observed by Gauthier (239) using a decerebrate preparation in which the animal was suspended. In both cases the reflex effects were evaluated in a limb that participated little or not at all in load-bearing and therefore there was no stabilization of the rhythm by other load-dependent afferent activity. It should be mentioned that the term *reversal* is used here in a broad sense, indicating that the same stimulus can give opposite responses. In the strict sense, one would expect that the reversal of reflexes implies that opposite responses of exactly the same latencies can be found under different conditions. As mentioned by Duysens et al. (200), these conditions are rarely met in mammalian systems.

The resetting of the rhythm also depended on the phase of the step cycle. It was most pronounced for stimuli given near the middle of swing or stance, while stimuli given at the transition points between ipsilateral flexion and extension phases were least effective in resetting the contralateral rhythm (187). More recently, ipsilateral rhythm resetting has been demonstrated as well (479). In general, the types of input that can delay flexion can facilitate the onset of extension as well. This input is much more specific than the one involved in the facilitation of flexion. For hip movements during fictive locomotion, it is only hip extensions and not hip flexions that have the potential to induce the extension period prematurely (8). For input from the foot in the premammillary cat, it is only the low-threshold skin and muscle afferents from this region (tibial nerve) that have the same potential (187, 190). Hence, in contrast to flexor enhancing input, the afferents that have been shown to enhance the swing to stance switch are highly specific and related to events that normally take place during this period (namely, hip extension and loading of the foot).

6. Hip sensory signals

The idea that there is a special hip signal that is important for the onset of flexion at the end of the stance phase is based on the notion that the swing phase is initiated when the hip passes through a particular threshold angle. The latter idea was originally based on the observations of Shik and Orlovsky (490), who found that raising the anterior or posterior part of a normal dog walking on a treadmill induces a prolongation of both the stance phase and the step cycle of the raised limbs. They reasoned that the prolongation of the stance phase in the raised limbs may have been correlated with an unchanged angular excursion of the hip and shoulder, and hence, they concluded that "the initiation of the transfer phase is determined by the onset of threshold extension of the limb, i.e., at definite values of the joint angles." Grillner and co-workers (7, 8, 456; for review, see Refs. 261 and 450) provided further evidence indicating that afferent signals from the hip are crucial for the reflex control of walking. They showed that direct input from hip afferents to the CPG is able to reset and/or entrain the locomotory rhythm. Using small-amplitude sinusoidal hip movement of a partially denervated hindlimb, Andersson and Grillner (8) could entrain locomotor rhythmicity in low spinal cats with L-dopa-induced fictive locomotion. Which receptors are involved? Two possible candidates are the receptors from the hip joint and those from hip muscles (420). Hiebert et al. (290) used selective stretches of various hindlimb muscles and were able to show that the flexor-inducing effects are mainly related to stretch of hip flexors (ankle flexors such as tibialis anterior had similar but weaker effects). As yet, it is unclear whether hip joint afferents contribute to the hip signal that has an important impact on the regulation of the CPG. In fact, little is known about the role of joint afferents in locomotion in

general. For the knee, Freeman and Wyke (232) showed that cats had great difficulty in walking along a narrow bar when their posterior and medial articular nerves were cut. However, Lindström and Norrsell (356), doing very similar experiments, were unable to detect any deficits at all. Joint afferents from the hip may be of greater importance, since it is conceivable that they play a dominant role in reflexly inducing the swing phase at the end of stance. However, hip denervation has very little effect. Kriellaars et al. (337) anesthetized the hip joints and found no effect on the ability of hip movements to entrain the fictive locomotor rhythm in decerebrate cats. In fact, their progressive denervation of the hip joint experiments showed how important just a few hip muscle afferents were in entraining the rhythm. Furthermore, the observation that bilateral hip denervation either in cats (192) or humans (256) does not induce major deficits in the pattern of locomotion or in position sense (256) indicates that joint afferents from the hip are not indispensable for normal locomotion.

7. *Critical periods for phase switching*

The effectiveness of a given input critically depends on the time of application of the stimulation in the motor process. A striking example is the cat respiratory system. The inspiratory phase consists of two parts. During the initial part it is not possible to terminate the inspiratory process by adding afferent input promoting the transition to expiration (Hering-Breuer reflex). In contrast, such transition can be induced by the same input given in the second part of the inspiratory phase. A similar subdivision can be made for the flexion phase of locomotion in cats. Touchdown is normally accompanied by an afferent barrage from the footsole (as demonstrated with cuff electrodes around the tibial nerve in cats; see Ref. 193). When this input is simulated by electrically stimulating the posterior tibial nerve in premammillary cats with one hindlimb fixed, then a flexor enhancing and prolonging effect is obtained for shocks given in early flexion period (187). However, the same input induces a premature extension period when given later in the flexion phase. The transition between these two parts of the flexion phase is very sharp.

Is there a similar division for the stance phase of locomotion and the expiratory phase of respiration? For the respiratory system of both cat and rat there is good evidence for the existence of two stages of expiration (445). Changes in respiratory rate are achieved by variations in the duration of the second phase, which starts after cessation of phrenic nerve activity. In contrast, the first stage, which appears immediately after inspiration, is relatively immune to feedback. The situation during locomotion is somewhat similar. The phase dependency of the "swing-blocking" effect is somewhat difficult to evaluate,

since often the duration of the stimulus trains used was quite long (200–300 ms). Nevertheless, it is clear that such stimuli, when applied to skin nerves of the foot, have little or no effect when given during the first part of the extensor burst in walking premammillary cats (187, 190). Most effective for delaying the next flexion phase are those stimulus trains that are given during the last period of the extensor bursts. At the behavioral level, corresponding results have been described in the stick insect (138).

Afferent input, which is able to induce flexor bursts prematurely, is also most effective near the final part of the extensor burst. For example, stimulation of the common peroneal nerve in the premammillary preparation has no effect on phase switching when given early in the extensor burst, but the same input shortens the ongoing extensor period extensively when given in the second half of the extensor activity period (187). Similarly, the premature induction of flexor bursts by using ramp movements of the hip seemed also more effective for stimuli applied in late than in early extensor period.

For the Ib stimulation, there are no data yet about the phase dependency of the swing-blocking effect. However, there are differences in the short-latency Ib reflex effects in the different periods. During fictive locomotion, the stimulation of presumed Ib afferents from extensors induces EPSP rather than inhibitory postsynaptic potentials in triceps surae MN (246). The size of these EPSP is largest at the transition from flexor to extensor periods (later EPSP may be artificially reduced due to occlusion). In the initial part of stance, the activity in extensors is primarily aimed at counteracting gravitational load, while during late stance these muscles are more and more involved in propulsion. Although occlusion may partly obscure some of the EPSP later in stance, it can be stated at least that the data of Gossard et al. (246) are consistent with an opening of Ib extensor facilitatory paths during the initial loading phase of stance.

In summary, there are many indications that there is a progressive facilitation of either the extensor or the flexor generating networks in the course of, respectively, the stance and swing periods (8, 186, 419). In this respect, the extensor period of locomotion resembles the expiratory phase of respiration in that the effects on the upcoming phase switch (ST-SW) are most pronounced for input given near this transition. Changes in the duration of the extension phase are rare for stimuli given at the beginning of the extensor period. There is no evidence for a sharp transition between the two parts of the extensor period however.

8. *Humans*

In humans, there is growing evidence for the existence of a spinal locomotor CPG (79–81, 167, 176, 177, 240, 273, 334, 448, 449, 487; for review, see Refs. 451, 452).

Some properties of this human CPG are very similar to what is found in cat (for example, late reflex discharges after electrical stimulation of the foot; Ref. 448 compared with Refs. 280, 318). Little is known on the role of load receptors on the human CPG, but some recent data suggest that there may be some striking similarities with the situation in the cat. Yang et al. (545) applied transient loading to infants during the stance phase of stepping and found that such loading prolonged the stance phase and delayed the swing phase, much as was observed in cats (see above). Furthermore, in adult humans, there are some indirect indications that unloading of extensors may be important for the initiation of swing in humans, much as in invertebrates and cats. For example, when humans change from standing to walking, they start by suppressing activity in extensors such as soleus and then, with a delay of ~60 ms, they contract flexors such as tibialis anterior (113, 118). This result is consistent with the idea that soleus Ib input has to fall below a given threshold before tibialis anterior can be activated. Similarly, both during walking and running, there is a tight coupling between the decrease in background activity in ankle extensors such as gastrocnemius lateralis and the onset of flexor activity in ankle flexors, such as tibialis anterior. Such observations would agree well with the idea that Ib activity from these extensors inhibits the generation of activity in the antagonist flexors. Unloading of these extensors at the end of stance reduces flexor suppression, making it possible to release activity in flexor premotor centers.

Very few studies have been concerned with load-compensating reflexes in humans with neurological diseases, yet it is of interest in the present context to mention that there is indirect evidence for the existence of facilitatory Ib paths to human ankle extensors in patients with neurological diseases in which the pathway for autogenic Ib inhibition is suppressed (Parkinsons' disease, Refs. 63, 160; spasticity, Ref. 159). An early inhibitory component (I1), following cutaneous stimulation of the hand, is also reduced in these patients. These abnormalities may contribute to the spastic muscle tone, although changes in intrinsic muscle stiffness may contribute as well (165).

For many patients with Parkinson's disease, the most difficult part is the initiation of walking. Is it possible that in Parkinson's disease the flexion at onset of swing is blocked by inhibitory pathways from Ib or cutaneous afferents? The difficulty in the initiation of walking is known to be related to the loss of dopaminergic cells in the substantia nigra. It is conceivable that this deficit leads to an inability to activate a locomotor CPG by descending pathways, but one should not overlook the possibility that part of the problem is related to continuous overactivity in pathways that inhibit the centers for the generation of flexion movements (flexor half-center).

Furthermore, it is worthwhile mentioning that there is a similarity between the stiff gait in these patients and in infants (220).

C. Concluding Remarks

In all species described, the afferent feedback due to loading during stance has three types of effects.

1) The stance muscle output always increases when load is augmented. The types of receptors differ, but the principle is the same. For example, in insects, the load-induced afferent input from the tibial CS serves exactly the same function as the stance muscle GTO in mammals, namely, to increase stance muscle activity at the onset of stance. The interpretation of these stance muscle-reinforcing effects can differ depending on the experimental conditions and on the parameters studied.

Sometimes these reflexes can be explained in terms of velocity feedback, but in other situations, it appears as part of force or position feedback (see also sect. VII).

2) There are many examples showing that moderately loading the extensors can prevent the onset of the next swing phase during walking. This appears more and more as a general basic rule that is functionally meaningful, since it allows the automatic scaling of the duration of the stance phase as a function of the load to be carried (see also Ref. 412). For the cat, the hypothesis was advanced that load-detecting afferents, both from muscles and skin, inhibit the center for the generation of flexion during the swing phase.

3) A series of examples has been described to show that load sometimes seems to induce flexion rather than to prevent it. In some cases, excessive loads are involved that may lead to rupture of extensors if the latter would be too stiff. Instead, extensor inhibition occurs under these circumstances in combination with a protective flexion reflex. This situation is very similar to what has been found in chewing. Slow moderate loading induces extensor reinforcement (mouth closing), but fast strong loading results in extensor suppression (mouth opening to prevent damage to the teeth).

In addition, both in invertebrates and in vertebrates, some afferent input that is specific for the end of the stance phase is used to automatically induce the subsequent swing phase. Although this principle is general, the implementation in the different species varies considerably. In some invertebrates, the afferent signal at end stance is derived from force-sensitive receptors in the exoskeleton, but position clearly is an important parameter too. In mammals, the main proprioceptive signal at end stance is derived from muscle stretch receptors in hip flexors. In both cases however, the reflex actions are the same, namely, a facilitation of the onset of the swing phase.

VII. PROGRAM- AND PHASE-DEPENDENT REFLEXES DURING WALKING

A striking similarity across species is observed in the way in which afferent input from load and position receptors is transformed into a direct motor response. This depends on the task in which the animal is involved. For example, one type of load-compensating reflex during standing may not be useful during particular phases of the step cycle, when another type of reflex would be more appropriate. The CNS, even of supposedly "simple" invertebrates, is capable of modulating load-compensating reflexes and guiding the input from load receptors into quite different pathways, depending on the requirements of the task in which the animal is involved (96, 523). For example, in the tadpole of *Xenopus*, a tactile stimulation is gated through dorsal IN and facilitates the MN at an appropriate time (494). These results demonstrate that several interneuronal pathways are selectively facilitated depending on the ongoing behavior. These variations in afferent connections imply not only facilitatory pathways but also some filtering action or inhibition. Hence, in this section, the question is not how afferent activity shapes the locomotor process, but instead, the issue is how locomotion modulates the activity in the different pathways to MN and to the CPG.

A. Invertebrates

Recent studies in invertebrates have demonstrated that reflexes often vary in intensity and even in sign depending on the ongoing motor task. A particularly good example of such task dependency is the reversal from resistance to assistance reflexes in the stick insect. Such reversal occurs when the animal changes from the "inactive" (resting) to the "active" (locomoting) state (25, 26, 31, 254). A femoral CO signals flexion and extension of the femur-tibia joint. When the animal is inactive, the mechanical stretch of this organ induces a resistance reflex and provides negative feedback. In contrast, when the animal is in the active state, stimulation of the same receptor induces mainly an assistance reflex, i.e., the muscles active during stance of forward walking receive extra excitation (positive feedback, the active reaction; see Refs. 26, 29, 32).

DiCaprio and Clarac (161) demonstrated a similar reversal in the crab. Sinusoidal stretch of the TCMRO initially caused a resistance reflex. Retractor movement induced a protractor response, whereas protractor movement caused activation of the retractors. However, this stimulation also caused a gradual increase in arousal and, when a given threshold was reached, the reflex inverted in sign (retraction movement now inducing retractor activation). This could be interpreted as an assistance reflex.

The reversal was thought to be due to the activation of the circuitry involved in rhythm generation. Direct evidence for this proposal came from experiments on an in vitro preparation of the crayfish (209). At rest, activation of the chordotonal induces a resistance reflex. After induction of fictive locomotion (by adding 10^{-5} M oxotremorine to the bath), the same type of stimulation induced an assistance reflex. In this latter case, the activation of a specific IN switches the reflex (443).

However, the situation is not simple. In both examples there is also experimental evidence for a negative feedback during stance. For the crayfish, the results of Barnes et al. (21) clearly show the effect of a negative-feedback system after an experimentally placed disturbance. In the stick insect, negative feedback in the walking animal was demonstrated in several investigations (123, 143, 147, 463, 466) in the active but fixed animal (526). Positive feedback is found in two ways. In one case, the influence passes a yes-no decision. This formally corresponds to a system with saturation that prevents the output of the positive-feedback system growing infinitely (129, 303). In the second case, a direct positive feedback could be shown to exist (133, 467). Here, infinite growth is inhibited by application of a high-pass filter, a phasic unit within the feedback loop. In the first case, the sense might be to stabilize the state of the ongoing behavior, for example, swing or stance. In the second case, the functional sense is to exploit the physical properties of the complicated mechanical system and thereby dramatically simplifying the computation necessary for proper coordination of the great number of joints in a multilegged animal. It is still unclear how we can have positive and negative feedback at the same time. A possible solution could be that error signals from negative feedback are used to change the gain of the positive-feedback circuit (133).

It is interesting that dynamic properties of the feedback system change from the standing to the walking state. Whereas in the walking animal the resistance reflex appears best described as to be velocity dependent, in the standing animal they are better described as being position dependent. Although height control in the stick insect was found in the standing (see above) and the walking animal (27, 28, 121, 148), it is best described as each leg being an individual height controller. The dynamic properties of the controllers are different for standing and walking. In the standing animal, there is a phasic response, whereas the walking animal does not show this effect (148). Another example for a program-dependent system is found in the gravity response of the stick insect. When the animal stands on or walks along an oblique surface, the body is rotated around its long axis to adjust its vertical axis more to the gravity vector. This effect is, however, much stronger during walking than during standing (161a). This also shows that in height control the

legs are not completely independent. Corresponding results have been found by Frantsevich et al. (230) for the beetle.

Still another example of program-dependent reflexes is described for stick insects. During standing, the avoidance response of a leg due to a mechanical stimulus is accompanied by an intersegmental leg placing reflex of an adjacent leg to keep a stable posture ("compensatory leg placing" reflex, Ref. 233). During walking, the same stimulus results in a leg-lifting response of the adjacent leg ("treading on tarsus" reflex, Refs. 251, 471). Such a mechanism seems to be quite universal and has also been described in the crayfish for FCO receptors (94, 98).

During an ongoing central motor pattern, some reflex pathways seem to be powerful and efficient only when the CPG is expressed. Activity in these pathways is also regulated in a phase-dependent manner. Similarly, in systems involved in the control of overground locomotion, there are parallel pathways that are modulated by the central rhythm. In this case, there are certain reflexes that assist in load bearing and that should be facilitated during stance. Equally important, however, is that there is then a simultaneous suppression of those pathways the activation of which is inappropriate (in this case the levator activating paths).

In general, in invertebrates the presence of CPG and their role in sensory modulation has been well established. In insects, however, there are still some uncertainties about their presence in walking. Some of these uncertainties may be related to methodological questions. Data on insects are usually collected on dissected animals but with most of the afferent inputs intact. Under these conditions, it is relatively difficult to reveal the working of a CPG. Isolation of the nervous system is difficult in insects due to the presence of tracheal respiration. In contrast, in some crustacean preparations, the thoracic or the abdominal ganglia (or the stomatogastric ganglion) have been totally isolated, thereby facilitating the demonstration of CPG activity. Nevertheless, in insects, a number of locomotor-related circuits have been identified. Three types of IN have been described in the locust, the cockroach, and the stick insect (66, 71, 73, 74, 347, 468): the local spiking IN on which converge a great number of afferent inputs, the intersegmental IN, and the local nonspiking IN that are premotor. These IN contribute to reflex activation, being intercalated between the afferent inputs and the MN by forming parallel and in part antagonizing pathways (74, 329). They organize the motor output to antagonistic muscles of the same joint as well as to other joints by lateral inhibitory connections, and they can adjust the gain of the local reflexes. They also integrate the activity of different afferent inputs and are able to redistribute the afferent message on different MN to a given muscle (329). In the femur-tibia control system of the stick insect, a great variety of IN is described that determine the pathways to the MN (32).

The IN have different properties and determine whether the feedback will be positive or negative. Whether they are active or not depends on the network. First results show that the pathways used by load receptors connect similarly to local spiking and nonspiking IN and then to MN (J. Schmitz and K. Schumann, unpublished data).

The data are related to the different afferents stimulated and have defined a "resistance state." When real locomotion can be simultaneously induced in the preparation, the reflex response can be reversed, and new interneuronal connections occur giving an "assistance reflex." Position, movement, and load receptors can be involved in such changes. Similar switches have been described in the crustaceans, but the changes have been related more to the synaptic modification or to the intrinsic properties of MN and IN.

Another mechanism of phase-dependent modulation concerns the gain of the resistance reflex through a presynaptic control implying GABAergic IN. Cattaert et al. (86) showed that primary afferent depolarization IN are activated during fictive in vitro locomotion induced by a cholinergic agent. These primary afferent depolarization IN are able to modulate the chordotonal sensory message depending on the CPG rhythms. Several other examples of presynaptic mechanisms have been described, e.g., during crayfish escape behavior (331) and on the TCMRO afferents during fictive locomotion (495). In insects, presynaptic inhibition also seems to be a very widespread phenomenon, but the different results have mainly demonstrated that such a mechanism is under the control of other sensory afferents via some specific IN (68), a situation also seen in crayfish.

B. Vertebrates

1. Program dependency of group I reflex effects in the cat

A selective method for the activation of Ib afferents is the stimulation of plantaris afferents. Conway et al. (111) used plantaris stimulation in experiments in immobilized spinal cats in which rhythmic locomotor neural activity was induced by injecting L-dopa. Low-intensity stimulation of the plantaris nerve increased extensor bursts and eliminated flexor bursts. In clonidine-treated spinal cats, Pearson and Collins (415) found that plantaris stimulation enhanced the ongoing activity in medial gastrocnemius MN during rhythmic locomotor activity, whereas the same stimuli had a suppressive action on these MN when there was no rhythmic activity. The switch from Ib inhibition to Ib excitation was further demonstrated at the intracellular level. McCrea et al. (377) were able to show

how Ib inhibitory postsynaptic potential (IPSP) disappeared entirely during the periods of rhythmic alternating flexor and extensor bursts.

A similar reversal from Ib IPSP at rest to Ib EPSP during bursts of fictive locomotion was shown by Gossard et al. (246). They were able to show that electrical stimulation of Ib afferents is able to produce EPSP in extensor MN, provided that the locomotor centers are activated (clonidine or L-dopa injection in spinal cats or stimulation of the mesencephalic locomotor region in decerebrate cats). They proposed that the primary action of the extensor Ib afferents is excitation of the extensor half-center (E) rather than inhibition of the flexor half-center (F, see Fig. 4). The main argument in favor of this bias toward E excitation is that large Ib EPSP can be evoked in extensors even in the absence of rhythmic flexor activity. However, this point is not very strong, since the F may be active at subthreshold level and therefore disinhibition of extensors (through inhibition of the inhibitory F) remains a possibility (for additional discussion on this point, see Refs. 111, 376). One point that is clear is that the suppression of the flexor activity by the group I input is indirect. Conway et al. (111) showed that the Ib induced hyperpolarization of flexor MN is not due to postsynaptic inhibition but to disfacilitation (the removal of excitation presumably coming from the flexor half-center).

A key feature for this line of research is the identification of the Ib excitatory IN. Gossard et al. (250) found that IN, thought to belong to CPG networks (lamina VII), receive excitatory input from presumed Ib afferents from plantaris during the extensor phase of fictive locomotion. The CPG centers are thought to be activated through an oligosynaptic pathway from the MLR (488). The short-latency EPSP produced in extensor MN by such MLR stimulation are facilitated by activation of plantaris Ib afferents (55). These observations would fit with the proposal that Ib afferents from extensors have excitatory projections onto the extensor half-center of the spinal locomotor CPG (270, 306). At any rate, both the data of Gossard et al. (246) and McCrea et al. (377) leave no doubt that there is a closing of an Ib inhibitory and opening of an Ib extensor facilitatory path during locomotion.

How "private" this facilitatory path is remains a largely unanswered question. Because activation of Deiters' nucleus is able to prolong extensor activity in the stance phase, one might expect that the currently described Ib extensor facilitatory path shares common IN with the projection from the lateral vestibulospinal pathway. Leblond and Gossard (350) tested this with the spatial facilitation technique, but they found no evidence for a common pathway.

How do these results from locomotion studies compare with those obtained under static conditions? As mentioned above, Lafleur et al. (343, 344) found a rapidly

declining Ib inhibition in a wide variety of both antagonist and agonist MN. It is not known whether these Ib induced inhibitions in flexor MN are also due to disfacilitation, as was observed by Conway et al. (111) during fictive locomotion. Hence, it is uncertain whether they are mediated by IN, which are part of the spinal CPG for locomotion. However, the short time course and the very wide distribution (involving both flexors and extensors) of these "static" inhibitions make this unlikely. It follows that extensor facilitatory pathways may be masked at rest and require to be studied during locomotion, when the CPG network is active (fictive and real locomotion; late flexor reflexes under L-dopa). In agreement with this, Jankowska (316) has proposed that the Ib pathways, involved in autogenic inhibition and rhythm resetting, respectively, are subserved by different sets of IN.

Does the extensor facilitatory pathway constitute an example of positive feedback? For a long time there has been resistance to this idea because it was generally assumed that positive feedback induces instability. However, Prochazka et al. (438) recently showed that positive force feedback can indeed provide stable load compensation, complementing negative displacement and velocity feedback. Based on experiments (437) and on simulations (438), they argued that positive force feedback is appropriate because inherent properties of the neuromuscular system prevent instability. The length-tension curve of muscle ensures that positive feedback is self-limiting, since shorter muscles produce less force (automatic gain control). Furthermore, they found that the introduction of long delays, compatible with the ones described for the Ib extensor facilitatory pathways described above, further stabilized the positive feedback (437, 438). In this way, positive force feedback could be shown to have interesting functional properties as to allow stable load compensation and to explain the puzzling results of high feedback delays; the stability of the positive-feedback system unexpectedly increased with increasing delay.

2. Phase dependency

The two main sources of afferent input related to limb loading are sense organs in the footpad (mechanoreceptors in the pad and in intrinsic foot muscles) and proprioceptors in leg extensor muscles. For both of these sensory inputs there is evidence for parallel pathways and for the ability to control these pathways during gait differentially. Cats with a high decerebration (premammillary cats) can walk spontaneously on a treadmill. Stimulation of the plantar surface of the foot in this preparation yields large extensor responses during stance, whereas the same stimuli evoke flexor facilitation during swing (187, 190). Similar results can be obtained by direct stimulation of the posterior tibial nerve at the ankle (112, 187; for decerebrate spinal cats injected with L-dopa) and by

stimulation of skin areas that may not be related primarily with load detection (218, 219, 223–225).

In principle, passive changes in limb position could underlie some of this switching between pathways (239, 258, 455; for review, see Ref. 52). However, phase-dependent switching between pathways persists during fictive locomotion of the motionless (paralyzed) spinal cat, treated with injections of Nialamide and dopa (6, 474, 475). The flexor EPSP, evoked by cutaneous stimulation, were usually largest during the rhythmic flexor burst, whereas the extensor EPSP were largest during extensor bursts. In general, Schomburg and co-workers (474–476, 478, 480) concluded that such EPSP appeared during the active phase of the recorded MN, whereas IPSP were present during the inactive phase. This modulation occurred for stimulus parameters that were similar to those used in the intact cat (188, 218). Similar results on phase-dependent modulation of transmission in cutaneous pathways have been reported for the forelimb (291). In some of these studies, the results on single cats are presented. One should be aware that such results are not always representative, since for some of the responses there is large intersubject variability (359, 361).

Furthermore, recent studies have challenged the generalized occurrence of phase-dependent modulation during fictive locomotion. Schmidt et al. (461, 462) found that phase-dependent modulation was only present in some MN [e.g., flexor digitorum longus (FDL)] and only to some types of input (saphenous and plantar nerves). Interestingly, the same authors were able to show that the FDL EPSP, evoked by the two nerves mentioned above, were differentially modulated during fictive stepping. The early components of the SP EPSP were enhanced during the early flexion phase, whereas those in plantar EPSP were markedly depressed during flexion (387). A similar picture of highly differentiated reflex pathways undergoing quite specific modulatory influences during fictive locomotion arises from the study of Labella et al. (339). The latter authors focused their attention on cutaneous reflexes in the different parts of the triceps surae. They showed that the reflexes to these muscles are generally largest during the phase of the cycle in which the nerves to these muscles are most active, but subtle deviations occur, and there are differences in amplitude of the responses of the various muscle parts.

A phase-dependent reversal from crossed extension to crossed flexion has been observed occasionally during fictive locomotion (spinal paralyzed cats treated with nialamide and L-dopa; Ref. 455). However, long stimulus trains were used, and the latencies of the responses were correspondingly much longer than those seen in the studies on the intact cats, where single shocks were used. It was noted that the reversal was much less constant than during decerebrate walking. In many cases, only crossed extension or crossed flexion was obtained. Rossignol et

al. (455) attributed this reduced potency of modulation to the absence of movement-related feedback during fictive locomotion.

At least part of the modulation during fictive locomotion seems to occur presynaptically on the afferent terminals (12–15, 180–182, 184, 185, 247–249; for review, see Ref. 506). Gossard et al. (245, 246, 249), for example, demonstrated presynaptic modulation of different cutaneous and group I afferents during fictive locomotion in the cat. It is likely that presynaptic inhibition also contributes to position-dependent modulation (35, 53, 454). In humans, the role of presynaptic inhibition in the phase and position dependency of various reflexes has been reviewed by Brooke et al. (52) and by Stein (506).

In the intact cat, the phase-dependent modulation of ipsi- and contralateral reflexes, as described above, could be due to supraspinal influences. Cortical influences may not be very essential, since phase-dependent modulation of crossed and uncrossed reflexes is present during locomotion of high decerebrate cats. Brain stem mechanisms could play a role to some degree. Drew (178) showed that microstimulation of the medullary reticular formation in the intact unanesthetized cat elicits maximal responses in flexors, not during the periodic locomotor activity but just before this period (when peripherally induced flexor responses are at a maximum as well). Nevertheless, the brain stem can be excluded as the only modulatory source underlying phase-dependent reflex gating. Forssberg and co-workers (218, 219, 223–225) showed that phase-dependent modulation of reflexes is present in the chronic spinal cat, walking on a treadmill.

Finally, it is worth mentioning that some data are available on humans as well. In intact humans, the phase-dependent modulation of sensations, cortical evoked potentials (195), and EMG responses in leg muscles after stimulation of cutaneous afferents has been studied extensively (196, 197, 533, 543). As in cats, electrical stimulation of skin nerves in humans induces facilitatory EMG responses in flexors, provided the responses are elicited near the transition from stance to swing (188, 199, 218, 543).

In patients with complete or almost complete spinal cord transection, rhythmic locomotor-like contractions are very rare (79–81, 177, 448), and it is not known whether phase-dependent modulation persists under such conditions. In humans, it is thus difficult to demonstrate whether such phase-dependent modulation is due to central or peripheral factors. Because a substantial part of the modulation of H reflexes persists during passive movements, there is a growing consensus that muscle stretch related to movement is an important element in amplitude modulation of H reflexes during locomotory movements (for review, see Refs. 52, 506). For cutaneous reflexes, the contribution of movement-related feedback has yet to be proven, whereas on the other hand, there is

evidence for a CPG-related modulation, based on indirect evidence related to backward locomotion (194). The central idea is that, in humans, the backward gait is produced by the central program for forward walking, but with the program working in reverse (517) and thus also producing a reversing of the order of the phase-dependent modulation of reflexes (201).

Furthermore, for the medium latency (P2) cutaneous reflexes from the foot, it has been argued that a spinobulbospinal (491) and/or a transcortical pathway may be partially involved (402). This is compatible with the observation that P2 responses have not been shown convincingly to be present in spinal human or cat. The reflexes survive only in patients with incomplete spinal cord injury lesions. Jones and Yang (323) showed that P2 reflexes (with a latency of ~75–80 ms) elicited through stimulation of the posterior tibial nerve (containing large cutaneous and other afferents from the foot) were present, but they were abnormally modulated in these spinal cord injury patients. In particular, in muscles such as tibialis anterior, there was no longer a phase-dependent reversal in these patients, because they lacked the suppressive responses normally seen at the end of the swing phase. The ankle extensor soleus was activated in reflexes in the swing phase. It was argued that this disordered activation pattern may be one of the causes of the frequent falls of these spinal cord injury patients. The abnormal modulation may reflect the contribution of supraspinal structures in the phase-dependent reflex changes (for review, see Ref. 508). Fung et al. (235), Yang and co-workers (542, 544), and Fung and Barbeau (234) found that improvement of gait was obtained by restoring the phase-dependent modulation of H reflexes through conditioning by cutaneous stimuli.

VIII. INTERLIMB COORDINATION

A. Invertebrates: Coordination in Multipods

It has been possible to manipulate load by adding weight to the entire animal or to a particular leg. A comparison with the unloaded animal demonstrates a change in the interleg coordination (see below). In the crayfish (18, 95, 268), it has been demonstrated that, within a given step cycle, a loaded leg shows a lengthening of its power stroke duration and not of its return stroke. On the other hand, Cruse and Müller (141) showed that return stroke duration is smaller when the vertical load is increased. This was also the case for the stick insect for small loads (227, 252). In contrast, Dean (153) reported a prolongation of swing movement when the stick insect walks under high loads. Prolongation of power stroke was also observed in the stick insect (227, 228), but such a prolongation might simply result from the mechanical effect due to the limited muscle force. Loading the whole animal shows a strong effect on the ipsilateral and contralateral coordination. Unloaded, the coordination is much weaker. In particular with respect to contralateral coupling, it can cover a complete range of values from in phase to out of phase. In a loaded animal, these phase values become more concentrated. Dean (153) found a quantitative influence on interleg phase for ipsilateral legs, but not for contralateral legs after loading a stick insect by externally applied force to the treadwheel. In several investigations, a number of coordinating mechanisms have been described between both ipsilateral and contralateral legs in the crayfish (3 mechanisms; Refs. 142, 391) and the stick insect (6 mechanisms; for review, see Ref. 128). Most of these mechanisms are described as depending on leg position. However, as was mentioned above, the PEP also depends on load, and therefore, all the position-dependent mechanisms may also indirectly be influenced by load. There are also influences that directly depend on load (coactivating mechanism, Ref. 125; prolongation of power stroke of adjacent rear leg, Ref. 470). Another one, the forward excitation (149), may well depend on load receptors of the posterior leg. In the decapod crustacean, a series of experiments emphasize the role of the CSD and FCO sensory receptors (91, 134, 330, 493, 353, 354).

It should, however, also be mentioned in this context that the effects of mechanical coupling should not be underestimated. If one leg lifts off the ground, the other legs are under higher load, and the opposite occurs when a leg finishes swing. Because load changes can have a direct influence on the local leg reflexes as discussed above, there is also at least an indirect influence on coordination between legs.

The FCO receptors, which are able to record load, control the interleg locomotor patterns. As mentioned in section vi*A1*, in the crab and in the rock lobster, stimulation of the FCO from one leg inhibits the stance muscle of that leg (the depressor) and facilitates its swing muscle (the levator). Moreover, it facilitates the stance muscles of the ipsilateral neighboring legs. In an in vitro crayfish preparation, such interleg connections have also been described (98). In the crab, if a leg (e.g., *leg 3*) is experimentally lifted from the ground and the animal walks freely, the two adjacents legs (*legs 2* and *4*) operate more or less out of phase, as if they were immediately neighboring legs. In the fixed leg, the depressor muscle is activated almost continuously. If, under these conditions, the FCO of the fixed legs are stimulated at the time when they would normally be activated in the step cycle, the depressor activation of the two neighboring legs changes to a pattern compatible with the situation when the fixed limb was really on the ground (353, 354). In the rock lobster, analogous interleg relations with "stance sensory receptor" controls have also been presented (389, 390).

This means a return to the pattern that these legs would show under normal conditions.

Increasing power stroke activity in one leg is correlated with a modification of the activation of the other legs. In the intact rock lobster walking on a treadmill, it is possible to block a leg during the stance phase, thereby substantially inhibiting the walking pattern of the other ipsilateral legs. An increase in the *leg 5* remotor activity by electrical stimulation (stance) inhibits the *leg 4* remotor (30, 92, 126, 134). A direct dependence of *leg 4* force on the *leg 5* swing has been proven by placing *leg 4* on a force platform while *leg 5* continues to step. *Leg 4*, which is immobile, exerts cyclical force on this platform. This force is maximal during *leg 5* swing and minimal during *leg 5* stance, as expected for alternating gait (134). Similar results have been described for the stick insect (29, 146).

Another experimental situation involving load has been the possibility of studying the effects of autotomizing a leg (253). On the basis of the results when locomotion is studied after amputation of one leg (changes in leg coordinations and in durations of return stroke and power stroke in the remaining stump), it can be assumed that load is a critical sensory influence (17, 91).

When all legs are autotomized, it is possible to see an erratic in-phase pattern involving buccal appendages (maxilliped), which are normally not involved in locomotion. These movements are in phase with the stumps of the legs. A similar pattern is observed in several decapod crustaceans when an animal is at rest provided the animal is supporting its weight by the back legs. In this case, the front legs are elevated above the ground. An in-phase pattern is observed with a succession of backward or forward movements of the front legs. This waving pattern (91, 409) involves only the first leg segment.

In the in vitro preparation of the thorax of the crayfish, in which all leg sensory afferent activity is suppressed, it was demonstrated that the fictive locomotor pattern, recorded from motor nerves of different thoracic ganglia, is more or less in phase (493, 496). In this case, the pattern is entirely of central origin. Nevertheless, it can be shown that some types of receptors may also be involved in maintaining in-phase patterns. For example, rhythmic activation of the TCMRO, a neuromuscular structure at the base of the leg, is able to stabilize the in-phase pattern and to entrain the central rhythm, accelerating or decreasing it.

Cruse (124) and Cruse and Graham (139) built a model where the influence of load changes of step phase duration in both the same leg and in neighboring legs.

In particular, return stroke duration is directly controlled by the load. The model predicts that, for small loads, return stroke duration decreases with increasing speed, and for high loads, return stroke duration is short and constant.

The model is in agreement with the following find-

ings. In a rock lobster, successive autotomy induces a pattern in the remaining stumps that is in phase with the front legs. The intact legs are always out of phase with the neighboring legs, independent of the number of autotomized legs. All the ipsilateral stumps move in phase with each other (91, 94). Similarly, when in the stick insect the middle leg was autotomized, the coxae moved in phase with the front legs (527).

B. Vertebrates: Interlimb Coordination in Cats and Humans/Effects of Elimination of Load Feedback

The studies on cat interlimb coordination have been summarized by Rossignol et al. (458) and by Cruse and Warnecke (150), while the effects of deafferentation have been reviewed as well (457). In agreement with the arthropod studies, it has been found that interlimb coordination becomes less precise following deafferentation (531). Such disturbance in the coupling between various limbs is especially prominent in the chronic spinal cat during air-stepping (241). In the context of the present review, it is of interest that the deafferentation effects are especially prominent during the load-bearing phase of the affected limb (531). Initially, the deafferented limb is overextended and dragged along during stance. In other cases, the stance phase is shortened dramatically as the animals fail to extend the limbs fully (531). Furthermore, the duration of the stance phase is no longer adequately adapted to the speed of the animal.

Little is known about the role of load receptors with respect to the neural substrate of the coordination between fore- and hindlimbs. In a recent review, English (211) describes the evidence for the involvement of two systems. First, long propriospinal cells that link lumbar and thoracic portions of the spinal cord have often been implicated (4, 500). Second, neurons of the ventral spinocerebellar tract may be involved, since they carry information about the timing of step cycles from more than one limb.

The coordination between fore- and hindlimbs during walking has been studied by several authors in the cat (150, 210, 212, 275, 382, 532). The main conclusions can be summarized as follows. *1*) Basically, there are two types of coordinating influences, namely, influences between ipsilateral neighboring legs and influences between contralateral neighboring legs. No evidence exists for direct connections between diagonally neighboring legs, even if diagonal coordination is stronger than ipsi- and contralateral coordination. Such an effect could be explained in the way that diagonal coordination may be supported by two ipsi-contralateral pathways, and this two-way influence becomes stronger than the two single pathways. *2*) In contrast to the arthropod species investigated (see Ref.

128), the contralateral coupling is stronger than the ipsilateral coupling in the cat.

Reflexes could be elicited from fore- to hindlimbs, or vice versa, yielding diagonal flexor and extensor patterns that were very reminiscent of the patterns of muscle activations used by these animals during locomotion (see Ref. 116 for review). It has been suggested initially that some reflex pathways from fore- to hindlimb could underlie some of the coupling seen during locomotion (381). However, the variability among the different interlimb patterns used is so large that it is unlikely that an association with simple neural circuitry can be made (210, 212, 532). One striking feature is the existence of a fast propriospinal inhibitory pathway from forelimb afferents to MN of hindlimb FDL (477, 478).

Hence, in summary, reflexes between fore- and hindlimb in the cat are present and often highly specific (FDL). They may involve load compensatory reactions, but they can, at present, not be linked to a specific form of interlimb coordination. The modulation of these reflexes during walking obeys the same rules as observed for crossed reflexes. Variations in the amplitudes of the reflexes depend primarily on the step cycle of the limb in which the reflexes are observed. As for ipsilateral and crossed (contralateral) reflexes, there is evidence that spinal motor centers underlie the observed phase-dependent modulation.

To study within which limits a cat can maintain stable interlimb coordination, some authors have used locomotion on split belts, moving at different speeds, thereby imitating walking in a circle (150, 222, 275, 338). Under such conditions, chronic spinal cats can maintain alternating stepping even for two- to threefold differences in belt speed. This is achieved mainly by prolonging the flexion or first extension phases of the limb walking on the "fast" belt and a shortening of the swing phase of the limb walking on the "slow" belt. One "rule" emerging from these studies was that bilateral overlap between different phases was allowed during alternating gait except for the E1 period (first extension phase before touchdown). Simultaneous bilateral occurrences of E1 phases were avoided, even if it meant that the limb had to "wait" a substantial period of time at the end of the flexion phase (see also Ref. 239 for this effect). On the other hand, Cruse and Warnecke (150) investigated free walking cats, and the results indicate that the start of swing is inhibited as long as the contralateral leg performs a swing. As mentioned above, similar effects were found in the stick insect (226, 228) when the legs of one side walk with twice the step frequency of the other side.

Whatever the building blocks of the neural substrate for interlimb coordination, it appears that the coupling between these blocks depends on an appropriate amount of movement-induced afferent input, some of it related to load. Grillner and Zangger (267) found that interlimb co-ordination during hindlimb walking deteriorated after deafferentation in the mesencephalic cat. Similarly, Giuliani and Smith (241) described that coupling between hindleg movements during unloaded locomotion (air stepping) was weaker after deafferentation of a hindlimb of a chronic spinal cat. They found that, during the majority of locomotor bouts, the bilateral stepping was characterized by irregular phasing with the intact hindlimb stepping at a faster frequency than the deafferented leg. Evidence for spinal mechanisms involved in the coordination of movements of the different limbs during locomotion of the cat is provided by the observation that such coordinated movements persist in the high spinal cat injected with dopa and placed on a treadmill (383). When movement feedback is absent, however, e.g., during fictive locomotion, then the coordination is generally more variable than when movements are allowed. The most common type of interlimb coordination is the alternation of activity in the limbs of one girdle, but occasionally a bilateral synchrony of flexion and extension was observed (384). The coordination of activity in fore- and hindlimbs is even more variable (89, 405, 522). There is also some evidence for diagonal coupling between forelimbs and hindlimbs (405). However, it was shown by a model calculation (392) that it is difficult to conclude the existence of neuronal diagonal pathways on the basis of measured coordination strengths, in the case that several parallel pathways could exist.

In conclusion, the results of various manipulations (e.g., split belt) have shown that the coordination between movements of the various limbs during walking is quite flexible. The spinal cord is able to produce much of this coordination as well as its flexibility. Load afferent feedback may be essential in strengthening the coordination.

In humans, compensatory reflexes due to unloading of one leg result in bilateral responses, provided the contralateral leg is performing a supportive role (38). Dietz et al. (164, 172) studied perturbations applied during stance on a treadmill with split belts. Bilateral displacements induced responses that were largest when both belts moved in the same direction and not in the opposite direction. Displacement in the opposite direction causes the body's center of mass to fall between the legs, and therefore, the compensatory responses do not have to be as large. This was shown to be due to automatic cocontraction of the homologous muscles of the respective contralateral leg. This leads to a lower level of leg muscle activity when both legs are displaced in the same direction and to a linear subtraction when they were displaced in opposite directions. On the basis of this and other studies, it was argued that load receptors in ankle extensors must be crucial for the maintenance of body posture.

IX. GENERAL CONCLUSIONS

Most movements are made against some type of resistance or load, whether it is our hand grasping an egg or our foot moving over ground during gait. Understanding how load is sensed by receptors and how this sensory information is used to guide these movements is a key issue in motor control studies. In recent years, the interest in this question is widening as there are more and more motor tasks that have to be performed with the help of man-made devices such as robots and prostheses. Just at the point where there is a broad need to understand load-compensating mechanisms, several new insights have emerged that have given an extra impetus to this field. These insights have mostly evolved from comparative studies, since it has been realized that basic principles concerning load regulation can be found in a wide variety of animals, both vertebrate and invertebrate. Major recent advances include the following.

1) Automated movements such as gait are regulated through feedback from load receptors onto central circuits involved in the generation of rhythmic locomotor output. Control of gravitational load is an essential element for the control of locomotion. Activation of load-detecting receptors is crucial for the control of the intensity and duration of the period during which a given limb acts against gravitational load (stance phase) in the step cycle. In invertebrates, it has long been known that this is achieved through feedback onto the central networks involved in the generation of the locomotor CPG. In the last 20 years, it has become clear that a similar principle applies to the control of locomotion in vertebrates such as the cat. In this animal, indirect evidence is accumulating that during the stance phase, afferent activity from various load detectors can activate the part of the CPG that generates extensor activity in this part of the cycle. This constitutes an example of reinforcing force feedback. At the same time, there is an inhibition of the CPG part generating flexion. The functional role of this arrangement is obvious. As long as the limb is loaded, activity in antigravity muscles should be promoted while the onset of the next flexion should be delayed.

2) Load-compensating reflexes are highly flexible, and their gain can be adapted to the task or to the phase of the ongoing movement. A next major finding was that reinforcing force feedback is not a constant feature but is task dependent. It appears only in situations where it is appropriate, such as during gait. In other conditions, such as in the immobile resting animal, such pathways are closed, and other reflexes may be more apparent. This type of switching between pathways has been observed in some invertebrates, but more recently, it was also shown to occur in cats. Traditionally in this animal, all experiments were done on immobile resting preparations, and this explains why only force-reducing pathways were revealed (autogenic inhibition from Ib afferents of GTO from leg extensors). Only through experiments under conditions related to locomotion has it become apparent that alternative pathways exist.

3) Load is a complex parameter that is recorded by very different types of receptor, although some are more directly involved than others. Feedback about load is not only derived from specific load receptors but also from other types of receptors that previously were thought to have other functions. In the CNS of many species, a convergence is found between specific and nonspecific load receptors. A redefinition of load receptors is required.

In invertebrates, most attention has been given to position and movement detectors (such as the hair plates, MRO, or the CO), but more recently, the cuticular receptors, such as the CS, which act as typical load receptors have been under detailed investigation. Similarly, in mammals, the question of load receptors is often reduced to a discussion of a single type of receptor, namely, the GTO of extensors. However, when a limb is loaded during stance, a wide variety of receptors are activated, including cutaneous receptors from the foot and spindles from stretched muscles. Input from these various sources (through Ia, Ib, and cutaneous afferents) is combined in reflex pathways at the spinal cord level, suggesting that a common message about limb loading has a high priority. One should add, however, that convergence in some pathways does not necessarily rule out modality specificity in other pathways.

4) Load feedback is intensity dependent. At low levels, the feedback may reinforce load-compensating actions, but at high levels, the actions are inversed, thereby protecting the system from overload.

Even within a given task it is not an advantage to have a reflex that is completely stereotyped. For example, load-resisting feedback is appropriate at physiological levels of load but not when load is excessive. In the latter case, the polarity of the feedback should change to protect the animal or subject from overloading. For example, in the crab and in other invertebrates, such switching does indeed occur. In cats, the outcome of contraction-induced reflexes was shown to depend on the ongoing force level. In humans, load-resisting reflexes through afferents from periodontal receptors occur at low levels of loading while, instead, jaw closing is inhibited at high load levels.

5) Load-compensating reactions not only involve several types of nervous feedback but also rely on the biomechanical arrangement of the biological structures. Resistance to load is due to a mixture of elements: passive resistance (e.g., passive muscle stiffness), feed-forward activation, and load-dependent feedback. The relative importance of each of these elements has been studied in a variety of tasks.

A hot topic in the debate on load compensation is related to the use of feed-forward versus feedback types of control, both for biological and for artificial systems. It is clear that in fast movements the role of anticipation prevails, but it is less clear what happens during movements of moderate speed.

6) Load plays a crucial role in shaping patterned motor output. Locomotor patterns (walking, swimming) depend on the medium in which the movements have to occur. This could indicate that these various forms of locomotion depend on the same neural substrate (CPG) but that the different patterns (walking, swimming) depend on the sensory context, in particular the afferent input related to load.

7) Proportional systems using positive feedback are usually neglected by engineers because such systems may show problems regarding stability unless those are prevented by saturation characteristics. However, an increasing number of examples of biological systems appear to use proportional positive feedback for position or force control. Conditions could be determined under which these systems are stable. Furthermore, positive feedback systems could be shown to solve different control problems by exploiting the physical properties of the system to be controlled. Some hybrid solutions, i.e., mixtures between position, force, or velocity feedback using positive or negative sign with interesting properties have been proposed. There is, however, a number of possible combinations that still deserve experimental and theoretical investigations.

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