Convergent evolution and locomotion through complex terrain by insects, vertebrates and robots[☆]

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Abstract

Arthropods are the most successful members of the animal kingdom largely because of their ability to move efficiently through a range of environments. Their agility has not been lost on engineers seeking to design agile legged robots. However, one cannot simply copy mechanical and neural control systems from insects into robotic designs. Rather one has to select the properties that are critical for specific behaviors that the engineer wants to capture in a particular robot. Convergent evolution provides an important clue to the properties of legged locomotion that are critical for success. Arthropods and vertebrates evolved legged locomotion independently. Nevertheless, many neural control properties and mechanical schemes are remarkably similar. Here we describe three aspects of legged locomotion that are found in both insects and vertebrates and that provide enhancements to legged robots. They are leg specialization, body flexion and the development of a complex head structure. Although these properties are commonly seen in legged animals, most robotic vehicles have similar legs throughout, rigid bodies and rudimentary sensors on what would be considered the head region. We describe these convergent properties in the context of robots that we developed to capture the agility of insects in moving through complex terrain.
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1. Introduction

Arthropods represent the most successful phylum on earth and among them insects are the most successful class. A large part of their success can be attributed to their agility in moving through virtually any environment. Insects readily climb over and around most objects, climb walls and walk on ceilings. In addition, many insects fly with agility unmatched in either the animal kingdom or by manmade devices. Clearly many lessons relevant to robot design can be learned by studying how these animals move through their environments. However, deciding how to take advantage of the principles found in insect locomotion is a challenge in itself.

One might simply attempt to copy the mechanical properties and control architectures in animals, hoping to capture their agility. Unfortunately, a strict bio-mimicry

strategy is rarely if ever successful for several reasons. First, even though insects are often referred to as simple animals, their mechanical and nervous systems are far more complex than that found in any current robot. Each leg has seven degrees of freedom. The muscles that control those movements are more efficient than any artificial actuators currently available. Thoracic ganglia contain thousands of neurons and head ganglia represent sophisticated sensory processing regions, memory banks and motor control centers (Gupta, 1987). Hundreds of sensors are found associated with each leg and on the head, antennae may have hundreds of thousands of sensors associated with them (Loudon, 2003). Beyond these complexities, scaling issues must be considered. Insects are small creatures and body plans may be optimized for the size and materials found in their bodies. As one scales up to larger devices typical of most robots and changes to materials such as aluminum or plastic, it is not clear that these designs will still be appropriate. Finally, neural circuits are rarely understood in their entirety and again have co-evolved with the size and materials of the insect's body. It is unlikely that an

incompletely understood neural circuit could readily control a device that is made to a different scale with different materials.

With these pitfalls in mind, some intelligent decisions must be made for a biorobotics effort to benefit from biological principles. Several strategies that go beyond bio-mimicry have been used with some success. In this paper, we describe two extreme examples from the robots designed by members of our group. In one, we attempt to incorporate the leg designs as much as practically possible into the design of the robot (Ritzmann et al., 2000). Dynamic simulation tools are used to limit degrees of freedom in each leg while leaving enough action to enable the vehicle to move appropriately for the behaviors that we hope to capture (Nelson et al., 1997). Rules derived from studies of the insect's kinematics and neural systems are used to control leg movements. This strategy leads to an iterative process whereby limitations in the robot's movement lead to further studies of the insect to answer questions that may increase the robot's agility. In the second example, a much simpler locomotion platform is generated and individual solutions to movement in complex terrain are identified in insects and implemented to improve the robot's agility (Allen et al., 2003). Here we use very abstracted principles derived from biological mechanisms. That is, we do not constrain ourselves to do things exactly like the animal does, but rather simply capture the principles that are found in the animal.

In both of these examples, we must decide which aspects of the animal's locomotion are most important to our robotic designs. Lessons of convergent evolution can guide these decisions. An examination of processes throughout the animal kingdom reveals numerous examples, where distantly related animals evolved similar solutions to various physical problems. It has been postulated that this convergence occurs because principles of physics limit the number of good solutions that are available (Conway Morris, 2003). Legged locomotion evolved independently by vertebrates and arthropods. Yet, many similarities are found in both groups. This convergence occurred because both animal groups must solve the same physical problems relevant to moving a body through natural terrain against forces such as gravity and friction. Because the robots which we design must solve these same problems, it would behoove engineers to consider points of convergence in disparate animals in their designs. Previous reviews pointed out similarities in the motor control systems of insects and mammals (Pearson, 1976, 1993). Here, we will describe three additional similarities in vertebrate and insect locomotion and explain how we are attempting to incorporate these properties into the types of robots that we are designing.

2. Basic walking patterns

2.1. Insect patterns

The basic walking patterns of insects have been studied for years and reveal several consistencies. At slow speeds, insects typically walk in a metachronal gait that evolves into a tripod gait as speeds increase (Wilson, 1966; Delcomyn, 1971). The tripod gait is in fact a form of metachronal gait but is distinguished by simultaneous swing and stance movements of the front and hind legs on one side along with the contralateral middle leg (Fig. 1). This statically stable tripod alternates with the tripod made up of the remaining three legs. Neural control of leg movements is found within the three thoracic ganglia that control each pair of legs. Pattern generation circuits have been demonstrated to exist in each hemi-ganglion and indeed may exist for each leg segment (Pearson and Fourtner, 1975; Bässler and Buschges, 1998). These oscillators are then coupled by sensory information derived from the wealth of sensory receptors associated with each leg (Akay et al., 2001).

The rules by which movements are coordinated both within each leg (intra-leg coordination) and between legs (inter-leg coordination) are described in detail in other articles within this issue (Dürr, Schmitz and Cruse and Zill, Schmitz and Büschges). Joint movements within a leg that are generated in this way can change to generate movements such as turning or righting. Specific timing of leg movements in different segments is influenced by sensory cues that monitor the states of adjacent legs (Cruse, 1990). In this way, coordination can be maintained at a very low level in a distributed manner that allows for efficient movement under a range of conditions.

Even within this basic pattern, we find some additional complexity. Although the legs that make up a tripod enter swing and stance at approximately the same time, the joint movements of each leg pair (front, middle and hind legs) are distinct as are the ground reaction forces that they generate. The hind legs make simple propulsive movements by extending the main leg joints (coxa–trochanter (CTr) and femur–tibia (FTi) joints) in nearly exact synchrony (Kram et al., 1997; Watson and Ritzmann, 1998) (Fig. 1). These actions generate positive ground reaction forces at the hind tarsi (feet) that move the animal's body forward (Full et al., 1991). During horizontal walking on flat surfaces, the hind legs make only small movements at the joint that connects the leg to the thorax (thorax–coxa (TC) joint) (Kram et al., 1997). The middle legs have to balance the lateral forces of the two contralateral legs of the tripod (Fig. 1). As with the hind legs, their CTr and FTi joints move in synchrony, but the FTi joint makes a smaller extension resulting in a more sweeping lateral movement (Kram et al., 1997; Watson and Ritzmann, 1998). The horizontal ground reaction forces for these legs during level walking include first a braking and then a propulsive phase. The front legs make much more complex movements than the other two (Fig. 2). They reach forward with variable movements (Tryba and Ritzmann, 2000) and generate braking ground reaction forces during horizontal walking (Full et al., 1991).

The movements that extend the front legs of the cockroach include a rotation of the front leg's coxal segment (Kram et al., 1997; Tryba and Ritzmann, 2000)
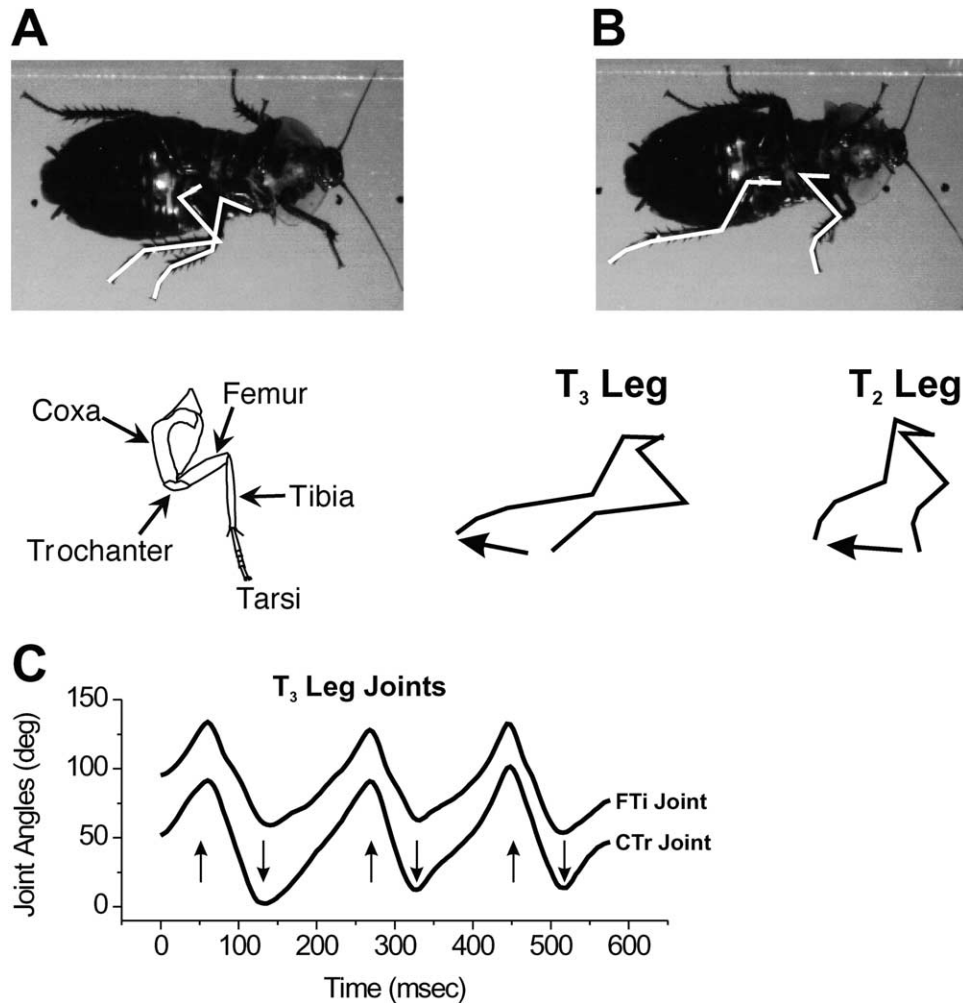
Fig. 1. Leg movements of *B. discoidalis*. A and B are frames from a high speed video record of a cockroach running in a tripod gait on a transparent treadmill. The two ventral views show extreme swing and stance of the legs. The right middle and hind legs are highlighted with white lines. (A) shows extreme flexion of the hind leg and extreme extension of the middle leg. (B) shows the opposite positions. The insets below these images include a diagram of a typical cockroach leg with the leg segments labeled and the leg movements shown in A and B. The leg movement inset was made by bringing together the white lines for each leg at the point where they meet the body, which represents a point that would not move relative to the body. The lines are also slightly expanded for viewing. (C) The FTi and CTr joint movements of the hind leg were digitized in the ventral view and smoothed to generate these records. Arrows indicate the points where the tarsus touched down upon the belt (downward arrows) at the beginning of stance and lifted off (upward arrows) at the onset of swing.

(Fig. 2). The front legs are unique in making extensive use of the three degree of freedom (DoF) TC joint even during typical walking movements. During swing, the coxa is rotated to move the leg foreword of the connection of the leg to the thorax at the TC joint (Fig. 2B). The action of the coxa is not as obvious in other insects such as locusts and stick insects where the legs are attached laterally to the thorax. Nevertheless, the forward extension of the front leg is consistent in virtually all insects and vertebrates.

The foreword extension of the front leg requires that CTr and FTi joint activity also be more complex than that seen in the other legs (Tryba and Ritzmann, 2000). During swing, the CTr and FTi joints of the front leg extend. Contrast this with the other legs where extension is typically associated with stance. After the front tarsi touch the substrate, the leg enters stance phase and is drawn backward. In many cases

the leg joints perform a second extension after the leg passes behind the axis of the TC joint.

2.2. Comparison to vertebrate patterns

The specific movements of the front and rear legs of the cockroach are in many ways similar to the actions seen in quadruped vertebrates, and especially mammals. Here we find our first lesson in convergent evolution. In mammals as in insects, we find specialization between rear legs that provide power for forward locomotion and front legs that provide braking and searching movements. Again, front legs extend forward from a perpendicular line from the shoulder joint to the substrate. In mammals, the forward movement of the front legs is accomplished largely by a skeletal element that rotates along the back. As with insects, gait changes
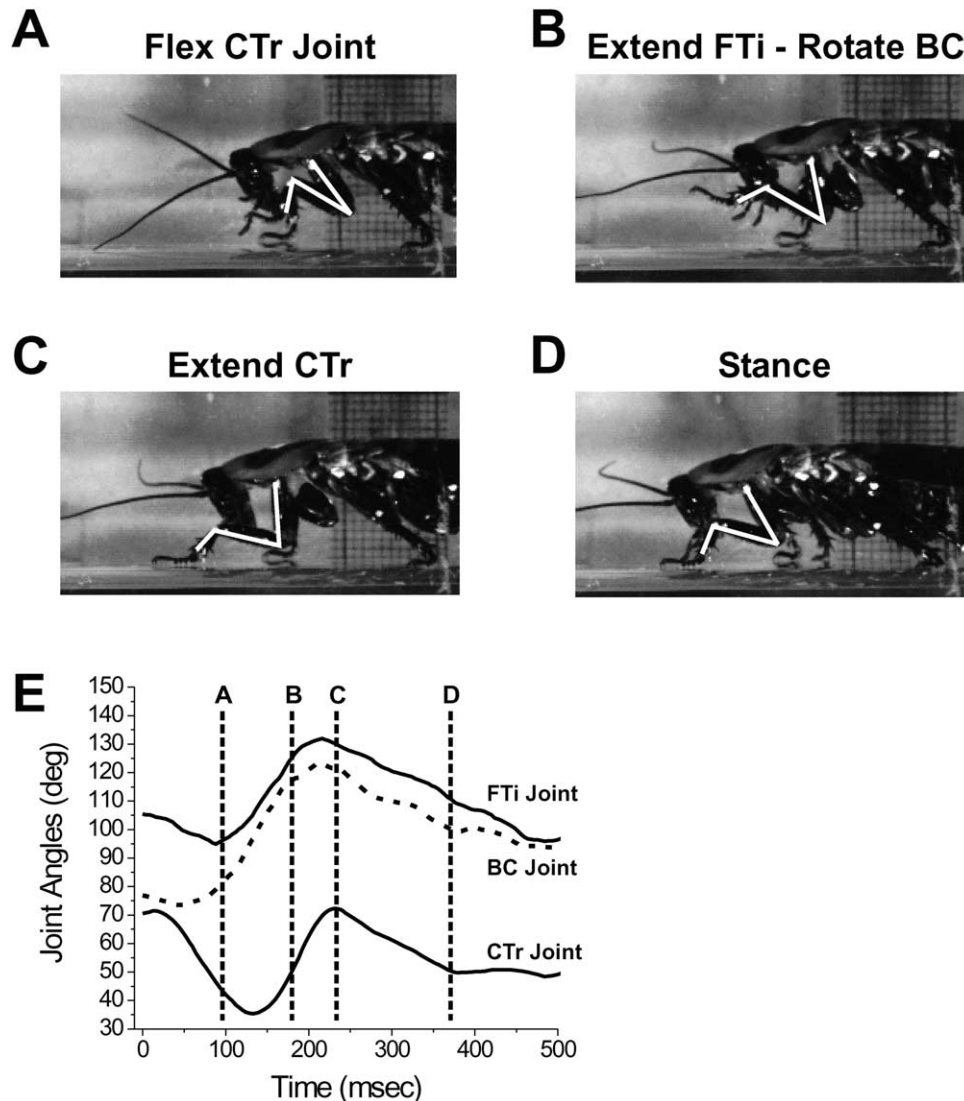
Fig. 2. The swing movements of the left front leg during horizontal walking are shown both as pictures and as graphs of joint angle changes. The pictures in A through D are frames from a side view high speed video record. A ventral view was also taken but is not shown here. With these two views the three dimensional joint movements cold be established using trigonometric functions. (E) The three dimensional joint movement of the FTi and CTr joint and the two dimensional movement of the TC joint (dashed line) is depicted graphically. The time at which each of the frames in A–D took place is indicated with dotted lines. Note that the leg lifts off (A) largely by flexing the CTr joint (joint angle decreases in E). In (B), the tarsus swings forward. That movement occurs by a rotation of the coxa leg segment at the TC joint along with an extension of the FTi joint (note parallel changes in E). In (C), the CTr joint has extended to bring the tarsus down to the substrate and begin stance. During stance (D) the body moves over the TC joint.

occur as quadruped mammals increase speed, going from 'symmetrical' gaits used in walking and trotting to 'in-phase' gaits found in galloping and bounding.

Specific leg structures varied as vertebrate evolution progressed from the two-segmented, sprawled tetrapod limb found in lower vertebrates to the three-segmented limb of mammals This change represents a decisive 'moment' in the evolution of mammalian locomotion (Fig. 3A and B). To appreciate the specializations found in front and rear mammalian legs, we must first understand how the leg segments are typically described. When we count the elements of a vertebrate limb, we neglect the most distal part (autopodium) because it has no or almost no propulsive component—except for the elongated mammalian metatarsus. Two of the segments in mammalian fore- and hindlimbs are serial homologues. They are the humerus and forearm of the front leg and the thigh and shank of the hind leg. However, in going to three segment limbs, the addition of a third element is achieved in different ways on the fore- and hindlimb. A proximal segment is added to the forelimb (the shoulder blade or scapula) whereas on the hindlimb an existing, distal element becomes a segment of its own with a specific ankle joint (Fig. 3A and B) (Jenkins and Weijs, 1979; Fischer, 1999; Fischer et al., 2002). Thus, as in insects, we also find distinct specialization of leg pairs in mammals. In the mammalian forelimb, the three segments
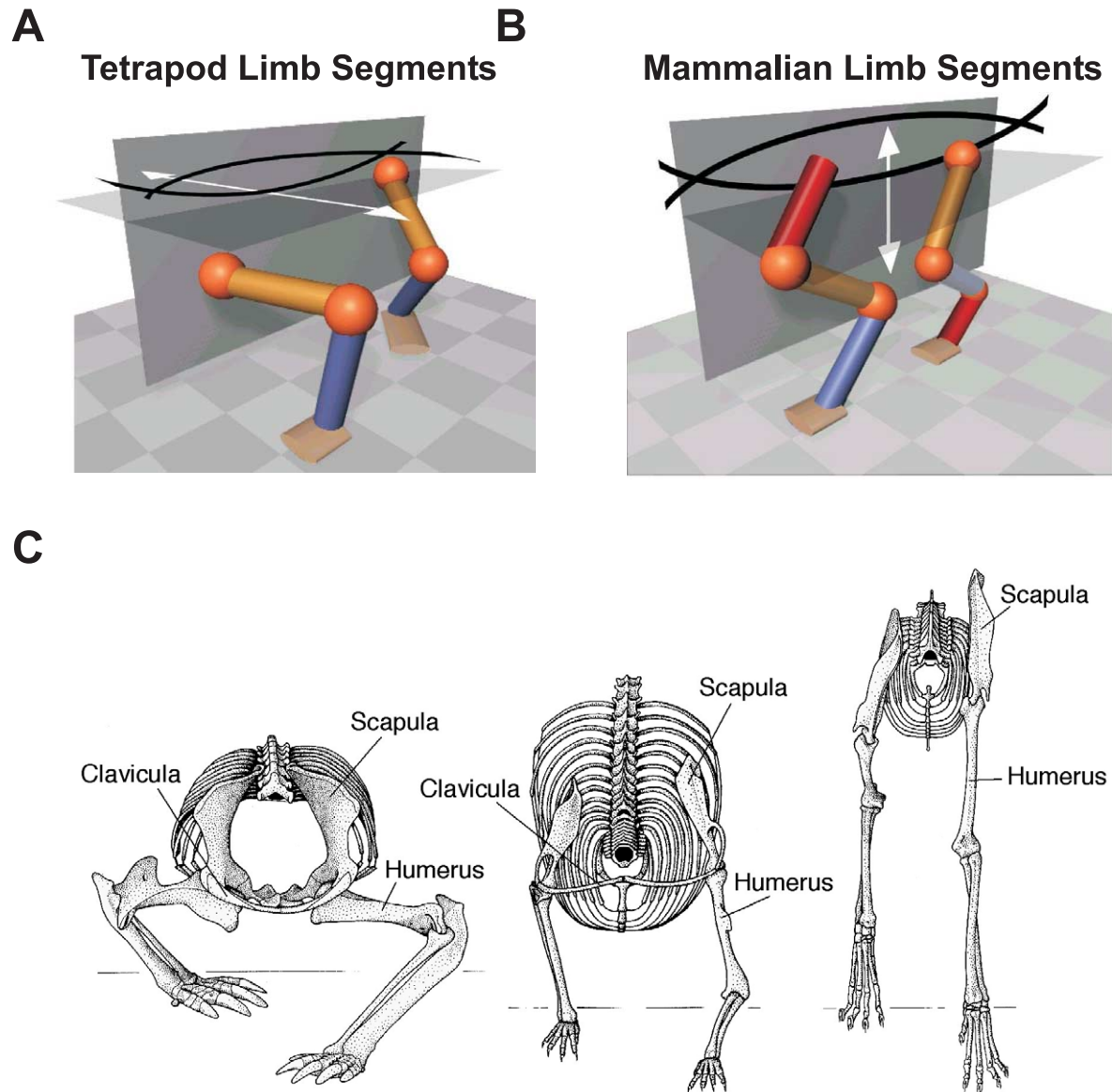
Fig. 3. (A) Leg design as seen in lower vertebrates such as salamanders. Note the body is depicted as moving laterally and the two legs have two segments each. (B) The design for mammalian limb segments have three segments each. The additional segments are red. The front leg has added a proximal segment while the hind leg has added a distal segment. (C) shows diagrams of skeletons of three different mammals (from left to right a monotreme called Tachyglossus, a rat and a cat) showing the front limbs and scapula of each.

are made up of the scapula, humerus and forearm (Fig. 3C), whereas in the hindlimb they are made up of the thigh, shank and foot.

There are important kinematic consequences of the reorganization of the vertebrate postcranial locomotory apparatus. The position of the forelimb's pivot now lies at the superior border of the shoulder blade. This position assigns to the scapula the dominant role in forelimb propulsion. In general, more than two-thirds of forelimb stance length (distance from foot down to foot up) is due to scapular rotation and translation (movement along the thorax) independently of the gaits. The new forelimb segment, the scapula, is either held by the clavicula or, as in most mammalian groups, is completely freed from any

connection with the trunk. The sliding movements of the shoulder blade are then purely guided by muscular forces with no articulation or ligament found on its border.

Forelimb movement relies largely upon pivoting the most proximal leg segment, the scapula (Fig. 4). Retraction of the scapula (sometimes referred to as 'extension', Miller and van der Meché (1975), English (1978a,b) and Boczek-Funcke et al. (1996) or 'caudal rotation', Fischer (1994, 1998)) starts from a minimum angle of around 40° (between the scapula and the horizontal plane) in the late swing phase. Touch down angles of the scapula are at $45° \pm 7°$ in all species and gaits (Fischer et al., 2002). Retraction of the scapula is continuous until the last quarter of stance phase. Then the rotatory movement stops, and in

aclaviculate species a displacement along the thoracic wall follows. Lift off angles are measured to be at 90° ± 11° (Fig. 4).

The effect of the scapular movement is similar to the rotation of the coxa seen in cockroach locomotion (compare Figs. 2 and 4). As with the scapula, the coxa of the cockroach's forelimb swings during most of the stance phase of that leg. Unlike the hind leg where coxa movement is limited and CTr extension dominates stance, in the forelimb the CTr joint serves primarily to lift the tarsus as the leg enters swing and set the tarsus down at the onset of stance. CTr extensions at the end of swing also serve to reach the tarsus somewhat more forward prior to entering stance.

2.3. Robotic leg patterns

Background on insect inspired robotics. Before describing how the patterns of leg design described above have been captured in our current robots, we first briefly provide some background on previous and current projects. Space does not permit an exhaustive review of these projects. Several of them are described elsewhere in this issue. The reader is also directed to other volumes for more information (Ayers et al., 2002; Muscato and Longo, 2003).

Ghengis was one of the first insect inspired robots and each of its six identical legs had two degrees of freedom (Brooks, 1989). Robot I (Espenschied et al., 1993), Robot II (Espenschied et al., 1996) and TUM (Pfeiffer et al., 1994) were the first robots to our knowledge to benefit from the stick insect coordination mechanisms (see Dürr, Schmitz and Cruse in this issue). These mechanisms modify the gait of a legged vehicle based upon its speed and other external and internal cues. TUM, inspired by stick insect, is one of the first hexapod vehicles to be designed with leg kinematics approximating those of a particular insect. Lauron, Lauron II, and Lauron III, have also been developed with the stick insect configuration and using 18 DC motors (Berns et al., 1994; Kepplin and Berns, 1999; Gassmann et al., 2001). Lauron III has successfully walked in many real world environments such as in forests and mountainous terrain. Protobot was one of the first robots to be designed with legs geometrically similar to cockroach legs (Delcomyn and Nelson, 2000). However each leg has only three degrees of freedom and is therefore kinematically different than a cockroach or Robot III discussed below.

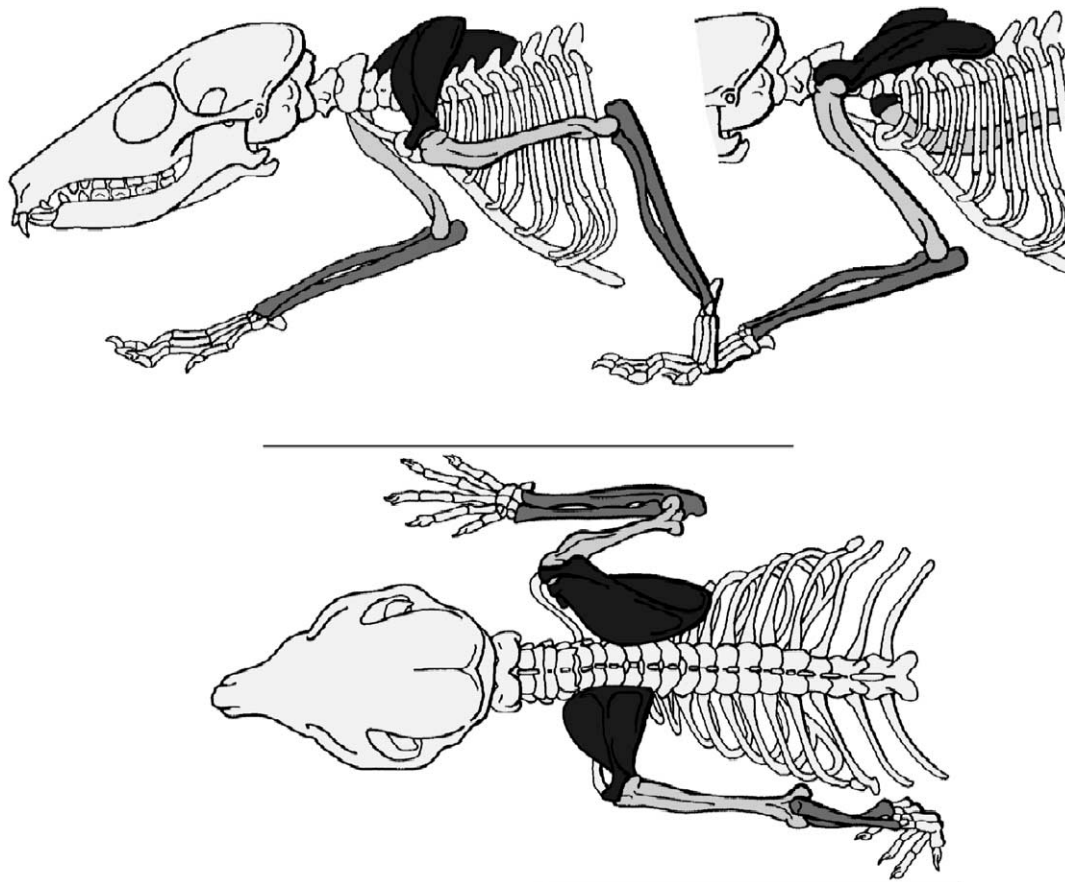*Cockroach inspired leg designs*. The consistently

Fig. 4. Diagrams of a Tupaia skeleton in side view and dorsal view with the front leg segments and scapula clearly indicated (shaded). Note the forward and rearward leg movement coupled with the rotation of the scapula. Compare these images to the front leg movements of the cockroach in Fig. 2 and especially compare the scapular movement with the rotation of cockroach coxa. This figure is courtesy to Dr Nadja Schilling.

specialized front and rear legs of both insects and vertebrates, that were described above, suggest important design principles, with hind legs maximized for driving force and front legs generating braking actions and variable reaching movements that allow the animal to explore the terrain it is entering. Nevertheless, most hexapod and quadruped robots ignore these principles and have similar legs at each position. There are some notable exceptions such as Protobot described above. Sprawlita is a hexapod with leg pairs that are similar in design, but they are oriented differently to abstract the different functions of the cockroach's leg pairs (Clark et al., 2001). The leg pairs of TUM are also oriented differently relative to its body to mirror the leg orientations of the stick insect (Pfeiffer et al., 1994).

One of our robot lines does in fact capture the joint and leg segment architecture of the cockroach. To design these robots, the movements of the cockroach were examined in high-speed video and the joint actions were digitized frame by frame. Those data were then used in a dynamic simulation to determine the minimum set of joint movements necessary to generate walking and climbing actions of the cockroach.

The dynamic models indicated why the designs found in the cockroach are important. In order to capture the mechanical actions of the cockroach in Robot III, we were actually forced to use distinctly different designs for each pair of legs (Nelson et al., 1997). The simple propulsive actions found in the hind legs required only three DoF and so we limited the design to those essential actions (Fig. 5). For walking, the middle legs could probably also be made with three DoF. However, during climbing, these legs must rotate the coxa to reorient the leg so that extension of the coxa–femur (CF) and FTi joints generate a rearing movement that pitches the front end up and allows the front legs to be placed on top of barriers. Note that the robot's legs do not have a separate trochanter segment, so here the coxa

connects directly to the femur. The cockroach's climbing behavior will be described in detail below. However, it is important in the leg design, because the rotation of the middle legs requires a fourth DoF (Fig. 5). The complex reaching actions of the front legs required five DoF including all three actions of the TC joint and the single DoF CF and FTi joints (Fig. 5).

The robot's TC joint is similar to that of the insect. It permits three independent, nearly orthogonal rotations of the coxa relative to the thorax. The CTr joint on the insect, which enables the femur to rotate relative to the coxa in the plane of the leg, is also preserved on Robot III, but the trochanter–femur joint on the insect, which enables out of plane rotation, is not included on the robot. The FTi joint on the insect, which enables rotations of the tibia relative to the femur in the plane of the leg, is preserved on the robot. The six segments that are connected by compliant mechanisms and make up the tarsus on the insect are abstracted as a single structure acting as a compliant foot on the robot.

A five DoF leg is difficult to manufacture, actuate and control. However, in order to capture the forward movement of front legs that appears to be important in both insects and vertebrates, we had to include all of these actions. Interestingly enough, the actions that are seen as Robot III's front legs go from stance to swing are very similar to those seen for the vertebrate depicted in Fig. 3, even though it was designed to capture the motions of the cockroach (Fig. 6).

Animal-like mechanics came with a price. With the complex designs of these legs, control became an issue. The problem was even greater given the pneumatic actuators that we used to generate forces necessary for large payloads and rapid locomotion. One problem associated with pneumatic actuators is their sluggishness as compared to electric motors. However, the associated time delay is similar to that found in the circuits of animals, and as such, should be surmountable.
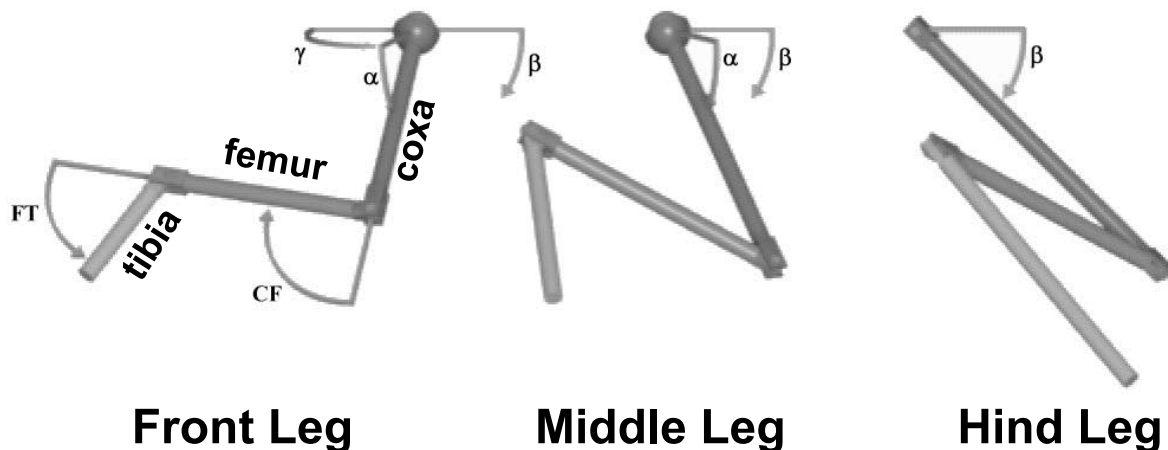

Fig. 5. Diagrams of the leg designs that were used for Robot III and subsequent hexapod robots in that series. The segments are labeled for the front leg. Note that the dimensions of the segments differ from leg to leg. Also, although all three legs have a degree of freedom (DoF) at each of the FT and CF joints, the thorax-coxa joint differs in the three legs. The rear leg has only one DoF (β), the middle leg has two (α and β) and the front leg has three DoF (α, β and γ).
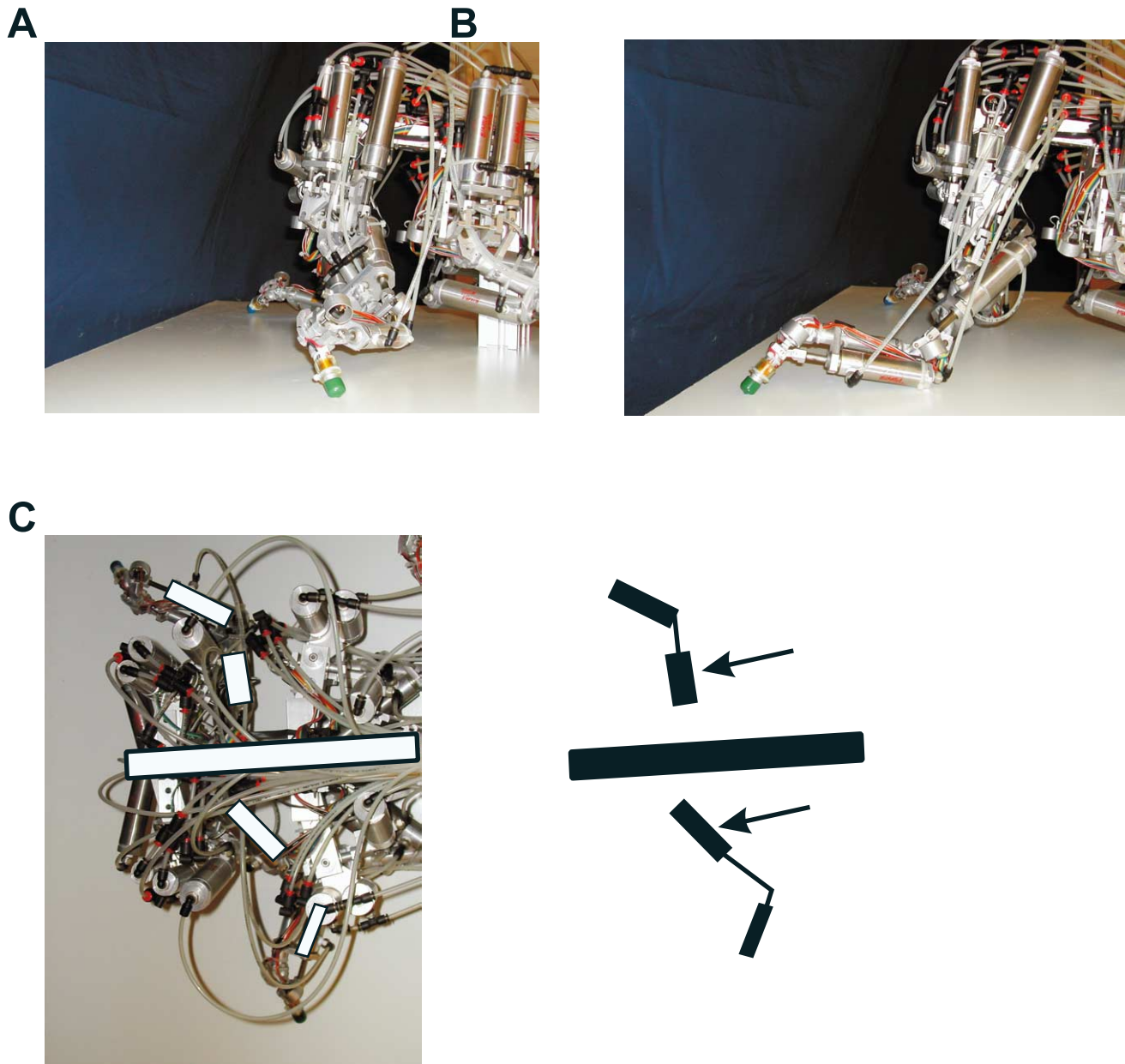
Fig. 6. Front leg actions of Robot III. (A) shows the front leg retracted at the end of stance. (B) shows the same leg extended at the end of swing (beginning of stance). (C) is an image of the robot from the top with the left leg as in A and the right leg as in B. Because pneumatic tubes clutter the view, coxa and femur actuators that are parallel to the coxa and femur segments are highlighted with white boxes along with the central skeleton and reproduced in black in the inset to the right. Compare these images to the pictures of the Tupaia skeleton in Fig. 4 and the cockroach leg movement in Fig. 2. Interestingly, the action of the proximal actuator (arrows) (one of the three thorax–coxa actuators) is very similar to the scapular movement, in spite of the fact that it was designed to capture the movement of the cockroach front leg.

The most elemental control problem that had to be solved was to cause a single joint on the robot to follow a specific trajectory. We chose to use simple proportional position control. Velocity control was found to be unnecessary because passive damping resulted from air flowing into and out of the actuators. The control torque at a joint was computed at a low level in the control circuit. It was equal to a control gain multiplied by the difference between the actual and desired positions of the joint. Joint motion can result when the desired foot position changed with time. At

the lowest level of the control system, the joint torque was converted to a duty cycle for pulse width modulation of the inlet and exhaust valves that controlled that joint.

The complexity presented by the front legs was particularly problematic. Moving the foot of one of Robot III's front legs in a cockroach stepping pattern requires coordinating the joints of the leg, which entails solving the inverse kinematics problem for a five DoF leg. This means that a set of joint angle trajectories must be determined that will cause the foot to move as desired. The problem is that a

leg with more than three DoF is said to be kinematically redundant because there is more than one set of joint angles that can place the foot in a particular position. In other words, the Jacobian matrix cannot be simply inverted to solve the inverse kinematics problem. A number of solutions have been published to solve kinematically redundant manipulator problems (Hollerback and Suh, 1985). We chose to use a variant of one presented by Mussa-Ivaldi and Hogan (1991), which is detailed in Nelson and Quinn (2001). This method provides a kinematic solution that minimizes the strain energy in the limb. It also preserves the instantaneous mobility of the limb by producing a solution for the joint angles that is as close as possible to their mid range positions.

When Robot III was suspended and this leg coordination circuit was coupled with the joint controller, each leg pair cycled its feet in the cockroach like stepping motion appropriate for that pair. The front legs extended to reach forward in swing far in front of their TC joints (Fig. 6), the middle legs cycled their feet fore and aft of their TC joints, and the rear legs moved their feet in a piston like manner well aft of their TC joints. However, without a gait controller, the legs moved independent of each other.

The next control problem was to coordinate the legs to produce insect gaits. The stick insect leg coordination network as reviewed by Cruse (1990) and simulated by Dean (1992) was used for this purpose. It is also described in another article in this issue (Dürr, Schmitz and Cruse). This remarkably simple network was shown to produce insect gaits efficiently and robustly in previous robots developed in the Case Biorobotics Lab as well as by other groups described above. Both Robot I and Robot II walked in metachronal gaits ranging from the wave gait to the tripod (Espenschied et al., 1993, 1996). However, Robot III is different from these previous robots in that it captures the unique design of each leg pair. This means that the joints of each pair have to move differently in order to move their feet through similar stance paths. Fortunately, this did not pose a problem after the inverse kinematics problem was solved as described above. With the joint, leg, and gait controllers implemented in its lower level control system, Robot III was shown to be able to cycle its legs smoothly in insect gaits while suspended above the ground.

Robot III has both the power and the leg designs to walk and climb over rough terrain. It can stand and lift a payload greater than its own weight and it can cycle its legs in cockroach-like patterns. However, animal-like locomotion has not been achieved because it has a low bandwidth actuation system and no passive actuator stiffness. A retrofit with additional valves such that air can be trapped in its air cylinders and provide passive stiffness would solve this problem. This has been shown to be the case for our newer cockroach robot, Robot V, which uses McKibben artificial muscles and has a valve configuration that enables air to be trapped in its actuators (Kingsley et al., 2003). Because of this passive stiffness it can stand and walk in a limited

manner with no sensor feedback. With a complete control system, it should be able to walk and climb barriers. Both of these robots have leg designs that would allow the robot to make the kinds of movements executed by the cockroach in walking and climbing.

Simplified leg designs. Robot III's control issues explain why designers of most legged robots opt to ignore the leg specialization found in both insects and vertebrates. Even though these principles may be required in order for an agent to walk like an animal, one can accomplish much with a simpler design. For example, it is not necessary to build a robot as complex as Robot III to accomplish a tripod gait. One of our earlier hexapod vehicles, Robot I, used only 12 electric motors to walk in the continuum of metachronal gaits (Espenschied et al., 1993). Furthermore, PROLERO, developed by the European Space Agency had only one motor per leg and walked in a tripod gait (Martin-Alverez et al., 1996). More recently, Saranli et al. (2000) and Altendorfer et al. (2001) developed a vehicle called RHex that also used only six motors to move in a tripod gait. The strategies employed in the design of RHex are described in detail in another article in this issue (Koditschek, Full and Buehler).

Our Whegs (© R. Quinn) line of robots generates a tripod gait with only one large propulsive motor (Quinn et al., 2002, 2003). These robots use three-spoke appendages called whegs that represent a compromise between wheels and legs (Fig. 7A). The tripod gait is accomplished by simply configuring the whegs with one spoke on each middle wheg in phase with a spoke on each of the front and rear whegs on the opposite side of the body. When a spoke of a wheg completes its stance phase, another spoke on the same wheg is two-thirds of the way through its swing phase and nearing stance, and the third spoke (the last to complete stance) is one-third of the way through its swing phase. Therefore, there is no need for a single spoke to be accelerated rapidly through its swing phase allowing the wheg to be driven at a constant speed while performing the function of a leg. As a result, a single motor can be used to drive all six whegs through chains and sprockets.

With this configuration, Whegs vehicles would have a fixed tripod gait and could not adapt to their environment as insects have been observed to do. For this reason, we have implemented torsionally compliant mechanisms in all six axles of the Whegs vehicles (Fig. 7B). Because the motor drives each wheg through a torsion spring, a wheg that encounters a large disturbance force is retarded as the spring is strained by the motor. These compliant mechanisms allow passive gait changes that bring whegs of the same segment into phase to climb over objects or walk up a hill.

Whegs robots have the advantage of simplicity and yet they can run quickly and climb large obstacles, benefiting from their passive gait adaptation. However, they lack the specialization that is described above for insects, vertebrates and Robot III. Can their performance in complex terrain be enhanced by providing some degree of leg specialization?

A   Hexapod Whegs Robot
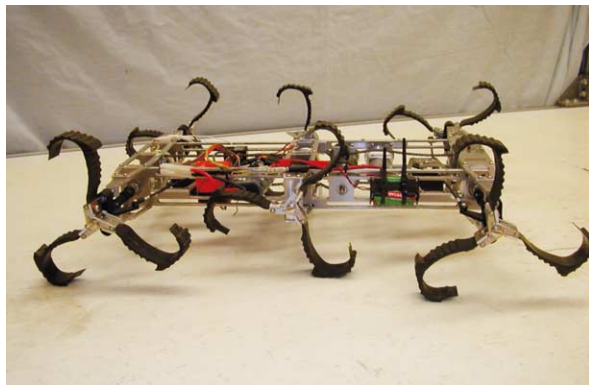
B   Diagrams of Torsionally Compliant Mechanism

Drive Shaft

Wheel Axle
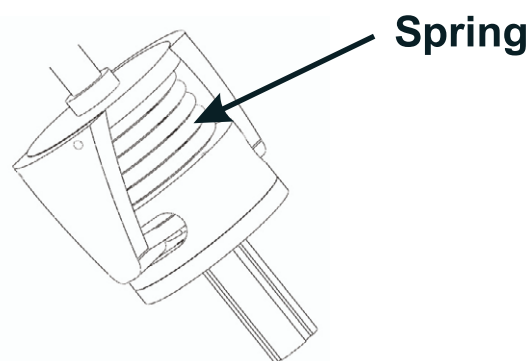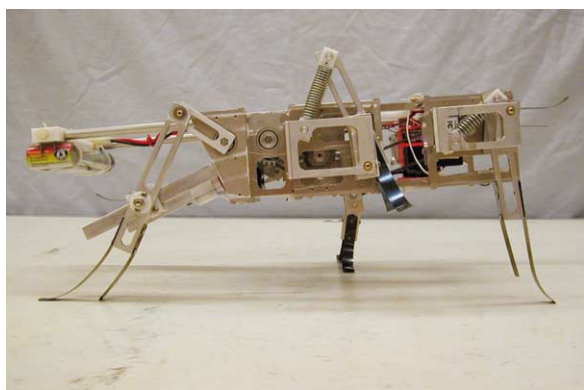
Spring
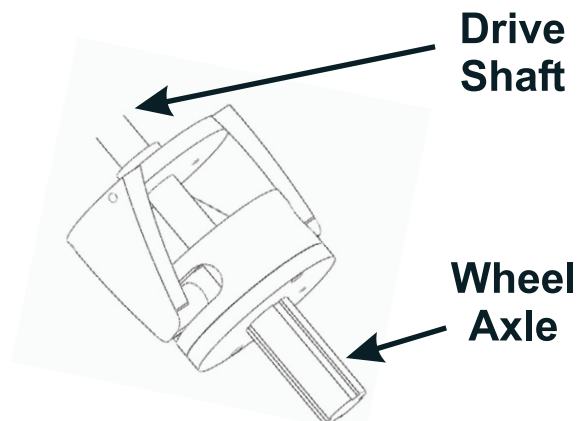
C   Mecha-Roach Robot

Fig. 7. Two examples of abstracted robots. (A) A picture of a hexapod Whegs robot clearly shows the three spoke whegs appendages, in this case ending with rubber feet. (B) These diagrams describe the torsionally compliant mechanism used in Whegs robots. The top diagram has the spring removed to show the axle and rotational limiting mechanism. The bottom diagram shows the same device with the spring in place. (C) Mecha-roach has similar rotatory actuation, but uses four-bar mechanisms to generate specialized movement of the front, middle and hind legs.

To examine this question, we are developing a third robot line that represents a compromise between our two extreme strategies. The first of these robots, Mecha-Roach (Fig. 7C), uses a single drive motor to move all six legs as is the case with Whegs (Boggess et al., 2004). However, specialized four-bar mechanisms replace the three spoke whegs. These mechanisms were designed to move the feet of each leg pair through paths that are similar to those observed in the cockroach. As a result, we have captured some of the pairwise leg specializations found in Robot III using reduced actuation. Mechanical coupling causes the legs to move in a tripod gait while being driven by the one large motor.

We are examining the performance of this robot with high-speed video imaging. Already, some benefits over the standard Whegs design have been noted. For example, because Mecha-Roach swings its front legs high in a cockroach like manner, it can climb obstacles leg high without changing its gait.

3. Body flexion

3.1. Vertebrate axial movements

Body flexion is critical for swimming vertebrates such as fish and marine mammals as well as terrestrial vertebrates such as salamanders and snakes that undulate laterally to generate forward motion. As with limb geometry, the orientation of the prevailing axial movements has also completely changed from amphibians and reptiles to therian mammals. While the ancient action was lateral bending, the mammalian vertebral column is flexed and extended dorsoventrally to generate a sagittal bend (Fig. 8) (see Fischer, 1998 for additional references). As a result, the fish caudal fin is vertical while the whale fluke is horizontal. Sagittal spinal movements are the effect of small intervertebral actions adding up to what is called pelvic movements. In addition, a complex three-dimensional
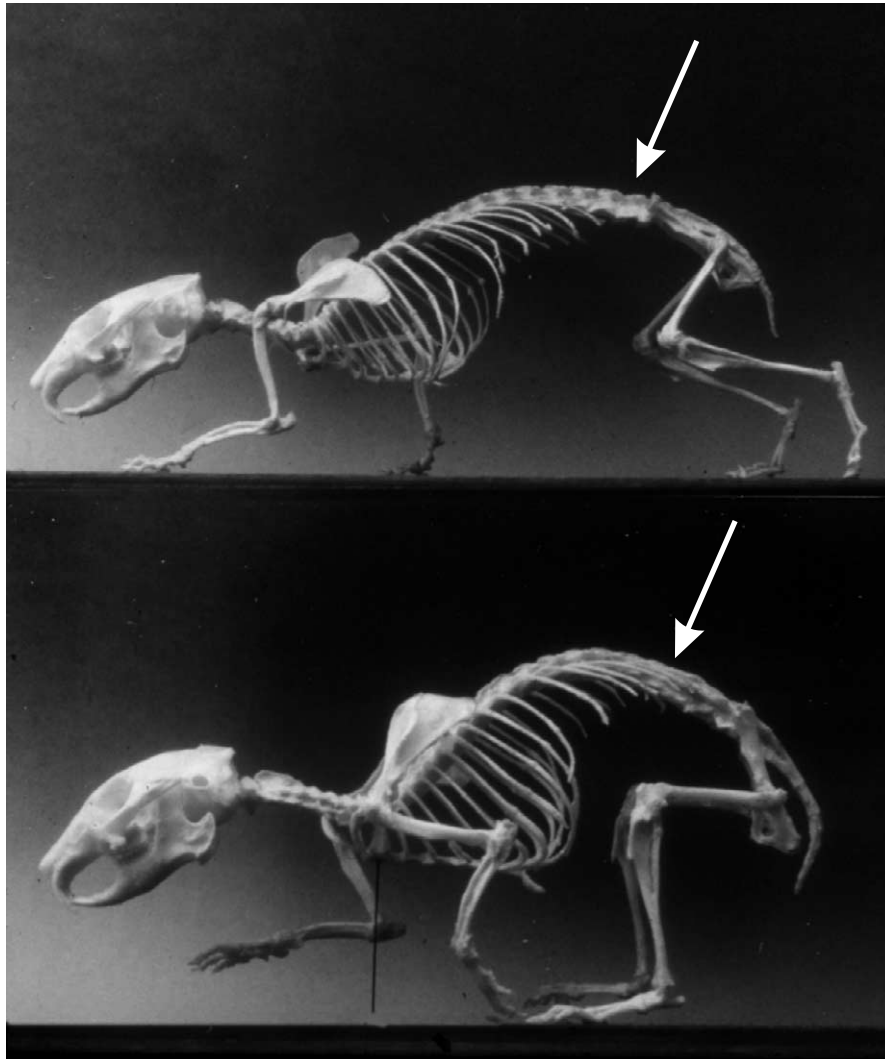
Fig. 8. A skeleton of a pika placed in two extreme positions that would be taken during a half-bound. Note the flexion of the spine (arrows) that is important to bringing the legs under the body.

movement ('tilting') of the pelvis occurs in therian mammals during symmetrical gaits (Jenkins and Camazine, 1977). This rotatory movement of the pelvis, which again is only the effect of additive lumbar spine actions, is especially pronounced in humans. Here the upper trunk rotates against the pelvis and vice versa in a constricted region or 'waist' (Witte et al., 1991; Witte, 2002).

During in-phase gaits (gallop, bound, halfbound) a composite of the lower back region and pelvis actually acts as a fourth functional segment (Fig. 8). Moreover, as the pelvis is immovably connected to the spine in the iliosacral joint, any movement of the spine will not only lead to a pelvic rotation but to a compulsory movement of the hindlegs. Thus, the hindlimbs of mammals are, strictly speaking, only three-segmented in symmetrical gaits (walk, trot), while in in-phase gaits they consists of a four-link chain.

Back limb drive is executed mainly in the hip joint in symmetrical gaits while in in-phase gaits sagittal move-

ments predominantly of the lumbar region take over a considerable part of propulsion (Fischer et al., 2002). More than half of hindlimb stance length is due to sagittal spine movements in in-phase gaits. While pelvis contribution is low in symmetrical gaits, it augments even more than 50% of total step length in in-phase gaits. This increase is accompanied by a strong decline in hip joint contribution, which is otherwise dominant in symmetrical gaits.

3.2. Body flexion in insects

A cuticular exoskeleton is one of the identifying characteristics of arthropods. However, far from being a rigid body, most arthropods have joints along their bodies with muscles that are capable of flexing the thorax dorsally or ventrally. The degree of motion varies from crabs, with rigid bodies, to insects such as cockroaches that have flexible joints at each thoracic segment.

Cockroaches use these body joints to maintain appro-

priate leg orientation as they traverse objects. For example, they flex their thorax as they climb over objects. In particular, the joint between the first and second thoracic segments bends downward as the animal reaches the top of a barrier (Fig. 9A). By so doing, the center of mass remains at an appropriate level and the legs maintain appropriate angles relative to the body to generate efficient movements. If the thoracic segments are held rigid by attaching a wooden splint across them, the animal high centers badly. That is, the animal's center of mass rises awkwardly high above the substrate. As a result, the legs must extend along the long axis of the body just to contact the top of the barrier. This leg orientation decreases mechanical advantage for those legs and makes efficient leg movements very difficult (Fig. 9B).

In click beetles, we find a particularly interesting use of body flexion. With a small modification of their first thoracic segment, these insects create an effective catapult. To generate this movement, the first thoracic joint is accompanied by a peg that restricts movement until flexion muscles contract to generate a large amount of potential energy (Evans, 1972). At that point, the peg slips allowing body flexion to proceed very rapidly. The resulting high acceleration propels the click beetle upward in a legless jump (Fig. 10A–D). The jump is effective enough to elevate a beetle that is less than an inch long up to a height of four inches above the substrate. This behavior inspired a similar catapult system for small Whegs robots that is described below (Fig. 10E).

3.3. Body flexion in robots

In spite of the importance of body flexion to locomotion in both vertebrates and many arthropods, most legged robots have rigid bodies. Indeed, this might be one of the reasons that they 'walk like robots' in a less fluid manner than that seen in animals. We tested this notion by incorporating body flexion into one of our Whegs robots.

Whegs I did not have a body flexion joint and this limited its performance in two ways. First, with its three-spoke wheg design it could only reach as high as 1.5 leg lengths and so it was limited to climbing over obstacles that were only slightly higher than that (Quinn et al., 2001). Second, when it climbed over large obstacles it high centered because it could not flex its body and reach its front whegs down toward the substrate (Fig. 11A). Because of this limitation, Whegs I and other whegs vehicles of similar design tend to flip over backwards when they try to climb very large obstacles (Quinn et al., 2001; Schroer et al., 2004).

Whegs II was designed with a bi-directional body joint that coincides with its middle axle (Allen et al., 2003). The upward motion makes up for one of the limitations of the Whegs design. In order to climb over a tall object, the cockroach rotates and extends its middle legs generating a rearing movement that allows it to place its front legs on top of an object (described in more detail below). Whegs I cannot do this because each wheg is limited to one rotation. However, Whegs II can rotate its body joint upward in a simulated rearing movement, so it can, in fact, place its front whegs on top of taller obstacles. Upon reaching the top of a barrier, the cockroach flexes its body to prevent high centering and maintain effective leg postures. Whegs II's body joint performs the same function and generates a fluid animal-like climb (Fig. 11B). Combining these body joint functions during obstacle climbs has resulted in Whegs II climbing over rectangular obstacles greater than twice its leg length.
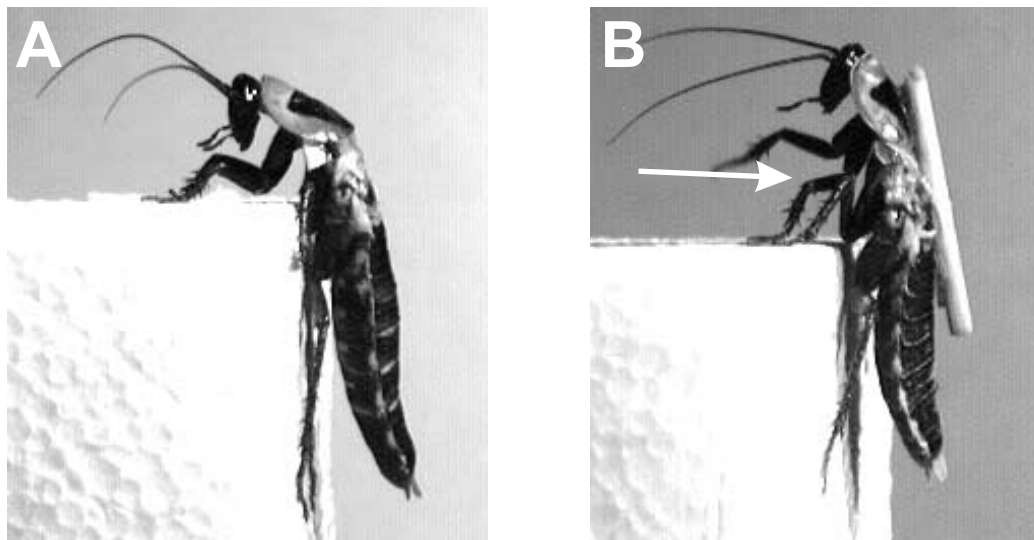

Fig. 9. The importance of body flexion to cockroach climbing is demonstrated in two frames from high speed video records. (A) An intact cockroach reaches the top of a large Styrofoam block and flexes the T_1–T_2 joint downward to keep the leg angles at good mechanical positions. (B) The same cockroach climbing the same block after the T_1 − T_2 joint movement is prevented by gluing a wooden splint over it. Now the animal high centers badly and shows inefficient leg positions with front legs extended awkwardly downward (arrow).
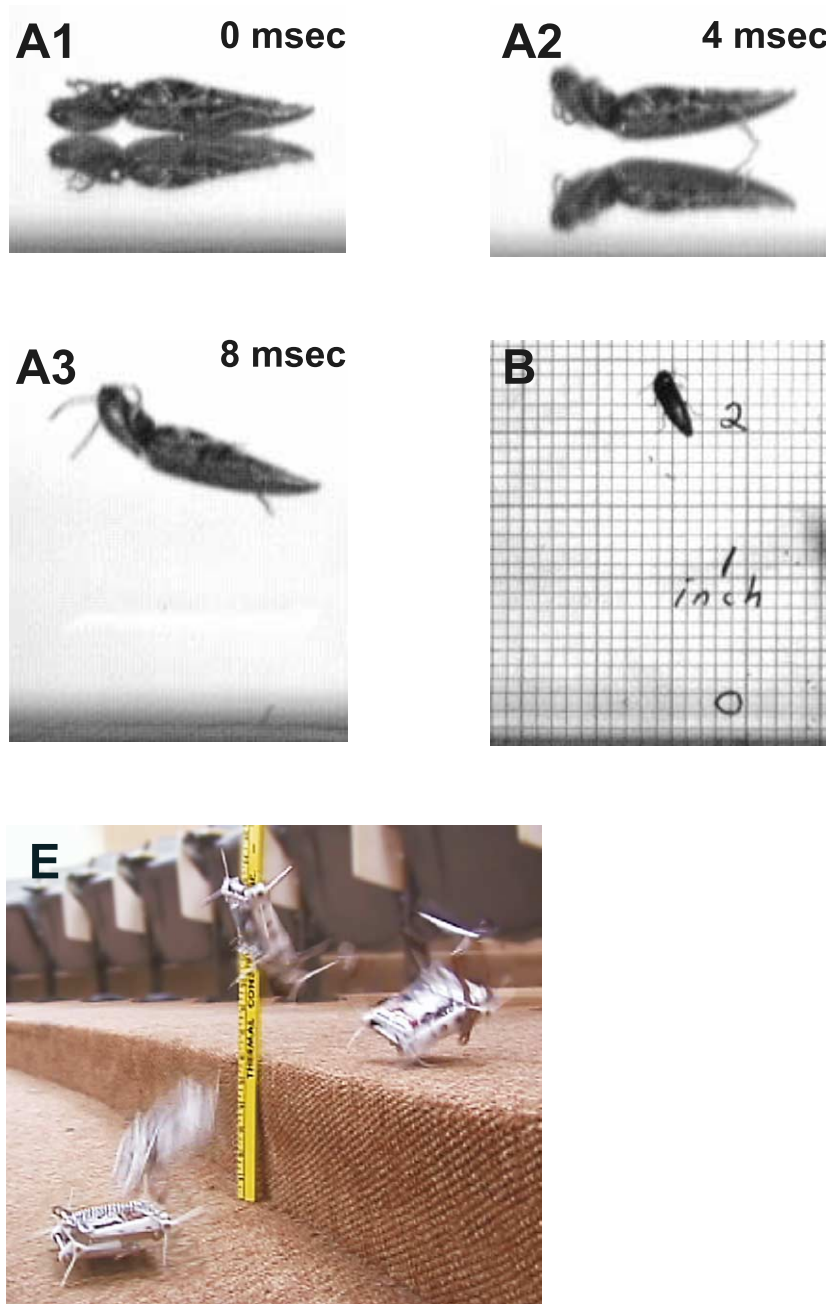
Fig. 10. The jump of the click beetle. A1 to A3 show three frames of a high speed video record taken during the jump of a click beetle. Time is indicated in each frame. The animal starts on its back, then within 4 ms the body has flexed upward (ventral flexion) and raised off the ground. By 8 ms the jump is well under way. (B) is a more distant image of another jump showing the beetle rising up above a two inch mark. Other jumps exceeded 4 in. (E) A small quadruped Whegs vehicle jumps over a step using a catapult device similar to the action of the click beetle. Multiple exposures are seen here.

The jump of the click beetle is an example of a behavior that is unique to a small subset of insects, but provides a particularly useful solution to some robots. Whegs vehicles can be designed to various scales. Mini-Whegs are small quadruped vehicles 8–9 cm in length that are very agile and robust (Morrey et al., 2003). They can scurry over 3.8 cm barriers with ease and fall down large stairs without damage, but, moving up stairs presents a serious problem. Even with a body joint, average size stairs would present an impossible barrier. However, a jumping movement similar to that found in the click beetle could allow the robot to proceed. To address this need, we implemented a jumping mechanism that winds up during walking and stores energy in much the same way that strain energy is stored in the click beetle's thoracic muscles. Release of this energy generates a vigorous movement allowing the robot to easily jump to the top of a 15 cm stair (Fig. 10E).

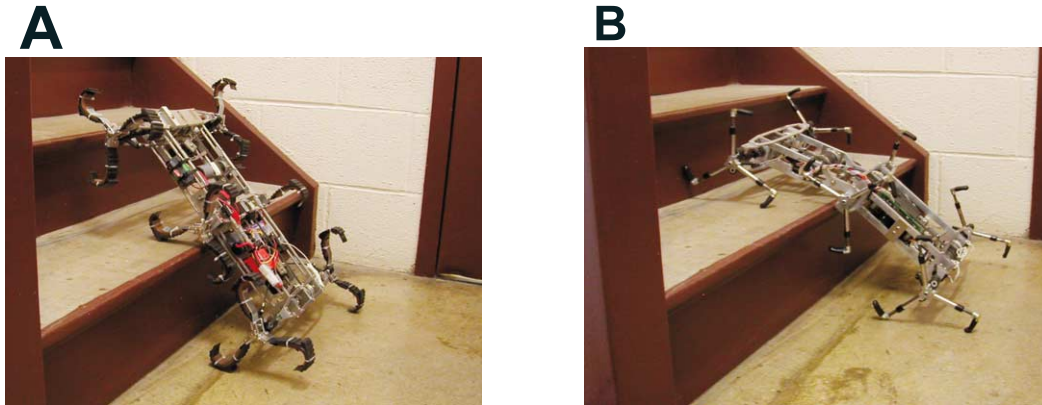**A**   **B**

Fig. 11. The importance of body flexion in robots. (A) shows a Whegs vehicle that lacks a body flexion joint climbing up a stair. It high centers and its front whegs are not touching the upper stair. (B) Another Whegs vehicle that does have a body flexion joint bends ventrally to keep its front whegs in contact with the substrate. By avoiding high centering, climbing is smoother, more efficient and more 'animal-like'.

4. Interaction with head sensors and ganglia

With specialization of leg design and function, animals or robots produce a preferred direction of movement. This asymmetry is not found in robots that have identical legs at each position. For example, an earlier robot produced by the Case Biorobotics Lab (Robot II) had a uniform leg design and walked equally well in either direction (Espenscheid et al., 1996). Whegs robots that lack body flexion also lack front to back specializations and can move in either direction or even upside down equally well. This bi-directionality can be beneficial when robots find themselves in tight crevices or fall over. However, the fact that most animals incorporate leg specialization along with movement in a preferred direction, suggests that this later plan has even more benefits. The cockroach-like leg specializations found in Robots III through V take advantage of powerful driving legs in the rear and more variable searching legs in the front (Kingsley et al., 2003).

With a preferred direction of movement, it is logical to create a head structure on which to place the majority of sensors that evaluate the environment that the robot or animal is entering. Thus, we find a wealth of sensors including visual, tactile, chemical and often auditory receptors located on the heads of most animals. By concentrating so many sensors on the head, it is appropriate to locate neural circuits that process the information from individual sensory modalities nearby in a brain (Gupta, 1987). This structure should also contain association areas that combine multisensory information into an image of the animal's surroundings and then use those data to generate commands for altering posture and changing patterns of leg movement as the animal negotiates barriers. In addition to sensory information, effective descending commands should be further influenced by the current state of the legs and previous experiences. Thus, brain circuits must include information that ascends from local motor control circuits as well as regions dedicated to short or long term memory.

Of course, our emphasis on the brain's role in guiding locomotory movements greatly simplifies its behavioral significance. Within the context of the animal's overall behavior, functions such as learning and memory, and selection and maintenance of specific behaviors reside in various regions of the brain. Thus, the insect brain is much more than a fusion of thoracic ganglia. Rather, we find unique neuropils such as the mushroom bodies (Mizunami et al., 1998) and central complex (Strausfeld, 1999) in highly developed brain regions. A thorough review of the role of higher centers in behavior is beyond the scope of this review. For more information on these topics, the reader is directed to several other excellent articles (Gupta, 1987; Homberg, 1987, Mizunami et al., 1998; Strausfeld, 1998; Staudacher, 1998; Strausfeld, 1998, 1999).

In both arthropods and vertebrates there is typically a gradient of influence on the various leg pairs, with hind legs moving largely independent of descending signals while front legs are greatly affected by them. In cockroaches, the front leg movements are much more variable than the middle and hind legs. Much of this variation may arise from a greater descending influence in the control of the front legs. Even in the escape response, which is often thought of as a reflexive behavior controlled by interneurons in the thoracic ganglia (Ritzmann and Eaton, 1997), we find a descending influence (Schaefer and Ritzmann, 2001). However, that influence shows a clear gradient with front legs affected much more than middle legs and hind legs affected the least. Thus, in cockroaches that have been decapitated or received bilateral cervical lesions, an escape response to wind or tactile stimuli include normal hind leg movements and reduced middle leg movements. However, the movements typically made by front legs are almost completely eliminated due to a severe reduction in the capacity for stimuli to activate fast motor neurons in front legs (Schaefer and Ritzmann, 2001).

A similar anterior to posterior gradient of descending influence is seen in vertebrates. Decerebrate or spinal cats can be trained to walk on a treadmill with their hind legs, but

their front legs typically do not participate (Rossignol, 1996). Also in cats, cortical neurons have been found that direct the movements of the foreleg, demonstrating a clear influence from the brain (Drew, 1993). Thus, it appears that there is a consistent rule that the forelimbs of legged animals are under much greater control by brain circuits than the more posterior appendages. As a result, forelimbs can generate variable searching movements, allowing them to function both as motor appendages and as sensory structures that examine the animal's immediate surroundings. In contrast, hind legs appear to be more purely involved in locomotor functions.

The general description in the previous paragraphs clearly indicates that the head is not simply a structure on which to mount antennae or visual systems, as is often found in 'heads' of robotic vehicles. The overwhelming amount of sensory receptors found on the heads of both arthropods and vertebrates requires a brain to process and utilize that information. For example, the large number of sensors located on the antennae of an insect creates a structure that is far more sophisticated than, for example, a feeler that is used to keep a vehicle from bumping into walls or other barriers. Rather it is used to influence complex changes in leg or wing performance or subtle changes in posture. These alterations can either anticipate movement around or over barriers or allow the animal to seek goals such as pheromones, food or mating calls. A discussion of these kinds of sensors and their implementation on robotic vehicles is found in another article in this issue (Webb, Harrison and Willis).

4.1. Directing climbing movements

The role of descending control from the head ganglia of insects can be appreciated by observing the animal's movement through complex terrain that requires evaluation and negotiation of barriers. Cockroaches of the species *Blaberus discoidalis*, readily negotiate barriers of various heights without the need for searching leg movements to reach the top of the object. When challenged with blocks that are lower than 6 mm, the cockroach simply continues to walk forward and moves over the barrier with little or no alteration in leg movement or motor activity (Watson et al., 2002b). The changes in posture and center of mass that must occur to lift the cockroach over the block are generated by direct interactions with the object. The front leg typically swings through an arc of approximately 6 mm. As a result, the tarsus of the front leg will land on top of a low object without any change in leg movement. The leg then pushes down and raises the body up so that normal extension of middle and hind legs drive the animal over the block. Thus, for these low barriers, alteration in body movement occurs as a consequence of interaction with the block rather than in anticipation of a required climbing behavior.

In order to negotiate blocks that are higher than its typical swing movements, the cockroach must do one of two things.

If it is running at high speed, it simply drives forward and relies upon the stability of its sprawled posture (Jindrich and Full, 2002) to stay upright as it scrambles over the objects. The properties that are important to these movements are discussed elsewhere in this issue (Koditschek, Full and Buehler).

At slower speeds, the cockroach alters the orientation of its middle legs in order to pitch its front end upward in a rearing movement that brings its front legs close to the top of the block (Fig. 12) (Watson et al., 2002a). Rearing height varies with the size of the barrier and is accurate enough that normal swing movements of the front legs can place their tarsi on top of the block without ever contacting the front of the object (Fig. 12) (Ritzmann et al., 2001; Watson et al., 2002a). Thus, the cockroach appears to have determined the height of the block prior to initiating a climb, making searching movements such as elevator reflexes unnecessary. During an elevator reflex, front legs would contact the barrier's front surface and respond by repeatedly swinging in higher and higher arcs until they reach the top of the object. These actions have been observed in climbs made by locusts (Pearson and Franklin, 1984) and under some conditions may also be used by cockroaches.

Once it has reared up, the cockroach extends the CTr and FTi joints of its middle and hind legs to push its center of mass upward. During this part of the climb, motor activity in the legs is enhanced to generate sufficient force to push the animal's body up and over the object. These changes in motor activity appear to result from reflex actions of local circuits within the thoracic ganglia (Watson et al., 2002a). Thus, a successful climb combines descending and local control. Descending pathways alter body posture relative to the height and location of the barrier then return control to local reflex circuits within the thoracic ganglia to adjust motor activity within the leg relative to this new posture.

4.2. Effects of brain lesions on climbing

If descending control is critical to the cockroach's capacity to negotiate barriers, it is not surprising that success is compromised by various types of lesions associated with the brain and suboesophageal ganglion. Cockroaches with bilateral cervical lesions take only a few steps with reduced coordination even after several days of recovery. In contrast, bilateral lesions of the circumoesophageal connectives actually increase the release of walking behavior (Roeder, 1937; Roeder et al., 1960). Indeed, for *B. discoidalis*, circumoesophageal lesioned animals (CoCLs) walk almost interminably (Pollack et al., 2003). This lesion leaves the suboesophageal ganglion attached to the thoracic ganglia but disconnects the brain.

CoCLs can climb over barriers but do so in a very different manner than that described above for intact animals. Rather than detecting and evaluating the object, CoCLs crash into the barrier and simply continue driving forward. Eventually, the animal slides up the front of its
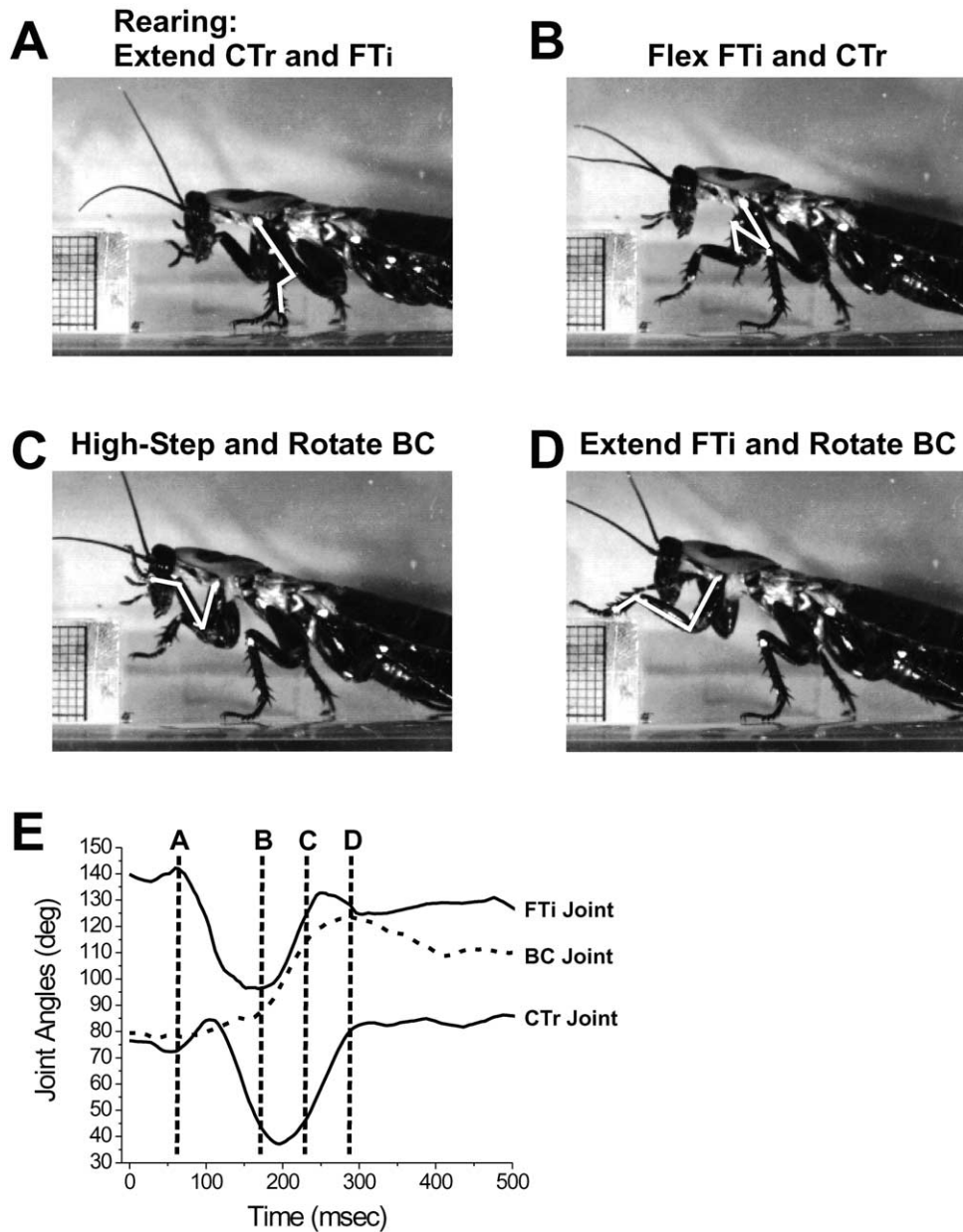
Fig. 12. Rearing movements of a cockroach climbing over a 12 mm plastic block. This figure is set up like Fig. 2 which depicts front leg movements over flat terrain. (A–D) are frames from a high speed video of the climb taken from the side. The front leg is highlighted with a white line. (E) The three dimensional joint angle changes for the FTi and CTr joints are shown graphically as is the two dimensional rotation of the coxa (dotted line). The timing of each frame in A–D is indicated by vertical dashed lines labeled appropriately. In A, the animal has rotated its middle leg to pitch its front end upward in a rearing movement. The left front leg (nearest the camera) remains on the ground by hyper-extending the FTi and CTr joints. In B, that leg is pulled upward by flexing the CTr joint. In C, the tarsus is pushed upward and forward by rotating the coxa at the TC joint and extending the FTi joint. In D, the tarsus comes down on the top of the block by extending the CTr joint. Note the similarity of the joint movements between B and D to the actions shown in Fig. 2 for swing movements associated with horizontal walking.

head and gets to the top of the block. Once its front feet have climbed onto the block, the rear legs will drive the animal over the object.

The block climbing deficits found in CoCLs are not surprising since these animals lack input from sensors mounted on their heads. However, the cause of another deficit associated with circumoesophageal connective lesion is less obvious (Pollack et al., 2003). CoCLs exhibit a subtle change in body posture that compromises the cockroach's ability to climb smooth inclines. They often walk with their body slightly higher off the ground than normal animals. Intact cockroaches rarely rise over a height of 11 mm from the substrate to the head. However, CoCLs walking on an incline rise above 11 mm about 60% of the time. When that occurs, attachment properties of tarsal pads are compromised (Jiao et al., 2000) and they have an increased

tendency to slip. As a result, CoCLs fall back while attempting to climb the incline. The implication is that inputs from head sensors contribute to control of body posture which in turn is critical to effective use of tarsal pads on each leg.

4.3. Implementing head functions in robots

The information on the role of head ganglia in controlling insect locomotion points to two stages of control that take place in insect brains. First, the wealth of sensory information from a wide range of sensors is fused into motor commands. Then these commands must interact with the motor control centers found in the thoracic ganglia in order to alter walking movements. The effects can be subtle postural changes, such as those seen during climbing or more complex alterations in patterns of leg movement such as the asymmetrical rearrangements seen in turning.

Our goal is to ultimately capture these functions in a robotic head. The head should be able to process different types of sensory information, fuse them into a sophisticated image of the robot's surroundings and then generate changes in forward locomotion.

In the first stages of this project, we have separated the functions of sensory integration from motor interaction. We are developing sensors that can control the simplified motor plant of a Whegs robot. In our first project, we implemented a circuit that was developed by Barbara Webb based loosely upon the cricket auditory system onto a Whegs robot (Horchler et al., 2003). The circuit allowed the robot to detect a recorded cricket mating call and guided the robot to the source. We are currently working on additional sensors that would need to be processed separately before bringing all the sensory information together into appropriate motor commands.

5. Conclusions

Animals such as insects are among the most sophisticated locomotory systems on the face of the earth. They process a tremendous amount of sensory information and use it to direct efficient leg and body movements that allow them to move effortlessly through a range of natural terrains that wheeled vehicles would have difficulty traversing. Although animal systems can provide exciting inspiration for designs of robotic vehicles, one cannot simply copy even the simplest animal system into a robotic design. The numbers of DoF and actuators not to mention the shear number of sensory receptors would pose a daunting task for any technical design. Thus, the robotics engineer is faced with the question of what animal properties she or he should incorporate into their designs.

At least one clue in choosing those aspects of animal locomotion to implement in robots is found in convergent evolution. Where animal groups evolved the same solutions

independently, aspects that are similar suggest excellent solutions to physical constraints. Legged locomotion provides such a situation. Remarkable similarities are found in insects and vertebrates, in spite of the fact that legs evolved independently in these two groups. The clear implication is that whether an agent is made out of skin and bone, chitin and muscle or aluminum and plastic, it must solve the same or similar physical problems for which there may be only a few very good solutions. Engineers are well advised to pay attention to those common solutions.

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