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Dynamic stabilization of rapid hexapedal locomotion

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Summary

To stabilize locomotion, animals must generate forces appropriate to overcome the effects of perturbations and to maintain a desired speed or direction of movement. We studied the stabilizing mechanism employed by rapidly running insects by using a novel apparatus to perturb running cockroaches (*Blaberus discoidalis*). The apparatus used chemical propellants to accelerate a small projectile, generating reaction force impulses of less than 10 ms duration. The apparatus was mounted onto the thorax of the insect, oriented to propel the projectile laterally and loaded with propellant sufficient to cause a nearly tenfold increase in lateral velocity relative to maxima observed during unperturbed locomotion. Cockroaches were able to recover from these perturbations in 27±12 ms (mean ± S.D., *N*=9) when running on a high-friction substratum. Lateral velocity began to decrease 13±5 ms (mean ± S.D., *N*=11) following the start of a perturbation, a time comparable with the fastest reflexes measured in cockroaches. Cockroaches did not require step transitions to recover from lateral perturbations. Instead, they exhibited viscoelastic behavior in the lateral direction, with spring constants similar to those observed during unperturbed locomotion. The rapid onset of recovery from lateral perturbations supports the possibility that, during fast locomotion, intrinsic properties of the musculoskeletal system augment neural stabilization by reflexes.

Key words: cockroach, *Blaberus discoidalis*, locomotion, mechanics, perturbation, stability, neural control.

Introduction

Many-legged animals with sprawled postures can be highly statically stable. The stepping patterns used by hexapods at slow and moderate speeds, for example, ensure that the center of mass falls within the polygon of support provided by their legs over the course of the entire stride (Alexander, 1982; Cruse and Schwarze, 1988; Delcomyn, 1985; Jander, 1985). Ting et al. (1994) showed that, while remaining statically stable over a wide range of speeds, at their highest speeds cockroaches are not statically stable and must rely on dynamic stability by using the momentum of the body to bridge periods of static instability. Animals or robots with fewer legs or aerial phases or both must rely on dynamic stability because the conditions necessary for static stability seldom apply (Raibert et al., 1984). Consequently, although static stability is useful to explain some aspects of morphology and behavior during slow, precise tasks, a consideration of dynamic stability is critical to understanding rapid locomotion (Full and Koditschek, 1999).

Although many types of periodic, dynamically stable motions are possible (Guckenheimer, 1982), one simple way of defining dynamic stability is the maintenance of an equilibrium trajectory over time: a defined pattern of positions and velocities that repeats with a characteristic frequency such as the stride frequency (Full et al., 2002). Following perturbations, dynamically stable systems return towards an unchanged equilibrium trajectory. Perturbations to neutrally stable systems persist in magnitude over time, and perturbations to unstable systems grow larger over time (Strogatz, 1994). Even simplified mechanical systems, such as inverted pendulum or spring-mass systems, can act as stable systems in some directions relative to their motion and as unstable or neutrally stable systems in others (Bauby and Kuo, 2000; Schmitt and Holmes, 2000a,b). A controller, such as the nervous system in animals, is necessary to stabilize systems with unstable components, even if the system is stable in some directions (Bauby and Kuo, 2000). Control may also be required to counteract perturbations in neutrally stable directions, such as desired movement direction or speed. Control is often active, taking the form of negative feedback from sensors to alter the state of a system. However, a consideration of the passive dynamic behavior of a mechanical system is critical for interpreting the effects of a controller (Full et al., 2002).

Two general mechanisms are available to maintain stability during legged locomotion. First, the initial condition of the legs at the transition from swing to stance can stabilize locomotion. For example, foot placement can stabilize bipedal locomotion (Townsend, 1985), and leg stiffness adjustments can compensate for substratum changes in humans (Ferris et al., 1999). In insects, foot placement plays an important part in stabilizing slow locomotion (Jander, 1985; Zollikofer, 1994). Control of step transitions can result in changes to leg stance, swing or stride periods in addition to changes in phase relationships among legs. Changes in leg placement, stepping periods and phase relationships have been used to identify mechanisms of neural control in arthropods (Cruse, 1990).

Movement need not be actively controlled to exhibit dynamic stability. For example, uncontrolled walking bipeds (McGeer, 1990) and sagittal-plane spring-mass systems (Seyfarth et al., 2002) with discontinuous stepping events can exhibit stability. In the horizontal plane, uncontrolled spring-mass models analogous to those of sagittal-plane running also exhibit stability (Schmitt and Holmes, 2000a,b). Parameters such as mass, moment of inertia, segment lengths, touchdown angles and segment compliance can determine the stability of an uncontrolled mechanical system (Schmitt et al., 2002; Seyfarth et al., 2002).

Coupled with uncontrolled, or 'passive' stabilization, the action of a controller acting at step transitions can contribute to dynamic stability. Whereas passive mechanisms contribute to stabilizing bipedal locomotion in the sagittal plane, humans use lateral foot placement to stabilize the unstable lateral direction during walking (Bauby and Kuo, 2000; Mackinnon and Winter, 1993). As for walking, control of leg placement and stiffness at step transitions is an important part of one successful control strategy used for dynamically stable three-dimensional hopping and running robots (Raibert et al., 1984).

An alternative to stabilizing locomotion at step transitions is to counteract perturbations within a step (Grillner, 1972, 1975). Within-step changes in joint torques could generate forces appropriate to counteract perturbations. Humans can modulate torque production to maintain constant-speed locomotion against an imposed force (Bonnard and Pailhous, 1991) and use changes in joint torques to counteract imposed force impulses when the impulses occur early in the step cycle (Yang et al., 1990). These dynamic changes in joint torques could serve to control movements about equilibrium trajectories during locomotion.

However, as animals move faster and stride periods decrease, the time available to recover from perturbations to movement within a step period decreases (Alexander, 1982). Neural delays in sensing a perturbation and in generating an appropriate motor pattern within the nervous system to arrest the perturbation, and delays involved in muscle activation and force generation, could limit the effectiveness with which neural feedback systems could continuously stabilize rapid movement (Full and Koditschek, 1999; Hogan, 1990; Joyce et al., 1974; McIntyre and Bizzi, 1993; Pearson and Iles, 1973).

Alternatively, stabilization of movement through non-neural mechanisms is also possible. The viscoelastic properties of muscles, skeletons and connective tissue, changing muscle moment arms and the length- and velocity-dependence of force production in active muscle all have the potential to contribute to the mechanical stabilization of musculoskeletal systems (Grillner, 1975; Seyfarth et al., 2001; Wagner and Blickhan, 1999). The potentially stabilizing properties of active muscles have been termed 'preflexes', since the stabilizing behavior of musculoskeletal systems may appear similar to neural reflexes but has the potential to occur very quickly before neural reflexes are able to act (Brown and Loeb, 2000). During rapid locomotion, musculoskeletal 'preflexes' could offer continuous stabilization, even at very high movement frequencies, and augment reflexive stabilization generated by the nervous system.

The goals of this study were to understand the mechanisms used by running insects to stabilize rapid locomotion. We therefore tested the following hypotheses: (i) that hexapods require step transitions to maintain stability during rapid running and are incapable of generating restoring forces to counteract perturbations within a step, and (ii) that non-neural 'preflexive' mechanisms contribute to the stabilization of rapid locomotion.

To test our hypotheses, we subjected cockroaches to laterally directed perturbations using a novel apparatus, a 'rapid impulsive perturbation' (RIP) device. The RIP apparatus was designed to be mounted directly above the center of mass of a freely running animal and to change the momentum of the animal's body by generating a brief force impulse. If the animal were to fail to generate an opposing force, the change in momentum caused by an impulsive perturbation would persist over time. If the animal were to generate a force impulse to oppose the perturbation and stabilize so their movements return to an equilibrium trajectory, the time necessary to stabilize to the equilibrium could be used to test whether step transitions are necessary for stability and whether musculoskeletal preflexes contribute to stabilization.

Three-dimensional kinematic measurements of body movement were recorded before, during and after perturbations as the animals ran freely on a Plexiglas track. We compared linear and rotational velocities from periods following perturbations with reference kinematics from unperturbed periods to determine the time at which recovery from perturbations occurred.

Materials and methods

Animals

We used the death-head cockroach, *Blaberus discoidalis* (Serville), with a mass of 2.69±0.8 g (mean ± S.D., *N*=9). Cockroaches were individually housed in plastic containers and fed dog food and water *ad libitum.*

Rapid impulsive perturbations

Since the timing of recovery from perturbations was important for testing our hypotheses, we designed the RIP apparatus to generate force impulses of as short duration as possible. We constructed an apparatus which employed a chemical propellant (black powder) to launch a small projectile, analogous to a miniaturized cannon mounted on the running animals. The RIP apparatus generated reaction force impulses of appropriate magnitude over a period of less than

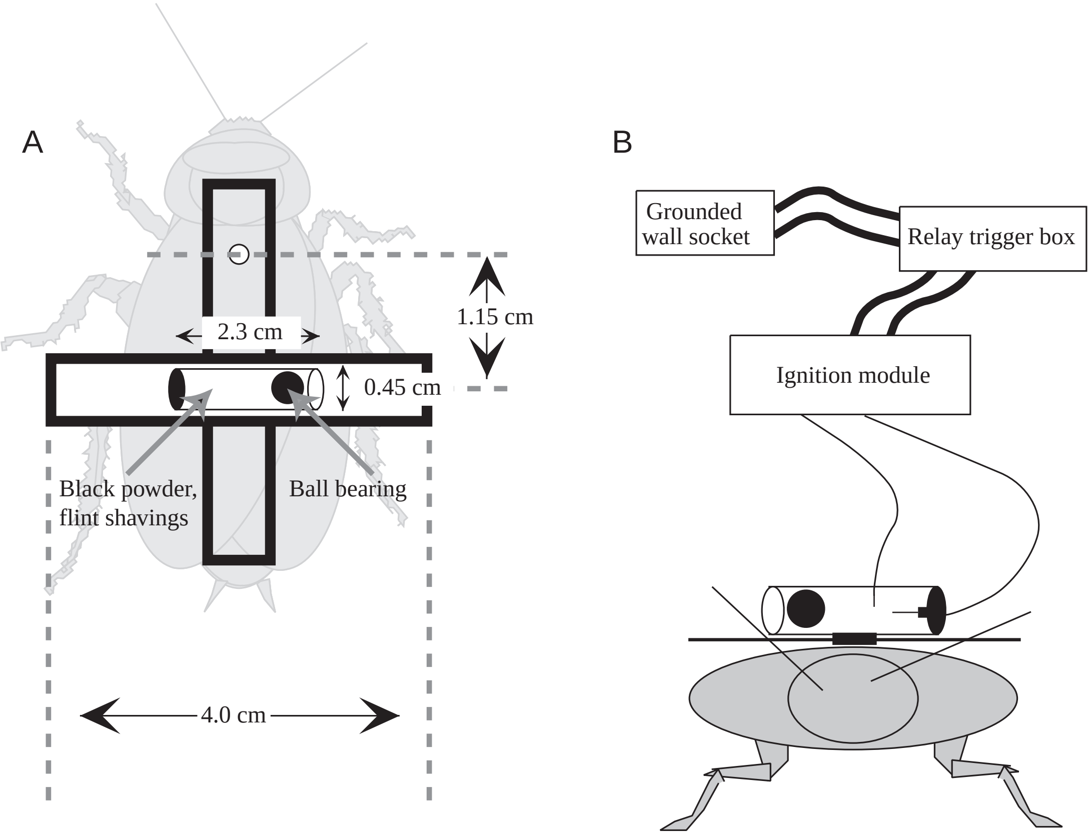

Fig. 1. The rapid impulsive perturbation (RIP) apparatus. (A) Diagram of the RIP apparatus, which consisted of a plastic cylinder placed laterally on a balsawood base. The apparatus was mounted on the mesonotum of the animal using small bolts. The cylinder was loaded with flint, black powder and a steel ball bearing. (B) The triggering system for generating RIPs. Flint and black powder were ignited using a spark generated from the ignition module, which was triggered manually.

10 ms, or less than 20% of the stance period of a cockroach running at its preferred speed.

To construct the RIP apparatus, we used a 2.3 cm long, 0.45 cm diameter plastic tube closed at one end. We added 6.3±1.4 mg (mean ± S.D.) of flint shavings (a low-ignition-temperature accelerant) to the tube. The flint shavings were necessary to ignite the black powder, but did not contribute substantial energy to the subsequent explosion. We then measured 3.2±0.7 mg of FFFF-grade black rifle powder (Goex, Inc.) and added it to the tube. A 0.13 g stainless-steel ball bearing was placed into the tube on top of the powder and held in place by a small piece of paper.

A spark from an ignition module (6520S0201, Harper-Wyman, Inc.) ignited the flint and black powder (Fig. 1B). Two 50 μm wires were connected to the ignition module at one end and soldered to two larger-diameter (0.6 mm) insulated wires at the other ends. The larger-diameter wires were threaded through holes in the base and side of the tube and glued to the outside of the tube with epoxy adhesive. The terminal 2 mm of the larger-diameter wires was uninsulated and served as the origin of the spark. The ignition module created sparks at approximately 3 Hz. The module and video cameras were triggered simultaneously *via* a relay switch.

Calibration of the RIP apparatus

We calibrated the RIP apparatus using a miniature force platform (Full and Tu, 1990). The RIP apparatus was mounted to a square plastic base and attached to the surface of the force platform using double-sided tape. We mounted the RIP apparatus vertically on the platform so that the ball-bearing was projected upwards, and sampled the output of the platform following an explosion at 10 kHz.

The RIP apparatus and the plastic holder weighed 14 g, and the added mass decreased the natural frequency of the force platform from 500 Hz (Full and Tu, 1990) to approximately 100 Hz. The forces measured by the force platform (Fig. 2A) are consistent with the hypothesis that the RIP apparatus generates a force impulse of duration less than half the period of oscillation of the platform/holder system (5 ms). No sustained force production was evident from the force platform recordings. Operating under this hypothesis, we considered the platform and RIP apparatus to be an elastic system. A near-instantaneous force impulse was hypothesized to accelerate the mass, and the platform generated a force to decelerate the mass in a spring-like manner. In this system, the area under the force curve between the beginning of the explosion and the time when the force begins to decrease (the peak force) is the force impulse necessary to arrest the momentum of the RIP apparatus. This

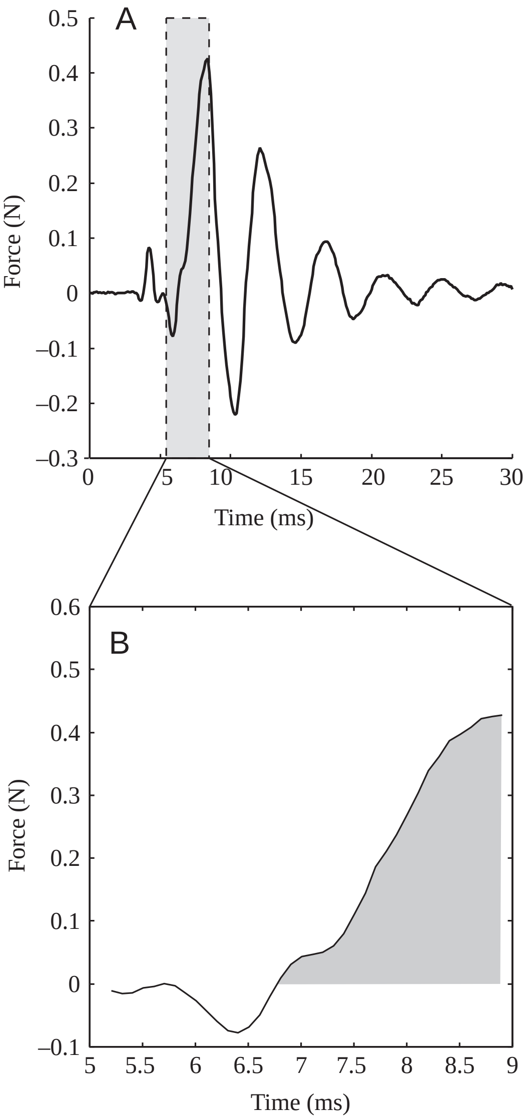

Fig. 2. Calibration of rapid impulsive perturbations (RIPs). (A) The RIP apparatus was placed vertically on a miniature force platform and triggered. Following the explosion, the RIP apparatus and force platform oscillated at a frequency of approximately 100 Hz. The time to the first force peak (gray area) was assumed to be the time necessary to arrest the RIP apparatus, which had been accelerated by a very rapidly generated force impulse. (B) The force impulse generated by the RIP apparatus was determined by integrating force with respect to time during the period between the beginning of the explosion and the first force peak. Small negative deflections before the positive force generated by the RIP apparatus were due to electromagnetic interference from the spark used to ignite the RIP.

force impulse must be equal in magnitude and in the direction opposite to the force impulse imparted by the RIP. We calculated the force impulse of the RIP apparatus by integrating the vertical force from the start of the explosion until the time at which peak force was reached (Fig. 2B). The mean impulse from 11 calibration trials using the miniature force platform was 0.84±0.87 mN s (mean ± S.D.). Noise in data acquisition from the force platform caused the variability in force impulse measurements. This average impulse is approximately 85% of the linear momentum of a 2.7 g cockroach carrying a 1.3 g RIP apparatus and running at 24 cm s^{-1}.

Attachment of the RIP apparatus to animals

The center of mass of cockroaches is 46% of the distance from the head to the tip of the abdomen, within the anterior portion of the abdomen directly behind the thorax (Kram et al., 1997). However, the abdomen of cockroaches is soft, and abdominal segments can move relative to one another. We consequently chose to attach the plastic tube to the crosspiece of a lightweight balsawood base (4.0 cm wide by 4.0 cm long; Fig. 1A) and attach the base to the stiffer thorax (Fig. 1A,B). The crosspiece was located 1.15 cm behind the most anterior bolt to place the centre of mass (COM) of the apparatus directly above the COM of the animals. The balsawood base not only provided a means of attaching the RIP apparatus to the body, but also facilitated digitization by amplifying thoracic rotation.

We used 1.1 mm diameter, 6.15 mm long brass bolts to attach the balsawood base to the animals. Using bolts allowed the RIP apparatus to be removed from the animal to be reloaded and facilitated the collection of COM and moment of inertia (MOI) data. We glued two bolts to the mesonotum with cyanoacrylate adhesive and 60 s epoxy adhesive, and a third bolt to an abdominal tergite. The second and third bolts fitted through small slots in the balsawood base. The second bolt ensured that the base remained aligned with the body axis, and the third bolt constrained lateral movements of the abdomen while allowing vertical motion of the abdomen relative to the thorax. The balsawood base was firmly attached to the most anterior bolt on the thorax with a small hex-nut. We attached the RIP apparatus so that the ball bearing was projected laterally towards the animal's right side, causing a reaction force that accelerated the animal to its left.

The RIP apparatus, including balsawood base, powder and ball bearing, weighed 1.3 g, approximately half the body mass of the animals. Attachment of the RIP apparatus must change both the COM and MOI of the animals. To minimize any effects that changing the COM location or MOI may have had on locomotory kinematics, our analysis (see below) compared kinematics from perturbed trials with kinematics from unperturbed trials in which the RIP apparatus was also mounted onto the animals.

Running track

A Plexiglas running track 91.4 cm long × 8.25 cm wide × 10.16 cm high was constructed to allow the animals free movement within a contained area. In its center, the track fitted over an 11 cm long × 8.25 cm wide balsawood platform, which allowed the animals to grip the substratum with their pretarsal claws. We did not visually observe any instances in which the legs slipped on the platform during running during unperturbed or perturbed trials.

Video recording

Each trial was recorded at a frame rate of 1000 Hz using a high-speed digital video system (Motionscope, Redlake Imaging). Three synchronized cameras focused on the space directly above the wood platform simultaneously recorded each trial. One camera was placed directly above the platform, and two cameras recorded from either side lateral to the average movement direction of the animals. Video frames had a resolution of 240×210 pixels. Lateral cameras had fields of view of 11 cm, and the camera above the platform had a field of view of 15 cm in the average movement direction.

Kinematic data analysis

During every experiment, a stationary calibration object was placed in the field of view to allow three-dimensional calibration. The calibration object was constructed from small plastic blocks (Lego systems, Inc.) and had dimensions of 6.5 cm×5 cm×2.5 cm, which was large enough to fill more than half the field of view of the lateral cameras in one dimension. The calibration object had 33 points identifiable in all three video cameras. The distances of 32 of the points from one point (which served as the origin) were measured with digital calipers (Omega Scientific, Inc) to an accuracy of 0.01 mm. An image of the calibration object was recorded prior to, and following, each experimental session. Cameras were not moved during an experimental session. Calibration errors in position were 0.11 mm in the x (fore–aft) direction, 0.21 mm in the y (medio–lateral) direction and 0.31 mm in the z (vertical) direction.

Digital video recorded during each trial was saved to computer disk as uncompressed AVI files, which were imported into a three-dimensional video analysis system (Motus, Peak Performance Technologies, Inc.).

Trials were selected for analysis if the perturbation occurred near the middle of the field of view of the video cameras and the animal and perturbation apparatus did not touch the wall during the trial. Selected trials were digitized using the video analysis system. Four points on the balsawood base (the rear of the base, the front of the base and the two lateral ends of the base; Fig. 1A) were digitized in two camera views (the vertical camera view and one of the lateral camera views). Raw coordinate data were filtered using a fourth-order zero-phase-shift Butterworth filter with a cut-off frequency of 100 Hz. Given the calibration and the filtered coordinate data, the video analysis system was used to calculate the three-dimensional location of each of the points relative to the origin of the calibration object using direct linear transformation (Biewener and Full, 1992). Resulting three-dimensional position data were filtered using a fourth-order Butterworth filter using a cut-off frequency of 50 Hz.

Experimental protocol

Prior to each experiment, we anesthetized the animals by placing them in a refrigerated (4°C) room for 1 h. We removed the wings from the animals (carefully cutting around the largest wing veins) using scissors and roughened the cuticle on the mesonotum by gently rubbing it with sandpaper. We glued the brass bolts to the mesonotum and allowed the animals to recover at room temperature in an unsealed plastic container for at least 1 h.

For each experimental trial, we carefully bolted the RIP apparatus into place. We placed the cockroach on the running track and encouraged it to run by lightly tapping its cerci. Typically, we conducted between five and ten unsuccessful running trials before attempting to trigger the RIP. When the cockroach appeared to run at constant average speed near the center of the video field of view, we manually triggered the RIP apparatus and video collection system. Since 300 ms elapsed between triggering and when the spark occurred (causing the explosion), it was necessary to anticipate the animal’s location and trigger the RIP before the animal was actually in the video field of view. After the RIP apparatus had been triggered, it was necessary to reload the apparatus with flint, black powder and the ball bearing. The RIP apparatus was carefully removed from the cockroach and reloaded between trials. The cockroach was placed in a plastic enclosure and allowed to rest for approximately 10 min.

Center of mass determination

Cockroaches were deep-frozen immediately following each experimental session and stored in airtight plastic containers. We determined the location of the center of mass for each animal (N=9) individually by suspending the animal from strings attached to three different points of the body. We filmed the animals while suspended from each location, and determined the vertical axis in each image by digitizing small pieces of reflective tape attached to the string. The COM lies at the intersection of the vertical axes in the three camera views (Blickhan and Full, 1992). We digitized the tail, head, left and right pronotum points and the four base points. To measure changes in COM position due to the RIP apparatus, we expressed the location of the COM in the coordinate frame set by the tail, head and left and right pronotum points. To calculate the COM position during running, we expressed the location of the COM in the coordinate frame set by the four base points.

Attachment of the RIP apparatus to the cockroaches shifted the COM –1.4±1.1 mm in the fore–aft direction (towards the tail), 0.6±0.6 mm in the medio–lateral direction (towards the left) and 3.6±0.8 mm in the vertical direction (upwards). These shifts represent less than 5% of body length in the fore–aft and medio–lateral directions, but a more than 25% shift in vertical COM position.

Moment of inertia determination

Since the perturbation apparatus was mounted on the animals and could potentially change the location of the COM and MOI of the animals, we directly measured the COM and MOI for each animal, with and without the apparatus. We determined the moment of inertia about the three principal axes (yaw, pitch and roll axes) by piercing the deep-frozen animals parallel to a principal axis with a long pin, which was balanced on razorblades

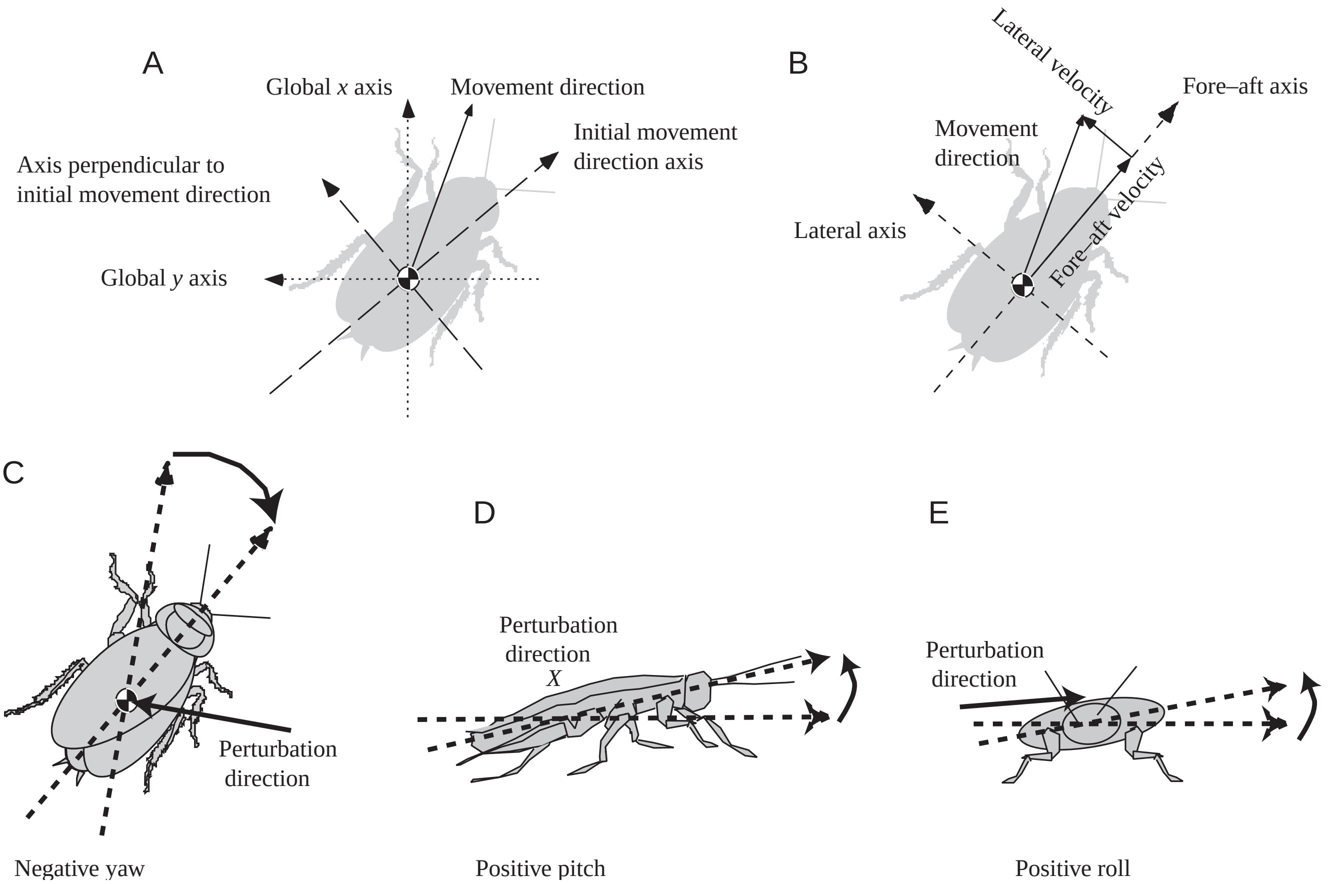
A
Global x axis
Movement direction
Initial movement direction axis
Axis perpendicular to initial movement direction
Global y axis
B
Lateral velocity
Fore–aft axis
Movement direction
Fore–aft velocity
Lateral axis
C
Perturbation direction
Negative yaw
D
Perturbation direction
X
Positive pitch
E
Perturbation direction
Positive roll

Fig. 3. Coordinate frames used to express kinematic data. (A) Translational positions and rotations were expressed in a coordinate (*X*,*Y*,*Z*) frame based on the mean direction of movement before perturbations and the global horizontal plane. (B) Translational velocities were expressed in a coordinate (*x*,*y*,*z*) frame based on the orientation of the fore–aft axis of the animals. (C–E) Rotation was expressed using yaw, pitch and roll Euler angles. Reaction forces from perturbations were directed towards the positive lateral axis.

and allowed to swing freely (Kram et al., 1997). We filmed the animals at 500 Hz, and measured the period of oscillation after lightly tapping the animals. We digitized points on the head and the tip of the abdomen, two points on either side of the pronotum and four points on the base (when the base was attached to the animal). Using the center of mass position calculated above, we determined the distance from the center of mass to the pin (*d*). We calculated the moment of inertia (*I*) about the given axis using the following formula derived from the parallel axis theorem:

$$I = \frac{9.81\tau_o^2 md}{4\pi^2} - md^2\,, \qquad (1)$$

where τ_o is the swing period and *m* is the mass (Kram et al., 1997; Ting et al., 1994). We did not remove the legs prior to moment of inertia calculations.

Coordinate frames

Kinematic data were expressed in two inertial reference frames with the origin at the instantaneous position of the COM, using custom-designed programs implemented in MATLAB (The MathWorks, Inc.).

First, the position of the COM in the three-dimensional global coordinate frame was calculated from the positions of the four base points for each sampled time frame. A natural coordinate system to use to express perturbations away from the initial (assumed to be the nominal or 'desired') movement direction is a rotational frame with one axis parallel to the average movement direction of the animal one stride before the perturbation and a second axis parallel to the global horizontal plane. We termed this coordinate (*x*,*y*,*z*) frame the 'initial movement direction frame' (Fig. 3A). Body orientation was calculated using the four digitized base points expressed in the initial movement direction frame and expressed as Euler angles in the order yaw, pitch, roll (Fig. 3C–E).

Since the animals were free to adopt a new average movement direction after being perturbed, a separate coordinate (*X*,*Y*,*Z*) system based on body orientation was employed to compare translational velocities and accelerations with reference data. We termed this frame a 'fore–aft' frame (Fig. 3B).

We differentiated the three-dimensional coordinates of the COM and the yaw, pitch and roll Euler angles with a fourth-order difference equation (Biewener and Full, 1992) to yield the instantaneous translational and rotational velocities of the body over time.

Step events

Insects typically employ an alternating tripod gait during rapid locomotion in which the front and hind legs on one side of the body step synchronously with the contralateral middle leg. For each stride of each trial, we recorded the time when each of the animals' legs switched from protraction to retraction and the time when each leg switched from retraction to protraction by visually inspecting video recordings from the two lateral views. The tarsi made contact with the ground (i.e. 'touchdown') at approximately the same time as the legs switched from protraction to retraction. Similarly, the tarsi left the ground at approximately the same time as the retraction–protraction transition (i.e. 'lift-off'). Consequently, we considered the stance period to be equal to the retraction period, and we considered the swing period to be equal to the protraction period. At times, shadows in the video image prevented accurate measurement of protraction, retraction, touchdown or lift-off step events. These steps were consequently not included in the analysis of stance and swing periods (consequently, the number of steps reported is not the same for all legs). We measured stride periods, stance duration, swing duration and phase relationships among legs during unperturbed and perturbed strides. We calculated stride period as the period between touchdown events and phase as the time of touchdown relative to the stride of a reference leg (Jamon and Clarac, 1995). Step event data from unperturbed trials and from strides prior to the perturbation formed an 'unperturbed' data set. Step event data from stride, stance and swing periods during which the perturbation occurred formed a data set 'during' the perturbation. Step event data from strides that occurred after the perturbed stride formed a third data set. Unperturbed and perturbed data were drawn from the same animals. For all data sets, we calculated mean values for each measure (i.e. phase and stride, stance and swing periods) for each condition and animal. Data sets from stride, stance and swing periods during and after the perturbation were compared with those from the unperturbed periods using an unpaired *t*-test implemented in MATLAB.

Reference data sets from unperturbed strides

We collected 12 unperturbed trials from eight of the nine animals used in the study to provide reference kinematics against which the perturbed trials could be compared. Animals were run with the perturbation apparatus loaded and attached to their thorax, but the RIP apparatus was not triggered during the trial. No animal contributed more than two trials to the reference data set. Whole-body kinematics and step event data over 1–3 strides were collected from each of the reference trials. Animals in unperturbed reference trials ran with an average fore–aft speed of $29\pm9\,\mathrm{cm\,s^{-1}}$, within the range $24–38\,\mathrm{cm\,s^{-1}}$ commonly observed in cockroaches running without the RIP apparatus (Full et al., 1991; Full and Tu, 1990).

Comparison of perturbed data with reference data

Scaling of unperturbed kinematics to stride periods of perturbed trials

To compare the kinematic data from perturbed trials with the reference kinematics, we scaled the reference kinematics in time and then normalized for differences in initial conditions. To scale the reference kinematics in time, we delimited stance periods for each trial by averaging the touchdown and lift-off times for legs of each stepping tripod. For the tripod containing the left front (LF), right middle (RM) and left rear (LR) legs, touchdown and lift-off times are identified as LF,RM,LR (abbreviated LF). Step events from the opposite tripod are identified as RF,LM,RR (abbreviated RF). Since stance and swing periods following perturbations were not significantly different from those for unperturbed running, and phase relationships among tripods did not differ by more than 5% from 0.5, we scaled the reference data to the stance and swing periods of the LF tripod of the perturbed trial.

To compare kinematics from perturbed strides with unperturbed kinematics, we first scaled the unperturbed data in time to yield the most representative reference data set corresponding to a period equal to the period of each perturbed step. For each stance period during or after a perturbation, we extracted unperturbed kinematics from all stance periods corresponding to the same tripod of legs of every reference trial. We scaled these kinematics from each unperturbed stance period to have the same number of samples as the selected perturbed stance period. Scaled, unperturbed (denoted by subscript U) kinematics are referred to as $\dot{p}_{\mathrm{U,LF}}$ and $\dot{p}_{\mathrm{U,RF}}$ for the LF and RF tripods, respectively. We averaged the scaled kinematics from all reference stance periods for each animal, resulting in eight reference stance data sets scaled to the length of each stance period of every perturbed trial. We termed the average of these eight unperturbed mean data sets $\bar{\dot{p}}_{\mathrm{U,LF}}$ and $\bar{\dot{p}}_{\mathrm{U,RF}}$ for the LF and RF tripods, respectively. Concatenating the average reference data for alternating tripods resulted in a mean reference data set for each perturbed trial.

After scaling in time, we normalized the reference kinematics to control for differences in position and velocity. We scaled the mean reference kinematics to have the same average position and velocity as the stride immediately before the perturbation.

Finally, we subtracted the scaled mean reference data from each normalized perturbation trial and measured the deviation in translational and rotational velocities from the reference mean. Statistical comparisons of maxima and minima of velocity deviations from the reference mean were conducted using a statistical package (JMP, the SAS Institute, Cary, NC, USA). We used a *z*-test to compare the measured populations of velocity deviation maxima and minima to a hypothesized mean of zero.

Criterion for recovery: deviation from the mean reference trajectory

Locomotion can be considered to be perturbed if observed movements are significantly outside the range observed during unperturbed locomotion. If the 'error', or the difference between a movement cycle and the mean unperturbed movements for an equivalent cycle, lies outside the range of errors observed during unperturbed locomotion, then the cycle can be considered to be perturbed. We measured movement error by calculating the mean-squared difference between movements over an entire locomotory cycle (Schwind, 1998). For each perturbed trial (denoted with subscript RIP), we selected one velocity direction (such as the lateral velocity, denoted with subscript y) and formed a vector from the velocity over one stance period. For the LF tripod, this vector is denoted $\dot{p}_{\mathrm{RIP,LFy}}$ and that for the RF tripod $\dot{p}_{\mathrm{RIP,RFy}}$. The magnitude of the error $E_{\mathrm{RIP,RFy}}$ or $E_{\mathrm{RIP,RFy}}$ between this vector and an equivalent vector from the scaled mean reference data set is:

$$E_{\mathrm{RIP,LFy}} = \sqrt{\sum_{t=0}^{t=\tau} \left[\dot{p}_{\mathrm{RIP,LFy}}(t) - \dot{\bar{p}}_{\mathrm{U,LFy}}(t) \right]^2} \qquad (2)$$

for the LF tripod, with a corresponding equation for the RF tripod.

We compared $E_{\mathrm{RIP,LFy}}$ and $E_{\mathrm{RIP,RFy}}$ with the population of errors from the unperturbed trials, which serves as an estimate of the variability of unperturbed running. To create a population of unperturbed errors for each scaled unperturbed trial, we calculated the error $E_{\mathrm{U,LFy}}$ or $E_{\mathrm{U,RFy}}$:

$$E_{\mathrm{U,LFy}} = \sqrt{\sum_{t=0}^{t=\tau} \left[\dot{p}_{\mathrm{U,LFy}}(t) - \dot{\bar{p}}_{\mathrm{U,LFy}}(t) \right]^2} \qquad (3)$$

for the LF tripod, with a corresponding equation for the RF tripod.

We compared $E_{\mathrm{RIP,LFy}}$ and $E_{\mathrm{RIP,RFy}}$ with the population of $E_{\mathrm{U,LFy}}$ and $E_{\mathrm{U,RFy}}$, respectively, using a z-test to determine whether movements over the cycle of the perturbed trial were significantly different from the mean unperturbed movements. A z-test determines whether a value lies outside confidence limits for a population. We used a one-tailed z-test with a significance level of 0.05 to determine whether $E_{\mathrm{RIP,LFy}}$ and $E_{\mathrm{RIP,RFy}}$ fell outside the population of $E_{\mathrm{U,LFy}}$ and $E_{\mathrm{U,RFy}}$ from the unperturbed trials. If $E_{\mathrm{RIP,LFy}}$ was not significantly different from the population of $E_{\mathrm{U,LFy}}$ values, $\dot{p}_{\mathrm{RIP,LFy}}$ was considered to be not significantly different from $\dot{\bar{p}}_{\mathrm{U,LFy}}$, with a comparable comparison for the opposite tripod.

If the perturbation resulted in a value of $\dot{p}_{\mathrm{RIP,LFy}}$ or $\dot{p}_{\mathrm{RIP,RFy}}$ that was significantly different from the corresponding value of $\dot{\bar{p}}_{\mathrm{U,LFy}}$ or $\dot{\bar{p}}_{\mathrm{U,RFy}}$ during the stance period containing the perturbation, then the stance period following the perturbation during which the velocity ceased to be different from the reference mean velocity was recorded. If the velocity ceased to be significantly different from the reference mean velocity for the stance period immediately following the stance period containing the perturbation, then the animal was considered to have recovered within the stance period during which the perturbation occurred.

Time to recovery

We considered the time to recovery to be the period between a perturbation and the time at which the velocity over an appropriate period was not significantly different from the reference mean. We chose the mean stance duration, a period assumed to be equal to a locomotory half-cycle, as the appropriate period for evaluating recovery. Following each 1 ms time sample after a perturbation, we constructed a vector for each variable (such as the lateral velocity, **y**) with length equal to the mean stance period. We compared this vector with equivalent vectors constructed from the unperturbed trials, appropriately scaled to phase in the step cycle. We constructed error vectors by subtracting the scaled reference mean from data from perturbed and unperturbed trials. Errors from perturbed trials were compared with the population of errors from unperturbed trials using a z-test with a significance level of 0.05. We repeated this measurement for each sample following the perturbation, sliding a window one mean stance period in length along the data sets and testing for significant differences. The time to recovery was considered to be the time sample after the perturbation at which error vectors from perturbed trials first failed to be significantly different from the reference mean. This indicates that the locomotory half-cycle beginning at this time is not significantly different from the population of unperturbed half-cycles of the same phase.

Values are presented as means ± S.D.

Results

Eleven of 237 perturbation trials fit all the criteria for acceptability and were included in the analysis. Fig. 4 shows a series of video images from a typical perturbation trial. Perturbations caused increases in lateral velocity (Table 1), which changed the movement direction immediately after the perturbation (Fig. 4).

Effects of perturbation

Translational position and velocity

Lateral velocity increased over the reference velocity to a maximum of 21.0±6.9 cm s^{-1} (z-test; $P<0.0001$), indicating that the perturbations imparted a force impulse that was on average 80% of the forward momentum of the animals. This impulse was not significantly different from the mean impulse of 85% generated by the RIP (t-test; $P>0.9$). Fig. 5 shows lateral velocity from a representative perturbation trial. In this trial, the perturbation occurred during the stance phase of the LF tripod and caused the lateral velocity to increase to a maximum value of 27 cm s^{-1} in 11 ms. For this trial, lateral velocity was significantly different from the reference velocity during the perturbed step (z-test; $P<0.05$), but was not significantly different in subsequent steps. In this trial, the lateral velocity recovered in 31 ms.

The mean time from the onset of the perturbation until the lateral velocity error began to decrease was 13±5 ms (Table 1). A decrease in lateral velocity must be caused by a force opposing the perturbation. This indicates that cockroaches were able to begin generating forces opposing the perturbation 13 ms following the onset of the perturbation.

The perturbation to lateral velocity resulted in a mean lateral displacement of 0.46±0.2 cm relative to the initial COM position (Fig. 6B). On average, 200 ms (approximately two

Table 1. *Responses to rapid impulsive perturbations during running*

	All trials (N=11)	Perturbation occurs during stance phase of tripod LF,RM,LR (N=6)	Perturbation occurs during stance phase of tripod RF,LM,RR (N=5)
Phase of perturbation in stride (%)	37±28	35±26	40±32
Maximum lateral velocity ($\mathrm{cm\,s^{-1}}$)	21.0±6.9	20.5±7.3	21.5±7.1
Time to lateral velocity decrease (ms)*	13±5	12±6	13±4
Minimum yaw velocity ($\mathrm{degrees\,s^{-1}}$)	−451±283	−438±293	−465±315
Time to yaw velocity decrease (ms)	14±9	12±6	16±12
Minimum pitch velocity ($\mathrm{degrees\,s^{-1}}$)	−498±364	−530±338	−467±435
Time to pitch velocity decrease (ms)	10±12	6±1	14±16
Minimum roll velocity ($\mathrm{degrees\,s^{-1}}$)	−596±837	−806±911	−336±746
Time to roll velocity decrease (ms)	14±26	21±35	6±1

Values are means ± S.D.

Reported velocities are increases or decreases in velocity relative to scaled mean reference velocities from unperturbed trials.

*Indicates the time from the beginning of the perturbation until the magnitude of relative velocity begins to decrease from its maximal value.

LF, left front leg; RM, right middle leg; LR, left hind leg; RF, right front leg; LM, left middle leg; RR, right hind leg.

strides) following the perturbation, the lateral position of the COM returned to 0.17±0.66 cm from its position before the perturbation (Fig. 6B). Even though the cockroaches were not constrained to run in a particular direction, the finding that perturbations to lateral position decreased after reaching a maximum suggests that cockroaches stabilize lateral COM position in addition to velocity when confronted with perturbations.

Lateral perturbations did not have a consistent effect on fore–aft or vertical velocity (Fig. 6A,E). Clear maxima or minima in fore–aft or vertical velocities were not evident. Consequently, velocity maxima are not reported in Table 1. Prior to the perturbation, animals ran at a fore–aft velocity of 23.9±5.4 $\mathrm{cm\,s^{-1}}$. Following perturbations, the animals ran at a mean velocity of 25.5±3.6 $\mathrm{cm\,s^{-1}}$, an insignificant difference. Changes in vertical velocity and position were variable, and many occurred more than 100 ms following the perturbation.

Rotational position and velocity

Lateral force impulses imparted by the RIP caused changes to yaw, pitch and roll velocity and to position (Fig. 7). Yaw velocity was affected by lateral perturbations above the COM. On average, yaw velocity decreased relative to the reference velocity by –451±283° $\mathrm{s^{-1}}$ (z-test; P<0.001), an approximately threefold increase over the maximum yaw velocities during unperturbed running (Kram et al., 1997). Yaw velocity began to increase from a minimum 14±9 ms following the perturbation (Table 1). Following a perturbation, the animals oriented in a yaw direction close to the orientation before the perturbation (Fig. 7A).

Since the RIP apparatus was approximately 5 mm above the COM, perturbations to roll would be expected as a result of the moment arm about the roll axis, particularly considering the low moment of inertia about the roll axis (Table 2). Surprisingly, the magnitude and timing of the effects of perturbations on roll were variable (Table 1). The mean change in roll velocity following perturbations was not significantly different from zero (z-test, P=0.052). Nearly 30 ms following the perturbation, however, there was a trend for cockroaches to roll in the direction opposite to the roll expected from the perturbation itself (Fig. 7E). Cockroaches appeared to stabilize perturbations to roll, but exhibited variability in roll orientation during locomotion following perturbations.

Perturbations caused an immediate negative pitch velocity, causing the head to rotate downwards. Pitch velocity decreased relative to the reference velocity, reaching a minimum of –498±364° $\mathrm{s^{-1}}$ (z-test; P<0.001). This decrease in pitch velocity is approximately 1–2 times the maximum pitch velocities observed during unperturbed running (Kram et al., 1997). Pitch velocity began to increase from this minimum 10±12 ms following the perturbation. This negative pitch velocity was followed by a positive pitch velocity, which caused the head to rotate upwards. Similar to changes in vertical COM position, the pitch response over longer time scales was variable.

Effects of perturbation did not depend on tripod perturbed

The effects of perturbations on translational and rotational velocity maxima and on the time to reach maxima did not depend on which tripod was in stance during the perturbation (t-tests, P>0.15 for all comparisons; Table 1). This difference is surprising, since the lateral force generated by the side of the body with two legs in stance is nearly twice the lateral force generated by the side of the body with one leg in stance (Full et al., 1991; Full and Tu, 1990). The LF tripod might be expected to generate forces opposing the perturbation more easily since the direction of the unperturbed net lateral force for this tripod is opposite to that of the perturbation. However, no effect of tripod was observed in our experiments.

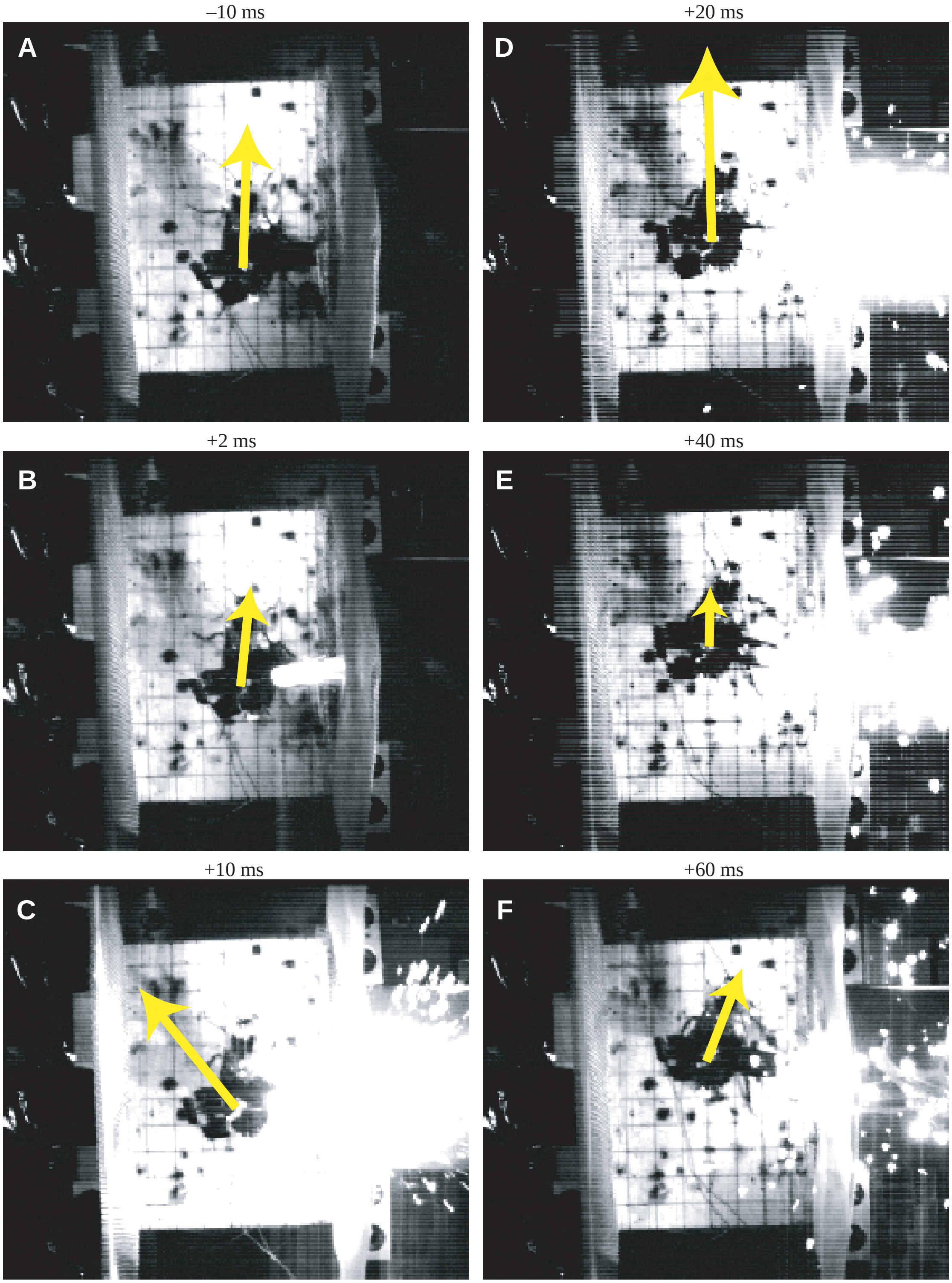
–10 ms
+20 ms
+2 ms
+40 ms
+10 ms
+60 ms

Fig. 4. Sequence of video images from a perturbation trial. Arrows superimposed on the images indicate the relative magnitude and orientation of the velocity of the center of mass before, during and after the perturbation. (A) Movement direction 10 ms before perturbation. (B) Movement direction 2 ms following start of perturbation. The rapid impulsive perturbation apparatus generates force, but the movement direction has yet to deflect substantially. (C) Perturbation causes the movement direction to be deflected towards the positive lateral direction, shown 10 ms following the perturbation. (D) At 20 ms following the perturbation, the movement direction has returned to a direction closer to the fore–aft axis. However, return towards the mean reference direction is not sufficient to indicate recovery. Recovery also requires the velocity to be not significantly different from the mean reference trajectory for an appropriate time period. (E) Velocity 40 ms following the perturbation. If animals continued running at velocities that did not differ from reference velocities over a locomotory half-cycle, such as lateral velocity in this trial, recovery was considered to have occurred. (F) Animals were free to move in any direction following the perturbation.

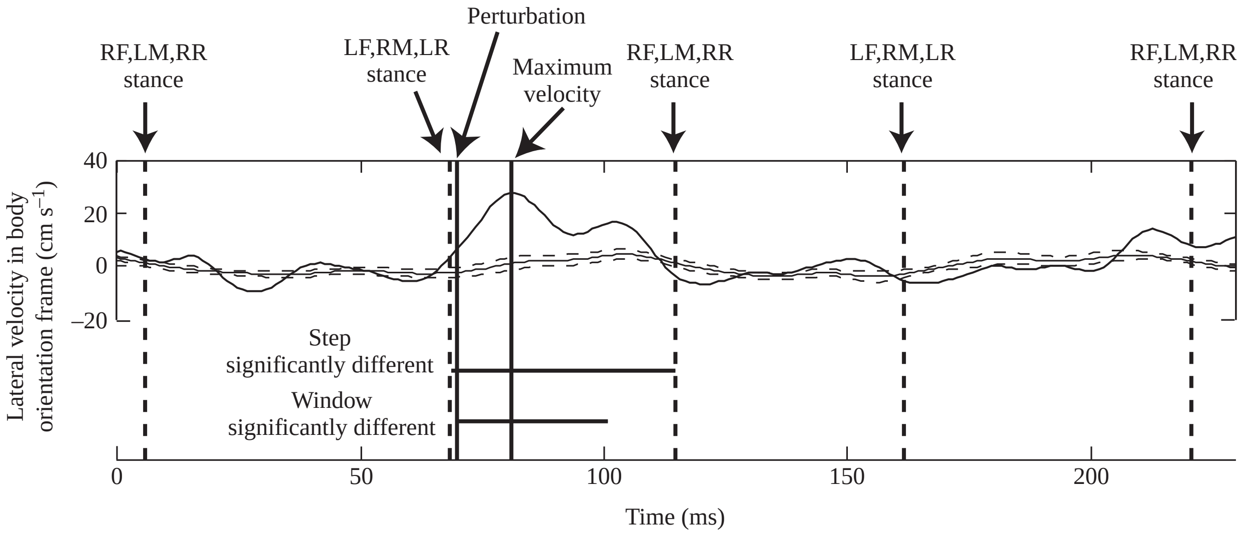

Fig. 5. Perturbation and recovery of lateral velocity from a representative trial. Lateral velocity was expressed in the fore–aft reference frame (see Fig. 3B). The thick solid line represents data from the perturbed trial. The thin solid line represents mean lateral velocity from reference trials scaled to the phase of the perturbed trial. Broken lines above and below the thin solid line represent reference mean ± 1 S.E.M. Vertical broken lines represent touchdown events for alternate tripods. 'RF,LM,RR stance' indicates the beginning of the period when the right front, left middle and right hind legs were in stance. 'LF,RM,LR stance' indicates the beginning of the period when the left front, right middle and left hind legs were in stance. Solid vertical lines indicate the time of perturbation and time at which maximum lateral velocity was reached. Horizontal lines below the lateral velocity represent the comparison of kinematics from steps of trial in which the animal was perturbed with reference kinematics. The perturbed trial is significantly different from the reference trial during the perturbed step, but not during subsequent steps. The horizontal line terminating near 100 ms indicates the time to recovery of the perturbed trial. Recovery was measured by comparing the kinematics of the trial in which the animal was perturbed with reference kinematics in a sliding window of length equal to the mean step period. The window began sliding at the time sample in which the perturbation occurred and moved forwards in time in 1 ms intervals. The perturbed trial ceased to be significantly different from reference trials 31 ms following perturbation.

Stride periods and leg phase relationships were not altered in responsfe to perturbations

Changes to leg placement at step transitions could be achieved through changes in stance or swing periods of individual legs during running. For example, to begin a step with the legs positioned more anteriorly than normal, the swing period could be lengthened to allow the leg to move farther forward than during unperturbed running. This change could also alter the stride period or the phase relationships among the legs following a perturbation.

Stride periods during and after perturbations did not differ from stride periods during unperturbed running for any leg (Table 3; $P>0.12$ for all comparisons). Stance duration during and after perturbations also did not differ significantly from unperturbed running, although there was a trend towards increasing stance duration in strides during and after perturbations (Table 3; $P\geq0.05$ for all comparisons). Swing periods of strides during and after perturbations also did not differ significantly from swing periods of unperturbed strides (Table 3; $P>0.32$ for all comparisons).

Leg phase relationships for strides during or following perturbations were not significantly different from phase relationships during unperturbed strides (Table 4; $P>0.09$ for all comparisons). Cockroaches maintained an alternating tripod gait during and after perturbations, resulting in phase relationships among legs that remained close to 0.5.

Recovery from perturbation

Translation

In all 11 trials, perturbations caused the lateral velocity to be significantly different from the reference velocity during the perturbed step (*z*-tests; $P<0.05$; Table 5). One trial which did not show recovery for any window following the perturbation, and one which showed instantaneous recovery, were excluded from the calculation of the time to lateral velocity recovery. For the remaining nine trials, lateral velocity recovered in 27±12 ms. This quick recovery caused lateral velocity to recover within the stance period during which the perturbation occurred in 45% of the trials. In a majority (5 of 7) of the trials in which the perturbation occurred within the first half of the stance period, the lateral velocity recovered within the perturbed stance period. Consequently, step transitions were not necessary to recover from lateral perturbations when the perturbation occurred sufficiently early in the stance period. In all trials in which the perturbation occurred in the second half of stance, the lateral velocity did not recover within the perturbed step. The phase of the step cycle during which the perturbation occurs appears to constrain the ability of the animals to recover from lateral perturbations. Perturbation magnitudes were not significantly different between trials recovering within one stance period and trials that failed to recover within one stance period (0.84±0.30 *versus* 0.84±0.29 mN s; *t*-test, $P>0.99$).

In six of 11 trials, perturbations caused the fore–aft velocity to be significantly different from the reference velocity during the perturbed step (*z*-tests; $P<0.05$; Table 5). Fore–aft velocity was significantly different from the reference velocity in the majority of steps (N=8) immediately following the perturbation and failed to recover during any window following the perturbation within the time period of the trial in four of 11 trials. In five trials, the perturbation caused a significantly different fore–aft velocity during the perturbed step and the fore–aft velocity recovered during the trial. In these trials, fore–aft velocity recovered in a period equal to 90% of the mean stride period of 111 ms (Table 3). Cockroaches did not appear to show within-step stabilization of fore–aft velocity following lateral perturbations, and we cannot reject the hypothesis that step transitions are important for maintaining fore–aft velocity.

Perturbations caused vertical velocity to become different from the reference velocity in 10 of the 11 trials (*z*-tests; $P<0.05$; Table 5), of which three recovered within the perturbed step and three recovered in a subsequent step in the trial. In two trials, the animals did not recover during a subsequent step period.

Rotation

Perturbations caused yaw velocity to become different from the reference velocity in six of 11 trials, of which one recovered within the perturbed step and four recovered in a subsequent step in the trial (*z*-tests; $P<0.05$; Table 5). Three trials that were not significantly different from the reference yaw velocity during the perturbed step became different during the step following the perturbation. Yaw velocity recovered in approximately 40 ms.

Perturbations caused pitch velocity to become different from the reference velocity in nine of 11 trials (*z*-tests; $P<0.05$; Table 5), of which two recovered within the perturbed step and five recovered in a subsequent step in the trial. On average, pitch velocity recovered in approximately 40 ms, similar to the yaw velocity.

Perturbations caused roll velocity to become different from the reference velocity in eight of 11 trials (*z*-tests; $P<0.05$; Table 5), none of which recovered within the perturbed step and one recovered in a subsequent step in the trial. For the three trials in which roll velocity recovered during a step period window, recovery occurred in approximately 100 ms.

Discussion

Controlled, rapid perturbations of running insects demonstrated the importance of characterizing dynamic stability in addition to static stability. Cockroaches showed a remarkable ability to recover from lateral perturbations that caused lateral velocity to increase nearly tenfold relative to maximal values during unperturbed locomotion ($20\,\mathrm{cm\,s^{-1}}$ *versus* $2.5\,\mathrm{cm\,s^{-1}}$; Full and Tu, 1990) (Figs 5, 6C). However, the force impulses generated by the RIP apparatus did not affect solely lateral velocity. Mechanical coupling caused lateral force impulses to result in perturbations to both linear and rotational velocity. Yaw velocity, for example, was also perturbed by laterally directed force impulses. By rapidly generating forces to oppose the effects of perturbations,

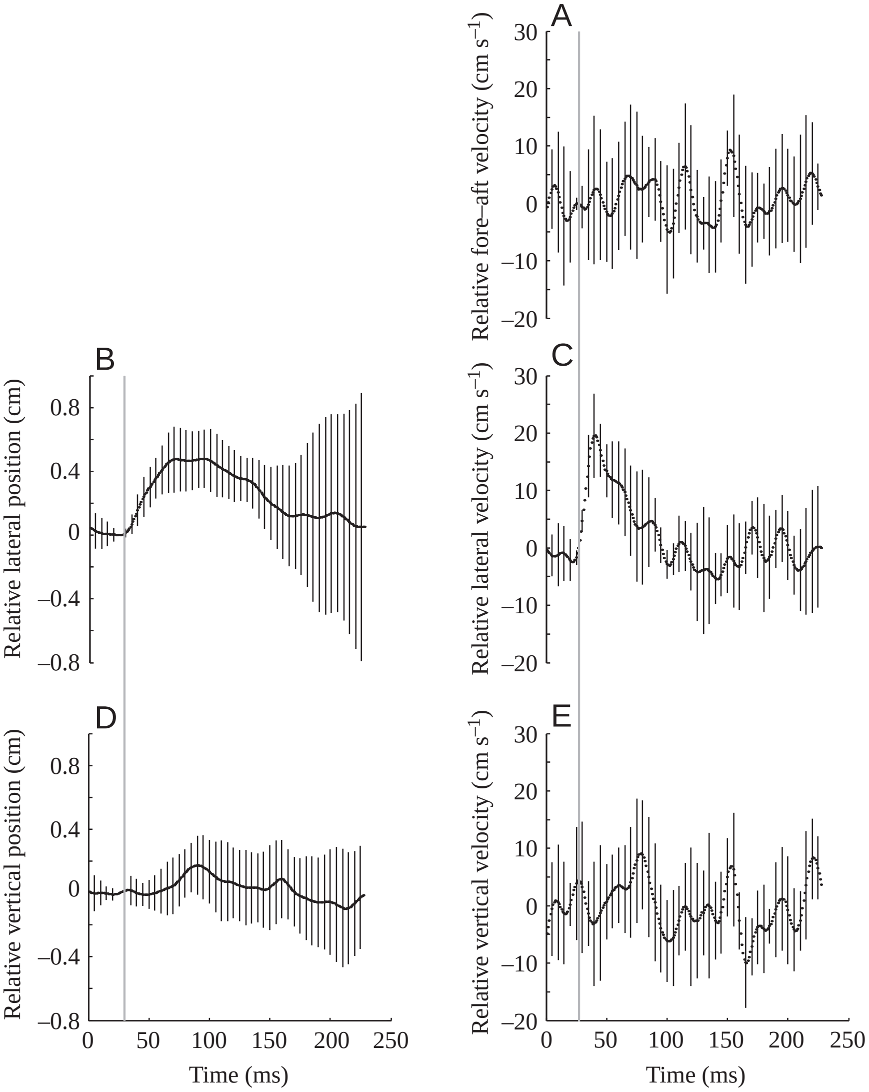

Fig. 6. Translational positions and velocities following perturbations relative to reference positions and velocities. Filled circles are values (mean ± 1 S.D.) for all perturbation trials. Velocities are 'errors': the difference between perturbed velocities and mean reference velocities collected from unperturbed trials at equivalent phases of the step cycle. Fore–aft and lateral velocities are in the body orientation coordinate frame. Vertical positions and velocities are in the global coordinate frame. Data from perturbed trials are normalized so that perturbations occur 30 ms from the beginning of the data set (indicated by gray vertical lines). N=11 perturbed trials and N=12 unperturbed reference trials.

cockroaches stabilized their lateral velocity in less than 30 ms and their yaw velocity in less than 40 ms (Table 5). These rapidly running insects were able to generate forces appropriate to recover from lateral perturbations without changing leg step periods or phase relationships. Moreover, cockroaches effectively counteracted perturbations irrespective of which tripod was in stance when the perturbation occurred.

Mechanical coupling results in complex responses to lateral perturbations

The complexity and non-linearity of musculoskeletal systems can cause forces, torques and motions in different directions to be interdependent (Zajac and Gordon, 1989). Even in highly simplified dynamic systems, mechanical coupling can cause perturbations to one variable to impact the dynamics of the entire system (Kubow and Full, 1999). Consequently, mechanical coupling can alter the control requirements for maintaining stability.

The laterally directed force impulses used in this study did not simply perturb lateral velocity, but also resulted in perturbations to other movement directions. For example, lateral perturbations caused yaw velocities to increase (in the negative direction) substantially (Table 1; Fig. 7A). A potential explanation for the coupling of yaw velocity to lateral COM velocity may be due to the position of the COM behind the point of attachment of the legs. The COM lies 3.5 mm behind the attachment of the hind legs to the body, 10 mm behind the attachment of the middle legs and 16 mm behind the attachment of the front legs (Kram et al., 1997). The position of the COM, and consequently the RIP apparatus, behind the legs creates a moment arm about the thorax in the fore–aft direction. This mechanical coupling may have caused the observed perturbations to yaw.

Cockroaches were able to generate moments about the vertical axis to recover from induced perturbations to yaw velocity. In five of six trials in which perturbations caused the yaw velocity to be different from the reference yaw velocity, the yaw velocity recovered within the trial (Table 5). In contrast to their rapid recovery in the lateral direction, however, cockroaches did not develop yaw torques sufficient to cause recovery in the yaw direction within one stance period in the majority of trials. This may be due to spring-like behavior in the lateral direction (Full et al., 2002) and to the large moment of inertia of cockroaches about the dorso–ventral axis (Table 2). The failure of yaw velocity to recover quickly from perturbations underscores the complexity of stabilizing rapidly moving dynamic systems. Even though the RIP apparatus directly caused perturbations to lateral movements, yaw velocity often remained altered after the lateral velocity had recovered.

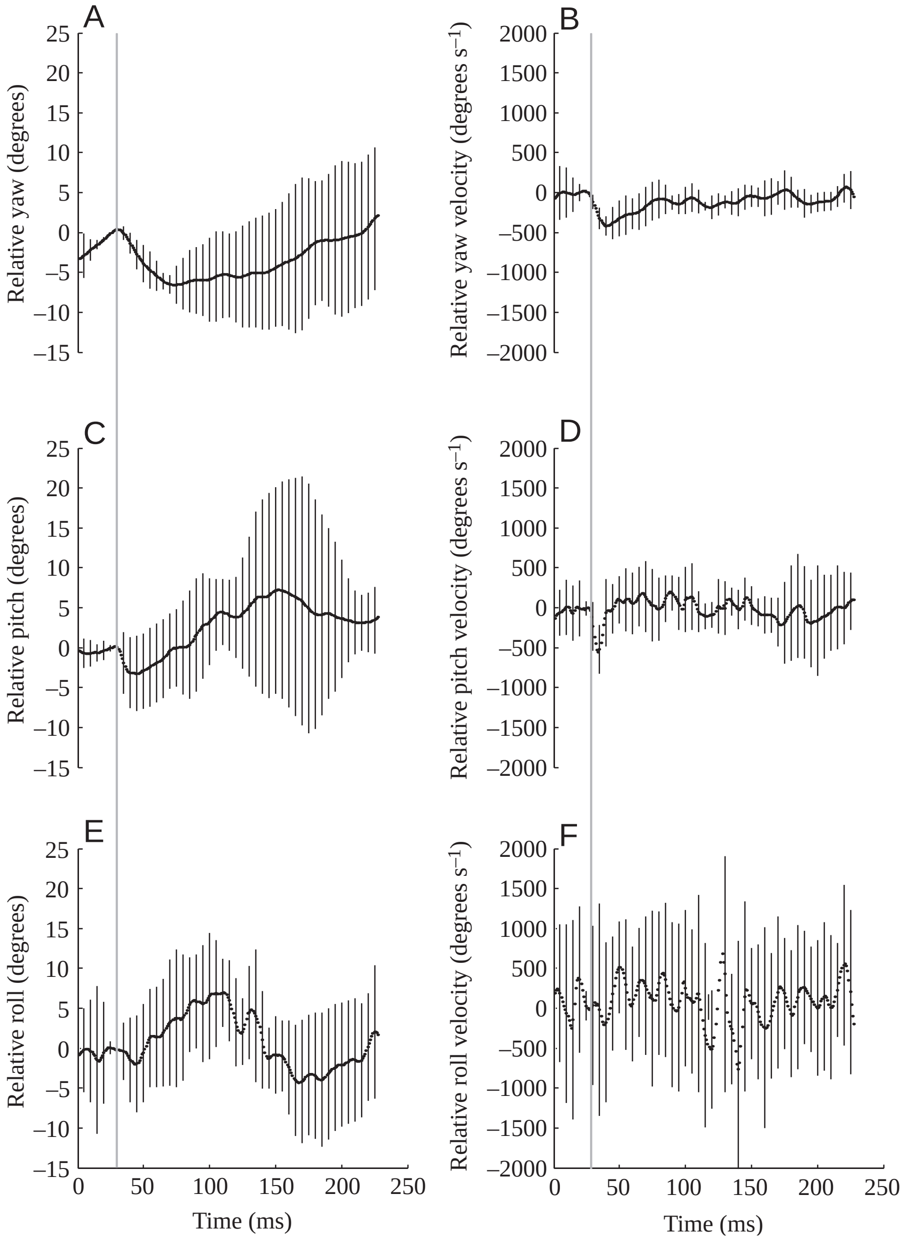

Fig. 7. Rotational positions and velocities following perturbations relative to reference positions and velocities. Points represent mean rotational velocity ‘errors’ normalized to reference velocities and to the time of perturbation (gray vertical lines) as in Fig. 6. Values are means ± 1 S.D. Yaw, pitch and roll Euler angles were calculated relative to a coordinate frame based on the initial movement direction of the animal (see Fig. 3A,C–E). *N*=11 perturbed trails and *N*=12 unperturbed reference trials.

Table 2. *Moments of inertia about the principal axes of inertia*

	Fore–aft, *x*, axis (roll)	Medio–lateral, *y*, axis (pitch)	Vertical, *z*, axis (yaw)
RIP apparatus absent (kg m^2)	$0.4\times10^{-7}\pm0.2\times10^{-7}$	$3.0\times10^{-7}\pm0.9\times10^{-7}$	$3.7\times10^{-7}\pm1.7\times10^{-7}$
RIP apparatus present (kg m^2)	$2.5\times10^{-7}\pm0.7\times10^{-7}$	$3.9\times10^{-7}\pm0.73\times10^{-7}$	$6.0\times10^{-7}\pm1.3\times10^{-7}$
Percentage change	740±400	135±33	209±153

RIP, rapid impulsive perturbation.

Values are means ± S.D. (*N*=9).

Table 3. *Stride, stance and swing periods for individual legs during unperturbed and perturbed running*

	Left			Right		
	Front	Middle	Hind	Front	Middle	Hind
Stride period (ms)						
Unperturbed	101±12 (8)	103±3 (8)	99±10 (8)	103±4 (8)	100±10 (8)	101±13 (8)
During perturbation	112±20 (9)	106±18 (7)	111±19 (7)	108±18 (7)	111±19 (9)	107±16 (6)
P	0.24	0.67	0.18	0.49	0.17	0.51
After perturbation	106±12 (9)	113±17 (8)	109±14 (7)	112±16 (6)	115±24 (7)	109±17 (7)
P	0.46	0.12	0.17	0.19	0.15	0.37
Stance duration (ms)						
Unperturbed	46±5 (8)	55±11 (8)	54±12 (8)	49±9 (8)	57±5 (8)	52±9 (8)
During perturbation	55±22 (5)	66±4 (6)	60±19 (4)	46±7 (5)	75±22 (3)	60±5 (3)
P	0.35	0.05	0.55	0.56	0.09	0.19
After perturbation	50±7 (8)	67±13 (8)	51±5 (9)	55±17 (6)	60±8 (9)	60±15 (7)
P	0.23	0.08	0.61	0.43	0.34	0.24
Swing duration (ms)						
Unperturbed	56±7 (8)	44±5 (8)	45±6 (8)	53±8 (8)	45±3 (8)	47±6 (8)
During perturbation	54±9 (4)	42±3 (4)	49±10 (5)	56±12 (5)	44±6 (5)	52±14 (3)
P	0.72	0.53	0.45	0.66	0.88	0.49
After perturbation	58±5 (8)	41±6 (8)	49±11 (9)	56±11 (6)	43±8 (9)	45±2 (7)
P	0.67	0.32	0.37	0.63	0.65	0.43

‘After perturbation’ refers to all steps occurring after the stride during which the perturbation occurred.

Numbers in parentheses indicate the number of samples used in the comparison.

Numbers below values indicate *P*-values for comparisons with unperturbed running.

Values are means ± S.D.

Table 4. *Phase relationships among legs during unperturbed and perturbed running*

	Unperturbed	During perturbation	*P*	After perturbation	*P*
Ipsilateral legs					
Left front in left middle	52±5 (8)	52±7 (5)	0.87	53±5 (8)	0.89
Left middle in left hind	48±4 (8)	45±3 (5)	0.19	47±3 (7)	0.73
Right front in right middle	53±6 (8)	56±4 (5)	0.33	50±8 (7)	0.51
Right middle in right hind	45±3 (8)	45±3 (3)	0.84	46±8 (7)	0.67
Contralateral legs					
Left front in right front	50±5 (8)	48±6 (5)	0.56	51±4 (6)	0.72
Left middle in right middle	51±3 (8)	50±3 (6)	0.54	48±6 (7)	0.27
Left hind in right hind	48±2 (8)	50±7 (4)	0.54	52±5 (7)	0.09

‘Left front in left middle’ indicates that the value corresponds to the phase during the step cycle of the left middle leg (touchdown-to-touchdown) at which the left front leg touches down and begins stance. For this comparison, the left middle leg is the ‘reference leg’. The leg listed second is the reference leg for each comparison.

Values are percentages of the stride period of the reference leg.

Numbers in parentheses indicate the number of samples used in the comparison.

Table 5. *Recovery from lateral perturbations*

	Significantly different, perturbed step (number of trials)*	Significantly different, step after perturbation (number of trials)	Mean number of steps to recovery	Number of trials recovering within first step	Phase of perturbation in step when animal recovered within first step (%)	Phase of perturbation in step when animal did not recover within first step (%)	Time to recovery (ms)
Fore–aft velocity	6	8	2.0±1.0 (4)	2	34±48	38±25	99±45 (5)
Lateral velocity	11	6	1.6±1.0 (9)	5	16±15	54±23	27±12 (9)
Vertical velocity	10	8	1.9±1.0 (7)	3	63±26	28±23	48±24 (8)
Yaw velocity	6	8	1.3±0.5 (5)	1	29	38±30	37±15 (5)
Pitch velocity	9	9	2.3±1.1 (7)	2	60±36	32±25	41±40 (7)
Roll velocity	8	11	3 (1)	0	NA	37±30	101±17 (3)

Values are means ± S.D.
*11 trials were used in the analysis.
Numbers in parentheses indicate the number of samples used in the comparison.
NA, not applicable.

Cockroaches did not require step transitions to recover from perturbations

Following lateral perturbations, cockroaches were able to stabilize lateral velocity before the transition to the next stance period occurred (Table 5). Cockroaches did not require step transitions to stabilize lateral velocity when subject to lateral force impulses of a magnitude equal to 85% of their forward momentum. However, the ability of cockroaches to recover from perturbations within a stance period depends on the substratum on which they run. Cockroaches do not exhibit within-step recovery on smooth surfaces (such as acetate) or on surfaces on which they have less purchase than soft balsawood (Jindrich, 2001). The influence of friction and other properties of substrata on stability and maneuverability during locomotion is an important area for research (Alexander, 1982).

Gait kinematics did not change in response to lateral perturbations

Changes in stance period, swing period or phase relationships among legs, which could indicate changes to leg kinematics at step transitions, were not evident (Tables 3, 4). This finding supports the hypothesis that kinematic changes at step transitions are not necessary to maintain stability in response to lateral perturbations and underscores the need to consider forces and inertias when studying rapid locomotion (Jindrich and Full, 1999). However, we did not directly measure leg or joint kinematics in response to perturbations. Changes in foot placement, leg configuration or stiffness could contribute to stability without requiring changes to step periods or phase relationships. We therefore cannot rule out the possibility that kinematic changes at step transitions augment within-step changes in force production and may be necessary to stabilize locomotion subject to perturbations of different magnitude or direction from those used in the present study.

Contribution of intrinsic musculoskeletal properties to stabilization of rapid running

The velocity maxima and minima following perturbations (Figs 6, 7) must result from forces generated by the animals. Forces opposing the perturbation are necessary to cause decreases in velocity. The short times to maximum lateral velocity (Table 1) indicate that the animals were capable of generating opposing forces 10–14 ms following the perturbation. This rapid force generation poses the question of whether neural reflexive feedback is likely to account for the ability of cockroaches to recover from perturbations within one step.

Neural feedback allows for precise control of leg kinematics and interleg coordination in slowly moving insects (Cruse, 1985a,b, 1990). Even during extremely rapid movements, some insects are capable of extraordinarily rapid and precise neural control. For example, flies are capable of cycle-by-cycle modulation of wing kinematics when beating their wings at 140 Hz (Tu and Dickinson, 1996). Reflexes involving chemical synapses can allow synaptic delays of less than 5 ms, and even faster electrical connections allow synaptic delays of less than 1 ms (Fayyazuddin and Dickinson, 1996). The capabilities of insect nervous systems clearly allow for the possibility that within-step stabilization is controlled by neural feedback.

For neural feedback to cause recovery from perturbations, three sequential events must take place. First, the perturbation must be detected by sensory cells. Sensors on the cerci (Camhi and Levy, 1988), the antennae (Camhi and Johnson, 1999), the exoskeleton (Schaefer et al., 1994), within the exoskeleton (Burrows, 1996) or even within the muscles (Matheson and Field, 1995) could sense the perturbation. Antennal or cercal sensors could detect air currents, noise or heat generated by the RIP, but these stimuli are less likely to provide information about the specific nature of the perturbation. Sensors on the exoskeleton such as campaniform sensilla (Ridgel et al., 1999) or chordotonal organs within the exoskeleton (Kondoh et al., 1995) can detect loading of the exoskeleton or joint position and velocity and are more likely to provide the specific information about the perturbed COM velocity necessary to generate an opposing force.

A brief force impulse does not necessarily produce an equally fast change in exoskeletal loading, joint position or velocity. Exoskeletal strain due to loading, which campaniform sensilla can detect, can occur when a segment is stressed axially or when muscles generate forces on the segment (Ridgel et al., 1999). Axial forces along leg segments opposing a perturbation would decrease the change in lateral momentum resulting from the perturbation. The agreement between the average force impulses generated by the RIP (85% of forward momentum) and the maximum lateral momentum measured following perturbations (80% of forward momentum) suggests that little immediate force is generated by axially loading the leg segments. Axial loading would be expected to decrease the degree to which the force impulse generated by the RIP results in increased lateral momentum. Substantial axial loading of the legs would generate a force impulse counter to the impulse generated by the RIP and cause the resulting change in lateral momentum to be smaller than the force impulse generated by the RIP. However, without direct measurements of exoskeletal strain or sensory output, it is not possible to exclude the possibility that campaniform sensilla can immediately sense perturbations. In the American cockroach, *Periplaneta americana*, campaniform sensilla have been shown to detect lateral substrate displacement, with latencies of 6.1±3,5 ms (mean±S.D., *N*=61) (Ridgel et al., 2001).

Hair plates and chordotonal organs can sense changes in joint position or velocity. However, some time may elapse before changes in velocity exceed the threshold of the sensors. The time necessary to sense a perturbation consequently depends on the sensor threshold and the magnitude of the perturbation.

The potential for a time delay between a perturbation and when sensors could detect position changes is magnified. In the 13 ms between a perturbation and the first stabilizing acceleration, lateral velocity changes by approximately 20 cm s^{-1} or almost 10 times the peak lateral velocity during unperturbed running. In the same time period, lateral position changes by only 0.15 cm, or 2.5 times the peak excursions during unperturbed running (Fig. 6B). In general, large position changes will lag behind velocity changes and, if sensors show comparable relative sensitivities, the time necessary to detect changes in position may be expected to be larger than the time necessary to detect changes in velocity or force.

The second event that must occur for neural feedback to stabilize a perturbation is that sensory information must be transmitted to the central nervous system (CNS) and processed, and an appropriate motor output must be sent to the muscles. Camhi and Nolen (1981) estimated a minimum neural latency, the time from stimulus onset to muscle stimulation, of 6.5 ms for the stereotyped escape response of *P. americana*, which, with a mass of less than 1 g, is smaller than *B. discoidalis* and can run at over twice the maximum leg cycling frequency of *B. discoidalis* (Full and Tu, 1991). It is reasonable to hypothesize that *P. americana* exhibits faster reflexes than *B. discoidalis*. However, it is unclear whether a neural response to a perturbation would be expected to show a shorter or longer time delay than the escape response.

Third, once the perturbation has been sensed and the appropriate motor output conducted to the muscles, the muscles must generate corrective forces. Muscles take time to begin to generate force because of delays inherent in excitation–contraction coupling. The estimate of 6.5 ms for minimum neural latency, coupled with the observed velocity changes 13 ms following RIPs, leaves 6.5 ms for the muscles to increase force production following stimulation. The time to force onset for individual muscles in *B. discoidalis* is almost 10 ms (Full and Meijer, 2001). Muscle kinetics alone could account for much of the time to recovery onset following perturbations, even if there were no neural latencies involved with sensing, processing and generating motor output.

Moreover, the time to peak force of active, shortening muscles for *B. discoidalis* is 36 ms (Ahn and Full, 2002). Similarly, K. Meijer (unpublished data) has subjected individual legs to rapid step position changes (1 mm change in fore–aft position in less than 2 ms) and found that, in passive muscles, peak force is developed on average 30±2 ms (mean ± S.D., *N*=8) following the step length change. The lateral velocity was observed to recover from the perturbations in slightly less than 30 ms (Table 5). Since the kinetics of relaxation is slower than the kinetics of force generation (Ahn and Full, 2002), if muscles could be stimulated immediately following a perturbation, peak force might be reached as much as 30 ms later. In this case, the lateral velocity might be expected to exhibit a large decrease (i.e. ‘overshoot’) after neurally stimulated muscles had generated forces to arrest the velocity imparted by the perturbation. Such an overshoot would prolong the time to recovery. We did not observe such a decrease in the perturbation trials (Fig. 6C).

In summary, to generate forces appropriate to counteract a perturbation, the perturbation must be sensed, sensory information must be integrated in the nervous system to generate appropriate motor output and the muscles must generate additional forces. Latencies due to sensing the perturbation, to integrating sensory information and generating motor output in the nervous system and to developing muscle forces could each separately account for a substantial proportion of the time to force onset observed following perturbations.

Several studies have directly measured the latency between the application of a stimulus and the generation of electrical (EMG) activity at the muscles or the onset of leg movement. This type of measurement accounts for the time necessary for the CNS to process a stimulus and, in the case of movement onset, some of the excitation–contraction kinetics of the muscle as well. Studies on *P. americana* report a wide range of time delays. Levi and Camhi (1996) reported a 25–50 ms delay (depending on the muscle) between a wind stimulus and EMG activity onset in *P. americana*. During walking, Camhi and Nolen (1981) reported a 14 ms delay between a stimulus and movement onset for *P. americana*. Schaefer et al. (1994) reported latencies to movement onset of 17 ms in response to a tactile stimulation, and Nye and Ritzmann (1992) reported a latency of 55 ms from wind stimulation to leg movement. The fastest reflex latencies measured for *P. americana* (14 ms) are longer than the mean time to lateral velocity decrease following RIPs (13 ms; Table 1). If *B. discoidalis* could sense perturbations immediately after they occurred, the time required to generate the observed forces would be comparable with the very fastest reflexes measured in cockroaches.

On the whole, a reflex-based mechanism for stabilizing locomotion could account for the extremely rapid force development observed following perturbations only if the time delays introduced in sensing and the neural processing of sensory information were close to the theoretical or measured minima. The extremely quick sensing and processing required of the nervous system, however, poses the question of whether the animals could sense the results of the perturbation accurately enough immediately following the perturbation to generate an appropriate motor response. Coupled with this problem, the likely magnitudes of both neural and muscular time delays calls into question whether reflex-based mechanisms could generate appropriate responses to the brief perturbations generated by the RIP apparatus. Consequently, the extremely rapid force generation and recovery times found in cockroaches support the hypothesis that musculoskeletal ‘preflexes’ contribute to stabilizing rapid locomotion. Measurements of EMG activity following perturbations will be an important next step to test this hypothesis.

A preflex can be considered as a ‘zero-delay, intrinsic response of a neuromusculoskeletal system to a perturbation’ (Brown and Loeb, 2000). Stabilization by musculoskeletal elements can result from the passive properties of muscles and connective tissue contributing to joint impedance (Brown et al., 1982; Esteki and Mansour, 1996; Hajian and Howe, 1997) and the length- and velocity-dependence of force production in active muscle (Grillner, 1972; Rack, 1970). For example, increased force generation by active muscle when subjected to lengthening could act to resist sudden length changes and counteract perturbations (Morgan, 1990; Rack and Westbury, 1974). Passive musculoskeletal elements and dynamic muscle properties can act to stabilize many-jointed musculoskeletal systems (Brown and Loeb, 2000; Seyfarth et al., 2001; Wagner and Blickhan, 1999).

The potential for musculoskeletal preflexes does not necessarily imply that recovery from a perturbation is instantaneous. Compliance in the musculoskeletal system can cause time delays in recovery from perturbations similar to the time delays that would arise from neural latencies (Campbell and Kirkpatrick, 2001). However, if the recovery from perturbations can be explained by the viscoelastic properties of the unperturbed neuromusculoskeletal system, it would provide additional support for the hypothesis that preflexes contribute to stabilization.

Spring-like recovery from brief perturbations is similar to spring-like dynamics during unperturbed running

Running animals employ a bouncing gait during unperturbed locomotion. The COM oscillates in a spring-like manner. Consequently, running animals can be modeled as compliant systems in the sagittal plane (Blickhan, 1989; Blickhan and Full, 1993; Farley et al., 1993; Full, 1989; McMahon and Cheng, 1990). Cockroaches also exhibit lateral oscillations of their COM during each stride (Full and Tu, 1990) and may act like spring-mass systems in the horizontal plane. Spring-like behavior during unperturbed locomotion may arise from the spring-like properties of active muscle and passive skeletal compliance without requiring reactive excitation of muscle.

Musculoskeletal properties that contribute to spring-like behavior during unperturbed locomotion could also contribute to stability. The ‘lateral leg spring’ (LLS) model of legged locomotion in the horizontal plane captures many aspects of insect locomotion without requiring a control system (Schmitt and Holmes, 2000a,b). Stability in yaw velocity and body orientation relative to the direction of COM movement emerges from the dynamics of the LLS model without the need for explicit control (Schmitt et al., 2002). If cockroaches act like spring-mass systems in the horizontal plane, then passive dynamic behavior analogous to that observed in the LLS model may contribute to stability. The direct lateral perturbations used in the present study provide the opportunity to determine whether cockroaches act like horizontal spring-mass systems.

Analysis of spring-mass systems in two dimensions is complex and non-linear (Schmitt and Holmes, 2000a; Schwind, 1998). Variables such as the length and touchdown angle of a ‘virtual’ leg are necessary to characterize the system, but have yet to be directly measured experimentally. To simplify our analysis and to allow for direct comparison with the mechanics of unperturbed locomotion (Full and Tu, 1990), we chose to constrain our analysis to movements in the lateral dimension. In one dimension, the frequency (ω) of a spring-mass system oscillating with a period equal to the step period (τ) is:

$$\omega = \pi/\tau\,. \tag{4}$$

If animals oscillate at their natural frequency in the lateral direction, the oscillation frequency is related to the mass (m) and lateral stiffness (k_{lat}):

$$\omega_{\mathrm{o}} = \sqrt{k_{\mathrm{lat}}/m} \tag{5}$$

or

$$k_{\mathrm{lat}} = m\omega^2\,. \tag{6}$$

The 4 g (animals, 2.7 g; apparatus, 1.3 g) cockroaches used in this study moved using a step period of approximately 50 ms

(Table 3). We would consequently predict a k_{lat} of $16\,\mathrm{N\,m^{-1}}$ for the weighted animals running at approximately $25\,\mathrm{cm\,s^{-1}}$.

To describe the mechanism used by cockroaches to recover from brief perturbations and compare it with the lateral spring-like behavior during unperturbed running, we fit a simple viscoelastic model to the kinematics of recovery from perturbations. This description can help to explain the relative contributions of position- and velocity-dependent components to the overall acceleration of the COM and to compare the recovery from perturbations with the compliance observed during unperturbed locomotion.

A 'viscoelastic' kinematic model hypothesizes that recovery from perturbations is due to position- and velocity-dependent acceleration, which act to arrest the momentum imparted on the animal by the RIP apparatus. The position-dependent acceleration can be considered as a 'spring' and the velocity-dependent acceleration as a 'damper'. In parallel, the spring and damper acting together is analogous to the Voigt model of viscoelasticity (Fung, 1993; Fig. 8A). Both the spring and damper are here assumed to be linear functions of lateral position.

The equation for the Voigt model can be written as:

$$\ddot{\mathbf{y}} + b\dot{\mathbf{y}} + k\mathbf{y} = 0\,, \tag{7}$$

where $\mathbf{y}$ is the lateral position, $\dot{\mathbf{y}}$ is the velocity and $\ddot{\mathbf{y}}$ is the acceleration; b is the damping coefficient and k is the spring coefficient. To fit a Voigt model to the perturbed data, the position of the COM in the direction perpendicular to the initial movement direction was filtered using a 25 Hz cut-off frequency and differentiated to yield velocity over time. The velocity was differentiated to yield acceleration. For each trial analyzed, we selected a period of recovery beginning at the time when lateral velocity begins to decrease (where the stabilizing acceleration first begins, on average 13 ms following the perturbation) until the end of the perturbed step. We estimated k and b from the position, velocity and acceleration for each trial using a least-squares method (Schwind, 1998).

For each trial, we predicted the acceleration using equation 7, the trial values of k and b and the position and velocity data for that trial. Fig. 8B compares the measured and calculated accelerations for one trial. In this trial, the Voigt model is better able to predict the measured acceleration than position-dependent (spring) or velocity-dependent (damping) components alone. By calculating the proportional root-mean-square error between the predicted and measured acceleration for each trial, we found that, over all trials, spring-dependent behavior was able to predict 44±23% of the total acceleration, damping was able to predict 30±21% of the acceleration and the full Voigt model was able to predict 74±17% of the trial accelerations following perturbations. Errors for the spring and damping models were not significantly different (t-test; $P=0.12$), but the Voigt model errors were significantly smaller than those for the spring and damping models alone (t-test; $P<0.0001$).

The mean value of k was $3800\pm3200\,\mathrm{s^{-2}}$, and the mean value of b was $26\pm14\,\mathrm{s^{-1}}$. Taking into account the mass of the animals, the lateral spring constant observed in response to perturbations is $15\,\mathrm{N\,m^{-1}}$, in reasonable agreement with the lateral spring constant ($16\,\mathrm{N\,m^{-1}}$) predicted for unperturbed, straight-ahead running calculated from the whole-body mechanics reported in Full and Tu (1990). Cockroaches act in a viscoelastic manner in response to brief perturbations. This may contribute to explaining why simple, self-stabilizing horizontal-plane spring-mass models can capture many aspects of cockroach locomotion (Schmitt and Holmes, 2000a,b). However, the ability of a linear Voigt model to describe recovery from perturbations with errors of 74% does not exclude the possibility that the stability characteristics of cockroaches could be better described by more complex or non-linear viscoelastic models.

This 'spring' constant of $15\,\mathrm{N\,m^{-1}}$ is 5–30 times the 'virtual leg' spring constants used in the LLS model (Schmitt and Holmes, 2000a,b). This difference is due to compression of the LLS 'virtual leg' by movement in both the fore–aft and lateral directions. Since cockroaches move approximately 10 mm in the fore–aft direction in one step, dependence on fore–aft movement results in larger 'virtual leg' spring compression than would be experienced by a purely lateral spring, with correspondingly lower spring constants. This difference is directly comparable with the higher vertical stiffness (k_{vert}) relative to leg stiffness (k_{leg}) observed for legged running in the sagittal plane (Farley et al., 1993).

Similarities between the spring-like component of the viscoelastic behavior observed during recovery from perturbations and the spring-like behavior observed during unperturbed locomotion lend additional support to the hypothesis that musculoskeletal preflexes contribute to stabilizing rapid locomotion. We hypothesize that the same spring-like properties that confer passive dynamic stability to horizontal-plane models of locomotion (J. Schmitt and P. Holmes, in preparation) contribute to the dynamic stabilization of rapid running.

Limitations

Using the RIP apparatus to perturb cockroaches during running is subject to several limitations, which should be taken into consideration. First, although the RIP apparatus was designed to mount to the cockroaches firmly with minimal changes to the location of the COM, the RIP apparatus increased body weight by approximately 50%. Increases in body weight have the potential to affect the mechanics, energetics and control of locomotion (Chang et al., 2000; Farley and Taylor, 1991; Taylor et al., 1980). However, adding mass equivalent to 50% of body weight above the COM does not appear to change locomotory kinematics substantially. The 10 Hz stride frequency observed in the cockroaches used in the present study is comparable with the stride frequency observed in unloaded cockroaches running at $29\,\mathrm{cm\,s^{-1}}$ (Full and Tu, 1990; Ting et al., 1994), and addition of load did not cause cockroaches to depart from the alternating-tripod gait observed during unloaded locomotion. The fore–aft velocity of animals

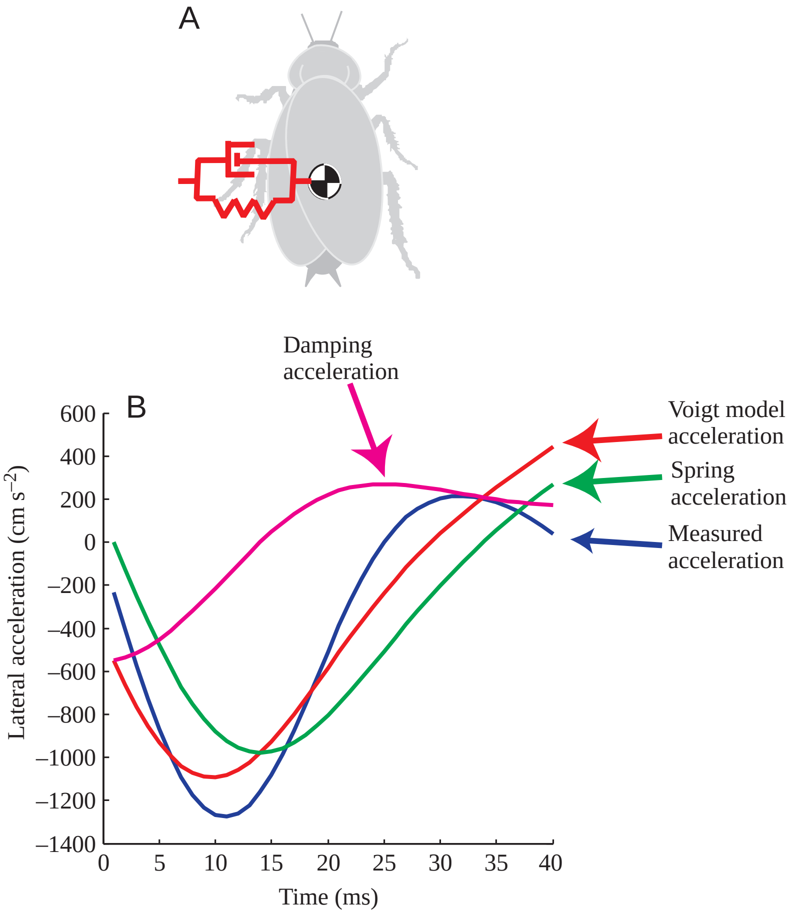

Fig. 8. Descriptive viscoelastic model fitted to the lateral recovery of cockroaches. (A) Voigt model for the mechanical behavior of cockroaches in the lateral direction. (B) Measured and calculated acceleration for a representative trial. The blue curve shows measured acceleration during recovery from a perturbation, and the red curve shows acceleration calculated from the Voigt model fitted to the cumulative trial data. The magenta curve shows the contribution of velocity-dependent acceleration (the damper) to calculated acceleration. The green curve shows the contribution of position-dependent acceleration (the spring) to calculated acceleration. The mean percentage error for the spring component alone for this trial was 40%, that for the damping component alone was 88% and that for the Voigt model was 17%.

carrying the RIP apparatus fluctuated around the average velocity by ±12%, in reasonable agreement with the ±8% fluctuations observed in unloaded cockroaches (Full and Tu, 1990).

Finally, in a separate study (D. L. Jindrich and R. J. Full, in preparation), we compared detailed leg kinematics between loaded and unloaded cockroaches. The anterior extreme positions (AEPs) and posterior extreme positions (PEPs) of unperturbed cockroaches carrying the RIP apparatus showed no significant differences from those employed by unloaded cockroaches. The kinematic similarities between unloaded cockroaches and cockroaches loaded with approximately 50% of body weight suggest that mounting the RIP apparatus on cockroaches does not result in qualitative changes in locomotory mechanics. Simulation studies suggest that, even if locomotory mechanics was altered by changing body mass or moments of inertia, these changes would be likely to decrease stability (Full et al., 2002). We therefore consider the stability observed when using the RIP apparatus to be a conservative estimate of the performance of these animals.

Future directions

Recent research advances have demonstrated that the passive dynamics of musculoskeletal systems, the properties of active muscle and neural control must all be considered together to understand animal movement (Dickinson et al., 2000). Moreover, the dynamics of the entire neuromechanical system must be taken into account when trying to understand any of its constituents. Neural motor output must be interpreted by muscles whose response to stimulation depends on many factors, including intrinsic muscle properties, system dynamics and previous activity. Muscles do not act solely as power generators, but also as springs, brakes, struts and, as our findings support, stabilizers.

We hypothesize that musculoskeletal preflexes contribute to stabilizing rapid locomotion. However, the nervous system remains necessary for coordinating movements and modulating the mechanical properties of the musculoskeletal system during locomotion. When subject to large or persistent perturbations, neurally mediated responses may be required for stability. Continued research on the dynamic interactions between neural control and musculoskeletal dynamics will be critical to understanding the exceptional performance of animals in their environment. Insights gained from neuromechanical studies of rapidly running insects have provided biological inspiration towards the design of simple, legged robots (Altendorfer et al., 2001).

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