

Effects of aging on behavior and leg kinematics during locomotion in two species of cockroach

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Summary

Aging is often associated with locomotor deficits. Behavior in aged *Blaberus discoidalis* cockroaches was analyzed during horizontal walking, climbing, righting and inclined walking. Adult animals showed a decrease in spontaneous locomotion with increasing age. Tarsal abnormalities, termed ‘tarsus catch’, were often present in aged individuals. In ‘tarsus catch’, the prothoracic leg catches on the mesothoracic leg during the swing phase. This deficit causes alterations of the gait, but animals are able to regain a tripod gait after the perturbation. The tibio-tarsal joint angle in individuals with ‘tarsus catch’ was significantly less than in intact animals. Structural defects were consistently associated with ‘tarsus catch’. The tracheal tubes in the tarsus and around the tibio-tarsal joint were often discolored and the tarsal pads were hardened in aged cockroaches. All aged individuals were able to climb. However, prior to climbing, some animals with ‘tarsus catch’ failed to show postural changes that are normally seen in young animals. Aged individuals can right as rapidly as 1-week-old adults. However, animals

with ‘tarsus catch’ take longer to right than aged intact individuals. Old cockroaches have difficulty climbing an incline of 45°, and leg slipping is extensive. Slipping may be caused by tarsal degeneration, but animals that are unsuccessful in inclined walking often show uncoordinated gaits during the attempt. Escape behavior was examined in aged American cockroaches (*Periplaneta americana*). They do not show normal escape. However, after decapitation, escape movements return, suggesting that degeneration in head ganglia may actually interfere with escape. These findings provide evidence for age-related changes both in the periphery and in the central nervous system of cockroaches and stress the importance of multi-level approaches to the study of locomotion.

Movies available on-line.

Key words: senescence, walking, arthropod, central nervous system, kinematics.

Introduction

In all animals, the aging process is accompanied by physiological and behavioral changes. Physiological changes, such as those associated with the nervous and musculoskeletal systems, often result in decreased or impaired locomotion in aged individuals (Fernandez et al., 1999; Hilleras et al., 1999; Le Bourg, 1987; Minois et al., 2001; Scimonelli et al., 1999; Siwak et al., 2002).

Age-related locomotor deficits are often the result of degeneration in the central and/or peripheral nervous systems. In mammals, loss of neurons and neurotransmitters in cortex and cerebellum can be associated with aging and motor impairment (Hilber and Caston, 2001; Kaasinen et al., 2000; Volkow et al., 1998). Sensory information from the limbs is important in postural control and reactions to perturbations (Maki and McIlroy, 1996; McIlroy and Maki, 1996). Degeneration in the peripheral nervous system could result in loss of vibration or cutaneous sense in the limbs and a decrease in the response time of reflexes (Shumway-Cook and Woollacott, 2000; Ulfhake et al., 2002).

Locomotor deficits in aged individuals can also be caused by non-neural degeneration in the musculoskeletal system. Aging is frequently associated with weakness and decreased mass in the muscles (Anderson, 2003). Muscle weakness in the elderly has been attributed to a reduction in the sliding speed of cross-bridging elements (Hook et al., 2001; Lowe et al., 2002). Muscle atrophy with aging is the result of a loss in the number of muscle fibers, rather than a reduction in fiber size (Lexell, 1993). Stiffness at the joints and ligaments, which can be caused by increases in collagen fiber cross-linkages and loss of elastic fibers, can also result in a decrease in the range of motion in aged individuals (Aigner and McKenna, 2002; Kerin et al., 2002).

Insects provide a useful model system for aging studies because they are short-lived compared with mammals. Decreases in spontaneous activity with increasing age have been well documented in fruitflies and honeybees (Fernandez et al., 1999; Minois et al., 2001; Parkes et al., 1999; Tofilski, 2000). However, none of these papers have examined changes

in leg kinematics and joint movement in aged insects. Furthermore, past studies have only looked at simple walking and have not studied more complex locomotion, such as 'transitional behaviors' that alter an animal's path of movement (Watson et al., 2002). Transitional behaviors often require altered leg movements and/or posture to complete the task. Examination of these types of locomotion is important in order to understand how an animal alters behavior in different environmental situations.

In the present study, we documented the adult lifespan of *Blaberus discoidalis* and *Periplaneta americana* cockroaches. We then examined behavioral and kinematic changes in locomotion with age in *Blaberus* during horizontal walking and transitional behaviors including righting, climbing and inclined walking. In addition, we studied the effect of advanced age on the kinematics of escape behavior in *Periplaneta* and compared these findings with those observed in young individuals and decapitated animals. Locomotor deficits were present in both species of cockroaches older than 60 weeks post-adult molt and the behavior of these animals was often different from that seen in younger animals. Our findings show that age-related deficits in locomotion are present in senescent cockroaches.

Materials and methods

Animal care

Male and female *Blaberus discoidalis* Serville (Blaberidae; death-head cockroach) and male *Periplaneta americana* L. (Blattidae; American cockroach) were collected upon adult ecdysis and placed into plastic containers on a weekly basis. Animals were maintained at 26°C on a 12 h:12 h light:dark cycle. Fragments of egg cartons were added for shelter. In addition, food (chicken chow) and water were provided *ad libitum*.

Spontaneous locomotion

Animals were placed into a 23 cm×30 cm×10 cm plastic container without any shelter. Spontaneous locomotion was defined as the amount of time an individual spent walking, tunneling or climbing the walls within a 10 min period (600 s). Tunneling was defined as the time in which an animal was moving the legs in a walking motion but the head was in contact with the wall. Climbing was defined as the time in which one or more of the legs were in contact with the wall of the arena and the legs were moving in a walking motion. Grooming and standing were not scored as locomotion. In order to maintain the novelty of the testing arena, animals were tested only once in each trial.

Horizontal walking

Animals were placed in a treadmill that allowed for observation from the side and from below *via* a mirror mounted at 45° (Watson and Ritzmann, 1998). High-speed video images (125 frames s⁻¹) were taken with a single camera. The position of the tarsus, the end of the tibia on each leg and the center of

mass (COM) were digitized using motion analysis software (WINanalyse; Mikromak, Berlin, Germany). The COM was estimated as a point 46% of the body length along the fore–aft axis from the tail point of the animal (Jindrich and Full, 1999; Kram et al., 1997). Digitized points were used to calculate the distance from the end of the tibia to the COM (r) and the angle of the end of the tibia relative to the fore–aft axis through the COM (Φ ; terminology from Jindrich and Full, 1999). The angle of the tibio-tarsal joint was calculated during the first frame of stance by digitizing the end of the tarsus and a point on the distal end of the tibia. Angles and distances were linearly smoothed with an 8 ms time constant using Data-Pac software (Run Technologies, Mission Viego, CA, USA) and plotted as polar coordinates (r , Φ). Stride length was calculated as the length of the distance between the anterior extreme position (AEP) and posterior extreme position (PEP) during each stance phase. Gait pattern and the speed of walking were determined by calculating the number of frames in which the legs were in stance and swing.

Tarsal anatomy studies

The external and internal morphology of the tarsi was examined under a dissecting microscope, and images were captured with a Nikon Coolpix 950 digital camera. To test the flexibility of the tarsal pads, the tarsus was secured, tarsal pads up, in a wax dish with insect pin staples so that it would not move. A single nylon filament attached to a glass rod and a micromanipulator was used to indent the most proximal pad until the filament buckled. The maximum force of the filament (29 mN) was determined by pushing it against a 10 g force transducer until it buckled. The force transducer was calibrated with small weights.

Block climbing, inclined walking and righting

To examine climbing in aging animals, acrylic blocks were placed across the path of the treadmill (Watson et al., 2002). Blocks of 5.5 mm, 11 mm and 16.5 mm height were used to test each individual. High-speed video images were taken with a single camera at 125 frames s⁻¹. Videos were examined and compared with previous studies (Watson et al., 2002).

The ability of aged individuals to successfully walk on an incline was tested by using a track with an acetate belt that was tilted to 45°. Two high-speed video cameras were used to visualize the animal from below and from the side. Foot placement was calculated as described above. Leg slipping was defined as a change in the position of the foot on the substrate during the stance phase and was tallied in all six legs in four consecutive steps. Within each animal, the probability of leg slipping was calculated as the number of slips per step in all trials. Probability values for slipping for each individual were used to calculate the mean and S.D. across the population.

Righting was examined by placing animals on their backs in a 23 cm×30 cm×10 cm plastic container that was lined with a piece of Styrofoam. The duration of righting was measured with a stopwatch. Each individual was tested four times and trials were averaged.

Escape behavior

To examine the effect of aging on escape behavior, we switched our focus to *Periplaneta americana*. The reason for this change is that most of the previous work, by far, on cockroach escape has been performed on *Periplaneta* (Camhi, 1988; Ritzmann, 1993; Ritzmann and Eaton, 1997). Indeed, in an earlier study (Simpson et al., 1986), a related blaberid species, *Blaberus craniifer*, failed to escape from a live predator or move away from a synthetically generated puff of wind at room temperature. Although *B. discoidalis* does make escape movements, they are not as vigorous as those of *Periplaneta*.

For escape studies, animals were tethered above a glass plate covered with microtome oil (Nye and Ritzmann, 1992; Tryba and Ritzmann, 2000). Two large pins were attached to a glass tube mounted on a manipulator and placed through the pronotum from the ventral surface on either side of the head. Animals were induced to escape using tactile stimulation, in a random order, to the left and right edges of the 3rd abdominal tergite (Schaefer and Ritzmann, 2001). Stimulation was delivered with a hand-held solenoid that moved a glass rod with a bent insect pin at the end. The stimulator was held approximately 1 mm above the cuticle, and activation of the solenoid produced a stimulus with a force of 0.18 N. Each individual was stimulated four times, and then the animals were decapitated and stimulated several more times. Escapes were recorded with a Redlake Motionscope camera at 250 frames s^{-1} . Leg joint angles were analyzed with Videoblaster card and Motion TV motion analysis software (DataCrunch Systems, San Clemente, CA, USA).

Results

Cockroaches are relatively long-lived insects. The maximum adult lifespan (period after last molt) of *Blaberus* in our studies ($N=63$) was 80 weeks. Only 11% of the *Blaberus* lived to 73 weeks after the adult molt (Fig. 1A). However, 50% of the individuals died by week 61. Therefore, we define aged *Blaberus* as those individuals ≥ 60 weeks post-adult molt. Although we did not systematically compare the lifespan of male versus female cockroaches, all of the individuals that lived more than 73 weeks were female. *Periplaneta* ($N=31$) did not survive as long as *Blaberus* (Fig. 1A). The maximum lifespan of *Periplaneta* was 64 weeks, and 50% of the population was dead by 56 weeks.

In adult *Blaberus* cockroaches, we measured a gradual, but significant, decrease in spontaneous locomotion with increasing age (regression analysis, slope = -3.4 , $r^2=0.839$, $P<0.01$; Fig. 1B). Aged animals walked more slowly than young individuals and spent more time grooming or standing still. In addition, they showed less climbing and tunneling behavior than young adults. Young *Periplaneta* readily showed walking movements on a tether, but old individuals showed little spontaneous movement while tethered.

Horizontal walking

To characterize locomotor deficits in aged *Blaberus*, we

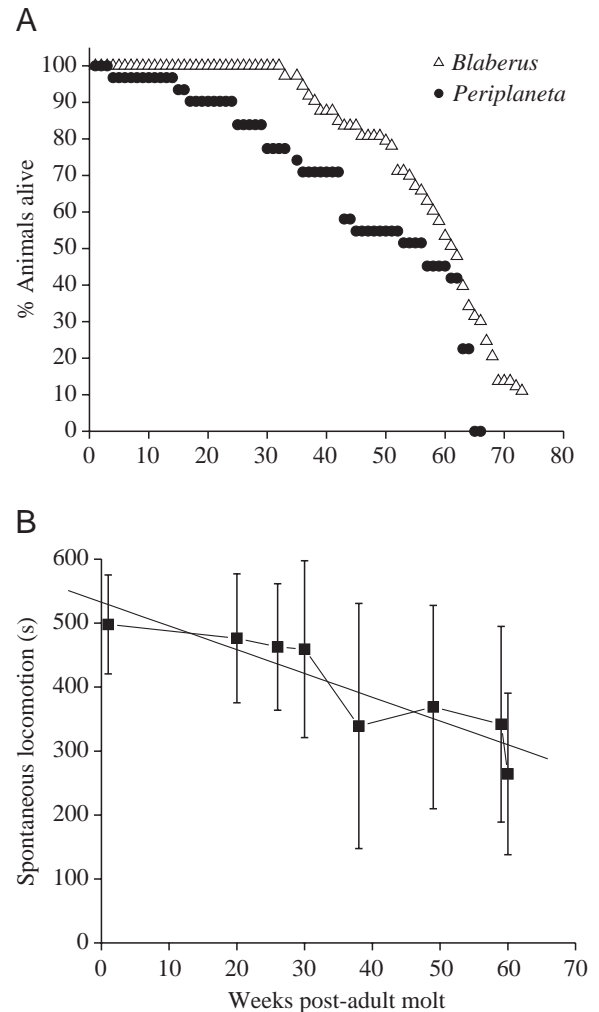
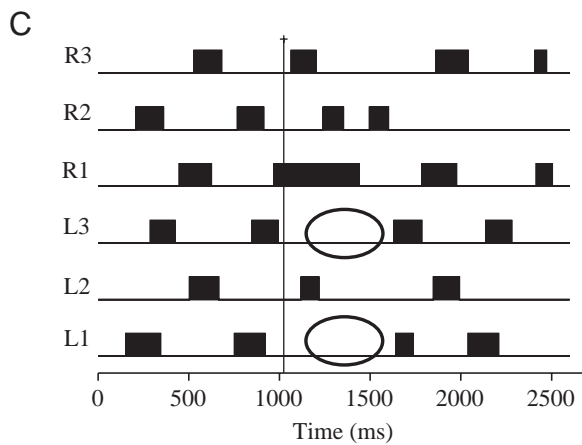
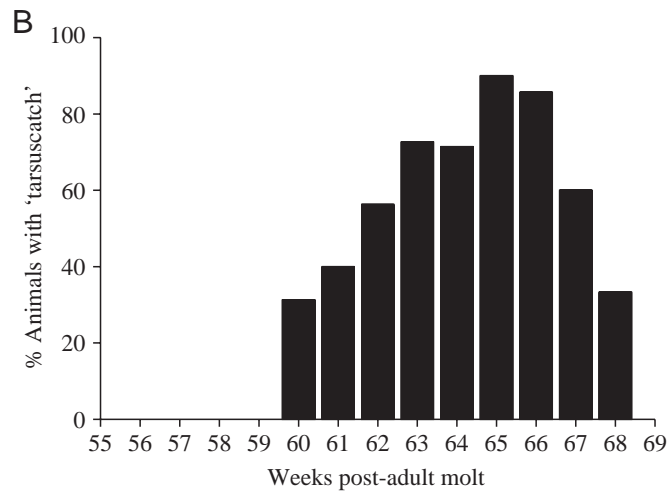
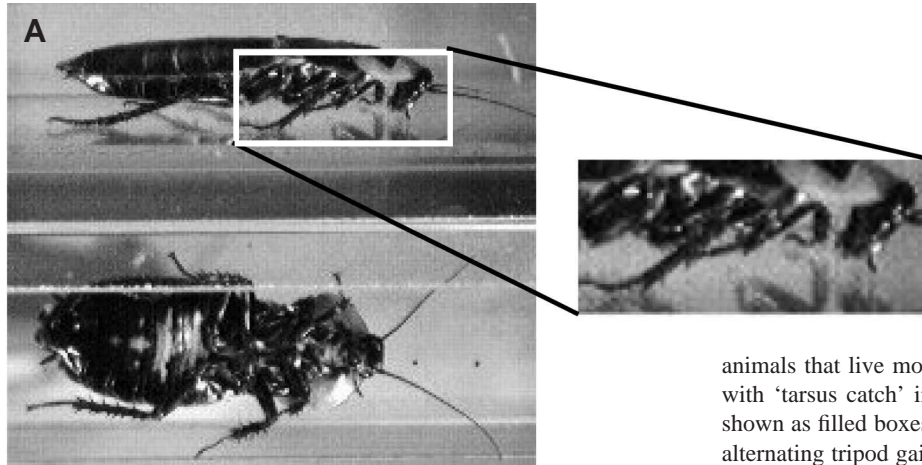


Fig. 1. Adult lifespan of cockroaches and spontaneous locomotion. (A) *Blaberus discoidalis* ($N=73$) and *Periplaneta americana* ($N=31$) cockroaches were placed in plastic containers immediately after molting to the adult stage. Containers were inspected weekly, and dead animals were counted and removed. *Blaberus* did not begin to die until week 36 post-adult molt, while *Periplaneta* showed a gradual dying-off. *Periplaneta* survived up to 64 weeks but *Blaberus* could live up to 80 weeks post-adult molt. 11% of the *Blaberus discoidalis* lived to 73 weeks after the adult molt. However, by week 61, 50% of the individuals were dead. (B) Spontaneous locomotion was defined as the total time spent walking, climbing or burrowing in a 10 min period. Spontaneous locomotion decreased significantly as adult cockroaches aged (regression analysis, slope = -3.4 , $r^2=0.839$, $P<0.01$).

examined the kinematics of walking on a horizontal surface ($N=21$ animals; age range, 60–71 weeks post-adult molt). A number of differences in behavior between young and aged adults were measured. First, the mean speed of walking in 1-week-old animals was 4.6 ± 1.7 steps s^{-1} ($N=6$ animals, 26 trials). By contrast, walking speed was significantly slower (2.7 ± 0.7 steps s^{-1}) in 60-week-old adults (independent t -test, $P<0.05$, $N=7$ animals, 13 trials). Second, an unexpected pathology, which we termed ‘tarsus catch’, was detected in



many of the aged animals. In these individuals, the tarsus of the prothoracic leg regularly catches on the spines of the femur or at the femur–tibia joint on a metathoracic leg (Fig. 2A; see Movie). ‘Tarsus catch’ was detectable in 90% of the animals observed at 65 weeks post-adult molt (Fig. 2B). The percentage of animals that showed ‘tarsus catch’ decreased after 65 weeks because the majority of individuals showing this pathology died shortly after that time.

Fig. 2. ‘Tarsus catch’ in aged animals. (A) Video image (from the side and below) of a 63-week-old adult with ‘tarsus catch’. Note that the right prothoracic tarsus catches on the tibia of the right mesothoracic leg. Inset: close-up of the tarsus catching on the mesothoracic leg. (B) ‘Tarsus catch’ is not evident until 60 weeks post-adult molt, and the percentage of animals exhibiting this behavior increases up to 65 weeks.

However, this percentage decreases in animals that live more than 65 weeks. (C) Gait pattern in an animal with ‘tarsus catch’ in the right prothoracic leg. The swing phase is shown as filled boxes. Prior to ‘tarsus catch’, this animal walks in an alternating tripod gait. The vertical line represents the time when the right prothoracic tarsus catches on the mesothoracic tibia. The ellipse illustrates the absence of swing in the left prothoracic and metathoracic leg due to ‘tarsus catch’. In addition, the length of the swing phase is reduced in the other legs to compensate for the absence of support by the left prothoracic leg. The animal recovers within one leg cycle.

‘Tarsus catch’ regularly results in an increase in the length of the swing phase in the prothoracic leg and a subsequent alteration of the gait pattern in the other legs. Prior to tarsus catch, 73% of aged individuals ($N=8$ of 11) walked with an alternating tripod gait (phase ≈ 0.5 for all neighboring legs). Fig. 2C shows an example of a gait pattern in which the right prothoracic tarsus catches on the right mesothoracic leg (shown by vertical line). While the prothoracic tarsus is caught on the mesothoracic leg, the tripod gait is disrupted, because the left front and left rear legs fail to swing (shown by circle). However, the alternating tripod gait quickly returns after the front leg tarsus is released. In the majority of individuals ($N=10$ of 11), only a single prothoracic leg showed ‘tarsus catch’. In these trials, the right and left prothoracic tarsi were affected equally (50% left leg, 50% right leg). However, one individual exhibited ‘tarsus catch’ in both prothoracic legs.

‘Tarsus catch’ was predominantly found only in prothoracic legs. Although it may be physically impossible for the metathoracic tarsi to catch on anterior legs, mesothoracic tarsi can catch. However, it is a rare occurrence. In one animal, the mesothoracic tarsus caught the ipsilateral metathoracic leg. That animal also showed prothoracic catch.

We studied leg placement during walking in aged animals to determine if ‘tarsus catch’ is caused by an alteration of leg kinematics. Specifically, we looked for changes in anterior extreme position (AEP) or posterior extreme position (PEP) of the legs in aged animals before and after ‘tarsus catch’ was present. These values are important because they denote the beginning and end of the swing phase of walking. Alteration in the PEP position of the front legs or the AEP of the middle legs could contribute to tarsus catch. We digitized the end of the tibia in all six legs and the COM (Fig. 3A). We then calculated the distance from the end of the tibia to the COM (r) and the angle of the end of the tibia (Φ) relative to the

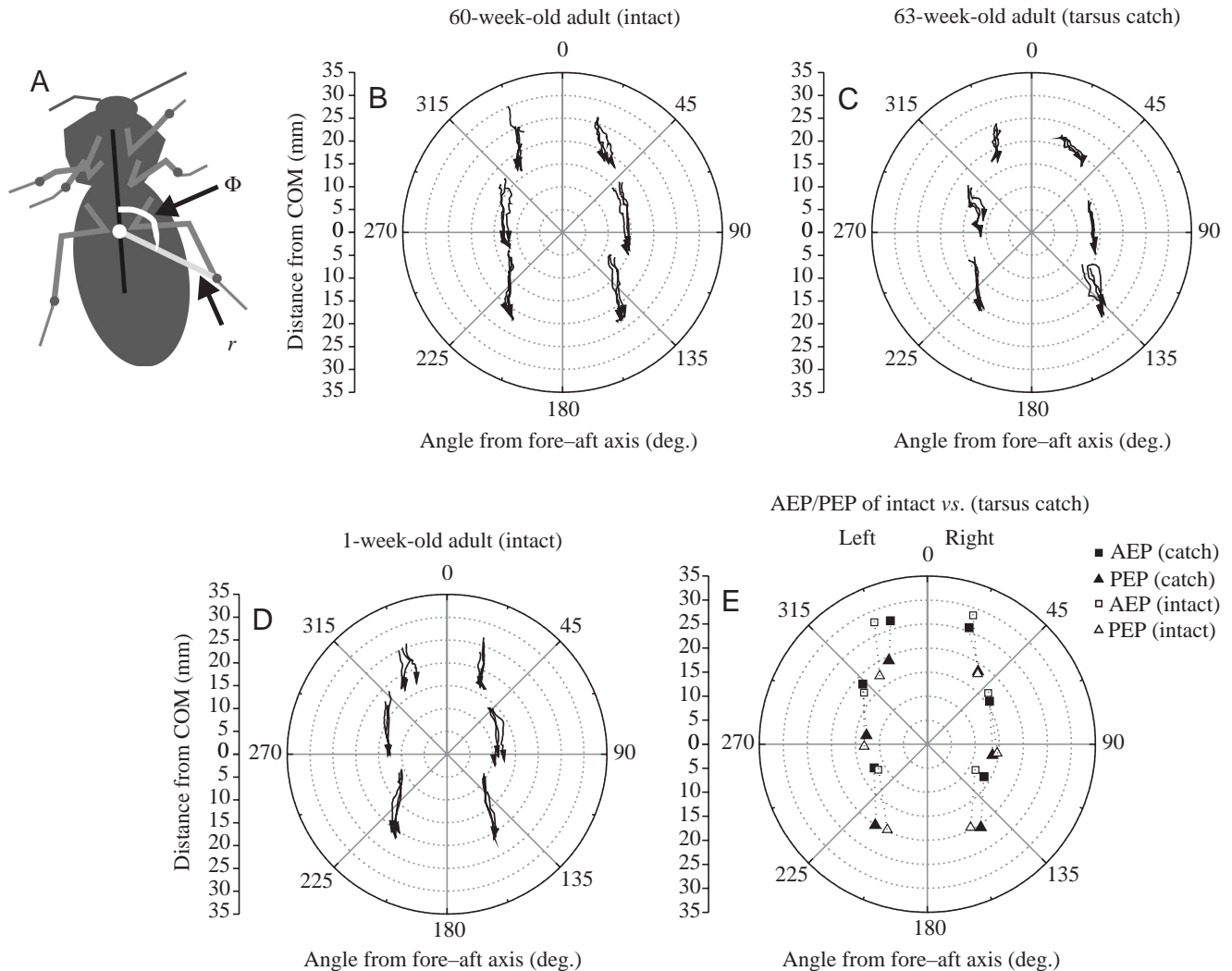


Fig. 3. Analysis of tibia placement in horizontal walking. (A) The end of the tibia (dark gray dots) and the center of mass (COM; white dot) were digitized using motion analysis software. These points were used to calculate the distance of the end of the tibia during the stance phase to the COM (r ; white line) and the angle of the tibia relative to the COM (Φ ; angle of white line and black line). (B) Leg placement values were plotted in a polar graph (r , Φ) for three successive steps in an intact aged animal (60 weeks post-adult molt). The start of the arrow shows the anterior extreme position (AEP), and the arrowhead represents the posterior extreme position (PEP). (C) As a comparison, leg trajectories for steps of the same animal shown in B were plotted after 'tarsus catch' was evident (week 63). This graph shows that tibia placement is altered slightly in trials with 'tarsus catch'. (D) Leg placement values in a 1-week-old adult. (E) Summary polar plot. Values of r and Φ during the AEP and PEP were averaged in the same-aged animals in trials before and after 'tarsus catch' developed. AEP and PEP Φ values of the left legs were converted to values between 0° and 180° for statistical analysis. Dotted lines between the AEP and PEP are only used to link the points within a single leg. Subtle differences between trials before and after 'tarsus catch' has developed are present (see Table 1). However, these differences could not be the cause of 'tarsus catch'.

fore-aft axis (represented by a line from the head to the tail and through the COM in Fig. 3A). We chose to digitize the end of the tibia because the orientation of the tarsus was often altered in aged animals (see Fig. 4). Fig. 3B shows a polar plot of the distance and angle values in all six legs during the stance phase of an aged animal before 'tarsus catch' developed (60 weeks post-adult molt). Each line represents a successive step and indicates the direction of leg movement relative to the fore-aft axis. The arrow originates at the AEP and terminates at the PEP; the beginning of the arrow is the AEP, while the

arrowhead denotes the PEP. Fig. 3C is a polar plot from the same animal, at week 63, after 'tarsus catch' is present. Leg placement in young adults is similar to that observed in old intact animals (Fig. 3D).

In an attempt to establish if changes in foot placement with aging are consistent within a population, we compared the mean values of r and Φ at the AEP and PEP in the same animals ($N=4$ animals, 8 trials, 56–64 steps) before and after they developed 'tarsus catch' (Fig. 3E). In trials after animals developed 'tarsus catch', we only analyzed steps before 'tarsus

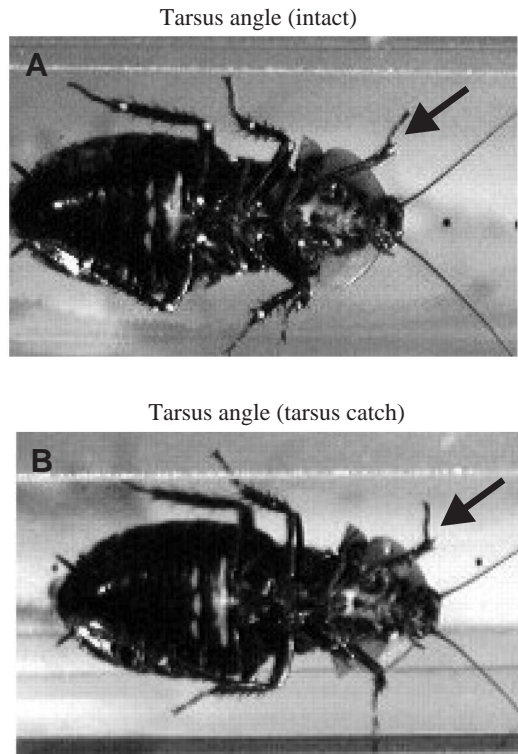


Fig. 4. Orientation of the tibio-tarsal joint in aged animals. (A) A 60-week-old intact animal. The arrow shows the tibio-tarsal joint of the right prothoracic leg. (B) The same animal as in A at 63 weeks with 'tarsus catch'. The angle of the joint is decreased in the animals with 'tarsus catch'.

catch' occurs. Overall, there were minor differences in foot placement among trials (Table 1; independent *t*-test, $P < 0.05$). These changes were not consistent from the left to the right side. The AEP Φ and the PEP Φ of all three legs (T1, T2 and T3) on the left side significantly decreased in trials after 'tarsus catch' was present. However, only the PEP Φ in the metathoracic leg was reduced. In addition, slight changes in the PEP and AEP r were present but not consistent among legs or among segments. Differences in the values of r and Φ at the AEP and PEP are subtle and result in a slight decrease in the horizontal position of the tarsi relative to the body (sprawl) in the front legs and an increase in the sprawl of the rear legs in individuals with 'tarsus catch'. Nevertheless, these changes are not sufficient to cause 'tarsus catch' in these animals.

While examining videos of horizontal walking, we noticed that the angle of the tibio-tarsal joint was altered in individuals with 'tarsus catch' (Fig. 4). The angle of the tibio-tarsal joint was $115 \pm 15.3^\circ$ in animals with 'tarsus catch' ($N = 12$ animals, 32 trials) and $155.3 \pm 20.8^\circ$ in intact cockroaches ($N = 5$ animals, 14 trials). The decrease in the angle of this joint in individuals with 'tarsus catch' is highly significant (independent *t*-test, $P < 0.01$). To determine the changes in the morphology of the tarsus with age, we examined the condition of the tarsal pads, trachea, tendons, nerves and muscles in young and aged animals. In young cockroaches, the tarsal pads and the tarsal

Table 1. Statistical summary of changes in anterior extreme position (AEP) and posterior extreme position (PEP) Φ and r values after 'tarsus catch' has developed in aged animals (independent *t*-test, $P < 0.05$)

		Left		Right	
		Φ	r	Φ	r
T1	AEP	↓	–	–	–
	PEP	↓	↑	–	–
T2	AEP	↓	↑	↑	–
	PEP	↓	–	–	↓
T3	AEP	↓	–	–	↑
	PEP	↓	–	↓	–

joints were flexible and white in color (Fig. 5A). By contrast, in aged animals, the joints were stiff and the tarsal pads were brown in color (Fig. 5B). Furthermore, the tarsal pads in young individuals were flexible and easily deformed with a nylon filament that produced 29 mN of force (Fig. 5C). Tarsal pads in aged individuals were hardened and did not deform when compressed with the nylon filament (Fig. 5D). The internal morphology of the tarsi was consistent with the external appearance. The trachea and tendon inside the tarsus of young animals were silver and shiny (Fig. 5E), while there was hardening and degeneration of the trachea and tendon in aged cockroaches (Fig. 5F).

Climbing

In light of the deficits seen in the horizontal walking trials, we tested the ability of aged animals to perform transitional behaviors such as climbing, righting and inclined walking. These types of behaviors often require altered gaits, body posture and leg positions to complete the task (Watson et al., 2002).

We examined block climbing (5.5 mm, 11 mm and 16.5 mm in height) in both aged and 1-week-old adults. Young individuals were easily able to surmount all blocks ($N = 6$ animals, 33 trials). Although old animals often show 'tarsus catch', they were also able to successfully climb blocks ($N = 16$ animals, 90 trials). Generally, all animals were able to climb a 5.5 mm block without alteration of gait or posture. Climbing strategies for larger obstacles (11 mm and 16.5 mm) were categorized as (1) 'rear up' (Fig. 6A,B) or (2) 'head butt' (Fig. 6C) according to the terminology of Watson et al. (2002). The most prominent strategy of all aged individuals (78% of trials of 'tarsus catch'; 100% of trials of 'no catch') was to change the body angle before placing the front legs on the block (Fig. 6D; rear up). This is consistent with previous reports (Watson et al., 2002). Cockroaches with 'tarsus catch' sometimes climb the obstacle by pushing the head against the block, thereby forcing the body over the obstacle (head butt).

There were additional differences in climbing behavior between intact aged cockroaches and those with 'tarsus catch'. Some animals with 'tarsus catch' appeared to use the

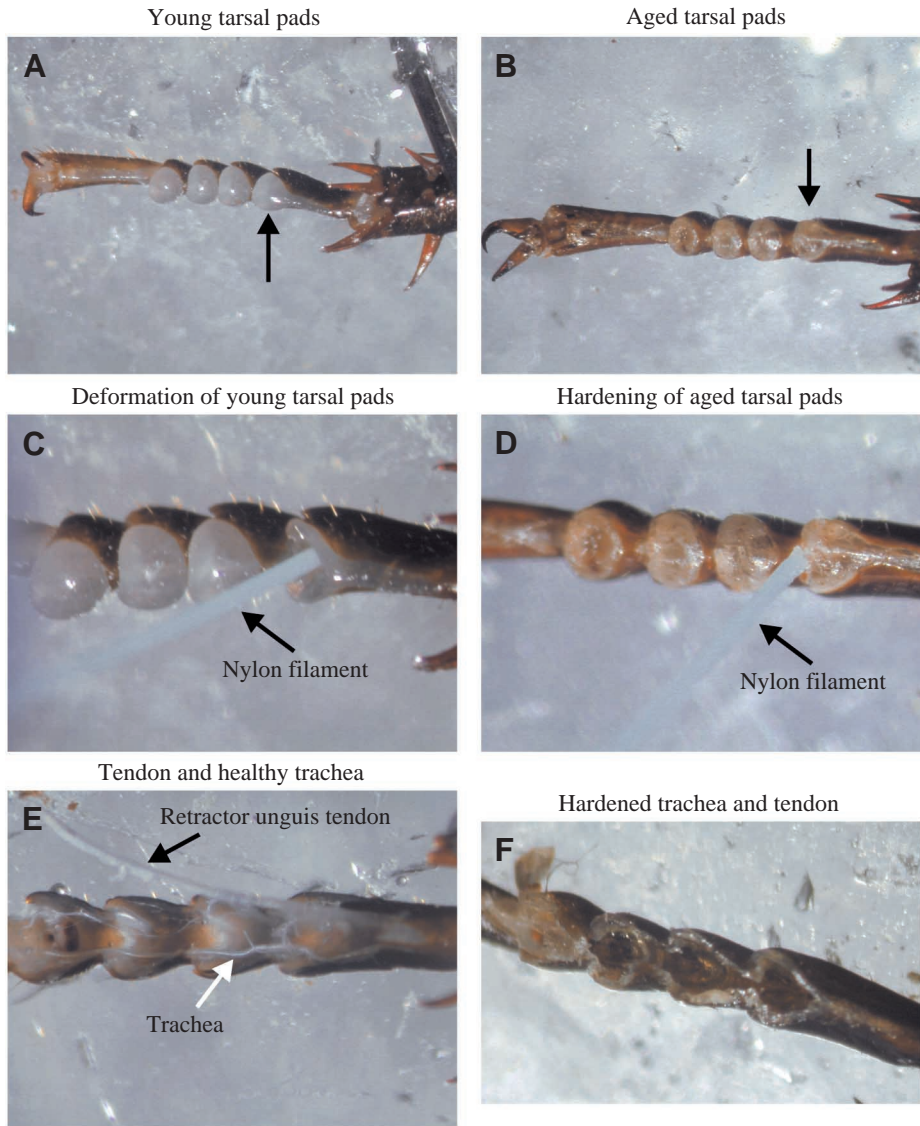


Fig. 5. Tarsus morphology in young and aged animals. (A) The tarsal pads of a 1-week-old adult are white in color (arrow), and the joints between the tarsal segments are flexible (not shown). (B) By contrast, the tarsal pads of an animal with 'tarsus catch' are brown in color (arrow) and the joints are often stiff. (C) A nylon filament, producing a force of 29 mN, readily deformed the tarsal pads in young animals. (D) Pads of old individuals were hardened and were not deformed by the nylon filament. (E) The cuticle of tibia was removed to examine the internal morphology of these leg segments. The trachea and tendon (arrow) in the tarsal segments were healthy and silver in color. (F) The trachea and tendon in the tarsus of aged cockroaches are discolored, hardened and degenerated.

cockroaches. Righting in cockroaches involves rotation about the fore–aft axis of the body while using the rear leg as an anchoring point and often includes dorsal flexions of the body (Camhi, 1977; Full et al., 1995). Aged individuals (59 weeks, $N=4$ animals, 16 trials; 60 weeks, $N=8$ animals, 24 trials; 63 weeks, $N=5$ animals, 20 trials) are readily able to right themselves as rapidly as 1-week-old adults ($N=9$ animals, 36 trials; Fig. 7). However, more variability in the duration of righting is present among aged individuals. Furthermore, there was a significant increase in the duration of righting in old adults with 'tarsus catch'

prothoracic legs to pull the body onto the block instead of extending the metathoracic legs to lift the COM over the obstacle (28% of the trials). However, they often had trouble grasping the top of the block with the prothoracic tarsi. Animals with 'tarsus catch' showed leg slipping in 85% of the trials ($N=47$) as compared with 18% of trials in intact aged individuals ($N=28$). The inability of these cockroaches to grasp the surface often results in the animals becoming 'high-centered' on the corner of the block. However, in all cases, they were able to recover and continue over the obstacle.

Righting

Righting behavior in cockroaches occurs when an animal is placed on its back and leg-to-ground contact is lost. With loss of ground contact, load receptors on the legs would not be activated as they are in standing or walking. In order to examine locomotory behavior under altered sensory conditions, we recorded the duration of righting in aged (59-, 60- and 63-week-old individuals) and 1-week-old adult

(4.96 ± 3.7 s, 60 and 63 weeks old, $N=5$ animals, 20 trials) when compared with intact aged animals (3.67 ± 2.4 s, $N=6$ animals, 24 trials; independent t -test, $P < 0.05$). These results show that old animals are able to right themselves, but cockroaches with 'tarsus catch' are slower at accomplishing this task.

Inclined walking

Aged animals ($N=13$ individuals, 27 trials) were placed in the arena, and trials were deemed successful if the animal moved the caudal end of the abdomen forward from the start of the incline (Start; Fig. 8A) to a point approximately one body length from the start (End; Fig. 8B). Young animals have no difficulty in performing this task. Only 58% of aged animals were able to climb the incline in at least one of the trials. However, the presence of 'tarsus catch' was not sufficient to determine if animals would fail in the inclined climbing task. Inclined walking was successful in 62.5% of the animals ($N=5$ of 8) that showed 'tarsus catch'. However, only 40% of individuals ($N=2$ of 5) without 'tarsus catch' were

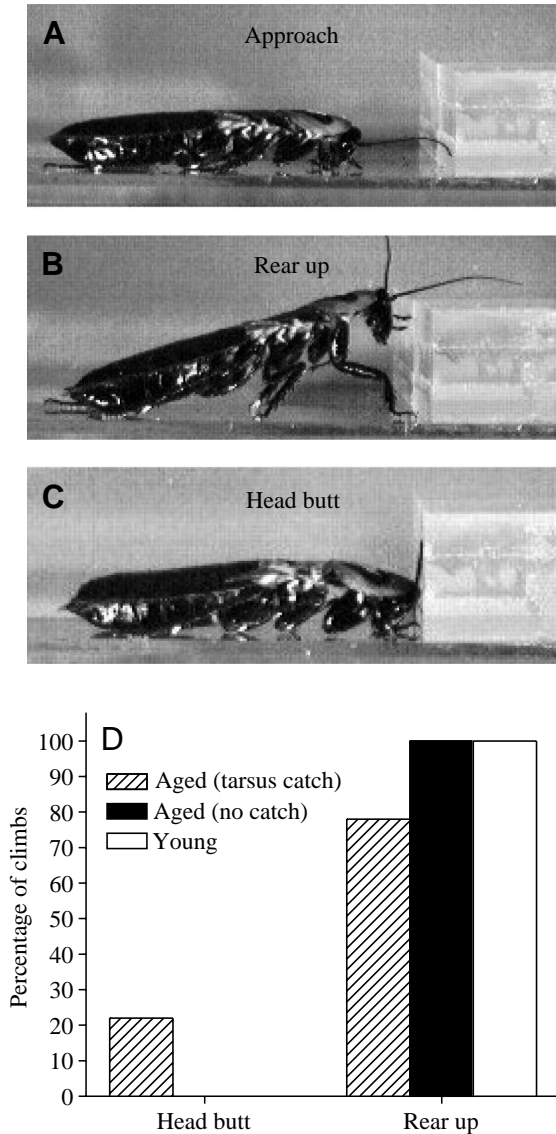


Fig. 6. Block climbing in aged and young cockroaches. (A) Posture of aged animal when approaching a three-block obstacle. (B) After detecting the obstacle, animals often change their body posture by rotating the mesothoracic legs forward and 'rearing up' the front of the body. (C) Some aged individuals do not alter their body angle and run into the side of the block ('head butt'). (D) Summary of climbing behaviors in aged and young cockroaches. In most of the trials, aged animals rear up before reaching the block (as seen in young animals). However, in a few trials, aged cockroaches with 'tarsus catch' run into the side of the block before climbing over it.

able to climb the incline. By contrast, all younger animals were successful ($N=13$ animals; A. J. Pollack, personal communication). Failure to climb the incline in aged cockroaches may simply be due to deterioration of the tarsal pads (see Fig. 5). 'Tarsus catch' may simply represent an extreme condition. However, these findings do not rule out the possibility that changes in the central nervous system (CNS) or muscular system in aging may also contribute to failure in inclined walking.

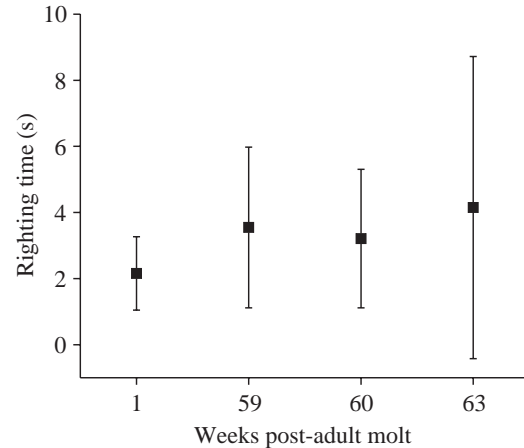


Fig. 7. Righting duration in aged versus young animals. Aged animals are readily able to right themselves, and righting duration is not significantly different from that recorded in 1-week-old adults. However, the variability in timing of righting is increased as animals increase in age.

Aged animals showed extensive leg slipping while walking on the inclined treadmill. In a few animals ($N=5$ of 13), the caudal end of the abdomen did not reach the start point. These trials were not used in the leg slipping analysis. Differences in the probability of leg slipping between intact animals ($N=3$ animals, 6 trials, 24 steps) and those with 'tarsus catch' ($N=5$ animals, 10 trials, 40 steps) were not detectable (Fig. 8C). Generally, the prothoracic legs slipped on the inclined acetate surface more often than the mesothoracic or metathoracic legs. However, there was significantly more leg slipping in the mesothoracic legs during failing trials ($N=3$ animals, 6 trials, 24 steps) than during successful trials ($N=6$ animals, 10 trials, 40 steps; $P<0.05$; Fig. 8D). Individuals that were able to climb the incline generally walked in a metachronal gait (Fig. 8E). By contrast, individuals that failed during inclined walking often showed uncoordinated gait patterns during the attempt (Fig. 8F). However, all aged animals that failed on the incline walked with a tripod gait on a horizontal surface.

Escape behavior

The escape behavior of *Periplaneta americana* is one of the most characterized behaviors in cockroaches and in arthropods in general (Ritzmann and Eaton, 1997; Comer and Robertson, 2001). The neural circuit underlying this behavior has been described in detail. Most of the neural control resides in the thoracic and abdominal ganglia. However, a descending influence has recently been demonstrated (Schaefer and Ritzmann, 2001). Given this background information, we decided to compare escape responses in young and aged cockroaches and to examine whether deficits were attributed to the basic thoracic circuitry or to the influences found in the higher centers (brain and subesophageal ganglia).

Tactile stimulation of the dorsal abdominal cuticle readily evokes escape responses in tethered American cockroaches (Schaefer and Ritzmann, 2001; Schaefer et al., 1994).

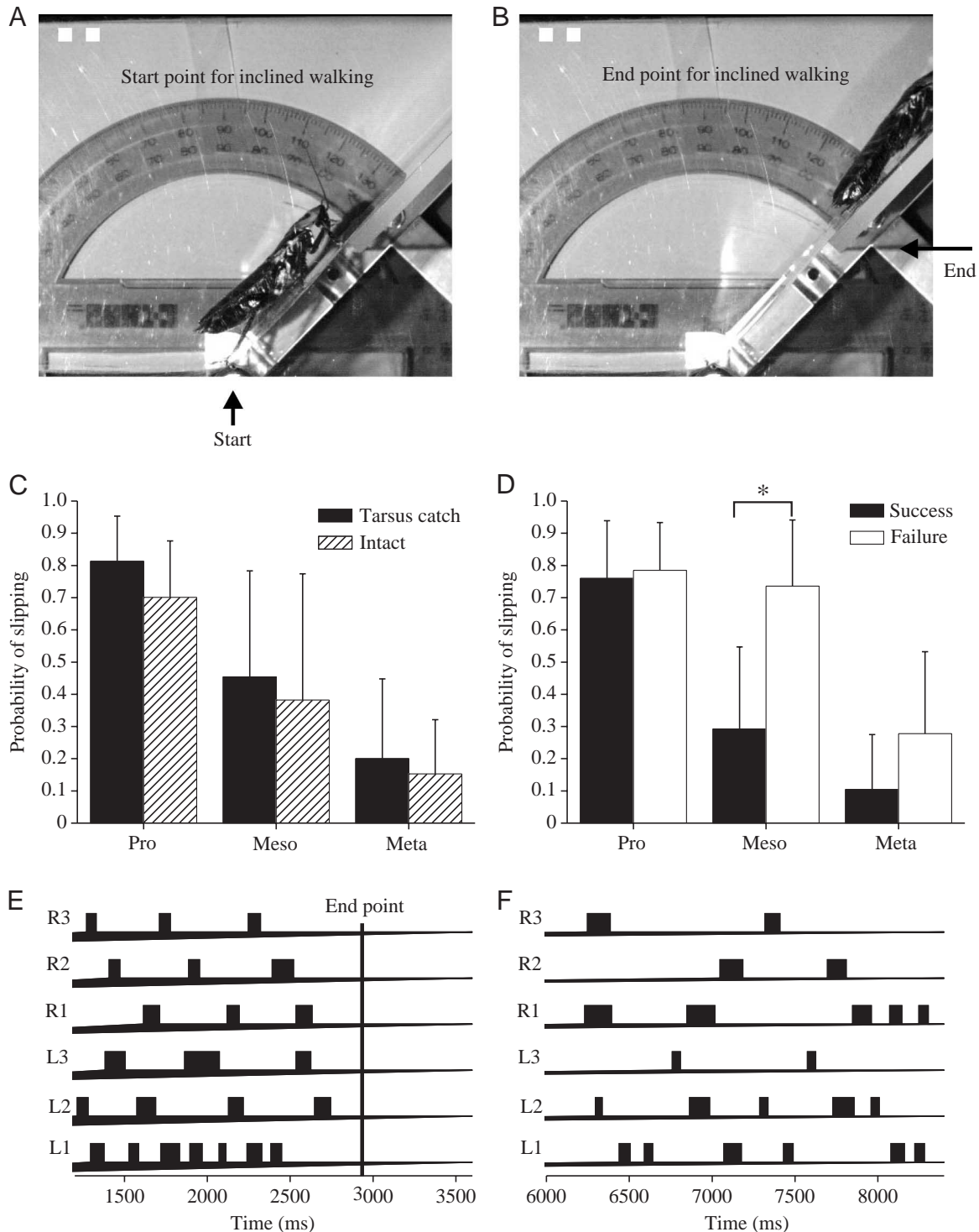


Fig. 8. Inclined walking in aged animals. (A) Animals were placed in a treadmill with an acetate belt that was tilted at a 45° angle. The analysis was started when the caudal end of the animal reached the beginning of the incline (START). (B) Trials were recorded as successful when the animal walked up the incline approximately one body length from the START point (END). (C) Leg slipping, defined as a change in the position of the foot on the substrate during the stance phase, was often present during inclined walking in aged animals. The probability of slipping was calculated as the number of slips per step for each animal. Probabilities for each individual were averaged across the population. There were no differences in the amount of leg slipping between animals with and without 'tarsus catch'. However, prothoracic legs slipped more often than the mesothoracic or metathoracic legs. (D) Data from the inclined walking trials were reorganized into successful and unsuccessful trials. Significantly more leg slipping in the middle legs was present in failing trials than in successful trials ($*P < 0.05$). (E) Gait pattern in an aged individual that successfully climbed the incline. Although the front legs often took multiple steps during inclined walking, these animals used a metachronal gait to surmount the incline. (F) Gait pattern in an aged individual that did not successfully climb the incline. Leg movements were not coordinated in this trial and leg slipping was extensive.

However, similar stimulation of aged animals (61 weeks post-adult molt) failed to evoke any escape responses (Fig. 9; $N=3$ animals, 12 trials). Interestingly, the capacity of aged animals to escape returned after decapitation, suggesting that the deficit associated with aging was, in fact, primarily focused within the head ganglia. After decapitation of aged cockroaches ($N=3$ animals, 22 trials), escape behavior was elicited in 72.7% of the trials. Of the evoked escapes post-decapitation, 25% were non-directional and one involved what appeared to be a turn towards the direction of the stimulus. Consistent with previous observations on decapitated cockroaches (Schaefer and Ritzmann, 2001), no subsequent runs were observed following escape behavior in decapitated individuals. However, uncoordinated and erratic leg movements occurred after the escape in two trials. To examine leg kinematics during escape behavior in aged animals, we measured joint angle excursions in the metathoracic and mesothoracic legs of decapitated 61-week-old cockroaches. Robust movements of the metathoracic legs were observed, with smaller excursions for the mesothoracic legs. These findings are similar to that observed in younger decapitated animals (Schaefer and Ritzmann, 2001). These data show that escape behaviors are disrupted in aged cockroaches and suggest that these deficits may be caused by age-related degeneration in the brain or subesophageal ganglia.

Discussion

In the present study, we have examined age-related deficits in a range of locomotor behaviors. The strategy can be powerful in understanding the complex effects of aging resulting from pathologies in the CNS, peripheral nervous system, muscles, cuticle and other skeletal elements. While behaviors such as horizontal walking may clearly emphasize some locomotor difficulties, others will be subtle. By examining a full range of locomotor behaviors, these subtle effects will be clearly brought forward.

We have shown that aged cockroaches have reduced activity levels and often have difficulty in complex locomotor tasks. Many of these animals also develop 'tarsus catch' in the prothoracic legs, which can temporarily disrupt normal walking activity. Old age does not limit the animals' ability to climb obstacles or right themselves. However, aged cockroaches show deficits in inclined walking and escape behavior. Reduction in motor activity in aged animals could be the result of deterioration in the musculature (Anderson, 2003; Rantanen, 2003), sensory neurons (Bergman and Ulfhake, 1998; Ulfhake et al., 2002) and/or motor neurons (Parkes et al., 1999). Deficits in each of these areas may have a significant or negligent effect during different behaviors. Our goal in this paper was to examine behavioral changes with age during many different types of locomotion in an effort to ultimately address physiological and anatomical changes that may be occurring in the nervous and musculoskeletal systems.

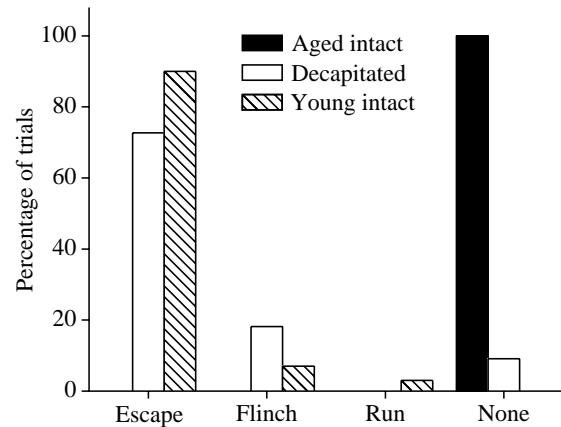


Fig. 9. Responses evoked by tactile stimulation of the lateral edge of the abdomen in 61-week-old tethered cockroaches under intact and decapitated conditions and young intact animals. Young intact animals readily show escape behavior when stimulated (data from Schaefer and Ritzmann, 2001). By contrast, intact 61-week-old cockroaches did not escape when stimulated. Following decapitation, however, forward directional escape responses (Schaefer et al., 1994) were easily elicited in aged individuals.

American and death-head cockroaches have similar adult lifespans and show reduced activity levels with increasing age

Our results are similar to other studies that have recorded the lifespan of adult cockroaches (Griffiths and Tauber, 1942; Pope, 1953; Willis and Lewis, 1957; Willis et al., 1957). There are a number of factors that could influence the lifespan of cockroaches including temperature, diet, reproductive experience, and degree of isolation (Griffiths and Tauber, 1942; Pope, 1953; Willis and Lewis, 1957; Willis et al., 1957). However, we have limited this variability by raising each of these cohorts under the same environmental conditions (temperature and diet).

Our findings that cockroaches show a decrease in spontaneous motor activity with age are consistent with studies in other insects (Fernandez et al., 1999; Le Bourg, 1987; Parkes et al., 1999; Tofilski, 2000) and mammals (Godde et al., 2002; Hilleras et al., 1999; Scimonelli et al., 1999; Siwak et al., 2002). In light of this study and others, the degree of spontaneous locomotion seems to provide an accurate measure of age in a number of animals.

Aged animals walk normally but often develop 'tarsus catch'

Although gait disruption was often present in aged animals, individuals were able to recover the tripod gait within one leg cycle. In the stick insect (*Carausius morosus*), it has been shown that coordinating influences at the level of the CNS are sufficient to regain normal coordination in the step directly following an interrupted step (Cruse and Schwarze, 1988). Therefore, degeneration at the level of the CNS could reduce the ability of the animal to recover the tripod gait after the perturbation (Pearson, 2000). Furthermore, changes in the placement of the legs during horizontal walking could be the

result of degeneration in the CNS of aged animals. Differences in leg placement were subtle and do not appear to contribute to tarsus catch. These changes might simply be the result of stiff and inflexible joints. In elderly humans, alterations of gait often occur as a result of arthritis in the leg joints (Elble et al., 1991; Mesure et al., 1999). However, further analysis is needed to determine whether changes in the CNS with aging are contributing to these gait changes.

Cockroaches with 'tarsus catch' also have hardening of the tarsal pads. These animals often have difficulty grasping the walking surface. The tarsi of insects provide friction with the substrate and are important in the generation of propulsive forces (Betz, 2002; Dai et al., 2002; Frazier et al., 1999). In order to generate sufficient adhesion on inclines, the tarsal pads exude adhesive materials and also deform their surface to expand over the substrate (Jiao et al., 2000). The hardening of the tarsal pads seen in aged cockroaches might be associated with decreases in the amount of adhesive that is released and most certainly reduces the capacity of the pad to deform on the surface. However, this deficit only causes temporary changes in gait and does not seem to affect the animals' ability to walk on a horizontal surface. These findings suggest that 'tarsus catch' is most likely to be the result of degeneration at the periphery.

Aged cockroaches are able to climb an obstacle, but postural changes are sometimes absent

When young and old cockroaches climb over small obstacles (less than 6 mm), the front legs reach the top of the block during normal swing movements of the leg (Watson et al., 2002). However, successful climbing of larger obstacles requires that the COM is raised to the height of the obstacle (Watson et al., 2002). Aged cockroaches are able to climb obstacles of up to 16.5 mm in height. The majority of aged animals show rearing behavior when climbing blocks greater than 6 mm. However, a small percentage of aged animals ran into the side of the block (head butt) before surmounting it. Cockroaches assess an obstacle, using visual or antennal inputs, in order to accurately change the body posture and place the foot on top of the block (Watson et al., 2002). Preliminary studies in our laboratory have suggested that the antennae play the primary role in the detection of the obstacle during climbing. Age-related structural changes in the insect brain, including loss of nerve cells, alteration in cell structure and decreased metabolic rate, have been documented (Kern, 1986). Therefore, it is possible that old animals that run into the obstacle have degeneration in the antennae detection system.

Aged cockroaches are able to right, but animals with 'tarsus catch' take longer

Stiffness in the leg joints and reduced mobility could negatively affect righting. However, degeneration in the higher CNS of aged animals would not necessarily affect righting behavior. Decapitated cockroaches are readily able to right themselves, and the mean duration of righting was only 12% greater than in intact cockroaches (Camhi, 1977).

Leg movements during righting are often uncoordinated and unpredictable (Camhi, 1977; Full et al., 1995). Although we did not systematically look at leg movements in aged animals during righting, previous studies (Sherman et al., 1977) have shown that cycle frequency of leg muscle activity and inter-leg coordination are similar during walking and righting. However, tactile and load feedback from the legs is altered from that of standing (Camhi, 1977; Sherman et al., 1977). Differences in sensory feedback result in shorter burst duration of leg muscles and decreased spike frequencies during righting (Sherman et al., 1977). Studies by Camhi (1977) showed that animals in which all six legs were amputated at the mid-coxal level did not show righting behavior. These findings illustrate that sensory information from the periphery is important for normal righting behavior. Our behavioral experiments showed that aged animals are able to right, although the duration of righting is longer when compared with that of younger animals. Therefore, either these aged animals do not have extensive sensory degeneration at the periphery or some types of peripheral degeneration do not have significant effects on the success of righting behavior.

Success in inclined walking is limited in aged individuals

On a horizontal surface, cockroaches generally walk with a tripod gait. However, our studies have shown that aged and young cockroaches use a metachronal gait to successfully climb an incline of 45°. By contrast, aged animals that were unable to climb the incline often had uncoordinated gaits. In a metachronal gait, more legs are on the ground at one time. This would increase the frictional forces between the legs and the surface and help to compensate for increases in load on the animals from the steeper slope (Pelletier and Caissie, 2001). Similar alterations of gait in sloped walking have been reported in potato beetles (*Leptionotarsa decemlineata*; Pelletier and Caissie, 2001) and cats (*Felis domesticus*; Carlson-Kuhta et al., 1998). During inclined walking, gravitational forces that oppose uphill movement are acting on the body. Therefore, alterations of posture and gait are often required to move an animal forward (Carlson-Kuhta et al., 1998; Pelletier and Caissie, 2001). In insects, force receptors on the legs would be important in the detection of changing gravitational forces during inclined walking (Duysens et al., 2000; Noah et al., 2001).

In our analysis, the presence of 'tarsus catch' was not a good predictor of failure in inclined walking. However, leg slipping was extensive in trials in which animals failed to climb the incline. Slipping could simply be due to age-related degeneration of the tarsal pads. Several studies have shown that pad deformation and tarsal secretion are of vital importance in attachment on smooth surfaces (Betz, 2002; Jiao et al., 2000). Adhesive properties of the tarsal pads are maximal when the contact area of the pad is large (Jiao et al., 2000). Indeed, the expansion of the pad is critical for developing sufficient adhesive force for climbing. Therefore, hardening of the tarsal pads may severely limit the ability of aged animals to grasp the surface. 'Tarsal catch' may well be

an extreme condition of tarsal degeneration that begins at earlier ages. Thus, even those individuals that do not exhibit 'tarsal catch' may have more limited pathologies in tarsal pad structure that would lead to slipping.

Degeneration of leg proprioceptors could also contribute to problems in incline walking. Leg slipping could certainly be detected by proprioceptive sensors on the leg, which could have a direct effect on the motor output and the gait pattern (Ridgel et al., 1999, 2001).

Escape behavior is absent in aged cockroaches

Age-related changes in the escape behavior were evident in *Periplaneta americana*. Aged animals did not escape to stimuli that normally evoked coordinated responses, and there was a loss or reduction of spontaneous locomotion. However, after decapitation, tactile stimulation of senescent animals evoked responses that are typical of headless cockroaches of younger ages (Schaefer and Ritzmann, 2001). Age-related changes in higher centers may disrupt normal descending inputs, which are important in modulation, coordination and adaptation of leg movements (Grillner et al., 2000; Kien and Altman, 1992). These findings suggest that descending inputs contribute to the observed age-related changes in escape behavior and that the thoracic circuitry and leg musculature are still capable of functioning 'normally' in the absence of descending inputs.

Sources of age-related behavioral deficit

This study has documented behavioral deficits in a range of locomotory behaviors that are readily performed by aged cockroaches. We have discussed potential sources of these deficits, which include CNS, peripheral nervous system, cuticle or skeletal problems. However, more research is required to identify the exact pathologies that lead to each of these problems.

Each of the behavioral deficits that we observed in aged animals is complex and could result from deficits in more than one of the areas listed above. Horizontal walking trials suggest that the behavioral deficits seen in aged cockroaches are the result of peripheral damage to the tarsi and the tibio-tarsal joint. However, analysis of transitional behaviors provides evidence that deficits in the CNS, especially the higher centers, may be present in aged cockroaches and these could certainly contribute to the problems seen in horizontal walking, albeit in a more subtle way. Anatomical analysis of the nervous system in old insects would complement these behavioral findings and could further elucidate the causes of locomotor changes with aging. A reasonable strategy for future research in this area would include anatomical studies of the nervous system and peripheral structures along with continued behavioral observations of a range of behaviors that document deficits associated with various different conditions. Moreover, a thorough understanding of the behavioral deficits associated with aging and the related structural pathologies could serve as naturally occurring lesions that lead to a greater understanding of the intact system.

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References

- Aigner, T. and McKenna, L.** (2002). Molecular pathology and pathobiology of osteoarthritic cartilage. *Cell. Mol. Life Sci.* **59**, 5-18.
- Anderson, J.** (2003). Muscle fibre type adaptation in the elderly human muscle. *Scand. J. Med. Sci. Sports* **13**, 40-47.
- Bergman, E. and Ulfhake, B.** (1998). Loss of primary sensory neurons in the very old rat: neuron number estimates using the disector method and confocal optical sectioning. *J. Comp. Neurol.* **396**, 211-222.
- Betz, O.** (2002). Performance and adaptive values of tarsal morphology in rove beetles of the genus *Stenus* (Coleoptera, Staphylinidae). *J. Exp. Biol.* **205**, 1097-1113.
- Camhi, J.** (1977). Behavior switching in cockroaches: transformations of tactile reflexes during righting behavior. *J. Comp. Physiol.* **113**, 283-301.
- Camhi, J. M.** (1988). Escape behavior in the cockroach: distributed neural processing. *Experientia* **44**, 401-408.
- Carlson-Kuhta, P., Trank, T. and Smith, J.** (1998). Forms of forward quadrupedal locomotion. II. A comparison of posture, hindlimb kinematics, and motor patterns for upslope and level walking. *J. Neurophysiol.* **79**, 1687-1701.
- Comer, C. and Robertson, R.** (2001). Identified nerve cells and insect behavior. *Prog. Neurobiol.* **63**, 409-439.
- Cruse, H. and Schwarze, W.** (1988). Mechanisms of coupling between the ipsilateral legs of a walking insect (*Carausius morosus*). *J. Exp. Biol.* **138**, 455-469.
- Dai, Z., Gorb, S. and Schwarz, U.** (2002). Roughness-dependent friction force of the tarsal claw system in the beetle *Pachnoda marginata* (Coleoptera, Scarabaeidae). *J. Exp. Biol.* **205**, 2479-2488.
- Duysens, J., Clarac, F. and Cruse, H.** (2000). Load-regulating mechanisms in gait and posture: comparative aspects. *Physiol. Rev.* **80**, 83-133.
- Elble, R., Higgins, C. and Hughes, L.** (1991). The syndrome of senile gait. *J. Neurol.* **239**, 71-75.
- Fernandez, J. R., Grant, M. D., Tulli, N. M., Karkowski, L. M. and McClearn, G. E.** (1999). Differences in locomotor activity across the lifespan of *Drosophila melanogaster*. *Exp. Gerontol.* **34**, 621-631.
- Frazier, S., Larsen, G., Neff, D., Quimby, L., Carney, M., DiCaprio, R. and Zill, S.** (1999). Elasticity and movements of the cockroach tarsus in walking. *J. Comp. Physiol.* **185**, 157-172.
- Full, R., Yamauchi, A. and Jindrich, D.** (1995). Maximum single leg force production: cockroaches righting on photoelastic gelatin. *J. Exp. Biol.* **198**, 2441-2452.
- Godde, B., Berkefeld, T., David-Jurgens, M. and Dinse, H. R.** (2002). Age-related changes in primary somatosensory cortex of rats: evidence for parallel degenerative and plastic-adaptive processes. *Neurosci. Biobehav. Rev.* **26**, 743-752.
- Griffiths, J. and Tauber, O.** (1942). Fecundity, longevity, and parthenogenesis of the American roach, *Periplaneta americana*. *Physiol. Zool.* **15**, 196-209.
- Grillner, S., Cangiano, L., Hu, G.-Y., Thompson, R., Hill, R. and Wallen, P.** (2000). The intrinsic function of a motor system—from ion channels to networks and behavior. *Brain Res.* **886**, 224-236.
- Hilber, P. and Caston, J.** (2001). Motor skills and motor learning in Lurcher mutant mice during aging. *Neuroscience* **102**, 615-623.
- Hilleras, P., Jorm, A., Herlitz, A. and Winblad, B.** (1999). Activity patterns in very old people: a survey of cognitively intact subjects aged 90 years or older. *Age Aging* **28**, 147-152.
- Hook, P., Sriramoju, V. and Larsson, L.** (2001). Effects of aging on actin sliding speed on myosin from single skeletal muscle cells of mice, rats, and humans. *Am. J. Physiol. Cell Physiol.* **280**, C782-C788.
- Jiao, Y., Gorb, S. and Scherge, M.** (2000). Adhesion measured on the attachment pads of *Tettigonia viridissima* (Orthoptera, Insecta). *J. Exp. Biol.* **203**, 1887-1895.
- Jindrich, D. L. and Full, R. J.** (1999). Many-legged maneuverability: dynamics of turning in hexapods. *J. Exp. Biol.* **202**, 1603-1623.
- Kaasinen, V., Vilkmann, H., Hietala, J., Nagren, K., Helenius, H., Olsson, H., Farde, L. and Rinne, J.** (2000). Age-related dopamine D2/D3 receptor loss in the extrastriatal regions of the human brain. *Neurobiol. Aging* **21**, 683-688.

- Kerin, A., Patwari, P. and Grodzinsky, A.** (2002). Molecular basis of osteoarthritis: biomechanical aspects. *Cell. Mol. Life Sci.* **59**, 27-35.
- Kern, M.** (1986). Brain aging in insects. In *Insect Aging: Strategies and Mechanisms* (ed. K.-G. Collatz and R. S. Sohal), pp. 90-105. Berlin: Springer-Verlag.
- Kien, J. and Altman, J.** (1992). Preparation and execution of movement: parallels between insects and mammalian motor systems. *Comp. Biochem. Physiol. A* **103**, 15-24.
- Kram, R., Wong, B. and Full, R. J.** (1997). Three-dimensional kinematics and limb kinetic energy of running cockroaches. *J. Exp. Biol.* **200**, 1919-1929.
- Le Bourg, E.** (1987). The rate of living theory, spontaneous locomotor activity, aging and longevity in *Drosophila melanogaster*. *Exp. Gerontol.* **22**, 359-369.
- Lexell, J.** (1993). What is the cause of the ageing atrophy? Assessment of the fiber type composition in whole human muscles. In *Sensorimotor Impairment in the Elderly* (ed. G. E. Stelmach and V. Homborg), pp. 143-157. Dordrecht: Kluwer Academic Publishers.
- Lowe, D. A., Thomas, D. D. and Thompson, L. V.** (2002). Force generation, but not myosin ATPase activity, declines with age in rat muscle fibers. *Am. J. Physiol. Cell Physiol.* **283**, C187-C192.
- Maki, B. E. and McIlroy, W. E.** (1996). Postural control in the older adult. *Clin. Ger. Med.* **12**, 635-658.
- McIlroy, W. E. and Maki, B. E.** (1996). Age-related changes in compensatory stepping in response to unpredictable perturbations. *J. Gerontol.* **51**, M289-M296.
- Measure, S., Azulay, J. P., Pouget, J. and Amblard, B.** (1999). Strategies of segmental stabilization during gait in Parkinson's disease. *Exp. Brain Res.* **129**, 573-581.
- Minois, N., Khazaeli, A. A. and Curtsinger, J. W.** (2001). Locomotor activity as a function of age and life span in *Drosophila melanogaster* overexpressing *hsp70*. *Exp. Gerontol.* **22**, 359-369.
- Noah, J. A., Quimby, L., Frazier, S. F. and Zill, S. N.** (2001). Force detection in cockroach walking reconsidered: discharges of proximal tibial campaniform sensilla when body load is altered. *J. Comp. Physiol.* **187**, 769-784.
- Nye, S. W. and Ritzmann, R. E.** (1992). Motion analysis of leg joints associated with escape turns of the cockroach, *Periplaneta americana*. *J. Comp. Physiol.* **171**, 183-194.
- Parkes, T. L., Hilliker, A. J. and Phillips, J. P.** (1999). Motorneurons, reactive oxygen, and life span in *Drosophila*. *Neurobiol. Aging* **20**, 531-535.
- Pearson, K.** (2000). Neural adaptation in the generation of rhythmic behavior. *Annu. Rev. Physiol.* **62**, 723-753.
- Pelletier, Y. and Caissie, R.** (2001). Behavior and physical reactions of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) walking on a slanted surface. *Biol. Cybern.* **84**, 269-277.
- Pope, P.** (1953). Studies of the life histories of some Queensland Blattidae (Orthoptera). *Proc. R. Soc. Queensland* **63**, 23-59.
- Rantanen, T.** (2003). Muscle strength, disability and mortality. *Scand. J. Med. Sci. Sports* **13**, 3-8.
- Ridgel, A. L., Frazier, S. F., Dicaprio, R. A. and Zill, S. N.** (1999). Active signaling of leg loading and unloading in the cockroach. *J. Neurophysiol.* **81**, 1432-1437.
- Ridgel, A. L., Frazier, S. F. and Zill, S. N.** (2001). Dynamic responses of tibial campaniform sensilla studied by substrate displacement in freely moving cockroaches. *J. Comp. Physiol.* **187**, 405-420.
- Ritzmann, R.** (1993). The neural organization of cockroach escape and its role in context-dependent orientation. In *Biological Neural Networks in Invertebrate Neuroethology and Robotics* (ed. R. Beer, R. Ritzmann and T. McKenna), pp. 113-137. San Diego: Academic Press.
- Ritzmann, R. and Eaton, R.** (1997). Neural substrates for initiation of startle responses. In *Neurons, Networks and Motor Behavior* (ed. P. Stein, S. Grillner, A. Selverston and D. Stuart), pp. 33-44. Cambridge, MA: MIT Press.
- Schaefer, P. and Ritzmann, R.** (2001). Descending influences on escape behavior and motor pattern in the cockroach. *J. Neurobiol.* **49**, 9-28.
- Schaefer, P. L., Kondagunta, G. V. and Ritzmann, R. E.** (1994). Motion analysis of escape movements evoked by tactile stimulation in the cockroach *Periplaneta americana*. *J. Exp. Biol.* **190**, 287-294.
- Scimonelli, T., Marucco, M. and Cleis, M. E.** (1999). Age-related changes in grooming behavior and motor activity in female rats. *Physiol. Behav.* **66**, 481-484.
- Sherman, E., Novotny, M. and Camhi, J.** (1977). A modified walking rhythm employed during righting behavior in the cockroach, *Gromphadorhina portentosa*. *J. Comp. Physiol.* **113**, 303-316.
- Shumway-Cook, A. and Woollacott, M.** (2000). Attentional demands and postural control: the effect of sensory context. *J. Gerontol.* **55**, M10-M16.
- Simpson, B. S., Ritzmann, R. E. and Pollack, A. J.** (1986). A comparison of the escape behaviors of the cockroaches *Blaberus craniifer* and *Periplaneta americana*. *J. Neurobiol.* **17**, 405-419.
- Siwak, C. T., Murphey, H. L., Muggenburg, B. A. and Milgram, N. W.** (2002). Age-dependent decline in locomotor activity in dogs is environment specific. *Physiol. Behav.* **75**, 65-70.
- Tofilski, A.** (2000). Senescence and learning in honeybee (*Apis mellifera*) workers. *Acta Neurobiol. Exp.* **60**, 35-39.
- Tryba, A. K. and Ritzmann, R. E.** (2000). Multi-joint coordination during walking and foothold searching in the *Blaberus* cockroach. I. Kinematics and electromyograms. *J. Neurophysiol.* **83**, 3323-3336.
- Ulfhake, B., Bergman, E. and Fundin, B.** (2002). Impairment of peripheral sensory innervation in senescence. *Auton. Neurosci. Basic Clin.* **96**, 43-49.
- Volkow, N. D., Gur, R. C., Wang, G. J., Fowler, J. S., Moberg, P. J., Ding, Y. S., Hitzemann, R., Smith, G. and Logan, J.** (1998). Association between decline in brain dopamine activity with age and cognitive and motor impairment in healthy individuals. *Am. J. Psychol.* **155**, 344-349.
- Watson, J. T. and Ritzmann, R. E.** (1998). Leg kinematics and muscle activity during treadmill running in the cockroach, *Blaberus discoidalis*. I. Slow running. *J. Comp. Physiol.* **182**, 11-22.
- Watson, J. T., Ritzmann, R. E., Zill, S. N. and Pollack, A. J.** (2002). Control of obstacle climbing in the cockroach, *Blaberus discoidalis*. I. Kinematics. *J. Comp. Physiol.* **188**, 39-53.
- Willis, E. and Lewis, N.** (1957). The longevity of starved cockroaches. *J. Econ. Entomol.* **50**, 438-440.
- Willis, E., Riser, G. and Roth, L.** (1957). Observations on reproduction and development in cockroaches. *Ann. Entomol. Soc. Am.* **51**, 53-69.