



Review

# Insights into age-related locomotor declines from studies of insects

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## Abstract

Locomotor deficits frequently accompany aging in animals. These deficits are often caused by degeneration in the nervous and musculoskeletal systems. Insects are an excellent model for age-related behavior studies because they are short-lived and have a reduced nervous system with fewer cells than vertebrates. Furthermore, they are highly mobile and display a complex set of locomotor behaviors. This review presents research that has examined age-related locomotor deficits in insects and discusses the value of these studies to understand aging processes in all animals.

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## 1. Introduction

Aging affects all organisms. Aside from being the most widely-represented group in the animal kingdom, insects have a pattern of post-embryonic development, which provides some useful advantages for studying the aging process. Most insects develop through a series of instars that are clearly demarcated by a molting process, where the animal escapes a previous exoskeleton and develops a new larger one. Within this framework, aging occurs in insects at a predictable time during the final, or adult, instar. The predictability of this insect development coupled with relatively short life spans can be exploited to further our understanding of the aging process and the properties that are essential for normal locomotor behavior.

Physiological changes during aging often result in decreased or impaired locomotor behavior. Age-related locomotor deficits can be caused by neural or musculoskeletal

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degeneration. Loss of neurons and neurotransmitters in the central nervous system has been associated with motor impairment in mammals (Hilber and Caston, 2001; Kaasinen et al., 2000; Robbins and Fahim, 1985; Volkow et al., 1998). In normal human aging, there is a decrease in the number of dopamine receptors in the brain (Kaasinen et al., 2000). Although loss of dopamine in healthy aged individuals does not reach the level present in patients with Parkinson's disease (80% loss), smaller losses can have an effect on motor behavior (Volkow et al., 1998). Furthermore, individuals with Parkinson's disease show gait disturbances, slowness of movement and failure of gait initiation. Degeneration in the peripheral nervous system often results in loss or reduction of proprioceptive sense in the limbs (Shumway-Cook and Woollacott, 2000; Ulfhake et al., 2002). Specifically, axon atrophy and demyelination are believed to be primarily responsible for loss of sensation (Ulfhake et al., 2002). Sensory information from the limbs is important in postural control and reactions to perturbations (Maki and McIlroy, 1996; McIlroy and Maki, 1996). Non-neural degeneration in the musculoskeletal system can also contribute to locomotor deficits in aged animals. Muscle weakness, decreased muscle mass and stiffness in joints and ligaments often accompany aging (Aigner and McKenna, 2002; Anderson, 2003; Lexell, 1993). 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 often the result of a loss in the number of muscle fibers (Lexell, 1993). Stiffness at the joints and ligaments is frequently caused by increases in collagen fiber cross-linkages and degeneration of elastic elements (Aigner and McKenna, 2002; Kerin et al., 2002). These deficits make sitting, standing, walking and turning difficult in aged individuals (Elble et al., 1991a,b).

Insects can provide useful insights into the problems of aging. There are a number of technical advantages to using them as a model system for aging. First, insects have short life spans (mean lifespan of a fruitfly is 37 days; Rogina et al., 2000) that can be compartmentalized into discrete and standard length stages each separated from the next by a molt. Insects typically have multiple nymphal (larval) instars and a single adult instar. Cockroaches go through 6–10 molts before they reach adulthood depending on the species (Willis et al., 1957). Furthermore, adult cockroaches have wings, which make them anatomically distinct from the nymphs. Insects also have reduced nervous systems with fewer numbers of cells than vertebrates. In cockroaches, the nervous system consists of two head ganglia (brain and the suboesophageal ganglion), three thoracic ganglia (one per leg segment) and a number of abdominal ganglia (Fig. 1A). Each thoracic ganglion contains a small number (500 in the mesothoracic ganglia of the cockroach) of motor neurons, which innervate muscles of the legs (Pearson, 1977). Many of these neurons have been identified and can be used to document changes in specific cells and circuits. Thus, they can be readily re-identified in young and aged individuals. In addition, there are fewer motor neurons per muscle in insects, which makes characterization of muscle properties easier than vertebrates. In the cockroach, each muscle may be innervated by as few as one to three excitatory and one to two inhibitory motor neurons (Guthrie and Tindall, 1968; Pearson and Iles, 1971; Usherwood, 1962). Another significant advantage to working on insects, and other arthropods, is the fact that their skeleton is on the outside of the body. Therefore, skeletal structures and many sensory structures of the legs are located on the surface of the exoskeleton and can be readily evaluated and manipulated. In fact, many insects have

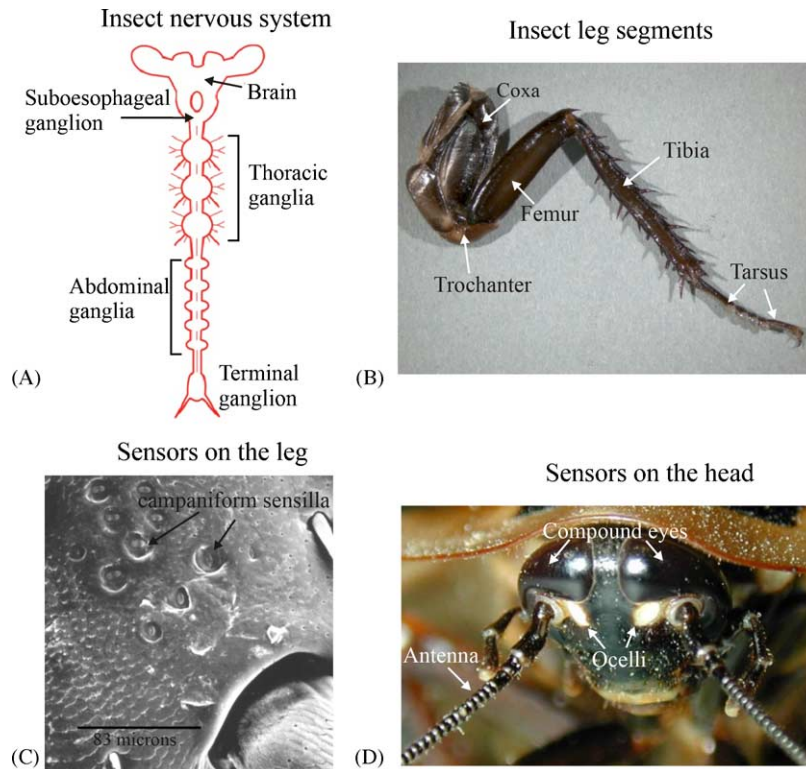


Fig. 1. Advantages to using insects as a model system for aging. (A) Insects have a reduced nervous system, which consists of a brain and the subesophageal ganglion in the head, three thoracic ganglia and a number of abdominal ganglia. (B) Insect legs have multiple segments: coxa, trochanter, femur, tibia and tarsus (foot). (C) Sensory structures of the legs are located on the surface of the exoskeleton and can be readily evaluated and manipulated. This scanning electron micrograph shows a close-up of the tibial campaniform sensilla located on the proximal part of the cockroach tibia. (D) There are many sensors on the head of an insect, which are important in surveying the environment such as compound eyes, ocelli and antennae. This image shows a close-up of the head of a *Blaberus* cockroach.

elaborate attachment structures on their feet to aid in walking in gravity defying situations such as up walls or over ceilings (Dai et al., 2002; Gorb et al., 2001; Jiao et al., 2000; Larsen et al., 1995; Pelletier and Caissie, 2001). Furthermore, the fruitfly provides an excellent model because it can be manipulated genetically and differences in aging between different strains can readily be examined. Finally, the very fact that insects are evolutionarily very distant from vertebrates provides an interesting situation. Vertebrates and arthropods (the phylum that contains insects) evolved legged locomotion independently. Nevertheless, remarkable similarities are found both in their leg designs (Ritzmann et al., 2004) and in the neural control of movement (Pearson, 1995, 2000). Both arthropods and vertebrates must solve the same physical impediments to legged locomotion and appear to have converged on a common set of solutions (Conway-Morris, 2003). Similarly, if one finds common

problems arising in the aging process in these disparate groups of animals, they may reveal fundamental principles of that process.

Insects are valuable for studies into the age-related declines in locomotor behavior because many are highly mobile both over land (walking and running) and in the air (flying). Locomotor movements in insects are fairly stereotyped. Therefore, deficits can be easily identified. Six-legged insects walk in a tripod gait during which the front leg and rear leg on one side and middle leg on opposite side move together during slow movement (Wilson, 1966). Within each of the thoracic ganglia are neurons that make up central pattern generators (Cohen, 1992; Selverston, 1999). These neurons are capable of producing rhythmic motor output, which activates the leg muscles. Insect legs consist of multiple leg segments including the coxa, trochanter, femur, tibia and tarsus (Fig. 1B, foot). Each leg joint is controlled by opposing muscles, which act to extend and flex the joint. Movement of the foot is controlled via a tendon, the retractor unguis, which originates in the tibia and attaches to the end of the claw of the tarsus (Frazier et al., 1999). Sensors on the legs act in synergy with central pattern generators for each leg to generate activity that is appropriate for movement in the context in which the insect finds itself at any given time (walking on even terrain, uphill, downhill or on a ceiling or carrying a load). Load sensors (campaniform sensilla, Fig. 1C) detect forces on the legs and act to limit leg extension and can initiate flexion of the leg (Akay et al., 2001; Noah et al., 2001; Ridgel et al., 2000, 2001; Zill et al., 1999). Joint sensors, such as hair plates, monitor joint position and can also initiate leg flexion (Wong and Pearson, 1976). Internal strands, called chordotonal organs, can detect joint position via gravitational sense and external vibration of a solid substrate (Field and Matheson, 1998).

Locomotion can be complex and variable. Depending on the locomotor task, different sensory and motor modalities may be at work. Recent studies in cockroaches have focused attention on ‘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., 2002b). Examination of ‘transitional behaviors’ is important to understand how animals alter their path of movement in different environmental conditions. In order for locomotion to be successful in a diverse environment, animals need to be able to detect obstacles and alter the path of movement. There are a number of sensors on the head of an insect, which are important in surveying the environment (Fig. 1D). Insects have a pair of compound eyes and multiple single-lens eyes called ocelli (Land, 1997; Mizunami, 1994). Furthermore, all insects have a pair of antennae. Each antenna is flexible, highly mobile and covered with many sensory structures. The primary functions of antennae are tactile and olfactory (Camhi and Johnson, 1999; Comer et al., 2003; Okada and Toh, 2000; Sakura et al., 2002; Ye et al., 2003). However, information from these head sensors must be integrated, packaged and sent to the thoracic circuits via descending pathways in order to influence posture or movement direction. An area in the brain, called the mushroom bodies, receives input from neurons carrying information from the antennae and is believed to be important in olfactory learning and place memory, as well as sensory discrimination (Heisenberg, 2003; Mizunami et al., 1998a,b). Another brain region, the central body complex has been suggested to play an essential role in integrating signals from sensors on the head with

information on motor activity in order to generate complex leg movements (Strausfeld, 1999).

Although thoracic neurons are capable of producing motor output consistent with walking, insects do not walk well without a head and locomotion is limited in animals, which have lesions that alter descending input to the brain. Animals with lesions of the circumoesophageal connectives (between the brain and the suboesophageal ganglia) walk with a tripod gait for long periods of time on flat surfaces. However, these animals show subtle deficits in postural control and have difficulty climbing steep inclines (Ritzmann et al., *in press*).

In light of the technical advantages, the short and predictable life span and the complex set of locomotory behaviors that can be generated by these animals, studies focused on the age-related changes in locomotion in insects will provide insight into the physiological and mechanical changes that may contribute to reductions or impairments which occur in all aged animals. Furthermore, the value can also work in the opposite direction. Aging could serve as a naturally occurring lesion in order to understand behavior in intact animals. Thus, aging studies can contribute to a better understanding of movement in healthy insects. The aim of this review is to discuss the age-related locomotor deficits in insects and remark on the value of multi-level approaches to the study of the control of locomotion.

## **2. Age-related changes in locomotor behavior**

### *2.1. Spontaneous locomotion/walking*

The majority of aging studies in insects have been done in fruitflies. Many of these experiments have examined the differences in age-related declines in locomotion between wild-type and mutant or transgenic flies. The most commonly used measure of age in insects is spontaneous locomotion. Generally, spontaneous locomotion is measured as any movement, including grooming, walking or climbing, during a given time period. Many studies in fruitflies have shown that spontaneous locomotion decreases with age in wild-type and mutant animals (Le Bourg, 1987; Le Bourg et al., 1993; Le Bourg and Minois, 1999; Martin et al., 1999; Minois et al., 2001). In addition, the rates of decrease in spontaneous locomotion have been shown to be altered in some transgenic flies. There has been an effort to find a mutation that can reduce the rate of aging, as estimated by behavioral studies, and to modulate the life span. Minois et al. (2001) hypothesized that fruitflies with overexpression of heat shock protein (HSP70) would age better and obtain higher scores during tests of spontaneous locomotion after heat shock than would control animals. They examined three different lines of animals in this study before and after heat shock induction: (1) a wild-type inbred line, (2) a line with extra-copies of the *hsp70* and (3) excision strain (chromosomal insertion without extra-copies of *hsp70*). This study found that Hsp overexpression did not have a dramatic effect on life span nor did it increase the locomotor ability of the animals. Fernandez et al. (1999) examined different strains of fruitfiles and documented how the genotypic background of an organism may affect aging and changes in locomotor behavior. This study provided evidence that the strains express different patterns of locomotor activity across the life span but did not discuss why these

differences might occur. Nevertheless, there was a general trend for mean activity scores to decline with age, from 7 to 35 days, in the all strains. Additional studies in fruitflies have examined the path of walking from the center of an arena to the outside. Aged animals have a tendency to move in a sinuous path from center, while young animals walk in a fairly straight line (Le Bourg et al., 1993). Despite variations in the rate of decline among strains of fruitflies, all studies showed decreases in spontaneous locomotor activity with increasing age.

Although fruitflies are short-lived and easy to manipulate genetically, they are not robust walkers and their small size precludes detailed examination of neural circuitry. Furthermore, aging research in fruitflies has not examined changes in leg kinematics or joint movement, which may contribute to reduced activity. Parallel studies in larger insects can augment fruit fly studies by examining the basis of locomotor deficits in greater detail. They can also contribute comparative data for aging studies on other animals such as mammals and even humans.

Cockroaches provide an excellent model for aging research because a great deal is known about the mechanics and neurobiology of locomotion in adult cockroaches (Camhi and Levy, 1988; Delcomyn, 1987; Full and Tu, 1990; Jindrich and Full, 1999; Ritzmann et al., in press; Schaefer et al., 1994; Tryba and Ritzmann, 2000; Watson and Ritzmann, 1998; Watson et al., 2002b). Recently, Ridgel et al. (2003) documented age-related changes in spontaneous locomotion and walking in the *Blaberus* cockroach using high-speed video analysis (125 frames/s). The maximum adult lifespan of these animals is 80 weeks and 50% of the cockroaches in our population died by week 61. Adult animals showed a decrease in spontaneous locomotion with increasing age (Fig. 2A). Aged animals (defined as those that are  $\geq 60$  weeks post adult molt) also showed a decrease in walking speed ( $2.7 \pm 0.7$  steps  $s^{-1}$ ) when compared to 1-week-old adult cockroaches ( $4.6 \pm 1.7$  steps  $s^{-1}$ ).

The age related decrease in activity was often accompanied by tarsal (foot) abnormalities, termed ‘tarsus catch’, in aged individuals. In ‘tarsus catch’ the prothoracic (front) leg catches on the mesothoracic (middle) leg during the swing phase, when the front leg is in the air and moving forward (Fig. 2B). ‘Tarsus catch’ was detected in 90% of the cockroaches observed at 65 weeks post-adult molt (Fig. 2C). This deficit causes temporary alterations of the gait, but animals are able to regain a tripod gait after the perturbation (Fig. 2D). In addition, the tibio-tarsal joint angle in legs, which exhibit ‘tarsus catch’ ( $115 \pm 15.3^\circ$ ) was significantly less than intact legs ( $155.3 \pm 20.8^\circ$ ).

Further examination of the tibio-tarsal joint and the tarsus in aged animals showed that structural defects were consistently associated with ‘tarsus catch’. In young cockroaches, the tarsal pads and the joints were white in color (Fig. 3A). In contrast, in aged animals, the joints were stiff and the tarsal pads were brown in color (Fig. 3B). Furthermore, the tarsal pads in young individuals were flexible and easily deformed with a nylon filament that produced 29 mN of force (Fig. 3C). The flexible nature of the pads is critical to their performance. In order to generate enough force to hold the insect onto a vertical structure, the pad must be flattened out (Dai et al., 2002; Gorb et al., 2000; Jiao et al., 2000; Niederegger and Gorb, 2003). The yellowed tarsal pads in aged individuals were, in fact, hardened and did not deform when compressed with a filament (Fig. 3D). The internal morphology of the tarsi was consistent with the external appearance. The trachea and



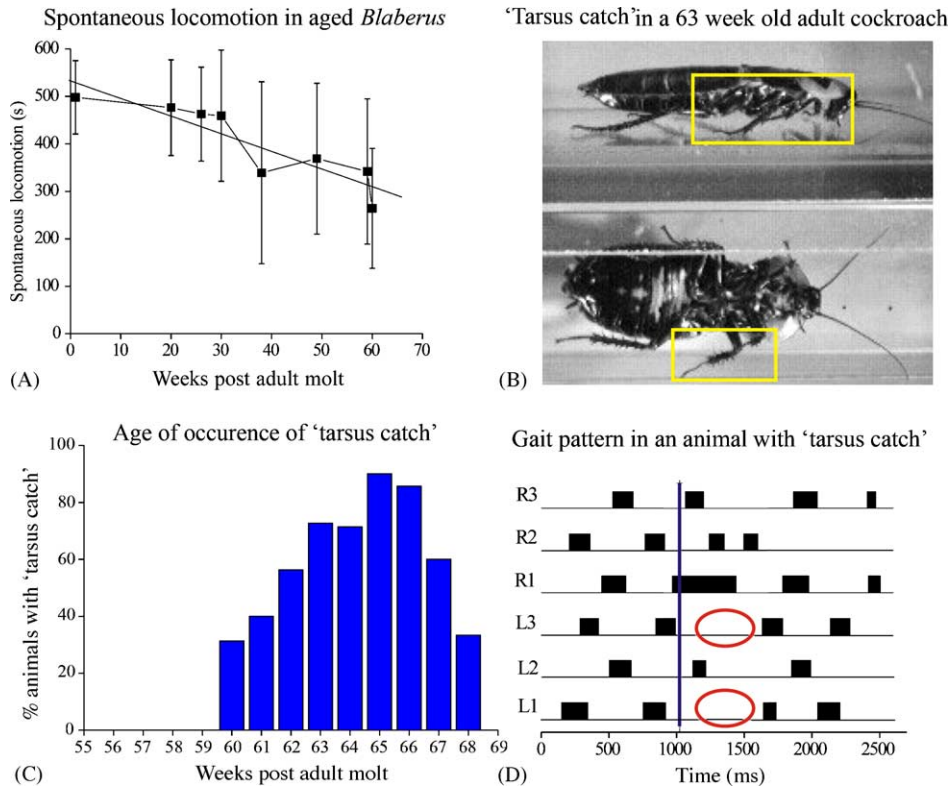


Fig. 2. Spontaneous locomotion and horizontal walking in *Blaberus* cockroaches. (A) Spontaneous locomotion was defined as the total time spent walking, climbing or burrowing in a 10-min period. Spontaneous locomotion decreases significantly as adult cockroaches age. (Regression analysis, slope =  $-3.4$ ,  $r^2 = 0.839$ ,  $p < 0.01$ ). (B) Video image (from the side and below) of a 63-week-old adult with 'tarsus catch'. Note that the right front tarsus catches on the tibia of the right middle leg (inside box). (C) '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. (D) Gait pattern in an animal with 'tarsus catch' in right front leg. The swing phase is shown as black boxes. Prior to 'tarsus catch', this animal walks in an alternating tripod gait. The vertical line represents the time when the right front tarsus catches on the middle tibia. The ellipse illustrates the absence of swing in the left front and middle leg due to 'tarsus catch'. The length of the swing phase is reduced in the other legs to compensate for the absence of support by the left front leg. The animal recovers within one leg cycle. R: right, L: left, 1: front leg, 2: middle leg, 3: rear leg (from Ridgel et al., 2003).

tendon inside the tarsus of young animals were silver and shiny (Fig. 3E), while there was hardening and degeneration of the trachea and tendon in aged cockroaches (Fig. 3F), suggesting a general degeneration of tissues in the distal region of the leg.

Currently, the physiological reason for degeneration of the tarsus in aged cockroaches is unknown. However, there are two likely possibilities. First, vascular insufficiency could be present in aged cockroaches. These animals have open circulatory systems and hemolymph is circulated throughout the body cavity by activity of the heart and the abdominal muscles (Wasserthal, 1996; Weis-Fogh, 1967). The hemolymph carries ions, amino acids, protein and hormones to the body tissues. Many insects have accessory hearts in the legs, which

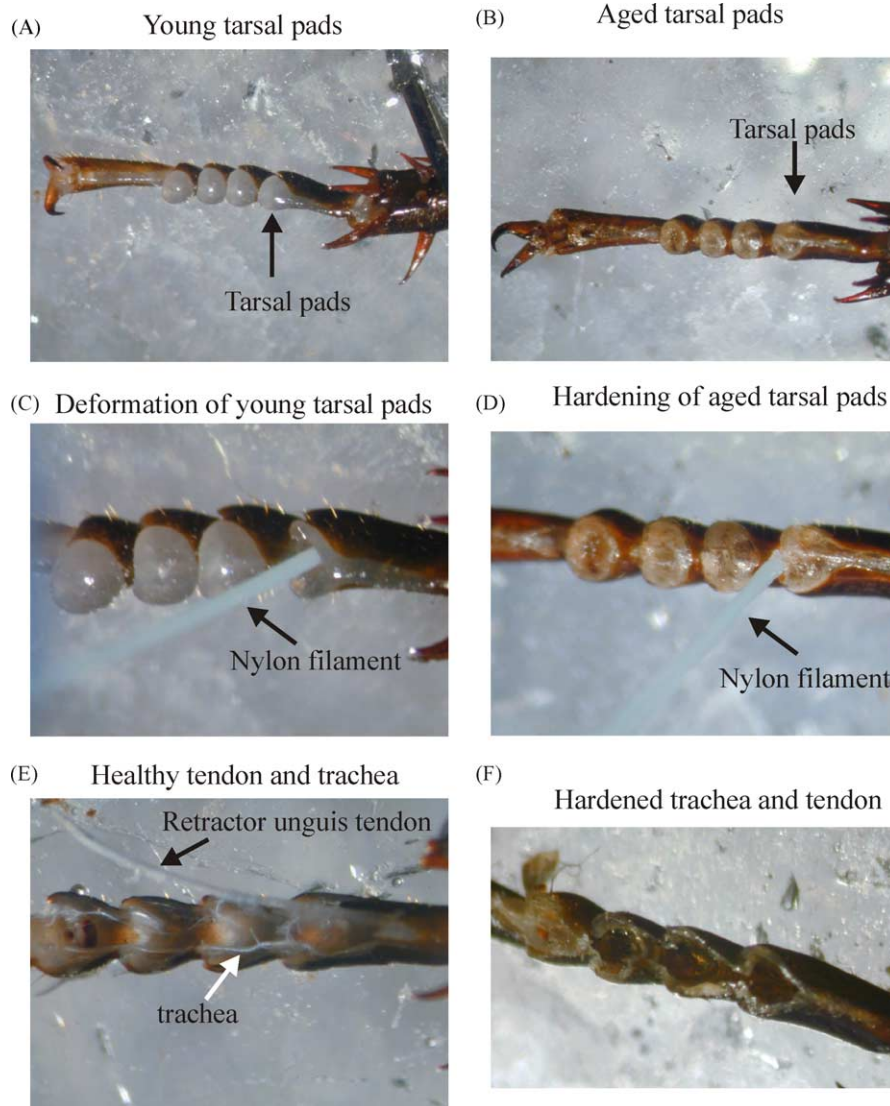


Fig. 3. Tarsus morphology in young and aged animals. (A) The tarsal pads of a 1-week-old adult are white in color (arrow) and the joints between the tarsal segments are flexible. (B) In contrast, the tarsal pads of an animal with 'tarsus catch' brown in color (arrow) and the joints are often stiff. (C) A nylon filament, producing a force of 29 mN, readily deformed the tarsal pads in young animals. (D) Pads on 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 (from Ridgel et al., 2003).



help to distribute hemolymph to the end of the legs (Pass, 2000), which, as a blind ending tube, presents considerable resistance to fluid circulation. However, if the circulatory mechanisms fail then tissues in the legs will die. Second, there may be degeneration in the tracheal system, which carries oxygen to the ends of the legs (Wasserthal, 1996; Weis-Fogh, 1967; Westneat et al., 2003).

## 2.2. Block climbing

Block climbing is different from horizontal walking because an animal must be able to detect the size of the obstacle, change body posture and alter the gait to move over the barrier. In studies by Watson et al. (2002a,b), cockroaches were videotaped as they climbed over plastic blocks of varying heights (5.5 and 11 mm). When an animal approaches a 5.5 mm block, the front legs do not alter the swing trajectory in order to reach the top of the obstacle. Furthermore, no change in body posture is necessary in these climbs. However, the legs do not lift high enough during horizontal walking to reach the top of an 11 mm block. Therefore, cockroaches had to change the body posture by tilting the body upwards in order to get the front legs on the obstacle. This alteration of posture was accomplished by rotation and extension of the joints in the middle leg.

Further studies in cockroaches have examined block climbing in both aged and 1 week after metamorphosis to an adult (Ridgel et al., 2003). Young individuals were easily able to surmount all blocks. Although old animals often show ‘tarsus catch’, they were often able to successfully climb blocks. Generally, all animals were able to climb a 5.5 mm block without alteration of gait or posture. Climbing strategies for larger obstacles (11 and 16.5 mm) were categorized as (1) rear up (Fig. 4A) or (2) head butt (Fig. 4B), according to the terminology of Watson et al. (2002b). The most prominent strategy of all aged and young individuals was to change the body angle before placing the front legs on the block (Fig. 4C, “Rear up”). Cockroaches with ‘tarsus catch’ sometimes climbed the obstacle by pushing the head against the block, thereby forcing the body over the obstacle (22% of trials—“head butt”). Some animals with ‘tarsus catch’ also had trouble grasping the top of the block with the tarsi of the front legs and showed leg slipping. The problems encountered by these animals demonstrate the importance of flexible tarsal pads for successful climbing behavior. This is an example of aging studies illuminating processes in young, healthy animals. The inability of aging 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.

## 2.3. Inclined/vertical walking

Vertical or inclined walking is different than horizontal walking because the animal’s weight has to be moved in the opposite direction to gravity. Studies in locust (Duch and Pfluger, 1995) and cockroaches (Larsen et al., 1995) have shown that step duration often increases, the swing phase of the leg decreases and flexor and extensor muscles often co-contract to compensate for the forces of gravity.

Studies in fruitflies and cockroaches have also examined changes in inclined or vertical walking behavior with aging. Vertical walking (negative geotaxis) in fruitflies was

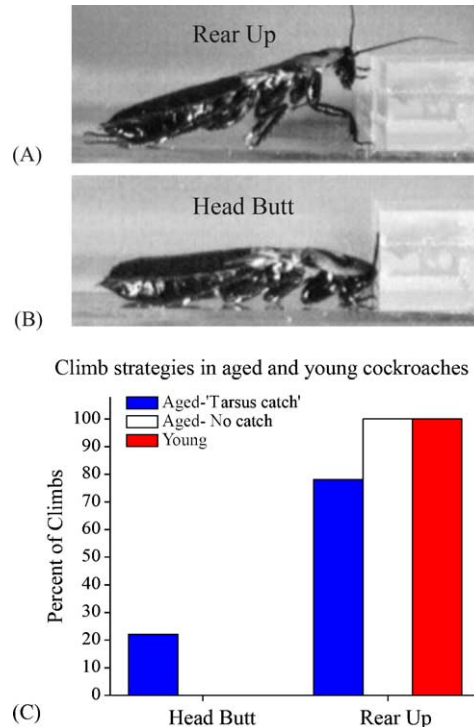


Fig. 4. Block climbing in aged and young cockroaches. (A) After detecting the obstacle, animals often change the body posture by rotating the middle legs forward and “rearing up” the front of the body. (B) Some aged individuals do not alter their body angle and run into the side of the block (“head butt”). (C) Summary of climbing behaviors in aged and young cockroaches. In most of the trials, aged animals ‘rear up’ before reaching the block. In a few trials, aged cockroaches with ‘tarsus catch’ run into the side of the block before climbing over it (from Ridgel et al., 2003).

measured as the net vertical distance walked for 10–15 s after animals were forced to the bottom of the tube by gentle tapping. The ability of wild-type fruitflies to perform this task and the distance moved up the tube in the time allotted decreased with age (Cook-Weins and Grotewiel, 2002; Goddeeris et al., 2003; Minois et al., 2001). Additional studies have examined climbing in mutant flies. Goddeeris et al. (2003) showed that age-dependent loss of vertical walking activity decreased in animals with mutations of the myospheroid (*mys*) gene. This gene encodes a cell surface receptor (integrin  $\beta$ PS) that mediates development, inflammation, tumor metastases and wound healing (Goddeeris et al., 2003). These findings suggest that  $\beta$ -integrins influence functional senescence in fruitflies. However, further analysis of vertical walking was not done in these studies. Therefore, it is difficult to determine the exact causes of reduced activity in aged fruitflies.

The ability of aged cockroaches to successfully walk on an incline was tested by using a track that was tilted to  $45^\circ$  (Fig. 5A). Young animals have no difficulty in performing this task. However, only 58% of aged animals were able to climb the incline in at least one of the trials. Failure to climb the incline in aged cockroaches may simply be due to deterioration of the tarsal pads. ‘Tarsus catch’ may simply represent an extreme condition.

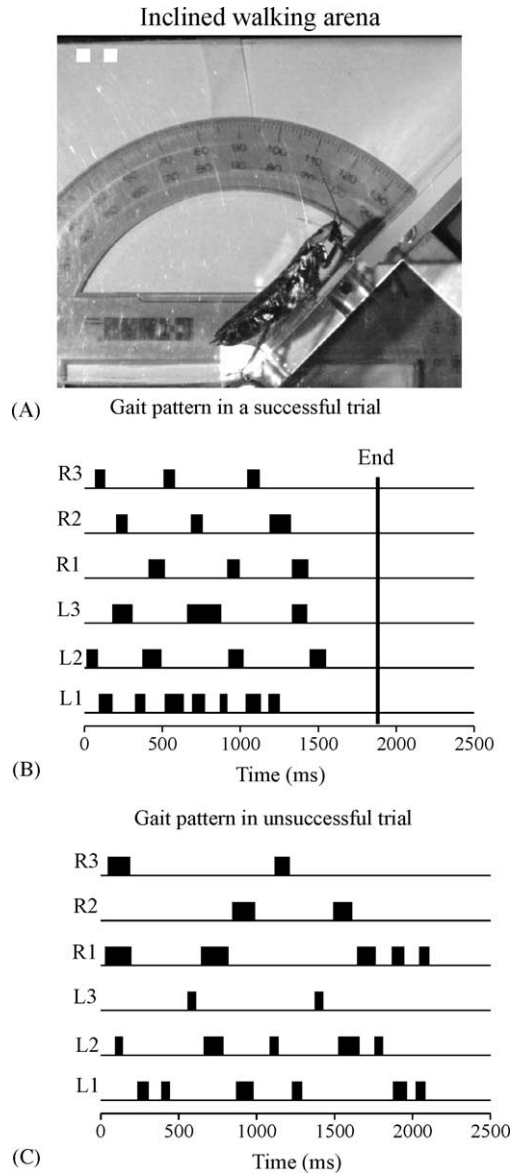


Fig. 5. Inclined walking in aged cockroaches. (A) Animals were placed in a treadmill with an acetate belt that was tilted at a  $45^\circ$  angle. (B) Gait pattern in an aged individual that successfully climbed the incline. Although the front legs often took multiple steps during inclined walking, these animals used a metachronal gait to surmount the incline. (C) 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 (from Ridgel et al., 2003).

However, these findings do not rule out the possibility that changes in central nervous or muscular system in aging may also contribute to failure in inclined walking. Indeed, young animals that have experienced bilateral lesion of the connectives between the brain and the suboesophageal ganglion also fail on similar inclines (Ritzmann et al., in press).

Aged animals showed extensive leg slipping while walking on an incline. Generally, the prothoracic front legs slipped on the inclined acetate surface more often than the middle or rear legs. However, there was significantly more leg slipping in the middle legs during failing trials than in successful trials. Individuals that were able to climb the incline generally walked in a metachronal gait, in which individual legs moved in a wave from the rear to the front (Fig. 5B). Metachronal gaits are sometimes used by slowly moving insects (Wilson, 1966). In contrast, aged cockroaches that failed during inclined walking often showed uncoordinated gait patterns during the attempt (Fig. 5C). Nevertheless, all aged insects that failed on the incline walked with a tripod gait on a horizontal surface. Thus, their ability to adjust to new tasks may be limited with age.

#### 2.4. Righting

Studies in aged cockroaches have further examined the ability of animals to right themselves (Ridgel et al., 2003). Righting behavior occurs when an animal is placed on its back and leg-to-ground contact is lost. This behavior 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). The mean righting duration was similar between all aged individuals and 1-week-old adults. However, there was a significant increase in the duration of righting in old adults with ‘tarsus catch’ ( $4.96 \pm 3.7$  s) when compared to intact aged animals ( $3.67 \pm 2.4$  s). These results show that old insects are able to right themselves, but cockroaches with mechanical pathologies associated with ‘tarsus catch’ are slower at accomplishing this task.

#### 2.5. Escape behavior

The escape behavior of the American cockroach, *Periplaneta americana*, is one of the most characterized behaviors in cockroaches and in arthropods in general (Comer and Robertson, 2001; Ritzmann and Eaton, 1997). During escape, cockroaches respond to puffs of wind by turning away from the source and running (Camhi and Tom, 1978). Generally, the front and middle legs determine the direction of the turn by flexing the femur-tibia joint on the leg contralateral to the stimulus and extending the same joint on the ipsilateral leg (Nye and Ritzmann, 1992). In addition, cockroaches also escape in a directional manner to tactile stimuli of the antennae or the body (Comer et al., 1994; Schaefer et al., 1994). Basic leg movements to tactile stimulation were very similar to escape elicited by wind.

Most of the neural control of this behavior resides in the thoracic and abdominal ganglia. However, a descending influence on escape has recently been demonstrated (Schaefer and Ritzmann, 2001). Decapitated cockroaches show decreased leg extension in response to threatening stimuli, with an anterior-to-posterior gradient. That is, hind legs are little affected by the lesion, front legs are greatly affected and middle legs show an intermediate effect.

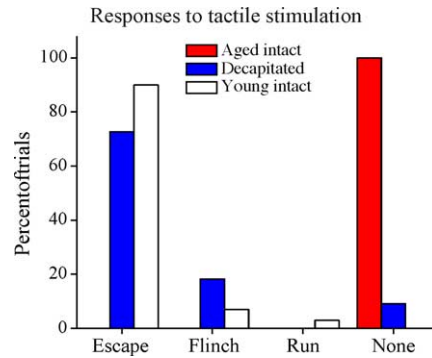


Fig. 6. Responses evoked by tactile stimulation of the abdomen in 61-week-old cockroaches under intact and decapitated conditions and young intact animals. Young intact animals readily show escape behavior when stimulated (data from Schaefer and Ritzmann, 2001). In contrast, intact 61-week-old cockroaches did not escape when stimulated. Following decapitation, however, forward directional escape responses (Schaefer et al., 1994) were easily elicited in aged individuals (from Ridgel et al., 2003).

Ridgel et al. (2003) compared escape responses in young and aged cockroaches and examined whether deficits were attributed to the basic thoracic circuitry or to the influences found in the brain and suboesophageal ganglia. Tactile stimulation of the dorsal abdominal cuticle readily evokes escape responses in young American cockroaches (Schaefer and Ritzmann, 2001; Schaefer et al., 1994). However, similar stimulation of aged animals failed to evoke any escape responses (Fig. 6). Interestingly, the capacity of aged cockroaches to escape returned after decapitation, suggesting that the deficit associated with aging was, in fact, primarily focused within the head ganglia. After decapitation, escape behavior in aged animals was elicited in 73% of the trials. These data show that escape behavior is disrupted in aged cockroaches and suggest that these deficits may be caused by age-related degeneration in the brain or suboesophageal ganglion. Pathologies in these structures appear to interfere with an otherwise functioning system. This effect is similar to that seen when a parasitic wasp stings a cockroach in the head ganglia rendering the escape system ineffective (Fouad et al., 1996; Haspel and Libersat, 2003; Weisel-Eichler et al., 1999; Weisel-Eichler and Libersat, 2002). These studies propose that venom injected into the head ganglia can affect the modulation of the thoracic portion of the escape circuitry. Thus, aging in cockroaches may also have an effect on modulatory pathways originating in the head ganglia.

### 3. Conclusions

This review has discussed studies that have documented reduced activity levels and difficulties in complex locomotor tasks in aged insects. Further research in this area should continue to examine behavior of aged animals in a full range of locomotor tasks. This strategy can be powerful in understanding the complex effects of aging resulting from pathologies in central nervous system, 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. Furthermore, behavioral deficits in aged insects could result from deficits in more than one of the areas listed above. In cockroaches, horizontal walking trials suggest that the behavioral deficits are the result of peripheral degeneration of 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 that these could certainly contribute to the problems seen in horizontal walking. Old age does not limit the cockroaches’ ability to climb obstacles or right themselves. Although some animals show delayed postural changes and decreased righting duration. However, aged cockroaches show significant deficits in inclined walking and escape behavior. A reasonable strategy for future research in this area would include anatomical and physiological studies of the changes in the nervous system and peripheral structures with aging along with continued behavioral observations of a range of behaviors that document deficits associated with various locomotor tasks. These results could be compared to effects of lesions generated in otherwise healthy young insects to localize the specific age-related pathologies.

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