Descending Influences on Escape Behavior and Motor Pattern in the Cockroach

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ABSTRACT: The escape behavior of the cockroach is a ballistic behavior with well characterized kinematics. The circuitry known to control the behavior lies in the thoracic ganglia, abdominal ganglia, and abdominal nerve cord. Some evidence suggests inputs may occur from the brain or suboesophageal ganglion. We tested this notion by decapitating cockroaches, removing all descending inputs, and evoking escape responses. The decapitated cockroaches exhibited directionally appropriate escape turns. However, there was a front-to-back gradient of change: the front legs moved little if at all, the middle legs moved in the proper direction but with reduced excursion, and the rear legs moved normally. The same pattern was seen when only inputs from the brain were removed, the suboesophageal ganglion remaining intact and connected to the thoracic ganglia. Electromyogram (EMG) analysis showed that the loss of or reduction in excursion was accompanied by a loss of or reduction in fast motor neuron activity. The loss of fast motor neuron activity was also observed in a reduced preparation in which descending neural signals were reversibly blocked via an isotonic sucrose solution superfusing the neck connectives, indicating that the changes seen were not due to trauma. Our data demonstrate that while the thoracic circuitry is sufficient to produce directional escape, lesion or blockage of the connective affects the excitability of components of the escape circuitry. Because of the rapidity of the escape response, such effects are likely due to the elimination of tonic descending inputs. J Neurobiol 49: 9–28, 2001

***Keywords: Periplaneta americana*; escape behavior; descending inputs**

INTRODUCTION

In most animals, the central nervous system is divided into multiple anatomically distinct areas. How these different areas act and interact to produce behavior has long been an issue of investigation (Sherrington, 1906). Initially, the "higher centers" of insects were thought to largely play an initiatory or inhibitory role on lower pattern generators (Roeder, 1963). However, from the study of a number of rhythmic systems, a more complex picture has emerged of higher centers interacting to initiate, maintain, and modulate behavior (Reichert and Rowell, 1986; Kien and Altman, 1992; Whelan, 1996; Canedo, 1997; Grillner et al., 1997). With such ongoing rhythmic behaviors, interaction is likely beneficial in producing advantageous behavior in a complex environment. Other behaviors such as startle responses are ballistic and have a very short latency. The circuits that produce such behaviors may well have different descending inputs vis-à-vis rhythmic locomotion, if they are under the influence of higher centers at all.

The escape response of the American cockroach, *Periplaneta americana*, is stereotyped and well documented. The most commonly studied stimulus for

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initiating escape is wind directed at the abdomen (Camhi and Tom, 1978). However, essentially the same response can be elicited by tactile stimulation to the body (Schaefer et al., 1994) or to the antennae (Comer and Dowd, 1993). The movement is composed of an initial directional turn that orients the animal away from the threat followed by a run of more random direction (Camhi and Tom, 1978). Two commonly elicited types of initial escape turns have been described (Nye and Ritzmann, 1992). In type 1 turns, both the metathoracic legs extend at the coxa-trochanter (CTr) and femur-tibia (FT) joints. The ipsilateral mesothoracic leg extends at the CTr and FT joints, while the contralateral mesothoracic leg typically extends at the CTr joint and flexes at the FT joint. The movements of the prothoracic leg joints are less stereotyped. Regardless of the actual joint movements, the prothoracic tarsi are driven posteriorly and towards the threat (Camhi and Levy, 1988; Nye and Ritzmann, 1992). The result of the movement of all six legs is that the animal is propelled forward and away from the stimulus (Nye and Ritzmann, 1992). In type 2 turns, the CTr and FT joints of the metathoracic and mesothoracic legs that are ipsilateral to the stimulus extend, while those joints on the contralateral metathoracic and mesothoracic legs flex. The prothoracic leg kinematics are again less stereotyped, but often mimic the tarsal tip movements of the mesothoracic legs (Camhi and Levy, 1988; Nye and Ritzmann, 1992; Schaefer et al., 1994). Type 2 escape turns produce a large magnitude rotation away from the threat, with no forward translation of the body. A third, less frequent response to front stimulation, type 3 escape, involves flexion of all CTr joints, causing the animal to back away from the threat before completing the movement with a type 1 or 2 turn.

The underlying circuitry has been described at the level of individually identifiable neurons (Ritzmann and Eaton, 1997). In general, sensory neurons associated with peripheral sensory structures (abdominal cerci or tactile structures in the cuticle) are activated by a threat (Westin, 1979; Pollack et al., 1995). The sensory neurons synapse onto modality-specific interganglionic interneurons such as the ventral giant interneurons (vGIs) (Westin et al., 1977), or tactile sensitive interneurons in the abdominal nerve cord (Ritzmann and Pollack, 1998). In each of the three thoracic ganglia the various modal pathways converge onto at least 13 pairs of interganglionic interneurons, known as type A thoracic interneurons (TI_As) (Ritzmann and Pollack, 1988, 1998; Pollack et al., 1995). The multimodal TI_As are thought to be the locus of control of the escape system, determining if an escape turn is to be initiated and in what direction the animal is to turn (Ritzmann, 1993; Ritzmann et al., 1991; Ritzmann and Pollack, 1994; Ritzmann and Eaton, 1997). The TI_As, in turn, connect to the leg motor neurons (MNs) in their own and adjacent ganglia both directly and indirectly via local interneurons (LIs) (Ritzmann and Pollack, 1990).

All of the neural circuitry necessary to account for basic oriented escape responses is found in the ventral nerve cord and thoracic ganglia. However, there is recent evidence of descending influences on the thoracic escape circuitry. First of all, identified interneurons from higher centers have been described that respond to mechanosensory cues directed at antennae (Burdohan and Comer, 1990, 1996). Cells have been described with their soma either in the supraoesophageal or suboesophageal ganglia. Some have dendritic morphology that is remarkably similar to the TI_As. Second, cockroaches stung by the wasp *Ampulex compressa* in the suboesophageal ganglion have a higher threshold for escape (Fouad et al., 1994, 1996), cockroaches with both antennae contacting barriers do not respond to stimuli that normally evoke escape (Watson and Ritzmann, 1994), and lesioning one neck hemi-connective produces a directional bias in escape responses elicited by wind (Keegan and Comer, 1993). Indeed, it has even been suggested that neural signals may have to ascend first to the brain and then descend back to the thoracic ganglia to generate an escape response (Burrows, 1996). Given this evidence, we sought to elucidate the nature of any descending influences on the escape system by examining the behavior following removal of descending neural inputs.

MATERIALS AND METHODS

Animals

Intact, adult, male *P. americana* were used in all experiments. Animals were housed in colonies in 30 gallon plastic garbage cans on a 12:12 light/dark cycle at 28°C. They had *ad libitum* access to Purina Chicken Starter Mash (unmedicated) and water.

Surgical Procedures

To sever the neck connectives, the animals were anesthetized with CO_2 and pinned ventral side up onto a Sylgard-filled dish. An incision was made into the soft neck cuticle, a glass probe was placed under the neck connectives, and microsurgical scissors were used to sever the cord. Care was taken to avoid the trachea.

To severe the circumoesophageal connectives, the animals were likewise anesthetized and pinned out. A razor blade was placed in the mouth above the mandibles, and an incision was made back to just below the compound eyes.

Free Ranging Observations

A Plexiglas™ arena was constructed measuring 32 × 24 × 9 cm. The floor was covered with acetate to provide sufficient traction. A mirror tilted at a 45° angle was mounted under the arena to allow videotaping of the animals from the ventral side.

Animals placed in the arena were given 10 min to adjust. A tactile stimulus was utilized because it has a shorter and less variable latency and because there is a more distinct tactile map in eliciting type 1 and type 2 responses than with wind (Schaefer et al., 1994). Tactile stimuli were delivered with a hand held solenoid that moved a 15 cm glass rod with a bent insect pin glued to its tip. Care was taken to hold the pin at the same distance (approximately 1 mm) above the cuticle prior to activation, though due to the hand held delivery there was some variability in exact height. Activation of the solenoid caused the head of the pin to contact the abdominal cuticle with a force of 0.18 N (measured with a WPI force transducer). The stimuli were delivered in a random order to the right and left edges of the pronotum and to the right and left edges of the 3rd abdominal tergite. There was 5 min between trials. Stimuli were only delivered to animals that were standing still. Immediately after two to four trials, the cockroaches were decapitated with a pair of scissors just caudal to the head capsule. Trials continued until the animal failed to respond two times in a row or until 12 trials had been administered.

Tethered Observations

The tether used was identical to that described in Schaefer et al. (1994). The animal's wings were removed. Thin pieces of steel were glued onto the animal's pronotum and abdomen with 3M Vetbond glue. Two magnets secured the animal via the metal pieces. The height of each magnet and distance between them were adjusted so the animal assumed a normal posture. Animals were tethered over a lightly oiled (microtome oil No. 288; Lipshaw Manufacturing) glass plate suspended over a mirror tilted at a 45° angle. This allowed videotaping of the leg movements from the ventral surface [see Fig. 1(A)]. The oil did not distort the video image.

Animals were allowed to adjust to the tether for 30 min. Tactile stimulus was delivered with the same solenoid as described for the free-ranging experiments, except that it was mounted onto a manipulator and the tip was placed 1 mm above the cuticle. The stimuli were delivered in a random order to the right and left edges of the pronotum and to the right and left edges of the 3rd abdominal tergite. There was 5 min between trials. Stimuli were only delivered to animals that were not attempting to move. Immediately after two to four trials, the cockroaches were decapitated with a pair of scissors just caudal to the head capsule. Trials continued until the animal failed to respond two times in a row or until 10 trials had been administered.

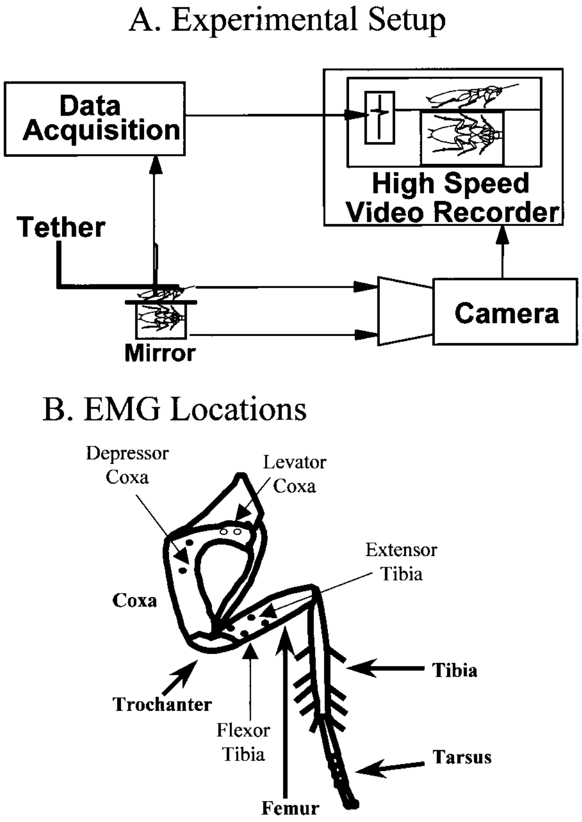

Figure 1 (A) The experimental setup for the behavioral experiments. The setup allowed for simultaneous high speed videography and electromyogram (EMG) recordings. (B) A schematic of a cockroach leg, depicting the location of EMG recording wire insertion points. Black dots represent ventral points, white dots represent dorsal points.

Videotaping and Kinematic Analysis

All video recordings were made with an NAC HSV-400 high speed video recording system sampling at 200 frames/s. A synchronized JSV-400 strobe provided illumination. The tethered preparation allowed simultaneous recording of the ventral and lateral views of the animal [see Fig. 1(A)]. Motion TV software was used in all kinematic measurements. For the mesothoracic and metathoracic legs, only the ventral view was used, as there is little movement about the body-coxa (BC) joint (Nye and Ritzmann, 1992). For measurements of the prothoracic tarsal tip displacement, only the ventral view was utilized. For the prothoracic joint kinematics, both the ventral and lateral views were used, and the three-dimensional movements were reconstructed using custom software developed in Mathcad (Marx et al., 1993).

Electromyograms

EMGs were recorded in additional tethered preparations. The electrodes were 50 μ bipolar wires insulated to the tip. The muscles recorded were the depressor coxa (177D in T3, 135D in T2, 85E in T1; Carbonell, 1947), levator coxa (182C in T3, 139C in T2, 88A in T1; Carbonell, 1947), tibial extensor (184a in T3, 142a in T2, 92 a in T1; Dresden and Nijenhuis, 1958), and tibial flexor (185 in T3, 146 in T2, 95 in T1; Dresden and Nijenhuis, 1958). To limit the possibility of recording electrodes affecting the animal's leg movements, we recorded EMGs from one leg per animal. Previous work has demonstrated that under these conditions, the wires do not impede leg movement in behaving animals (Watson and Ritzmann, 1998). Given the stereotypical nature of the escape turn, comparisons between animals do not pose problems in interpretation. A pair of electrodes was inserted into each muscle recorded in a given preparation. Figure 1(B) shows the recording sites. One additional ground wire was inserted into the thorax. The wires were secured with cyanoacrylate glue. For further details on the recording sites and implantation methods, see Watson and Ritzmann (1998).

EMGs were amplified via AC amplifiers and the signal was digitally recorded on VHS tape using a VCR equipped with an analog to digital converter. A wave inserter superimposed one EMG record onto the video [see Fig. 1(A)]. Additionally, the strobe timing pulses from the NAC HSV (200 Hz) were recorded as a timing train, the onset of which was also recorded on the video by the activation of an LED. These two techniques facilitated synchronization of the kinematic and EMG data, which was done with Data-Pac III software (Run Technologies).

Nerve Recordings

For these experiments, the cockroaches were anesthetized by placing them in a refrigerator (3°C) for 10–15 min. Their wings and legs distal to the CTr joint were removed, and they were pinned dorsal side up onto a cork platform. The dorsal cuticle was removed from the neck to A6. The gut was removed, and the ventral nerve cord was exposed. Surrounding tissues were removed. Extracellular nerve recordings were made with silver bipolar hook electrodes insulated with a mixture of petrolatum and mineral oil. The nervous system was superfused with Wafford and Sattelle (1986) cockroach saline. Electrical signals were recorded on a Hewlett-Packard 3968A reel-to-reel tape recorder, and examined using Axotape and Axoscope software.

RESULTS

Free Ranging Behavior

First, we examined the general effects of removing descending inputs on behavior *in toto*. Fifty-one free-ranging cockroaches were either decapitated ($n = 43$) or had their cervical connectives cut ($n = 8$), and their behavior was observed. Either manipulation removes all descending neural inputs from the higher centers to the thoracic and abdominal ganglia. Such animals often immediately showed a burst of frantic movement, such as "running" in circles, or spastic, uncoordinated leg movements.

The decapitated and lesioned animals responded readily to tactile stimulation, and their responses were videotaped. Though we were unable to measure specific leg kinematics in free-ranging animals, their body movements were consistent with escape in 89 out of 137 trials (Schaefer et al., 1994). In the remainder of the trials, there was little or no evoked response. Presumed type 1 turns involved forward motion, type 2 turns involved rotation in place, and type 3 turns involved rearward motion of the animal's body. Subsequent runs were never seen, though an apparent additional subsequent type 1 escape turn was seen in two trials, and flightlike movement of the wings was seen during or following an escape in 12 trials. No actual flight was observed.

Lesioned and decapitated animals showed other notable behavioral defects. There was a marked decrease in spontaneous locomotion. The animals moved little if at all without external stimuli, and when they did move, they exhibited neither metachronal nor tripod coordinated gaits. Locomotion, when it did occur, was produced by the rather jerky movements of a single pair of legs. Spastic jumps were observed, and viewing tethered animals showed them to be spontaneous type 1 escapes. A hyperextended posture brought about by extension at the CTr and FT joints was seen, though not in all animals. The animals frequently fell over onto their backs as a result of their own movements, whether spastic jumps or attempts at walking, and had difficulty righting themselves. The righting movements, however, were recognizably similar to those of intact animals. Searching with the prothoracic legs and grooming of the cerci and abdomen with the metathoracic legs were readily observed, and appeared normal. The animals occasionally exhibited peristaltic movements of the abdomen, or would arc up the posterior tip of the abdomen. There were no obvious behavioral differences between decapitated and lesioned cockroaches.

Tethered Kinematics: Direction of Leg Movements

To get a more detailed analysis of leg movements, we also observed animals mounted on a tether over a lightly oiled glass plate. Twenty-five animals were tethered, and mechanical stimulation was applied to

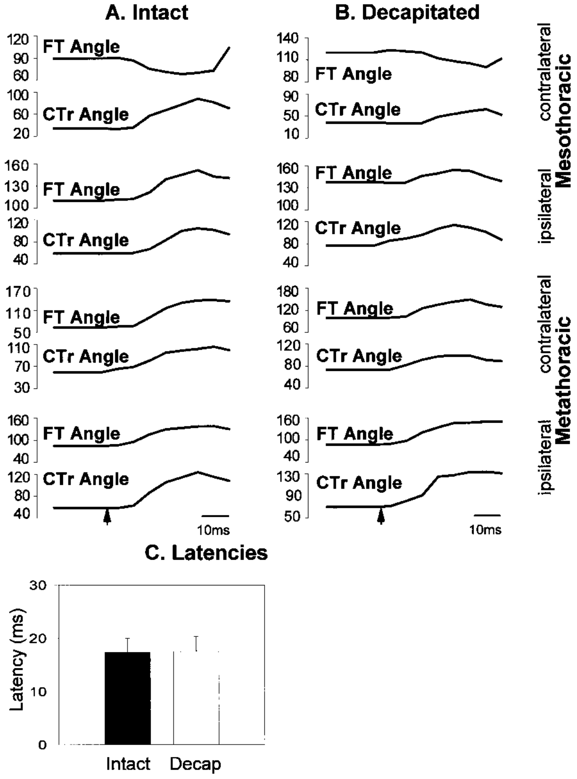

Figure 2 (A) Metathoracic and mesothoracic CTr and FT kinematics for all four legs during a single type 1 escape response. The arrow under the bottom record indicates when the tactile stimulus was delivered. (B) Metathoracic and mesothoracic CTr and FT kinematics of a type 1 escape response in the same animal as in (A) after decapitation. The arrow indicates when the tactile stimulus was delivered. (C) Graph showing the mean latency from stimulus delivery to initiation of the escape turn for the intact and decapitated trials. The error bars indicate one standard deviation.

the cuticle of the animals before and after decapitation. Tethering over an oiled glass plate minimizes passive movements produced by the actions of other legs and joints. Readily identifiable escape turns were still evoked in headless animals; 57 escapes were elicited in intact animals out of 64 trials, and 55 out of 88 in the animals postdecapitation. The escapes were still composed of the coordinated movement of all six legs (Fig. 2). The latency of the escape behavior was not affected [Fig. 2(C)].

Are the escape turns directionally appropriate in the lesioned animals? Keegan and Comer (1993) showed that lesioning a single cervical hemi-connective produced a directional bias. Moreover, it is possible that one type of escape (e.g., a type 1 turn) is the default, and descending inputs are required to produce larger angle turns such as type 2 turns. Figure 3 shows the responses elicited from mechanical stimulation of the abdomen and pronotum under intact and headless conditions. The front/back directional pattern of escape turns is maintained in decapitated cockroaches. That is, mechanical stimulation of the pronotum elicits type 2 turns, whereas stimulation of the abdomen produces type 1 turns. There was an increase in the number of atypical, yet somewhat coordinated, leg movements that may or may not produce a functional escape (i.e., flinches), and, with stimulation of the pronotum, there was an increase in the failure to respond. This increased number of failures could po-

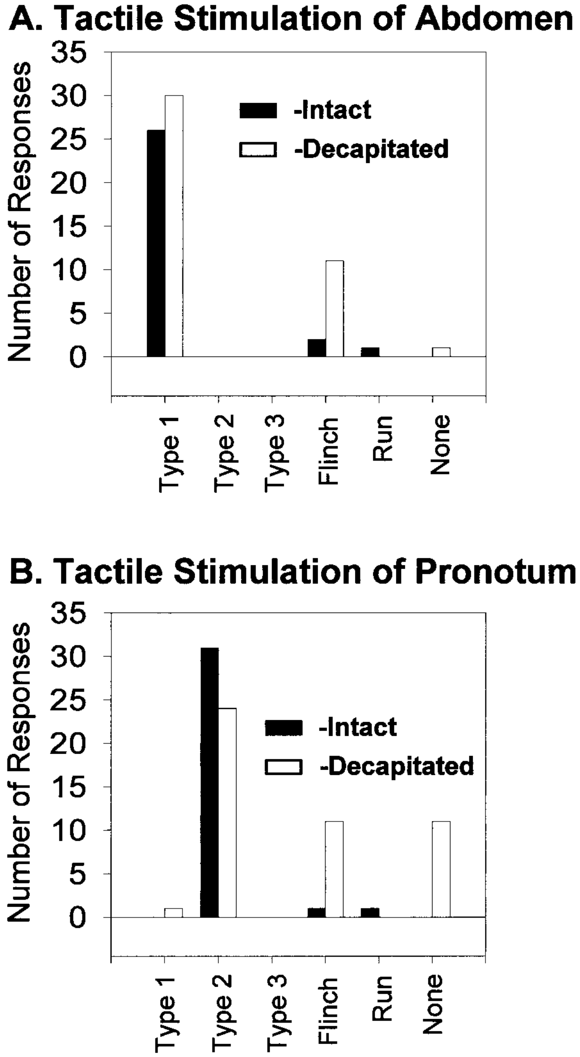

Figure 3 (A) Responses evoked by rear tactile stimulation of the lateral edge of the abdomen in tethered cockroaches under intact and decapitated conditions. Type 1 turns predominate under both conditions. (B) Responses evoked by front tactile stimulation of the lateral edge of the pronotum in tethered cockroaches under intact and decapitated conditions. Type 2 responses predominate under both conditions, although an increase is seen in nonstandard leg movements (flinches) and no responses.

tentially be due to the role of sensory structures on the head, such as the antenna, or in thoracic sensory neurons projecting to the suboesophageal ganglion, in detecting anterior mechanical stimulation (Altman and Kien, 1987). Loss of these structures or pathways with decapitation could reduce the amount of sensory drive reaching the TI_As. Nonetheless, the front/back directionality of the escape turns was maintained.

Left/right directionality was also maintained without descending inputs. Intact type 1 turns are characterized by extension of the ipsilateral mesothoracic FT joint and flexion of the contralateral mesothoracic FT joint (Nye and Ritzmann, 1992), and this pattern was maintained subsequent to decapitation (for example see Fig. 2). For type 2 turns, there is extension at the ipsilateral mesothoracic and metathoracic CTr and FT joints, whereas these same joints on the contralateral legs flex [see Fig. 4(B)]. Again, this is consistent with intact behavior (Nye and Ritzmann, 1992). With both escape types, turns toward the wrong direction were not observed in decapitated animals. However, in a minority of type 1 escapes (25% of intact, 28% of decapitated), there was extension at both mesothoracic FT joints. Such escapes were termed nondirectional, as they did not exhibit the characteristic directionality of FT kinematics described by Nye and Ritzmann (1992). There was no significant difference in occurrences of nondirectional escapes between intact and decapitated escapes (chi-squared test, *p* = .92).

The subsequent run typically following the escape turn in intact animals was observed on only one occasion with the decapitated animals (Fig. 4). The one run observed was very brief, lasting only four step cycles after the initial turning movements, whereas intact animals usually ran for several seconds. Additionally, in the one run observed in a decapitated animal, interleg coordination was disrupted. Although the legs started off in a tripod, this broke down by the fourth step cycle, when the hind legs were then moving in phase. The interjoint coordination within each individual leg appeared normal. In five trials with decapitated animals, a second type 1 turn was seen approximately 100 ms after the stimulus was applied.

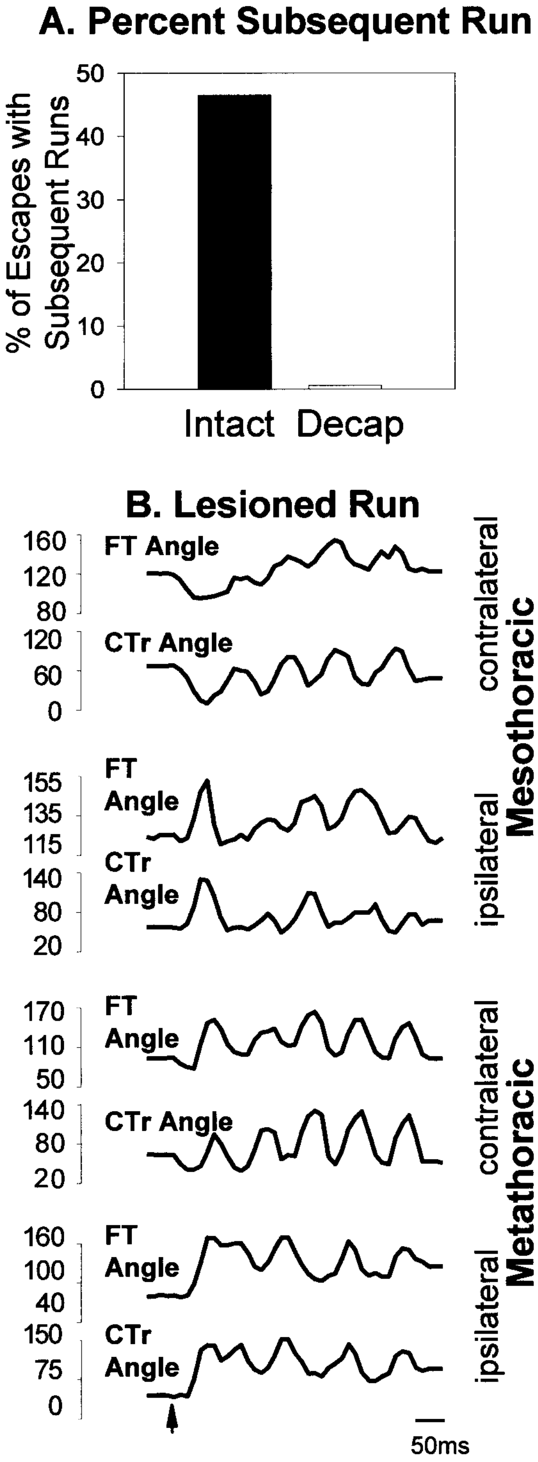

Figure 4 Subsequent runs in decapitated cockroaches. (A) Percentage of escape turns with subsequent runs in cockroaches under intact and decapitated conditions. (B) Metathoracic and mesothoracic kinematics of the one subsequent run evoked under decapitated conditions. There is initially a type 2 escape turn. This is followed by joint angle changes typically associated with running. While the run starts off in a normal tripod, by the fourth (and last) step, the two metathoracic legs are moving in synchrony. Intraleg coordination appears normal; that is, in each leg the FT and CTr joints move in tandem. The arrow indicates when the tactile stimulus was delivered to the pronotum. The angles are in degrees.

Quantitative Analysis of Joint Angle Excursions during Escape Turns

The preceding analysis indicates that the legs moved qualitatively in the appropriate direction after the higher centers were removed. This is perhaps not surprising, given that the known circuitry is in the thoracic and abdominal ganglia. However, it is still possible that joint excursions could be altered quantitatively. Graham (1979) showed that while decerebrate stick insects still showed coordinated walking, there were subtle but significant changes in timing and coordination. Because of this, a more detailed kinematic analysis is warranted. As we seek ultimately to relate behavioral effects to changes in circuitry, we focused on the type 1 response. Effects specific to type 2 responses would likely be due to effects of TI_As preferring wind from the front, and in all of the recordings of TI_As, such a cell has only been recorded once (Westin et al., 1988).

The rear legs display normal joint kinematics without descending inputs from the higher centers. In a type 1 response, the metathoracic legs typically drive the animal forward. We analyzed the changes in metathoracic joint angle in animals pre- and postdecapitation. The joint angle excursions showed no significant changes in excursion between intact and decapitated escape turns (Fig. 5).

Quantitative changes were seen in the mesothoracic legs (Fig. 6). The mesothoracic kinematics typically orient the animal away from the stimulus and also drive it forward. The basic kinematic pattern was maintained after decapitation. However, there were significant reductions in the excursions of the ipsilateral CTr joint ($p = .03$), the ipsilateral FT joint ($p = .02$), and the contralateral CTr joint ($p < .01$). There was no significant change in the contralateral FT joint, though this joint shows a relatively small mean extension and may require a larger sample size to elucidate any significant changes [Fig. 6(D)]. This small mean extension is paradoxical, as typically one sees flexion at this joint. In the majority of trials the joint did flex or remain motionless. However, there were a few cases of large extensions in nondirectional escapes, which produced the small mean extension. Overall, while the basic directionality of the mesothoracic leg joints is unaltered, there is a quantitative effect of decapitation on the joint excursion.

Are these changes restricted to the mesothoracic legs or do they extend to the prothoracic legs? Even in intact animals, the prothoracic kinematics are much more variable than the other two pairs of legs, making measurements of joint kinematics problematic. This variability is due to the extensive movement at the body-coxa (BC) joint that is not seen during the escape turn in the mesothoracic and metathoracic legs (Nye and Ritzmann, 1992). Nevertheless, a casual observation showed that in decapitated animals, the prothoracic legs typically moved little, and often not at all. Sometimes there would be movement at only one joint. Thus, it was possible to assess the changes in prothoracic legs by simply examining the net movement of the tip of the prothoracic tarsi from the beginning to the end of the escape turn, normalizing for the size of the image of the cockroach's body. Figure 7 shows the changes in net movement. The reductions were significant ($p << .01$ for both ipsilateral and contralateral legs).

Thus, a somewhat unexpected gradient of the descending influences on the escape turn emerged. The rear leg kinematics are unaffected, the middle leg kinematics are appropriate in direction but reduced in magnitude, and the front legs move little if at all.

These effects were seen with decapitation, which results in the removal of both the suboesophageal ganglion and the brain. Is the influence distributed to both of these structures or limited only to one? Earlier observations indicated that descending influences from the brain inhibited locomotion, while inputs from the suboesophageal ganglion maintained constant walking (Roeder, 1963). One might then expect that a lesion between the brain and the suboesophageal ganglion would result in a different pattern with no loss of activation in the prothoracic ganglion.

To address this question, we tethered 10 additional animals that had received lesions to the circumoesophageal connectives, and elicited type 1 escape responses. Postmortems were performed to ensure that the connectives had been fully lesioned. Escape turns were still readily elicited, with 19% of the type 1 escapes being nondirectional (not significantly different from intact occurrences; Fisher's Exact, $p = .35$). Neither subsequent runs nor spontaneous locomotion was observed.

The joint kinematics of the mesothoracic and metathoracic legs in the animals with circumoesophageal connective lesions were essentially identical to the decapitated and neck connective lesioned animals. Again, the metathoracic legs showed no significant differences in joint angle excursions with the intact escapes elicited in the other population of animals (Fig. 5), and the mesothoracic legs showed significant reductions in the ipsilateral CTr joint ($p < .01$), ipsilateral FT joint ($p = .04$), and contralateral CTr joint ($p < .01$) compared to the intact escapes (Fig. 6). The prothoracic legs also showed little or no movement, with significant reductions compared to the intact escapes ($p << .01$ for both ipsilateral and contralat-

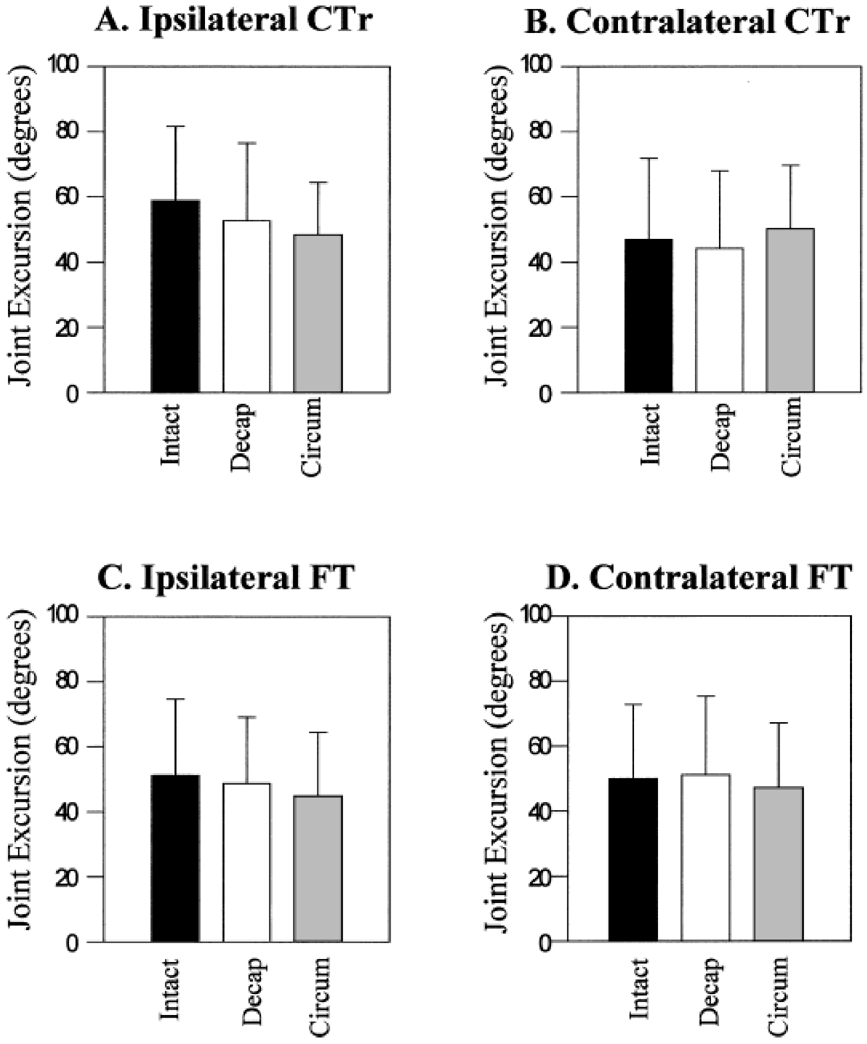

Figure 5 Metathoracic legs of decapitated and circumoesophageal connective lesioned animals move through normal excursions in type 1 escape turns. Metathoracic CTr [(A) and (B)] and FT [(C) and (D)] joint excursion during escape turns of cockroaches under intact and decapitated (Decap) conditions, and in cockroaches with the circumoesophageal connective lesioned (Circum). The error bars indicate one standard deviation. There were no significant differences (ANOVA, $p > .05$) in any of the leg kinematics between the various data sets for a given joint. The number of trials for each bar is as follows: contralateral CTr-intact = 22, decapitated = 30, circumoesophageal = 59; contralateral FT-intact = 22, decapitated = 30, circumoesophageal = 59; ipsilateral CTr-intact = 22, decapitated = 30, circumoesophageal = 59; ipsilateral FT-intact = 22, decapitated = 30, circumoesophageal = 59.

eral legs) (Fig. 7). This suggests that influences from the brain are participating in the observed effects. The data also suggest that the pattern of changes seen is not simply due to disruption of the tracheal system or transection of the gut in the neck. Additionally, this lesion was performed more anteriorly along the nerve cord, yet produced the same effects as decapitation, demonstrating the pattern of effects is not merely due to absolute proximity to the injury.

Motor Pattern

The kinematic changes in the escape turn could result from a decrease in motor activity to the relevant leg muscles or an increase in cocontraction. To investigate this point, we characterized the leg motor activity during the initial escape turn. We initially recorded EMGs of the coxa depressor, extensor tibia, and flexor tibia muscles during tactilely elicited type 1 escape

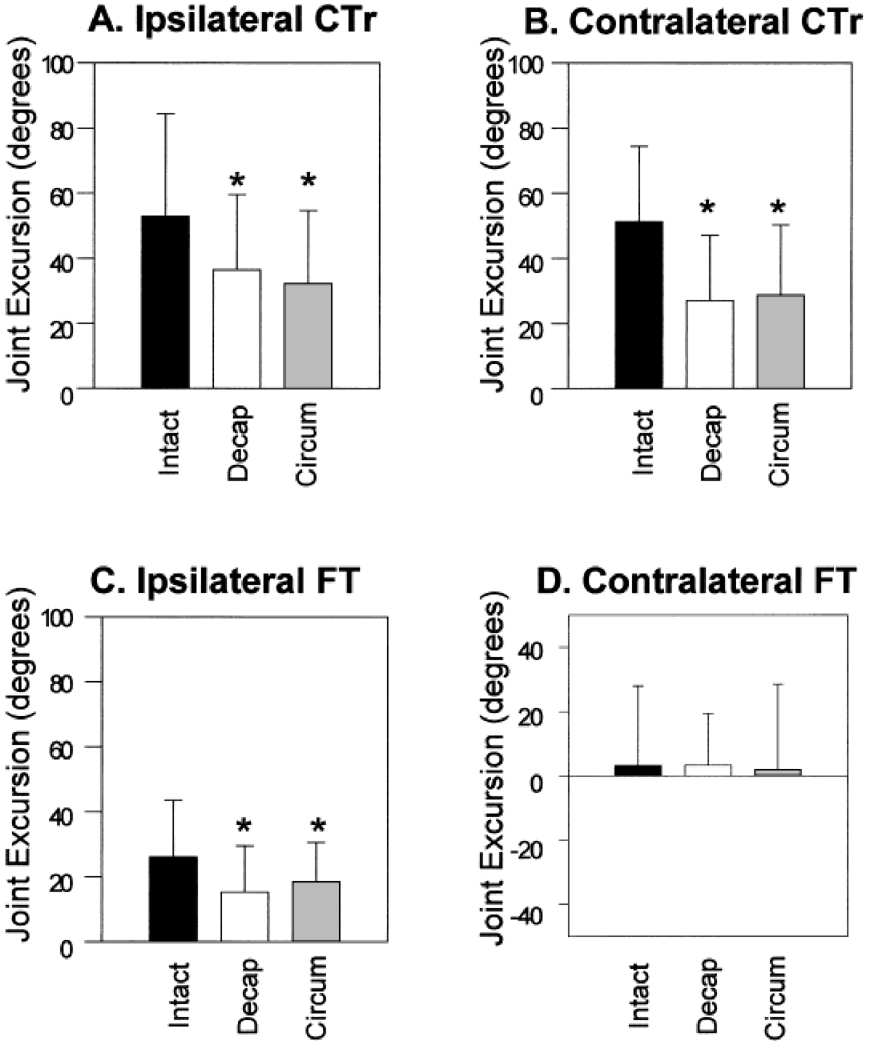

Figure 6 In both decapitated and circumoesophageal connective lesioned animals, the mesothoracic joints move appropriately in type 1 escape turns, but with a reduced excursion. Mesothoracic CTr [(A) and (B)] and FT [(C) and (D)] joint excursion during escape turns of cockroaches as in Figure 5. Positive numbers indicate extension, negative numbers indicate flexion. There were significant differences in excursion between the intact and the two lesioned data sets in the ipsilateral CTr, contralateral CTr, and ipsilateral FT joints (Bonferoni's correction, $p < .05$), as indicated by the asterisks. There were no significant differences in the contralateral FT excursion (ANOVA, $p > .05$). The number of trials for each bar is as follows: contralateral CTr-intact = 22, decapitated = 30, circumoesophageal = 56; contralateral FT-intact = 19, decapitated = 30, circumoesophageal = 56; ipsilateral CTr-intact = 22, decapitated = 30, circumoesophageal = 55; ipsilateral FT-intact = 19, decapitated = 30, circumoesophageal = 55.

responses in tethered animals, and comparisons were made between pre- and postdecapitation. For the metathoracic legs, we recorded the motor activity of the various muscles of interest in eight animals; there were 30 evoked escapes under intact conditions, 21 after decapitation. For the mesothoracic EMGs, there were 33 intact escapes and 42 headless escapes with 20 animals. Prothoracic EMGs were recorded in 13 animals, with 38 escapes elicited while intact, and 45 postdecapitation. Table 1 shows the mean number of fast MN spikes seen in the various muscles of interest in intact and decapitated escape turns.

Figure 8(A) shows typical metathoracic EMG recordings during an intact type 1 response. They are shown along with joint kinematics to link the timing of motor activity to joint movement, and for comparison to previous kinematic data taken from animals with no wires implanted. Ipsilateral and contralateral

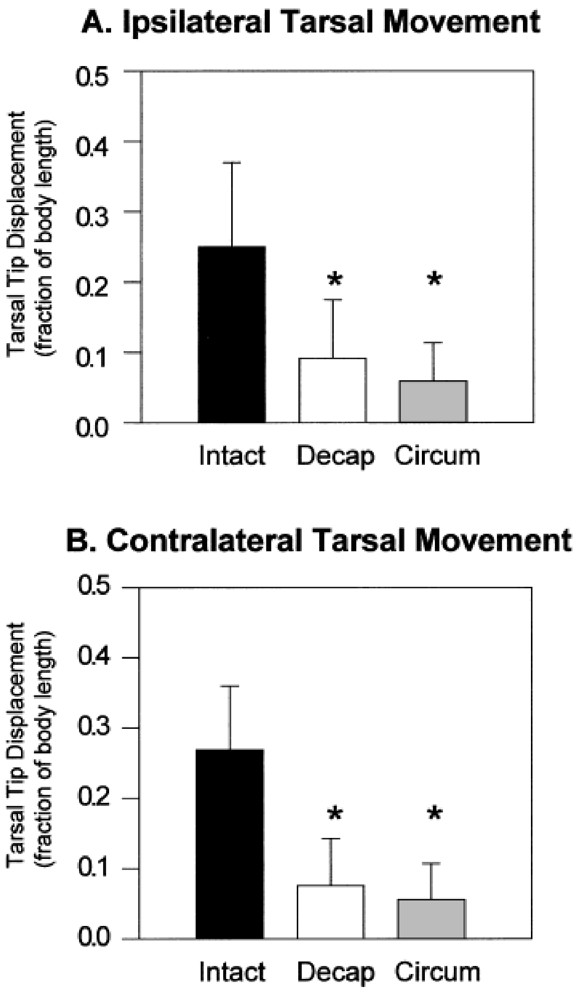

Figure 7 The prothoracic legs in both decapitated and circumoesophageal connective lesioned animals moved little if at all. Ipsilateral (A) and contralateral (B) prothoracic tarsal tip displacement in type 1 escape turns, normalized to the size of the body. There were significant differences in displacement between the intact and the two lesioned data sets in the ipsilateral and contralateral legs (Bonferoni's correction, $p < .05$), as indicated by the asterisks.

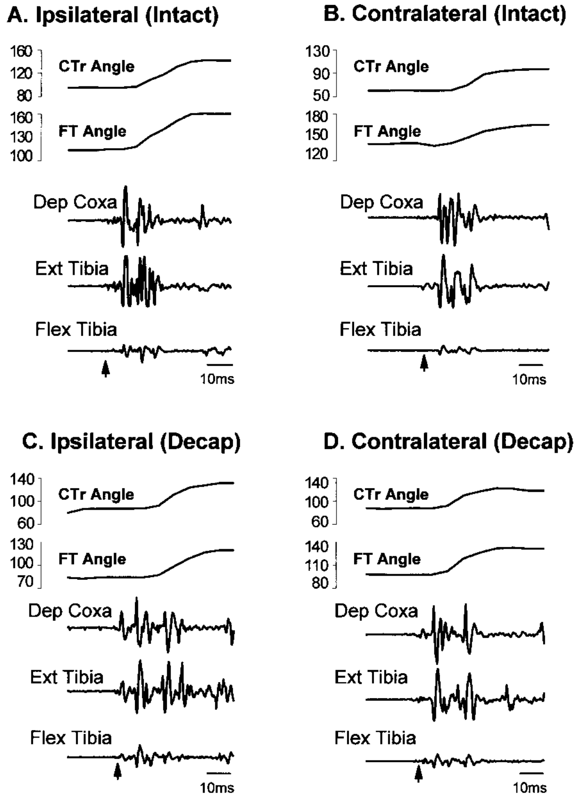

Figure 8 The metathoracic EMGs are similar under intact and decapitated conditions. Examples of kinematics and EMGs of type 1 escape turns in the metathoracic legs under intact [(A) and (B)] and decapitated [(C) and (D)] conditions. There is extension at both CTr and FT joints. Angles are in degrees. Fast EMG activity is seen in the depressor coxa and extensor tibia, but not in the flexor tibia. The arrows indicate when the tactile stimulus was delivered to the abdomen.

legs gave similar results. Slow activity was seen in all joints, while fast activity mirrored the kinematics. That is, there was extension at the CTr joint along

Table 1 Mean (±S.D.) Number of Fast EMG Spikes Recorded in the Various Muscles During Type 1 Escape Turns

	Ipsilateral		Contralateral	
	Intact	Decapitated	Intact	Decapitated
T1 Df	2.4 ± 1.5	0.6 ± 0.7*	1.2 ± 0.9	0.1 ± 0.2*
T2 Df	1.8 ± 1.0	0.4 ± 0.5*	1.6 ± 0.8	0.3 ± 0.5*
T2 FETi	2.0 ± 0.9	1.1 ± 0.6*	0.5 ± 0.9	0.3 ± 0.6
T2 FF	0.0 ± 0.0	0.2 ± 0.6	1.3 ± 1.0	1.5 ± 1.2
T3 Df	1.5 ± 0.7	1.9 ± 0.8	1.8 ± 1.1	1.7 ± 0.8
T3 FETi	1.7 ± 1.3	1.6 ± 0.7	1.8 ± 0.9	2.2 ± 0.9

Significant differences (student's *t*-test, $p < 0.05$) between intact and decapitated conditions are indicated by an asterisk following the decapitated data. A pattern similar to that seen with the kinematics emerges. That is, there are no significant changes in the metathoracic legs, a loss or reduction in fast activity in the mesothoracic legs, and a loss of fast activity in the front legs.

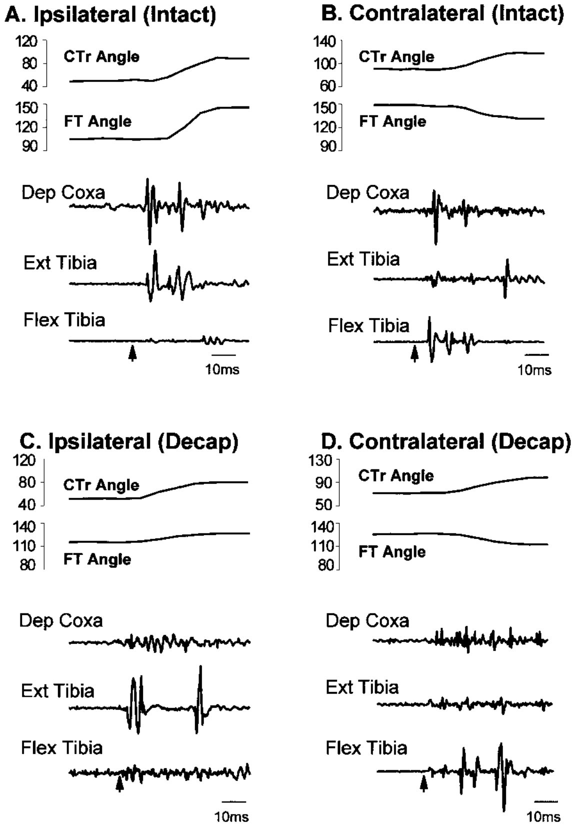

Figure 9 The mesothoracic EMGs exhibit changes in fast activity with decapitation. Examples of kinematics and EMGs of type 1 escape turns in the mesothoracic legs under intact [(A) and (B)] and decapitated [(C) and (D)] conditions. There is extension at both CTr joints and the ipsilateral FT joint, while the contralateral FT joint flexes. Angles are in degrees. For the intact ipsilateral leg (A), fast EMG activity is seen in the depressor coxa and extensor tibia, but not in the flexor tibia. For the contralateral leg (B), fast EMG activity is seen in the depressor coxa and flexor tibia, but not in the extensor tibia. There is a reduction or loss of fast activity under decapitated conditions, especially evident in the depressor coxa records. The arrows indicate when the tactile stimulus was delivered to the abdomen.

with Df firing. There was also extension at the FT joint as FETi was excited. In each of these joints, fast activity occurred at or near the beginning of the initial motor burst, and continued throughout. In contrast, flexor activity was typically limited to slow muscle activity. Following decapitation, the same pattern of EMG activity was observed [Fig. 8(B)]. There were no significant changes in the mean number of fast spikes, which is consistent with the lack of kinematic changes.

Figure 9(A) and (B) shows typical intact kinematics and EMGs from the mesothoracic legs during a type 1 escape turn. Again, slow activity was present in all the muscles, and it typically was more vigorous in the muscles appropriate for the observed motion. Likewise, fast activity was seen predominately in certain muscles consistent with the observed joint movements. Both mesothoracic legs extend at the CTr joint, and both legs showed Df activity. This is consistent with observations made previously by Levi and Camhi (1996) on the motor activation of mesothoracic CTr joints. We extended their observations to the FT joints of those legs. The two mesothoracic legs showed the typical difference in the kinematics of the FT joint. The leg ipsilateral to the stimulus extended at the FT joint, while the contralateral leg flexed at that joint. The ipsilateral leg's mean number of FETi spikes was 2.0 ± 0.9, and the mean number of fast flexors was much lower, at 0.1 ± 0.2. Conversely, the contralateral mesothoracic leg's mean number of FETi spikes was 0.5 ± 0.9, and the mean number of fast flexor spikes was 1.3 ± 1.1. Thus, the mean fast activity in intact animals is consistent with the typical joint kinematics.

In decapitated cockroaches, the decreased excursion of mesothoracic legs was associated with decreases in fast motor neuron activity [Fig. 9(C,D)]. There was no evidence for increased cocontraction in the related EMGs. However, there were significant decreases in the number of Df spikes in both the ipsilateral and contralateral legs ($p < .01$ for both), and in the number FETi spikes for the ipsilateral leg ($p < .01$) (Table 1). Thus, the changes in kinematics seen in the mesothoracic legs can be accounted for by a decrease in the recruitment of fast MNs.

There were a minority of trials (20% of intact trials, 19% of beheaded trials) that exhibited atypical EMG patterns consistent with a nondirectional escape response (Fig. 10). In these trials we recorded more fast extensor spikes than fast flexor spikes in the muscles controlling the FT joint of the contralateral mesothoracic leg. The atypical EMG patterns for these trials were consistent with the observed joint kinematics. That is, in these trials the FT joint of the contralateral mesothoracic leg extended rather than flexed. Thus, all of the joints for all four legs extended to approximately the same degree in a movement that would be consistent with an escape that would drive the animal straight ahead. In contrast, there were no intact trials, and only one beheaded trial, in which the ipsilateral mesothoracic EMG pattern was reversed, i.e., more fast flexors than extensors.

As the greatest behavioral effect was seen in the prothoracic legs, we sought to roughly characterize their EMG pattern, focusing primarily upon the muscles controlling the CTr joint. Extensors and flexors of the tibia were only successfully recorded in three

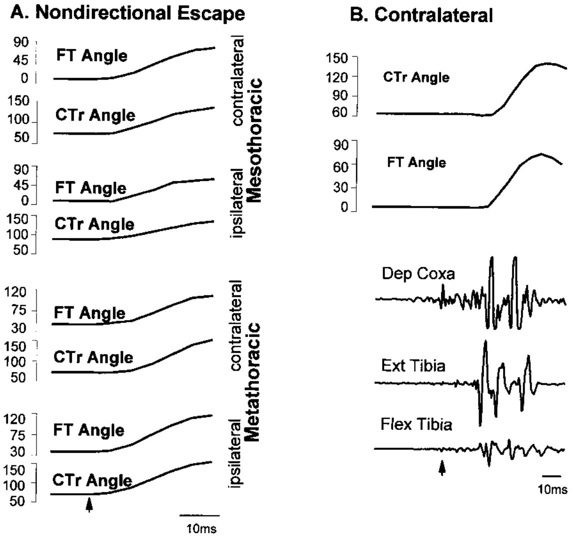

Figure 10 A minority of trials exhibited nondirectional escapes. (A) Example of mesothoracic and metathoracic CTr and FT kinematics in a nondirectional escape of an intact animal. There is extension at both CTr and FT joints in both sets of legs. Note especially the extension at the contralateral mesothoracic FT joint, which normally flexes. Angles are in degrees. (B) An example of the EMGs in the contralateral mesothoracic leg in an intact animal. Consistent with the kinematics, fast EMG activity is seen in the depressor coxa and extensor tibia, but not in the flexor tibia. The arrows indicate when the tactile stimulus was delivered to the abdomen.

animals (six intact trials, eight decapitated). Slow activity was seen in all of the muscles. Not surprisingly, Df spikes were seen in the ipsilateral and contralateral depressor coxa EMGs. However, the latency to Df activation was often much longer than that seen for the other legs. Figure 11(E) is a histogram showing the latencies of the first Df action potential in each pair of legs from the time the mechanical stimulator contacted the abdominal cuticle. The peak of the metathoracic latency distribution occurs at the 4.5 ms bin, the peak of the mesothoracic latency is around 9 ms, and the prothoracic latency distribution shows peaks at 10.5 and 18 ms.

The delay to firing of the Df motor neuron in the prothoracic legs was considerable, particularly in the second peak. While exact three- dimensional characterization of the prothoracic joint kinematics is beyond the scope of this work, we examined the kinematics in some trials in an attempt to account for the extremely long latency of Df activation. Figure 11(A) and (B) shows the escape kinematics and depressor coxa EMG from an ipsilateral and contralateral prothoracic leg. Unlike the other pairs of legs, there is a CTr flexion preceding the joint extension. This change is accompanied by movement at the BC joint as the coxa swings from pointing anteriorly to posteriorly. In contrast to the metathoracic and mesothoracic levators, the prothoracic fast levators were activated in all of the intact escapes in which they were successfully recorded (19 intact trials, 15 decapitated). A typical recording is shown in Figure 11(D). The fast levators fired at the beginning of the escape activity when there was flexion, followed by Df activity. Thus, the unusually long latency for Df activation may be due to an active flexion prior to CTr extension.

Consistent with the changes in kinematics, the motor activity that controls front legs showed dramatic changes with decapitation. The number of Df spikes in prothoracic legs markedly dropped, though bursts of slow activity were still observed in some trials [Fig. 11(C,D)]. This further demonstrates that the leg movements associated with the initial escape turn are primarily due to fast motor neuron activity.

Effects Specific to Nontraumatic Removal of Descending Inputs

There is the possibility that the observed effects of decapitation are the result of the trauma of decapitation instead of a result of simply removing descending neural inputs. To test this possibility, we sought to block the descending inputs without the associated injury. To this end, we decided to utilize an isotonic sucrose solution placed on the nerve cord, which blocks conduction of action potentials. To assure that the sucrose solution was effective, we tested it on the abdominal nerve cord (five preparations). Stimulating and recording extracellular hook electrodes were placed on the cord, and the animal was perfused with saline [Fig. 12(A)]. The intervening well initially contained normal saline. A stimulation was delivered, producing a burst of activity in the cord that was seen on the far side of the well. Then, the intervening well was changed to the isotonic sucrose solution. With the sucrose block in place, stimulation to the cord failed to yield action potentials at the recording electrodes. Upon refilling the intervening well with normal saline, conduction was restored with the same stimulation.

With the efficacy of the sucrose block established, we could use it to reversibly block descending neural inputs. For this test we used a reduced *in situ* preparation that permitted stimulation of the abdominal nerve cord while recording from the 5r1 nerves in the metathoracic and prothoracic legs (containing only Df, Ds, and the common inhibitor neuron; Pearson

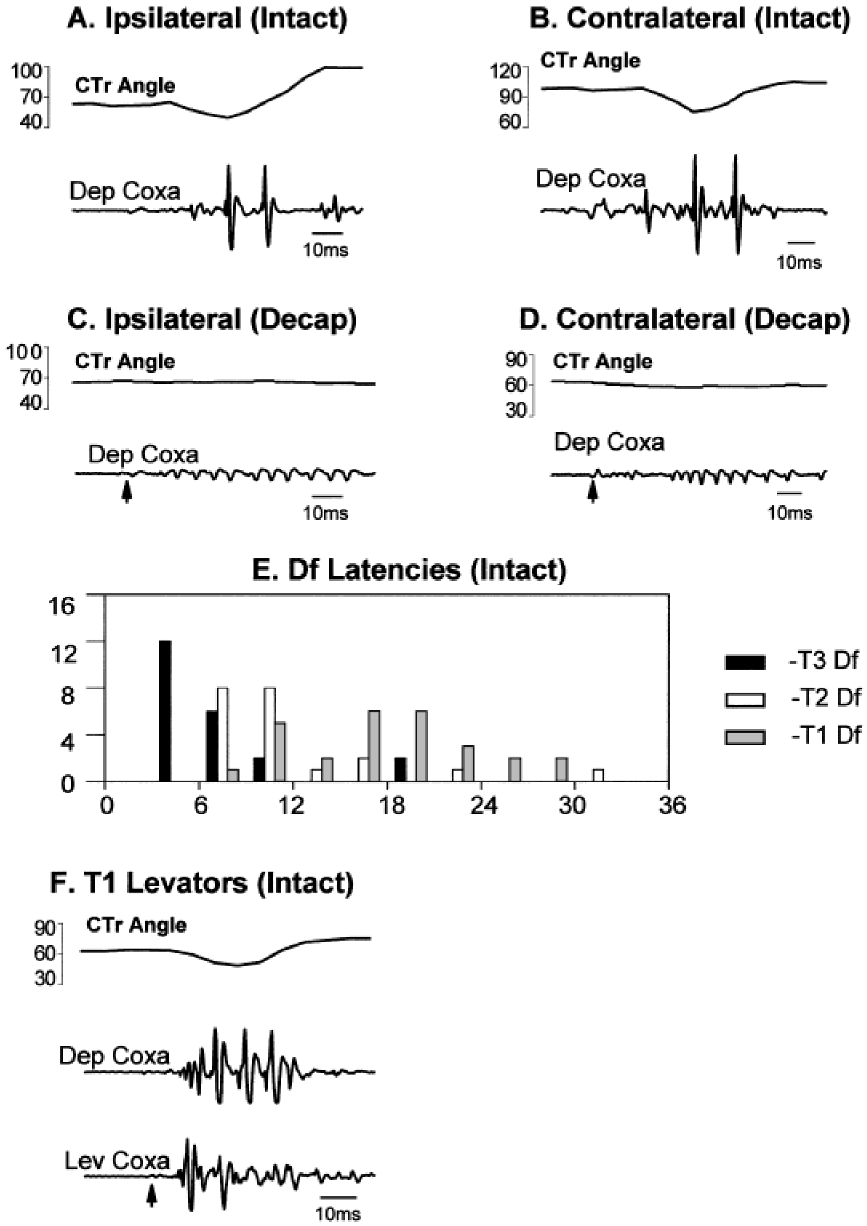

Figure 11 The prothoracic legs show complex type 1 escape CTr kinematics. Examples of prothoracic CTr kinematics and EMGs [(A) and (B)]. The kinematics show both extension and flexion of the CTr joint during the same turn. Df activity is present. Under decapitated conditions [(C) and (D)], movement is not seen and Df activity is absent. (E) A histogram shows that the prothoracic Df activity often exhibits a surprisingly long latency compared to mesothoracic and metathoracic Df activity. (F) The longer latency and initial flexion may be accounted for by initial fast levator activity. All angles are in degrees. The arrows indicate when the tactile stimulus was delivered to the abdomen.

and Iles, 1971). A well was created in the neck to create the block of the cervical connectives ($n = 2$).

With the normal saline in the neck well, the abdominal cord stimulation at a level sufficient to stimulate vGIs and other axons activated Df in the nerve roots. The saline in the neck well was then replaced with the isotonic sucrose solution and the abdominal nerve cord was stimulated at the same level, again generating activity in GIs and other interneurons. Df activity was still seen in the metathoracic 5r1 recording, but was abolished in the prothoracic recording. Thus, blocking conduction to and from the head gan-

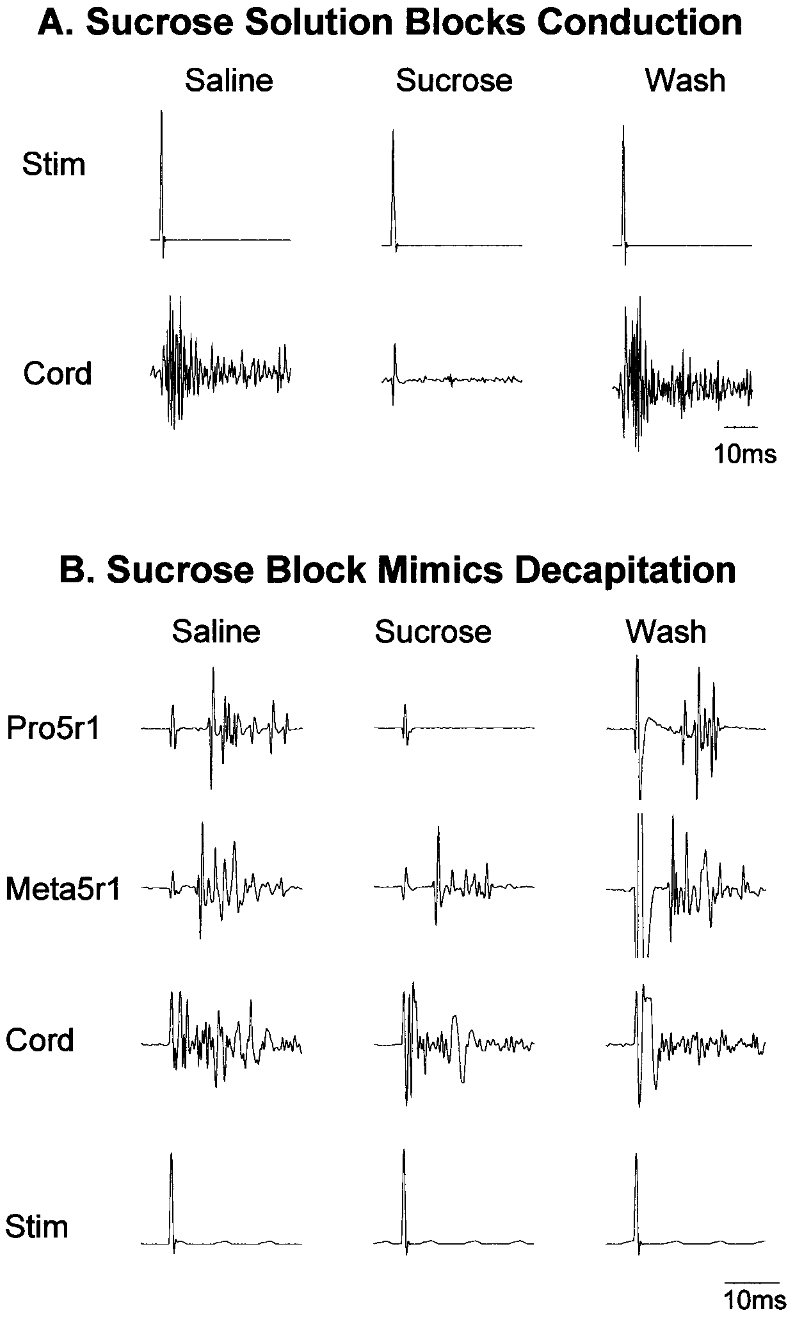

Figure 12 Blocking descending neural inputs mimics decapitation. (A) A sucrose solution blocks conduction of evoked activity along the ventral nerve cord. Stimulating and recording electrodes are placed on the cord, and between them a well is inserted. A brief stimulus delivered to the cord evokes activity recorded on the far side of the well when the intervening well contains saline. If the intervening well is filled with an isotonic sucrose solution, activity evoked by the same stimulus does not reach the electrode past the well. The block is fully reversible when the well is refilled with normal saline. (B) The same well is placed on the neck connectives, which would not directly interfere with transmission through the escape circuit. If filled with normal saline, a brief shock to the ventral nerve cord elicits GI and other activity, producing one Df and several Ds action potentials in the prothoracic and metathoracic 5r1 nerves. If the well is filled with sucrose, after 2 min the same stimulus evokes similar activity in the metathoracic nerve root, but not in the prothoracic, similar to what is seen with the decapitated EMGs. The recording in the nerve cord is unaffected by the sucrose block, because it is well posterior to the site of the well. This effect is fully reversible.

glia and the rest of the nervous system produced results consistent with decapitation on the EMG motor pattern. Upon returning normal saline to the neck well, Df activation was restored to the prothoracic nerves [Fig. 12(B)]. Therefore, the effect of blocking descending inputs was reversible. These data support the claim that the observed effects of decapitation on the escape system are due to removal of descending inputs, and not a result of a more general response to trauma. Additionally, the data demonstrate that the detected descending influences act via neural inputs and not neurohormone release from the various neurosecretory regions in the brain and suboesophageal ganglion.

DISCUSSION

Data presented in this paper demonstrate the importance of descending neural influences on the escape behavior and its related motor pattern in the cockroach. The changes we observed demonstrate that there is a descending influence on the thoracic escape circuitry, and thus, the higher centers are important for producing normal escape responses. However, the thoracic circuitry absent higher centers still produces directionally appropriate escape turns, refuting the notion that information must first ascend to the brain and then descend back to the thoracic ganglia to initiate an escape turn (Burrows, 1996). This also supports the hypothesis that directionally specific neurons in the thoracic ganglia control the directionality of the escape turn (Ritzmann, 1993; Ritzmann and Eaton, 1997).

We observed an interesting pattern of kinematic changes with removal of higher centers: the rear legs were unaffected, the middle legs exhibited a quantitative reduction in excursion, and the front legs were qualitatively altered, showing little if any movement. Thus, there is a front to back "gradient of changes." A similar pattern is seen in decerebrate or spinal cats trained to walk on a treadmill. Their rear legs participate in walking, but not their front legs (Rossignol, 1996). Additionally, cortical neurons have been shown to specifically affect the foreleg kinematics in cats (Drew, 1993) and arm movements in apes (Georgopoulos et al., 1988). Therefore, a close association between descending influences and motor control of the most rostral appendages has been observed in a wide range of phylogenetically distinct systems.

The loss of or reduction in movement in the middle and front legs was accompanied by a loss of or reduction in fast MN activity. This suggests a net loss of excitability within the circuitry. However, the front legs retained the ability to move vigorously during searching, righting, and occasionally during uncoordinated locomotion. This, in turn, suggests that such alterations to excitability may be specific to the escape circuitry.

What are the likely targets of the descending inputs within the escape circuitry? The fact that the metathoracic legs move appropriately suggest that the conducting interneurons are carrying the signal normally. This notion is supported by the observation that in two cases where the excitability of the escape system is decreased via descending inputs [quiescent roaches (Watson and Ritzmann, 1994) and those stung by the wasp *A. compressa* (Fouad et al., 1996)], the vGIs fire normally. That intraleg coordination is still intact and other legged behaviors are affected differentially suggests that the observed changes are not due to alteration of local circuitry for each leg. Additionally, descending neurons typically interact with thoracic interneurons as opposed to MNs (Strausfeld et al., 1984; Tryer et al., 1988; Gronenberg and Strausfeld, 1990; Hensler, 1992; Roth et al., 1994). A population of thoracic interneurons, the $\mathrm{TI_A}$s, is thought to be the multimodal locus of control of the escape response. They integrate sensorimotor information and then contribute to the decision of whether or not to escape (Ritzmann, 1993; Ritzmann and Eaton, 1997). Therefore, the $\mathrm{TI_A}$s make a reasonable target for the initial examination of neural correlates of these behavioral changes.

Comparison to Previously Reported Escape Movements

The leg movements associated with escape turning have been well documented previously, and our data on intact animals were consistent with those reports (Camhi and Levy, 1988; Nye and Ritzmann, 1992; Schaefer et al., 1994). The leg movements are grouped into two categories, called type 1 and 2 turns. Both involve extension of the rear and middle CTr and FT joints on the side ipsilateral to stimulation. In type 1 turns the contralateral rear joints also extend, as does the CTr joint on the contralateral mesothoracic leg. However, the contralateral, mesothoracic FT joint flexes to pull the animal away from the threat. In type 2 turns, which are generated by stimulation from the front of the animal, the contralateral CTr joints flex to enhance body rotation.

In both lesioned and intact animals, we observed some atypical type 1 escapes where the contralateral FT joint extended instead of flexed. This would likely produce a forward escape. Directionality could still be provided by differences in the excursion of the two FT joints. That is, a small contralateral extension coupled with a large ipsilateral FT extension would still turn the animal away from the threat. This observation is still consistent with previous data sets. Nye and Ritzmann (1992) also observed cases of contralateral FT joint extension of the mesothoracic leg when stimulating with wind. Because contralateral FT joint movements are typically small, a slight difference in the number of these extension movements can determine whether the mean value of a number of trials indicates an overall flexion or extension of the FT joint. In our data, the mean indicated slight extension, while Nye and Ritzmann (1992) reported slight flexion. In fact, the distribution of individual movements was actually very similar.

Additionally, the data clearly show the importance of fast MN activity in the escape turn, extending Levi and Camhi's (1996) finding of the importance of fast activity to additional legs and joints, including the mesothoracic FT joints. This observation is important, because actions of the mesothoracic FT joint play a major role in determining the left-right direction of the escape turn (Nye and Ritzmann, 1992). Slow activity by itself typically was not sufficient to produce the rapid joint movements associated with escape.

Previous Examinations of Decapitated Cockroaches

Our observations of free-ranging decapitated cockroaches are consistent with the observations of Roeder (1963) and Zill (1986). They are also consistent with sparser descriptions provided by other researchers, which note loss of walking and coordination, yet normal grooming (Reingold and Camhi, 1977; Pringle, 1940; Keegan and Comer, 1993). In terms of escape behavior, previous workers observed that decapitated animals "escaped" directionally via jumps (Roeder, 1963; Hughes, 1965; Keegan and Comer, 1993). We determined these jumps to be bona fide type 1 escape turns without the subsequent run.

There are some contradictions with the literature. Libersat et al. (1999) claimed that cockroaches with their brain removed but the suboesophageal ganglion intact exhibited spontaneous locomotion and escape turns with subsequent runs that were significantly slower than normal. This is in contrast to our observations that animals with lesioned circumoesophageal connectives did not display coordinated locomotion, nor did they run subsequent to escape turns. There was a difference in the timing of testing relative to surgery. Libersat et al. (1999) tested the animals 1 day after surgery, whereas we tested within an hour after the lesioning. Thus, the animals Libersat et al. (1999) examined would have had more time to recover from surgical trauma. We were less concerned about this effect in our studies, because the effects that we observed on the escape motor pattern with decapitation were reproduced using the minimally traumatic sucrose block technique. Thus, we were confident that trauma was not producing the observed changes associated with the escape turn. It is possible that the extra time for recovery would increase the incidence of running subsequent to the escape turn. Because the influence of suboesophageal ganglion versus brain centers on walking was not the primary focus of our study, we did not further pursue that possibility.

Loading might also be a factor. Libersat's group tethered animals by pinning them through the tip of their abdomens, whereas we suspended animals from their dorsal cuticle. Therefore, our animals were not supporting their own weight, while theirs were. Loading is important in controlling the force generated during stance (Pearson, 1972; Pearson and Iles, 1973; Bässler and Büschges, 1998). Decreased loading may then decrease the motor drive in running, which would be compounded with loss of descending inputs.

We should note that the use of reversible blocking techniques to uncover descending control with minimal trauma has been done previously. Thompson (1986) used a cold block technique to remove descending inhibition to the pattern generation circuitry that controls oviposition movements in the locust.

Other Behaviors of Decapitated Cockroaches

Removing descending inputs had varying effects upon different behaviors. In general, behaviors that are not thought to rely upon the higher centers, such as righting and grooming, were minimally affected (Zill, 1986; Berkowitz and Laurent, 1996), while those that are known to rely on input from higher centers, such as posture and locomotion, were profoundly affected (Kien, 1990a,b; Bohm and Schildberger, 1992; Horak and Macpherson, 1996). Across behaviors, interleg coordination was disrupted, though intraleg coordination seemed less affected. Also, movements involving changes in load, such as walking, may be more profoundly altered than behaviors such as searching and grooming in which the legs are typically unloaded.

It is perhaps surprising that the recognizable, coordinated escape turns were easily evoked in decapitated animals, whereas other behaviors involving interleg coordination, such as running, were profoundly disrupted. Both are locally controlled by thoracic circuitry (Fourtner, 1976; Pearson, 1976; Ritzmann, 1993; Ritzmann and Eaton, 1997). However, the interleg coordination associated with escape may be achieved in a fundamentally different manner from that associated with walking. Walking is an ongoing behavior that involves a complex interaction of pattern generation and sensory input between legs (Cruse, 1990). Thus, the coordination is at the motor or premotor level. In addition, walking likely requires the capacity for interaction with descending inputs in order to generate turns and climbing movements as dictated by anterior sensory structures and computational regions (Watson et al., 1998). So, for running and walking, loss of those inputs can be a serious disruption. In contrast, the escape turn is more reflexive and the coordination that occurs may well happen simply because of the projection of the TI_As to adjacent ganglia. Therefore, this simpler coordination in the escape system relative to walking might explain the difference in the effect of removing descending inputs.

Our data does suggest that descending commands are very important to the subsequent run that typically follows the escape turn. The effect seen on escape related running is consistent with previously observed disruptions of walking in locusts (Kien, 1990a,b), crickets (Bohm and Schildberger, 1992), mantids (Roeder, 1963), fruit flies (Strauss and Heisenberg, 1993), and cats (Whelan, 1996) upon lesioning descending pathways. Similarly, Zill (1986) found the locomotory EMG pattern in decapitated cockroaches to be highly uncoordinated. It would seem that the ascending signal is almost never sufficient to produce coordinated gaits, and that descending inputs are key to producing coordinated locomotion. However, the fact that on at least one occasion a brief tripod run was produced in a decapitated animal shows that the higher centers are not necessary for generation of this gait.

Brain versus Suboesophageal Ganglion

Decapitation removes both the brain and the suboesophageal ganglion. The effects that we report on the escape turn cannot be attributed solely to neurons in the suboesophageal ganglion. The observed deficits were also found by lesioning the circumoesophageal connective, thereby leaving the suboesophageal ganglion intact and connected to the thoracic ganglia. This is perhaps not surprising given the complex spatial, sensory-motor integration, and associative and coordination functions ascribed to brain regions in cockroaches and other insects (Homberg et al., 1989; Strauss and Heisenberg, 1993; Muller et al., 1997; Strausfeld et al., 1998; Heisenberg, 1998; Mizunami et al., 1998a,b; Ehmer and Hoy, 2000), and the role of brain neurons ascribed to other legged behaviors in insects as well as vertebrates (Kien and Williams, 1983; Kien and Altman, 1984, 1992; Ramirez, 1988; Reichert and Rowell, 1986; Bohm and Schildberger, 1992; Horseman et al., 1997; Strausfeld et al., 1984; Gronenberg, 1990; Strauss and Heisenberg, 1993; Whelan, 1996; Grillner et al., 1997).

Although our data demonstrate that the brain is essential for a normal escape response, they should not be taken to suggest that the suboesophageal ganglion is not playing an important role. Most of the neurons descending directly from the brain send collaterals to the suboesophageal ganglion. This parallel descending pathway is thought to relay information about the overall level of activity coming from the brain (Kien and Williams, 1983; Strausfeld et al., 1984; Altman and Kien, 1987; Kien and Altman, 1992). Additionally, some brain descending neurons terminate in the suboesophageal ganglion, where they relay their signal to suboesophageal descending cells (Kien and Altman, 1984; Altman and Kien, 1987; Kien et al., 1990; Roth et al., 1994). Thus, it is possible that the proximate control resides in the suboesophageal ganglion, with the ultimate source being the brain.

General Remarks

Many if not most studies that have sought to understand the neural control of legged behaviors have focused upon local control circuitry. Such work has greatly advanced our understanding of the field. However, factors beyond local circuitry can be of great import as well. Legged locomotion evolved to allow animals to traverse complex terrain, and they do it better than any manmade vehicle (Ritzmann et al., 2000). Although animals that have experienced decapitation, spinal section, or cervical lesions can produce rudimentary walking movements, deficits are certainly apparent (Zill, 1986; Kien, 1990a,b; Rossignol, 1996; Whelan, 1996). We demonstrated that even in a ballistic, reflexive movement like the escape turn, descending influences have a significant effect. Just as a complete understanding of rhythmic movements such as flying or running must take into account the role of sensory input (Pearson et al., 1983), a full understanding of locomotion must take into account the role played by descending influences. These roles may be tonic, as is probably the case in escape, or they may provide directional or postural adjustment.

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