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In vivo neural stimulation for locomotion control of cockroaches

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ABSTRACT

We demonstrated that a controlled locomotory response in American cockroaches (*Periplaneta americana* L,) can be elicited using an electrical stimulation directed toward the thoracic ganglia. This was done on a tracking apparatus where the cockroach's walking trajectory corresponding to electrical signal was recorded. Walk and turn initiation was achieved by directly stimulating the lateral regions of the prothoracic ganglion. We characterized the turning behavior and endurance to stimulation which were evaluated against the input parameters such as voltage and frequency. It was found that the frequency had a more dominant role in steering a roach than the input voltage. The response endurance can be significantly enhanced by giving consecutive stimulation at proper time intervals.

KEYWORDS: neural stimulation, american cockroach, locomotion control

INTRODUCTION

The possibility of manipulating the behavior of an organism through direct electrical stimulation of its neural system has been of great interest [1-3]. Locomotion in insects has been largely studied and it has served as a biological model for neurological research [4-9]. In engineering, controlling locomotion in insects by using electrical input not only benefits the studies of mechanical robots [10, 11], but being able to control insects can also serve as courier to locations unreachable by human beings.

The insect's neural system is many orders of magnitude simpler than that of many mammals [12]. With the small number of motorneurons involved in insect locomotion, electrically stimulating the neurons responsible for rhythmic activity patterns seems to be a promising approach for manipulating the insect's locomotion. Further, the American cockroaches live as adults for about one year and they are one of the few insects that can be commonly found throughout the world's populated regions. They are easy to rear and to handle. Cockroaches are cursorial insects which attest for a maximum sustainable stride frequency with their well engineered body structures [13]. These characteristics make American cockroaches efficient subjects that are potentially unique as a platform for deployment purpose.

An insect's motor behavior is controlled by a system of nerve centers (ganglia) that are located in each segment of the body [14-16]. In 1970, Pearson has first described the neural mechanisms underlying the rhythmic motor output. He confirmed the connections and the functions of the levator

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motoneurons and depressor motoneurons in the metathoracic ganglion of American Cockroach. Bursting interneurons excite the levator motoneurons while simultaneously inhibiting the depressor motoneurons [17, 18]. Later work further supported the assumption that a collection of neurons is directly responsible for generating and maintaining the rhythm of locomotion in a variety of insects [19]. The coordination mechanisms during normal walking of stick-like insects rely upon the centrally coupled burst-generating systems in each segment of the thorax [20, 21]. The model proposed to explain the leg movements in walking cockroach and also suggested a mutual coupling between levator burst-generating systems in the ipsilateral legs [20]. Previous studies in the American cockroach (*Periplaneta americana*) have shown a relationship between the orientation angle of the antennae and the direction of the insect's locomotion [22]. Tactile and electrical stimulation of the antenna has also provided some directional control of locomotion [12, 23]. However, the sensory antennae of the head, while capable of influencing the direction of the insect, are unlikely to be directly involved in the production of locomotion.

The neural circuitries, which control the initiation of movement, have been well studied in cockroaches. Tactile and wing stimulus of receptor can lead to oriented escape output from the thoracic ganglia via giant interneurons [24, 25]. We reasoned that electrical stimulation of the thoracic ganglia might therefore be more efficient in manipulating the walking behavior of insects. It is desirable to evaluate the effectiveness of stimulating and manipulating movement in a quantitative manner.

In the present research, we develop a methodology for the direct control of an American cockroach by a simple stimulating protocol. We have attempted to initiate the turns by giving asymmetric electrical stimulus to the prothoracic ganglion. We characterized the success rates and the behavioral output of the cockroach elicited by electrical input. The effect of electrical stimulation on locomotion and endurance of American Cockroaches was also studied. Here we identify parameters that are most effective in the control of the insect movement.

MATERIALS AND METHODS

Insect and preparation

Adult cockroaches (*P. americana*) were used for this study, and were reared in our laboratory. Colonies were fed and kept in the same environment as described earlier [26]. Our initial experiment focused on effectively triggering the turning behavior of these cockroaches. Influence on movement of each thoracic ganglion was tested through electrical stimulation. The empirical results showed that stimulating the prothoracic ganglion resulted in turning behavior while stimulating the meso- and meta-thoracic ganglion resulted in a more anterior-posterior movement. Preliminary tests done in our laboratory showed that applying electrical impulses in internal regions of the roach's body, but not directly in or close to the thoracic ganglia, either resulted in no movement or erratic movements of the legs. In this paper, the study of locomotion response to electrical stimulation focuses on stimulating the first thoracic ganglion.

Prior to the experiments, the insect was anesthetized by carbon dioxide and fixed to a plastic plate by gluing the pronotum. The antennae of American cockroach serve as a sensory organ, which are innervated by different receptors [27]. The tactile cue gather by the antennae have a clear influence in the locomotion of the American cockroach [28]. The antennae were thus amputated prior to the experiment. This was done in order to ensure that the locomotory response was only affected by the electrical stimulus. A pair of copper wires (Ø 150 μr each) attached to each other were used as the electrode. A small pinprick was made using acupuncture needles (40 gauges) at the prosternum near the femur of front legs. The copper electrodes were then inserted through the puncture to reach the ganglion. The relative locations of electrodes and ganglion are shown on a micro CT scan images (Fig. 1). The center of the bright light indicates the position of the close-paired electrode. Although the scattering and noise due to the low optical transmittance of the copper electrode cast a shadow near the position of ganglion, we were still able to confirm that the electrode site is within the periphery of the ganglion. The insect was kept on the tracking apparatus an hour prior to the stimulation to recover from the surgery. Only the insects which performed normal walking rhythm (forward, turning) after the surgery were tested. This indicates that the insect was accustomed to the tracking apparatus and the implanted electrodes.

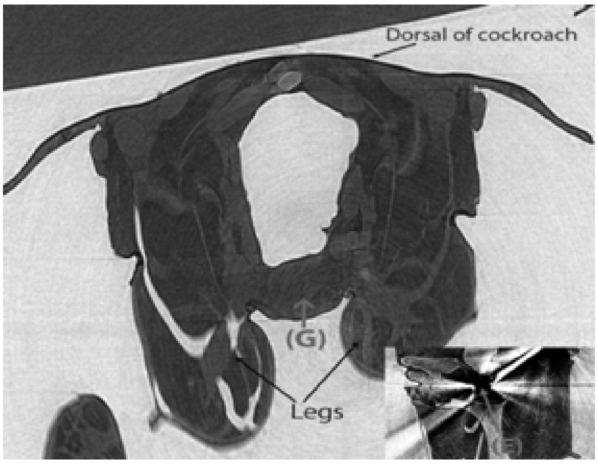

Fig. 1. Micro CT image. The image represents the cross section view of cockroach's thorax (the image is the superposition of 9 images in which the thickness is 9x3600 nm). Point G indicates the position of ganglion, where point E indicates the position of implanted copper electrodes.

Tracking ball setup

A tracking apparatus was used to monitor and record the locomotor response of the cockroach to electrical stimulation (Fig. 2). A tethered American cockroach was mounted on a light-weight styro-foam ball 10 cm in diameter which rests on top of large tube (10.2 cm in diameter). A plastic plate was glued to the pronotum to hold the cockroach in place. The plate was connected to the positional manipulator to center the cockroach's position to the ball. An optical mouse mounted in the inner tube (6 cm in diameter) was placed underneath the ball to monitor the movement of the ball. The ball was suspended on a cushion of air provided by a small fan, which was adjusted to provide the ball with friction-free movement. The bottom of inner tube was sealed only allowing the air stream to flow in between outer and inner tubes. Straws were placed between the tubes to ensure flotation of the ball on a smooth, and laminar flow of air. The optical mouse recorded the trajectory movements of the sphere in the opposite direction of the cockroach's movements. The recorded information

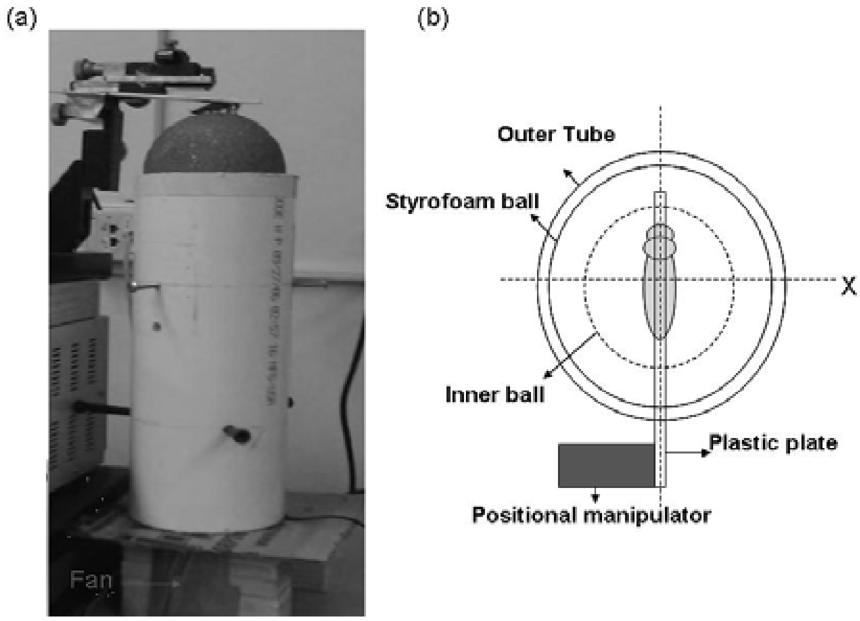

Fig. 2. Tracking apparatus. (2a) Experimental apparatus of tethered American cockroach on the styro-foam ball. (2b) Top view of the experimental setup. The cockroach was tethered to the plastic plate which is connected to a positional manipulator to center the insect to the sphere.

was decoded by a Linux system in a resolution of 1 mm/incr and returned the absolute position along the trajectory, which can be plotted in X-Y coordinates. The summation of each recorded trajectory displacement represents the movement of the sphere (Fig. 3). The mirror image of the sphere movement therefore represents the walking trajectory of the insect. The actual trace of insect was linearly fit using trend line to determine the angular turning tendency.

Signal generator

The electrical stimulation was directly driven by a computer connected with a USB high-performance data acquisition device (National Instrument, USB-6229). The electrical input frequency was preset in the range of 1HZ~80HZ. The voltage was varied between 1 and 8 volts. Positive potential pulses of rectangular signal with pulse duration at 1 ms were used during stimulation. Electrical input signals were controlled through the Labview program interface. Through the Labview program,

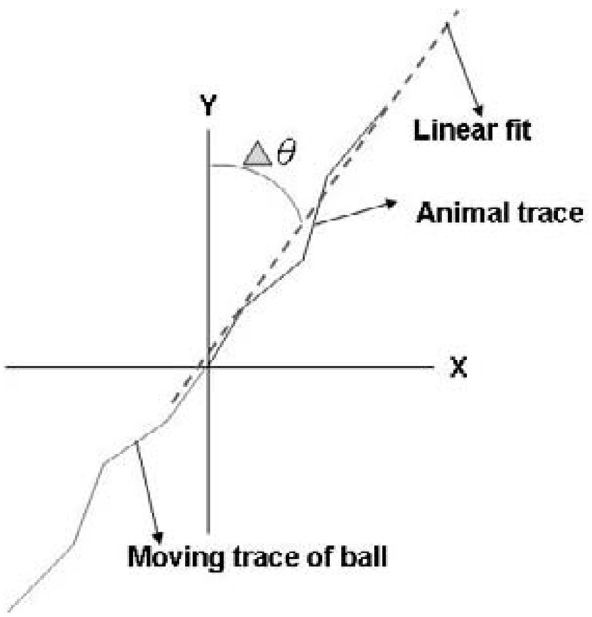

Fig. 3. Method for analyzing insect's moving trajectory. The summation of every recorded ball displacement represents the overall moving trajectory of the sphere. The mirror image of sphere's moving trace represents the insect's moving trace. The overall insect's moving trajectory was linearly fitted and the deviation to the y-axis was converted to θ, which represents the insect's turning angle.

the input electrical stimuli can be equally and consistently alternated between left and right side of the ganglion.

RESULTS

The stimulation was applied to the insect, which showed no sign of moving behavior, to initiate the walk and turn. All tests were performed in a dark room. The asymmetric electrical potential pulses reproducibly generated walking and turning behavior of tethered American Cockroach with a success rate of 72%. Typical tracking curves are shown in Fig. 4. It was found that the turn could be elicited by 1V, 5Hz potential pulses applied to either left or right side of the prothoracic ganglion. The insect turned in an opposite direction to the stimulated side. Median walking duration in response to the asymmetric electrical stimulus was 62.4 sec in a range from 17-240 seconds. Given the initial data of an insect's turning behavior in response to the electrical stimulation, we extended the study to quantify the turning behavior under different electrical signal input. The walking endurance measurements were also performed to test the response duration of insect to the electrical stimulation.

Turning behavior

In the following series of experiments, the turning angle of the cockroach to the stimulation was measured under varied frequencies and voltages. The experiments were terminated, and the trace recorded, when the cockroach stopped walking. The turning tendency of the cockroaches were derived by fitting the trace with a straight line where the slopes were converted to the amount of deviation to the Y-axis (θ). The value for each stimulation parameter was selected for repeatability: 20 tested results in which the insects were successfully triggered to initiate walking behavior by stimulation were used.

Results derived from stimulation in left side of prothoracic ganglion under 2V input voltage with varied input frequency are shown in Fig. 5. The turning tendency increases while the input frequency is increased. While above 10Hz, the increasing rate reaches a plateau at 20Hz input frequency. Likewise, when the stimulation was applied to the right side of the ganglion, the cockroach went toward the left.

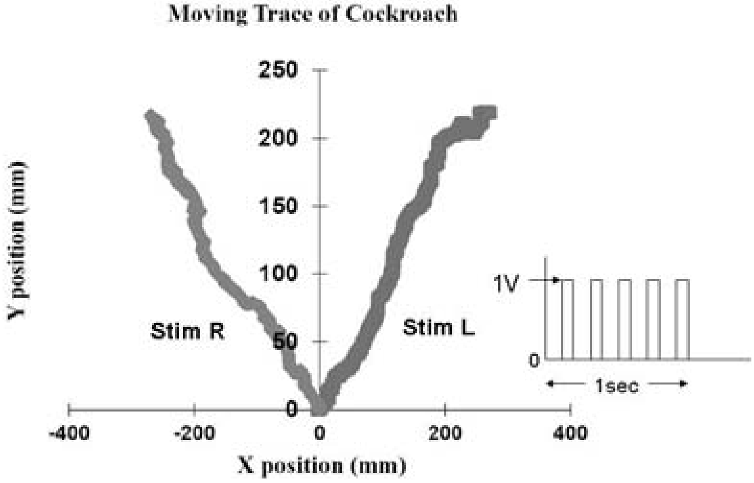

Fig. 4. Moving trajectory of Cockroach under 1V, 5Hz asymmetric electrical input applied to the pro-thoracic ganglion. The insect turned against the stimulated side (i.e. Left side stimulation results in right turn of insect and vice versa).

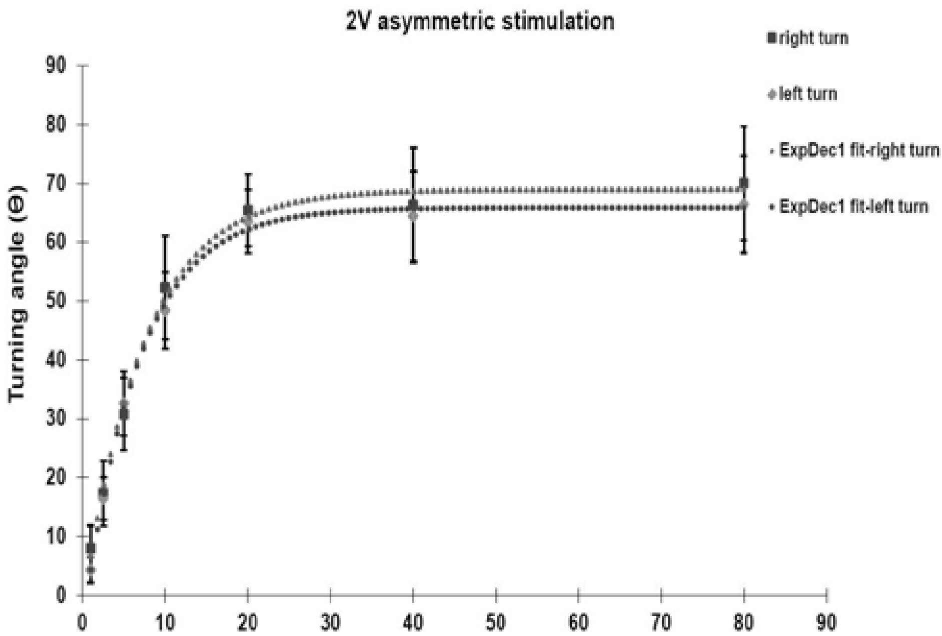

Fig. 5. Turning tendency of insect as the result of 2V input signal to the prothoracic ganglion with different input frequencies. Each median value and standard deviation (error bar) was delivered by 20 tested subjects. Most notably, the turning tendency reaches an asymptotic value after input frequency was increased to 20Hz for left and right side asymmetric stimulation. The fitting curve was generated by Expdec1 model (Origin8).

The turning tendency also reached a plateau at 20Hz (Fig. 5). No further turning was found even when the input frequency reached 80Hz for either left or right asymmetric stimulation. The results for left and right side of stimulation show similar turning behavior. The effects of varied input voltages at fixed frequency to the turning behavior were also investigated. Two input frequencies were chosen - 20Hz and 10Hz- and stimulation was applied to the left prothoracic ganglion (Fig. 6). The input voltages were set from 1V-8V. At 1V, the effect of input voltage is less significant. The turning tendency becomes more diverse when the input voltage increased to 2V. The stimulation effect starts to show similar increasing trend at 2V for both input frequencies.

Endurance behavior

For response endurance tests, two sets of close-paired copper electrodes were placed near the left and right side of the prothoracic ganglion. The electrical input was equally and repeatedly alternated between left and right electrode with different given time intervals (Fig. 7). The input signal at each close-paired electrode is exactly out of phase to each other. The schematic walking trace shown in Fig. 7 represents the corresponding turn of insect to the alternating stimulation signal. Ensuring no further locomotory responses were observed, the stimulation was terminated 40 seconds after the insect stopped walking. The walking duration (time in sec) and trace (X-Y coordinate) in response to the stimulation were recorded. As in the turning test, only the insect with movements initiated by electrical stimulation were used to monitor the responding endurance. Each parameter was conducted 30 times for repeatability.

The walking traces in different alternating given time intervals under 8V-20Hz electrical input signal are shown in Fig. 8. Series of electrical pulses alternated between the left and right side of ganglion (Fig. 7) resulting in the corresponding turning direction of the insect (i.e. left stimulation results in turning right and vice versa). The zigzag patterns shown in Fig. 8 (5 and 10 sec given time interval) represent the insect's corresponding turning response to the alternated stimuli. This indicates the controllability of insect's movements through alternating the stimuli between left and right side of prothoracic ganglion. However, increasing the given time interval to 20 sec, the insect didn't turn back after the stimuli alternated to another side.

Fig. 9 shows the results of response duration of the insect to 8V-20Hz electrical input signal with

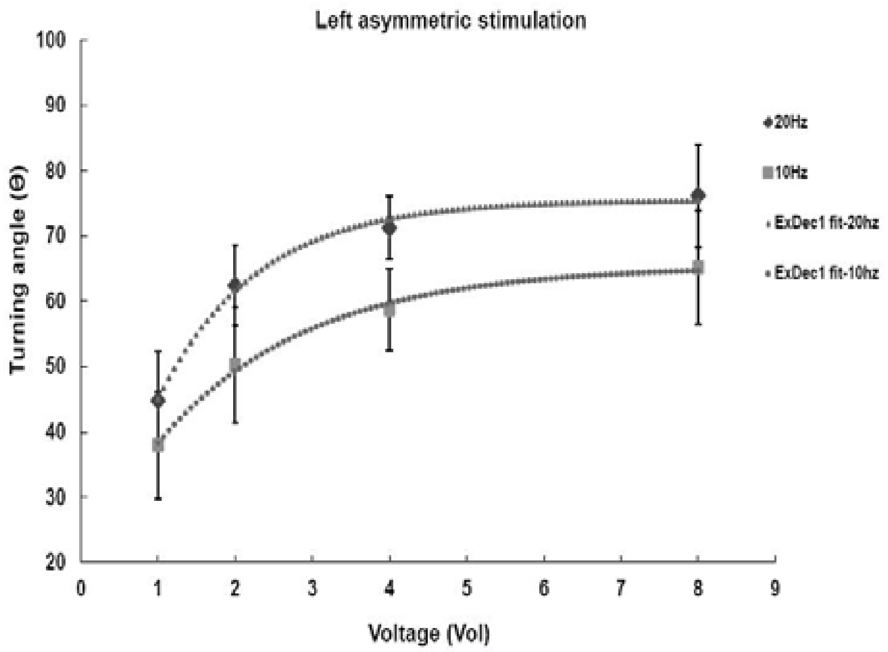

Fig. 6. Turning tendency of insect as the result of 10Hz, and 20Hz input signal of left side asymmetric stimulation with different input voltages. Each median value and standard deviation (error bar) was delivered by 20 tested subjects. The increasing trends of turning tendency show similarity in all conditions (1V~8V). The fitting curve was generated by Exdec1 model (Origin8).

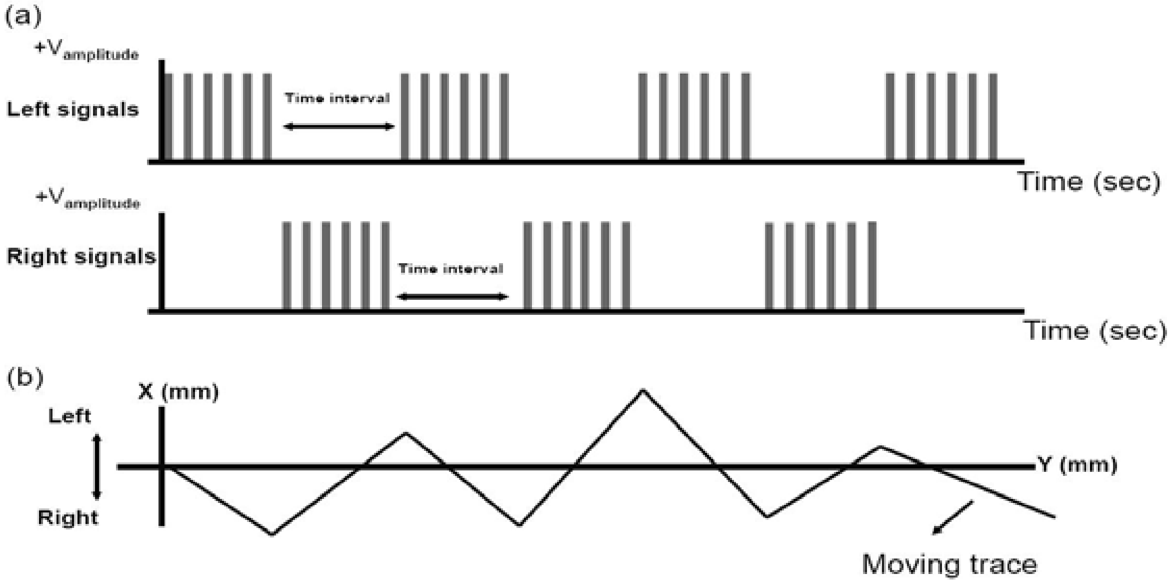

Fig. 7. Illustration of alternating stimulation. (7a) Electrical signals were given from left and right of the prothoracic ganglion. Electrical input for both side were given at the same amplitude and frequency. The input signal at each close-paired electrode is exactly out of phase to each other. The pause between each ipsilateral electrical pulse series were defined as time interval. (7b) The corresponding movements of insect to the alternating stimulation. The insects moved toward the right while the signal was given from the left, and followed by the movement toward the left when the signal switched to the right.

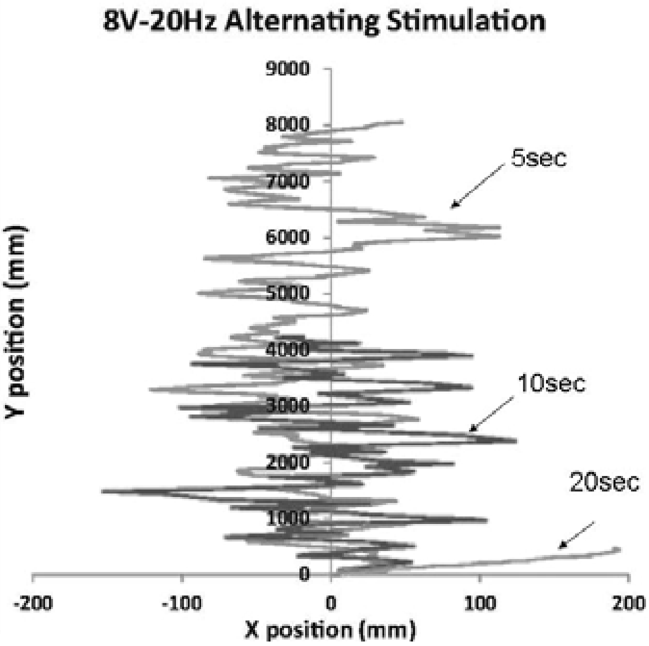

Fig. 8. Moving trajectory of insect in response to 8V-20Hz alternating stimulation. 5, 10, and 20 sec represent the given time interval defined in Fig 7a. The zigzag trajectory result of 5 and 10 sec given time interval indicate that the insect continuously switched turning directions corresponding to the alternated stimuli. This result shows the controllability of the insect locomotion whereas the result of 20 sec given time interval, the insect didn’t turn back.

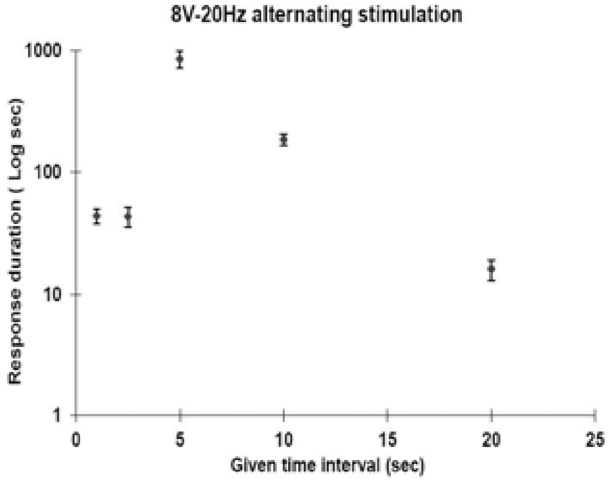

Fig. 9. Response duration of insect as the result of 8V-20Hz alternating stimulation with different given time intervals. The response duration shows remarkable increase at 5 second given time interval where the insect continuously responded to the electrical input in average of 15 mins. The shortest response duration occurs at 20 sec given time interval where the insect only responded to the stimulation for 17 sec. Each median value and standard deviation (error bar) was delivered by 30 tested subjects.

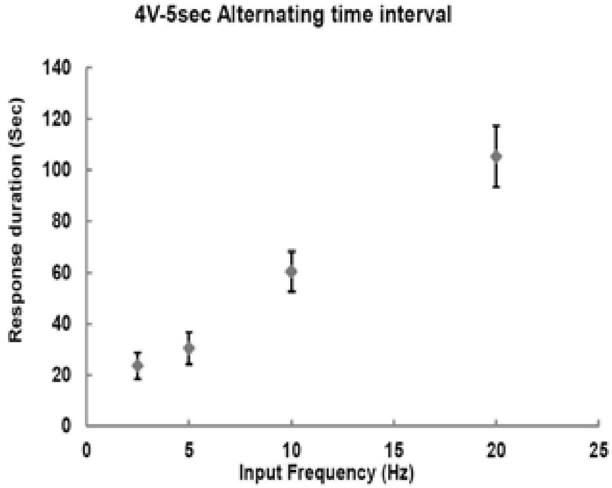

Fig. 10. Response duration of insect as the result of 4V-5 sec given time interval alternating stimulation with different input frequencies. An increasing trend of response duration as increase the input frequency is noted. Each median value and standard deviation (error bar) was delivered by 30 tested subjects.

different alternating given time interval. The median response duration at 1 sec and 2.5 sec given time interval is around 43 sec. The median response duration remarkably increases to 850.5 sec as the given time interval was increased to 5 sec. However, the response duration drops down to 184.4 sec as the time interval increase to 10 sec. Furthermore, the median response duration of insect only lasts 16 sec at 20 sec given time interval. All tested subjects under this parameter showed less than 20 sec response duration. This explains the fact that no turning back trace can be seen in Fig. 8 (20 sec given time interval). The adaptation of insect to the electrical stimuli occurred much faster when the stimuli were applied for more than 10 sec.

The effects of electrical signals under various input voltages and frequencies were monitored under the same given time interval (5 sec). Fig. 10 shows the result of 4V, 5 sec alternating given time interval with different input frequencies. No prominent changes of response duration under 1Hz and 2.5Hz are found where the median response duration is 22.63 seconds. The insect exhibits increasing response duration while the input frequency was

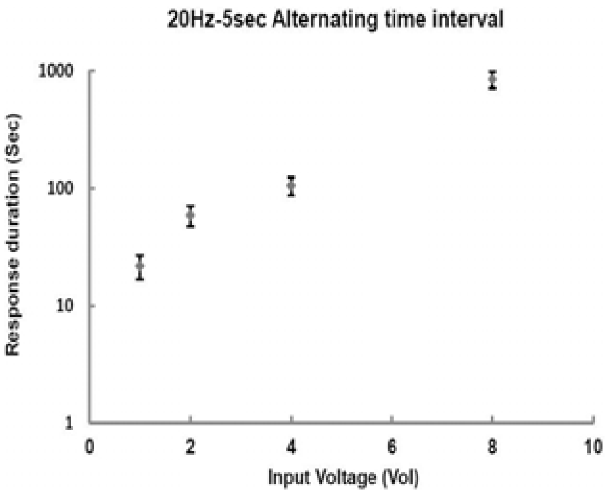

Fig. 11. Response duration of insect as the result of 20Hz-5 sec given time interval alternating stimulation with different input voltages. The insect response duration strongly increase from 105 sec to 850 sec while the voltage was increased from 4V to 8V. Each median value and standard deviation (error bar) was delivered by 30 tested subjects.

increased where the median response duration at 20Hz is 105.26 sec. Fig. 11 shows the result of 20Hz, 5 sec alternating given time interval with different input voltages. The response duration increases with increments of input voltage where remarkable response duration is revealed from 105.26 sec (4V) to 850.5 sec (8V).

DISCUSSION

Results from this study showed visible effects of electrical input on tethered American cockroach's turning. The turning tendency of the insect can be altered by modulating the electrical input. During stimulation, the moving preference of the insect was against the asymmetric stimulation. Similar behavior was also found in electrically stimulating the cockroach's antenna and beetle's basalar muscle [3, 12]. The turning initiation of insect might be due to the avoidance and escape response to the electrical stimuli. The overall successful rate of walking and turning initiation by asymmetric electrical stimulation is 72%. Individual successful rate corresponding to each asymmetric stimulation parameter varies from 61%~78%, which could be caused by the variation of implant position in each surgery. This could also result in large standard deviation ($\theta>10$) (Fig. 5) of the turning response.

The first order exponential growth fitting method was used to generalize the relationship between input parameter and turning tendency as is shown in Fig. 5. The turning angle increases as the input frequency increases. However, this increase becomes proportionately less and reaches asymptotic value. Similar situation was found in the frequency-fixed condition Fig. 6. The function representing the relationship of turning angle and input parameter is shown as follows:

$$\boldsymbol{\theta=\theta_0+Ae^{-x/t}}$$

here $\boldsymbol{\theta}$ represents the turning angle, $\boldsymbol{X}$ represents either input frequency or input voltage corresponding to the controlled condition. $\boldsymbol{\theta_0}$, **A** and **t** are constant. The constant values of fitting equation for each controlled condition are shown in Table 1. Result of voltage and frequency fixed conditions show increasing effect on the turning tendency. The increasing rate of turning tendencies were compared under voltage fixed and frequency fixed conditions to determine the input-dominance of the electrical stimulus. The turning tendency increases 22% when the input frequency was doubled whereas turning tendency increases 1.6% when the input voltage was doubled. The fitting results also show that the increasing speed of turning tendency of frequency dependent condition is faster than the voltage dependent condition. This suggests that the input frequency has stronger influence in affecting the turning behavior of cockroach than input voltage.

In cockroaches, walking and turning dynamics rely on the coordination of a tripod gait that is controlled by both the neural and the neuromuscular system [19, 20, 29-32]. The insect initiates a turn against the stimulus when evasive responses of cockroaches are elicited by wind or tactile stimulation of the antenna [33-35]. Our stimulation protocol shows the same result by asymmetrically stimulating the prothracic ganglion even with full antennal amputation. This suggests that the electrical stimuli affects the tripod coordination, and hence leads to an alteration of motor output. In the present work, we are unable to determine which neuron(s) within the ganglion were excited. The signal pathway, or locomotive generator, that led to the results presented here were not determined. Since the physiological mechanism of the stimulation is beyond the scope of this paper, we will leave it for future investigation.

Table 1. Curve fitting results.

Controlled condition	*y0*	*a1*	*t1*	*Adj.R-square*
Voltage (2V-left stim)	68.93914	-71.3235	7.36679	0.99753
Voltage (2V-right stim)	65.8548	-71.3418	6.76168	0.99776
Frequency(20Hz-left stim)	75.52656	-66.7417	1.27566	0.98243
Frequency(20Hz-right stim)	65.43232	-45.58899	1.92174	0.98408

CONCLUSION

It has been demonstrated that asymmetric electrical stimulation on the prothoracic ganglion elicits a directional response of cockroach locomotion. Such controlled stimulation can be used to modulate the turning preference of a cockroach's locomotion. Input frequency has a more prominent effect on turning tendency modulation than input voltage. Further increases in the input frequency could cause the insensitivity of cockroach to the frequency variation. A mathematical equation was created to predict the insect's turning behavior under controlled stimulation parameters.

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