ISSN 0022-0930, Journal of Evolutionary Biochemistry and Physiology, 2008, Vol. 44, No. 3, pp. 288—293. © Pleiades Publishing, Ltd., 2008.
Original Russian Text © V. S. Gorelkin, I. Yu. Severina, I. L. Isavnina, V. L. Svidersky, 2008, published in Zhurnal Evolyutsionnoi Biokhimii i Fiziologii, 2008, Vol. 44, No. 3, pp. 245—249.

COMPARATIVE AND ONTOGENIC PHYSIOLOGY

Effect of Static Load on Motor Behavior of the Cockroach *Periplaneta americana*

V. S. Gorelkin, I. Yu. Severina, I. L. Isavnina, and V. L. Svidersky

Sechenov Institute of Evolutionary Physiology and Biochemistry, Russian Academy of Sciences, St. Petersburg, Russia

Received May 14, 2007

Abstract—Effect of static load on activity of motor centers controlling motor activity (walking, flight) was studied in the American cockroach *Periplaneta americana* L. It has been established that under effect of load on the animal body the relative excitability of these centers increases. A suggestion is put forward about the presence of common neuronal elements in the generator networks providing motor acts in the American cockroach; a role of afferent systems in control of excitability of locomotor centers functioning in the regime of static load is shown.

DOI: 10.1134/S0022093008030046

Key words: insects, motor control, excitability, locomotor centers.

INTRODUCTION

Recently, a particular attention of many authors has been paid to study of motor behavior of different animals both in norm and under effect of various external stimuli [1–4]. The increased interest to this problem seems to be due to search for systems and mechanisms able co control and operate the animal locomotion. One of the ways of initiation and regulation of motor activity is known to be exposure of an animal to its starting mechanisms present under natural conditions as well as stimulation of various sensory systems [5–9]. However, as shown by observations, such stimulation not always leads to unequivocal responses. It can be thought that such organism reaction might be connected with a change of excitability of the centers controlling the animal motor behavior at different external actions on it and the degree of activity of some particular sensory systems.

Study of these processes in insects is of particular interest because, as shown by observations, the main principles of control of movements in these animals are much similar with those in vertebrates [10–17]. This allows using in several cases the obtained results for analysis of more complex relations existing in analogous system of control in the higher vertebrates.

The aim of the present work consisted in study of effect of static load of different values applied to the insect body on character of its motor behavior and activity of the motor center controlling various motor acts.

MATERIALS AND METHODS

The study was carried out on adult cockroaches *Periplaneta americana* L. capable for normal flight. Chosen for the experiments were males with length no less than 3.6 cm and weight no less than 0.85 g. All animals were designated by numbers. Experiments were performed during the light day period

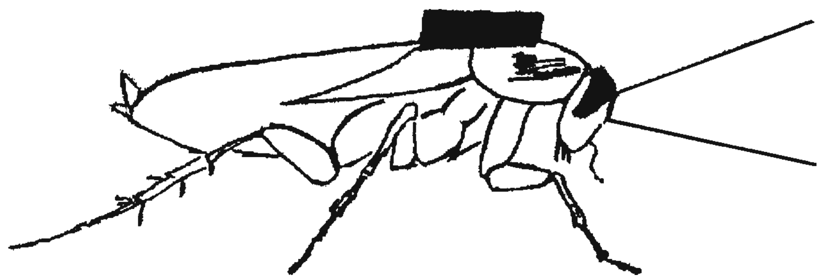

Fig. 1. Scheme of fixation of load on the cockroach *Periplaneta americana*.

at the air temperature of 20.0 ± 2.0°C. As a load, we used standard lead plates measuring 0.5 × 0.8 cm and weighing from 0.5 to 1.5 g in different combinations. The plates were fixed with a MK-2 medical glue on the animal dorsal side in the area of promezonotum (Fig. 1). For their installment, a part of wings of the anterior and posterior pairs were cut off. To record animal movements, a metallic rectangular groove, 100-cm long and 5-cm wide, limited with 2.5-cm high walls, was designed. For better adhesion of the animal extremities with the groove surface, a filter paper band was placed on its bottom. Motor activity of the animals was initiated by stimulation of cercuses with a soft brush. As a test-reaction to determine the level of relative excitability of the flight locomotor centers, there was used the animal natural reaction to start flying movements during the loss of the support by the animal extremities (Fraenkel's reflex) [18]. Duration of the evoked flight was recorded by a special device described earlier [19]. The relative excitability of the centers controlling the cockroach walking was assessed by the rate of the animal movement during its passing the designed territory without the load on the body.

Results of the experiments were processed on a computer with aid of the ANOVA test.

RESULTS AND DISCUSSION

The work was carried out at several stages: we studied dynamics of the cockroach motor activity in norm, in the static load regime, and at the moment of its elimination, as well as analyzed interaction of the motor centers providing various motor act under these conditions.

It is known that the cockroach activity can be triggered by a mechanical stimulation of the animal abdomen or cercuses as well as by gentle air puffs of these areas [20–22]. It has been established that the rate of the cockroach movement on a horizontal plane at the ambient temperature of 20–25°C varies from 20 to 40 cm/s in individual animals. As a rule, a cockroach is running until the border of arena or some shelter and sometimes stops briefly. Such peculiarities of the cockroach motor activity are to be noted as rather pronounced uniformity and linearity of the cockroach movement on the free arena under these conditions. Sometimes the movement along the great radius is observed. It is shown that any additional stimulation of various cockroach body areas as well as unexpected modifications of external conditions change markedly the movement direction and rate. At this moment, the animal rate can reach 60 cm/s according to our calculations (according to some literature data, 80–130 cm/s [23]). We believe that such rather high maneuver-ability and rate (1.5–3 km/h) of movement are quite sufficient to compensate weak flying possibilities of these animals, which allows considering walking as the main form of locomotion in this animal group. Taking this into account, it is analysis of this motor activity type that we focused on in our studies.

In the next series of experiments, we tried to find out whether the static load affects, and if does, how, the dynamics of the cockroach motor behavior. The load of 0.5–1 g on the insect body (with the cockroach body weight of 0.85–1.0 g) was shown to have no effect on the locomotor activity rate and character. The cockroach behavior did not differ from control. Subsequent rise of the load changed

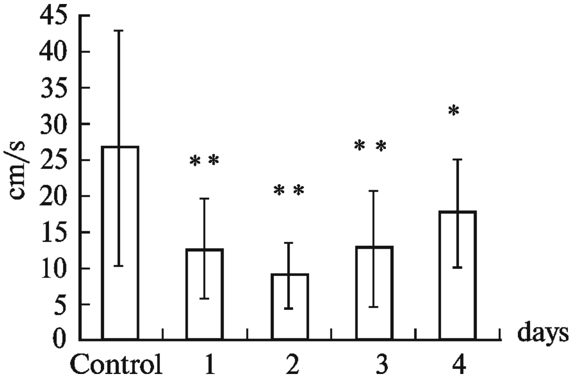

Fig. 2. Rate of cockroach movement on horizontal plane with load of 1.5 g. *Abscissa*: days of recording, *ordinate*: rate of movement (cm/s). *Asterisks* indicate statistically significant differences from control: *—$p < 0.05$, **—$p < 0.01$.

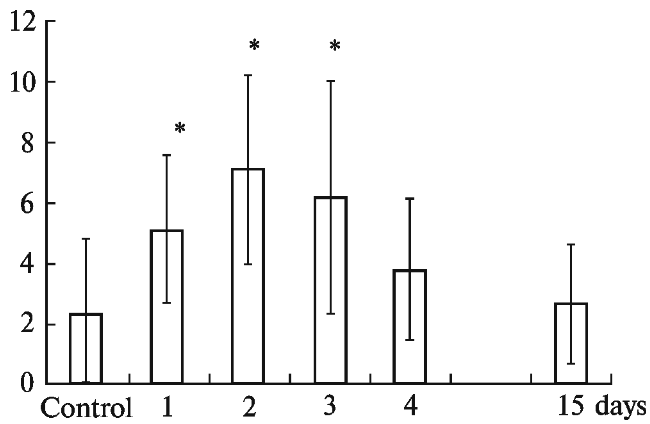

Fig. 3. The number of stimulations of cockroach during movement on horizontal plane with load of 1.5 g. *Abscissa*: days of recording, *ordinate*: the number of stimulations. *Asterisks* indicate statistically significant differences from control—$p < 0.01$.

sharply the picture. An increase of the load on the animal body up to 1.5 g was established to lead for the first moment to a significant decrease of the movement rate (Fig. 2). As seen from the averaged data presented in this figure, a decrease of the movement rate (by up to 50%) is observed for the first two days, then its gradual restoration occurs. The activity restoration (up to 60–70%) is observed by 4–5 days from the moment of the load. The complete (or almost complete) return to the initial level is recorded in the majority of individuals as late as by 12–15 days (see Fig. 5, the first and second columns). At the transient period, not only the rate, but also the character of movement has been shown to change: the animal stops many times. To maintain continuous cockroach movement at this period at its passing the designed territory, mechanostimulation of the circus area is needed (Fig. 3).

In the course of the experiment there also was revealed some difference in the motor behavior dynamics in cockroaches with different initial activity level in response to the load. It is clearly seen from Figs. 4a, 4b, that effect of the load on the motor behavior is less pronounced in animals with the initially low activity level than with the high one. Results of these experiments allow suggesting that the descending signals coming from the higher CNS parts into segmentary motor centers in response to the load–induced stimulation with a of receptor systems of extremities and exoskeleton seem to produce more efficient regulatory (correlating) effect on the generator network activity in this particular group of animals. This suggestion agrees well with data obtained by other authors, for instance, by Pearson [24], at study of effect of activity of the bell-shaped sensillae located on insect extremities on the body posture and motor pattern. He has shown the regulatory effect from activity of these receptor structures to occur mainly during walking at slow and middle rates, whereas during rapid walking this effect is less pronounced. It is undoubtedly that other receptors, such as chordotonal organs and hair plates, also can participate in control of work of generator of the motor activity rhythm at some particular external action on the insect.

Analysis of the cockroach motor behavior dynamics in response to the additional load increase (by 1.5 g more) at the 15th day of experiment in the static load regime (in this case the total weight of the load amounted to 3 g) allowed revealing, like in the previous series, several activity periods (Fig. 5). Thus, the centers providing walking are characterized, like in the previous experiments, by two main periods: the short one associated with a sharp activity decrease (1–3 days) and the long one—the restoration period. Thus, results of the experiments have shown adaptation to loads and transition to the period of the restoration of the

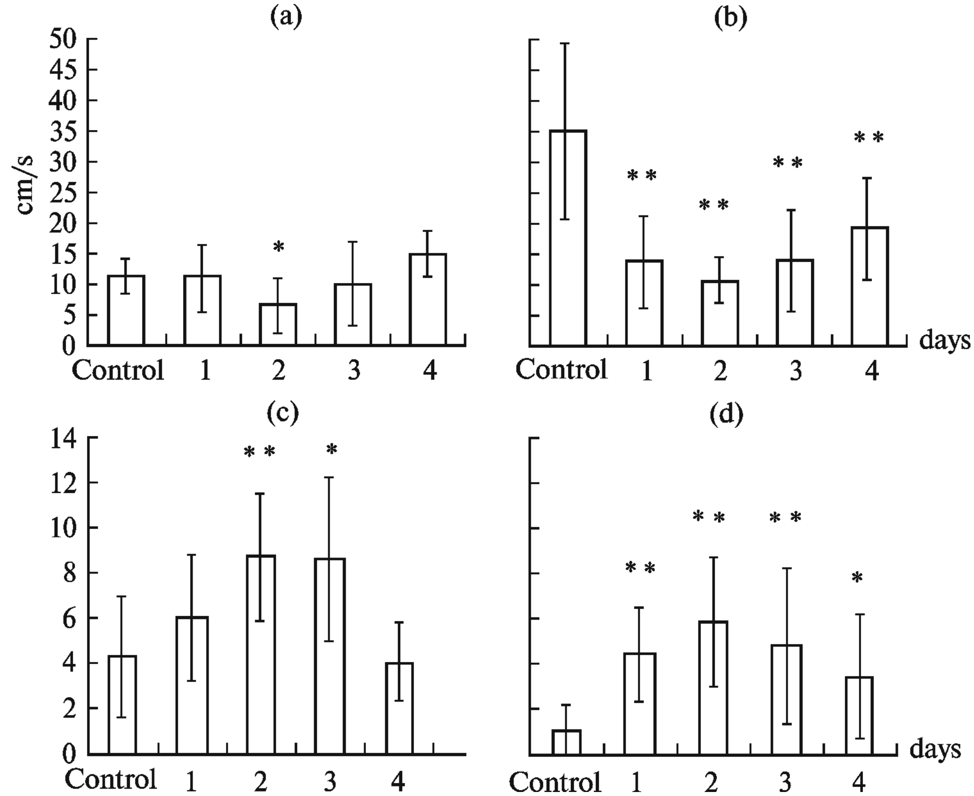

Fig. 4. Rate of movement of cockroach with different activity levels on horizontal plane with load of 1.5 g. (a) and (b): *abscissa*: days of recording, *ordinate*: the rate of movement (cm/s). c and d: *abscissa*: days of recording, *ordinate*: the number of stimulations. Cockroaches with the initial activity level: (a) and (b)—low, (c) and (d)—high. *Asterisks* indicate statistically significant differences from control: *—$p < 0.05$, **—$p < 0.01$.

initial motor activity rate in cockroaches to occur rather rapidly (for 3–4 days). It is established that this process is possible under the condition that the load weight does not exceed the weight of the insect itself more than 3 times (the coefficient—K ≤ 3). At the transient period, maintenance of the cockroach continual motor activity needs repeated stimulation of the animal. Experiments showed the load heavier than 3 times (K > 3) to lead to a further sharp fall of the locomotor activity. The movement rate amounted to about 1 cm/s. In this case, to initiate and maintain the uninterrupted walking, multiple stimulation was needed. Even under these conditions it was impossible to maintain the long walking of the American cockroach: during the walking the animal soon fell on its side or stuck into a track with the head.

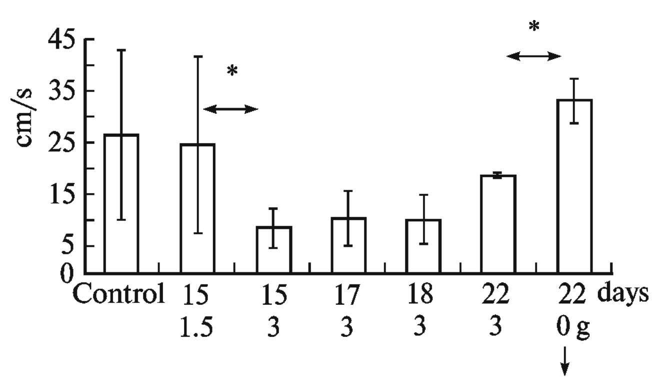

Fig. 5. Rate of cockroach movement on horizontal plane with load of 3.0 g. *Abscissa*: days of recording and weight of the load (g), *ordinate*: rate of movement (cm/s). *Arrow*—removal of the load. *Asterisk* indicates statistically significant differences at addition and removal of the load—$p < 0.05$.

It is to be noted that action of the load affects excitability not only of the centers controlling the animal walking, but also of the centers providing

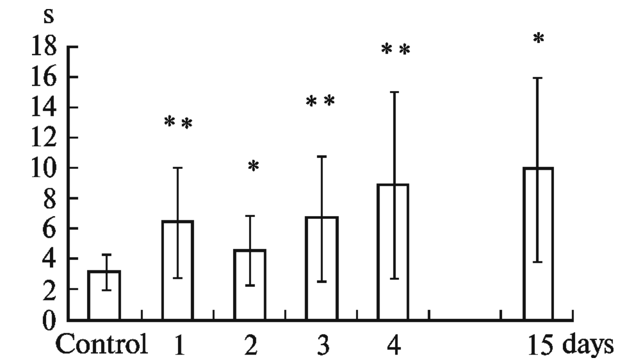

Fig. 6. Duration of the flight caused by tarsal reaction in cockroach with load of 1.5 g. *Abscissa*: days, *ordinate*: duration of the induced flight (s). *Asterisks* indicate statistically significant differences from control: *—$p < 0.05$, **—$p < 0.01$.

its flight (Fig. 6). Analysis and comparison of the data obtained in this series of experiments have allowed revealing seemingly quite different character of action on these centers. From the data summarized in Fig. 6, it is seen that duration of the cockroach flight caused by the tarsal reaction is increasingly enhanced under effect of this load. From the data summarized in Fig. 6 it is seen that duration of the cockroach flight induced by the tarsal reaction steadily increases under effect of this load. By the 4th day of experiment this duration has been established to rise by 70–80% of the initial one and to be kept at this high level throughout the entire experiment (until 15 days). Interestingly, at the same period of time, activity of the centers controlling the cockroach walking was restored to the same level (up to 60–70%) (compare Figs. 2 and 5). Analysis of these data allows suggesting the existence of common neuronal mechanisms underlying regulation of excitability of these locomotor centers. This suggestion can be confirmed, in our opinion, by the data obtained after removal of the load. The tarsal reaction duration is known to be usually recorded under conditions of fixed flight. Under these conditions the load is as if to be compensated by an up-ward force and hence should have not affect essentially some particular receptor systems on extremities at the moment of loss of their contact with the support. This might be suggested to modulate conditions associated with a brief load removal and to form thereby prerequisite for instantaneous recording of traces of the previous excitation of the corresponding motor centers. In all these cases, the experiment established a consecutive increase of excitability of the centers connected with the wing apparatus work, which is seen from the above data as a significant rise of the tarsal reaction duration. If our suggestion about the presence of common neuronal mechanisms in the system of control of activity of locomotor center is true, a similar reaction of the centers controlling the American cockroach walking under conditions of the static load also might be expected. And, indeed, the experiments show the removal of the load to lead to a significant increase of the cockroach movement rate (Fig. 5, the last column). In individual animals the rate increment could achieve 50–60% of the initial rate. Several hours later the rate returned to norm.

Analysis of the data and their comparison with results obtained earlier have allowed concluding that in the generator networks controlling activity of both locomotion centers, in all probability, there are common neuronal elements providing their close interaction and supporting the level of excitability of segmental centers, necessary for functioning, by traces of the preceding excitation of some particular locomotor systems. We believe that the choice of the animal response to stimulation is determined not only by possibilities of the system providing initiation of this motor act, but also by the excitability level of the "neighbor" locomotor centers combined into the single generation system by common neuronal elements.

REFERENCES

1. Beer, R.D., Chiel, H.J., Quinn, R.D., and Ritzmann, R.E., Biorobotic Approaches to the Study of Motor System, *Curr. Opin. Neurobiol.*, 1988, vol. 8, pp. 777–782.
2. Gorelkin, V.S., Kuznetsova, T.V., and Severina, I.Yu., Change of Activity of Locust Locomotor Centers under Effect of Increased Gravitation, *Zh. Evol. Biokhim. Fiziol.*, 2001, vol. 37, pp. 286–289.
3. Hooper, S.L. and Dicaprio, R.A., Crustacean Motor Pattern of Generator Networks, *Neurosignals*, 2004, vol. 13, pp. 50–69.
4. Delcomyn, F., Insect Walking and Robotics, *Ann. Rev. Entomol.*, 2004, vol. 49, pp. 51–70.
5. Camhi, J.M. and Tom, W., The Escape Behavior

of Cockroach *Perplaneta americana*, I. Turning Response to Wind Puffs, *J. Comp. Physiol.*, 1978, vol. 128, pp. 193–201.

6. Zill, S.N., Selective Mechanical Stimulation of an Identified Proprioceptor in Freely Moving Locusts: Role of Resistance reflex in Active Posture, *Brain Res.*, 1987, vol. 417, pp. 195–198.
7. Laurent, G., Sensory Control in Locomotion of Insect, *Curr. Opin. Neurobiol.*, 1991, vol. 1, pp. 601–604.
8. Matsuura, T., Kanou, M., and Yamaguchi, T., Motor Program Initiation and Selection in Crickets with Special Reference to Swimming and Flying Behavior, *J. Comp. Physiol.*, 2002, vol. 187, pp. 987–995.
9. Ye, S., Leung, V., Khan, A., Baba, Y., and Comer, C.M., The Antennal System and Cockroach Evasive Behavior. I. Roles for Visual and Mechanosnsory Cues in the Response, *J. Comp. Physiol.*, 2003, vol. 189, pp. 89–96.
10. Svidersky, V.L., Nervous Control of Fast Rhythmical Movements of Insect Muscles, *Tr. Vsesoyuzn. entomol. ob-va* (Proceed. All-USSR Entomol. Soc.), 1969, vol. 53, pp. 91–131.
11. Svidersky, V.L., *Neirofiziologiya poleta nasekomykh* (Neurophysiology of the Insect Flight), Leningrad, 1973.
12. Svidersky, V.L., *Osnovy neirofiziologii nasekomykh* (Grounds of Insect neurophysiology), Leningrad, 1980.
13. Svidersky, V.L., *Lokomotsiya nasekomykh. Neirofiziologicheskie aspekty* (Insect Locomotion. Neurophysiological aspects), Leningrad, 1988.
14. Peason, K.G., Common Principles of Motor Control in Vertebrates and Invertebrates, *Annu. Rev. Neurosci.*, 1993, vo. 16, pp. 265–297.
15. Svidersky, V.L., Generation of Motor Rhythms, *Zh. Evol. Biokhim. Fiziol.*, 1999, vol. 35, pp. 358–367.
16. Duysens, J., Clarac, F., and Cruse, H., Load-Regulating Mechanisms in Giant and Posture, Comparative Aspects, *Physiol. Rev.*, 2000, vol. 80, pp. 83–133.
17. Svidersky, V.L. and Plotnikova, S.I., Insects and Vertebrates: Similar Structures in the Higher Integrative Brain Centers, *Zh. Evol. Biokhim. Physiol.*, 2002, vol. 38, pp. 492–501.
18. Fraenkel, G., Untersuchungen über die Koordination von Reflexen und Automatischenervosen bei Insekten, *Ztschr. Vergl. Physiol.*, 1932, vol. 16, pp. 371–392.
19. Gorelkin, V.L. and Severina, I.Yu., Role of Central and Peripheral Mechanisms in Control of Excitability of Segmental Motor centers in Insects, *Zh. Evol. Biokhim. Fiziol.*, 2004, vol. 40, pp. 508–513.
20. Camhi, J.M. and Levy, A., Organization of Complex Movement: Fixed and variable Components of Cockroach Escape Behavior, *J. Comp. Phusiol.*, 1988, vol. 163, pp. 317–328.
21. Schaeffer, P.L., Kondagunta, V., and Ritzmann, R.E., Motion Analysis of Escape Movements Evoked by Tactile Stimulation on Cockroach *Periplaneta americana*, *J. Exp. Biol.*, 1994, vol. 190, pp. 287–297.
22. Levi, R. and Camhi, J.M., Wind Direction Coding in the Cockroach Escape Response: Winner Does not Take All, *J. Neurosci.*, 2000, vol. 20, pp. 3814–3821.
23. Mc Connel, E. and Richards, A.G., How Fast Can a Cockroach Run? *Bull. Brooklyn Entomol. Soc.*, 1955, vol. 50, pp. 36–43.
24. Pearson, K.G., Central Programming and Reflex Control of Walking in Cockroach, *J. Exp. Biol.*, 1972, vol. 56, pp. 173–193.