

SHORT COMMUNICATION

CONTROL OF CERCAL POSITION DURING FLIGHT IN THE COCKROACH: A MECHANISM FOR REGULATING SENSORY FEEDBACK

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In a flying cockroach, the response of cercal wind receptors to standard wind stimuli was reduced by 40 % compared with when the animal was at rest. While flying, rhythmic bursts of action potentials, phase-locked to the wingbeat rhythm, descended the nerve cord. These bursts appeared responsible for a phase-locked rhythmic discharge of cercal motor neurones. This, in turn, evoked a cercal displacement, maintained throughout flight. It is suggested that this displacement causes a pressure block of the sensory nerve, since it has recently been shown that experimental displacement of the cercus in a non-flying cockroach causes a similar degree of sensory reduction (40 %) by means of such a mechanism (Libersat, Goldstein & Camhi, 1987). The functional significance of this means of sensory reduction is discussed.

Rhythmic behaviours such as locomotion are known to be produced in part by pattern generators within the central nervous system (Delcomyn, 1980; Selverston & Moulins, 1985). As a result of an animal's locomotion, it receives considerable sensory feedback, much of which is also used to help control the movements (Burrows, 1976; Libersat, Clarac & Zill, 1987; Pearson & Wolf, 1987). However, some of this feedback is not useful and could even perturb the behaviour if not filtered out (Kennedy, Calabrese & Wine, 1974).

When a cockroach flies, its forward progression plus the beating of its wings produce strong wind stimuli to the cerci, paired wind-sensitive appendages located posteriorly on the abdomen. Each cercus bears about 220 filiform hairs that detect air displacement (Nicklaus, 1965). They are stimulated by minute air currents, such as those produced by the approach of a predator (Camhi, 1980). Currents of 1 cm s^{-1} are sufficient to evoke an evasive run. The wind generated by flying is roughly 300 times this velocity and could thus activate an inappropriate escape movement during flying, and could habituate the escape circuit. We demonstrate here that the cockroach partly circumvents this problem by means of a novel mechanism involving cercal movements made during flight (Fig. 1A).

Adult male *Periplaneta americana* were anaesthetized with CO_2 and the legs, supra-anal plates and wings were removed. The medial cercal nerve (containing

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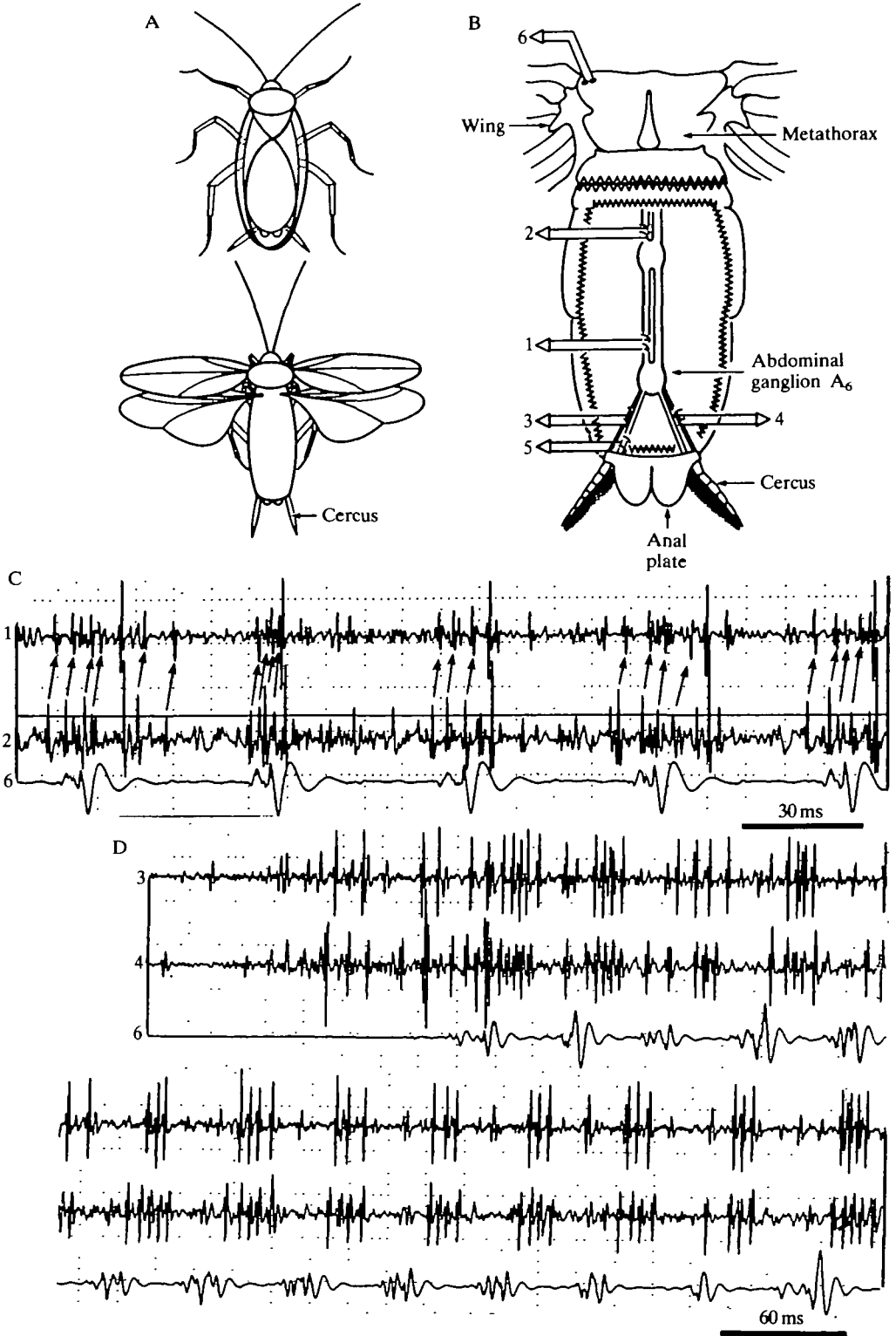


Fig. 1

the wind receptor axons), the lateral cercal nerve [containing motor axons to the cercal muscles (Bernard, Gobin & Callec, 1983)] and the nerve cord were exposed for recording (Fig. 1B) and the preparation was perfused with saline (Callec & Satelle, 1973).

To record electromyograms from elevator muscles of the metathoracic wings, pairs of 50 μm diameter copper wires, insulated to their tips, were inserted through small holes made in the cuticle of the anterior tergal process of the third thoracic segment (Carbonell, 1947). Pairs of hooks were used to record from or stimulate the nerve cord, and to record from the medial and lateral cercal nerves (Fig. 1B).

Sequences of flight activity were triggered either by puffing air onto the head or by electrical stimulation of the nerve cord (pulses of 200 μs duration, at 200 s^{-1} for 700 ms) (Ritzmann, Tobias & Fourtner, 1980). These stimuli caused the wing stumps to open and beat rhythmically, and caused the flight muscles to fire rhythmically at 20–30 s^{-1} , within the natural range of wingbeat frequency for this species (Roeder, 1951). Once flight had begun, a sensory response was evoked in the cercal nerve by a controlled wind puff delivered from a tube (Westin, Langberg & Camhi, 1977). All recordings were stored on tape for further analysis. Sensory nerve recordings were passed through a window discriminator to select action potentials which exceeded a preset level (generally chosen as the baseline noise level during rest) and all the selected signals were counted for an interval of 200 ms using a digital counter. By this means, sensory responses to a wind puff during flight were compared with those during rest.

Recordings were made during flight from a single connective of the cord at two different anterior–posterior locations, and showed bursts of small-amplitude spikes descending the nerve cord, phase-locked to the EMG of the flight muscle (Fig. 1C). This descending rhythm was seen in all 60 bouts of flight recorded in seven animals. Descending bursts were often followed by one or two ascending action potentials of larger amplitude (Fig. 1C), an analysis of whose activity will be reported elsewhere (F. Libersat & J. M. Camhi, in preparation).

Immediately upon receiving a wind puff or electrical stimulation to trigger flight, the animal displaced both cerci medially and vibrated them slightly, by contracting its cercal muscles. These muscles receive innervation from a group of

Fig. 1. (A) The cockroach *Periplaneta americana* at rest and flying. During flight, the cerci are displaced medially. (B) Placement of wire electrodes: 1 and 2 record the activity on the nerve cord; 3 and 4 record the motor activity of both lateral cercal nerves; 5 records the sensory activity of the medial cercal nerve; 6 records the wing muscle EMG. (C) Recording of the rhythmic activity in the nerve cord at anterior and posterior locations, showing both descending (arrows) and ascending action potentials during flight. An arrow was drawn from each spike in the bottom trace (2) that exceeded the window setting (straight line) and for which a subsequent spike was found on the top trace (1). Numbers indicate recording locations shown in B. (D) Recording of the rhythmic motor activity of both lateral cercal nerves at the initiation of and during flight; continuous record.

motor neurones in the last abdominal ganglion that send their axons through the lateral sensory-motor cercal nerve (Bernard *et al.* 1983). When the lateral cercal nerves were cut distally, only the motor action potentials to these muscles were recorded (Fig. 1D). At the onset of flight, the initial cercal displacement was characterized by an intense burst of spike activity in the motor neurones. As soon

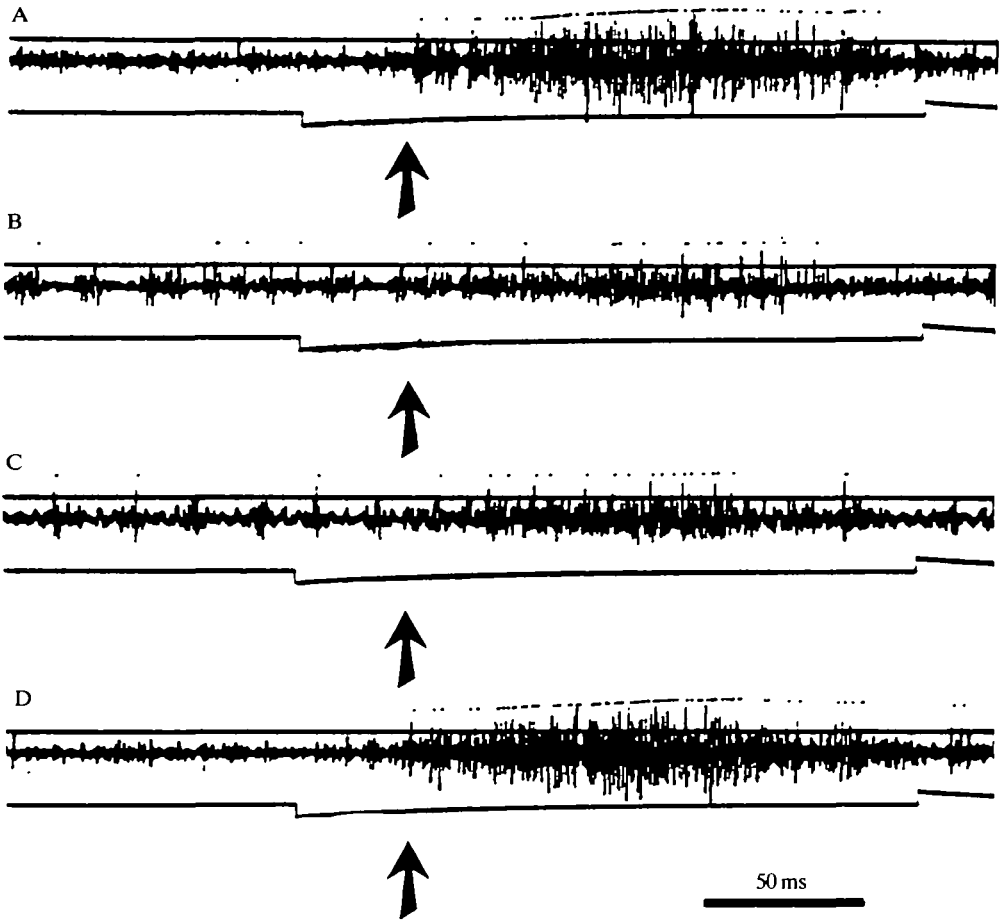


Fig. 2. Sensory responses to controlled wind puffs under different experimental conditions. All recordings from the same animal. (A–D) The nerve recording is from the medial cercal nerve (5 in Fig. 1B). The setting level of a window discriminator is shown by the line above the record traces. The bottom traces represent a 200 ms interval during which spikes that exceeded the setting level were counted. Each counted spike produced a dot above the record. Each wind puff began at the time shown by the arrow. (A) Animal at rest (cerci in their resting position; Fig. 1A top). (B) Animal flying in response to a brief wind puff on its head delivered about 2 s earlier (cerci moved parallel to the animal's long axis; Fig. 1A bottom). (C) Animal flying in response to electrical stimulation of the nerve cord (cerci moved parallel to the animal's long axis). (D) Animal at rest again (cerci again in their resting position).

as flight started (indicated by rhythmic EMG activity in the bottom trace), the motor activity was organized into regular bursts. These bursts in both lateral cercal nerves were phase-locked with the EMG from the wing muscle (Fig. 1D). Such bursts were seen in each of 50 bouts of activity studied in five animals.

Each motor burst began on average 5 ms after the end of the previous descending burst in the cord. This timing is consistent with the possibility that each descending burst in the cord evokes the subsequent motor burst.

Previous experiments have shown that either continuous stimulation of the cercal motor neurones, which evokes a similar cercal displacement when the animal is at rest, or manual cercal displacement induces a reduction of sensory activity in response to controlled wind puffs (Libersat *et al.* 1987). We wished to determine whether the cercal movements which occur naturally during flight are also accompanied by a decrease in the wind-sensitive input. Recordings made from the medial cercal nerve with the cockroach at rest showed a vigorous train of action potentials in response to a controlled wind puff (Fig. 2A). During flight, controlled wind puffs elicited a response reduced by a mean of $39 \pm 6\%$ (S.E.M., $N = 70$ stimuli flying and 70 at rest, in seven animals) (Fig. 2B,C) relative to rest. This reduction was highly significant ($P < 0.001$, paired t -test, $N = 75$ bouts). After the sequence of flight, the cerci returned to their original position, and the wind response returned to normal (Fig. 2D).

We conclude that during flight, the response of the cercal nerve to wind is substantially reduced, concomitant with a maintained cercal displacement. In a resting animal, the sensory reduction upon displacing the cercus does not result from the altered cercal angle relative to the wind stimulus. Instead, the displacement appears to impose a pressure block on the sensory nerve, reducing the number of sensory action potentials by roughly 40% (35% for manual displacement and 45% for displacement by electrical stimulation of the lateral cercal nerve) (Libersat *et al.* 1987). The close correspondence between the sensory reduction in non-flying and flying animals suggests that the same mechanism accounts for both.

The results presented here indicate that a copy of the flight rhythm, descending the nerve cord from the thorax, is responsible for the sensory reduction, and that it will be effective for just the duration of flight. A sensory reduction of the amount we report here has been shown to lead to a substantial reduction of wind-evoked activity in the giant interneurons that mediate the escape response (Goldstein & Camhi, 1987). Therefore, this sensory reduction could help to prevent inappropriate activation of escape movements during flight and/or help protect the escape circuit from habituation.

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