Organization of the antennal motor system
in the sphinx moth *Manduca sexta*

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Abstract. The antennae of the sphinx moth *Manduca sexta* are multimodal sense organs, each comprising three segments: scape, pedicel, and flagellum. Each antenna is moved by two systems of muscles, one controlling the movement of the scape and consisting of five muscles situated in the head capsule (extrinsic muscles), and the other system located within the scape (intrinsic muscles) and consisting of four muscles that move the pedicel. At least seven motoneurons innervate the extrinsic muscles, and at least five motoneurons innervate the intrinsic muscles. The dendritic fields of the antennal motoneurons overlap one another extensively and are located in the neuropil of the antennal mechanosensory and motor center. The density of motoneuronal arborizations is greatest in the lateral part of this neuropil region and decreases more medially. None of the motoneurons exhibits a contralateral projection. The cell bodies of motoneurons innervating the extrinsic muscles are distributed throughout an arching band of neuronal somata dorsal and dorsolateral to the neuropil of the antennal mechanosensory and motor center, whereas the cell bodies of motoneurons innervating the intrinsic muscles reside mainly among the neuronal somata situated dorsolateral to that neuropil.

Key words: Antenna – Antennal muscles – Motoneurons – Brain, insect – Deutocerebrum – *Manduca sexta* (Insecta)

Introduction

In the giant sphinx moth *Manduca sexta*, as in other moths and many other insect orders, the antennae are

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multimodal sensory organs comprising three segments: scape, pedicel, and flagellum (Sanes and Hildebrand 1976a). The long, distalmost segment of the antenna, the flagellum, is made up of about 80 annuli, each of which bears several types of cuticular sensilla innervated by sensory receptor cells (Sanes and Hildebrand 1976a; Lee and Strausfeld 1990). In moths, including *M. sexta*, the antenna is principally an olfactory organ, and most of the olfactory sensilla are situated on the anterior (Leading) half of the flagellum (Sanes and Hildebrand 1976a; Schweitzer et al. 1976; Hildebrand et al. 1980; Matsumoto and Hildebrand 1981; Christensen and Hildebrand 1984; Keil 1989; Kaissling et al. 1989; Lee and Strausfeld 1990). In addition to olfactory sensilla, the flagellum of a moth's antenna possesses smaller numbers of sensilla subserving functions such as hygro-, thermo-, and mechanoreception (Sanes and Hildebrand 1976a; see reviews in: Schneider 1964; Boeckh et al. 1965; Altner and Prillinger 1980; Kaissling and Thorson 1980; Steinbrecht 1984; Keil and Steinbrecht 1984; Zacharuk 1985; McIver 1985; Kaissling 1987; Lee and Strausfeld 1990). The two basal segments of the insect antenna, the scape and pedicel, bear discrete fields of hairlike mechanosensory sensilla called Böhm bristles (Böhm 1911; Schneider and Kaissling 1956, 1957; Gewecke 1972; Arbas 1986). The pedicel also contains the mechanosensory Johnston's organ (Schneider and Kaissling 1957; Vande Berg 1971), and additional mechanoreceptors are assumed to be distributed between the antennal segments and between the annuli of the flagellum (see Gewecke 1972).

Movements of a moth's antenna are controlled by two sets of muscles: the scape is moved by muscles originating on the tentorium within the head and inserting on the base of the scape, and the pedicel is moved by muscles originating in the scape and inserting at opposite points on the pedicel (Schneider and Kaissling 1956; Schneider 1964; Eaton 1988). There are no muscles in the flagellum. Previously we found that the cell bodies of the motoneurons innervating these muscles reside among neurons adjacent to the "dorsal lobe," or antennal mech-

anosensory and motor center (AMMC), of the deutocerebrum and that these motoneurons have dendritic arborizations in the AMMC neuropil, overlapping with the terminals of axons projecting from the mechanoreceptive Johnston's organ in the pedicel of the antenna and Böhm-bristle hair plates on the scape and pedicel (Camazine and Hildebrand 1979; Hildebrand et al. 1980; S. Camazine and J. Hildebrand, unpublished observations). In contrast to the numerous published studies of antennal sensilla and antennal lobes, however, a detailed analysis of the antennal motor system has been reported for only a few species, including crickets (Honegger et al. 1990a), honey bees (Snodgrass 1956; Kloppenburg 1990, 1995), and locusts (Bauer and Gewecke 1991).

As has been described for the butterfly *Aglais urticae* L. (Niehaus and Gewecke 1978), different antennal positions can be recognized in *M. sexta*, which correlate with different behavioral states. The antennae of a resting moth recline under the folded wings, whereas those of an aroused or flying moth are pivoted forward and held upright. In this "flight position", the antennae may serve as air-current sensors: bending due to aerodynamic drag on the elevated antennal flagella probably is monitored by the mechanoreceptors of the Johnston's organs (Ge-wecke and Niehaus 1981; Niehaus 1981). Thus movement of the antennae by the antennal motor system is likely to be important for the control of flight.

This report describes the muscles and motoneurons controlling antennal movements in the sphinx moth *M. sexta*. The findings from this study and its future extensions should contribute to understanding the roles of the antennae in the control of flight in moths.

Materials and methods

Manduca sexta (Lepidoptera: Sphingidae) were reared on artificial diet (modified from that of Bell and Joachim 1976) under a long-day photoperiod regimen (17 h light, 7 h dark) at 25° C and 50–60% relative humidity. All insects used for these studies were adults within 3 days posteclosion.

To study the intrinsic musculature of the antennae, we cut holes of different sizes in the cuticle of the scapes of antennae either attached to or isolated from the head. The muscles were observed under a stereomicroscope in fixed or unfixed preparations. We used the same fixation procedure for both the muscles and the brain (see below). The extrinsic musculature of the antenna was studied similarly. The head capsule was opened by cutting a window between the compound eyes and the antennal joints. The muscles were exposed by removing the palps, cibarial pump, and connective tissue.

To study the nerves containing the axons of motoneurons, we removed the muscles and pinned the opened head capsule in a Sylgard-coated plastic culture dish. The nerves innervating the antennal muscles were stained by backfilling. The nerves were cut near the muscles they innervate, and the nerve stumps were immersed in 2–5% Lucifer yellow solution in distilled water (modified from Strausfeld et al. 1983). After the stain had been allowed to diffuse into the nerves for 2–4 h at room temperature, the brains were fixed for 1–12 h (2.5% formaldehyde and 3% sucrose in 0.1 M phosphate-buffered saline solution, pH 7.2), dehydrated, embedded in plastic (Spurr 1969), and sectioned at 20–40 μm. The sections were photographed with a fluorescence photomicroscope (Nikon) or a laser-scanning confocal microscope (Bio-Rad 600). Selected intracellularly stained neurons were reconstructed from photographic slides.

The general organization of the brains was visualized in silver-stained preparations (method of Bodian 1936, modified by Gregory 1980).

Results

Muscles

Two sets of muscles, intrinsic and extrinsic to the antenna, control its movement. The extrinsic muscles (five for each antenna) originate on the tentorium (Fig. 1), which is formed by invaginations of the head cuticle, and insert at the base of the scape. The scape is set in the antennal socket on the head (Fig. 2). The intersegmental membrane between the head and the scape is wide except
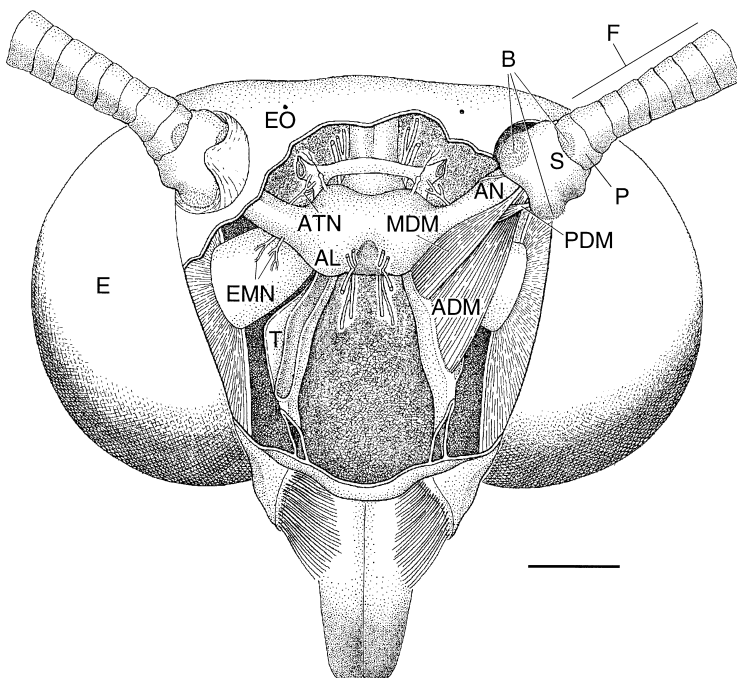

Fig. 1. Dorsal view of the adult *Manduca sexta* head with portions of the cuticle and underlying structures removed to reveal the brain and extrinsic antennal muscles: posterior levator muscle (*PLM*), anterior depressor muscle (*ADM*), posterior depressor muscle (*PDM*), mesal depressor muscle (*MDM*). These muscles originate on the tentorium (*T*) and insert in the scape (*S*). The antennal nerve (*AN*) enters the deutocerebrum dorsolaterally. Also shown are the nerves (*EMN*) to the extrinsic antennal muscles, the external ocelli (*EO*), and the anterior tegumentary nerve (*ATN*). On the scape (*S*) and pedicel (*P*) are the arrays of Böhm bristles (*B*). The sensilla and scales on the flagellum (*F*) are not shown, and only 7 of the more than 80 annuli of the flagellum have been included. *AL*, Antennal lobe; *E*, compound eye; *PTN*, posterior tegumentary nerve. *Bar:* 1 mm
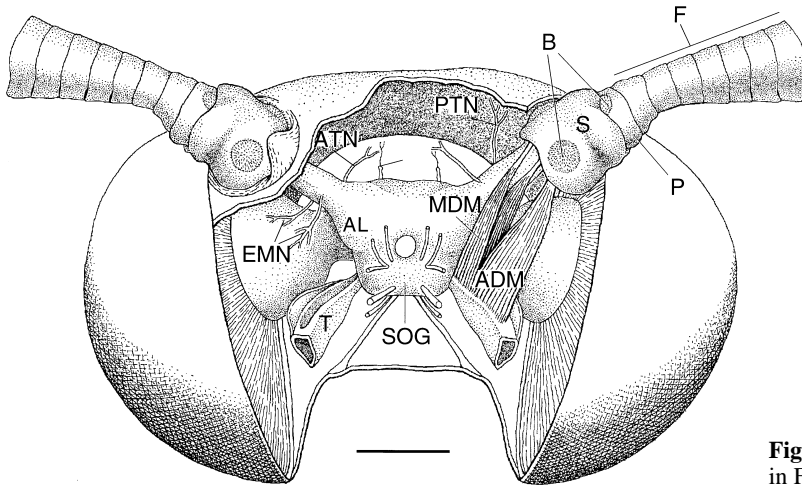
Fig. 2. Frontal view of the adult *M. sexta* head, labeled as in Fig. 1. *Bar:* 1 mm
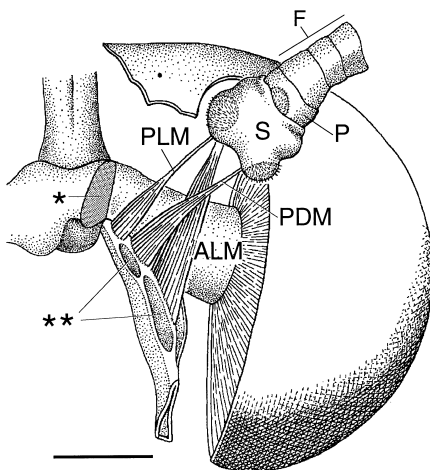

Fig. 3. Dorsal view of a portion of the adult head (compare with Fig. 1) after removal of the mesal and anterior depressor muscles (from positions marked ✶✶) and part of the deutocerebrum (✶). The three underlying extrinsic antennal muscles are revealed: posterior levator muscle (*PLM*), anterior levator muscle (*ALM*), posterior depressor muscle (*PDM*). Other labeling as in Fig. 1. *Bar:* 1 mm
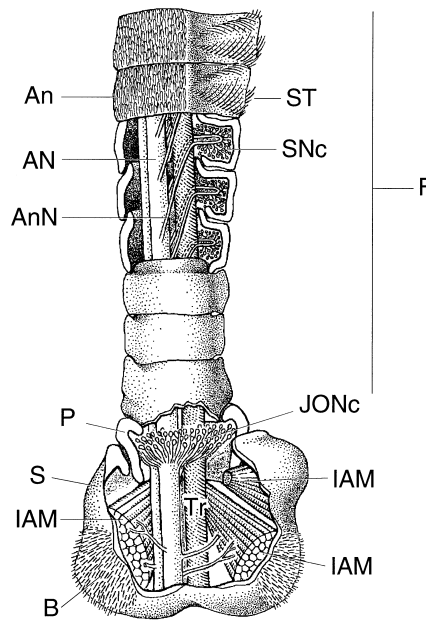

Fig. 4. Internal anatomy of the male *M. sexta* antenna, showing a dorsal view of the base of the antenna with portions of the cuticle removed to reveal internal structures. The antenna comprises three segments, the scape (*S*), pedicel (*P*), and flagellum (*F*), of which 8 of the ca. 80 annuli (*An*) are shown. The intrinsic antennal muscles (*IAM*; three of four are shown) move the pedicel and flagellum in a "hingelike" manner. Small nerves to the Böhm bristles (*B*) and to intrinsic muscles branch from the antennal nerve within the scape. A trachea (*Tr*) runs the length of the antenna. Within the pedicel, Johnston's organ nerve cells (*JONc*) join the two trunks of antennal nerve (*AN*). Nerve cells of the flagellar sensilla (*SNc*) contribute to the annular nerves (*AnN*). The only sensilla shown are the long, male-specific sensilla trichodea (*ST*). *Bar:* 100 μm

where the antennifer, a knob of head cuticle (see Schneider 1964; Chapman 1982), comes nearly into contact with the scape to form a point of articulation that allows the antenna to pivot in all directions. The extrinsic muscles have been described by Fleming (1968), and his nomenclature has been adopted here. Two muscles, the anterior and posterior levators, elevate the antenna. Three muscles, the anterior, posterior, and mesal depressors, lower the antenna (Figs. 1, 2, 3, 6).

The intrinsic muscles (two pairs of muscles in each antenna) originate and reside within the scape and insert at opposite points on the proximal lip of the pedicel, allowing a more limited, "hingelike" movement (Figs. 4, 5). No muscles have been found in the flagellum of the antenna.

Antennal nerves

Within the antennal flagellum the axons of sensory receptor cells innervating the sensilla on the annuli form two nerve trunks. The sensilla of the dorsal and ventral sides of each annulus supply separate fine nerve branches, which enter the dorsal and ventral nerve trunks, respectively. Each of the nerve branches enters the nerve trunk approximately two annuli proximal to the origin of the branch (Fig. 4; see also Sanes and Hildebrand 1976b).

Within the scape, fine nerves arise from sensory receptor cells associated with the Böhm bristles and per-
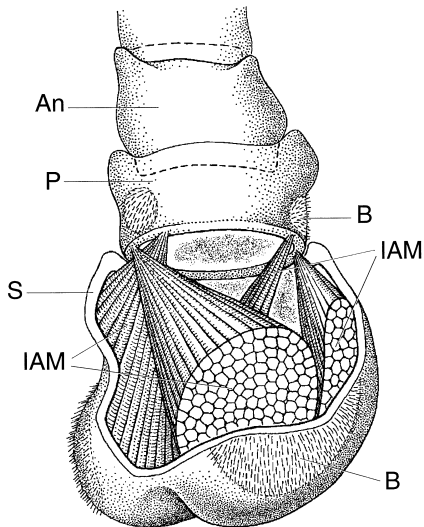
Fig. 5. Oblique view of the base of an adult antenna showing the scape (*S*) and pedicel (*P*) and a flagellar annulus (*An*). The four intrinsic antennal muscles (*IAM*) of the scape have tendons attaching to the lip of the pedicel. The patches of Böhm bristles (*B*) on the scape and pedicel are illustrated. Other structures within the antenna are not shown. *Bar:* 500 μm
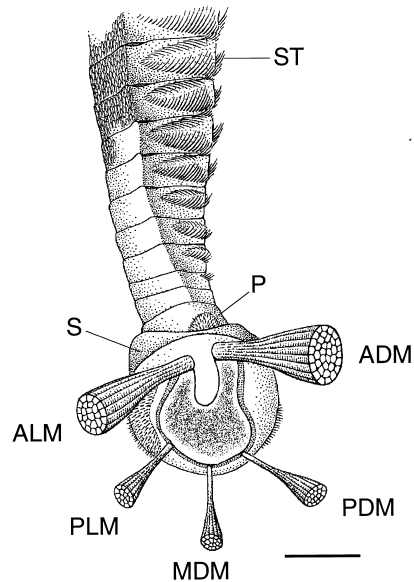

Fig. 6. View of the base of the antenna showing the insertions of the five extrinsic muscles on the proximal lip of the scape (*S*); anterior levator muscle (*ALM*), posterior levator muscle (*PLM*), anterior depressor muscle (*ADM*), posterior depressor muscle (*PDM*), and mesal depressor muscle (*MDM*). Ten flagellar annuli are shown, bearing the male-specific sensilla trichodea (*ST*); other sensilla are not included. *Bar:* 500 μm
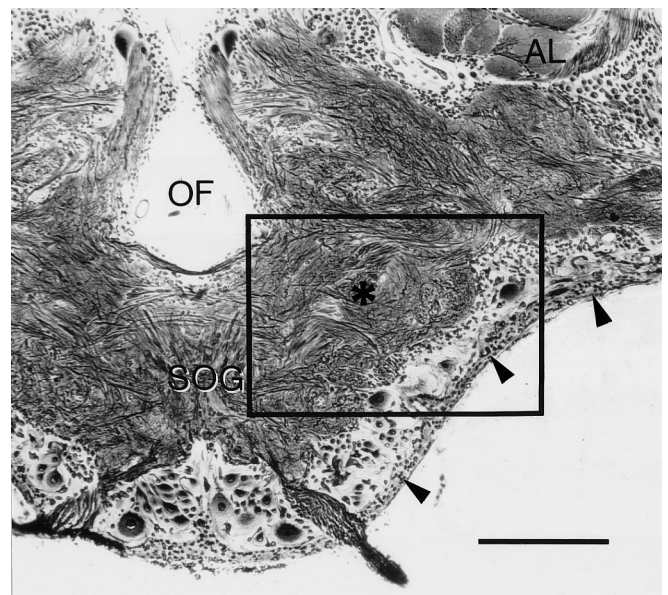
haps other unidentified sensilla and join the antennal nerve. The sensory nerves that emanate from Johnston's organ within the pedicel surround both the antennal nerve and the antennal trachea (Fig. 4) and join the antennal nerve. Distinct nerve branches also arise from the Böhm bristles and perhaps from other sensilla that may be present.

The axons of motoneurons to the antennal muscles project through the basal part of the antennal nerve and small motor nerves that branch from the antennal nerve intracranially for the extrinsic muscles (Figs. 1, 2) and within the scape for the intrinsic muscles (Fig. 4). Thus, the proximal part of the antennal nerve is a mixed, sensory and motor nerve, while the remainder of the antennal nerve beyond the intrinsic motor branch is believed to be exclusively sensory (Sanes and Hildebrand 1976a, b).

Several small nerves in addition to these motor nerves branch from the antennal nerve between the brain and the base of the antennal flagellum. The most proximal of these nerves, the anterior tegumentary nerve (ATN in Figs. 1, 2; compare with Snodgrass 1956 and Strausfeld 1976), joins the medial side of the antennal nerve intracranially, proximal to the bifurcation of the antennal nerve into two nerve trunks. The fine branches of this small nerve course among the tracheae overlying the brain and appear to originate near the head capsule. The ATN originates from sensilla on the dorsal surface of the head.

Deutocerebrum

The deutocerebrum of adult *M. sexta* receives antennal sensory inputs and contains the antennal motoneurons.

Fig. 7. Frontal view of a Bodian-stained section through the antennal mechanosensory and motor center (✶) and adjacent neuropil regions. The *framed area* corresponds approximately to the regions shown in Figs. 8A–F and 9A–F and includes part of the lateral array of neuronal somata (*arrowheads*). *AL*, Antennal lobe; *OF*, oesophageal foramen; *SOG*, suboesophageal ganglion. *Bar:* 100 μm

There are two main divisions of the deutocerebrum on each side of the brain: the antennal lobe (AL) and ventral and adjacent to it, the AMMC (reviewed in Homberg et al. 1989), which in other insects has been called the dorsal lobe (e.g., see Mobbs 1985). Each antennal nerve enters the brain at the level of the ipsilateral AL, as
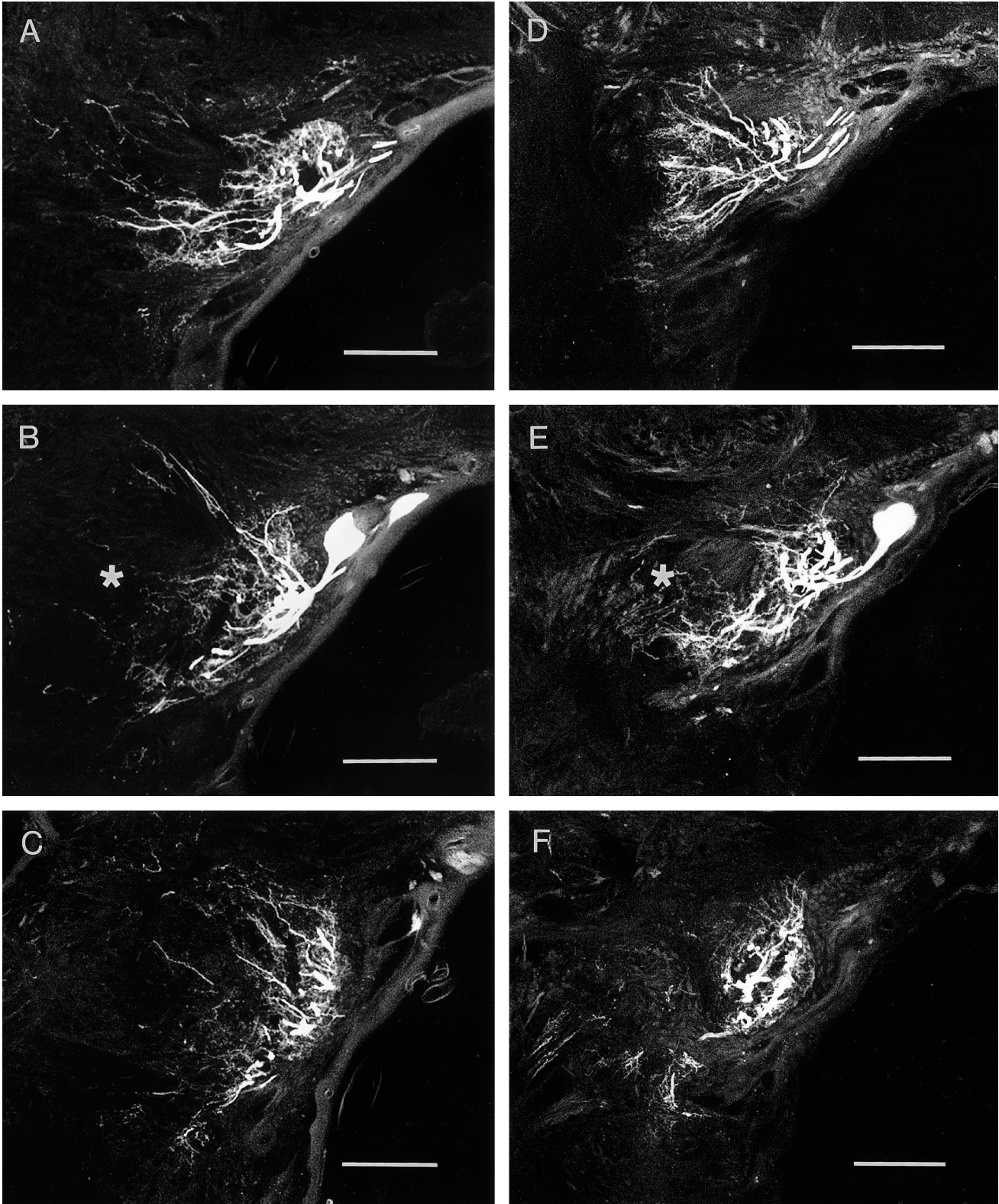
Fig. 8A–F. Frontal view of the antennal motoneurons in section (20 μm) from preparations stained with Lucifer yellow. **A–C** Extrinsic motoneurons controlling the movement of the scape. With respect to the frontal brain surface, the section shown in **B** is 60 μm more posterior than the section in **A**, and the section shown in **C** is 40 μm more posterior than the section in **B**. **D–F** Intrinsic motoneurons controlling the movement of the pedicel (and with it, the flagellum). With respect to the frontal brain surface, the section shown in **E** is 60 μm more posterior than the section in **D**, and the section shown in **F** is 40 μm more posterior than the section in **E**. In **B** and **E**, the location of the ✻ corresponds approximately to that in Fig. 7. *Bars:* 100 μm
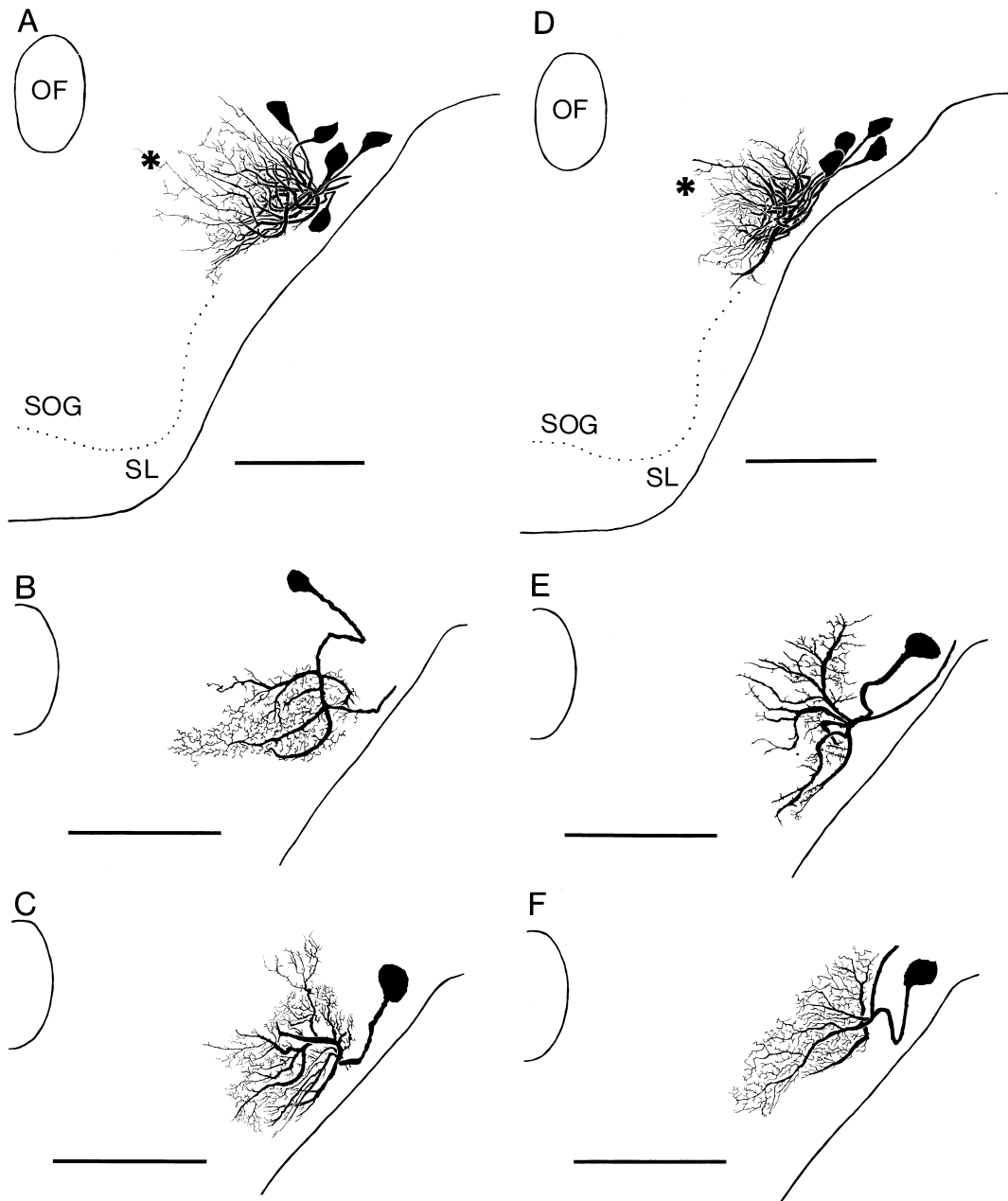
Fig. 9A–F. Reconstruction of antennal motoneurons from Lucifer yellow-stained preparations (frontal view). **A–C** Motoneurons of the extrinsic muscles. **A** Reconstruction of the backfilled cell shown in Fig. 8A–C. **B, C** Single motoneurons of the extrinsic antennal muscles. **D–F** Motoneurons of the intrinsic muscles. **D** Reconstruction of the backfilled cells shown in Fig. 8D–F. **E, F** Single motoneurons of the intrinsic antennal muscles. In **A** and **D** a *dotted line* indicates the boundary between the neuropil and the cortical soma layer (*SL*); other labeling as in Fig. 7. In **A** and **D**, the location of the ✶ corresponds approximately to that in Fig. 7. *Bars:* 100 μm

shown in Figs. 1 and 2. The functional organization of the AL of *M. sexta* has been described elsewhere (Hildebrand et al. 1980; Christensen and Hildebrand 1984; Hildebrand and Montague 1986; Homberg et al. 1989; Hildebrand et al. 1992).

The second main division of the deutocerebrum, the AMMC, is a poorly delimited region, with no clear borders to the tritocerebrum or the suboesophageal ganglion (Homberg et al. 1989). The AMMC neuropil does not appear to be organized into glomeruli or other obvious subdivisions (Fig. 7). This region receives projections of mechanosensory axons from the antennae, including those of the Johnston's organ and Böhm bristles, and from mechanoreceptive sensilla on the head (Camazine and Hildebrand 1979; Hildebrand et al. 1980; Hildebrand and Montague 1986).

Antennal motoneurons

Antennal motoneurons were stained by Lucifer yellow backfilling of the nerves that branch from the antennal nerve and innervate the antennal muscles. These experiments have shown that at least seven motoneurons innervate the extrinsic muscles of the antenna and at least five
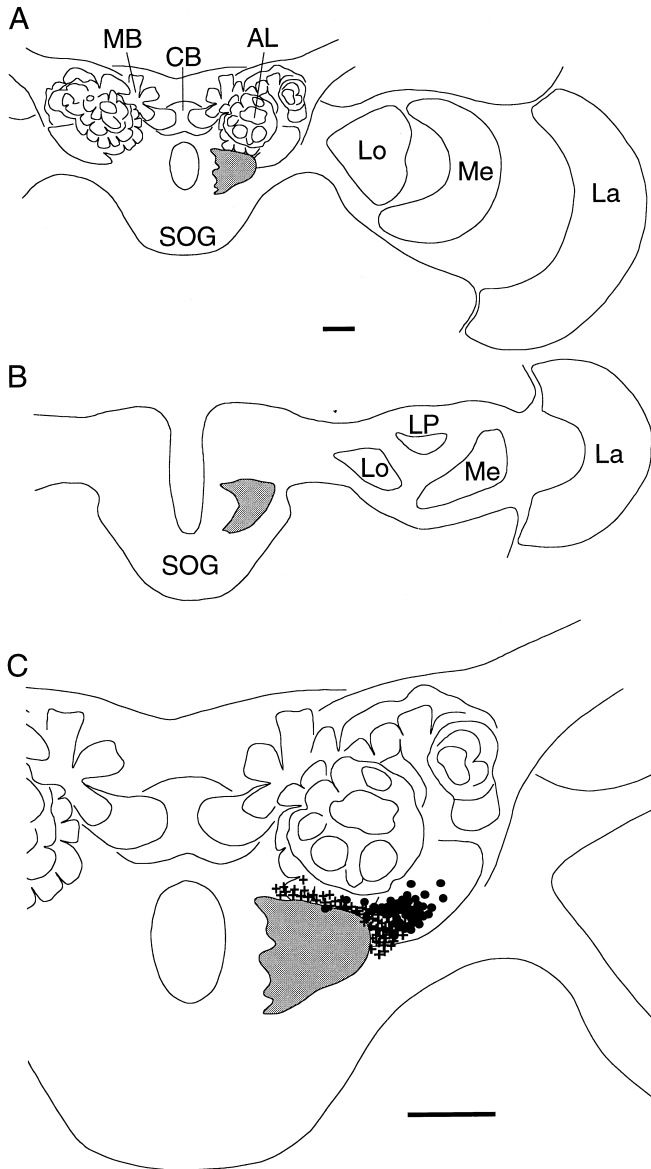
Fig. 10. Diagrammatic representation of all antennal motoneurons included in this study. **A** and **B** show the composite dendritic fields within the brain (*shaded area*) of the motoneurons innervating the intrinsic and extrinsic antennal muscles (**A** frontal view; **B** dorsal view, ventral to the antennal lobes). **C** Diagram (frontal view) of the antennal motoneurons, showing their composite dendritic fields and the distribution of their cell bodies. The crosses (+) represent the cell bodies of motoneurons innervating the extrinsic muscles, and the solid circles (•) represent the cell bodies of motoneurons innervating the intrinsic muscles. The dendritic fields of both populations of motoneurons share a common region of neuropil (*shaded area*) in the antennal mechanosensory and motor center of the deutocerebrum. This figure is based on 35 preparations (19 for extrinsic muscles, including 69 motoneurons; 16 for intrinsic muscles, including 46 motoneurons), each containing 1–7 motoneurons. *AL*, Antennal lobe; *CB*, central body; *La*, lamina; *Lo*, lobula; *LP*, lobula plate; *MB*, mushroom body; *Me*, medulla; *SOG*, suboesophageal ganglion. *Bars:* 100 μm

motoneurons innervate the intrinsic muscles. Impregnation of the stumps of cut nerves innervating the muscles failed to stain sensory neurons (with somata in the periphery), suggesting that these nerves exclusively carry axons of motoneurons.

From stained preparations, it was evident that the primary neurite of each antennal motoneuron gives rise to many branches that arborize in the neuropil of the AMMC. Staining of single motoneurons demonstrated that their dendritic fields overlap extensively, if not completely, in the AMMC neuropil (Figs. 8, 9). Together, the overlapping dendritic fields of the antennal motoneurons constitute a collective dendritic field for the ensemble. Arborizations of motoneurons occupy the entire lateral region of the AMMC neuropil, extending laterally to and defining its curving margin (Figs. 8, 9). The density of arborizations of motoneurons is high, and their neurites have the largest diameters of all processes in this lateral neuropil region. The density of arborizations is reduced in more medial regions, and the collective motoneuronal dendritic field has no sharp medial border. Anteriorly the collective dendritic field ends below the AL. Posteriorly, single neurites closely approach the suboesophageal ganglion. Overall the collective motoneuronal dendritic field, from its posterior to anterior margins, is about 400 μm deep. The motoneurons have no contralateral projections.

Motoneurons innervating the extrinsic muscles are illustrated in Figs. 8A–C and 9A–C. The cell bodies of these "extrinsic motoneurons" are distributed throughout the arching band of neuronal somata dorsal and dorsolateral to the AMMC neuropil (Figs. 8–10). Motoneurons innervating the intrinsic muscles are illustrated in Figs. 8D–F and 9D–F. The dendritic arborizations of these "intrinsic motoneurons" overlap extensively in the AMMC neuropil with arborizations of extrinsic motoneurons (Figs. 8, 9). In contrast to the cell bodies of the extrinsic motoneurons, the cell bodies of the intrinsic motoneurons are concentrated in the dorsolateral region of the arching band of neuronal somata adjacent to the AMMC (Figs. 8–10).

Discussion

The antennal motor system of *M. sexta* consists of five extrinsic muscles, situated in the head and controlled by at least seven motoneurons that move the scape, and four intrinsic muscles situated in the scape and controlled by at least five motoneurons that move the pedicel (and with it, the flagellum). The dendritic arborizations of both classes of motoneurons share a common region of the AMMC neuropil. Although the functional significance of the extensive overlap of the motoneuronal dendritic fields is not yet known, it seems likely that there are synaptic contacts among the motoneurons to foster coordinated activity in this population of functionally related neurons. For example, direct synaptic contacts have been found between motoneurons of antagonistic muscles in the hind leg of *Locusta migratoria* (Burrows et al. 1989). Investigations of flight motoneurons in *L. migratoria* (Burrows 1977) and *M. sexta* (Rind 1983), however, have shown that overlap of dendritic fields does not necessarily correlate with the presence of monosynaptic contacts. A common dendritic field could have the additional advantage of providing different motoneurons with similar input from either sensory neurons or central interneurons.

As in crickets (Honegger 1990a), honey bees (Kloppenburg 1990, 1995), and locusts (Bauer 1988; Bauer and Gewecke 1991), the antennal motoneurons in the moth do not project to the contralateral side of the brain. This finding suggests the involvement of central interneurons in the bilateral coordination of the antennae. There are other examples in which motoneurons innervating exoskeletal muscles have arborizations confined to central neuropil regions ipsilateral to the muscles they innervate (Wilson 1979; Phillips 1981; Honegger et al. 1984; Pflüger et al. 1986). Nevertheless, the absence of contralateral projections of antennal motoneurons contrasts with findings for other bilateral motor systems, e.g., the mouthparts of the honeybee (Rehder 1987, 1989), for which extensive contralateral projections of the motoneurons exist. Consequently there is an extensive overlap of the dendritic fields of motoneurons of both sides.

In *M. sexta* the dendritic fields of the antennal motoneurons overlap with primary mechanosensory projections from the antennae (Camazine and Hildebrand 1979; Hildebrand et al. 1980). Antennal mechanosensory information is very important for control of flight and is essential for controlled movement of the antennae. Presumably the overlap of the dendritic arborizations of the motoneurons and the terminals of the antennal mechanosensory axons permits the formation of a feedback loop, providing information about the positions of the antennae to the antennal motor system. Monosynaptic connections between antennal mechanosensory neurons and motoneurons have been found in flies (Burkhardt and Gewecke 1965).

The plurality of motoneurons, with respect to the muscles they control, that we report here is consistent with the pattern reported for antennal motor systems of other insects: the number of motoneurons typically exceeds the number of muscles innervated (crickets: Honegger et al. 1990a; honey bees: Kloppenburg 1990, 1995; locusts: Bauer 1988; Bauer and Gewecke 1991). In crickets, Honegger et al. (1990a) demonstrated that certain muscles with similar functions are innervated by the same motoneurons. If insect skeletal muscles are innervated by three or more motoneurons, they often include slow and fast excitatory motoneurons and an inhibitory motoneuron (Hoyle 1974). This pattern has been found in one of the muscles of the antennal motor system of *Locusta* (Bauer and Gewecke 1991). Common inhibitory neurons, innervating most or all muscles, have been found in the antennal motor system of locusts (Bauer and Gewecke 1991), crickets (Honegger et al. 1990b), and crustaceans (Sandeman and Wilkens 1983).

To build on the findings reported here, future studies will emphasize identification of individual antennal motor neurons, neurophysiological assessment of functional interactions among antennal motoneurons and mechanosensory affererents to the AMMC, and physiological and cytochemical characterization of muscle types among the intrinsic and extrinsic muscles of the antenna.

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