and perhaps only Y-cells project to the magnocellular laminae. While our electrophysiological data support their latter conclusion, we found no evidence for W- or Y-cell input to the parvocellular laminae. If owl and rhesus monkeys share a common retino-geniculate pattern, this is an apparent noncorrespondence between anatomical and physiological observations of the parvocellular laminae, and it cannot yet be explained.

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Dendritic Reorganization of an Identified Motoneuron During Metamorphosis of the Tobacco Hornworm Moth

Abstract. *In the tobacco hornworm, many larval motoneurons become respecified and supply new muscles in the adult. Changes in the morphology of one such neuron were examined through metamorphosis. The dendritic pattern of the adult comes about both by outgrowth from the primary and secondary branches of the larval neuron and by the development of new branches that are unique to the adult.*

Since the classic studies of Lyonet (*1*) over 200 years ago, it has been known that "complete" metamorphosis of insects is accompanied by an extensive reorganization of the nervous system. In examining these changes, a number of investigators have concluded that at least part of the adult system is constructed from preexisting larval neurons (*2*, *3*). Thus, differentiated larval neurons must redifferentiate during metamorphosis and assume new functions in the adult. We report that in an identified motoneuron this change in function is accompanied by an extensive alteration of the dendritic morphology. We also examined the extent to which the larval structures of the neuron contribute to the final adult form.

In adult *Manduca sexta*, 89 percent of the motoneurons in the fourth abdominal ganglion (ganglion A_4) are derived from motoneurons that were present in the larva (*3*). Since the larva and adult show extreme differences in the musculature of segment A_4, it was apparent that some neurons must innervate different muscles and consequently have different functions in these two stages. Male last instar larvae, diapausing pupae, and pharate (*4*) adults were used. Possible changes in dendritic morphology of motoneurons were examined by back diffusion of $CoCl_2$ through the proximal stump of peripheral nerves (*3*, *5*) into ganglion A_4. The cobalt served to impregnate the neurons that sent axons out of the respective nerves. After precipitation of the cobalt with ammonium sulfide (*5*), ganglia were fixed in alcoholic Bouin's solution, dehydrated, embedded in paraffin, and serially sectioned at 10 μm. The cobalt was then intensified by silver precipitation according to a modification of Timm's method (*6*). In favorable preparations this procedure revealed dendritic twigs down to 0.5 μm in diameter. Portions of the neuron on each section were traced by using a Leitz drawing tube and a 40 $\times$ planar objective and subsequently assembled into a two-dimensional reconstruction of the particular neuron.

The main trunk of the dorsal nerve (*7*) of ganglion A_4 was filled from beyond the second branch. In the pupal and adult stages this procedure filled only two neurons that had their cell bodies and dendritic areas in A_4. Motoneuron MN1 [numbering system according to (*3*)] had a contralateral cell body situated in the ventral lateral region of A_4, anterior to the entry of the other dorsal nerve. A second motoneuron (MN4) had a ventral midline cell body and an axon that divided and sent branches out through both dorsal nerves. Similar staining of larval ganglia revealed a third neuron (MN6). This neuron, which subsequently degenerates during metamorphosis (*3*), had an ipsilateral cell body situated in the dorsomedial region of A_4. Since MN1 had the only large cell body in the ventral lateral region of ganglion A_4 anterior to the dorsal nerve, it was chosen for study. Two other neurons in the larva and only one other neuron in the pupa and adult filled from beyond the second branch of the dorsal nerve, so the dendritic structure of MN1 was not obscured by the branching of many other neurons.

The fact that a neuron with a large cell

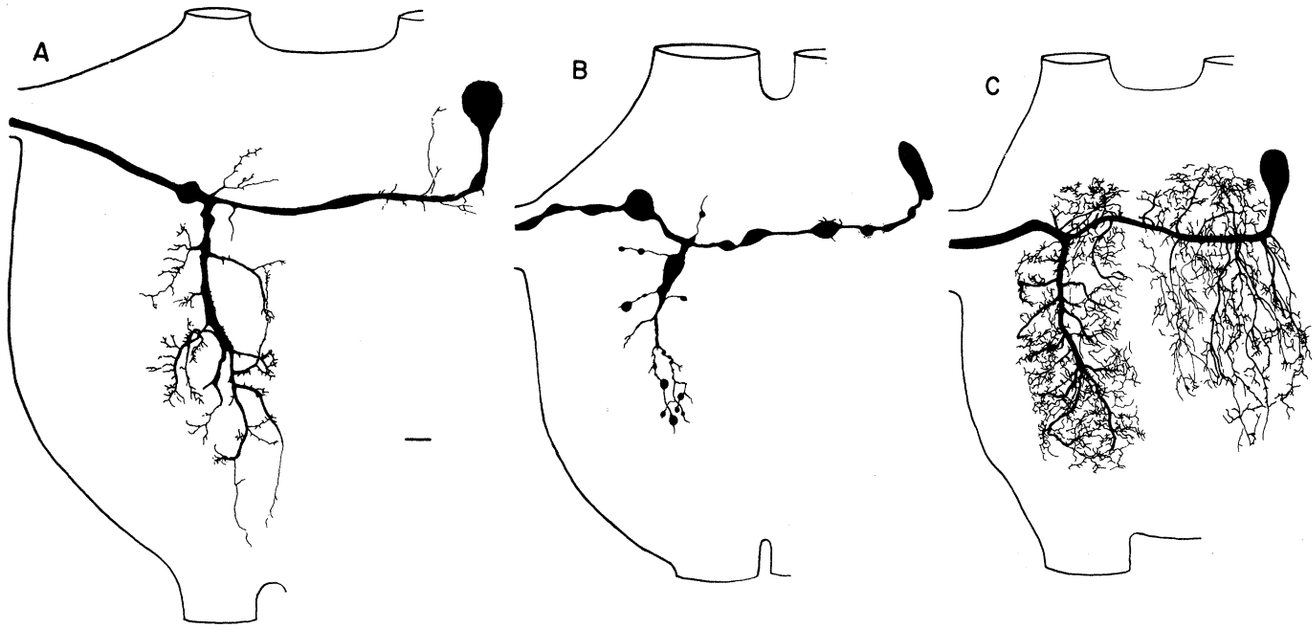

Fig. 1. Dorsal view of a reconstruction of MN1 in the fourth abdominal ganglion of *Manduca sexta*; (A) larva, (B) diapausing pupa, and (C) pharate adult. Scale bar, 20 μm.

body in a characteristic location was consistently observed when larval, pupal, and adult ganglia were stained by the same technique suggested that the neuron persisted through metamorphosis. But to eliminate the possibility that MN1 was replaced during metamorphosis by another neuron in the same location, abdominal ganglia were fixed in Carnoy's solution, stained in a 1 percent aqueous solution of toluidine blue, and prepared as whole mounts. The ventral lateral region anterior to the dorsal nerve was examined in at least ten ganglia from each day starting with the premetamorphic larva and ending 8 days into adult development. The number of large neurons (cell body < 25 μm in diameter) was determined. Of 143 ganglia examined, 137 showed only one large cell in this region of the hemiganglion and 6 had two large cells. Examples of the latter condition were found at each developmental stage and probably represent a normal variation in the position of the cell bodies of the other large motoneurons. In addition, 1 to 3 days after pupation the small

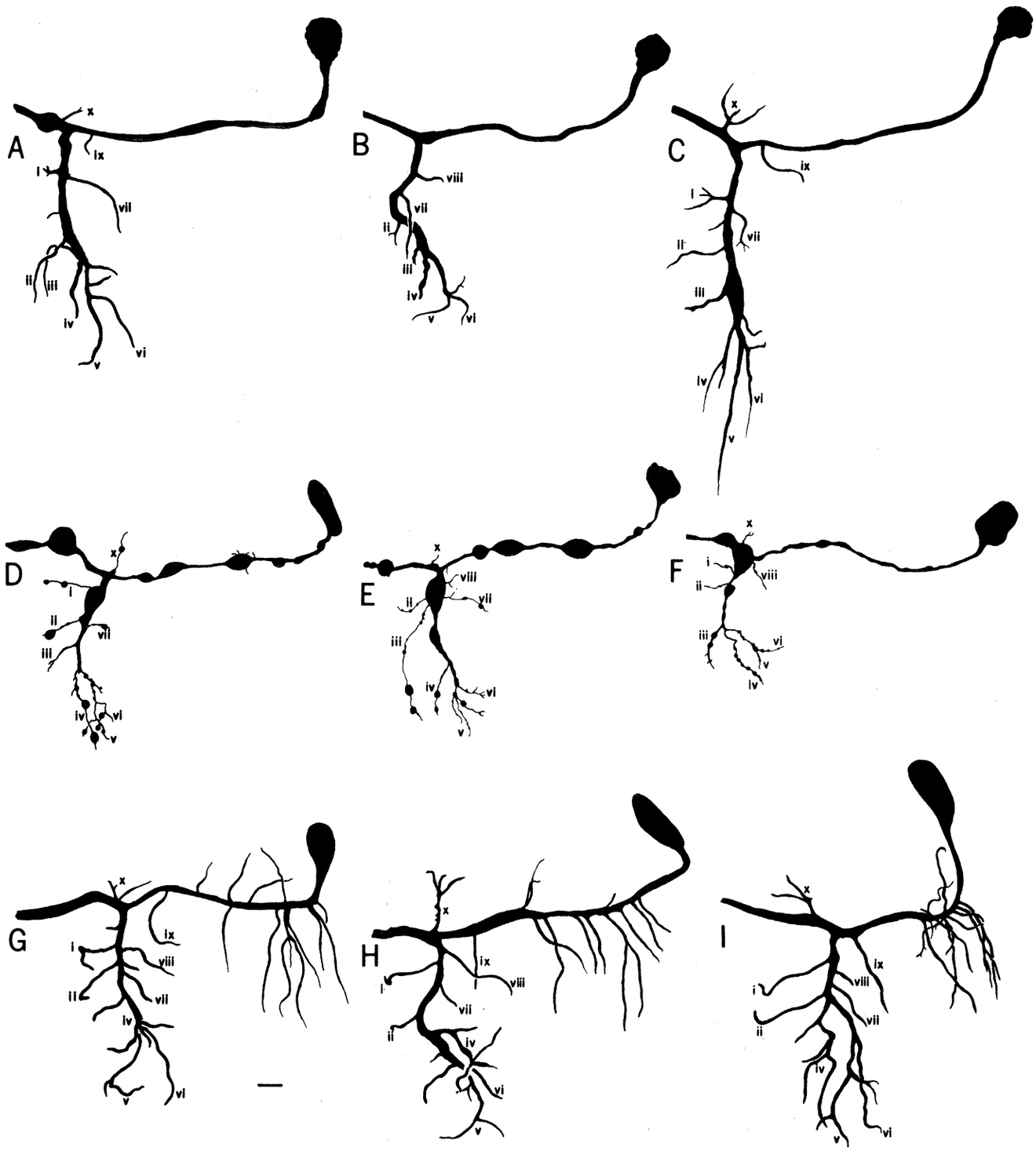

Fig. 2. Dorsal view of reconstruction of MN1 showing only the primary and secondary dendritic branches. Neurons are from (A to C) larvae, (D to F) diapausing pupae, and (G to I) pharate adults; *i* to *x* represent presumably homologous dendritic branches. The first neuron in each series is the one shown in Fig. 1. Scale bar, 20 μm.

number of larval motoneurons that do not persist through metamorphosis (for example, MN6) can be seen to be degenerating. But no degenerating cells were seen in the region of MN1 at this time. We conclude that at least in the case of MN1, a single neuron persists through metamorphosis from larva to adult.

In pharate adult *Manduca*, the portion of the dorsal nerve beyond the second branch extends past the spiracle and supplies the dorsal internal longitudinal muscles and the dorsal external muscles. The former muscles are innervated by motoneurons whose cell bodies are located in the next, more anterior ganglion (*8*). Therefore, MN1 probably controls one of the dorsal external muscle groups. These muscles are not present in the larva or the pupa but differentiate during the course of adult development. Knowledge of the exact target of MN1 in the larva and the adult must await electrophysiological examination of the nerve and the muscle groups.

Figure 1 gives an example of the dendritic morphology of MN1 in the larva, the diapausing pupa, and the pharate adult of *Manduca sexta*. In all stages the initial process extended posteriorly from the cell body, then made a 90° turn and crossed the dorsal neuropil to the opposite side of the ganglion. A primary branch extended from the initial process posteriorly through the dorsal neuropil on the side contralateral to the neuron cell body. In the larva, ten secondary dendritic branches could be identified in fills of MN1 (*i* to *x* in Fig. 2, A to C). The amount of third- and fourth-order branching was modest and less than that seen in some other larval neurons (for example, MN6). The initial process leading from the cell body was bare except for a few thin processes ipsilateral to the soma. In some larval preparations, extension of the neuropil a short distance into the posterior connective caused a distortion in the dendritic tree of MN1 (Fig. 2C). But the typical pattern of secondary branching of this cell could nevertheless be resolved.

The morphology of MN1 changed markedly in the diapausing pupa (Fig. 2, D to F). Cobalt filling of the neuron revealed only the primary and secondary branches. Typically, the branches consisted of occasional swollen areas joined together by very thin processes. The swellings were consistently found in pupal material and appeared at relatively characteristic sites along the initial process and primary dendrite of the pupa. Similar swellings were only rarely observed in larval or adult material. The number of secondary branches in the pupa was relatively constant and the branches appeared to be homologous with those found in the larva.

After adult development, MN1 showed a marked branching and subbranching. Secondary branches that were apparently homologous to those of the larva persisted into the pharate adult stage, with the possible exception of branch *iii*. Branch *iv* extended dorsally in the adult (as it did in the larva), but minor changes in the orientation of the ganglion during sectioning resulted in this branch appearing either to the right (Fig. 2H) or to the left (Fig. 2, G and I) of the primary dendrite in the reconstruction. The neuron showed extensive third- and fourth-order branching, and processes extended throughout the dorsal neuropil on the side of the ganglion contralateral to the cell body. The most striking change in the adult MN1 was the development of a second dendritic field. A number of dendritic branches left the initial segment and extended through the dorsal neuropil ipsilateral to the cell body. This new dendritic area presumably grew out from the thin processes that were undeveloped in the larva and the pupa. It is possible that the complete dendritic pattern seen in the adult was present in the larva and pupa, but that the processes were very thin and were not penetrated by the cobalt. We feel that this possibility is unlikely, but it can be excluded only through an electron microscopic study.

During metamorphosis of the peripheral nervous system in the silkmoth *Antheraea polyphemus*, the distal portions of the motor axons degenerate and new processes are sent out to supply the myoblasts of the adult muscle (*9*). Events in the central nervous system seem to be analogous. In *Manduca* during the transition from larva to pupa, most of the larval dendritic branches appear to degenerate or to be resorbed, leaving only the primary and secondary branches at the pupal stage. The extensive swollen areas consistently observed in the pupal neurons may represent accumulations of resorbed axoplasm. With the advent of adult development, extensive outgrowth then occurs from the secondary branches. Also, additional areas of the neuropil are invaded by new branches formed by the metamorphosing neuron. Thus, in this instance the construction of the adult neuron is accomplished by using the "skeleton" of the larval neuron as well as by the development of branches that are unique to the adult.

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Human Babesiosis: Reservoir of Infection on Nantucket Island

Abstract. *Examination of blood films from six species of rodents and lagomorphs on Nantucket Island disclosed infections with* Babesia microti *in all of five* Microtus pennsylvanicus *(field mice) and 31 of 39* Peromyscus leucopus *(white-footed or deer mice). Six human cases of clinical babesiosis have recently been diagnosed on the island.*

Human babesiosis presents two distinct epidemiological patterns: (i) isolated cases in persons who had previously undergone splenectomy and (ii) cases in a group of persons with intact spleens who live on a small island. Of the four reports concerning patients who had splenectomies, two originated from Yugoslavia in 1957 (*1*) and 1969 (*2*), one from Ireland in 1967 (*3*), and one from California in 1966 (*4*). Each case was ascribed to infection with one or another *Babesia* species known to parasitize ungulates. The reports involving persons with intact spleens are limited to residents of Nantucket Island (*5, 6*), located in the Atlantic Ocean approximately 50 km south of Cape Cod, Massachusetts. All seven of the Nantucket cases diagnosed to date were due to a piroplasm of rodents, *Babesia microti* (*7*), which was isolated in hamsters in all seven cases