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Morphological and physiological changes in central auditory neurons following unilateral foreleg amputation in larval crickets

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Summary. 1. In view of the surprising recent demonstration that developmentally one-eared female crickets can track sound sources (Huber et al. 1984), we have looked for correlates in the morphological and physiological properties of auditory interneurons of these animals. One foreleg was amputated in the 3rd/4th or penultimate (8/9th) larval instar; in both cases the leg regenerated without developing a functional ear. In the adult stage, these animals were studied first for their phonotactic behavior and then by intracellular recording and staining; three types of auditory interneurons in the prothoracic ganglion were identified: the omega neuron ON1, and the ascending neurons AN1 and AN2.

2. Of these three neuron types, those that normally receive excitatory input from the side now deafferented send dendrites across the midline of the ganglion, along specific pathways, to end in the auditory neuropil of the intact side (Figs. 1–4).

3. The new connections are functional, as shown by the responses of the neurons to synthesized calling songs presented to the remaining ear. With respect to the copying of chirp structure, threshold curves and intensity characteristics, these neurons respond like cells in intact animals that are presented with the same stimulus on the side ipsilateral to the main input region of the neurons (Figs. 2–4). The implication is that in animals with one ear missing, functional pathways within the central nervous system are reorganized, resulting in better orientation of one-eared animals.

Introduction

Female crickets deprived of auditory input from one ear are still capable of recognizing the conspecific song and locating the sound source (Huber et al. 1984). Some animals lacking one auditory organ and associated tympana, presumably through developmental disturbances, walked in a more stable direction than animals having a foreleg amputated as adults. Better orientation of monaural animals with developmental disturbances might be brought about by compensatory mechanisms such as altered synaptic efficacy or by the formation of new connections within the auditory system.

Compensation phenomena in cases of unilateral deficit have been observed, for example, in the vertebrate labyrinth (von Holst 1950; Precht 1978) and in the cercal system of the cockroach (Vardi and Camhi 1982a, b). The compensation in escape behavior of the cockroach could be explained by restoration of the directional characteristic of the interneurons on the deprived side. Such restoration is possible in the cercal system, because one cercus alone has access to all the necessary information about wind direction (Dagan and Camhi 1979; Westin 1979).

The phonotactic compensation of one-eared crickets must be based on a different mechanism. In intact crickets the only information available concerning sound direction resides in differences of sound pressure level at the two ears which vary according to the direction of sound incidence. This information is ambiguous for one-eared animals, however, because sound pressure changes due to intensity differences for a given direction cannot be distinguished from those that result from changes in the direction of a sound.

Before the orientation of 'developmentally one-eared' crickets can be understood, the quality of behavioral compensation and parameters affecting it must be elucidated so that comparisons may be made with animals that have undergone foreleg

Abbreviations: ON Omega neuron; *AN* ascending neuron

amputation as adults. Furthermore, it must be established whether or not morphological and physiological changes in afferent auditory nerve fibers and central neurons will provide a basis for interpreting this compensation. Some morphological and physiological changes due to deafferentation have been reported for an auditory interneuron in the cricket *Teleogryllus oceanicus* (Hoy et al. 1978, 1985; Hoy and Moiseff 1979; Pallas and Hoy 1984). Because the orientation ability of one-eared animals can vary widely among individuals, the question of neuronal mechanisms can be answered only if the behavior of the individual in which neuronal responses are studied can also be recorded, either previously or simultaneously.

In our present work, we first evaluated acoustic orientation of one-eared animals, after which each was prepared for recording from central neurons (see Wohlers and Huber 1982). The morphology and physiology of identified neurons in these animals will be described here, the correlation between neuronal responses and behavior and a quantitative study of phonotaxis in one-eared animals will appear in a subsequent paper (Schmitz et al., in preparation).

Material and methods

Fifty-four female larvae of *Gryllus bimaculatus* de Geer were used in these experiments. One foreleg was amputated at the coxa-trochanter joint during the 3rd/4th instar in 20 animals and during the penultimate instar in 34 others. Those crickets which lost a leg in the 3rd /4th instar regenerated a foreleg varying in length from 45 to 100% of the intact, opposite leg and bearing a posterior tympanum with an area 0–60% of normal. Following the operation in the penultimate instar, the leg regenerated 0–60% of normal length; the posterior tympanum, however, was completely absent. An anterior tympanum was never observed on any regenerated leg. In 22 of these animals, auditory interneurons in the prothoracic ganglion were identified.

Electrophysiology. Intracellular recordings from auditory interneurons in the prothoracic ganglion were made at room temperature (20–23 °C) under two sets of conditions. In the first, the animals were mounted on a holder with the ventral surface up; the prothoracic ganglion was exposed. The intact foreleg was placed within a 'legphone', a device through which sound from a 1/4″ microphone (Brüel and Kjaer 4135; see Kleindienst et al. 1981) is delivered to the ear in isolation. In the second case the animal was fixed to a holder with the dorsal side up and the prothoracic ganglion was exposed by dorsal dissection. Sound stimuli were presented, in a calibrated acoustic free field, using a high-frequency loudspeaker mounted ipsilateral to the intact ear at an angle of 50° to the long axis of the body and a distance of 30 cm. In both situations the stimulus consisted of an electronic simulation of the conspecific calling song, having appropriate temporal parameters (four syllables per chirp, chirp interval 500 ms, chirp duration 140 ms, syllable repetition interval 40 ms, syllable duration 20 ms). The carrier frequency was varied between 2 and 20 kHz and the sound intensity between 35 and 95 dB (RMS) relative to 20 μPa. The carrier frequency was increased by 1 kHz steps (from 12 to 20 kHz, 2 kHz steps) between chirps, starting at 2 kHz. In the last chirp of a series 5 kHz was tested again, after which the intensity was raised by 5 dB and the frequency sweep repeated. The differences in the neuronal responses to the first 5 kHz chirp and the last chirp (also 5 kHz) of a particular frequency sweep at constant intensity was always smaller than the differences between the responses to 5 kHz chirps differing by 5 dB in intensity. No systematic difference between the threshold curves and intensity characteristics in the two experimental arrangements was observed. Sound intensities were considered above-threshold when at least two stimulus-correlated action potentials per chirp were observed. Intracellular neuronal activity was stored conventionally.

Anatomy. When the physiological tests had been completed, the recorded neurons were marked with the dye lucifer yellow by passing hyperpolarizing D.C. current, 2–6 nA, for 5–15 min. The tissue was then fixed in 4% formaldehyde (phosphate-buffered) for 1–4 h, dehydrated and cleared. Whole-mounts were photographed immediately and then embedded in Spurr's medium. The preparations were sectioned (20 μm thick) and photographed again. All reconstructions were made from these sections.

Results

Omega neurons ON1

The omega neurons (ON1s) are bilaterally arborizing local interneurons of the prothoracic ganglion responding to acoustic stimuli (Casaday and Hoy 1977; Wohlers and Huber 1978). The soma of a given ON1 is found in the lateral part of the ganglion, anterior to nerve N2 and halfway between the dorsal and ventral surfaces of the ganglion. Arborizations found medially within the left and right auditory neuropils also extend laterally toward opposing leg nerves; they are connected medially by the prominent omega-shaped axon. The dendrites on the cell-body side are thin and smooth, whereas those on the contralateral side have thickened end structures (Popov et al. 1978). ON1s of intact animals receive excitatory input from the ear ipsilateral to the soma and inhibitory input from the contralateral ear (Wohlers and Huber 1982). They are tuned to the conspecific calling song frequency (4–5 kHz) and copy the temporal structure of the chirp.

Four different morphological (and associated physiological) types of changes were encountered in ON1s of adult animals following the amputation of a foreleg in larval stages (Figs. 1, 2).

(i) Omega neurons with the cell body on the deafferented side ($N=4$, omega cells of the deafferented side) send branches to the contralateral (intact) side by way of the anterior ring tract; these arborize extensively in the contralateral auditory

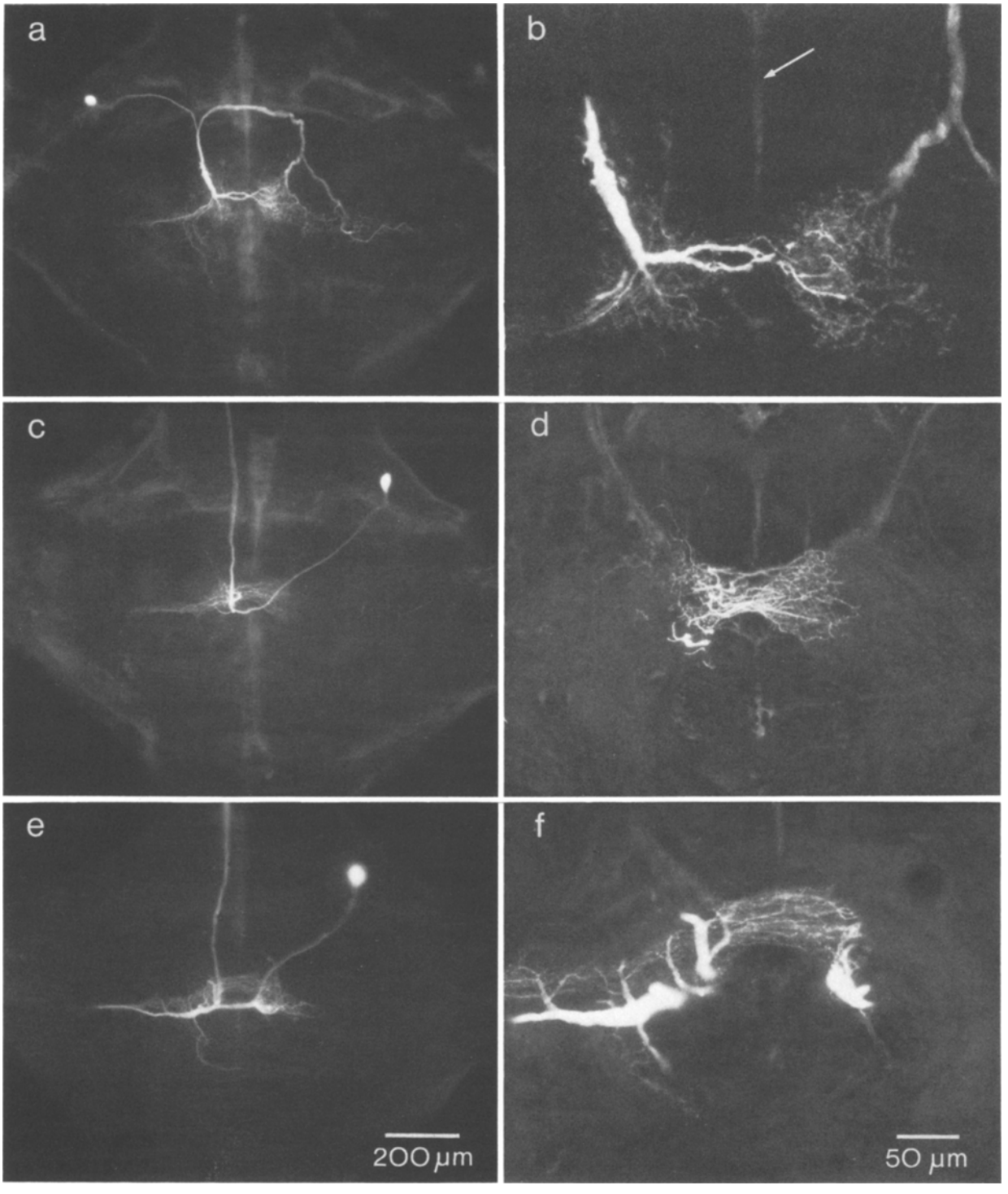

Fig. 1 a–f. Auditory neurons in the prothoracic ganglion of animals with a regenerated leg, viewed horizontally; the operated side is always left. Left column: whole mounts of lucifer yellow stained neurons; right column: horizontal sections from the same preparations at the level of the anterior ring tract. **a, b** Omega Neuron ON1; dendrites grow from the integrating segment of the deafferented side to the contralateral auditory neuropil; note sprouting in anterior parts of the integrating segment. **c, d** Ascending Neuron AN1; fine, dense arborizations project from the integrating segment of the deafferented side through the anterior ring tract to the auditory neuropil of the intact side. **e, f** Ascending Neuron AN2; arborizations grow from a single trunk of the deafferented side through the anterior ring tract into the contralateral neuropil. Note that arborizations of the intact side are increased in number and density over those found in intact animals. Arrow in **b** denotes the ganglion midline

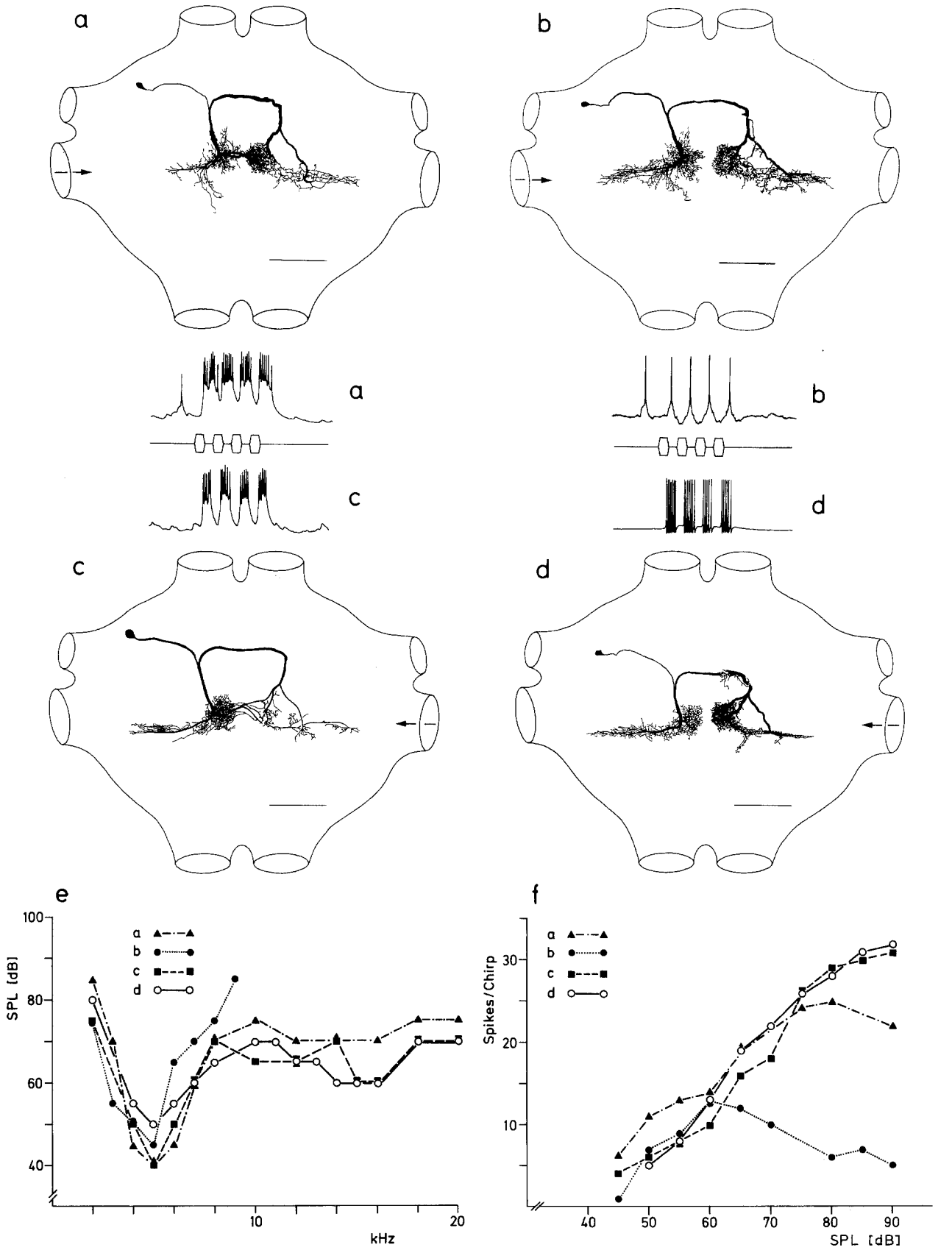

Fig. 2a–f. Morphology and physiology of Omega Neurons (ON1s) in unilaterally deafferented animals. Reconstructions of cells from the deafferented side (**a, b**) and the intact side (**c, d**). Arrows denote the deafferented side; scale 200 µm. The response of each cell to one chirp of the simulated song (5 kHz, 80 dB SPL) is shown below (**a, b**) or above the reconstruction (**c, d**). The recordings in a–c were made from the soma-ipsilateral (left) side, in d from the soma-contalateral (right) side. **e** threshold and **f** 5 kHz intensity/response functions of the drawn neurons (the letters a–d correspond to the lettered drawings)

neuropil (Figs. 1a, b; 2a). Stimulation of the ear contralateral to the ON1 soma elicited an excitatory response in the deafferented animal (Fig. 2a) rather than strong inhibition which is observed in intact animals. All these ON1 neurons are both morphologically and physiologically distinguishable from type ON2, which even in intact animals send dendrites to the contralateral side.

(ii) One ON1 of the deafferented side did not sprout branches to the intact side (Fig. 2b). Physiologically, this ON1 was weakly excited via the intact (normally inhibitory) ear, indicating that in some way functional excitatory connections were made through the contralateral auditory network.

(iii) Omega neurons with somata on the intact side (omega cells of the intact side, $N=2$) exhibited a marked reduction in the amount of arborization on the deafferented side. Surprisingly, several branches originating on the deafferented side sprouted to the intact side (Fig. 2c). These two animals had been operated on in the 3rd/4th instar. Here, normal excitation from the intact side was observed in the absence of any apparent inhibition.

(iv) In most omega cells ($N=7$) of the intact side no sprouting across the midline was observed (Fig. 2d). In five cells (leg amputated in penultimate instar) density, shape and position of the arborizations in the auditory neuropil were indistinguishable from those in intact animals. The other two neurons (leg amputated in 4th instar) exhibited a marked reduction in the density of arborizations on the operated side in addition to a marked extension of the lateral-most branch of arborization (not shown). A few branches of arborization along the axon anterior to the auditory neuropil were observed in all seven cells. The physiological responses consisted of excitation from the intact side.

Frequency threshold curves and intensity plots at 5 kHz are shown in Fig. 2e and f for examples of the four types of morphological changes. Types i, iii, and iv exhibit curves which are grossly similar to those from ON1s of intact animals (see Wohlers and Huber 1978). The differences seen in curves for type ii, namely, decreased sensitivity to higher frequencies (Fig. 2e) and strongly depressed response at higher intensities (Fig. 2f), may be the result of combined excitation and inhibition. In all four types the most effective sound frequency is about 5 kHz, the major frequency component of the conspecific calling song.

Ascending neurons AN1

The cell body of the ascending neuron AN1 occupies a position near that of ON1. The AN1 arborizes only within the auditory neuropil of the contralateral side, where its branches are densely packed. From this region the axon ascends to the brain (Boyan and Williams 1982; Wohlers and Huber 1982; Schildberger 1984).

In intact animals, AN1 is excited only through the ear contralateral to the soma, i.e. the ear ipsilateral to the dendritic field. No sign of excitation or inhibition via the opposite ear has been observed in AN1 type neurons. AN1 is tuned to the carrier frequency of the conspecific calling song and copies the temporal structure of the chirp (Wohlers and Huber 1982).

Identified AN1 neurons ($N=3$) with the cell bodies contralateral to the deafferented side (AN1 neurons of the deafferented side) send dendritic outgrowths from the deafferented to the intact side (Figs. 1c, d; 3a, b; compare with AN1 of an intact animal, 3c). They cross the midline in the anterior ring tract and arborize profusely within the intact auditory neuropil, exhibiting densely packed, very fine endings. Those dendrites remaining on the deafferented side are clearly reduced in density. Such AN1s are strongly excited by soma-ipsilateral stimulation (Fig. 3a, b) which elicits no apparent response in intact animals. The temporal pattern of the chirp is copied accurately and the neurons are maximally excited at 5 kHz. The shape of the threshold and intensity curves is similar to that of AN1s from intact animals (Fig. 3d, e). In amputees, the AN1s of the intact side were morphologically and physiologically indistinguishable from AN1s of intact animals.

Ascending neurons AN2

AN2 is morphologically similar to AN1 except for 2 major differences. First, in addition to the area of arborization within the auditory neuropil on the side contralateral to the soma, branches of AN2 further extend laterally toward the leg nerve, as is also observed in arborizations of ON1. Additionally, in intact animals, a small area of arborization can always be observed within the auditory neuropil on the side ipsilateral to the soma (Fig. 4c; see also Popov and Markovich 1982; Wohlers and Huber 1982; Moiseff and Hoy 1983).

AN2 is excited by the ear contralateral to the soma. Stimulation of the ipsilateral ear produces marked inhibition, and in some cases also weak excitation. This neuron does not copy the conspecific chirp structure as accurately as AN1, and it is usually tuned to higher frequencies (>10 kHz), though it often has a second sensitivity maximum

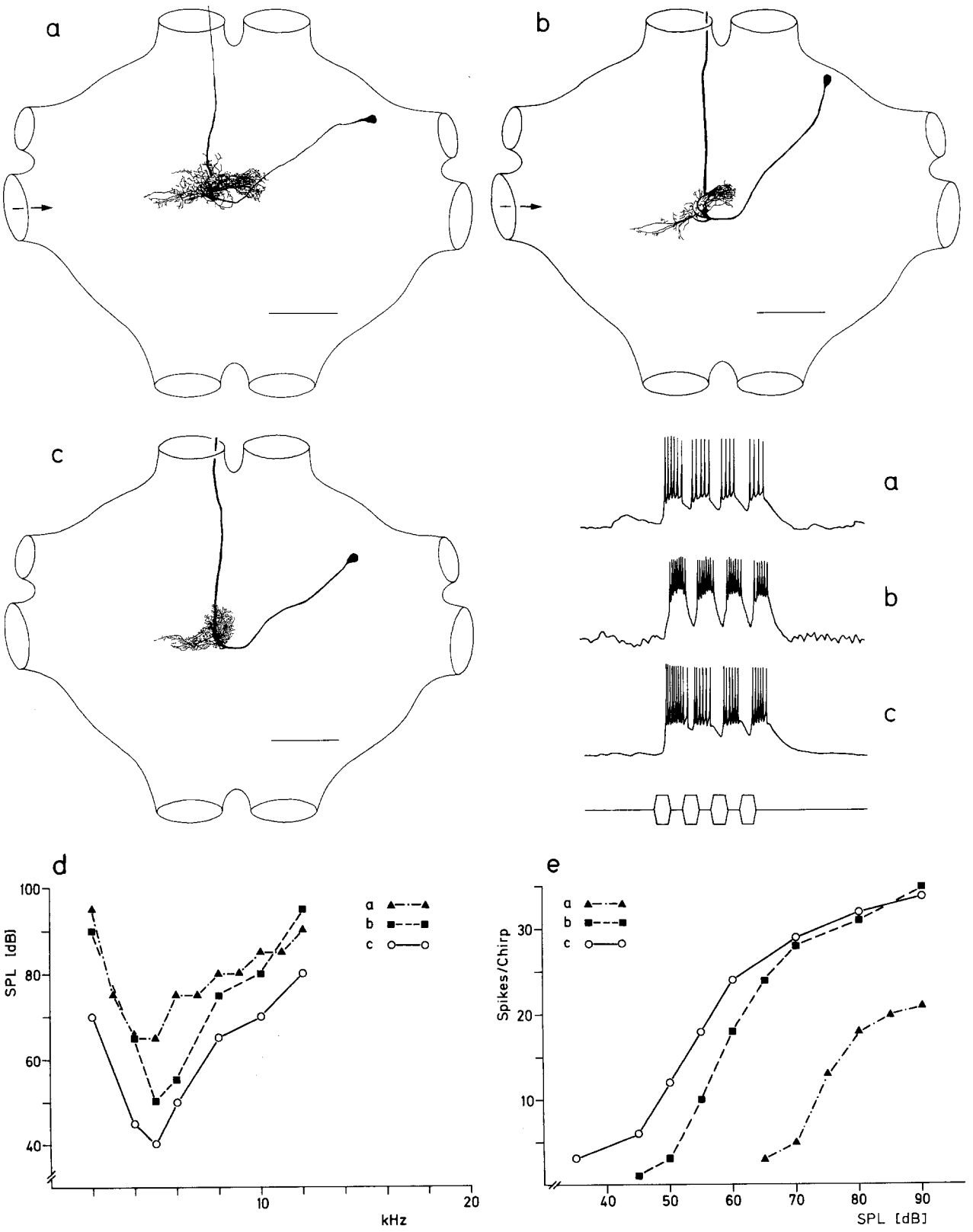

Fig. 3a–e. Morphology and physiology of Ascending Neurons (AN1s) in unilaterally deafferented (**a, b**) and intact (**c**) animals; arrows denote the deafferented side, scale 200 μm. Responses to one chirp of the simulated song (5 kHz, 80 dB SPL) are shown. **d** threshold and **e** 5 kHz intensity/response functions of the drawn AN1 cells (the letters a–c correspond to the lettered drawings)

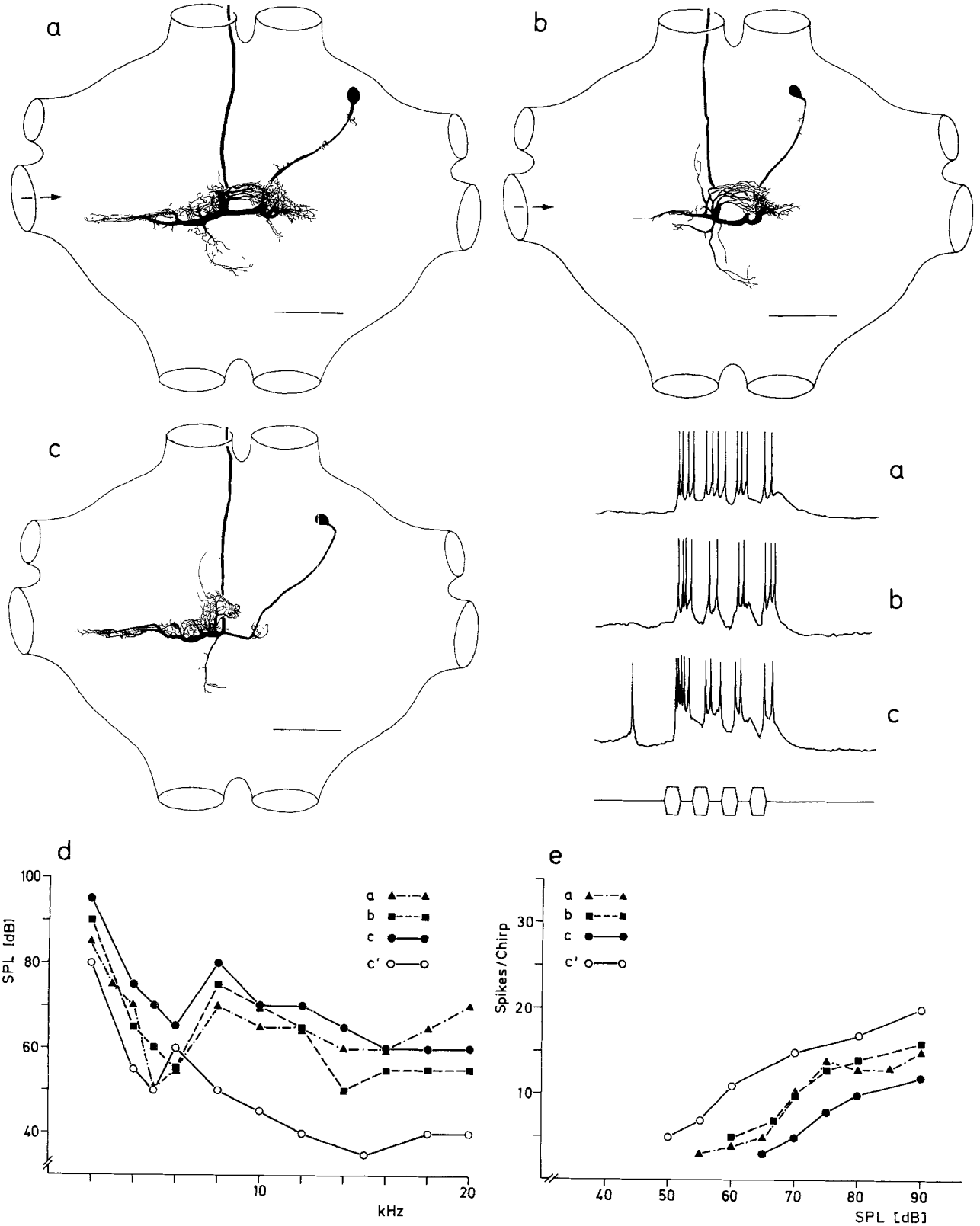

Fig. 4a–f. Morphology and physiology of Ascending Neurons (AN2s) in unilaterally deafferented (**a, b**) and intact (**c**) animals; arrows denote the deafferented side, scale 200 µm. Responses to a chirp of a simulated song (5 kHz, 80 dB SPL) are shown. **d** threshold and **e** 5 kHz intensity/response functions of AN2 neurons. **a–c** denote those curves relating to the corresponding drawn neurons (**a–c**). The normal range of variability in AN2 responses is outlined by curves c and c′, which are taken from two separate intact animals

at 5 kHz. Absolute thresholds can vary greatly among individuals.

AN2s with major arborizations on the intact side (AN2s of the intact side) in unilaterally deafferented animals are grossly similar to those in intact animals. However, the identified AN2s of the deafferented side ($N=5$) sprout branches which cross (via the anterior ring tract) from the deafferented side to the auditory neuropil on the intact side (Figs. 1e, f; 4a, b). The amount of arborization on the operated side is greatly reduced, and arborizations originating on the soma side also branch much more profusely than they do in intact animals. Finally, small fields of arborization are observed along the neurite, often very close to the soma itself.

Physiologically, AN2s show no sign of inhibition from the intact (soma-ipsilateral) ear, but rather strong excitation (Fig. 4a, b). Copying of chirp structure, threshold curves and intensity characteristics of these AN2s exhibiting extensive sprouting are all within the ranges observed for AN2s of intact animals (Fig. 4d, e).

Discussion

Regeneration, transplantation and lesion experiments are often used in two kinds of studies: to follow the differentiation, specificity and determination of sensory and motor systems (Sperry 1944, 1963; Palka and Edwards 1974; Clark 1976; Murphey et al. 1975, 1976, 1981; Murphey and Levine 1980; Denburg 1982; Schmidt 1982; Whitington and Seifert 1982; Murphey and Lemere 1984), and to analyze compensation mechanisms in behavior (von Holst 1950; Precht 1978; Vardi and Camhi 1982a, b; Page 1983). A model system for the clarification of such questions at the level of identified neurons has been provided by the cercus-to-giant fiber system found in cockroaches, crickets and grasshoppers. Here the entire cercus regenerates with all its sensory neurons which project to the normal target region in the terminal ganglion and make connections with appropriate interneurons (Palka and Edwards 1974; Murphey and Levine 1980; Murphey et al. 1981; Vardi and Camhi 1982a). Contrastingly, the cricket tympanal organ shows little or no sign of regeneration or differentiation of sensory neurons in regeneration and transplantation experiments (Ball 1978; Biggin 1981). One reason for this difference may lie in the delayed postembryonic development of the cricket tympanal organ (Ball and Young 1974; Ball and Hill 1978).

Although in both systems a directed behavioral response remains after permanent unilateral deafferentation (see Vardi and Camhi 1982b; Huber et al. 1984), the interneurons that receive input from the two sense organs are affected differently by the operation. The cercal interneurons do not alter their projection areas; the only morphological effect is a shortening of their dendrites (Murphey et al. 1975, 1976; Murphey and Levine 1980; Murphey and Lemere 1984). By contrast, the auditory interneurons of the cricket send dendritic outgrowths across the midline to invade contralateral auditory neuropil, evidently making new functional connections with auditory afferents on that side. This phenomenon was first reported for an auditory interneuron (Int-1) of the cricket *Teleogryllus oceanicus* (Hoy et al. 1978, 1985; Hoy and Moiseff 1979; Pallas and Hoy 1984); it may be homologous to the neuron AN2 of *Gryllus bimaculatus*.

The newly developing dendrites pass along the anterior ring tract to the opposite half of the ganglion. Branches of the ON2 neuron in intact animals, which connect the two neuropils, also lie in this tract (Wohlers and Huber 1985). That is, the developing dendrites make use of a pre-existing pathway to reach the contralateral neuropil. The end points of the projections are in regions where the auditory neurons of the intact side also terminate.

In the cercal system, deafferentation in the larval stage or in the adult animal increases the excitatory response of interneurons to stimulation of the remaining contralateral cercus (Murphey and Levine 1980; Vardi and Camhi 1982b). Murphey and Levine propose that a possible cause of this effect may be the elimination of inhibitory influences from the contralateral cercus and a change in the cable properties of the dendrites; Vardi and Camhi tend more to regard an enhancement of existing excitatory synapses as an explanation. In the auditory system of the cricket, on the other hand, strong contralateral excitation of neurons of the deafferented side, at least in the case of AN1, can be explained only by new connections between the interneurons and the afferents of the contralateral side, because in the intact animal this cell is apparently neither excited nor inhibited by stimulation of the opposite ear. The cells ON1 and AN2 receive inhibitory inputs from the contralateral ear. In an otherwise intact animal, when one omega cell is eliminated, both the mirror-image partner cell and the AN2 of the contralateral side are no longer inhibited; additionally, weak excitation via

the contralateral ear is unmasked (Selverston et al. 1985). However, this contralateral excitatory influence is much too weak to account for the strong excitatory responses of ON1s and AN2s reported here, and is even more striking because the mirror-image omega cell is still present.

The conclusion drawn from the morphological and physiological data is that all three types of auditory neurons of the deafferented side establish functional contacts on the intact side. Thus, the responses differ from those of the same cell types in intact animals only in that the excitation is coming from the 'wrong' ear. The resemblance between the threshold curves of these neurons and those from intact animals implies that similar sets of afferents are recruited. AN1 remains sharply tuned to 5 kHz and AN2 remains a broad-band neuron. The efficacy of the synapses also appears to be normal, in view of the finding that the intensity characteristics are within the range of intact animals. It may be that particular receptor types, regardless of the side of the animal on which they originate, have a chemical specificity that causes the appropriate interneurons to make contact with them. In the case of the omega neurons, the correlation of dendrite growth with the response properties is particularly clear. That is, a normal response occurs only if the dendrites have reached the intact auditory neuropil. If they fail to do so, the excitation is distinctly weaker and the response decreases strongly at higher intensities. This is probably due to the inhibition mediated by the omega cell of the intact side. The remaining excitation in this case could come either directly from receptor fibers originating on the intact side that had grown across to the deafferented side, or from other neurons with bilateral connections.

Even in an animal with only one ear, the central nervous system retains functional auditory pathways on both sides. Assuming that the neurons considered here are involved in acoustic orientation, their post-operative properties should have some consequences for phonotaxis. The fact that animals with regenerated legs lacking one ear show much more accurate tracking than animals with a foreleg amputated as an adult (Huber et al. 1984; Schmitz et al., in prep.) finds a surprising correlate in these modified prothoracic cells. Although a correlation with the behavior is not yet clear in detail, one may speculate about ways the resulting bilateral activity might underlie orientation. The direction of a sound source could be determined, for instance, by successive measurement and comparison after circling movements. In this case a functional pathway on the deafferented side would not be necessary, but could be used for more accurate determination of the direction of the highest sound pressure level. The precise shape of the intensity curve and the balance of neurons would be unimportant. But if orientation results from comparison of the excitation of the right and left members of these prothoracic cell pairs even in one-eared animals, a threshold difference and a difference in the slope of their intensity characteristics is necessary. Given this prerequisite, if the directional characteristics of the two sides – resulting from the different intensity functions of the central neurons – do not intersect, the result must be continuous circling in one direction. If they do intersect, there is a point of excitatory equilibrium and hence a stable course direction only at certain intensities. The results of behavioral tests may provide some evidence for this kind of mechanism. Consistent lag angles occur in animals that were deafferented in a larval instar over an intensity range of 20–30 dB (Schmitz et al., in prep.). In contrast, the range of consistent tracking is about 40–50 dB in intact animals (Schmitz 1985). However, further behavioral and electrophysiological studies will be required to determine if one of the mechanisms discussed here is responsible for the one-eared phonotaxis of crickets.

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