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Excitable Properties of Olfactory Receptor Neurons

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Action potential-generating properties of olfactory receptor neurons in the olfactory epithelium of the salamander, *Ambystoma tigrinum*, were studied in control animals, and 2 and 4 weeks after olfactory nerve transection. The threshold for impulse generation in response to injected current was extremely low (74 ± 46 pA). In addition, the discharge frequencies of the receptor neurons were exquisitely sensitive to small increments of injected current. These high sensitivities may be characteristic of small neurons and stand in contrast to the much lower sensitivities reported for large neurons. The high sensitivity has important implications for the input–output functions of this cell. After nerve transection, both the threshold and the frequency sensitivity decreased. These changes appear to be associated with increased potassium conductance, suggested by prominent membrane rectification and reduced amplitudes of later membrane action potentials in the spike trains. The olfactory receptor neuron appears to be a favorable model for exploring these properties.

The olfactory epithelium is a unique structure with the capacity in the adult for generation of new sensory receptor neurons from stem cells (Graziadei, 1973). Normally, the sequence of receptor neuron differentiation, maturation, and death proceeds at a slow rate during adult life (Graziadei and Monti Graziadei, 1978). Transection of the olfactory nerve, which contains the axons of the receptor neurons, provides a powerful stimulus to the system: virtually all the receptor neurons degenerate and are replaced by a new population of receptor neurons differentiated from the stem cells (Graziadei, 1973).

Analysis of the physiological properties of olfactory receptor neurons following nerve transection began with the pioneering studies of Simmons and Getchell (1981a, b) using extracellular recording techniques. Building on these studies, we have carried out an intracellular analysis that characterized the membrane properties of 3 types of epithelial cells—mature receptor neurons, immature receptor neurons, and supporting cells (Masukawa et al., 1983, 1985a, b)—in the normal and regenerating epithelium. We report here an extension of that study, in which we have first analyzed the sensitivity of the normal receptor neuron to injected current. The results show that this neuron combines a low threshold for impulse initiation with a high sensitivity of impulse frequency to small increments of injected currents. Both the threshold and the frequency sensitivity increase following nerve transection. These changes appear to be correlated with differences in membrane properties of newly developing neurons.

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Materials and Methods

Experiments were carried out on olfactory epithelia from normal tiger salamanders (land phase), *Ambystoma tigrinum*, and 2 and 4 weeks after olfactory nerve transection. The techniques used for transection were identical to those described previously (Masukawa et al., 1985b). Briefly, the animal was cooled and immobilized on ice and subcutaneously injected with xylocaine in the area of the surgery. The olfactory nerves were exposed and cut bilaterally with ultrafine scissors. A small piece of gelfoam was placed over the transection site to control bleeding. The surgical area was closed and cleansed with 70% alcohol.

The procedures for surgery and for maintaining the animals after surgery were similar to those used by Simmons and Getchell (1981a, b). Most animals seemed to tolerate the surgery well; those that did not typically did not survive more than 1–2 d. The animals were maintained in plastic boxes, which were periodically cleaned, and kept at room temperature. Animals surviving for the different periods, 2 and 4 weeks, were active and appeared healthy.

Animals were sacrificed after 2 or 4 weeks, and their dorsal epithelia were removed and used for intracellular recording. The completeness of transection was verified by inspection under the dissecting microscope during removal of the epithelium for recording and, in some cases, by histological preparations of serial sections through the rostral portions of the olfactory bulbs. After the recordings, several epithelia at each time period were prepared for histological examination. These showed changes in the histology of the epithelium produced by the transections that were essentially identical to those described by Simmons and Getchell (1981a).

Intracellular electrical recordings were made from these epithelia as described earlier (Masukawa et al. 1983, 1985a, b). The chamber was perfused by normal oxygenated Ringer's solution (104 mM NaCl, 1.82 mM KCl, 3.6 mM $CaCl_2$, 0.71 mM $MgCl_2$, 26 mM $NaHCO_3$, 11 mM glucose) and bubbled with 95% O_2, 5% CO_2, pH 7.3, at room temperature. Microelectrodes were filled with 4 M potassium acetate; they had tip resistances of 150–200 MΩ. Receptor cells were distinguished from supporting cells by several criteria (see Masukawa et al., 1985a), including the relative depth of penetration, magnitude of the resting membrane potential and input resistance, and action potential generation. Current was passed through the recording electrode using an active bridge circuit amplifier capable of balancing electrode tip resistances up to 300 MΩ. Changes in the electrical properties as examined in normal olfactory receptor cells were determined in cells after nerve transections. Recordings were made in the central region of the dorsal epithelial tissue. The cell input resistances were determined using hyperpolarizing pulses (Masukawa et al., 1985a, b).

As previously noted (Masukawa et al., 1983, 1985a, b), receptor neurons are difficult to record from, presumably because of the small size of these cells (cell body diameter is 10–12 μm: Simmons and Getchell, 1981a). A yield of 2–3 successful penetrations in a preparation was typical, with stable recording conditions lasting 5–15 min. Similar criteria for successful penetrations applied for all 3 experimental groups (control, and 2 and 4 weeks posttransection).

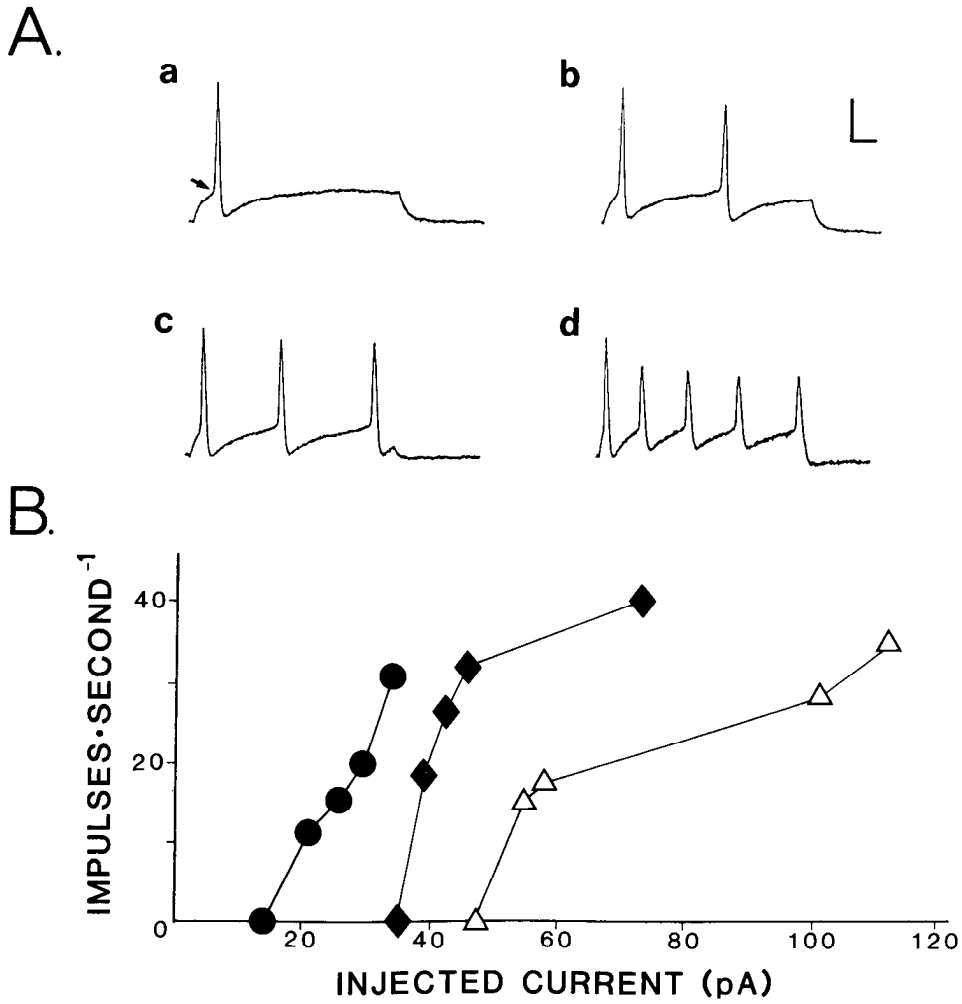

Figure 1. Impulse response of control receptor cells to current injection. *A*, Intracellular responses of a receptor cell to depolarizing current injections of different intensities. The strength of the injected current pulse increases from *a* to *d*. Resting membrane potential was −45 mV, and the input resistance was 160 MΩ. *Arrow* indicates point of threshold measurement in this cell. *B*, Firing frequency of the second action potential (inverse of the time interval between the first and second action potential in the train) plotted against amount of injected current. Different symbols refer to 3 representative cells. The values from the cell in *A* are plotted as ◆s. The threshold currents for eliciting the first action potential in each cell are indicated along the abscissa. Calibration bars, 40 mV and 20 msec.

The data were recorded on FM tape (bandwidth, DC–5000 Hz) and digitized and stored in a LSI 11/23 computer. A program written in BASIC 23 (Cheshire Data) was used for data acquisition, analysis, and display.

Results

Properties of repetitive discharge in normal receptor neurons

In the normal epithelium we analyzed 11 olfactory receptor neurons for the present study (resting membrane potential, −57.4 ± 21.4 mV; input resistance, 259 ± 157 MΩ; means ± SD). All cells satisfied the physiological criteria established by Masukawa et al. (1985a) for mature receptor neurons, including a high input resistance (at least 80 MΩ), a moderate resting membrane potential (at least −30 mV), and the ability to generate impulses in response to injected depolarizing current.

In response to injected currents, these cells showed patterns of impulse generation typical of neuronal responses, as seen in Figure 1*A*. Part *a* shows the single impulse response characteristically generated near threshold by a very weak injected current. Note the slowly rising charging transient, the smooth conformation of the action potential, and the prominent afterhyperpolarization phase. Slightly higher currents are represented in Figure 1*Ab* and 1*Ac*. This produced a faster rising charging transient leading up to the first action potential, which was followed by later impulses. Note the slowly rising depolarization leading to generation of the later impulse, as is typical of slowly firing neurons (cf. Granit et al., 1966a, b). With a large current (Fig. 1*Ad*) there was a very fast initial depolarization, and the first action potential was followed by a multiple-impulse discharge. The action potentials at higher frequencies characteristically had smaller amplitudes.

The frequency response for this cell is plotted in Figure 1*B* (diamonds). The first point (on the abscissa) indicates the threshold current for eliciting the first spike of approximately 35 pA. The firing frequency calculated for the first interspike interval can be seen to increase sharply with small amounts of added current. At the highest current level, the curve is less steep.

Threshold for initial action potential generation

An outstanding property of the response of the receptor neurons was the low threshold current needed for generation of the initial impulse. The values for the threshold currents ranged from 11 to 144 pA, with an average value of 74 ± 46 pA (mean ± SD). The variation between cells was not correlated with differences in resting membrane potential.

A related property of interest was the threshold voltage for eliciting the initial impulse. In the example shown in Figure 1*Aa*, the point on the charging transient from which the action potential arose at threshold is indicated by the arrow; in Figure 1*Aa* the threshold was 22 mV. The values for the population of cells ranged from 9 to 38 mV (average, 21.2 ± 10.0 mV). As

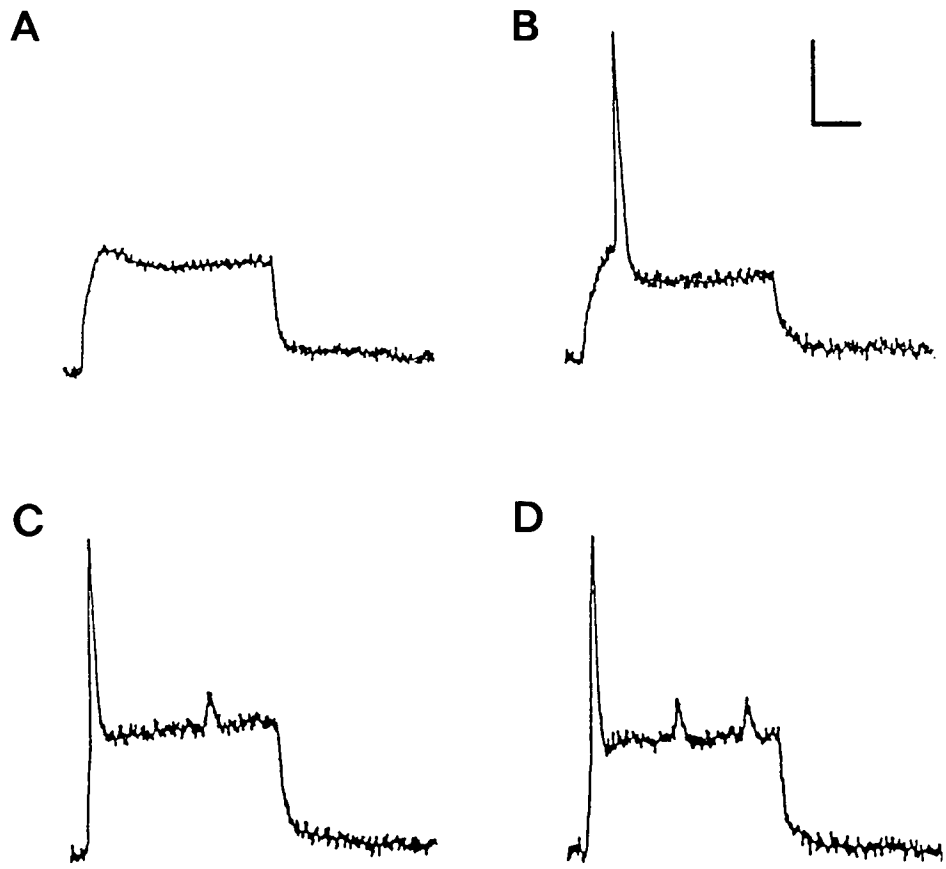

Figure 2. Intracellular responses of a receptor cell 2 weeks after olfactory nerve transection to depolarizing current injections of different intensities. The strength of the injected current pulse increases from *a* to *d*. Calibration bars, 40 mV and 20 msec.

in the case of threshold currents, the threshold potentials did not appear to be significantly correlated with resting membrane potentials. The penetrated cells in this sample did not show signs of injury discharges; resting rates of impulse firing were <1 Hz.

Properties of repetitive discharges

The properties of repetitive discharges in this cell population are indicated in 2 further examples in Figure 1*B*. These 3 examples summarize several important features of the responses in the normal epithelium. First, up to approximately 20 impulses sec^{-1}, action potential frequency increased as a linear function of injected depolarizing current. In most cells the curves extended upwards in a linear fashion from the threshold values for the initial impulse. At higher current intensities, some cells gave evidence of lower sensitivity (flatter curves) in the current–frequency relation (e.g., ◆ and △).

In order to make a more quantitative assessment of the current–frequency relations, we calculated the increases in frequency produced by increases in injected current in our most completely characterized cells. Six cells showed a simple linear current–frequency relation throughout the range of currents tested. The most sensitive cell in this group showed an increase in frequency of firing from 6 to 28 impulses sec^{-1} in response to an increase in current intensity of 13 pA. This gave a value of approximately 0.9 impulses sec^{-1} pA^{-1}. This ratio of impulse frequency to injected current is a measure of the frequency sensitivity of the impulse-generating membrane to injected current. The values of this ratio for this group of cells ranged from 0.6 to. 1.7 impulses sec^{-1} pA^{-1} (mean, 1.0 ± 0.4). Two other cells showed very high sensitivities at lower frequencies (2.3 and 2.9 impulses sec^{-1} pA^{-1}) and very low sensitivities at higher frequencies (0.3 and 0.5 impulses sec^{-1} pA^{-1}).

Properties of repetitive discharge in receptor neurons during regeneration

A total population of 20 cells was studied after transection, 8 cells 2 weeks after olfactory nerve transection (48 ± 4 mV, 329 ± 96 MΩ) and 12 cells 4 weeks after transection (39 ± 7 mV, 258 ± 145 MΩ). All of the cells 4 weeks after transection satisfied the physiological criteria established by Masukawa et al. (1985a) for mature receptor neurons, as mentioned above.

Two weeks

Two weeks after nerve transection, olfactory receptor neurons responded to injected currents with only a single impulse (4 cells) or with multiple but low-amplitude spikes (4 cells) (Masukawa et al., 1985b). An example of a cell able to generate a spike train is shown in Figure 2. As the strength of the current pulse was increased (Fig. 2, *A* and *B*) a single impulse was generated. When the current was increased further (Fig. 2, *C* and *D*), a second and then a third action potential were generated. The amplitude of the first impulse was not affected when the current strength was increased, but the amplitudes of the later action potentials were greatly attenuated. Note the marked long-duration rectification, as seen in the response sag in Figure 2, *A* and *B*.

In the cells studied 2 weeks posttransection the threshold for impulse initiation ranged from 100 to 220 pA, with an average of 176 ± 41 pA (Fig. 3). This value is significantly higher ($p < 0.05$) than that in the population of control cells (see above). This higher threshold is illustrated by the graph of Figure 3, in

which the threshold for the cell of Figure 2 (▲) and another cell (□) are compared with that of a cell in normal epithelium (◆).

As in control epithelia (see above), no correlation was found between threshold potentials and resting membrane potentials. The threshold values ranged from 16 to 50 mV, with an average value of 38.4 ± 12.7 mV.

Since repetitive firing was limited in cells 2 weeks posttransection, being either absent or confined to very small spikes that tend to merge with the baseline noise, it was not possible to analyze the sensitivity of repetitive firing to injected current as closely as in controls. In several examples, there appeared to be a tendency toward a lower sensitivity (Figs. 2, 3).

Four weeks

Four weeks after olfactory nerve transection most of the recorded olfactory neurons were able to generate action potential trains, as previously reported (Masukawa et al., 1985b). An example is shown in Figure 4. In this cell population the threshold currents for impulse potential initiation were still significantly higher than in the normal receptor cells. The values observed at this time period ranged from 95 to 340 pA, with a mean of 191 ± 71 pA. The threshold potentials were independent of resting membrane potentials. The values for the threshold potentials ranged from 16 to 40 mV (mean, 29.3 ± 13.4 mV), not significantly different from the values observed in control cells.

Plots of the current–frequency relation for 2 cells showing repetitive firing are given in Figure 5, together with the plot for the control response from Figure 1*B*. The current sensitivities were calculated for each of the cells analyzed. Below 20 impulses sec^{-1} there was a sensitivity of 0.5 ± 0.3 impulses sec^{-1} pA^{-1}, while above 20 impulses sec^{-1} there was a sensitivity of 0.1 ± 0.1 impulses sec^{-1} pA^{-1}. Both these values were lower than in normal controls.

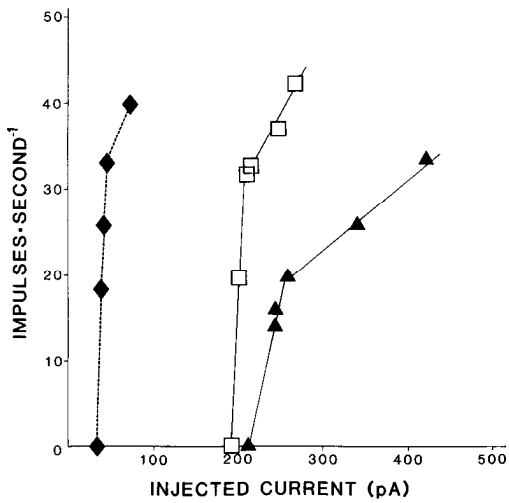

Figure 3. Firing frequencies of action potentials 2 weeks after olfactory nerve transection plotted against amount of injected current. Different symbols refer to 3 representative cells; values from the cell represented in Figure 2 are plotted as □s. Control cell values from Figure 1*A* are also plotted for comparison (◆). The threshold current pulse eliciting the first action potential in each cell is indicated along the abscissa.

Discussion

Threshold for action potential initiation

The results show that the threshold currents needed to elicit an impulse in the normal olfactory receptor neuron of the salamander are extremely low (11–144 pA). Similar results have been reported in the lamprey (19–400 pA) (Suzuki, 1977). To our knowledge these ranges include the lowest thresholds yet reported for action potential initiation in a neuron using conventional intracellular techniques. For comparison, it can be estimated from the report of Gustafsson et al. (1978) that the impulse threshold for cat dorsal spinocerebellar tract neurons was in the range of 0.5–1.0 nA (see their fig. 3C). Other reported values are 10 nA for cat motoneuron (Granit et al., 1966a, b), 0.3–0.5 nA for hippocampal pyramidal neurons (Schwartzkroin and Slawsky, 1977), 0.1–2 nA for slow pyramidal tract neurons, 0.7–3.1 nA for fast pyramidal tract neurons (Oshima, 1969), and 0.25 nA for thalamocortical cells (Llinás and Jahnsen, 1982). Thus, the lowest threshold currents for the olfactory receptor neurons are an order of magnitude below those for the other neurons, and 3 orders of magnitude lower than those for motoneurons.

The low value of threshold current in the olfactory receptor neuron reflects the fact that this is a very small neuron with a very high input resistance. In the salamander, the receptor cell body has a diameter of 10–12 μm (Graziadei, 1973; Getchell, 1977; Graziadei and Monti Graziadei, 1978; Rafols and Getchell, 1983); there is a single dendritic process, 50–150 μm in length and approximately 1 μm in diameter, and an unmyelinated axon approximately 0.2 μm in diameter. We have verified these dimensions in salamander receptor neurons by intracellular injection of Lucifer yellow (Masukawa et al., 1985a).

The high sensitivity to small currents reported here has important functional implications. As noted previously (Masukawa et al., 1985a), the receptor neuron is very electrotonically compact. The high input resistance (219 ± 92 MΩ, as recorded intracellularly by Masukawa et al., 1985a) means that a small conductance change in the receptor membrane in the cilia gives a large receptor potential, and the electrotonic compactness means that this potential spreads to the axon with relatively little decrement. A computational compartmental model has shown that for a neuron with a low threshold to injected current (e.g., such as the cells in Figs. 1 and 2), the same threshold transient could be generated by a sensory conductance change of as little as 180 pS (Hedlund et al., 1984). Such a small conductance change could be obtained by the synchronous opening of only a few channels, if the conductances were in the range of those of channels at the neuromuscular junction (see Latorre and Miller, 1983). This in turn implies that olfactory neurons may respond at threshold to the presence of only a few odor molecules (Hedlund et al., 1984). These results support the suggestion that small neurons in the nervous system can display high sensitivities, such that a single synapse could elicit an impulse output, in contrast to large neurons, in which summation of many inputs is necessary to reach firing threshold (Hedlund et al., 1984). Dryer (1985) drew a similar conclusion from binding studies.

Recently, Firestein and Werblin (1985), who used whole-cell patch recordings from freshly dissociated salamander olfactory receptor neurons, reported input resistances ranging up to 2 GΩ (2×10^9 Ω). These results thus give even stronger support to the present evidence regarding the high current sensitivity and electrotonic compactness of the olfactory receptor neuron. The lower values of input resistance obtained with conventional recordings, such as in the present study, could be due to Ca^{2+}

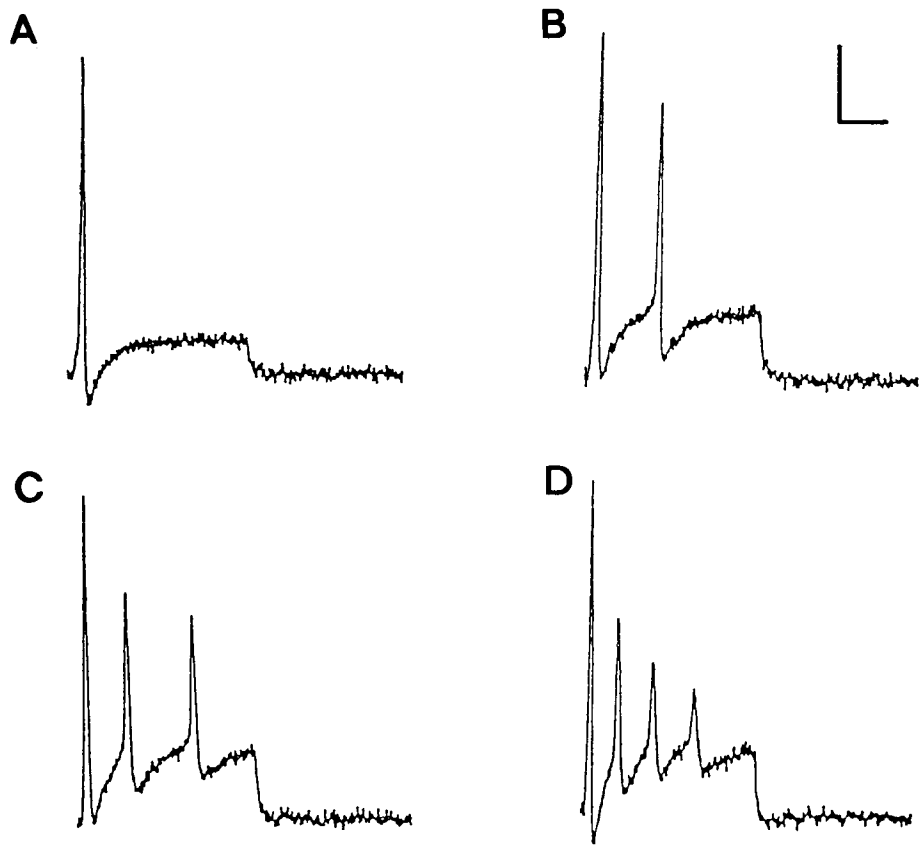

Figure 4. Intracellular responses of a receptor cell 4 weeks after olfactory nerve transection to depolarizing current injections of different intensities. The strength of the injected current pulse increases from *a* to *d*. Resting membrane potential was −40 mV, and the input resistance was 150 MΩ. Calibration bars, 40 mV and 20 msec.

influx at the site of penetration, activating a calcium-dependent K conductance that lowers the input resistance while maintaining the membrane potential relatively polarized (Walsh and Singer, 1980; A. Marty, personal communication). Conversely, washout or inactivation of channels by the seal of the pipette tip could contribute to the whole-cell patch recordings (Galvan et al., 1985). Careful comparisons of results obtained with the 2 methods in the same laboratory (Galvan et al., 1985) should help to resolve this question in different neurons.

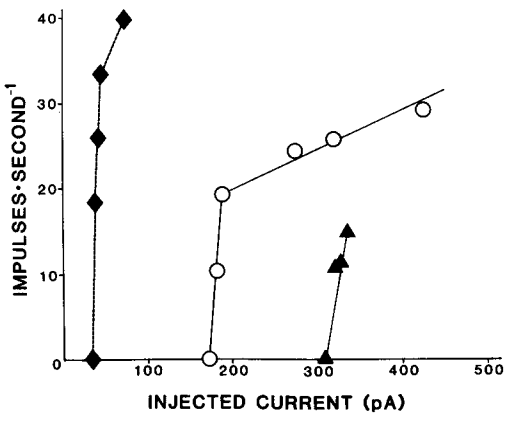

Figure 5. Firing frequencies of action potentials 4 weeks after olfactory nerve transection plotted against amount of injected current. Different symbols refer to 3 representative cells; values from the cell represented in Figure 4 are plotted as ▲s. Control cell values from Figure 1*A* are also plotted for comparison (◆). The threshold current pulse eliciting the first action potential in each cell is indicated along the abscissa.

Repetitive firing in response to injected current

Associated with very low thresholds are very small currents needed to elicit repetitive impulse firing in normal neurons. The current sensitivity was close to 1 impulse sec^{-1} pA^{-1}, i.e., for each added pA of current above threshold there was an increase in firing frequency of 1 impulse sec^{-1}. This sensitivity contrasts markedly with values for other neurons reported in the literature, for example, approximately 0.001 impulses sec^{-1} pA^{-1} for motoneurons (fig. 1, Granit et al., 1966a, b), 0.008–0.03 impulses sec^{-1} pA^{-1} for pyramidal tract neurons (fig. 2, Oshima, 1969; fig. 4, Calvin and Sypert, 1976), and 0.07 impulses sec^{-1} pA^{-1} for dorsal spinocerebellar tract cells (fig. 1B, Gustafsson et al., 1978). Thus, repetitive firing by the olfactory receptor neuron is 3 orders of magnitude more sensitive to injected current than in the motoneuron, and more than one order of magnitude more sensitive than the next most sensitive cell, the dorsal spinocerebellar tract neuron. As in the case of the very low impulse threshold, the high-frequency sensitivity appears to be associated with the high input resistance of the receptor neuron, such that small increments of current result in relatively large increments in the membrane depolarizations that underlie repetitive impulse generation.

The modulation of impulse discharges demonstrated in the present study occurs over a range of very low firing frequencies. The highest rates, approximately 50 Hz, appear nonetheless to be near the physiological maximum for these cells, as judged from the literature (Suzuki, 1977; Getchell and Shepherd, 1978a, b; Trotier and MacLeod, 1983) and by the appearance of attenuated action potentials during discharges with the strongest stimulation. The olfactory receptor neuron thus appears to be adapted not only to respond at very low threshold, but also to

fire at relatively slow discharge rates. These low firing rates may be controlled by transient K^+ conductances, as in other neurons with low firing frequencies (Connor and Stevens, 1971).

Posttransection changes in excitable properties

Several specific changes have been observed in the excitable properties of olfactory receptor neurons in the 2–4 week period after olfactory nerve transection. First, the threshold for generation of the initial impulse response to injected current is significantly higher compared to normal receptor neurons. Second, there is prominent rectification and spike afterhyperpolarization, suggested as due to increased membrane potassium conductances. Third, there is a decreased frequency sensitivity to injected current, which is also likely to be correlated with increased membrane potassium conductance. Small spike-like potentials during the response to current injection indicate the presence of more than one site of action potential initiation.

The functional significance of these changes in membrane excitability is not yet clear. Since olfactory nerve transection results in synchronous generation of new receptor neurons, it may be assumed that these changes are associated with the differentiation of new neurons and the maturation of the excitable properties of these neurons. The earliest events must be associated with differentiation of new neurons from the stem cells. It is interesting to note in this respect that K channels play a prominent role in mitogenesis of lymphocytes (Cahalan, 1985); we similarly hypothesize a role for K^+ in mitogenesis of receptor neurons following nerve transection. Subsequent changes in electrical properties may be related to the sequence of outgrowth of the axon, contact by the axonal growth cone with the olfactory bulb, and establishment there of synaptic contacts with bulbar neuronal dendrites in the olfactory glomeruli. The higher impulse thresholds and attenuated repetitive responses appear to be immature properties of neurons that have not yet established fully functional synapses in the olfactory bulb; these properties may protect the neuron from overstimulation.

It appears therefore that the immature neuron expresses several types of membrane potassium conductances that may be involved in mitogenesis and subsequently exert control over depolarizing (Na and Ca) conductances and limit thereby the activity of the neuron. Maturation of low-threshold, slowly adapting impulse responsiveness must then involve anterograde signals from the receptive dendritic sites and retrograde signals from the axonal synaptic sites that control the expression and insertion of channel proteins in their appropriate numbers and sites. The posttransection olfactory epithelium should provide a valuable model for documenting membrane properties of a defined neuronal population in relation to these events.

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