THE DUAL ACTIONS OF THE CENTRIFUGAL NERVOUS SYSTEM IN THE Olfactory BULB

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Two kinds of potential waves have been well known in the olfactory bulb. One is the intrinsic wave which appears spontaneously in the bulb (Adrian, 1950). The other one is the induced wave which appears in accordance with respiration (Hasama, 1934, Adrian, 1950) or in response to electrical or natural stimulation of the olfactory epithelium (Ottozon, 1959 b, Takagi & Shibuya, 1960 a, b, Takagi, Shibuya, Higashino & Arai, 1960). The influences of the higher brain centers upon these two kinds of bulb activities were studied in the cat by Kerr & Hagbarth (1955) and Hernández-Péon, Lavín, Alcocer-Cuaron & Marcelin (1960), in the rabbit by Yamamoto & Iwama (1960) and in the frog by Ottozon (1959 a). However, in these studies stimulation was electrically applied by means of metal electrodes inserted into the high brain centers. The effects of natural sensory stimulation upon the activity of the olfactory bulb have been poorly investigated (Hernández-Péon et al., 1960).

In this paper, the effects of various sensory stimulations upon the induced activity of the olfactory bulb are studied. Thus, it is intended to clarify the mechanism of the centrifugal nervous activity in the bulb. The biological role of the nervous system is considered.

METHOD

Preparations. Frogs, Rana nigromaculata were used. In case of visual, auditory, and gustatory stimulation, frogs were decapitated, and the heads were put on the cork plate. In case of cutaneous stimulation, frogs were anaesthetized by nembutal and put on the cork plate. The olfactory epithelium and the whole brain were exposed.

In case of cutaneous stimulation, the other sense organs, namely tympanic membranes, eyeballs, and tongue were removed before experiment in order to get rid of the influences from other sources. By the same reason, in case of visual, auditory and gustatory stimulation, two out of these three sense organs were removed.

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respectively. At least thirty minutes were supposed to be necessary before the after-effect of the above surgical operation disappears. Each experiment was started after this interval.

Stimulation. As cutaneous stimuli, pain, touch, warmth and cold were applied. Pain was given to the limbs, the fingers or the hip by pricking with a needle or pinching with forceps. Touch was given to the limbs, the dorsum or the sides of the abdomen. Warmth and cold were given to the above parts by means of cotton wools containing warm (about 40°C) and cold water (near 5°C) respectively. As visual stimulus, light of 20 to 30 lux was put on at a distance of 10 cm above the eyeballs after enough dark adaptation. As auditory stimuli, sounds of 100 to 8,000 c.p.s. were given for a second at the magnitudes of 40 to 50 phones by means of an electronic oscillator. As gustatory stimuli, a few drops of distilled water, sodium chloride solution (5%), cane sugar solution (5%), acetic acid solution (1%), and quinine solution (1%) were dripped on the tongue.

In order to induce the activity of the olfactory bulb, the olfactory epithelium was stimulated with an electrical pulse or an odour. For electrical stimulation, a pair of thin silver wires were put across the olfactory eminentia. For odour stimulation, the saturated vapour of ether was used (TAKAGI et al., 1960). It was drawn into a 20 ml syringe and was applied onto the olfactory epithelium through a thin lucite tube at a constant velocity. In order to obtain clearer results, electrical stimulation was chiefly employed. Odour stimulation was tried only complementarily.

Recording. The bulb potentials were picked up with silver wire electrodes. They were amplified by RC coupled amplifiers with a time constant of 0.1 sec. and recorded by an ink-writing recorder.

RESULTS

I. Cutaneous stimulation. When pain was given, the induced waves due to odour stimulation were always inhibited (FIG. 1). It was shown that the 'on'- and 'off'-induced waves appear by the application of ether vapour (TAKAGI et al., 1960). It seemed that 'off'-waves were inhibited more markedly than the 'on'-

![Fig. 1. Potential waves of the olfactory bulb induced by the application of ether vapour. Top: Control. Bottom: Inhibition of the induced wave by previously applied pain. A broken line and continuous lines indicate the application of pain and ether vapour respectively.](image-url)
waves. It is noteworthy that the degree of inhibition increases in accordance with the degree of pain stimulation. Thus, Fig. 2 shows that the electrically induced wave gradually decreased its amplitude and finally disappeared, when the intensity of pinching was increased little by little. Moreover, it shows that the induced wave reappeared immediately after pinching was stopped, but it did not recover the original amplitude for some time. This latter phenomenon may probably be due to the remaining dull pain which lasts for some time after stimulation was stopped. The results are summarized in Table 1.

When touch was given, the electrically induced wave showed an increase in amplitude by twenty to thirty microvolts in most cases (Fig. 3). Similarly, the induced waves due to odour stimulation were also augmented in many cases. The results were not different, even when cutaneous stimulation was given to different parts of the body.

When warmth was given, the electrically induced wave decreased its amplitude in some cases, but it did not show any change in other cases. On the contrary, when cold was given, the electrically induced wave increased its amplitude in some cases (Fig. 4), but it did not show any change in other cases. Similar results were obtained in case of odour stimulation. The results are summarized in Table 1.
II. Visual stimulation. When light was switched on above a dark-adapted eye, the electrically induced wave usually decreased its amplitude (Fig. 5). The results are summarized in Table 2.

III. Auditory stimulation. The actions of the sounds of various frequencies on the electrically induced wave were studied. No significant changes were found in many cases. But whenever some changes were found, they were inhibitory. Inhibition occurred more often in the frequencies of 500 to 3,000 per second than in the other frequencies. Similar results were found in case of natural olfactory stimulation. The detailed results are shown in Table 3.

IV. Gustatory stimulation. When distilled water was dripped on the tongue, the electrically induced wave increased its amplitude in most cases. On the contrary, the reverse was generally the case, when the solutions of sodium
TABLE 3
Auditory stimulation

<table>
<thead>
<tr>
<th></th>
<th>Augmentation</th>
<th>Inhibition</th>
<th>No change</th>
</tr>
</thead>
<tbody>
<tr>
<td>100 cps</td>
<td>0</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td>500 cps</td>
<td>0</td>
<td>13</td>
<td>16</td>
</tr>
<tr>
<td>1000 cps</td>
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</tr>
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<td>1500 cps</td>
<td>0</td>
<td>13</td>
<td>10</td>
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<tr>
<td>2000 cps</td>
<td>0</td>
<td>12</td>
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</tr>
<tr>
<td>3000 cps</td>
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<td>13</td>
<td>14</td>
</tr>
<tr>
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<td>0</td>
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<td>18</td>
</tr>
<tr>
<td>6000 cps</td>
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</tr>
<tr>
<td>8000 cps</td>
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<td>25</td>
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TABLE 4
Gustatory stimulation

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<th></th>
<th>Augmentation</th>
<th>Inhibition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distill. water</td>
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<td>4</td>
</tr>
<tr>
<td>5% NaCl</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>5% Sugar</td>
<td>3</td>
<td>11</td>
</tr>
<tr>
<td>1% Acetic Acid</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>1% Quinine</td>
<td>3</td>
<td>12</td>
</tr>
</tbody>
</table>

chloride, cane sugar, acetic acid and quinine were applied. Similar phenomena were found in case of natural olfactory stimulation. The results are summarized in Table 4.

DISCUSSION

Since CAJAL'S study (1911), the centrifugal nervous pathways from the higher brain centers to the olfactory bulb have been investigated by several histologists (HERRICK, 1924, ALLISON, 1953). Electrophysiological analysis of the functions of these pathways was also attempted. KERR & HAGBARTH (1955) found that the activity of the olfactory bulb of a cat is augmented by low frequency stimulation of the anterior commissure, while it is depressed by high frequency stimulation of the same position. YAMAMOTO & IWAMA (1960a, b) showed that the activity of the olfactory bulb of a rabbit is depressed by stimulation of the reticular formation, while it is augmented by stimulation of the anterior hypothalamus.

It is well known that the olfactory bulb is composed of three kinds of cells. The mitral cell is located in the third (external plexiform) layer and conveys olfactory messages from the glomeruli to the higher olfactory centers. The tufted cell is also in the third layer and conveys the messages to the opposite bulb through the anterior commissure. The granule cell is large in number and is located in the fifth (granular) layer. This is the cell which receives the
centrifugal nerve fibers from the higher centers and extends its axon up to the external plexiform layer to end in contact with the dendrites of the mitral and tufted cells. This is the only histologically known pathway from the higher center to the mitral and tufted cell. Though the precise mechanisms of synaptic actions in the olfactory bulb is entirely open to question, the results obtained by the above physiologists show that there are two groups of centrifugal nerve fibers to the olfactory bulb. Our results support the presence of the two groups and indicate that the activity of the bulb is augmented or inhibited by either of these fibers, depending on the kinds of sensory stimulation.

Hernández-Péon, Sherrer & Jouvet (1956) recorded the click responses in the cochlear nucleus in unanaesthetized unrestrained cats. They found that the responses are diminished in amplitude, while the cat is visually attentive to mice in a bottle, or while it is attentively sniffing fish odour. This indicates that the concentration of attention inhibits the nervous activity of various sensory modalities other than those pertaining to the subject of attention. This was supposed to be the nervous mechanism underlying conversion of attention. From the above and our findings, it can be supposed that sensations of pain, light and sound cause conversion of attention from the olfactory bulb.

On the contrary, the increase in amplitude of the induced wave was observed in case of touch and cold sensation in the skin and water taste in the tongue. They belong to very weak sensations and are presumed to have different roles from the other stimuli which produce clear and strong sensations, such as pain, light and etc. In other words, it is probable that the former sensations only arouse the curiosity, while the latter ones produce pleasant or unpleasant sensations including nociceptive ones. If so, the former sensation may probably raise the attention level of not only the pertaining sensory organ but also of all the other ones. This may be a mechanism for the centrifugal augmentation of the induced activity of the olfactory bulb.

In conclusion, our results suggest that sensations can be divided into two groups: one group of sensations are pleasant or unpleasant and cause concentration of attention to the pertaining sensory nervous system, resulting in conversion of attention from the others, while the other group only causes curious sensation and raises the attention level of general sensory nervous systems. What kinds of sensations belong to which group may depend upon the kinds of animals and in part upon the intensity of stimulus.

SUMMARY

1. The actions of various sensory stimulation upon the induced wave of the olfactory bulb of a frog were studied.
2. The induced waves were inhibited by the application of pain and warmth.
on the skin, light to the eye and sound to the ear. They were also inhibited by the application of sodium chloride, cane sugar, acetic acid and quinine solution onto the tongue.

3. On the contrary, the induced waves were generally augmented by the application of touch and cold on the skin as well as distilled water on the tongue.

4. These findings support the view that there are facilitatory and inhibitory fibers in the centrifugal nervous system from the higher brain centers to the olfactory bulb. The biological functions of these two fiber systems were considered.

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