FUNCTIONAL CHARACTERISTICS OF SINGLE NEURONS IN PIGEON CORTEX

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Cerebral reactions to photic and acoustic stimuli have been studied in birds from recordings of potentials in generalized form (electroencephalograms, electrocorticograms, evoked potentials) [1, 8, 10, and others]. It is still not known how cortical neurons in birds react to other forms of stimulation (tactile, proprioceptive, etc.), and whether response reactions to these different forms of stimulation are produced by different or by the same neurons.

As the solution of these problems is important for an understanding of the functional structure of the cortex from both evolutionary and ecological standpoints, an attempt was now made to examine the detailed arrangement of receptor fields and the connections which individual neurons in the pigeon cortex have with different systems.

METHOD

The experiments were carried out on 28 adult pigeons, in which 106 neurons situated in different parts of the cortex at depths of not more than 1 mm in the medial regions and 0.3-0.6 mm in the lateral regions were examined.

The skull was trephined under local anesthesia. After removal of the dura mater, an annular silver electrode was placed in the trephine opening, which was 2-3 mm in diameter, for the recording of electrocorticograms, required for continuous observation of the functional state of the cortex. The indifferent electrode was attached to the skin in the midline of the frons. Flaxedil or Listenon was injected and artificial respiration instituted.

The spike potentials of single neurons were recorded from within the cell by means of a wolfram microelectrode, the external diameter of the glass-insulated tip being 1-4 μ. A hydraulically operated micromanipulator was used to insert the microelectrodes. The cathode follower used has been described previously [4]. The electrical phenomena were recorded on cinefilm from the oscillograph screen. During an experiment continuous analysis and recording of changes from moment to moment in the impulse rates were maintained, so that the nature and degree of change in background activity could be followed exactly, and receptor field could be quickly discovered and outlined. This record was produced by an electronic ink-writing potentiometer with an integrator [4].

The photic stimulation employed was diffuse illumination of the eyes (300 lux); the acoustic stimulus was a tone of 2000 c/s; tactile stimulation was produced by touching and moving the feathers with a fine brush; and movement of wing, leg, or tail provided proprioceptive stimulation. The pigeon was in a heated atmosphere throughout the experiment, and its body temperature was maintained between 38 and 40°C.

RESULTS

The background activity of the cortical neurons examined varied in rate from 1 to 35 impulses per sec (11.6 ± 1.7), but the rate was generally about 10 impulses per sec. In most cases background activity took the form of single spike potentials, occurring at more or less regular intervals in some, but irregularly in other cases. Less frequently the activity was in the form of rapid bundles and groups of spike potentials (Fig. 1, a-c). Mixed forms were also observed (Fig. 1, b). In practically no case could the spike activity be correlated with the slow waves in

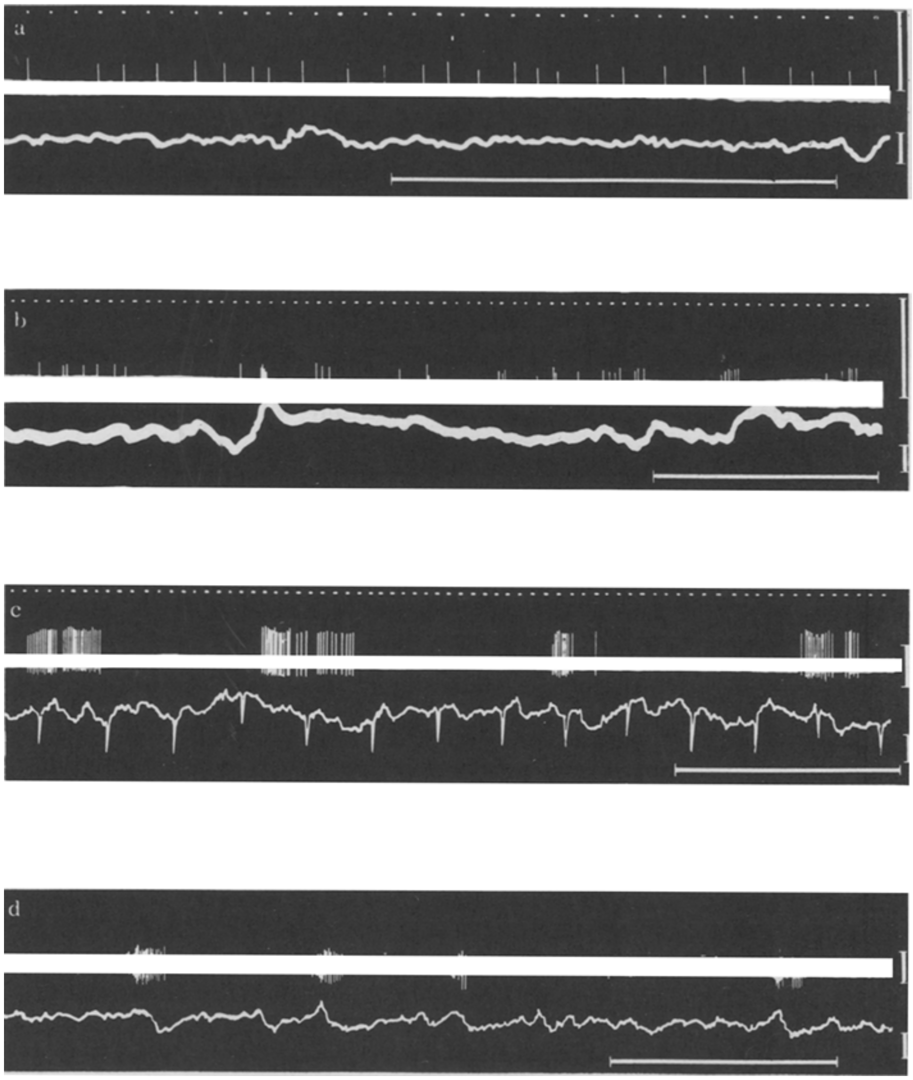

Fig. 1. Types of background activity observed in individual neurons of pigeon cortex (upper tracings). a) Continuous impulsation in form of single spikes; b) mixed type of impulse activity – single and grouped spikes; c) series of spike potentials; d) same type as in c, but impulse activity only seen in association with large waves in electrocorticogram. Lower tracings) superficial electrocorticograms. Scale for microelectrode channel) 5 mV; and for electrocorticogram) 100 μV. Time scale) 1 sec. In c, ECG is superimposed on electrocorticogram.

the surface electrocorticogram (see Fig. 1, a-c). Only occasionally were spike potentials seen to develop concurrently with certain waves (generally large waves) in the electrocorticogram (Fig. 1, d).

The background activity of neurons in the pigeon cortex is thus similar to that of cortical cells in other warm-blooded animals (cat, rabbit, guinea-pig, rat, etc.) [5, 14, 15, 16, 20, 21, and others].

With natural forms of stimulation (photic, acoustic, tactile, etc.) the neuronal reactions manifested themselves either as fast bundles of spike potentials or in the form of more numerous impulses generally, with shorter intervals; inhibition was seen as slowing or, it might be, complete suppression of activity. In the latter case it was difficult to determine latent periods. Reactions in the form of parcels of impulses were seen with photic and acoustic stimuli, while the second type of reaction was generally associated with tactile and proprioceptive forms of stimulation, particularly the latter.

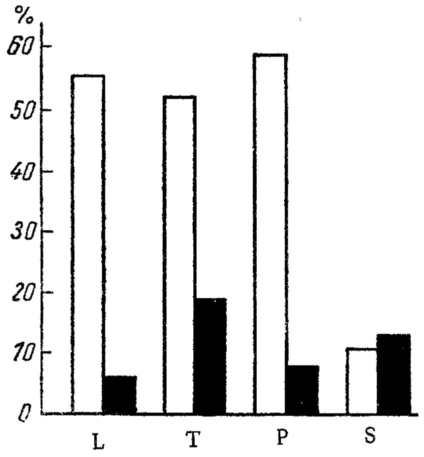

Fig. 2. Distribution of frequencies of activation of cortical neurons of pigeon on photic stimulation of light-adapted retinal (L), tactile (T), proprioceptive (P), and acoustic stimulation (S). White columns) neurons giving positive reactions (including those with inhibitory fields in addition). Black columns) neurons with only inhibitory receptor fields within given system.

The reactions of cortical neurons to light and sound, which were either of "on" or "on-off" type, presented some noteworth features. In occasional cases the "on" component was combined with inhibition when the stimulus was switched on. The latent period for light and sound ranged from 60 to 100 msec. When the photic stimulus was applied rhythmically (every 2-4 or more sec), the reactions to light and sound were suppressed in 14 of 35 neurons examined with this form of stimulation. Recovery took several minutes.

As these experiments were arranged, it was impossible to determine at what level the evoked reaction was suppressed, and special analysis is obviously required. This feature of evoked reactions in cortical neurons has also been noted in other animals [5, 16, 17], and it points to the possible involvement of these neurons in orientation reflex mechanisms.

In connection with the analysis of the receptor fields of individual neurons, it was found that reactions to light (observed in 62% of the animals) took the form of excitation or excitation combined with inhibition in 55%, and of inhibition of background activity in 7% (Fig. 2). Reactions to sound were observed in 24% of the neurons examined, the reactions being purely inhibitory in 13%, and excitatory (or combined excitatory and inhibitory) in 11%. Like light, tactile and proprioceptive stimulations produced mainly excitatory reactions (52 and 58% of neurons respectively), and purely inhibitory reactions in 19 and 8%.

Certain features of the reactions to tactile and proprioceptive stimulations and the distribution of the receptor fields merit attention. The receptor fields were on the same or opposite side of the body with equal frequency. In no case was a local receptor field noted; the fields were generally extensive and might, for example, include the surface of the neck, wing, trunk, and legs; or indeed the entire skin surface. Particularly intense reactions were observed when the neck or anterior surface of a wing was touched. Reaction magnitude depended on strength of stimulation.

Purely inhibitory reactions were seen in occasional cases (the frequency of these reactions is shown in Fig. 2). Additional inhibitory fields could be demonstrated when the excitatory receptor field did not cover the entire skin surface. The relative positions of the two types of field might vary considerably for different neurons. The inhibitory fields generally bordered on the excitatory field. The positions of the excitatory and inhibitory fields for three separate neurons are shown in Fig. 3.

An important point is that an overwhelming majority of the neurons reacted to afferent impulse activities of several kinds. Thus, 75% of the neurons which reacted to light also reacted to tactile and proprioceptive forms of stimulation. All neurons which reacted to sound were activated in response to photic stimulation. Only isolated

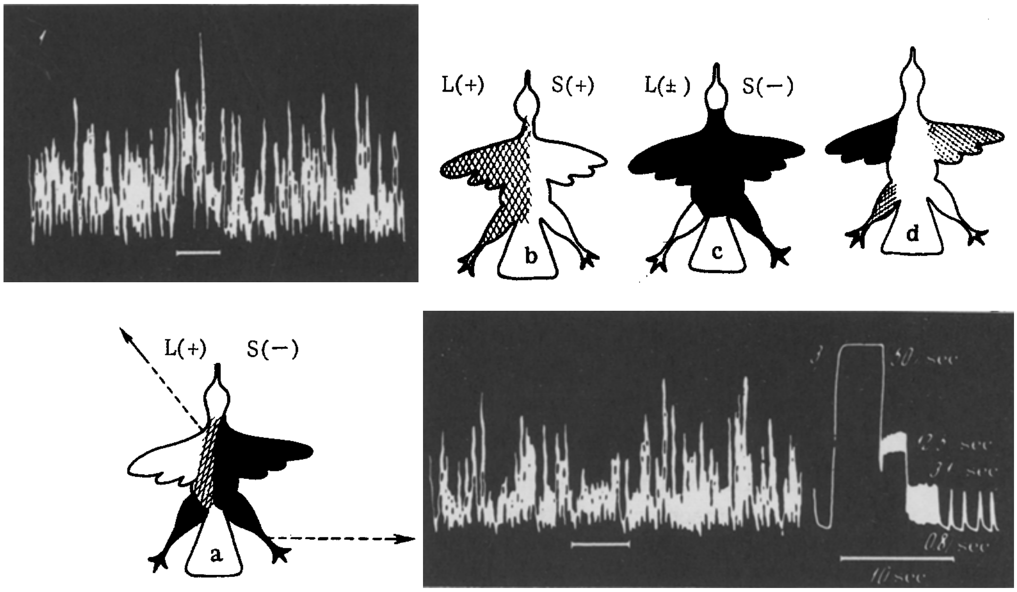

Fig. 3. Examples of the distribution of receptor fields for individual neurons. a) Neuron activated on tactile stimulation from ipsilateral half of body and neck and on photic stimulation: L(+). Inhibitory reaction to sound: S(−); and from contralateral half of neck, body, wing, and both legs: 1) electronic potentiometer recording of rates of impulse activity during tactile stimulation of neck – reaction of activation; 2) inhibitory reaction tactile stimulation of contralateral leg; 3) scale; b) neuron with excitatory receptor field extending to almost entire ipsilateral half of body and positive reactions to light and sound; c) neuron with inhibitory tactile receptor field. Reaction to light: on-positive; off-inhibitory; d) distribution of inhibitory and excitatory receptor fields in neuron in c for proprioceptive stimulations. Inhibitory reaction on passive movement of ipsilateral wing, excitatory on movement of contralateral wing and ipsilateral leg.

neurons were found to react to one kind of stimulation only. A significant proportion of cortical neurons in the pigeon have associative organization of their receptor fields, integrating different kinds of afferent impulse activity.

It is suggested that the frequency of activation (or the probability of a connection with one or another system) will depend directly on the ecological importance of a particular form of stimulation for the species concerned [2, 3, 10, 11].

This multiplicity of the receptor fields of individual neurons would suggest that the avian cortex has functional properties very similar to those of neuronal structures in the archipallium and paleocortex of other vertebrates [6, 7, 9, 12, 13]. The predominance of reactions to light, tactile and proprioceptive stimulations confirms the view, expressed earlier, that the avian cortex is a special variant of the visuosomatic cortex in the evolution of the vertebrate forebrain [18, 19], in which associative type neurons, receiving many kinds of afferent impulses, predominate.

SUMMARY

Analysis of background and induced activity in individual cortical neurons (corticoid lamina) in pigeons showed similarity of their reactions to the activity of neurons of the neo-, paleo-, and archicortex in other vertebrate animals.

The overwhelming majority of neurons react to stimuli which are the most important ecologically (light, tactile and proprioceptive). An insignificant part of neurons respond to sound.

These findings allow us to regard the cortex in pigeons as an original variant of the optico-somatic ancient cortex in the evolutional development of the forebrain in vertebrate animals.

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