Histological and electrophysiological investigations on the vibration-sensitive receptors (Herbst corpuscles) in the wing of the pigeon (Columba livia)

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Summary. The Herbst corpuscles (HCs) of the pigeon's wing were investigated both histologically and electrophysiologically. All HCs found in the wing were lamellated, basic type corpuscles without any specialized structures. Their lengths ranged from 67 to 853 µm (mean = 310 µm). Unexpected findings were their large number (about 1000 in the manual part of the wing), their irregular distribution and their preferred orientation (approximately parallel or at right angles to the primary feather follicles). The HCs were highly sensitive to vibrational stimuli applied to wing feathers. Their electrophysiological behaviour has the following characteristics: no spontaneous activity, phase-locked nerve impulses, a 1:1 stimulus-response relation up to at least 660 Hz at sufficiently high stimulus amplitudes, and a sensitivity to stimulus frequencies up to 1800 Hz. The best frequencies of 52 receptive units for which complete threshold curves were obtained lay between 100 and 900 Hz, 67% of the best frequencies were between 200 and 400 Hz. The threshold amplitudes at best frequency ranged from 0.5 to 150 µm. Two virtually non-overlapping mechanosensitive areas on the wing were identified. One is a very narrow band along the frontal edge and the other covers a large area of the remaining wing. They correspond with the two branches of the radial nerve. The histological and electrophysiological findings suggest that the HCs are part of a vibrational sensory system that is principally involved in flight control. The complex stimulus situation at the wing raises the question about the sensory structures involved in the reception of the efficacious stimuli. Many of these stimuli contain acceleration components. As mechanoreceptive lamellated corpuscles are very sensitive to acceleration (Herbst corpuscles = HCs; Gottschaldt 1974; Pacinian corpuscles = PCs; Kornhuber 1972) this type of mechanoreceptor is of special interest for the analysis of vibrational stimuli.

Pacinian corpuscles support the hypothesis that they evolved from a unique ancestral lamellar receptor.

Key words: Pigeon - Vibrational receptor - Receptor arrangement - Vibrational sensitivity - Flight control

Introduction

A variety of mechanical stimuli impinge on the body surface of birds during flight. The complexity of these stimuli bear a great amount of information. As they reflect critical air current changes, their reception and analyses must be important to flying birds. Because of its central function as a flight effector the wing is especially exposed to permanently changing stimulus conditions and therefore has a special significance for the perception of mechanical stimuli. The complex stimulus situation at the wing raises the question about the sensory structures involved in the reception of the efficacious stimuli. Many of these stimuli contain acceleration components. As mechanoreceptive lamellated corpuscles are very sensitive to acceleration (Herbst corpuscles = HCs; Gottschaldt 1974; Pacinian corpuscles = PCs; Kornhuber 1972) this type of mechanoreceptor is of special interest for the analysis of vibrational stimuli.

HCs are lamellated mechanoreceptors only found in birds. Morphologically they are quite similar to mammalian PCs (Polacek 1969). The central sensory nerve fiber ending is surrounded by two lamellary systems, the inner and outer core. Flattened perineural cells enclose the receptor and form a capsule (Malinovsky 1967). Detailed ultrastructural descriptions of the corpuscles are given by Andres (1969); Gottschaldt (1980); Ide et al. (1988); Munger et al. (1988). From electrophysiological studies it is also known that the stimulus-response behaviour of isolated HCs is very similar to that of the PCs (Gottschaldt 1974). Both receptors are extremely sensitive to vibrational stimuli, typically producing a sin-
gle spike per cycle in response to sinusoidal displacement stimulation up to frequencies of about 1000 Hz (Bolanowski and Zwislocki 1984; Gregory 1973; Hörster et al. 1983).

HCs are found in several parts of the avian body including the deeper layers of the skin (Abraham 1978), the beak (Berkhoudt 1980; Gottschaldt 1971; Gottschaldt and Lausmann 1974; Gregory 1973), tongue (Herbst 1850), leg (Dorward and Mcintyre 1971; Schildmacher 1931) and wing (Dorward 1970; Herbst 1848; Necker and Reiner 1980). When HCs concentrate in a certain body region, they can constitute a functional unit or sense organ. This could be shown for the leg of several species, where numerous corpuscles lie between the tibia and fibula in a so called ‘strang’ or cord (Schildmacher 1931). In pigeons, this organ is very sensitive to vibrational stimuli responding to displacement amplitudes of only 0.05 μm at 500 Hz (Shen 1983; Shen et al. 1983). This high sensitivity enables pigeons to detect faint substrate oscillations.

Another body area where HCs cluster is the bill tip organ of ducks and geese involved in the control of food intake (Berkhoudt 1980).

Until recently only few experiments have been carried out on the HCs in the wing (Dorward 1970; Necker 1983), and nothing is known about their biological function. The present histological study is conceived as a step towards a functional analysis and aimed at providing information about the quantity and distribution of HCs in the wing. Additionally electrophysiological experiments were done to record the neuronal responses of single receptor units to vibrational stimuli applied to different wing feathers or skin areas. Preliminary results have already been published elsewhere (Hörster et al. 1983).

Materials and methods

Histology. The defeathered wings of 3 perfused pigeons (Columba livia) were fixed in 1.25% glutaric aldehyde solution for 5 days. Rectangular pieces of tissue (side lengths: 10–25 mm) were removed, dehydrated through an alcoholic series, left in benzoic acid methyl ester for 24 h, and embedded in paraplast. Serial sections were cut at 20 or 24 μm and stained with hematoxylin-eosin. Seven series involving a total of 2178 single sections were examined with the microscope. The length and diameter of the HCs as well as their position in the wing tissue was either measured directly with an ocular micrometer scale or determined by scaled reconstruction drawings. The sizes of all tissue pieces were measured before and after dehydration. A mean shrinkage of 10% was taken into account for HCs length data. The orientations of identified HCs were marked in sketches of the tissue pieces, both having the same enlargement scale. Thus the receptor density and the orientation of their long axes could easily be established.

Four further series of sections from different wing areas were evaluated qualitatively to assess the arrangement of receptors.

Stimulation and electrical recording. Ninety-two pigeons of both sexes weighing 311–553 g (mean weight: 429 g) were used. They were anesthetized with Nembutal (6% pentobarbital-sodium solution, 0.07 ml per 100 g body weight) and artificially resired using the method of Schwartzkopff and Bremond (1963) to avoid movement artefacts. Sine-wave vibrational stimuli were produced by a Brüel&Kjaer minivibrator (type 4810), driven by a function generator (Burchard II), and applied to different skin areas or feather shafts of the wing with an aluminum stylus (tip diameter: 0.3 mm). After the tip of the stylus was brought into contact with the feather shaft or skin surface it was lowered for one further millimeter so that the area to be stimulated tracked the full stylus movement forwards and backwards; during the experiments the contact between stimulator and stimulated tissue was under permanent visual control.

The skin was always stimulated at the center of a receptive field. This was not possible for feather stimulation; but if a receptive unit could be excited by stimulating several different feathers, the vibrational stimulus was applied to the feather that elicited the strongest responses.

Action potentials from single fibers of the radial nerve were recorded differentially with two platinum hook electrodes (diameter: 0.1 mm) after removing the perineural sheath and dissecting the radial nerve with insect needles into fine fiber bundles. The spikes were amplified (Tektronix, type 122) and stored on tape simultaneously with the stimulus signal. The data were later filmed from an oscilloscope; the films allowed a detailed quantitative analysis that related the spike patterns to different vibrational stimulus parameters (e.g. frequency, intensity, repetition rate). The interspike intervals could be measured with an accuracy of 0.3 ms; this was of special importance for estimating the phase locking of the stimulus responses.

Results

1. Histological findings

a) Size and shape of HCs in the wing. From 7 representative pieces of wing tissue (including skin, musculature