

rolled sheet and tested in the tensile mode at an elongation rate of  $53.2 \times 10^{-6} \text{ m s}^{-1}$  over the range 25 to 45 °C. Propolis exhibits an unusual behaviour on tensile deformation: there is a linear relationship between load and elongation from the origin of the curves to the maximum sustainable load. Thus, the yield stress coincides with the ultimate strength of the material. But, propolis like beeswax, is an entirely plastic material in the range 25 to 45 °C so that this linearity is not an elastic one. On yield, propolis is highly ductile and flows about 200% before the necking thread finally fails.

The tensile strength of propolis decreases 8-fold over the range of temperatures tested, and the yield strain some 3-fold over this range (Table 1). The stiffness remains virtually constant at lower temperatures with a major transition between 35 and 40 °C. The work to yield also decreases with increasing temperature as does the ductility of the substance.

Honeybee combs must bear the weight of the bees, their brood and all their provisions as well. Because feral bees build their nests to hang vertically, their combs are loaded in tension. Thus tensile strength is of great importance to the structural integrity of the nest. Over the range of temperatures tested, beeswax is at least four times stronger than propolis. Even so, the combs of bees in warm countries sometimes fail in hot weather. Propolis at its strongest is comparable to beeswax at its weakest over the range of temperatures that are likely to impinge on the nests of honeybees.

Received June 27 and August 13, 1984

1. Michener, C.D.: The Social Behaviour of the Bees. Cambridge: Harvard Univ. Press 1974
2. Alfonsus, E.C.: Glean. Bee Cult. 61, 92 (1933)
3. Hepburn, H.R., Armstrong, E., Kurstjens, S.P.: S. Afr. J. Sci. 79, 416 (1983)

## Avian Primary Auditory Neurons

### The Relationship between Characteristic Frequency and Preferred Intervals

G.A. Manley and O. Gleich

Institut für Zoologie der Technischen Universität München,  
D-8046 Garching

In 1979, one of us (G.A.M.) reported the existence of unusual patterns in interval histograms of spontaneous activity in primary auditory nerve fibers of a reptile (*Gekko gecko*) and a bird (starling, *Sturnus vulgaris*) [1]. Instead of showing a smooth exponential decay of intervals with increasing interval duration, a high proportion of lower-frequency fibres showed preferred intervals in their discharge patterns. These are inter-spike intervals which appear much more often than expected. Their interval durations corresponded roughly to the period, or multiples of the period of the characteristic frequency (CF-period) as measured using tone bursts. Evidence was presented to demonstrate that this activity was not due to responses to acoustical noise or inadvertent stimulation. Since that report similar phenomena have been demon-

strated in nerve fibres of the red-eared turtle [2]. Also, in an analysis of intracellular recordings from single hair cells of this turtle, Crawford and Fetiplice [2] showed that the spontaneous membrane noise of such cells had a spectral energy maximum near the CF of the individual cell. Removing the tympanic membrane and cutting the middle-ear ossicle did not affect the strength of these oscillations, neither was "body noise" an adequate explanation in their supravital (isolated half head) preparation system. Their data indicate that the source of the frequency-tuning characteristics of the primary input to the auditory neurons system in the red-eared turtle may be at least partly traceable to electrical filtering properties of the hair cell membrane. The possible cellular mechanisms and the similarities to the fre-

quency selectivity and temperature sensitivity of the electroreceptors of fish have already been discussed [1, 3].

We report here the pertinent results of a more detailed investigation of this phenomenon in the starling (*Sturnus vulgaris*). Details of the preparation technique have already been or will soon be published [4] together with a complete description of the activity patterns of primary auditory fibres in this species [5]. The activity described here was recorded from the cochlear ganglion of Nembutal-anaesthetized birds held at normal body temperature in a sound-proofed and anechoic chamber. All units were active in the absence of sound stimuli, with a unimodal distribution of rates between 10 and 160 spikes  $\text{s}^{-1}$ . The average rate was 44 spikes  $\text{s}^{-1}$  ( $N=134$ ). Interval histograms of spontaneous activity were derived using a DEC-MINC computer (time resolution generally 0.01 ms) from 90 neurons of a total of 134 of known CF. CF's were determined using audiovisual criteria, with frequency steps of 10 Hz below 300 Hz, 50 or 100 Hz above. In the lower frequency range of CF's (73 cells with CF up to 1.5 kHz), histograms from 35 cells showed preferred intervals and most were adequate for this detailed analysis. Our primary interest focused on the question as to how well the "basic" preferred interval length (as defined in Fig. 1 legend) corresponded to the CF-period for a given unit. We demonstrate here that on average the basic preferred interval length does not correspond exactly to the CF-period but is approximately 15% longer. Secondly, although many units do not show multiple preferred intervals, their most common interval (mode of the histogram) lies more often near the CF-period than one would expect from a truncated Poisson distribution of intervals.

Fig. 1A shows a "normal" interval histogram; Fig. 1B is an example of a histogram showing obvious preferred intervals. On the premise that the second, third, etc. peaks represent multiples of a certain oscillation period, a "basic interval" for each cell was calculated. Since the position of the first histogram peak may well depend on the cell's refractory period, only the second and later peaks were included in this analysis. Preferred intervals var-

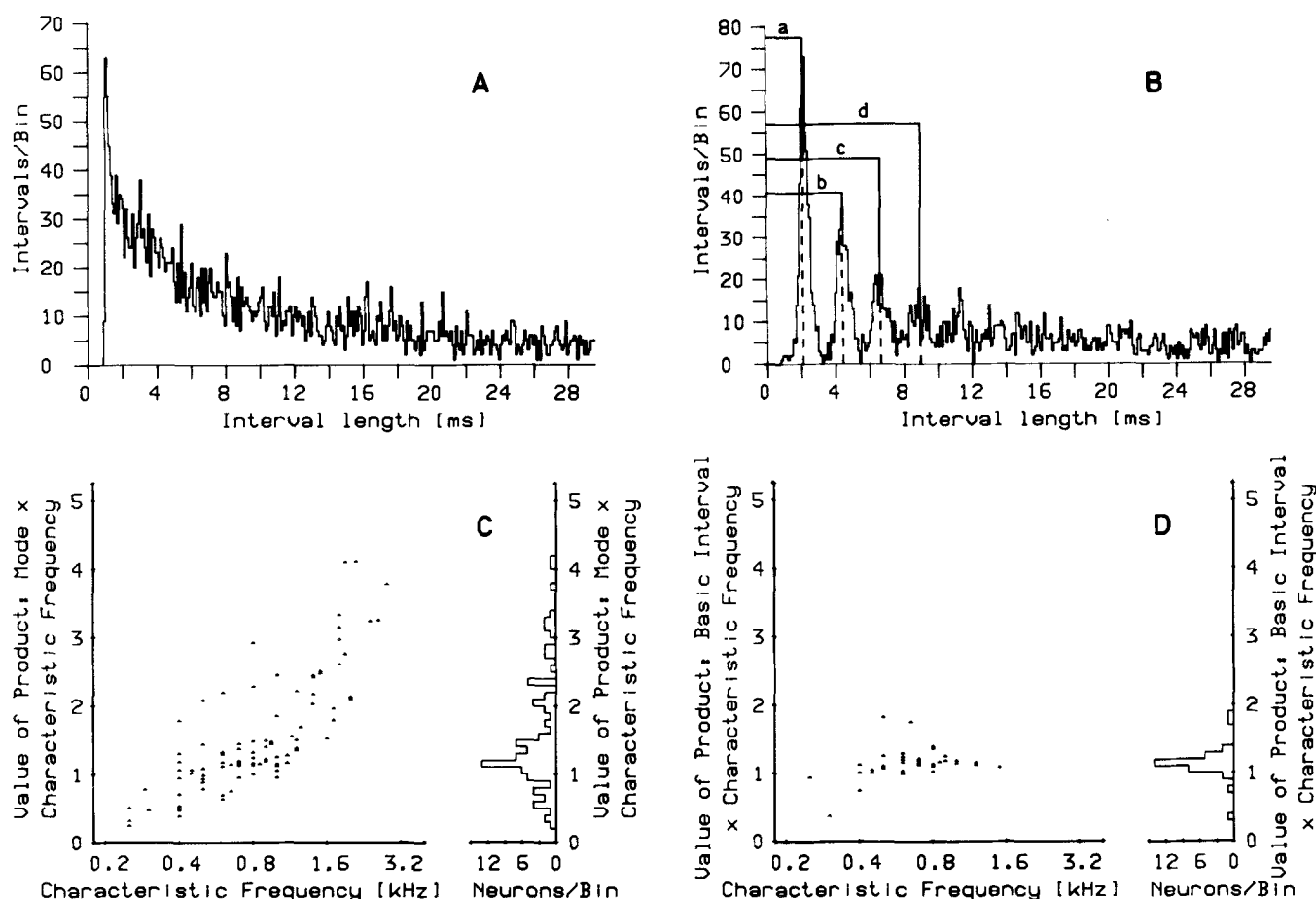


Fig. 1. A) Typical time-interval histogram (TIH) of spontaneous activity of a primary auditory nerve fibre of the starling (truncated Poisson distribution: bin width 0.1 ms; CF=2.0 kHz; 3205 intervals; spontaneous rate 59.3 spikes/s). B) Typical TIH of spontaneous activity from a cell showing preferred intervals. This histogram demonstrates the method of calculating the "basic" interval as referred to in the text. The interval *a* is the mode of the histogram (see Fig. 1C). The preferred intervals *b*, *c* and *d* were used as follows: "basic" interval for this unit =  $(b/2 + c/3 + d/4)/3$  (see Fig. 1D). Bin width 0.1 ms; CF=0.45 kHz; 2332 intervals; spontaneous rate 48.6 spikes/s. C) Graph of the value of the product of the modes of all histograms ( $N=90$ ) multiplied by the corresponding CF as a function of CF. A correspondence between mode and CF-period would give a product value of 1. The histogram of the distribution of product values on the right demonstrates a tendency for the product values to cluster near 1.15 (see text). D) Graph of the product of "basic" interval (as calculated in B) multiplied by CF for histograms showing preferred intervals (as in Fig. 1B) as a function of CF. The histogram of the distribution of product values on the right demonstrates a clear tendency for product values to average approximately 1.15 (see text)

ied within one histogram randomly  $\pm 5\%$  around multiples of the basic interval. These individual basic intervals were multiplied by the corresponding CF's, so that a perfect agreement of the basic preferred interval and CF-period would give the numerical product of 1, longer intervals a product greater than 1, etc. The result of this analysis is shown in Fig. 1D. There is an obvious tendency for the basic preferred interval to be about 15% longer than the CF-period. Possible sources of scatter in the data, such as inaccurate determination of the actual CF's, inadequate resolution of the computer analysis, etc., fail to explain the *systematic* ten-

dency to basic intervals longer than the CF-period.

A corresponding analysis of the histogram modes (most common interval; range 0.95 to 4.45 ms) was carried out on all histograms, including those showing no preferred intervals. In all cases, the mode was multiplied by the CF, so that a mode corresponding exactly to the CF-period would give a numerical product of 1. In Fig. 1C it is clear that there exists a tendency not only for the mode to be related to the CF-period, but that the mode is also on average slightly longer. The picture is more confused than in Fig. 1D, since some modes correspond to slightly

more than *double* the CF-period, but also because for CF's below 0.4 kHz and above approximately 1.4 kHz (due to the refractory period) the modes are shorter or longer than the CF-period, respectively. Apart from these special cases, it is legitimate to regard the most frequent interval as a special case of a preferred interval.

We conclude from these data that in this species, the spontaneous activity of the majority of primary auditory fibres with CF's below about 1.6 kHz show non-randomness in their interval distributions. This phenomenon manifests itself in a characteristic distribution of intervals, such that the mode and cer-

tain longer intervals are emphasized at the expense of interval durations which lie between. Seen as a whole, however, the truncated Poisson pattern is preserved. The simplest explanation of these data is that oscillations near the CF-frequency are superimposed on the membrane noise or random phenomena which cause spontaneous transmitter release from the hair cell [1–3].

We cannot at present offer a satisfactory explanation for the fact that the mode and other preferred intervals tend on average to be 15% longer in duration than expected from the known CF's. Error in CF determination should only lead to a broadening of the scatter of data, but no systematic shift. One possible explanation may be derived from further work of Crawford and Fettiplace [6]. In turtle hair cells, injected current pulses initiate oscillations whose frequency lies near the CF for small current pulses but progressively higher for larger depolarisations or lower for hyperpolarisations, respectively. If it were the case that the threshold discharge rate increase in the starling nerve fibres corresponded to a

significant hair cell depolarisation above the potential present during spontaneous activity, the resulting frequency shift would be in the right direction to explain the phenomena we describe here. Thus one might expect, at least near the CF threshold, a threshold-criterion-dependent CF value. Although Sachs et al. [7] showed in the pigeon no shift of CF for progressively higher threshold criteria, it is possible that their initial criterion (50% rate increase) was too high to observe the near-threshold phenomenon which may be operating here. This possibility remains to be investigated. That these oscillation phenomena at the hair-cell level are reflected in the discharge patterns of primary nerve fibres is remarkable, as the meagre data available indicate that nerve fibres in birds and reptiles contact several hair cells. Although some evidence for indirect electrical coupling of hair cells exists (see [3] for discussion), it is difficult to conceive of an adequate coupling in all species. It may be that the unravelling of the mechanism of co-ordination of oscillations between hair cells will ex-

plain the difference we report here between nerve-fibre acoustic CF and the modes and/or preferred intervals of interval histograms of fibre spontaneous activity.

Supported by the Deutsche Forschungsgemeinschaft under the programme of the Sonderforschungsbereich 204, "Gehör". We thank Horst Oeckinghaus and Peter Narins for commenting on the manuscript.

Received August 20, 1984

1. Manley, G.A.: *Naturwissenschaften* 66, 582 (1979)
2. Crawford, A.C., Fettiplace, R.: *J. Physiol. (Lond.)* 306, 79 (1980)
3. Eatock, R.A., et al.: *J. Comp. Physiol.* 142, 203 (1981); Eatock, R.A., Manley, G.A.: *ibid.* 142, 219 (1981)
4. Manley, G.A., Leppelsack, H.-J.: *Collog. INSERM* 68, 127 (1977)
5. Manley, G.A., et al.: in preparation
6. Crawford, A.C., Fettiplace, R.: *J. Physiol. (Lond.)* 312, 377 (1981); 315, 317 (1981)
7. Sachs, M.B., et al.: *Brain Res.* 70, 431 (1974)

## Naturwissenschaften

## Buchbesprechungen

**Johann Beckmann.** Von M. Beckert. Leipzig: Teubner 1983. 119 S., 16 Abb., 8,60 M.

Sieht man von einer etwas unvermittelt auftauchenden Querverbindung am Ende des Buches ab, die über Gedanken von Karl Marx zu einem Programm der SED führt, so ist dem Autor mit diesem Bändchen eine geschlossene Darstellung, ein lebendiges Bild vom Leben und Schaffen des Johann Beckmann gelungen, eingebettet in das wissenschaftliche Umfeld Europas und in die geistigen Strömungen der Zeit. Zwar konnte der Autor nur noch auf die gedruckten Tagebücher, nicht mehr auf den schriftlichen Nachlaß Beckmanns zurückgreifen, dennoch wird unter Rückbezug auf seine Bücher und Abhandlungen die historische Leistung anschaulich herausgearbeitet, „Tech-

nologie“ und „Warenkunde“ als eigenständige Wissenschaften begründet zu haben. Es ist das Verdienst der Herausgeber der Reihe und speziell des Autors dieses Bandes, historische Zusammenhänge auf einem Gebiet bewußt zu machen, das leider allzusehr den „Fortschritt“ nur als Phänomen unserer Zeit versteht. W. Ludwig (Heidelberg)

**Römpps Chemie Lexikon,** Band 3, H.-L. Von O.-A. Neumüller. Stuttgart: Franckh 1983. 868 S., 183 Abb., DM 195,—.

Der dritte Band des Römpp/Neumüller beginnt auf Seite 1577 mit *h* (Plancksches Wirkungsquantum) und endet mit dem Stichwort *D-Lyxose* auf Seite 2430. Die Sorgfalt und Genauigkeit der Stichworte bis zu den Verästelungen

der Chemie zu geologischen, biologischen, medizinischen, physikalischen und biographischen sowie wirtschaftlichen und firmenkundlichen Angaben sind wie in den vorangegangenen Bänden schier unübertrefflich. Ein einziges Stichwort sei als Beispiel genannt: „Immunologie“. Hier findet man 4 Spalten Stichworttext und dazu 6 Spalten Literaturzitate, zumeist Hinweise auf Bücher aus der neuesten Zeit (wie denn überhaupt die Aktualität des Werkes hervorragend ist; es führt Literatur aus seinem Erscheinungsjahr in reicher Zahl auf!). Ein besonderes Lob ist dem Herausgeber dadurch gewiß, daß er die sich (leider) immer mehr verbreitenden Akronyme bringt, vor denen der Nicht-Spezialist oft hoffnungslos überfordert steht, und das nicht nur bei Warenzeichen, sondern eben auch z.B. in der