A Hypothesis Concerning the Sharp Pitch Discrimination Observed in the Sleeping Cat

The ability of a cat to discriminate between tones of different frequencies appears to improve when the animal passes from the wakeful state to a condition of high voltage sleep (HVS)[1,2]. This statement reflects experimental results such as those summarized in Figure 1A, taken from BUENDÍA et al.[2]. They pertain to a cat submitted to an instrumental avoidance training routine in which a 'positive' tone of 5 Kcps was followed by punishment when the animal failed to perform a certain response and 'negative' tones of 5.1, 5.5, 6.0, 7.2 and 10.0 Kcps were never followed by punishment. The 'proportion of successes with a tone of a given frequency' (i.e. the ratio 'number of responses/number of presentations') is plotted as a function of 'pitch' or tone frequency for the cat awake (open circles) and asleep (black circles). This proportion is an estimate of the probability with which that pitch will evoke the response; the vertical bars indicate the 95% confidence intervals for the probability, based in each case on 250 presentations[3]. The change in reactivity which occurs when the animal falls asleep justifies the initial statement and is characterized by the following basic features (Figure 1A): (i) a small decrease in the efficiency of the very effective 'positive' tone (5 Kcps); (ii) a small decrease in the efficiency of the least effective 'negative' tones (7.2, 10.0 Kcps); (iii) a marked decrease in the efficiency of the intermediately effective 'negative' tones (5.1, 5.5, 6.0 Kcps); and (iv), as a consequence of (i), (ii), and (iii), an increase in the differentiation gradient that goes from 'positive' to 'negative' pitches.

These results indicate that the mechanisms which mediate the responses to the various pitches are not affected uniformly by the HVS process, but suffer in a selective manner that depends on the pitch. A priori, there are two interpretations. First that all mechanisms have the same susceptibility, but that the influence of HVS distributes itself in a non-uniform manner determined by the previous training experience. Second, that the influence of HVS distributes itself in a uniform manner, but that the mechanism for each pitch has a different susceptibility determined by the previous training experience. In the author's opinion, the second interpretation is more acceptable, since it does not require an extreme plasticity of the sleep producing mechanism. This paper summarizes a hypothesis which proposes a certain organization and certain properties for the neurophysio-

logical mechanism involved in producing a conditioned response; this hypothesis would explain the peculiar shift in responsiveness that is observed when the preparation passes from alertness to HVS. It applies regardless of whether the conditioned response considered is a specific act, a behavioral arousal or an EEG 'arousal'[2]. We make the following assumptions. (A) The production of the learned response involves three stages: (a) a 'receptor' stage which detects the stimulus; (b) a 'trigger' stage T which 'decides' on presentation of each stimulus whether or not the response will occur (T involves N neurones); (c) an 'effector' stage which responds to a 'go' signal from the trigger by producing the organized pattern which constitutes the response. Assumption (A) is discussed by BUENDÍA et al.[2]. (B) The necessary condition for the response to occur on presentation of a given stimulus is that any n or more of the total N cells in the trigger be activated by that presentation. The number of T units responding to each presentation is not a fixed value, but a random variable taking the values 0, 1, ..., n, ..., N according to a certain discrete probability mass function. Each probability function is defined for a given state (awake, HVS, etc.) and for a given pitch ($p1$, $p2$, etc.). These functions depend of course on the response-probability values of the individual cells in T; this dependence will not be discussed here. Figure 2 shows hypothetical functions in the wakeful (upper row) and sleeping (lower row) animals for the 'positive' ($p3$) and for two negative ($p1$, $p2$) pitches. Continuous probability density curves are used for simplicity in the drawing; normal-like curves are shown but the only constraint that is necessary is that they exhibit a central mode and that probability values become smaller at one or both ends. As postulated above the probability that a given pitch ($p1$, $p2$, or $p3$) will evoke the response under given conditions (awake or asleep) is the probability that it will mobilize n or more trigger units; it is represented in Figure 2 for each case by the heavily shaded area under the curve and to the right of the vertical line through n. The situation in the wakeful cat is shown in the upper row. Note that pitches can be

[1] N. BUENDÍA, M. GOODE, G. SIERRA, and J. P. SEGUNDO, Exper. 19, 208 (1963).

[2] N. BUENDÍA, G. SIERRA, M., GOODE, and J. P. SEGUNDO, EEG Clin. Neurophysiol. Suppl. 24, 199 (1964).

[3] D. A. S. FRASER, Statistics: an Introduction (John Wiley and Sons Inc., New York 1958).
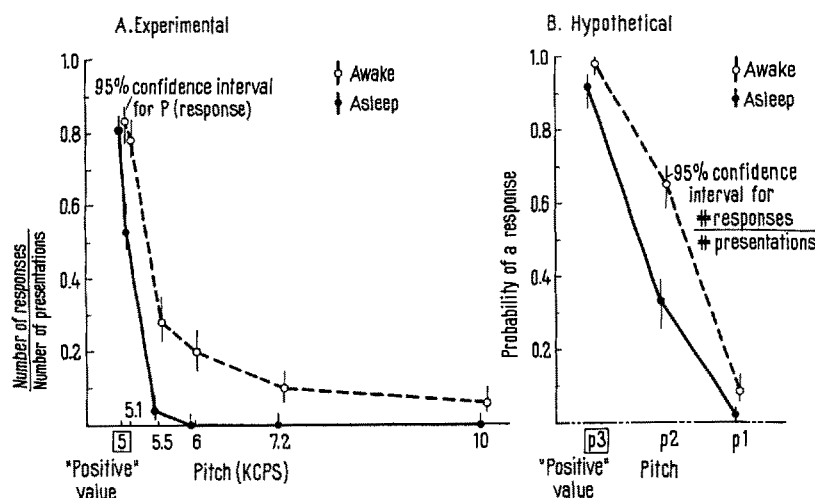
Fig. 1. The essential features of curve B inferred from the hypothetical situation depicted in Figure 2 are the same as those of curve A constructed with real data taken from BUENDÍA et al.[2].
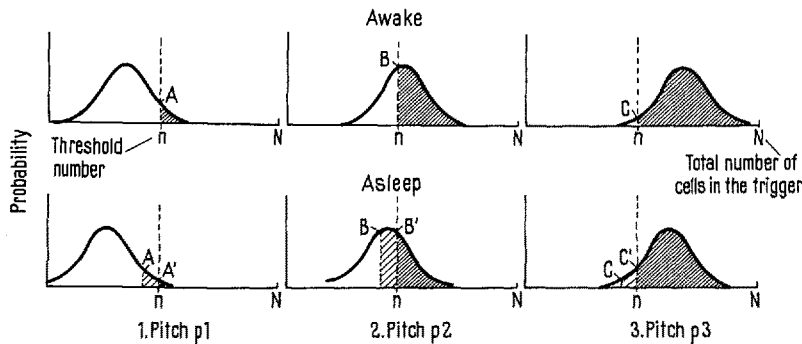
Fig. 2. Hypothetical situation. On abscissae, number of trigger cells responding to a presentation of a given pitch. N is the total number of cells in the trigger mechanism; n is the threshold number of cells (i.e. on a given presentation, the response will occur whenever any n or more trigger cells respond). On ordinates, respective probabilities. Upper row, curves awake; lower row, curves asleep. Left, center and right columns correspond to pitches p1, p2 and p3 respectively. See text.

divided into three differently effective categories according to where the curve is intersected by the n line (at A, B and C respectively): pitches like $p3$ for which most of the area under the curve is to the right of n and that are, therefore, very effective; pitches like $p2$ for which the area is divided into similar parts and that are moderately effective; pitches like $p3$ for which most of the area is to the left of n and are the least effective.

If the sleep process exerts a relatively uniform influence upon the mechanism that mediates the response, this may be reflected by a uniform shift of all probability curves to the left, without a major change in their shapes. The situation in the sleeping cat is shown in the lower row of Figure 2. Curves now intersect line n at A', B' and C', to the right of A, B and C, respectively. As can be inferred from comparison of the upper and lower rows the probability that a given tone will mobilize n or more T units and evoke the response is reduced, on passing from wakefulness to HVS, by a value represented by the lightly shaded areas between A and A', B and B' and C and C', respectively. On the basis of obvious geometrical features, it is apparent that the decrease in probability will be greater for $p2$ (whose density curve mode crossed the n line when the animal fell asleep) than for $p1$ (whose density curve left tail crossed the n line) and $p3$ (whose density curve right tail crossed the n line). The hypothetical situation just described is summarized in Figure 1B. The *'probability of a response for a tone of a given frequency'* is plotted as a function of *'pitch'*, for the cat awake (open circles) and asleep (black circles); the vertical bars indicate the 95% probability intervals for the proportion of successes in 250 presentations[3]. The change in reactivity which occurs when the animal passes from wakefulness to sleep in the hypothetical case (Figure 1B)

exhibits the same basic features as in the real experimental situation (Figure 1A). Namely: (i) the small decrease in the efficiency of the very effective 'positive' tone $(p3)$; (ii) the small decrease in the efficiency of the least effective 'negative' tone $(p1)$; (iii) the marked decrease in the efficiency of the intermediately effective 'negative' tone $(p2)$; and (iv), as a consequence of (i), (ii) and (iii), the increase in the differentiation gradient that goes from the 'positive' to the 'negative' pitches. Note that a similar effect could be produced if, instead of the curve having shifted as a consequence of HVS, the threshold value n had increased. In summary, the hypothesis presented here, based upon assumptions and subject to constraints that are not altogether unreasonable, appears to explain a somewhat surprising experimental finding[4].

Résumé. Une hypothèse est présentée pour expliquer la discrimination tonale précise du chat endormi. Postulats: (A) Un mécanisme de déclenchement détermine si la réponse aura lieu ou non[2]; et il faut qu'une quantité minime de neurones de déclenchement soit activée. (B) Le nombre de cellules activées par chaque ton est une variable aléatoire avec une distribution qui possède certaines caractéristiques.

J. P. Segundo

Anatomy Department and Brain Research Institute, University of California, Los Angeles (USA), December 9, 1963.

CONGRESSUS

Österreich

Gemeinsame Tagung
Deutsche Gesellschaft für Biophysik E.V., Österreichische Gesellschaft für reine und angewandte Biophysik, Schweizerische Arbeitsgemeinschaft für Strahlenbiologie

Wien, 14.–16. September 1964

in Zusammenarbeit mit der Wiener Medizinischen Akademie. Hauptthemen: Allgemeine Biophysik, Molekularbiophysik, Strahlenbiophysik-Strahlenbiologie, Kybernetik in der Biologie.

Wiss. Sekr.: Dr. A. Locker, Wiener Medizinische Akademie, Wien IX., Alserstrasse 4.

Japon

Neuvième congrès international du cancer

du 23 au 29 Octobre 1966 à Tokyo

Sous les auspices de l'Union Internationale Contre le Cancer (U.I.C.C.).

Président: Prof. Tomizo Yoshida, M.D. Secrétaire générale: Prof. Kunio Oota, M.D., c/o Cancer Institute, Nishisugamo, Toshima-ku, Tokyo (Japon).