

evoked only by a stimulus of a different modality. The relationship was commonly reciprocal: if a cell responded to B after attenuation of A, it would respond to A after attenuation of B.

Results can be discussed from two view points. From that of the general susceptibility of reticular units to sensory stimuli, these experiments suggested that certain concepts should be broadened. Firstly, the notion of reticular responsiveness should include susceptibility to sensory stimuli which are natural and complex, as opposed to the more currently used shocks, flashes, etc., which are less so. Secondly (and as pointed out by AMASSIAN and DE VITO¹), the notion of exclusively widespread receptive fields should be substituted by the recognition of many varieties, including some that are quite restricted (e.g. to the digits of one paw). Thirdly, the notion of convergence of different modalities upon single neurons should take into account cells which respond to several weak and complex natural stimuli (e.g. light brushing, illumination and voice); in certain cases the latter were effective only within limited receptive fields, as in the case of a unit sensitive to tapping only on the left foreleg and part of the thorax and to hand passing only in the left visual field. The complexity and variety of these sensory response patterns at cellular level resist theorizing as to the function of these units as a coordinated whole.

From the point of view of repetitive stimulation, low following frequencies and attenuation were outstanding. This behavior reflected a type of responsiveness different from that of primary sensory systems where high following rates and equilibration are the rule (for work on unanesthetized preparations see ²⁻⁴). These features of reticular activity may be shared by units in other areas: e.g. recent experiments have indicated that low rates and attenuation are found in certain cells of the somatic sensory cortex⁵.

With regard to attenuation, one is struck by the similarities (effectiveness of a stimulus when novel, decay on repetition, specificity, etc.) between it and habituation; the actual relationship, however, cannot be stated more precisely without further experimentation⁶.

Résumé. L'activité des neurones de la formation réticulaire mésencéphalique du chat est modifiée par l'effet de stimuli physiologiques, quelque fois très complexes: la convergence hétéro-sensorielle est très évidente et les champs récepteurs ont différentes étendues et distributions. Soumises à de hautes fréquences de stimulation, les cellules présentent une réactivité limitée. Au fur et à mesure que la stimulation est répétée, les réponses diminuent et, finalement, disparaissent; cette diminution de réactivité est souvent spécifique de la stimulation utilisée.

C. BELL, N. BUENDIA,
G. SIERRA, and J. P. SEGUNDO

*Department of Anatomy and Brain Research Institute,
University of California at Los Angeles (U.S.A.),
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¹ V. E. AMASSIAN and R. V. DE VITO, *J. Neurophysiol.* 17, 575 (1954).

² R. GALAMBOS and V. G. VERNIER, *Amer. J. Physiol.* 188, 233 (1957).

³ R. JUNG, in E. ROSENBLITH, *Sensory Communication* (J. Wiley & Sons Inc., New York 1961).

⁴ V. B. MOUNTCASTLE and G. F. POGGIO, *Bull. John Hopkins Hosp.* 106, 280 (1960).

⁵ V. L. BROOKS, P. RUDOMIN, and C. L. SLAYMAN, *J. Neurophysiol.* 24, 286 (1961).

⁶ Supported by USPHS M-5183-02.

Nuclear and Radicular Distribution of Cardio-Inhibitory Neurons

Cardio-inhibitory fibres have been traced into the cardiac branches of the vagus nerve from both the vagal and the bulbar-accessory roots^{1,2}. Since the vagal and the bulbar-accessory components show similar functional, reflex properties³, and parallel patterns of peripheral distribution to the nodal structures of the heart², a systemic organization of the two sets of neurons within the dorsal motor nucleus and the radicular output is presumptive. The radicular distribution of the cardio-inhibitory effects has therefore been investigated, in comparison with that of visceromotor effects, which represent the most extensive output of the dorsal motor nucleus through the vagal root; and the two populations of cardio-inhibitory neurons have been localized according to the distribution of the retrograde changes following chronic section of either vagal or bulbar-accessory cardio-inhibitory rootlets.

The experiments were carried out on 21 adult dogs (7-10 kg). In 9 animals, anaesthetized with chloralose (80 mg/kg), the trachea was cannulated and the vago-accessory roots were exposed bilaterally by opening largely the posterior fossa: on one side the rootlets were sectioned and stimulated (peripheral stump) with small, bipolar, silver electrodes, in groups or one by one; on the other side, to rule out possible current diffusion effects, the dorsal motor

nucleus was stimulated with stereotactically placed, concentric electrodes, and the vago-accessory rootlets were interrupted in sequence.

Femoral blood pressure and the average changes in the intraluminal pressure of the digestive tract (upper and lower oesophagus, stomach and duodenum) were routinely recorded by means of two Samborn pressure transducers connected to a femoral catheter or to an air-filled rubber balloon, respectively, and coupled with a Samborn Twin-Viso recorder through carrier pre-amplifiers.

In 12 animals the intracranial section of different groups of rootlets was carried out, unilaterally, under pentothal anaesthesia and with full aseptic precautions, and the cardio-inhibitory and visceromotor effects, obtained 3 weeks later by the electrical stimulation of the normal or partially degenerated vagal trunk (peripheral stump), were comparatively analysed and related to the distribution of the retrograde changes following the chronic radicotomy, occurring within the dorsal motor nucleus (serial, Nissl-stained, cross sections of the medulla).

The following results were obtained: (i) Intracranial stimulation of the bulbar-accessory root was found to

¹ L. SPERTI and E. XAMIN, *Exper.* 16, 556 (1960).

² L. SPERTI, M. MIDRIO, and E. XAMIN, *Exper.* 18, 96 (1962).

³ L. SPERTI, M. MIDRIO, and E. XAMIN, *Exper.* 18, 97 (1962).

bring about marked cardio-inhibitory effects without collateral changes in the intraluminal pressure of the digestive tract. Upon selective stimulation of the bulbar-accessory rootlets, the cardio-inhibitory effects appeared to be often confined to the three cranialmost rootlets. On the other hand, acute or chronic unilateral section of the bulbar-accessory root was found to reduce the bradycardiac response to the electrical stimulation of the ipsilateral dorsal motor nucleus, or vagal trunk, respectively, without affecting in both cases the visceromotor response.

(ii) Strong cardio-inhibitory and visceromotor effects were constantly evoked by electrical stimulation of either the dorsal motor nucleus or the vagal root. With selective stimulation of the different vagal rootlets, the cardio-inhibitory effects were obtained only from the most caudal group of rootlets (caudo-vagal rootlets) and were rarely accompanied by visceromotor effects, limited to the upper portion of the oesophagus. The unilateral section of these caudo-vagal rootlets was found to reduce the bradycardiac response to the electrical stimulation of the ipsilateral dorsal motor nucleus, or to abolish it when performed in addition to a bulbar-accessory radicotomy. Moreover, electrical stimulation of the ipsilateral vagal trunk in animals with chronic section of the bulbar-accessory and caudo-vagal rootlets evoked motor responses of the digestive tract not significantly different from those elicited from the contralateral vagal trunk, but not negative chronotropic effects, even with supramaximal stimulus intensities.

(iii) Intracranial stimulation of the vagal rootlets, except the caudo-vagal ones, caused motor responses of the upper and lower oesophagus, stomach and duodenum, not accompanied by negative chronotropic effects. Acute or chronic intracranial section of this group of vagal rootlets completely prevented the motor response of the digestive tract to the electrical stimulation of the ipsilateral dorsal motor nucleus or vagal trunk, respectively, without affecting in both cases the bradycardiac effect.

(iv) In all the animals submitted to a chronic radicotomy, retrograde changes, consisting mainly in a marked loss of cells, were observed 3 weeks later in the medial aspect of the ipsilateral dorsal motor nucleus, with a rather constant distribution. Such retrograde changes were found to occur in the upper part of the caudal half of the nucleus, in cases of bulbar-accessory radicotomy; in the basal part of the cranial half of the nucleus, in cases of caudo-vagal radicotomy; in both of these areas, with more marked loss of cells at the border, in cases of combined bulbar-accessory and caudo-vagal radicotomy (Figure C).

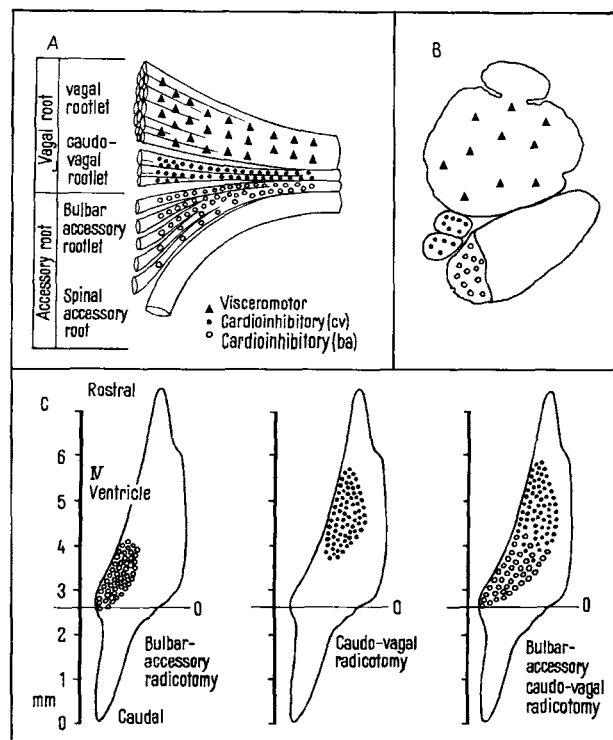
(v) Serial cross sections of the vago-accessory complex have shown that the 5–7 caudalmost vagal rootlets, referred to as caudo-vagal in (ii), (iii) and (iv), cluster together and, instead of merging into the collected vagal root, enter the jugular foramen as separate strands of fibers lying in the dorso-caudal angle between the vagal and the accessory roots, close to the bulbar portion of the latter (Figure B)^{4,5}.

The above results (summarized in the Figure) suggest that in the dog the cardio-inhibitory neurons are localized in the medial aspect of the middle 2/4 of the dorsal motor nucleus, where they are arranged in the same caudo-cranial sequence as the bulbar-accessory and caudo-vagal rootlets by which the axons leave the medulla, the bulbar-accessory neurons lying caudally to, and partially overlapping with, the vagal ones.

The bulbar-accessory and caudo-vagal rootlets do not contain general vegetative efferent fibres, motor for the digestive tract, which appear to be collected in the re-

maining vagal rootlets; but the possible presence of general vegetative efferent fibres for the respiratory tract must be borne in mind in the quantitative analysis of the cardio-inhibitory neurons.

The arrangement in sequence of the cardio-inhibitory fibres across the border between bulbar-accessory and vagal roots accounts for the debated question of their anatomical appurtenance⁶.



Radicular distribution of cardio-inhibitory and visceromotor effects in the vago-accessory roots of the dog (A, B), and distribution of the retrograde changes, consecutive to chronic section of the cardio-inhibitory rootlets, within the dorsal motor nucleus. A: Schematic representation of the vago-accessory roots. B: Outline of a cross section of the vago-accessory roots, taken at the level of the distal end of A. C: Outline of the horizontal projection of the dorsal motor nucleus; line O marks the opening of the central canal into the IV ventricle.

Riassunto. Nel cane, le fibre cardioinibitrici escono dal bulbo con le radicole bulbari dell'accessorio e con quelle più caudali del vago. Tali radicole non contengono fibre motrici per il tratto digerente, che sono contenute nella porzione craniale della radice vagale. Nel nucleo motore dorsale i neuroni cardioinibitori sono localizzati nella porzione mediale dei 2/4 intermedi, e sono distribuiti nello stesso ordine caudo-craniale delle radicole con le quali gli assoni escono dal bulbo.

L. SPERTI and M. MIDRIO

Istituto di Fisiologia Umana dell'Università di Padova (Italy), November 14, 1962.

⁴ M. MOLHANT, *Le Névralgie* 11, 137 (1910).

⁵ M. R. CHASE and S. W. RANSON, *J. comp. Neurol.* 24, 31 (1914).

⁶ F. JOURDAN and S. J. G. NOWAK, *Arch. int. Pharmacodyn.* 53, 121 (1936).