Comp. Biochem. Physiol., 1969, *Vol.* 28, *pp.* 961 *to* 965. *Pergamon Press. Printed in Great Britain*

AVIAN AFFERENT VAGAL ACTIVITY RELATED TO RESPIRATORY AND CARDIAC CYCLES

DAVID R. JONES

Department of Zoology, The University, Bristol, 8

(*Received* 10 *June* 1968)

Abstract—1. Attempts have been made to record afferent activity from the cervical vagi of fifty-two birds.

2. Afferent activity from stretch receptors stimulated by inspiration and from mechano-receptors located in the central cardiovascular area has been recorded.

INTRODUCTION

THE CONTROL mechanisms invoked to account for the respiratory and cardiovascular reflexes shown by birds are largely based on inference from the mammalian situation. Recent reviews have pointed out, in some detail, the differences between avian and mammalian respiratory and circulatory responses to vagal section and stimulation (Johansen & Reite, 1964; King, 1966). Although these reviews have clarified the general picture, the finer details are obscure and must remain so in the absence of precise information about the nature of afferent and efferent activity normally present in the nerves innervating the respiratory and circulatory organs. This note describes afferent activity recorded from the cervical vagus nerve of birds which is related to respiratory and cardiac cycles.

MATERIALS AND METHODS

The cervical vagi of fifty-two birds (domestic duck (*Anas domesticus*), Muscovy duck (*Cairina moschata*), Khaki Campbell (*Anas* sp.) mallard (*A. platyrhynchos*), dove (*Columba* sp.), pigeon (*Columba livia*)), have been investigated using conventional recording techniques (Jewett, 1964). Before an experiment birds were sedated by intramuscular injection of paraldehyde (1–2 ml/kg). This level of anaesthesia was maintained throughout the experiment by further injections of paraldehyde. Exposure of the cervical vagus was completed under local anaesthesia (2% Xylocaine). More extensive operative procedures, performed when attempting to localize the site of origin of afferent activity, were done under deep anaesthesia induced either by intravenous injection of 15–20 mg/kg sodium thiomylal or ether inhalation. Heart rate was recorded bipolarly (Lead II) and respiratory frequency by a pneunograph as described previously (Butler & Jones, 1968).

In birds one vagus predominates in regard to cardiac chronotropic control (Johansen & Reite, 1964; Butler & Jones, 1968). Section of the "active" vagus causes a marked increase in heart rate and has variable effects on respiratory frequency and amplitude. Consequently in these experiments both vagi were kept intact. Identification of the nature of recorded activity was usually done by correlation with respiratory or cardiac cycles. Small bundles of nerve fibres were sectioned to determine whether activity was afferent or efferent. Precise localization of the site of origin of afferent activity was attempted in seventeen animals by punctate stimulation of appropriate regions of the lungs, air sacs, heart or central blood vessels.

RESULTS

Mass activity (Fig. 1a) initiated by the inspiratory phase of the respiratory cycle was investigated by recordings from smaller numbers of units. Three types of discharge were found to be associated with inspiration although from no single

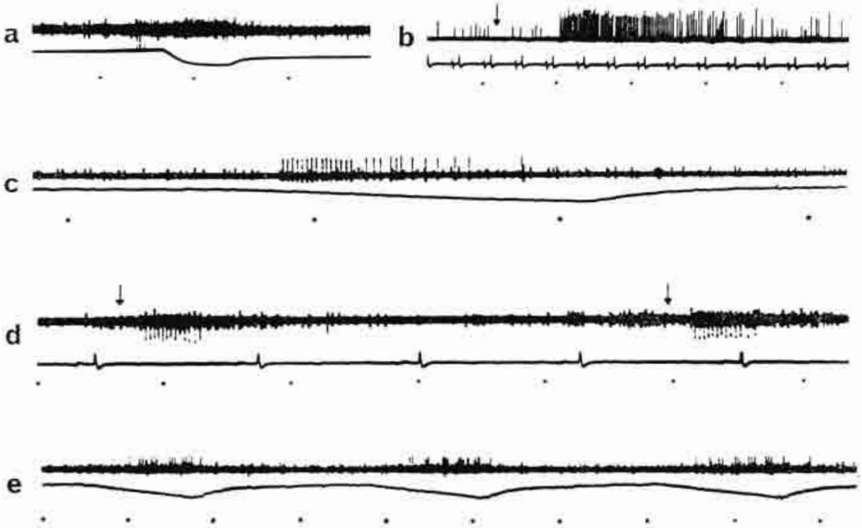

FIG. 1. Afferent activity associated with the respiratory cycle. a. Domestic duck (*A. domesticus*). Upper trace, mass discharge from a vagal slip. Middle trace, displacement of sternum (down on trace = inspiration). b. Muscovy duck (*C. moschata*). Upper trace, afferent activity during maintained inflation of the lung (retouched). Arrow marks start of inflation. Middle trace e.c.g. c. Muscovy duck (*C. moschata*). Upper trace, afferent activity during normal inspiration. Middle trace, displacement of sternum (down on trace = inspiration). d. Khaki Campbell (*Anas* sp.). Upper trace afferent activity during rhythmic artificial ventilation. Arrows mark start of inflation. Middle trace e.c.g. e. Muscovy duck (*C. moschata*). Upper trace, afferent activity during normal inspiration. Middle trace, displacement of sternum (down on trace = inspiration). In all records the bottom trace is a 1-sec time mark.

bird were all types recorded: Firstly, rapid discharge which adapted fairly slowly to maintained inflation (Fig. 1b). Secondly, low-frequency discharge initiated after a displacement of the sternum of 20 per cent of maximum, and stopping some 300 msec before maximum, displacement (Fig. 1c). The instantaneous frequency at 10 per cent sternal displacement increments was averaged for ten similar discharges. This average is plotted, in Fig. 2, against sternal displacement during inspiration. This type of activity could be evoked by artificial ventilation (closed chest preparation) (Fig. 1d). Thirdly, bursts of activity, the number of spikes per burst increasing as inspiration continued. These bursts of activity showed no correlation with the cardiac cycle. Activity continued until peak inspiration (Fig. 1e).

In all cases onset of activity lagged behind displacement of the sternum by some 200 msec.

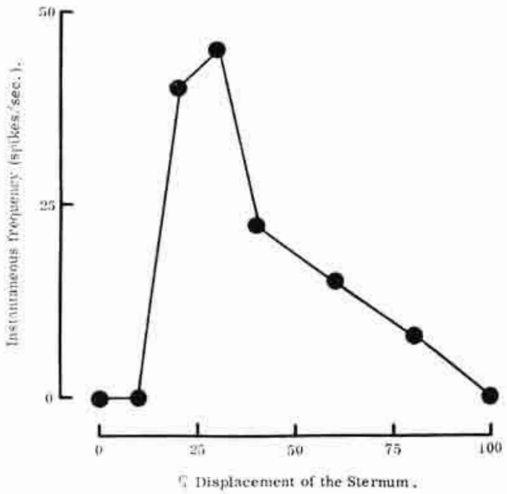

FIG. 2. Analysis of instantaneous frequency of ten discharges of the type shown in Fig. 1c against percentage displacement of the sternum during inspiration.

Two other types of single-fibre activity modified by the respiratory cycle were recorded. In one case a constant low-frequency discharge, of 140 spikes/min, present during expiration, was reduced to about 50 spikes/min during inspiration. The other pattern of activity which was recorded from the whole vagus of both the domestic duck (*Anas domesticus*) and dove (*Columba* sp.) showed an opposite response to inspiration. Low frequency discharge (135 spikes/min) during expiration doubled on inspiration. On some occasions this activity stopped for about half of the expiratory cycle. No activity was recorded solely associated with expiration during the performance of normal respiratory movements. No successful attempts were made at locating the source of these afferent discharges associated with the respiratory cycle.

Mass discharges related to the cardiac cycle showed a grouping of impulses around the period of the repolarization wave of the electrocardiogram (Fig. 3a). So far three types of activity associated with this period have been isolated. Two of these were single discharges occurring soon after the Q.R.S. complex (e.g. Fig. 3b), and the other an impulse train which occurred during and after repolarization (Fig. 3d). Placing a glass probe in the region of the pulmonary artery caused increased activity of one of the single discharges with every cardiac contraction (Fig. 3b (i) and (ii)). Punctate stimulation of the area between the atria and ventricles, near the base of the ascending aorta, increased the rate of firing of the other, although the relationship with heart rate was not maintained. The source of the burst of impulses (Fig. 3d) which occurred after the repolarization of the

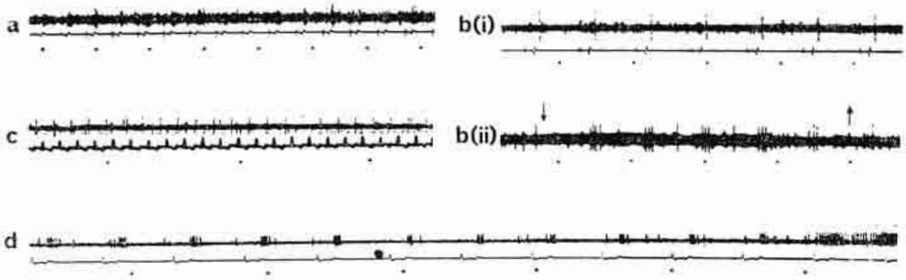

FIG. 3. Afferent activity associated with the cardiac cycle. a. Muscovy duck (*C. moschata*). Upper trace, mass discharge associated with the cardiac cycle. Middle trace, e.c.g. b. Muscovy duck (*C. moschata*). (i) Upper trace, single discharge occurring soon after the Q.R.S. complex. Middle trace, e.c.g. (ii) Effect of locating a probe in the region of the pulmonary artery. Probe positioned at the downward-pointing arrow and removed at the upward-pointing arrow. c. Khaki Campbell (*Anas* sp.). Upper trace, afferent discharge associated with the *P* wave of the e.c.g. Middle trace, e.c.g. d. Muscovy duck (*C. moschata*). Upper trace, afferent discharge associated with the repolarization wave of the e.c.g. The discharge continues during inspiration, marked by discharge similar to that shown in Fig. 1c. Middle trace, e.c.g. In all records the bottom trace is a 1-sec time marker.

ventricle (*T* wave) was not located. However, a constant and definite relationship with this period of the cardiac cycle was maintained whilst recording over a hundred heart beats on several separate occasions. Activity persisted throughout inspiration and the number of spikes in each discharge tended to decrease as expiration was prolonged (Fig. 3d). On one occasion activity was recorded just before or shortly after the *P* wave of the electro-cardiogram (Fig. 3c). Most commonly this was a single discharge but occasionally two spikes occurred during this period. The pattern of discharge was unaffected by inspiration. Heart rate was high and the animal died before localization could be effected.

DISCUSSION

From these results it can be stated that stretch receptors are stimulated during normal inspiration and that mechano-receptors, of one kind or another, are located in the central cardiovascular area. However, a much more detailed study is required in order to elucidate the role of these receptors in the maintenance of respiration and circulation in birds. In this respect an improved technique is required in that, using the present system of recording, mass discharges from vagal slips were not easily detectable and this rendered isolation of single fibres a somewhat hit-or-miss affair. Sections of the cervical vagus of ducks have shown that the majority of fibres are below 5 μ in diameter; fibres in the 6–10 μ range are comparatively rare. The relative paucity of large-diameter myelinated fibres in birds may in part account for the difficulties experienced in recording.

Acknowledgements—I am grateful to the Severn Wildfowl Trust, Slimbridge, Glos. for the gift of twelve mallards (*A. platyrhynchos*).

REFERENCES

BUTLER P. J. & JONES D. R. (1968) Onset of and recovery from diving bradycardia in ducks. *J. Physiol.* (*Lond.*) **196**, 255–272.

JEWETT D. L. (1964) Activity of single efferent fibres in the cervical vagus nerve of the dog, with special reference to possible cardio-inhibitory fibres. *J. Physiol.* (*Lond.*) **175**, 321–357.

JOHANSEN K. & REITE O. B. (1964) Cardiovascular responses to vagal stimulation and cardioaccelerator nerve blockade in birds. *Comp. Biochem. Physiol.* **12**, 479–487.

KING A. J. S. (1966) Afferent pathways in the vagus and their influence on avian breathing: a review. In *Physiology of the Domestic Fowl* (Edited by HORTON-SMITH C. & AMOROSO E. C.). Oliver & Boyd, Edinburgh.