On the Fine Structure of the Carotid Body of the Bird, 
Uroloncha domestica

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Received August 2, 1969

The chief cell of the mammalian carotid body has long been believed to be a chemoreceptor. However, some authors have recently reported that it makes synaptic contacts with nerve endings of efferent nature (Kobayashi, 1968; Abraham, 1968). Hence there occurred the question as to what type of ending is responsible for the exquisite sensitivity of the carotid body and as to whether this cell is really a chemoreceptor at all. Although there are many reports on the electron microscopy of the mammalian carotid body (for reference see Kobayashi, 1968), detailed description of the synapse in the avian carotid body has not yet been made as far as the author knows. The carotid body of little birds is known to be characteristically enclosed by the parathyroid, like the relation of the medulla to the cortex in the mammalian adrenal, to form the so-called parathyroid-carotid body complex (see Adams, 1958). Thus the avian carotid body, if studied by electron microscopy, seems to provide a key for elucidating the function of this organ.

Methods

Adult love birds, Uroloncha domestica were decapitated and the thorax was widely opened. The brachiocepharic artery was dissected. A thin polyethylene tube was inserted into this vessel through which the fixative (2.5% glutaraldehyde in 0.1 M phosphate buffer at pH 7.1) was injected. The carotid body, together with its surrounding tissue, was taken and further fixed for 2-6 hrs by immersion in the same fixative. The tissue was then rinsed for about 15 min in the phosphate buffer and finally postfixed in a 1.3% OsO4 solution for about 8 hrs. After dehydration in progressively increasing concentrations of alcohol the material was embedded in Epon (Luft, 1961). Ultrathin sections were made with a Porter-Blum microtome and stained with uranylacetate and lead tartarate (Millonig, 1961). Observations were made with a Hitachi HS 7s electron microscope.

Thicker sections of Epon embedded materials were stained with buffered toluidine blue (Yamamoto, 1963) and were studied light microscopically.

Results

The carotid body of the love bird was bilaterally located at the base of the neck just lateral to the common carotid artery 0.6–0.9mm beyond the origin of the subclavian artery. Small aberrant carotid bodies sometimes were scattered around the wall of the common carotid artery. In the same region, there were the thyroid,
Fig. 1. A light micrograph showing the parathyroid-carotid body complex of the love bird. Note the arrows indicating the communication between the capillary of the carotid body and that of the parathyroid. *as* Air sac, *cc* common carotid artery, *adt* adipose tissue. ×150

Fig. 2. Higher magnification of the small area enclosed in the rectangle on Figure 1. The parathyroidal tissue encloses the carotid body. The chief cells are scattered between the blood vessels (*v*) and myelinated nerve fibers (*mn*). ×650
Fig. 3. A low power electron micrograph showing a junctional area between the parathyroid and the carotid body. A chief cell having contacts with four nerve terminals (n) is seen in a myelinated nerve bundles. s Schwann cell, v blood vessel, p parathyroidal cell, f fibroblast. ×3,500
thymus, parathyroid and ultimobranchial body. The parathyroid almost completely enclosed the carotid body (Fig. 1).

The blood supply of the carotid body came from the common carotid artery which also supplied the adjacent organs above mentioned. In the light microscope profiles of small arteries occurred especially in the hilar region. There were abundant capillaries in the carotid body, and unions between capillaries of the carotid body and those of the parathyroid were commonly found as shown in Figure 1. Electron microscopy revealed that the endothelium of the capillaries adjacent to the chief cells of the carotid body and the parathyroidal cells was fenestrated.

There were both isolated or grouped chief cells surrounded by non-myelinated nerve fibers, nerve terminals and Schwann cells in the meshes of a well-developed capillary net in the carotid body. Thick myelinated nerve fibers were abundantly found in the connective tissue spaces, and fairly often there occurred isolated ganglion cells between the chief cells.

Figures 3 to 5 are electron micrographs showing the fine structure of the chief cell. The most characteristic feature of the cytoplasm of the chief cell was the occurrence of cored vesicles which were similar in appearance to the catecholamine granules of the adrenal medullary cell. The cytoplasmic organelles such as centrioles, endoplasmic reticulum, lysosomes, mitochondria, and the Golgi complex essentially corresponded in their structure and distribution to those in the mammalian carotid body (Lever, Lewis and Boyd, 1959; Biscoe and Stehbens, 1966; Hess, 1968; Kobayashi, 1968; Grimley and Glenner, 1968; Al-Lami and Murry 1968; Chiarugi, 1968; Zapata, Hess and Eyzaguirre, 1969).

There were aggregated nerve terminals around the chief cell. These aggregations were enveloped by a sheet of Schwann cell cytoplasm. They were distinguished from nerve fibers passing through the Schwann cell by the presence of small vesicles which were believed to correspond to synaptic vesicles. There were considerable variations in the ultrastructure of the individual nerve terminals, e.g. in the size of the terminals, density of the axoplasm, appearance of mitochondria and number of the synaptic vesicles (Fig. 4–8).

It was often seen that several terminals of different appearance lay adjacent to each other forming desmosome-like membrane thickenings. The synaptic vesicles were not always restricted to one side of the junction between two nerve terminals, but occurred frequently on each side of the apposed membranes which showed an increased electron density (Fig. 6, 7).

On the other hand, a chief cell could be recognized to be in contact with many nerve terminals, some of which were, in their turn, in contact with other nerve terminals on the opposite side to the chief cell (Fig. 4, 5). When the nerve terminal ended on the chief cell, the synaptic vesicles were always found on the nervous side.

Discussion

The parathyroid-carotid body complex is most common in small birds, though it occurs also in reptiles and even in mammals (Adams 1958). Some authors regard this intimacy as an example of "neurotropism" analogous to that between the adrenal cortex and the medulla, while others postulate a functional interrelationship
Fig. 4. A chief cell of the love bird's carotid body which makes contacts with five profiles of nerve elements. Arrows indicate the probable synaptic junctions. ×13,000
Fig. 5. A portion of a chief cell of the love bird's carotid body, around which many nerve endings are seen. Three nerve terminals are making contacts with the chief cell. There are desmosome-like structures between nerve terminals (arrows). s Schwann cell, ct connective tissue space. ×15,000

Fig. 6. Nerve endings around the chief cell in the love bird's carotid body, showing synaptic contacts between nerve endings themselves. s Schwann cell. ×30,000
Fig. 7. Nerve endings of the love bird’s carotid body. Note the occurrence of the synaptic vesicles on both faces of membrane thickenings. ×30,000

Fig. 8. Nerve endings of the love bird’s carotid body. There are considerable differences in the ultrastructure between different nerve terminals. ×25,000
of both organs suggesting that the “secretion” of the one influences the other (for reference see Adams, 1958). The present author (Kobayashi, 1969) has recently revealed the presence of catecholamines in the love bird’s carotid body using the histochemical fluorescence method. Considering his findings by the use of serial sections on the vascular architecture of the parathyroid-carotid body complex, he proposed a hypothesis that, in the love bird, the carotid body is an endocrine organ which secretes catecholamines into the blood stream presumably to influence the function of the parathyroid which encircles it.

The morphological relationship between the nerve fibers and the chief cells seems to be one of the most important points in the interpretation of the function of the carotid body. Earlier investigators have revealed that, in electron micrographs showing synapses in the central nervous system, the nerve terminal is separated from the apposed synaptic element by a cleft about 300 Å in width (see Eccles, 1964; Gray, 1969). It seems now to be the general view that the synaptic vesicles occur in the presynaptic element. Accordingly, if the chief cell represents a chemoreceptor, the conglomeration of synaptic vesicles must be expected on the side of the chief cell, as it is the receptoneural junction as in the case of the visual cells (Sjöstrand, 1958) and the taste bud (Hirata, 1966). The results in present and previous works (for reference see Kobayashi, 1968), however, give a reverse relation, i.e. the occurrence of synaptic vesicles on the nervous side, suggesting the efferent nature of the synapse. However we must be careful to decide the efferent nature of the innervation of the chief cell only on the basis of electron microscopy until we get more ample data from morphological and physiological investigations.

The present paper seems to be the first to report the probable synaptic contacts between nerve terminals themselves in the carotid body. A similar type of synapses is known to be common in some regions in the central nervous system, e.g., in the lateral geniculate body (Peters and Palay, 1966; Szentágothai, 1968; Hámori, 1968; Jones and Powell, 1969). In these regions large numbers of pre- and postsynaptic profiles come together to form the so-called synaptic glomeruli. The glomeruli usually contain a central dendrite. Their outer part is built up closely packed axon terminals. Thus, if we regard the chief cell in avian carotid body as an equivalent of the central dendrite of the glomeruli, it may be possible to consider that many morphological features in the avian carotid body correspond to those of the synaptic glomeruli.

In the central nervous system, the contact between nerve terminals seems restricted to the sites where at least two different types of axon terminals may not only influence the dendrites of a single cell but also may interact with each other by means of axo-axonic contacts (Gray, 1962; Hirata, 1964; Hámori, 1968; Jones and Powell, 1969). The occurrence of different profiles of nerve terminals around the chief cell in the avian carotid body seems to suggest the different nature of these terminals. Further studies must be done to verify the origin of nerve terminals around the chief cell.

The present finding on the occurrence of aynaptic vesicles on both sides of an axo-axonic synapse seems to correspond to the descriptions in the synaptic glomeruli of the central nervous system (Szentágothai, 1968). When we accept the general view on the one way transmission and on the presence of synaptic vesicles on the
presynaptic side in the chemical transmitting synapse, we cannot interpret this type of junction without some contradictions. Thus, it may be argued that, in the contact between nerve terminal themselves, accumulations of synaptic vesicles seem not necessarily to indicate a presynaptic nature; similar opinions have already been proposed by Szentágothai (1968).

The synapse between a chief cell and a nerve terminal having further synaptic contacts with other terminals described in the present study is similar to the so-called serial synapse described elsewhere (Gray, 1962; Kidd, 1962; Eccles, 1964; Gray, 1969). This type of complex synapse may appear as a simple synapse between two terminals or between a chief cell and a nerve terminal when the sectioned plane does not favour the appearance of one of two serial synaptic regions. In the central nervous system some authors have considered this type of synapse as the morphological basis of presynaptic inhibition; the first nerve terminal influences the second terminal to reduce the output of the second terminal’s excitation transmitter and hence reduce or block the excitation of the third component of the serial arrangement (Gray, 1962; Eccles, 1964; Gray, 1969). It is attractive to apply this hypothesis to the interpretation of the present result on the avian carotid body, though we must be careful in deciding “presynaptic inhibition” without physiological certification.

**Summary**

1. The carotid body of *Urolocha domestica* was studied by light and electron microscopy.
2. The ultrastructure of the chief cell essentially corresponded to that of the mammalian carotid body.
3. Many nerve terminals occurred around a chief cell, some of which made synaptic contacts with the latter. The synaptic vesicles were on the neural side as in the mammalian carotid body, and it was considered that these nerve terminals were of efferent nature.
4. Synaptic contacts were described between nerve terminals themselves around the chief cell. The synaptic vesicles occurred frequently on both sides of this axo-axonic synapse. In this type of synapse accumulations of synaptic vesicles may not necessarily indicate a presynaptic nature.
5. Synapse between a chief cell and a nerve terminal having further synaptic contacts with other terminals was illustrated and discussed. This type of synapse was similar to the so-called serial synapse regarded by some authors as a possible morphological basis for presynaptic inhibition.

**ジューシマツの頸動脈小体の微細構造について（内容自抄）**

1. ジューシマツの頸動脈小体を光線顕微鏡と電子顕微鏡で観察した。
2. 主細胞の微細構造は基本的には哺乳類のそれに一致していた。
3. ひとつの主細胞の周囲に多数の神経終末がみられ、そのうちのいくつかは主細胞とシナプスを形成していたが、シナプス小胞は神経側にあることからこれらの終末は哺乳類の頸動脈小体におけると同様に遠心性と考えられた。
4. 神経終末同士の間にもシナプスが見出された。この場合、シナプス小胞はしばしばシナプス結合の両側にあり、シナプス小胞の存在の有無が必ずしもシナプスの方向を示すとは限らないと考えられた。

5. 主細胞とシナプスを形成している神経終末が他方で別の神経終末とシナプス結合している像が観察された。これらは presynaptic inhibition の形態学的示標とされるいわゆる serial synapse であろうと考えられた。

References


