Serial and Triadic Synapses in the Cerebellar Nuclei of the Cat

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Summary. A quantitative electron microscopic investigation of the nucleus interpositus in cat cerebellum reveals that about 1.5% of all observed synapses are established between synaptic vesicle-bearing profiles. It is shown by serial sections that 70% of these synaptic complexes are triadic arrangements and 30% are serial synapses. Further analysis discloses that the first presynaptic element in the triadic and serial synapses may be one of four different axonal types: (A) Purkinje-cell axons; (B) and (C) afferent fibers containing large round vesicles and originating from the brain stem (probably mossy and climbing fiber collaterals); and (D) axon terminals containing small round vesicles. Indirect evidence suggests that type D profiles are the recurrent axon collaterals of the projective neurons. The second, postsynaptic and presynaptic, vesicle-bearing process in these complexes is either a class D terminal, or a somewhat more “dendrite-like” profile (Class E) containing flattened vesicles, and identified as belonging to processes of local Golgi type II interneurons.

Key words: Cerebellum – Nuclei – Triadic synapses

Introduction

Synapses in the central nervous system of vertebrates were thought to be either axo-somatic or axo-dendritic on the basis of classical light microscopy and even by early electron microscopic criteria. Other synaptic contacts, however, were recognized later. Serial axo-axonic synapses were first described in the spinal cord (Gray, 1962, 1963; Ralston, 1965) and then in other regions of the CNS (Colonnier and Guillery, 1964; Walberg, 1963; Valverde, 1966; Szentágothai et al., 1966; Pappas et al., 1964; Hámori, 1968). The observation of dendrites and somata exhibiting both presynaptic and postsynaptic sites (olfactory bulb, retina, several thalamic nuclei, etc.) complicated even more the classification and functional interpretation of synapses by introducing dendro-dendritic (Andres, 1965; Rall et al., 1966; Price, 1968; Famiglietti, 1970; Ralston, 1971; Morest, 1971; Harding, 1971; Lieberman and Webster, 1972, 1974; Lieberman, 1973;
Pasik et al., 1973), somato-dendritic (Sétaló and Székely, 1967; Wong, 1970; Pasik et al., 1976), dendro-somatic (Hámori et al., 1974; Pasik et al., 1976), and even somato-somatic (Hoppsu and Arstile, 1965) synaptic types. From the studies so far available, it looks as if these unorthodox synaptic patterns are frequent but not evenly distributed in the CNS. They appear to be confined mainly to certain sensory structures and their thalamic nuclei (retina, olfactory bulb, ventrobasal complex, geniculate nuclei). They are absent or very rare (Sloper, 1971) in the cerebral cortex and upper brain stem nuclei that contain mainly classical types of axodendritic and axosomatic synapses. In the subcortical relay nuclei, especially in the thalamus, the capacity to establish nonconventional synaptic contacts appears to be linked directly to the presence of local, specialized Golgi II type interneurons, which by their presynaptic dendrites (and somata) contribute to the formation of synaptic triads (Famiglietti and Peters, 1972; Hámori et al., 1974). These latter structures may be of special importance in information processing within these nuclei (Lábos, 1977).

In one of the most thoroughly studied brain regions, the cerebellar cortex (Eccles et al., 1967; Palay and Chan-Palay, 1974), most interneurons similar to those found in the cerebral cortex do not seem to have presynaptic dendrites and appear to be classical neurons, both structurally and functionally. Moreover, the cerebellar cortex is apparently devoid of any type of serial synapses. In the cerebellar nuclei of the cat, however, apparent axo-axonic synapses are found, although their occurrence is considered to be rare (Angaut and Sotelo, 1973). During recent quantitative morphological studies of the cat cerebellar nuclei in this laboratory (Palkovits et al., 1977), it was observed that serial synapses occur regularly though not as frequently as in the thalamic nuclei. The aim of the present study is to identify the participating elements in these complex synaptic arrangements, by means of experimental and quantitative morphological

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**Fig. 1.** Neuropil islet exhibiting synaptic contacts (arrows) between synaptic vesicle-containing processes. The presynaptic axon in these combinations exhibits either large round vesicles (C) or pleomorphic and flattened vesicles (A). The postsynaptic processes (D) have small, round vesicles mixed with a few ovoid vesicles. Class D processes are also presynaptic to dendritic spines (ringed arrow). Note also characteristic axodendritic synaptic contact between a Purkinje-cell axon (A₁) and a “regular” dendrite (d). Nucleus interpositus. Scale: 1 μm

**Fig. 2.** Two synaptic junctions (arrows) between synaptic vesicle-bearing processes in a neuropil islet. The Purkinje axon terminal (A) is presynaptic to a profile (D) containing small spheroid and a few ovoid vesicles. Class D axon terminal at right bottom is presynaptic to a process (E) containing ovoid vesicles and a few endoplasmic cisterns. Ringed arrow indicates axo-dendritic synaptic contact between Class D process and a “regular” dendrite. Nucleus interpositus. Scale: 1 μm

**Fig. 3.** “Axo-axonic” synapse lying close to a neuronal perikaryon (cb). The postsynaptic element containing large spheroid vesicles and a few dense core vesicles is considered as Class B, the postsynaptic process with small round vesicles as Class D. Nucleus interpositus. Scale: 1 μm

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1 In agranular cerebellar cortex, Sotelo (personal communication) has found presynaptic dendrites and identified them as processes of Golgi neurons