

The vascular responses to spinal heat stimulation were, on principle, the same at all applied stimulus intensities, even if panting was additionally evoked by strong heating. During vertebral canal cooling, a response like that shown in Figure 1 was observed only at perfusion temperatures around 30°C, which correspond to an average vertebral canal temperature of 35.5°C⁷. Stimulation with higher perfusion temperatures seemed too weak to induce a definite vascular response. At stronger cooling, shivering, in addition to skin blood flow reduction, was evoked, which seemed to obscure the vascular response in the intestine by changes of muscle blood flow¹.

Figure 2 shows the effects of thermal stimulation of the *hypothalamic temperature sensors*. In the example demonstrated, the thermodes were perfused during cooling with water of 30°C, which lowered hypothalamic temperature to 33.8°C, and during heating with water of 44.5°C, which elevated hypothalamic temperature to 40.7°C. The circulatory responses induced by these stimuli were obviously identical with those evoked by thermal stimulation of spinal temperature sensors. Increase of skin blood flow during heating as well as reduction during cooling were accompanied by opposite changes of intestinal blood flow. Arterial mean pressure was not affected by hypothalamic thermal stimulation.

In the case of hypothalamic thermal stimulation, the demonstrated responses were observed, only with quantitative differences, at all stimulus intensities. Depending on stimulus intensity panting was additionally evoked during heating and shivering during cooling.

The thermoregulatory effects of heat stimulation of both hypothalamic and spinal temperature sensors were reflected by the courses of rectal temperature. Its slight

fall during central heating, as visible in the figures, was apparently caused by increased heat loss from the skin following cutaneous vasodilatation at cool ambient conditions. During central cold stimulation no such changes of core temperature attributable to thermoregulatory adjustments of skin blood flow could be observed, probably because at warm ambient conditions the possible fluctuations of conductive heat loss from the body surface were reduced.

Conclusions. The pattern of regional blood flow adjustments during central thermal stimulation in the conscious dog is in agreement with the vascular responses observed in the anesthetized, paralyzed animals. Therefore, with respect to the underlying mechanisms, the same conclusions are justified. The results reported thus indicate that evocation of antagonistic changes of activity in sympathetic efferents of the cutaneous and intestinal resistance vessels may occur in the conscious dog as a typical thermoregulatory response of the autonomic nervous system.

Zusammenfassung. Am wachen Hund wurde bei selektiver thermischer Reizung von Rückenmark und Hypothalamus ein regionaler Durchblutungsantagonismus für das kutane und intestinale Gefäßgebiet als thermoregulatorische Antwort nachgewiesen.

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Evidence of Direct Nervous Connections Between the Neuromasts of the Lateral Line System of Fishes

According to text books, the sense organs (neuromasts) of the lateral line system of fishes are innervated by the so-called lateralis components of certain brain nerves. These include a pro-otic group which consists of components of the trigeminal nerve and the facial nerve, and a meta-otic group which is associated with the vagus nerve and, in some cases, with the glossopharyngeal nerve. These lateral nerves run to different series of neuromasts and supply single organs of these series by means of side branches.

In the course of studies on the anatomy and development of the lateral line system in the Genus *Tilapia* (Cichlidae)¹, evidence was obtained which indicated that apart from the above-mentioned lateralis nerves there exist nervous bundles which connect the neuromasts directly with one another. Studies of the classic literature revealed, surprisingly, that direct cellular connections between the neuromasts of the lateral line system of fishes had already been intensively discussed in the early papers. The most important of these publications, in so far as the present question is concerned, is that by CLAPP² on the lateral line system of *Batrachus*. No paper before or after has portrayed the structures in question with such detail. Her excellent figures (pl. XX, compare Figures 22 and 23) clearly show that the neuromasts, which are spread over the various parts of the head and the trunk of *Batrachus* are not only supplied by the commonly known lateralis nerves but are also endowed with direct connections, one with another. CLAPP calls these connections 'connecting strands' and remarks that they 'had the

appearance of the commissures connecting the ganglia of the sympathetic system, and from the fact that it resisted the action of nitric acid, I inferred that it was nerve tissue'. However, having discussed her observations on the connecting strands as well as the interpretations by other authors, she left the question of their nature open.

Other authors of this period either considered the connecting strands to be lymphatic canals or else suggested that they were simply remnants of the embryonic development and were devoid of function¹. It was SOLGER³ who, alone, in 1880, definitely asserted that the connecting strands were nerve bundles, 'marklose, von kernführender Schwann'scher Scheide umschlossene Nervenfasern'. This conclusion was based upon observations of *Acerina* and *Lota*. In 1882 SOLGER⁴ referred to 'nervöse Verbindung der Einzelorgane zu einer Organkette'. This is an interesting formulation which indicates a vague idea about the physiological implications of the fibers.

In the following decades, the controversy concerning the 'connecting strands', important as it was, fell gradually

¹ A more detailed publication is being prepared. Compare also O. H. SPIESER, Anatomische Untersuchungen an den Hirnnerven von *Tilapia* (Cichlidae, Teleostei). Diss. Math.-Naturw. Fakultät Tübingen (1970).

² C. M. CLAPP, J. Morph. 15, 223 (1899).

³ B. SOLGER, Sitz. ber. naturf. Ges. Halle Jg. 1880, 105 (1880).

⁴ B. SOLGER, Zool. Anz. 5, 660 (1882).

into oblivion. RAUTHER⁵, working on syngnathids, was among the few later authors who paid attention to these enigmatic structures. Others gave fairly complete descriptions of lateral line systems without being aware that 'connecting strands' existed. Some workers did make observations on them but did not realize that they had already been the subject of much disputation in the literature. Thus, BERGEIJK and ALEXANDER⁶, working on *Fundulus*, were surprised to find strands between neuromasts and believed that nobody before was aware of them except for DENNY⁷. Like some of their predecessors, BERGEIJK and ALEXANDER interpreted the connecting strands as remnants of the lateral line embryonic tissue.

Indeed, from the time of the earliest studies, the common opinion was that these strands are derived from the embryonic anlage of the lateral line system. In young embryonic stages this anlage consists of rows of cells within the epidermal epithelium. These rows anticipate the pattern of the lateral lines. The neuromasts form along them, probably directly from cells belonging to these rows. In the course of differentiation of the neuromast anlagen into sense cells and supporting cells, the cells of the cord lying between them become lengthened and form connecting strands (Figure 1). These strands first lie at the base of the epidermis. However, when the lateral line canals are formed they are displaced downwards together with the neuromasts so that they eventually lie on the floor of the canals (Figure 2). Because the connecting strands of adult fishes are so fine one may understand why many observers, who were not aware of their existence, overlooked them.

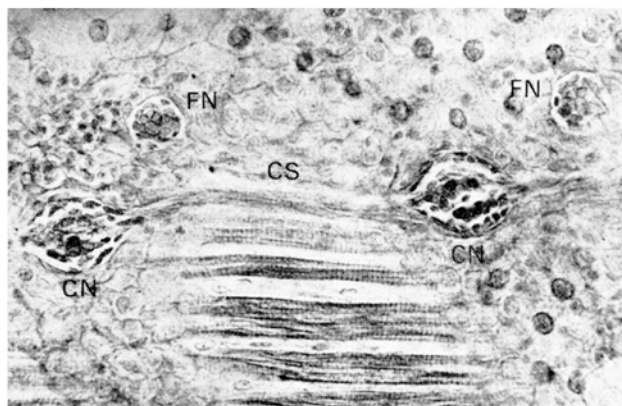


Fig. 1. Surface section from a young *Tilapia mariae* (10 mm long) showing 2 neuromasts CN of the upper trunk lateral line connected by a strand CS. During adult development such neuromasts are displaced into scaly canals. FN, anlagen of free neuromasts which remain on the epidermal surface. Distance between two neuromasts (CN) 0.12 mm. Preparation stained by the Bodian procedure.

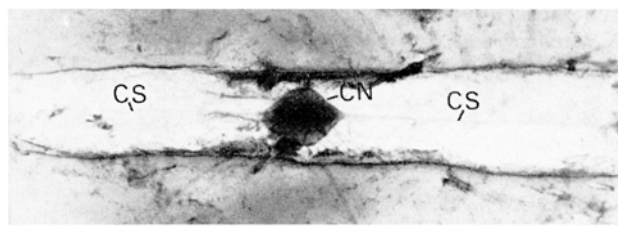


Fig. 2. *Tilapia nilotica* (total length 192 mm). Canal within a scale of the lower trunk lateral line. CN, neuromast. The roof of the canal has been removed in order to display the connecting strands CS more clearly. Length of the canal 3.1 mm. Preparation stained by the Hematoxylin technique after maceration with nitric acid.

The present author has studied these strands in *Tilapia nilotica* and in other *Tilapia* species mainly in the region of the upper and lower lateral lines of the trunk, and to a certain extent in the head region. The general pattern of distribution of the strands closely resembles the description given by CLAPP for *Batrachus*.

There is strong evidence that the statement by SOLGER^{3,4} indicating that the connecting strands function as nervous structures, is correct. This supposition receives support for the following reasons: 1. Microscopic observations have shown that the connecting strands of adult *Tilapia* are similar in structure to nerves derived from ganglia in the main sympathetic chain (compare CLAPP). 2. The connecting strands can be selectively stained by the EL-BADAWI and SCHENK method⁸. This histochemical test reveals the presence of acetylcholinesterase. The enzyme can be traced by brownish red copper ferrocyanide.

Fresh, unfixed, cryostat sections (20 and 30 μ m) were incubated for 1 h at 37°C. Acetylcholinthiodide (SERVA) was used as a substrate. Eventually the sections were fixed in 4% formalin, for 10 min, and then embedded either directly in glycerine gel or, after being treated with alum hematoxylin (Meyer's Haemalaun⁹), in DePeX.

This demonstration was most successful with connecting strands of young fishes 10 mm long. In fishes whose neuromasts were already enclosed in canals the strands could be followed only short distances due to the difficulty of obtaining complete series of sections. In older *Tilapia*, scales have completely formed; these are extremely hard and render cryostat sectioning difficult.

The only argument for the neural nature of the connecting strands still lacking should eventually be provided by electrophysiology. However, such experiments do not lie within the framework of the present author's studies. One would like to speculate about the physiological function of the connecting strands, for instance with respect to peripheral integration. But such speculations may be somewhat premature. At any rate, considering the renewed interest in the lateral line system of fishes, electrophysiologists and neurocytologists should take into account those direct connections between the neuromasts.

Zusammenfassung. Auf histochemischer Basis wird an *Tilapia* (Cichlidae, Teleostei) die bereits 1880 von SOLGER geäußerte und später in Vergessenheit geratene Auffassung bestätigt, dass die Verbindungsstränge zwischen den Neuromasten in den Seitenkanälen bei Knochenfischen marklose Nervenfasern, ähnlich jenen des vegetativen Nervensystems, sind.

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⁵ M. RAUTHER, Fauna e Flora del Golfo di Napoli, 36. Monogr. (1925).

⁶ W. VAN BERGEIJK and S. ALEXANDER, J. MORPH. 110, 333 (1962).

⁷ M. DENNY, J. comp. Neurol. 68, 49 (1937).

⁸ A. EL-BADAWI and E. A. SCHENK, J. Histochem. Cytochem. 15, 580 (1967).

⁹ B. ROMEIS, Mikroskopische Technik, 16. Aufl. (Oldenbourg, München-Wien 1968).

¹⁰ Acknowledgments: I am most grateful to Dr. K. REUTTER (Anatomisches Institut der Universität Tübingen) who undertook the histochemical investigations for this account. This work was supported by the Deutsche Forschungsgemeinschaft.