# AURICULAR-VENTRICULAR INTERACTING MECHANISMS IN THE SYSTEMIC HEART OF THE CUTTLEFISH SEPIA OFFICINALIS L. (CEPHALOPODA)

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# AURICULAR-VENTRICULAR INTERACTING MECHANISMS IN THE SYSTEMIC HEART OF THE CUTTLEFISH *SEPIA OFFICINALIS* L. (CEPHALOPODA)

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CEPHALOPODA
*SEPIA OFFICINALIS*
CUTTLEFISH
CIRCULATORY SYSTEM
HEART
PACEMAKER

ABSTRACT. – Our physiological examinations on the systemic heart of the cuttlefish *Sepia officinalis* L. revealed that the auricle as well as the ventricle each has a myogenic automatism of its own. The results presented in this paper support the hypothesis that the ventricular pacemaker is located within the atrio-ventricular junction, while the auricular myogenicity seems to be diffuse. Because examinations of perfused systemic hearts indicated that the ventricular automatism is influenced by the pulsating auricle, it is supposed that the ventricular pacemaker is subordinated to the myogenicity of the auricles. According to histological and physiological examinations, the concept of a hydro-mechanical interaction between the auricle and the ventricle has been developed. It suggests that the auricle transforms the peristaltic contractions of the efferent branchial vessel into a kind of pulse wave, which causes the opening and stretching of the AV-valves during the ventricular diastole, inducing a reflex-like contraction of the ventricle. Proceeding from this hypothesis, it is assumed that the auricles are the primary pacemakers of the coleoid cephalopod systemic heart.

CEPHALOPODA
*SEPIA OFFICINALIS*
SEICHE
SYSTÈME CIRCULATOIRE
CŒUR
PACEMAKER

RÉSUMÉ. – Mécanismes interactifs auriculo-ventriculaires du cœur de la Seiche *Sepia officinalis* L. (Cephalopoda). Nos recherches physiologiques sur le cœur systémique de *Sepia officinalis* L. ont démontré que l'auricule, comme le ventricule, ont chacun un automatisme myogénique qui fonctionne séparément. Les résultats que nous présentons soutiennent l'hypothèse que le pacemaker ventriculaire est localisé à la jonction atrio-ventriculaire tandis que la myogénicité auriculaire semble être diffuse. Les études portant sur des cœurs systémiques perfusés indiquant que l'automatisme ventriculaire est influencé par l'auricule contractant-décontractant, on suppose que le pacemaker ventriculaire est subordonné à la myogénicité des auricules. Les études histologiques et physiologiques permettent de développer la conception d'une interaction hydro-mécanique entre l'auricule et le ventricule. Celle-ci suggère que l'auricule transforme les contractions péristaltiques du vaisseau branchial efférent en une sorte d'onde de pression qui fait que les valves-AV s'ouvrent et s'étendent pendant la diastole ventriculaire produisant ainsi une contraction réflexe du ventricule. En se basant sur cette hypothèse on pourrait conclure que les auricules sont les pacemakers primaires du cœur systémique des Céphalopodes Coleoidés.

## INTRODUCTION

Numerous physiological investigations on isolated ventricles of bivalves, gastropods and cephalopods (for review see Krijgsman & Divaris 1955) revealed a myogenic, stretch-dependent automatism of the molluscan heart. E.g. an isolated, 'Straub-cannulated' ventricle of *Sepia officinalis* L. shows only rhythmical contractions if it is stretched by a filling pressure of at least 20 mm water-column. A further increase of the pressure leads to a linear acceleration of the frequency up to a maximum value of 58 ± 12 beats/min (Kling 1985). This correlation between filling pressure and excitation is characteristic of molluscan ventricles and has been described by several authors who examined the ventricles of gastropods (*Aplysia* : Straub 1904; *Helix* : Willems 1932; Almquist 1973; *Dolabella* : Matsui 1945), bivalves (*Mercenaria* : Smith 1985) and cephalopods (*Eledone* : Smith 1981a; *Octopus* : Foti *et al.* 1985). However, though a lot of work has been done to investigate the physiology of the molluscan ventricle, all attempts to localize a distinct pacemaker area within the systemic heart have so far failed. For that reason it is still being discussed where the automatic activity of the molluscan ventricle originates. In general it is proposed that the rhythmicity of the molluscan heart is governed by a diffuse myogenicity, i.e. the automatic activity originates in each myocardial cell (Krijgsman & Divaris 1955 ; Hill & Welsh 1966). Some authors, however, observed *in vivo* (Wells 1979), *in vitro* (Smith 1981b; Wells 1983) and even in tissue culture (Versen, unpublished) that the origin of the cephalopods' ventricular contractions is located in the area of the atrio-ventricular junction. Proceeding from these observations, it is a matter of interest that in whole systemic heart preparations of *Sepia officinalis*, perfused synchronously via both auricles, the auricles and the ventricle contracted as *in vivo*, i.e. alternately with the same rate of beats (Jakobs 1991a, b). However, although Jakobs used the same filling pressure as Kling (1985) in the 'Straub-cannulated' ventricle preparations, the perfused systemic hearts contracted in an evident lower frequency (17 ± 7/min.) than the 'Straub-cannulated' organs.

These results suggest that the myogenic automatism of the ventricle is being influenced by the auricles. Proceeding from the assumption that there is an interaction between both compartments of the coleoid cephalopod systemic heart, it seems probable that the supposed ventricular pacemaker is located next to the auricle, i.e. within the AV-junction.

The following observations and experiments were carried out to elucidate the presence of an auriculo-ventricular interaction within the systemic heart of *Sepia offcinalis* L. and to give further evidence that the myogenic automatism of the cephalopod ventricle is organized into nodal pacemaker areas.

## MATERIAL AND METHODS

Advanced juvenile (mantle-length 8-11 cm; body weight 60-110 g; Bassin d'Arcachon) and adult animals (mantle-length 11-17 cm; body weight 200-400 g; Mediterranean near Banyuls-sur-Mer) of both sexes of *Sepia officinalis* L. were used in this study. All animals were anaesthetized by 1.5 % ethanol/seawater (SW) before surgical procedures and dissections were carried out.

Scanning Electron Microscopy : The preparations were fixed in 4 % formalin/SW and postfixed with 2 % osmium tetroxide in sodium cacodylate buffer (0,1M; pH 7,4; 1 000 mOsm). The specimens were dehydrated through a graded series of acetone, critical point dried (Technics, Alexandria), sputter coated (Polaron equipment) and viewed with a scanning electron microscope (Jeol Ltd., Tokyo).

Light microscopy : Material fixed in buffered formalin or Bouins solution was embedded in paraffin. Paraffin sections (7 µm) were stained with Massons trichrome modified by Goldner and Bodian's nerve coloration.

Physiological Preparations : Filtered aerated seawater-glucose solution (1.7 g/l; pH 8.3) was used as physiological solution, bathing- and perfusion medium. All experiments were performed at temperatures of 18-20 °C.

*a. Ring-shaped preparations* : Ring-shaped segments (length 4-5 mm) of the left or right auricle, the atrio-ventricular junction (AV-junction), the central part of the ventricle and the ventricular area next to the cephalic aorta were mounted on stainless steel clasps. These preparations were isometrically suspended (auricle 1 ± 0.5 cN; AV-junction 2.5 ± 0.5 cN; ventricle 0.5-4 cN; ventricle/cephalic aorta 2.5 ± 0.5 cN) in a 50 ml water jacketed organ bath with one clasp anchored and the other fixed to a strain gauge (Statham UC2). The pressure transducer was connected to a DC bridge amplifier (HSE type 300) and its signals were registrated on a thermographic recorder (Watanabe Mark V).

*b. Auricle-ventricle preparations* : The isolated systemic heart, including both auricles, was mounted in a flat organ bath and the genital and renal artery as well as the cephalic aorta were closed by ligatures. In each experiment one auricle was used to place an input cannula inside the ventricle. All potential electrical connections between this auricle and the ventricle were prevented through the fixation of the cannula by a ligature at the AV-junction. The second input cannula was placed into the other auricle and fixed by a ligature at the end of the efferent branchial vessel. For the 'open-valve' preparations, the AV-valve of this auricle was kept intact and functioning. For the experiments in which the hydro-mechanical coupling between auricle and ventricle should be interrupted, the AV-valve was sealed with a tissue adhesive (Histoacryl, Braun Melsungen).

The tightness of the seal was tested after the experiments by filling of the auricle with a 0.1 % Evans Blue/Seawater solution. Both input cannulas were connected with separate perfusion reservoirs which enabled controlled preload pressures for the auricle (4 cm $H_2O$) and for the ventricle (9 cm $H_2O$). To record the pressure pulse and the contraction rate of the isolated preparations, pressure transducers (auricle : HSE W101 ; ventricle : surgical 'single-use' transducer, Braun Melsungen) were installed between the cannulas and the perfusion reservoirs. The signals of the transducers were amplified by two HSE bridge amplifiers and displayed simultaneously on a two-channel xt-recorder (Watanabe Mark V).

## RESULTS

### *Ring-shaped preparations*

Whereas all examined auricles (n = 25) showed, with (0.5-1 cN) or without stretching, spontaneous rhythmical contractions (3.5 ± 1/min.) for several hours, remarkable differences between the tested ventricle-preparations could be recorded (Fig. 1, Aa).

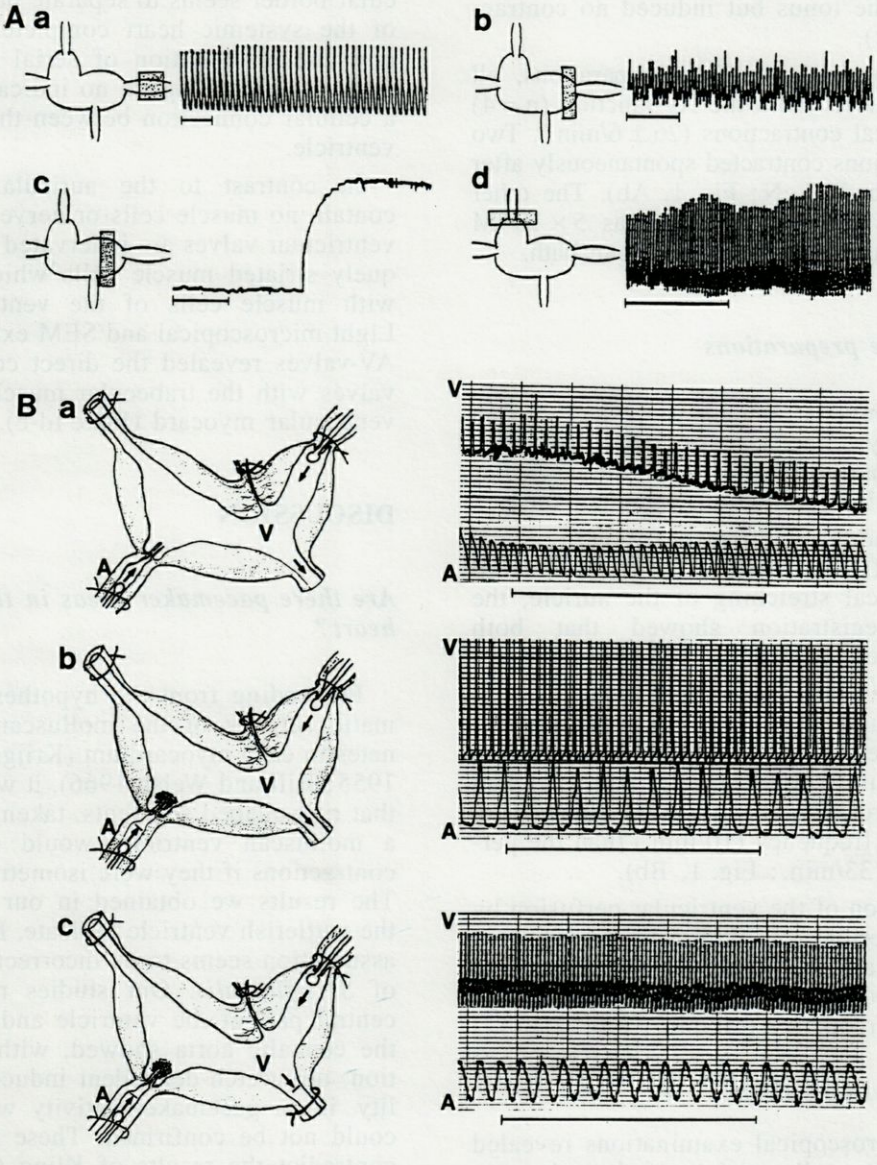



Fig. 1. – A, Actograms of isometrically suspended ring-shaped preparations taken from different parts of the systemic heart of *Sepia officinalis* (Scale bar 1 min.). a, Spontaneous contractions of an auricle preparation. b, Stretch-induced contractions of an AV-preparation. c, Increasing tonus of a ventricle-preparation after catecholamine stimulation. d, Catecholamine-induced contractions of a preparation from the ventricular area next to the cephalic aorta. B, Simultaneously recorded actograms of the auricle-ventricle preparations (Scale bar 1min.). a, 'Open valve' preparation; auricle (A) and ventricle (V) contract with the same frequency. b, Occlusion of the AV-valves; auricle and ventricle contract with different frequencies. c, Closure of the posterior aorta; the increasing ventricular frequency does not affect the auricular contraction rate.

Only one of the ring-shaped segments (n = 6), taken from the ventricular area next to the cephalic aorta, showed spontaneous contractions (35/min.) when they were isometrically suspended (3 cN). Two of these specimens started to contract for a short period as we applied $5 \times 10^{-6}$ M noradrenaline into the organ-bath (Fig. 1, Ad). The other preparations didn't show any contractions, neither by an increase of the stretching force nor by a higher noradrenaline stimulation ($10^{-5}$M).

The ring-shaped preparations from the middle area of the ventricle (n = 2) showed, even if they were forcefully stretched (4 cN), no contractions. The application of noradrenaline ($10^{-5}$M) led to an increase of the tonus but induced no contractions (Fig. 1, Ac).

In contrast to these ventricle preparations, all ring-shaped segments from the AV-junction (n = 4) showed rhythmical contractions (26 ± 6/min.). Two of these preparations contracted spontaneously after they were stretched (3 cN; Fig. 1, Ab). The other two preparations started to contract as $5 \times 10^{-6}$M noradrenaline was applied into the organ bath.

### *Auricle-ventricle preparations*

The experimental arrangement we had chosen to perfuse the systemic heart of *Sepia officinalis* provided the possibility to record the auricular and the ventricular contractions simultaneously.

Though we had to use different filling pressures (auricle : 4 cm $H_2O$; ventricle 9 cm $H_2O$) to avoid an unphysiological stretching of the auricle, the simultaneous registration showed that both compartments were contracting with the same frequency (20 ± 10/min.; Fig. 1Ba).

As we interrupted the luminal connection between the auricle and the ventricle by sealing the AV-valves, the unperfused auricle, still stretched with a filling pressure of 4 cm $H_2O$, showed an obviously lower frequency (10/min.) than the perfused ventricle (33/min.; Fig. 1, Bb).

The interruption of the ventricular perfusion by closing the posterior aorta with a ligature did not affect the contraction frequency of the auricle (10/min.), but led to a remarkable acceleration of the ventricular frequency (60/min.; Fig. 1, Bc).

### *Morphological examinations*

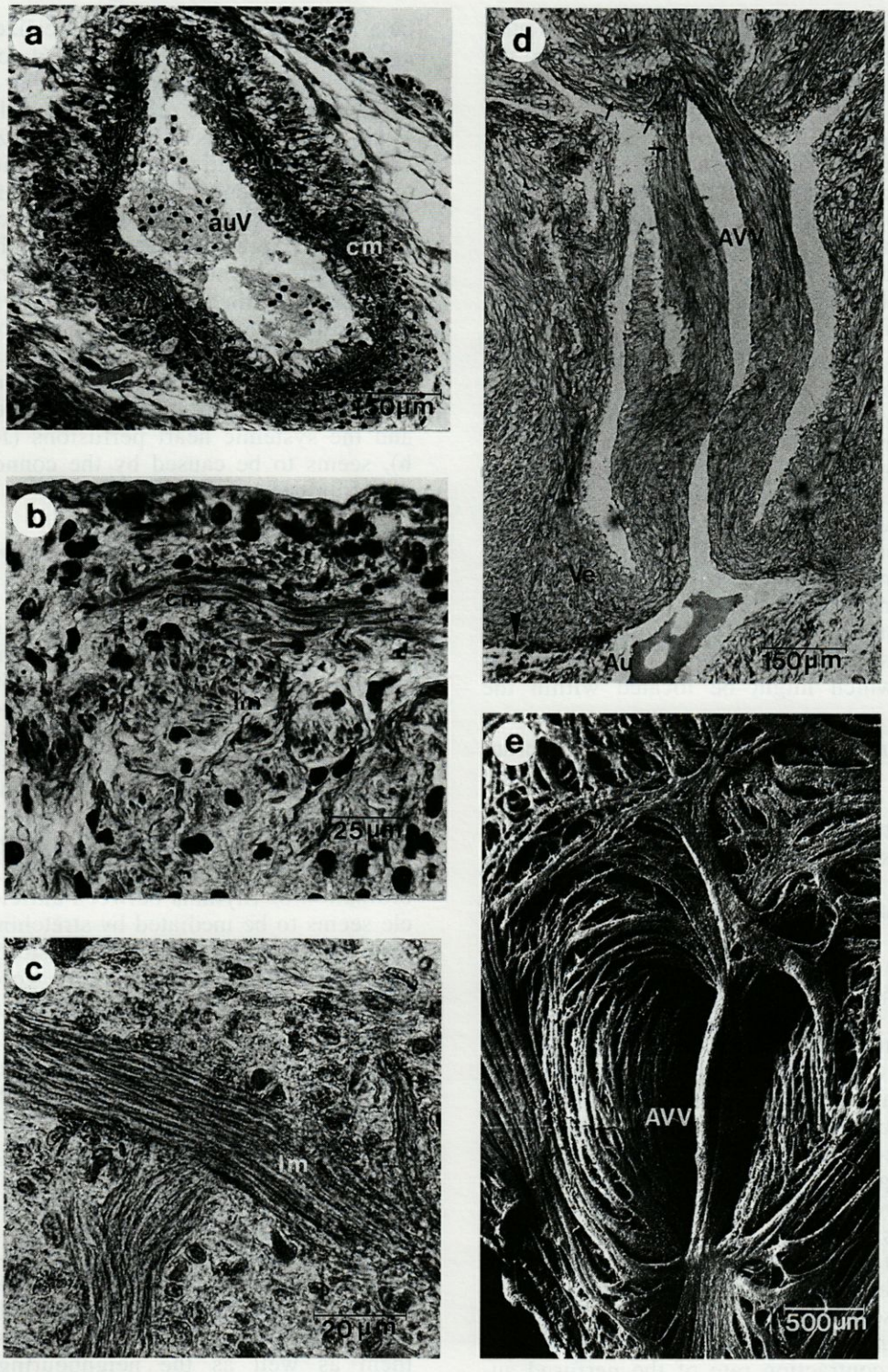
The light-microscopical examinations revealed that the auricular wall consists of three layers : the epi-, myo– and the endocard. The epicard is built by cubic cells of the coelom epithelium with a continuous lamina basalis, connected to the myocardium by a thin layer of collagenous fibers. The muscle cells of the myocard branch several times and show a clear oblique striation. At the base of the gills, where the auricular valves form a sharp border between the efferent branchial vessel and the auricle, the muscle cells are circularily arranged similar to those whithin the Tunica media of the efferent branchial vessel (Plate Ia). Towards the middle area of the auricle, however, the muscle fibers near the auricular lumen are longitudinally orientated and the outward running fibers show a transversal-circular orientation (Plate Ib). Whithin the auricular myocard next to the ventricle, all muscle fibers show only a longitudinal orientation (Plate Ic). There they insert on a collagenous layer which separates the auricle from the ventricle (Plate Id). This auriculo-ventricular border seems to separate both compartments of the systemic heart completely, because until now the examination of serial longitudinal sections of this area gave no indication that there is a cellular connection between the auricle and the ventricle.

In contrast to the auricular valves, which contain no muscle cells or nerve fibers, the atrioventricular valves are innervated and contain obliquely striated muscle cells which are connected with muscle cells of the ventricular myocard. Light microscopical and SEM examinations of the AV-valves revealed the direct conjunction of the valves with the trabecular muscle bundles of the ventricular myocard (Plate Id-e).

## DISCUSSION

### *Are there pacemaker areas in the coleoid heart?*

Proceeding from the hypothesis that the automatic activity of the molluscan ventricle originates in each myocardium (Krijgsman and Divaris 1955; Hill and Welsh 1966), it would be expected that ring-shaped segments, taken from any part of a molluscan ventricle, would show rhythmical contractions if they were isometrically suspended. The results we obtained in our examinations of the cuttlefish ventricle indicate, however, that this assumption seems to be incorrect for the ventricle of *S. officinalis*. Our studies revealed that the central part of the ventricle and the area next to the cephalic aorta showed, with a single exception, no stretch-dependent induction of contractility, i.e. a pacemaker activity within these areas could not be confirmed. These findings seem to contradict the results of Kling (1985), who described a stretch-dependent automatism of the cuttlefish ventricle. But it must be considered that the 'Straub-cannulation' of the ventricle will stretch each part of the organ, also the AV-junction. And here we found a stretch-inductable contractility in our preparations.




Pl. I. – a, Cross section of the auricular area next to the gills with circularily orientated muscle fibers (cm). The auricular valves (auV) contain no muscle fibers. b, Cross section of the middle area of the auricle with circularily (cm) and longitudinally (lm) orientated muscle fibers. c, Longitudinal section of the auricular area next to the ventricle with longitudinally orientated muscle fibers (lm). d, Longitudinal section of the AV-valves (AVV). A connective tissue layer (➤) separates the auricle (Au) from the ventricle (Ve). The muscle fibers of the valves are connected with the ventricular myocard (→). e, SEM-view of the AV-valves (AVV) and the inner surface of the ventricle. Note the ramifications of the trabecular network and its conjunction with the AV-valves.
*Abbreviations* : Au, auricle; auV, auricular valves; AVV, Atrio-Ventricular valves; cm, circular muscle fibers; lm, longitudinal muscle fibers; Ve, ventricle.

Since Skramlik (1941) observed a particular sensitivity of the *Octopus* ventricle within the AV-junction, other authors also supposed that the myogenicity of the cephalopod ventricle is not diffuse (Wells 1979; Wells 1983; Smith 1981b; Wells and Smith 1987). Though we are still not able to localize the assumed pacemaker precisely, our results support the hypothesis of Smith (1981b) that the diffuse automatism of the cephalopod ventricle is in fact organized into nodal areas, located in the region of the auriculo-ventricular junctions.

The results of Jakobs (1991a, b) suggest, however, that the ventricular pacemaker only works autonomously if the ventricle is isolated and stretched alone. In complete systemic heart perfusions the ventricles contract with the same frequency as the auricles, but though the same filling pressure was used, obviously slower than in 'Straub-cannulated' preparations. Based on these findings and the observation that also *in vivo* the auricles and the ventricle contract with the same rate of beats, it must be considered that the ventricular automaticity seems to be subordinated to a further pacemaker, which might be located within the auricles.

These connections between the efferent branchial vessels and the ventricle have not been studied as much as the ventricle. Some authors, who observed that isolated oyster auricles are able to beat by themselves with a regular rhythm, concluded that they seem to function as a whole with a similar mechanism as the ventricle (Jullien and Morin 1931; Oka 1932). Our studies revealed, however, that the mechanism of the auricular contractility seems to be different from those of the ventricle. Corresponding to the findings with the oyster auricle, we observed that isolated auricles of the cuttlefish systemic heart show slow regular contractions (3.5 ± 1/min.). But in contrast to the ventricular preparations, each part of the auricular ring-shaped segments contracted without any stretching and the frequency was not accelarated if the preparations were isometrically expanded. The assumption that the missing nerve control might be the reason for the low contraction rate of the isolated auricle was disproved, as we perfused some auricles (n = 5), using the same filling pressure as in the auricle-ventricle examinations. The contraction rate of the perfused auricles was accelerated to the same values (20 ± 10/min.; Versen, 1996 unpubl.) we obtained in the 'open-valve' preparations. In these experiments, the ventricle contracted simultaneously with the same frequency as the auricle, though it was directly stretched with a considerably higher filling pressure than the auricle.

Based on these results it is stated that both compartments of the systemic heart have their own myogenic automatism. But while the ventricular automatism seems to be localized in distinct areas, there are no indications until now, to contradict the assumption that the auricular myogenicity originates from each myocardium (Hill and Welsh 1966). Despite this different organization of the myogenic automatism, the examinations of isolated auricles (Versen, 1996 unpub.) and ventricles (Kling 1985) revealed that in both compartments, the luminal pressure seems to be the mediating factor that coordinates the contraction of the muscle fibers within the auricular as well as in the ventricular myocard. However, the results of the 'open-valve' experiments indicate that the considerable discrepancy between the ventricular frequencies of the 'Straub-cannulated' examinations and the systemic heart perfusions (Jakobs 1991a b), seems to be caused by the connection of the ventricle to a pulsating auricle.

### *How do the auricles influence the ventricular contractility?*

The means by which the auricles influence the ventricular automatism are still being discussed. Based upon morphological examinations, it had been supposed that there might be a cellular conduction pathway between both compartments of the systemic heart (*Sepia* : Jakobs and Schipp, 1992). Examinations of the systemic hearts of gastropods (*Helix* : Willems 1932; *Dolabella :* Matsui 1945) and bivalves (*Crassostrea* : Uesaka *et al.* 1987a, b) indicated, however, that the coordination of rhythms between auricle and ventricle seems to be mediated by stretching. Nevertheless, the morphological and physiological results we obtained in our studies gave good reasons to suppose that there might be a different form of interaction.

The histological examinations indicated that the specific orientation of the muscle fibers within the auricular myocard enables the auricle to transform the peristaltic contractions of the efferent branchial vessel into a contraction mode which creates a kind of a pulse wave. I.e. each auricular contraction pushes the haemolymph with a fast increase of pressure towards the AV-valves, causing an opening of the valves in the ventricular diastole. The SEM-examinations of the AV-valves suggest that an opening of the valves will stretch them as well as the neighbouring ventricular areas. Stretch sensitive cells within this area could create an excitation if the valves were stretched. The multiple ramifications of the ventricular muscle cells and their close coupling would permit the transmission of this excitation from cell to cell, inducing a ventricular contraction wave which originates at the AV-junction (Kling and Schipp 1987).

Though this theory is only based upon histological examinations, nevertheless it corresponds in

many respects with the results of several authors, e.g. the alternate contractions of the auricle and the ventricle (Uesaka *et al.* 1987a, b), the sensitivity of the AV-junction (Skramlik 1941) or the spreading of the ventricular contraction wave (Smith 1981b; Wells and Smith 1987).

### *Is there a hydro-mechanical interaction between auricle and ventricle?*

Because also an electrical- or a stretch-mediated interaction between the two compartments would explain the observations described above, we repeated the auricular-ventricular experiments, with the difference that the AV-valves were sealed with a tissue adhesive. This occlusion of the valves only interrupted the luminal connection between the auricle and the ventricle, while a potential electrical or mechanical interaction should not be affected. The results of these experiments show that though we used the same filling pressures as in the 'open-valve' experiments, the auricle and the ventricle contracted with different frequencies. While the auricular contraction-rate still corresponds with the frequencies we obtained in the isolated auricle perfusions, the perfused ventricle obviously contracted faster than in the 'open-valve' preparations respectively complete systemic heart perfusions (Jakobs 1991a, b). Assuming that the electrical and the mechanical connection between the auricle and the ventricle was not interrupted, it must be supposed that the independent contractility of the auricle and the ventricle in this experiment could only be caused by the occlusion of the luminal connection between the both compartments.

The assumption that only stretching is the mediating factor for the coordinate contractility of the systemic heart (Uesaka *et al.* 1987a, b) does not explain why the auricular frequency was not accelerated, induced retrogradely by the increasing contraction rate of the ventricle, after we closed the posterior aorta with a ligature. The frequencies we recorded here correspond with the ventricular contraction rates of the 'Straub-cannulated' preparations (Kling 1985), indicating that the ventricular frequency is considerably higher if the AV-valves are disabled and the ventricle, or the AV-junction which contains the ventricular input-cannula, is stretched by a constant luminal pressure.

These results suggest that the coordination between the independent automatisms of the auricle and the ventricle is caused by a hydro-mechanical interaction between the compartments. According to our results and the findings of other authors, it is supposed that there is a ventricular pacemaker within the AV-junction, being subordinated to the auricular automatism, which acts as the primary pacemaker of the systemic heart.

Though there are still many questions left which have to be answered for the complete understanding of the cuttlefish systemic heart physiology, the results presented here, substantiate the hypothesis that the auricles are not only connections between the efferent branchial vessels and the ventricle, but have a definite regulatory function in the circulatory system of cephalopods.

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