Biol. Rev. (1984), **59**, *pp.* 255–270
Printed in Great Britain

CONNECTIVE TISSUE CATCH IN ECHINODERMS

BY TATSUO MOTOKAWA

Department of Biology, University of the Ryukyus, Nakagusuku, Okinawa, 901–24 Japan

(*Received 7 September, accepted 2 November* 1983)

CONTENTS

I. INTRODUCTION

The mechanical properties of collagenous connective tissues usually do not change in a short period. Although typical mammalian collagenous connective tissue such as tendon becomes stiffer with increase in age, the change is very slow and the physiological significance of the stiffening is not understood (Viidik, 1979*a*). In echinoderms, however, collagenous connective tissues with changeable mechanical properties are found in all classes of this phylum (Table 1). The change is rapid and sometimes reversible. These connective tissues can be regarded as nervously controlled mechano-effectors which control the body tone by changing the mechanical properties. Jordan (1914, 1919) was the first to demonstrate that the body-wall connective tissues of sea cucumbers change their mechanical properties and that the change is possibly controlled by nerves. Later Uexküll (1926) claimed that the body-wall dermis was catch muscle. Although the dermis is a connective tissue and not muscle, his interpretation that the dermis plays a role similar to that of the catch muscles of molluscs is correct. He also studied the spine 'muscle' of sea urchins and here again he described two kinds of 'muscle' layers: a 'fast muscle' layer and a 'catch muscle' layer (Uexküll, 1900). Takahashi (1966, 1967*a*, *b*) established that the 'catch muscle' layer is in fact a collagenous connective tissue, yet it changes its mechanical properties: in a stiff state it can hold the spine, whereas in a soft state it allows the muscle to move the spine. Again Uexküll was right about the role of this connective tissue. Takahashi named this tissue the 'catch apparatus' after its function. The means whereby the stiffness-changeable connective tissues control the body tone is called the 'connective tissue catch' (Rüegg, 1971).

Table 1. *Catch connective tissues in echinoderms*

Tissue	Function	Reference
Holothuroidea		
Body wall dermis	Control of body tone	Motokawa (1981)
Tendon of pharyngeal retractor muscle	autotomy	Smith & Greenberg (1973)
Echinoidea		
Catch apparatus	Control of spine posture	Takahashi (1967*b*)
Central ligament	Prevention of spine disarticulation	Motokawa (1983)
Ophiuroidea		
Intervertebral ligament	Autotomy	Wilkie (1978*a*)
Crinoidea		
Syzygial ligament	Autotomy	Holland & Grimmer (1981*a*)
Cirral ligament	Control of flexibility of cirrus	Wilkie (1983)
Asteroidea		
Spine ligament	Control of spine posture	Motokawa (1982*b*)

Literature on the connective tissue catch is limited, and evidence for its existence in all the five classes of echinoderms has been presented only recently. The aim of this review is to introduce this unique and relatively unknown phenomenon. I will first review how the catch connective tissues are used in the five classes of Phylum Echinodermata, and then discuss the control and the molecular mechanism of the stiffness change of the tissue.

II. MORPHOLOGY AND FUNCTION OF CATCH CONNECTIVE TISSUES

(1) *Holothuroidea*

Sea cucumbers stiffen their body walls when touched (Uexküll, 1926; Serra-von Buddenbrock, 1963). The body wall is composed mainly of a collagenous connective tissue dermis. The isolated dermis changes mechanical properties in response to mechanical (Stott *et al.*, 1974; Motokawa, 1984*a*), chemical (Motokawa, 1981), electrical (Motokawa, 1981), and photic (Motokawa, 1984*b*) stimulation. At evisceration a part of the body wall of sea cucumbers becomes quite soft and the viscera are extruded from that part. Dendrochirote holothurians eviscerate not only the viscera but also the aquapharyngeal bulbs. The tendons of the pharyngeal retractor muscles lose tensile strength and break at evisceration (Smith & Greenberg, 1973; Byrne, 1982). Some sea cucumbers undergo fission of their bodies (Emson & Wilkie, 1980). The body wall becomes soft enough to be torn at autotomy and fission. *Stichopus japonicus* Selenka aestivates: during summer months the animal crawls under rocks and becomes dormant; the body wall becomes quite stiff during this summer sleep (Mitsukuri, 1903). This stiffening helps the animal to spend the dormant period safely. The softening at autotomy and the stiffening at aestivation are the extreme degrees of the stiffness change of the dermis. The stiffness controllability of the dermis is quite likely also used in body tone control during the usual activities of sea cucumbers, although there is no measurement of the mechanical properties of the dermis *in vivo*. I observed the behaviour of *Stichopus chloronotus* Brandt and 'felt' the stiffness of the body wall by

palpation. The animal sometimes moves with propagating peristaltic waves, and the body wall is soft at that time. When the animal extends the front part, the extension is soft, whereas the unextended hind part is stiff. This seems reasonable because, if all the body wall were to become soft, selective extension by hydrostatic pressure would be impossible. Wolcott (1981) suggested that the tonus generated by the body wall connective tissue helps the action of the cloacal pump.

The body-wall dermis is composed mainly of extracellular materials: collagen fibres and a matrix of ground substance. In *Thyone briareus* (Lesueur) the collagen fibres associate to form a lamella. The fibres of adjacent lamellae are oriented nearly perpendicularly to one another (Menton & Eisen, 1970). In *Holothuria tubulosa* Gmelin, *Stichopus japonicus*, and *S. chloronotus* the collagen fibres do not have such strict orientations: they make loose, felt-like, three-dimensional networks (Serra-von Buddenbrock, 1963; Kawaguti, 1966; Motokawa, 1982*a*). The presence of acid mucopolysaccharides has been shown in the matrix histochemically (Krishnan, 1968). Sulphated mucopolysaccharides have been isolated from several sea cucumber body walls (Maki & Hiyama, 1956; Motohiro, 1960; Cássaro & Dietrich, 1977). The cells frequently found in the dermis are morula cells and cells with processes, possibly neurosecretory, which are filled with electron-dense granules. Muscle cells are found only in the walls of water-vascular canals (Motokawa, 1982*a*). Therefore the observed stiffness change of the dermis is very likely caused by the change in the mechanical properties of the extracellular components of the dermis.

(2) *Echinoidea*

In sea urchins two connective tissues have been shown to change their mechanical properties: the catch apparatus and the central ligament. Sea-urchin spines are mounted on tubercles, forming a ball-and-socket joint (Takahashi, 1967*c*). The spine is mechanically connected by two cone-shaped layers of soft tissue: the muscle layer and the catch apparatus. The muscle is responsible for movement of the spine. The catch apparatus is a collagenous connective tissue which can change its mechanical properties (Fig. 2*a* and Takahashi, 1967*a*, *b*). When it is stiff, it can hold the spine at an angle and make it immovable. Sea urchins living in holes in rocks, such as *Echinometra mathaei* (de Blainville), anchor their bodies against the walls of the hole by their spines. The catch apparatus is stiff during such a condition. When the animals move their spines, for example to come out of the holes, the catch apparatus becomes soft, in order not to impede the spine movement caused by muscles.

Some sea urchins such as *Diadema setosum* Leske have another ligament, in addition to the catch apparatus, at the spine joint. This is the central ligament, and it can also change its mechanical properties (Motokawa, 1983). Although both of the spine ligaments can support the spine, the roles of these ligaments seem to be different. The catch apparatus locks the spine at an angle when it is stiff; the central ligament cannot lock the spine, but it limits the angle of inclination of the spine during the stiff state. The spine is free to incline to a certain angle, but further inclination, and thus the disarticulation of the spine, is prevented by the central ligament.

The catch apparatus (Kawaguti & Kamishima, 1965; Takahashi, 1966, 1967*a*; Smith *et al.*, 1981; Hidaka & Takahashi, 1983; Motokawa, 1983) and the central ligament (Motokawa, 1983) have similar ultrastructures. These ligaments are composed of

parallel collagen fibres. Cell elements frequently found in these tissues are morula cells and possible neurosecretory cells with processes filled with electron-dense granules. The main difference between these tissues is that the catch apparatus contains a few muscle cells whereas the central ligament contains none; the fact that the central ligament can change its stiffness thus indicates that muscles are not responsible for the change.

Other candidates as catch connective tissues in sea urchins are the connective tissue layers of the tube feet (Florey & Cahill, 1977) and the stalk ligament of globiferous pedicellariae, which break off from the test after having bitten an enemy (Chia, 1970). The breaking of the pedicellaria can be described as attack autotomy (Emson & Wilkie, 1980), and the connective-tissue ligament may lose tensile strength as in other examples of echinoderm autotomy.

(3) *Ophiuroidea*

Brittle stars autotomize their arms. The arm ossicles are connected by intervertebral ligaments which are composed of parallel collagen fibres associated with a ground substance containing a carbohydrate–protein complex. The ligaments lose tensile strength and are easily broken at autotomy (Wilkie, 1978*a*). This softening of the ligament is not a one-way response: Fig. 2*b* shows that the softening is reversible, which suggests that the invertebral ligament changes the stiffness not only at the catastrophic occasion of autotomy, but also in everyday life, thus controlling the flexibility of the arms. For example *Ophiothrix fragilis* (Abildgaard) extends the arms upwards into tidal currents and suspension feeds (Warner, 1982). The intervertebral ligaments of the extended arm are probably stiffened to maintain the posture of the arm.

On the surface of the intervertebral ligament there are juxtaligamental cells, which send processes into the ligament. These processes contain large electron-dense granules, which Wilkie (1979) has suggested may be neurosecretory.

(4) *Crinoidea*

Crinoids are rheophilic suspension feeders (Meyer, 1982): they extend their arms against the current and suspension-feed. The arms are rigid in this feeding posture. The collagenous ligaments that connect the arm ossicles may become stiff to maintain the postures (Meyer, 1971). Three types of skeletal articulations are known: synostosis, syzygy, and synarthry. The geometry of the articulation suggests that the animal can flex the body mainly at the synarthries. Autotomy, however, seems to occur mainly at the other two articulations (Emson & Wilkie, 1980). It is tempting to suggest that the ligament at the synarthries changes in stiffness for controlling the flexibility of arms, whereas the ligaments at the synostosis and syzygy soften at autotomy. The ligament at syzygy is composed of parallel collagen fibres and nerve-like cell processes which contain electron-dense granules (Holland & Grimmer, 1981*a*).

The cirri are the jointed appendages that grasp the substrate to anchor the animal. The ossicles of the cirri are connected by collagenous ligaments which contain no muscles, yet the cirri deform actively (Holland & Grimmer, 1981*b*). The flexibility of the cirri is also variable. When comatulids grip a substrate, the cirri are rigid, but, when the animals are walking, the cirri are flexible. Holland & Grimmer (1981*b*) suggested the possible role of the epithelial cells for contraction, and also suggested that the stiffness change of the cirri is caused by the catch activity of the connective-

tissue ligament. The reversible softening of the ligament by sea water containing excess potassium concentration was directly demonstrated by Wilkie (1983). The ligament contains possible neurosecretory cells with electron-dense granules (Holland & Grimmer, 1981*b*).

(5) *Asteroidea*

The body wall of starfish is sometimes quite rigid and sometimes quite flexible. For example, the aboral body wall of *Ctenodiscus crispatus* (Retzius) swells out to make an epiproctal cone at low oxygen tension (Shick, 1976). The body wall is quite likely soft during this rapid extension. The body wall becomes soft when the animals autotomize their arms (Anderson, 1956). When a starfish mounts a clam and tries to open it, the body wall of the animal becomes stiff enough to resist the force exerted by the tube feet (Eylers, 1976*a*). The body wall of the starfish is composed of ossicles which are connected by both collagenous connective tissues and muscles. The stiffening and relaxation of the body wall may well be caused by the muscles, but it is reasonable to suppose that the actual stiffness of the body wall is dependent on connective tissues, as in the body walls of sea cucumbers.

The only connective tissue whose stiffness is shown to change by mechanical tests is the tissue at the spine joint of the crown-of-thorns starfish *Acanthaster planci* (L.) (Motokawa, 1982*b*). The tissue is a collagenous tissue with muscle fibres in it. The spines usually stand upright, but, when the animal passes through a narrow space, the spines bend at the joint. The tissue is probably soft at that moment. The tissue becomes stiff or soft in response to factors isolated from the coelomic fluid of the sea cucumber. Because these factors change the stiffness of holothurian dermis and echinoid spine ligaments in a similar manner, it can be concluded that the stiffness change of the starfish spine-joint tissue is caused by the connective tissue, not by the muscles.

In summary, echinoderms seem to use catch connective tissues for control of the tone of the tissues on many occasions during their daily activities. Autotomy is the most spectacular case, in which the stiffness change can be readily observed. In other cases, especially in the cases of stiffening, the activities of the connective tissue and that of the muscles are often difficult to distinguish. Studies on chemical substances that selectively affect the connective tissue alone reveal the distribution of the catch connective tissues in echinoderms (Motokawa, 1982*b*).

III. MECHANICAL PROPERTIES AND THEIR CHANGE

Few attempts have been made to describe quantitatively the stiffness change of echinoderm connective tissues. Because the catch connective tissues are viscoelastic materials, the conventional Young's modulus is not adequate to describe the mechanical properties of the tissues. The most complete description is derived from tests performed on the dermis of body walls of the sea cucumbers *Actinopyga echinites* (Jäger) and *Holothuria leucospilota* Brandt (Motokawa, 1984*c*). When the dermis is quickly stretched to some length and that length is held, the force exerted in the dermis at stretch gradually declines and finally approaches zero. The stress–relaxation curve thus obtained (Fig. 1) can be closely simulated by that given by the four-element mechanical model shown in Fig. 1 inset. The model parameters of the dermis in artificial sea water

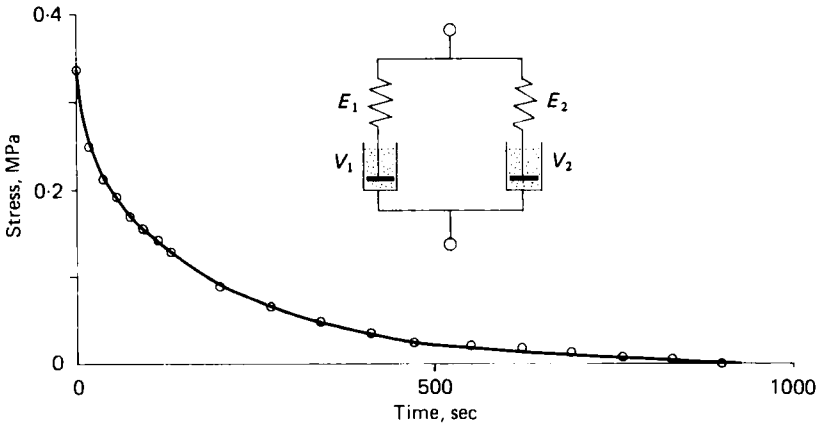

Fig. 1. Stress–relaxation of the dermis of the sea cucumber *Actinopyga echinites* (Jäger) in artificial sea water with normal composition. The dermis was stretched to 0·5 strain at time 0, and that strain was maintained. The stress in the dermis (hollow circles) decreased with time, and it finally approached 0. This stress relaxation behaviour could be simulated with the four-element mechanical model shown in inset. E_1 and E_2 are the elastic moduli of the springs, and in this particular case 0·19 MPa and 0·49 MPa, respectively. V_1 and V_2 are the viscosities of the dashpots, and in this case 3·3 MPa·s and 98 MPa·s, respectively. This model generated a stress–relaxation curve, which agreed well with that of the dermis, as is shown in the figure.

Table 2. *Model parameters of* Actinopyga echinites *in artificial sea water* (ASW) *and artificial sea water with elevated* (100 *mM*) *potassium concentration* (KASW)†

	Elasticity		Viscosity		Relaxation time	
	E_1	E_2	V_1	V_2	t_1	t_2
	(0·1 MPa)	(0·1 MPa)	(MPa·s)	(10 MPa·s)	(s)	(s)
ASW	3·97	5·84	3·71	5·73	12·4	109
KASW	4·70	8·98	19·5*	63·9*	26·9*	661**

† The parameters of the four-element mechanical model shown in Fig. 1 inset are shown. Because the viscosities and relaxation times showed large variations, the median values are given. The relaxation times, t_1 and t_2, are defined as follows: $t_1 = V_1/E_1$, $t_2 = V_2/E_2$. The number of experiments was 18 for ASW and 15 for KASW.

*, ** The value is statistically different from that in ASW at the level of 5 % and 1 %, respectively.

of normal composition and those of the dermis in artificial sea water with elevated (100 mM) potassium concentration are compared (Table 2). The viscosities greatly increase in excess K^+ solution, whereas the elasticities change only slightly, thus the relaxation times increase. The viscosities in normal artificial sea water differ from sample to sample: the variation ranges through more than two orders of magnitude, but the variation of the elasticities is small. The wide variation of the viscosity value in normal artificial sea water reflects the ease of change of the viscosity: the dermis may be either in a 'relaxed' state, in an 'intermediate' state, or in a 'catch' state. Artificial sea water with excess K^+ will stimulate the dermis in the 'relaxed' and 'intermediate' states so as to increase the viscosity to the 'catch' state. A one-hundredfold viscosity change can actually be observed in a single dermis (Motokawa, 1984*c*).

Another piece of evidence that the viscosity changes greatly but the elasticity little is obtained from the tensile test performed on the catch apparatus of a sea urchin (Hidaka

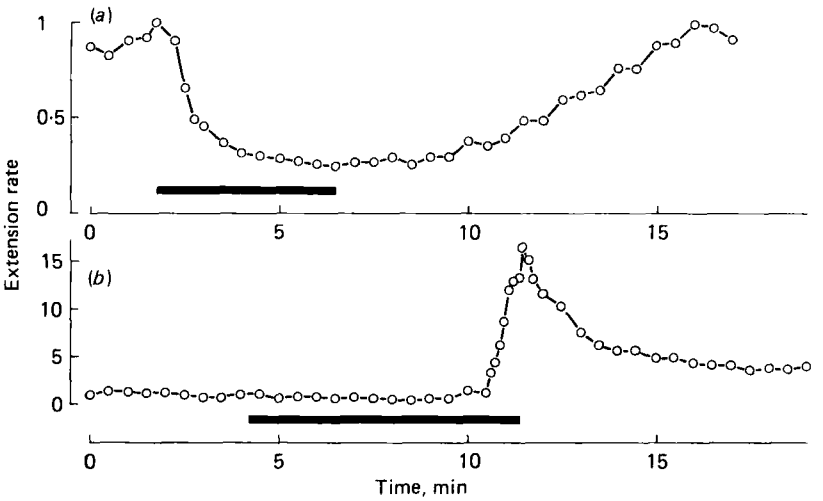

Fig. 2. Effect of artificial sea water containing high (100 mM) potassium concentration on the isotonic elongation of the catch connective tissues. (*a*) The catch apparatus of the sea urchin *Diadema setosum* Leske. (*b*) The intervertebral ligament of the brittle star *Ophiomastix lütkeni* Pfeffer. The ordinate is the extension rate which was normalized by that of the time just before the application of high potassium solution. The bars indicate the periods of application of the high potassium solution. Notice that the high potassium solution induced catch state in the catch apparatus, whereas it relaxed the intervertebral ligament. Assuming that the elasticity does not change, the high potassium solution increased the viscosity to four times that before application (*a*), and it decreased the viscosity to one-sixteenth of that before application (*b*).

& Takahashi, 1983). The apparent elastic stiffness depends on the speed of stretch: at a low speed the stiffness is high in an acetylcholine-treated sample and low in an adrenaline-treated one; at a high stretch speed the difference disappears. These results imply that the viscosity increases in acetylcholine and decreases in adrenaline, but the elasticity remains unchanged.

The creep test, which measures the elongation of the tissue under a constant load, has been preferred in most other studies (catch apparatus: Takahashi, 1967*b*; Smith *et al.*, 1981; Motokawa, 1982*b*; sea-urchin central ligament: Motokawa, 1983; ophiuroid intervertebral ligament: Wilkie, 1978*b*; holothurian dermis: Jordan, 1914, 1919; Eylers, 1976*b*, 1982; Motokawa, 1981, 1982*c*, 1984*a*, *b*, *c*; crinoid cirral ligament: Wilkie, 1983; starfish spine ligament: Motokawa, 1982*b*). All the catch connective tissues except the cirral ligament show continuous elongation or flow, even under a light load. The stimulation changes the flow rate. The change in the flow rate is the measure of the change in the viscous element which lies in series with the applied force. The viscosity of this element is generally called the normal viscosity. Catch connective tissues change the normal viscosity (Fig. 2). The reaction time varies from several seconds to several minutes. The change is usually reversible. The extent of the change in normal viscosity is sometimes as large as 10- to 100-fold. Because normal viscosity of the central ligament of sea urchins (Motokawa, 1983), and that of the body wall dermis of sea cucumbers (Motokawa, 1984*a*, *c*) in sea water with normal composition, show quite a wide variation (more than two orders of magnitude), the catch connective tissues are likely to control the viscosity by 100-fold *in vivo*.

In summary, the catch connective tissue is a viscoelastic material whose viscosity (not elasticity) can be changed rapidly and reversibly by a factor of more than 100.

IV. NERVOUS CONTROL

The stiffness change caused by nerve stimulation was demonstrated by Maeda (1978) in the catch apparatus of the sea urchin *Anthocidaris crassispina* (A. Agassiz). Electrical stimulation of the radial nerve softens the catch apparatus. Electrical stimulation applied to the adjacent body surface transiently increases the stiffness and then greatly reduces it. Mechanical stimulation applied to the adjacent body surface, which elicits the convergence response of spines, softens the catch apparatus. The softening of the catch apparatus allows the spine muscle to move the spine easily. Thus the stiffness of the catch apparatus is controlled in a manner coordinated with the spine movement.

Nervous control of the stiffness of the body-wall dermis of sea cucumbers was suggested by Jordan (1919), based on the observation that a piece of dermis is softer when it is isolated with a radial nerve attached. The dermis of *Stichopus chloronotus* and *Isostichopus badionotus* (Selenka) becomes quite a soft gel when vigorous mechanical stimulation is applied. The softening is suppressed by anaesthesia (Hill & Reinschmidt, 1976; Motokawa, 1981). The dermis of *Holothuria leucospilota* becomes stiff under photic stimulation, which causes the stiffening through stimulating the 'photoreceptor' in the epidermis (Motokawa, 1984*b*). These observations strongly suggest that the stiffness of holothurian dermis is controlled by nerves.

Because autotomy is a nervously mediated phenomenon (Emson & Wilkie, 1980), the softening of the connective tissue at autotomy can be inferred to be controlled by nerves. Arm autotomy by *Ophiocomina nigra* (Abildgaard) and evisceration by the sea cucumber *Thyone briarieus* are induced by isotonic KCl, and the responses are suppressed by anaesthesia (Wilkie, 1978*b*; Smith & Greenberg, 1973).

Smith & Greenberg (1973) found that the coelomic fluid taken from the eviscerating *Thyone briareus* induces the evisceration in other animals. The coelomic fluid causes the loss of tensile strength in the tendon of the pharyngeal retractor muscle. These authors isolated the active substance from the coelomic fluid and also from the tissues of the sea cucumber. It is a small molecule of unknown character. A survey of coelomic fluids of other echinoderms revealed that all the coelomic fluids cause a change in stiffness when tested on the catch apparatus (Motokawa, 1982*b*). Some coelomic fluids stiffen, some soften, and some first soften and then stiffen the connective tissue. From the coelomic fluid of the sea cucumber *Stichopus chloronotus*, which causes stiffening of the body wall dermis, both a stiffening factor and a softening factor have been isolated (Motokawa, 1982*c*). These factors affect the stiffness of the catch apparatus, the central ligament, and the spine ligament of crown-of-thorns starfish in a manner similar to the holothurian dermis (Motokawa, 1982*b*). As these factors work similarly on a variety of catch connective tissues, the control mechanism for stiffness change in these tissues appears to be similar. The finding that echinoderm coelomic fluids contain factors that modulate the stiffness of the catch connective tissues does not necessarily mean that the stiffness of the tissues is hormonally controlled. As these factors are also found in several tissues of sea cucumbers (Smith & Greenberg, 1973; Motokawa, 1981), they are likely to have diffused out from the tissue where they function, to the coelomic fluid.

The effects of putative neurotransmitters have been surveyed in several catch

connective tissues. The dermis and the tendon of sea cucumber pharyngeal retractor muscle, and the ophiuroid intervertebral ligament do not respond to the usual neurotransmitter substances, such as adrenaline, noradrenaline, 5-hydroxytryptamine and glutamic acid (Smith & Greenberg, 1973; Wilkie, 1978*b*; Motokawa, 1981). γ-Amino-butyric acid is not effective on the intervertebral ligament or on the sea-cucumber body wall. 1-Methyladenine is not effective on sea-cucumber tendon and body wall. Acetylcholine transiently increases the viscosity of the holothurian dermis, and later it decreases the viscosity to less than the value before application (Motokawa, 1981, 1984*a*). Acetylcholine has no effect on the tendon of the pharyngeal retractor muscle nor on the intervertebral ligament. Because the usual neurotransmitters are not effective, unknown ones may be working in these connective tissues. Candidates for these are the factors found in the coelomic fluids.

In contrast to other catch connective tissues, the catch apparatus of sea urchins responds to a variety of putative neurotransmitters. Acetylcholine, 5-hydroxytryptamine, and glutamic acid stiffen, whereas adrenaline, noradrenaline, dopamine, and γ-amino-butyric acid soften, the ligament (Takahashi, 1967*b*; Maeda, 1978). The stiffening effect of acetylcholine is transient, as it is in the holothurian dermis (Hidaka & Takahashi, 1983). The central ligament of the sea urchin also increases in viscosity when acetylcholine is applied, and decreases when adrenaline or noradrenaline is applied (Motokawa, 1983). The above observations and the result of electric stimulation (Maeda, 1978) suggest that sea-urchin spine ligaments are controlled by two kinds of nerves: the stiffening nerve and the softening nerve.

A solution containing higher potassium concentrations than that of sea water changes the stiffness of catch connective tissues. Because the effect of excess K^+ is suppressed by anaesthesia (Smith & Greenberg, 1973; Wilkie, 1978*a*, 1983), the excess K^+ solution may stimulate the nervous elements in the tissues. Excess K^+ elicits different responses in different tissues (Wilkie, 1983): it stiffens the echinoid catch apparatus (Fig. 2*a*), the echinoid central ligament and holothurian dermis (Table 2), whereas it softens the tendon of holothurian pharyngeal retractor muscle, the ophiuroid intervertebral ligament (Fig. 2*b*), the spine ligament of crown-of-thorns starfish, and the cirral ligament of crinoids. The difference in response may be interpreted as follows. Some catch connective tissues may have only one kind of nerve. For example, the tendon of pharyngeal retractor muscle is specialized for autotomy and it is quite possible that the tendon is innervated by the softening nerve alone, and thus the response to excess K^+ is softening. Other connective tissues may have both stiffening and softening nerves, the apparent response determined by which nerve is more accessible to excess K^+ stimulation.

The morphological evidence for nervous control is that the neurosecretory-like cell processes, which contain large electron-dense granules, are found in all the catch connective tissues (catch apparatus: Smith *et al.*, 1981, Hidaka & Takahashi, 1983; central ligament: Motokawa, 1983; tendon of pharyngeal retractor muscle of the sea cucumber: Byrne, 1982; holothurian dermis: Motokawa, 1982*a*; intervertebral ligament: Wilkie, 1979; syzygial ligament: Holland & Grimmer, 1981*a*; cirral ligament: Holland & Grimmer, 1981*b*). The morphology of the cells has been studied in detail by Wilkie (1979) in the intervertebral ligament of ophiuroids. The perikarya of the cells are concentrated in a ganglion-like node, which is located on the surface of the ligament

and is innervated by hyponeural nerves. The cells send processes into the ligament. The processes contain spherical or oval granules of very large size (up to 0·7 μm long). The morphology of the cell strongly suggests that the cell is neurosecretory. Because the granule-containing cell processes are the only cell elements that are distributed abundantly in catch connective tissues, these cells no doubt control the mechanical properties of the extracellular substances of the tissue.

V. MECHANISM OF VISCOSITY CHANGE

It is known that the stiffness change of catch connective tissues is not caused by muscular activity, because some connective tissues have been shown to contain no muscle cells in the tissues (holothurian dermis: Motokawa, 1982*a*; echinoid central ligament: Motokawa, 1983; ophiuroid intervertebral ligament: Wilkie, 1978*a*; crinoid ligaments: Holland & Grimmer, 1981*a*, *b*). Catch apparatus of sea urchins contains thin muscle fibres which occupy 1–3 % of the cross-sectional area of the tissues. Even if these muscles are assumed to exert the force that is the largest known for muscles in the literature, the increase in passive tension in the catch state is more than that expected from the muscles (Smith *et al.*, 1981; Hidaka & Takahashi, 1983). The role of the muscle in the catch apparatus may be to control the length of the catch apparatus. Slow contraction of the catch apparatus is observed (Takahashi, 1967*b*). Because other cells that could be candidates for the development of tension are not found in the connective tissues, a viscosity change in the extracellular matrix is the most likely mechanism.

The collagenous connective tissues can be regarded as a network of collagen fibrils embedded in a proteoglycan matrix. That the collagen fibrils do not critically determine the mechanical properties of the catch apparatus is indicated by the results obtained by Hidaka & Takahashi (1983). They observed that, in the catch apparatus, the axial band pattern of collagen fibrils does not change, irrespective of the tissue length. The observation contrasts with that in the mammalian tendon, where the band periodicity increases with tendon length, and the elongation of the collagen fibrils accounts for the tension of the tissue (Viidik, 1979*b*). In the catch apparatus, collagen fibrils slip past one another when stretched. The stretch resistance of the catch apparatus is therefore not determined by the elastic stiffness of the collagen fibrils but is determined by the cohesive forces between collagen fibrils, between collagen and proteoglycan, and between proteoglycan molecules. The creep behaviour of the other catch connective tissues also indicates that the collagen fibrils are not continuous, or, in other words, that they are not covalently bonded at each end. The elastic stiffness of the collagen fibrils does not determine the mechanical properties of the tissue directly. Collagens are likely to work as fillers, as has been proposed for the body wall of a sea anemone (Gosline, 1971).

The viscosity, not the elasticity, changes in the catch connective tissues. The relaxation times of two Maxwell elements in the mechanical model of the dermis of *Actinopyga echinites* are of the order of 10–100 sec (Table 2). The relaxation time in this range is likely to be caused by the translational movement of the macromolecules in the dermis (Goto, Hirai & Hanai, 1962). The viscosity is determined by the resistance to this translation; in other words, the strength and the number of the weak (non-covalent) bonds between the macromolecules. The change in the relaxation time and thus viscosity is the result of the change in the interactions between macromolecules in the dermis.

Proteolytic enzymes may well reduce the viscosity of the connective tissue, as proposed for the formalin-induced degradation of holothurian dermis (Junqueira *et al.*, 1980). Most of the viscosity change in the catch connective tissues are, however, rapid and reversible. Rapid digestion and resyntheses of the connective tissue molecules by enzymes seem unlikely.

Both collagen and sulphated mucopolysaccharides, which are known to exist in the holothurian dermis (Tanikawa, 1955; Hiyama & Maki, 1956; Motohiro, 1960), are polyelectrolytes. Ionic environment greatly affects the electrostatic interactions between polyelectrolyte molecules, and also affects the shape of the molecules, which in turn influences steric interactions (such as molecular entanglement and excluded volume effects). Both electrostatic and the steric interactions profoundly influence the viscosity of polymer solutions (Nagasawa, 1978). The effects of ionic environment on the viscosity of catch connective tissues have been studied in some echinoderms (catch apparatus: Smith *et al.*, 1981; Hidaka, 1979, 1983; holothurian body wall: Eylers, 1982; intervertebral ligament: Wilkie, 1978*b*). Among these studies Hidaka's work on the catch apparatus is most detailed. Increase in ionic strength reduces the viscosity of the catch apparatus. This effect can be expected from the fact that the counter ions reduce the electrostatic interactions between the molecules. Chelation of Ca^{2+} with EGTA reduces viscosity to the value that compares with that in 10^{-4} M adrenaline. The effect of adrenaline is antagonized by the increase of Ca^{2+} concentration. Increase in Ca^{2+} concentration above the normal increases the viscosity a little. Calcium ions are known to provide electrostatic cross-bridges between polyelectrolytes in a number of systems such as alginate gel (Reid, 1978). The pH greatly affects the viscosity. The viscosity is lowest at pH 5, increases as pH becomes more basic, and at pH 9 the viscosity compares with that in 10^{-4} M acetylcholine. These results suggest the following viscosity control system in the catch apparatus (Fig. 3): adrenaline causes a decrease in Ca^{2+} concentration, which reduces the number of Ca^{2+}-mediated cross-bridges and thus decreases the viscosity; acetylcholine causes an increase in pH which increases the negative charges on the macromolecules; calcium ions bind to these sites to make cross-bridges and thus increase the viscosity. Both decrease in ionic strength, and excess Mg^{2+} and Ca^{2+}, increase the viscosity of holothurian dermis (Eylers, 1982). Excess Ca^{2+} increases the viscosity of intervertebral ligament (Wilkie, 1979*b*). These results are in accord with those of the catch apparatus. Effect of pH on the viscosity of the intervertebral ligament is quite different from that of the catch apparatus. The viscosity of intervertebral ligament is lower in a basic pH. This experiment, however, was done in 0·05 M buffer solutions. Because the ionic environment of experimental solutions is quite different from natural conditions, the observed result may be due to factors other than pH (Wilkie, 1978*b*).

Because the manipulation of the ionic environment causes large and reversible change in the viscosity, regulation of the ionic environment is the most likely mechanism for the *in vivo* control of the viscosity of the catch connective tissues. Caution must be exercised, however, because the ionic environment may affect both the extracellular materials and the cells that control the viscosity. For example it is possible that Ca^{2+} concentration affects the secretory activity of the possible neurosecretory cells and thus affects the viscosity (Wilkie, 1983). Eylers (1982) tried to eliminate this effect by killing the cell element by soaking the holothurian dermis in distilled water before experimentation. This procedure, however, will cause loss of water-soluble proteins

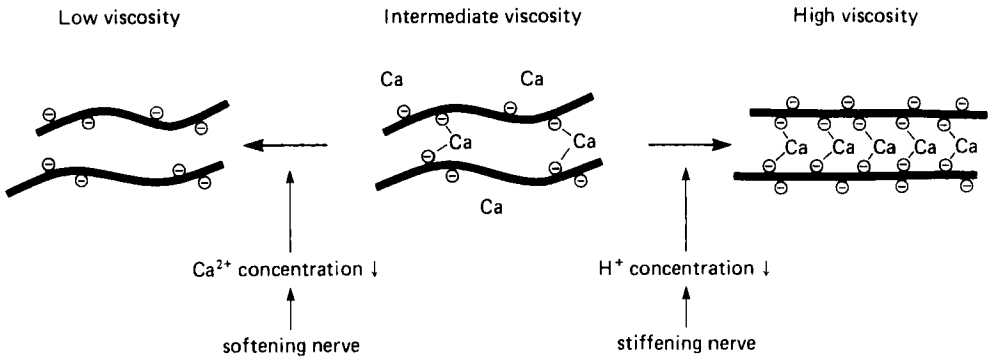

Fig. 3. Hypothetical schemata of the viscosity control system of catch connective tissues based on the work of Hidaka (1983) on sea-urchin catch apparatus. The viscosity is assumed to be determined by the number of cross-links, which are mediated by calcium ions, between negatively charged macromolecules. The charge distribution of the macromolecules is controlled through pH in the tissue, which is altered *via* the 'stiffening' nerve. The concentration of calcium ions is controlled through the 'softening' nerve.

from body walls (Tanikawa, 1955). More work is needed with a system in which the activities of cells are suppressed by several different methods.

Holland & Grimmer (1981 *a*) found that after autotomy the surface of crinoid ossicles of syzygy looks smooth. They suggested that either a chelating agent or an acid is secreted from the granules in the neurosecretory-like cell processes at autotomy. In the intervertebral ligament of ophiuroids, the presence of a Ca^{2+}-binding substance is suggested in the neurosecretory-like cell processes (Wilkie, 1979). Experiments to detect the change in pH or change in Ca^{2+} concentration in the tissue at the change in mechanical properties, and experiments to identify the granule contents in the cell processes, will bear fruitful results.

VI. CONCLUSIONS

The catch connective tissue is defined as the collagenous connective tissue whose mechanical properties can be changed rapidly (in seconds or minutes) under nervous control. At present only a few tissues have been shown to be catch connective tissues. Behavioural observations of echinoderms, however, suggest that the catch connective tissues are widely distributed in echinoderms.

So far few related phenomena have been found in the collagenous connective tissues of other phyla. Mammalian uterine cervix becomes more extensible at parturition. The increase in extensibility is caused by degradation of collagen by collagenase, whose activity is controlled by hormones (Jeffery & Koob, 1980). It is well known that the collagenous connective tissues becomes more brittle as the result of aging (Viidik, 1979*a*). This is a slow change caused by the increase of non-reducible cross-links between collagen molecules. The change in mechanical properties in collagen diseases is caused by the disturbance of collagen metabolism (Adam, Deyl & Miterová, 1981). In the examples given above, the change in the mechanical properties takes place in a day (uterine cervix) to years (aging), and not so rapidly as in the catch connective tissues of echinoderms. Their change involves enzymatic alteration in the composition of connective tissue molecules, enzymatic digestion, or enzymatic induction of covalent

cross-links. The mechanism of change in mechanical properties seems to be different from that of catch connective tissue.

Why can catch connective tissues of echinoderms rapidly change mechanical properties? Collagen molecules of echinoderms seem to be not so different from those of mammals (Matsumura, 1972). The difference among collagens is that the collagen fibrils are not covalently cross-linked in catch connective tissues, whereas in many usual collagenous connective tissues the collagen fibrils are covalently bonded continuously, end to end (Wainwright *et al.*, 1976). This implies that in usual collagenous tissues the elastic modulus of the tissue under large strain is determined by that of the collagen, which seems to change little. This is one reason for the stability of the mechanical properties of usual connective tissues. The mechanical properties of catch connective tissues are not dependent on the mechanical properties of collagen, but rather on those of the matrix. The chemistry of the matrix molecules may be different in catch connective tissues, but almost nothing is known about this. The presence of neurosecretory-like cells in catch connective tissues is one critical difference, and these cells seem to control the ionic environment of the tissues, thus controlling the viscosity. In mammalian connective tissues, the interactions between collagens, between collagen and proteoglycans, and between proteoglycan molecules, depend also on ionic environment such as pH and ionic strength (Comper & Laurent, 1978). Therefore the stability of the ionic environment in the usual collagenous connective tissues is one reason for the stability of their mechanical properties. The homeostasis of the ionic environment, however, may change with developmental stages and with disease. The ionic environment will be different in the collagenous connective tissues of different species. 'Anyone who can know about all these things and not rush off to initiate an enormous research project on the ionic control of tensile properties in collagenous connective tissues in development, evolution and disease must be either cynical or tired' (Wainwright, 1980).

When catch connective tissue is viewed as structural material, it provides a new category, that of adaptive materials. The catch connective tissue adjusts its mechanical properties by judging the force applied. We have no such 'intelligent' materials for industry and for artefacts. This kind of material may be found in other phyla, if we re-examine the collagenous connective tissues without the preconception that their mechanical properties do not change.

VII. SUMMARY

(1) Catch connective tissue is defined as the collagenous connective tissue whose mechanical properties can be changed rapidly (in seconds or minutes) under nervous control.

(2) Catch connective tissues are found in all five classes of Echinodermata. They function in tone control of the tissues and in autotomy.

(3) The change in mechanical properties occurs in viscosity.

(4) Muscle cells are not responsible for the viscosity change.

(5) The viscosity change is controlled by nervous activities. Neurosecretory-like cells with large electron-dense granules are found in all the catch connective tissues so far studied.

(6) The viscosity change is quite likely caused by the change in the ionic environment

in the connective tissues, which alters the weak (non-covalent) interactions between extracellular macromolecules in the tissue.

VIII. ACKNOWLEDGEMENTS

I am indebted to Professor Keiichi Takahashi for his encouragement. I thank Dr K. M. Muzik and Dr M. Hidaka for critical reading of the manuscript.

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