Abstract—Catch connective tissue (CCT) is the connective tissue that shows large stiffness changes in response to stimulation under nervous control. The dermis of sea cucumbers is a typical example of CCT. Mechanical properties of the dermis are determined by the extracellular materials that are made of collagen fibrils embedded in a hydrogel of proteoglycans. The dermis takes 3 mechanical states soft (S_a), standard (S_b) and stiff (S_c). Different molecular mechanisms of stiffening have been found in the transition S_a → S_b and in the transition S_b → S_c. In this article I will review my works on this intelligent material.

Index Terms—catch connective tissue, sea cucumber, stiffness change, intelligent material

I. INTRODUCTION

Skin of sea cucumbers is made of catch connective tissue (CCT) or mutable collagenous tissue that shows large stiffness changes in response to stimulation under nervous control [1, 2]. CCT is the tissue specific to echinoderms and are found in body walls and ligaments connecting skeletal elements. Examples are the body-wall dermis of sea cucumbers and starfish [3, 4], sea-urchin catch apparatus that connects spines to a test [5] and brittlestar intervertebral ligaments connecting arm vertebræ [6]. Stiffness changes are reversible and apparent in seconds to minutes. Animals use stiffening in defense and posture maintenance. Softening also serves for defense and is used in postural changes, fission and autotomy. The main component of the dermis is extracellular materials that are composed of collagen fibrils embedded in a matrix made of hydrogel of proteoglycans [7, 8]. The stiffness of the extracellular components determines that of the dermis [9]. As the sea-cucumber dermis is the most studied material among CCTs I will mainly review my works on this intelligent material in this article.

II. BODY-WALL STRUCTURE

The body wall of sea cucumbers consists of several layers: from outside to inside, a layer of thin cuticle, thin epidermis, thick dermis that occupies most of the thickness of the body wall, and a circular muscle layer that is interrupted at five places by pairs of longitudinal muscles. The body wall encircles the coelom in which viscera are stored [10]. The water content of individual sea cucumbers is ca. 80%. Among the tissues the dermis is the main component that occupies ca. 60% of the wet weight; muscle content is only 7 % [11]. The dermis is composed of a voluminous extracellular matrix in which cellular elements are sparsely distributed. The examples of cell types are nerve cells, juxtaligamental cells containing secretory granules that are supposed to contain proteins controlling stiffness of extracellular materials, and morula cells whose inclusion are supposed to contain materials for the extracellular matrix [12]. Muscle cells are not found in the dermis except in the walls of the water-vascular canals occasionally found in the dermis.

III. MECHANICAL PROPERTIES AND THEIR CHANGES

A. Mechanical properties

Our dynamic mechanical tests revealed that the dermis takes 3 different mechanical states, soft state (S_a), standard state (S_b) and stiff state (S_c) [13]. The stiffness increases in the order S_a < S_b < S_c whereas the energy dissipation ratio decreases in the order S_a > S_b > S_c. The notable mechanical property of S_a is the strain softening in which the application of repetitive strain larger than 10% invokes drastic softening that leads the dermis to “melt” into a viscous mass with non-measurable stiffness. Such a mass could recover the original shape before melting. This drastic softening works in fission and defensive behavior including evisceration and autotomy.

B. Nervous control

The mechanical states of CCT are under nervous control and thus we can regard CCT as one of neutrally controlled mechano-effectors such as muscles. When stained with the antibody specific to echinoderm nerves sea-cucumber body wall is supplied with immunoreactive fine fibers running among the collagen fibrils [14]. Pharmacological experiments suggested the presence of two types of cholinergic systems, one is the nicotinic one involved in the dermal stiffening and the other is the muscarinic one involved in softening [15]. The presence of the cholinergic system was supported
by the neuropeptide stichopin that inhibits the action of stiffening cholinergic systems [16]. Stichopin is one of four new peptides we have found in the dermis of sea cucumbers. Other ones are the neuropeptide NGIWYamide that stiffens the dermis and two holokinins that soften the dermis.

The stiffening of the body wall is found when shade falls on sea cucumbers; this response probably works for the defense against the potential predators that attack from above. The shadow-induced stiffening is observed in the isolated dermis to which epidermis is attached but not in the epidermis-free dermis [17]. The shadow response vanishes when the preparation is treated with anesthesia, which also supports the involvement of nerves in this response. The clear evidence of nervous control of CCT is found in the shadow reflex of sea urchin Diadema setosum [18]. When a shadow falls on a sea urchin it waves its spines vigorously. This reaction is regarded as being a defense response to fish; some fish bite the tip of a spine to lift a sea urchin in order to turn it over to expose the unguarded oral surface for attack [19]. The shadow reflex is the reflex in which radial nerves are involved. In this reflex the waving of spines is associated with coordinated spine-muscle contraction and softening of catch apparatus, the ligament connecting spines to the test of sea urchins. The electrical stimulation of the radial nerve can mimic the shadow reflex: it provokes both spine waving and softening of catch apparatus. The softening of catch apparatus would permit muscles to move spines with less force during the softened period and thus with less energy expenditure. This example clearly shows that the mechanical properties of CCT are controlled in a coordinated way with muscle contraction through nerves.

IV. MOLECULAR MECHANISMS OF STIFFNESS CHANGES

In the early history of studies on CCT muscles were suspected to be the cause of stiffness changes because muscles are found in many CCTs although their amount is quite small [20]. The evidences against this suspicion was the finding of CCTs containing no muscle cells [21, 22] and the experiments showing that CCT kept the ability of large stiffness changes still after its cellular elements had been disrupted by detergents or by freeze-thaw cycles [23].

The break through in the study of the mechanism of stiffness changes was the finding of tensilin that was extracted from the sea-cucumber body wall [24]. This protein stiffens the isolated dermis and aggregates collagen fibrils isolated from sea-cucumber body walls. We found another protein softenin in sea-cucumber body walls: it softens the dermis and inhibits the aggregating action of tensilin [25]. A detailed mechanical tests revealed that tensilin is responsible to the change Sₐ→S₈ but not S₈→S₉ [26]. As the diameter of collagen fibrils in S₈ is larger than that in S₉ by the electron microscopic observations, tensilin likely increases cohesive forces between subfibrils constituting collagen fibrils that make fibrils thicker and thus stiffer [27]. CCT can be regarded as a fiber-reinforced material whose fibers are made of collagen. The stiffening of the reinforcing fibers increases the stiffness of the fiber-reinforced materials. This is not the only mechanism of stiffening of the body wall though. A new stiffening factor (NSF) was extracted from the sea-cucumber body wall. This protein causes the transition S₈→S₉ [28]. As this transition is associated with exudation of water from the dermis the formation of hydrophobic bonds between macromolecules may responsible to S₈→S₉ [29]. The electron-microscopic observation suggested another stiffening mechanism. Cross bridges between collagen fibrils are found and the number of bridges increases in the order S₈<S₉<S₃ [30]. The chemical nature of the bridge is yet to be determined. Based on these findings we have proposed a “nested fiber-reinforced composite model” in which the dermis is regarded as a collagen-fiber reinforced material and the collagen fiber is again regarded as a composite reinforced by fibril [27]. We have assumed three stiffening mechanisms in this model: 1. Tensilin makes collagen fibrils stronger and stiffer in S₈→S₈ through the increase in cohesive forces between subfibrils; 2. Cross-bridges makes fibrils to be a continuous network of collagen bundles both in S₈→S₈ and S₈→S₉; 3. The matrix embedding the fiber component becomes stiffer in S₈→S₈, which was produced by bonding associated with water exudation.

We know little about the stiffening mechanism of CCTs other than sea-cucumber dermis. A gene coding a tensilin-like protein has been found in sea-urchin genome [30]. The protein synthesized after the code has, however, little stiffening effect on sea-urchin CCT. Different mechanism and different proteins may be working in CCTs other than sea-cucumber dermis.

V. ENERGETICS AND EVOLUTION

The energy consumption in three mechanical states has been measured in three CCTs, dermis of sea cucumbers and starfish and catch apparatus of sea urchins. The values measured were similar irrespective of the kinds of CCTs: when compared with the energy consumption rate of S₈, that of S₉ is about twice greater and that of S₃ is about ten times greater [31]. The energy consumption rate of the body-wall muscles of sea cucumbers and their contraction forces were measured. With these data we could conclude that sea cucumbers maintain their posture by CCT with only 1/100 of energy if they were to use muscles instead of CCT in posture maintenance. The notable character of echinoderms is its low metabolic rate that is 1/10 the value of other invertebrates. Low energy consumption and high body content of CCT no doubt contribute to this low metabolic rate of sea cucumbers. The exceptionally low metabolic rate satisfies the prerequisite for sea cucumbers to feed on foods of low energy contents such as sands.
All five classes of extant echinoderms have CCT, which suggests that CCT was already present in their common ancestors [32]. Early echinoderms were sessile organisms that fed on small organic particles carried by water currents. Their body was covered with imbricate small skeletal plates. The arrangement of plates suggests that plates worked as sliding joints so as animals to be able to change their body shape: they could possibly take a feeding posture extending their bodies so that they could reach the layer of faster water currents. The body walls covered with imbricate small skeletal plates are found in modern starfish. The plates are connected with CCT and with minute muscle cells forming active sliding joints. Starfish can change their body shape by sliding the joints and they can “freeze” and keep that posture making joint CCT stiff [4]. A similar mechanism might have worked in the early echinoderms.

In animals other than echinoderms both posture change and maintenance are performed by muscles alone. To have a tissue specific to postural maintenance of course needs extra energy and thus evolution of such a tissue would be possible only in the situation in which the cost of posture maintenance by muscles exceeds the total cost of CCT that is the cost of posture maintenance by CCT plus the costs of developing and keeping CCT. The large economy of CCT in posture maintenance has been shown; the costs of making and maintaining CCT seem to be far lower than those of muscles because it is mainly made of extracellular materials not cells.

Connective tissue might have been used both in posture changes and in posture maintenance in ancient echinoderms. Sea lilies are regarded as the oldest one among the extant echinoderm classes and we found contractile ligaments in them [33, 34]. Ligaments connecting ossicles in arms and cirri are devoid of muscle cells and yet they show slow contractions. Some ancestral echinoderms have been believed to have no muscles associated with skeletal ossicles [35]; such animals would have used connective tissue both in posture change and maintenance.

The sea-cucumber dermis can be regarded as an intelligent material that alters the stiffness to meet the needs of animals. The isolated dermis itself can sense the mechanical strain applied and responds by stiffening or softening to protect animals. The dermis also changes the stiffness under the control of nerves. The rapid and large stiffness changes and the adaptability of the dermis have been attracting the interest of materials scientists and giving inspiration to them. The results are some synthesized materials with adaptable stiffness [36, 37]. Sea cucumbers have no brain and thus we usually regard them as animals without intelligence. They are, however, intelligent in their body walls. This intelligence together with the toxin in the body walls enabled sea cucumbers to lead their lives exposed on sands feeding on sands, which are the life without cares to eat and to be eaten by possible predators although they are sluggish without developed sense organs and brains.

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