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Role of extracellular matrix in development of skeletal muscle and postmortem aging of meat

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ABSTRACT

The integrity of skeletal muscle is maintained by the intramuscular connective tissues (IMCTs) that are composed of extracellular matrix (ECM) molecules such as collagens, proteoglycans, and glycoproteins. The ECM plays an important role not only in providing biomechanical strength of the IMCT, but also in regulating muscle cell behavior. Some ECM molecules, such as decorin and laminin, modulate the activity of myostatin that regulates skeletal muscle mass. Furthermore, it has been shown that decorin activates Akt downstream of insulin-like growth factor-I receptor (IGF-IR) and enhances the differentiation of myogenic cells, suggesting that decorin acts as a signaling molecule to myogenic cells. With animal growth, the structural integrity of IMCT increases; collagen fibrils within the endomysium associate more closely with each other, and the collagen fibers in the perimysium become increasingly thick and their wavy pattern grows more regular. These changes increase the mechanical strength of IMCT, contributing to the toughening of meat. However, in highly marbled beef cattle like Wagyu, intramuscular fat deposits mainly in the perimysium between muscle fiber bundles during the fattening period. The development of adipose tissues appears to disorganize the structure of IMCT and contributes to the tenderness of Wagyu beef. The IMCT was considered to be rather immutable compared to myofibrils during postmortem aging of meat. However, several studies have shown that collagen networks in the IMCT are disintegrated and proteoglycan components are degraded during postmortem aging. These changes in ECM appear to reduce the mechanical strength of IMCT and contribute to the tenderness of uncooked meat or cooked meat at low temperature. Thus, the ECM plays a multifunctional role in skeletal muscle development and postmortem aging of meat.

1. Introduction

From a consumer standpoint, texture is the most important factor in determining the quality of meat (Dransfield et al., 1984). Meat texture depends on the structure and composition of skeletal muscle, which is mainly composed of muscle fibers and surrounding intramuscular connective tissues (IMCTs). Muscle fibers consist of myofibrils, which are composed of numerous proteins including actin and myosin that are major proteins of thin and thick filaments respectively. The integrity of skeletal muscle is maintained by three layers of IMCT: 1) the endomysium, which encloses individual muscle fibers; 2) the perimysium, which bundles groups of muscle fibers; and 3) the epimysium, which ensheathes the whole muscle. The IMCT is composed of extracellular matrix (ECM) macromolecules such as collagens, proteoglycans (PGs), and glycoproteins. These ECM macromolecules interact with each other and form a supermolecular network that can both withstand and transmit the contractile forces generated by muscle fibers (Fig. 1, Voermans et al., 2008).

Skeletal muscle contains collagen types I, III, IV, V, VI, XII, and XIV (Listrat, Picard & Geay, 1999; Listrat et al., 2000; Nishimura, Ojima, Hattori & Takahashi, 1997). The major types of collagen in skeletal muscle are type I and III (Bailey & Light, 1989), which align into a quarter-stagger array to form fibrils in tissues. Proteoglycan is composed of a central core protein with covalently attached glycosaminoglycan (GAG) chains. The GAG is a polymer of disaccharide repeats that are highly sulfated and negatively charged. Typical GAGs attached to the core protein of PGs are chondroitin sulfate (CS), dermatan sulfate (DS), and heparan sulfate (HS). In skeletal muscle, there are several types of PGs with various sizes of core protein and kinds of GAG chain (Brandan, Fuentes & Andrade, 1992; Nishimura, Hattori & Takahashi, 1996b; Parthasarathy, Chandrasekaran & Tanzer, 1991).

Decorin is one of the most studied members of the small leucine-rich proteoglycan (SLRP) family (Kresse & Schönherr, 2001). The decorin molecule is composed of a core-protein to which a CS/DS chain and small number oligosaccharides are covalently attached. Decorin associates with fibrillar collagen, types I, II, and III collagens (Scott, 1988; Vogel & Trotter, 1987), and has been identified in various tissues

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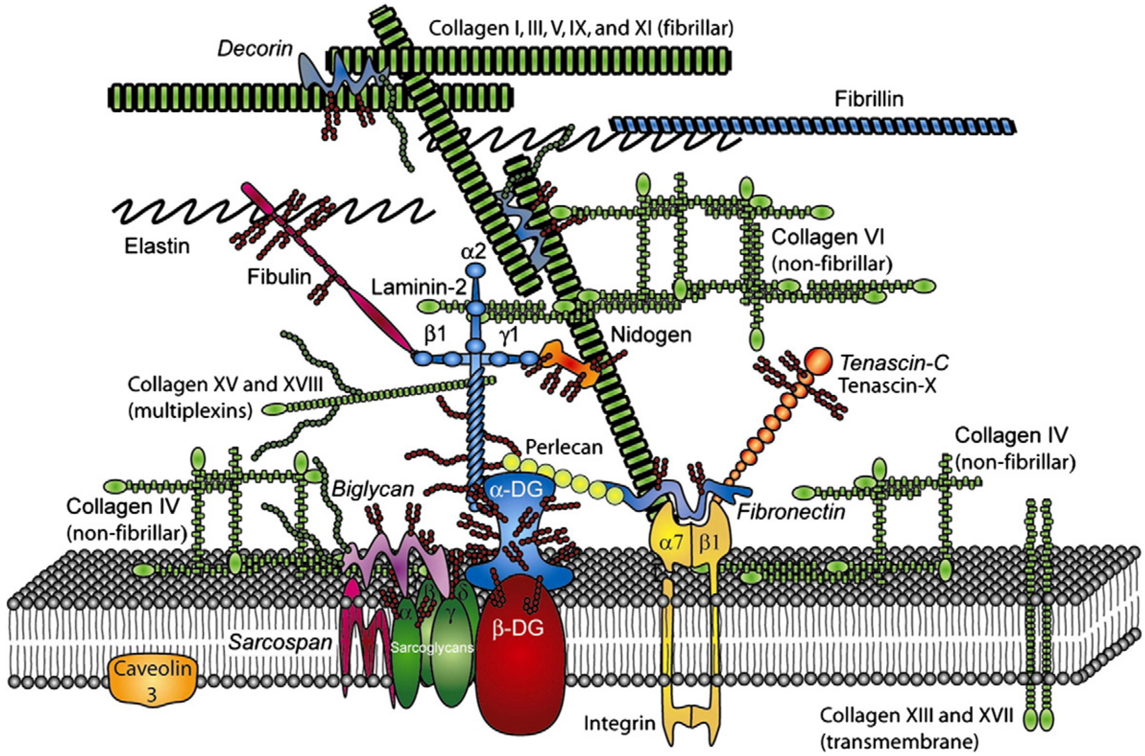

Fig. 1. Schematic representation of the ECM surrounding skeletal muscle. Individual molecules are depicted at their approximate location in relation to the sarcolemma. Well-established molecular interactions between individual ECM molecules are portrayed. From Voermans et al. (2008).

including skeletal muscle (Eggen, Malmstrom & Kolset, 1994; Lennon, Carrino, Baber & Caplan, 1991; Parthasarathy et al., 1991). Danielson et al. (1997) demonstrated that targeted disruption of decorin in mice leads to abnormal collagen fibril morphology and skin fragility, suggesting that decorin plays an important role in collagen fibril formation and organization of fibril networks. Decorin also participates in cell growth by modulating some growth factors (Li, McFarland & Velleman, 2008; Riquelme et al., 2001; Yamaguchi, Mann & Ruoslahti, 1990) and by signaling directly to cells (Schönherr, Sunderkotter, Iozzo & Schaefer, 2005; Suzuki, Kishioka, Wakamatsu & Nishimura, 2013).

This article aims to provide a review of roles of ECM in muscle cell growth and the organization of IMCT during skeletal muscle development, and also changes of ECM during the postmortem aging of meat.

2. Role of ECM in myogenesis

The ECM supports cells and provides tissues with mechanical strength and elastic properties. In addition to the maintenance of tissue structure, ECM has also been recognized as an important regulator of cell growth, either through modulation of growth factor activities or through direct involvement in cell signaling. Kanematsu et al. (2004) have shown that type I collagen interacts with basic Fibroblast Growth Factor (bFGF) and that collagen matrix can control the release of bFGF, resulting in regulation of its activity. Furthermore, collagen has been reported to serve as a ligand via the discoidin domain receptor (Hou, Vogel & Bendeck, 2001; Shrivastava et al., 1997; Vogel, Gish, Alves & Pawson, 1997). These studies suggest that collagen plays an important role not only in providing shape and biomechanical strength to organs and tissues, but also in regulating cell behavior. In fact, the inhibition of collagen synthesis suppresses the differentiation of myoblasts in vitro, suggesting that collagen is necessary for myogenesis (Nandan, Clarke, Ball & Sanwal, 1990; Saitoh, Periasamy, Kan & Matsuda, 1992).

Proteoglycans have been similarly recognized not only as an organizer of ECM but also a modulator of growth factor activities (Kresse & Schönherr, 2001). Perlecan, a HSPG, which is an intrinsic constituent of basement membranes, participates in the activation of tyrosine kinase receptors by bFGF, a strong inhibitor of myogenic differentiation (Larraín, Alvarez, Hassell & Brandan, 1997). The membrane-associated HSPGs, glypican-1 and syndecan-4, are expressed in myogenic satellite cells (Powell, McFarland, Cowieson, Muir & Velleman, 2014) and affect the expression of myogenic regulatory factors, MyoD, myogenin, and MRF4 (Harthan, McFarland & Velleman, 2013). Syndecan-4 and glypican-1 regulate muscle cell proliferation and differentiation by modulating cellular responsiveness to fibroblast growth factor 2 (FGF2) (Velleman, 2012).

Decorin is a small leucine-rich PG containing a single covalently attached CS or DS to the core protein. The induced expression of decorin in Chinese hamster ovary cells leads to an inhibition of cell proliferation (Yamaguchi & Ruoslahti, 1988), which might result from inhibition of transforming growth factor-β1 (TGF-β1) activity (Yamaguchi et al., 1990). Decorin binds to TGF-β through its core-protein (Schönherr, Broszat, Brandan, Bruckner & Kresse, 1998) and sequesters TGF-β by trapping it in the ECM (Markmann, Hausser, Schönherr & Kresse, 2000). TGF-β1 is a strong inhibitor of both the proliferation and differentiation of myogenic cells. Li et al. (2008) showed that over-expression of decorin in skeletal muscle satellite cells significantly increases cell proliferation by decreasing sensitivity to TGF-β1 signaling. However, Riquelme et al. (2001) showed that decorin prevents the terminal differentiation of C2C12 muscle cells by increasing sensitivity to TGF-β1 signaling. Decorin stimulates TGF-β-dependent signaling via lipoprotein-receptor related protein (LRP-1) in non-differentiated myoblasts, but inhibits signaling by sequestering TGF-β in differentiated myotubes that express low levels of LRP-1 (Cabello-Verrugio & Brandan, 2007; Droguett, Cabello-Verrugio, Riquelme & Brandan, 2006). These results suggest that decorin has differential effects on TGF-β-dependent signaling at the early and late stages in differentiation. Thus, decorin plays important roles in myogenic cell growth by regulating cellular responsiveness to TGF-β1.

Several growth factors including HGF, IGF, FGF, and the TGF-β superfamily are involved in controlling the proliferation and differentiation of