

which may form pliant but slightly elastic intrinsic ligaments. Conversely, the articular fibrous capsule of the IMJ and ISJ contains numerous elastin fibers.<sup>19</sup> In our previous study, we have found that the PA layer and synovium of young rat MJ were distributed with dense collagen fibers and a network of ESFs.<sup>39</sup> Transmission electron microscopy on ESFs in the synovium of joints in the present study revealed that the synovium of the mature IMJ and ISJ contained elastic fibers, while the synovium of the completed MJ and AL of the mature SVJ contained pre-elastic elaunin. Histology suggested similarities between the periosteal area and AL, both of which differentiated from embryonic mesenchyme.

Collagen fibrils and hydrated glycoaminoglycans have been shown to be the ECM components providing most of the tensile strength and capability, respectively, to withstand compressive stress. Some studies have stressed that while large-diameter ECM fibrils provide many of the tensile properties, small-diameter fibrils contribute to the creep-resistant properties of the tissue; both therefore enhance the resilience of connective tissues.<sup>11,21</sup> In another ECM fibersystem, the ESFs comprising elastin-associated microfibrils (oxytalan fibers), elaunin and true elastin (elastic fibers) are essential in tissues requiring elasticity. Microfibrils and amorphous elastin represent mechanically force-sustaining fibrils and a rubber-like shock absorber, respectively.<sup>20,26,28-30,40-42</sup> Moreover, some studies have stated that collagen fibrils are largely responsible for tensile strength to retain the original state while ESFs are closely related to elasticity of the connective tissue.<sup>43,44</sup> The associated ESFs intervening within the collagen network construct a complicated fibrillar network in accordance with the dynamic necessities of the organ; the ESFs oriented parallel to the direction of applied force can readily be straightened to 2- to 2.5-fold the original length before the laminated collagen fibers become stretched, and therefore the fibre networks in the connective tissue sustain the mechanical force.<sup>27,30,45</sup>

Although many studies on elastogenesis in connective tissues have reported deposition of amorphous elastin onto microfibrils, accumulation of microfibrils does not seem an essential precursor to deposition of

elastin.<sup>47-51</sup> Some studies have indicated that deposition of elastin does not exactly accompany microfibrillar accumulation, and *vice versa*; yet both the ratio of elastin-to-microfibrils and elastin fibre diameter increase in consecutive stages of normal elastogenesis, such that mature elastic fibers contain up to 90% amorphous elastin but lack microfibrils.<sup>22,23,52-56</sup>

Elastin material gives rise to fibers, bundles and lamellae of different shapes and sizes in various organs. These structures grow heterogeneously, essentially depending on the strength and direction of the forces working on the aggregating materials.<sup>27</sup> The present study indicates that maturation of ESFs in the IMJ, ISJ, SVJ and MJ is intimately related with pneumanization of the middle ear, tooth eruption and joint function (Table 1). By studying ESFs in synovial ECM, we also observed that the SVJ and MJ, of mesenchymal origin developing at sites subject to specific and periodic stress, display particularly abundance of mechanically-resistant elaunin fibers. Nevertheless, age-related changes in the fibrillar component involving replacement of collagen by elastin material, substitution of elaunin with mature elastic fibers or disintegration of ESFs followed by an increase of collagen fibers were not observed in either the mature SVJ or immature MJ<sup>57,58</sup>. One study has observed a decrease in cellular components in aging SVJ, but other studies have stated that both the component and proportion of cells and ECM fibrils in synovia do not vary with site, gender or aging process of the joints.<sup>2,20,59</sup> In contrast, histological studies of elastogenesis in the periodontal ligament have observed distribution of pre-elastic oxytalan and elaunin fibers in the syndesmotomic joint, and suggested a feedback mechanism responding to stresses of different duration and level in the stress-bearing tissue, thus initiating a rapid turnover of ESFs as a functional requirement.<sup>21,60</sup>

Our observations indicate that the AL and PA, by remodelling the ECM of articular tissue, are most responsible for the adjustment, modification and adaptation of the mechanical properties of the SVJ and MJ. Furthermore, growth of ECM fibers in the joints is not only closely related to morphological completion and maturation of the joints, but also reflects the functional significance of the articular tissues.