

Temporal bone adaptations in response to protrusive function in juvenile and young adult rhesus monkeys (*Macaca mulatta*)

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Summary. Temporal bone adaptations to protrusive function are described in both growing and non-growing animals. In juvenile monkeys fitted with a functional protrusive appliance, a discrete sequence of microanatomical changes in the temporal joint component is described. The most pronounced of these involved the deposition of new bone in the posterior region of the mandibular fossa (fossa roof and postglenoid spine). In a sequence which paralleled in time that of the condylar cartilage response to protrusion, new bone continued to be deposited in weeks 2-6 following appliance placement, was consolidated into layers in weeks 8-12, and had ceased by 24 weeks. The response in young adult animals was much more variable, possibly of reduced magnitude, and occurred at a slower pace. However, a response qualitatively similar to that in juveniles was observed in one-third of the experimental sample. It is suggested that the osteogenic response may be triggered by periosteal tension transmitted by fibres of the posterior portion of the articular disc. As skeletal adaptations reduce the need for habitual anterior posturing of the lower jaw by the lateral pterygoid muscles (after 8 weeks), tension in the disc fibres diminishes to levels present during normal jaw excursions and the stimulus for further osteogenesis is eliminated.

Review of literature

Over the past decades, a number of studies utilizing animal models have been undertaken to investigate the adaptability of the craniofacial complex in response to procedures that mimic orthodontic treatment regimens. Because of the capacity for growth of the condylar cartilage, the adaptive potential of the condyle has been the object of numerous studies by researchers in both basic sciences and clinical disciplines. In particular, the efficacy of anterior posturing of the lower jaw for stimulating increased growth at the mandibular condyle in experimental animals has been well documented (Häupl and Psansky, 1939; Breitner, 1940; Baume and Derichsweiler, 1961; Charlier *et al.*, 1968; Petrovic *et al.*,

1975; Petrovic *et al.*, 1981; Stöckli and Willert, 1971; McNamara, 1972, 1973, 1980; McNamara and Carlson, 1979; McNamara *et al.*, 1982). However, the temporal component of the TMJ - specifically, the mandibular (glenoid) fossa and articular eminence - has received considerably less attention. Yet there are indications that specific adaptations take place in this region in association with changes occurring at the condyle. Although little studied or described, these adaptations are of interest from the point of view of basic connective tissue biology, and their elucidation should form an integral part of our understanding of the consequences of clinical procedures involving orthopaedic manipulation of or even extirpation of the mandibular condyle.

Changes in temporal component micro-

anatomy have usually been briefly described as part of studies focussing on the mandibular condyle. In rodents, such descriptions have dealt with the joint response to unreduced condylar fractures (Gilhuus-Moe, 1969; Sprinz, 1970), to condylectomy (Jolly, 1961), and to bite splints (Ingervall *et al.*, 1972; Folke and Stallard, 1966). However, most accounts are incidental to the larger study and offer only limited information on tissues of the mandibular fossa (see Gilhuus-Moe, 1969 for a notable exception). In fact, one of the few studies to declare the response of the mandibular fossa as its primary object of study was purely radiographic (Hayes, 1961) and included no histology. In monkeys, which exhibit temporal component anatomy that resembles more closely that in humans, descriptions of histological response of the TMJ to orthopaedic procedures have placed little emphasis on changes other than those taking place at the condyle. Although limited descriptions of temporal bone microanatomy are a part of most efforts (cf., Breitner, 1940, 1941; Adams *et al.*, 1972; McNamara, 1972, 1973; Stöckli and Willert, 1971; Joho, 1973; McNamara and Carlson, 1979), changes are often noted at only one stage of the experimental protocol, and are figured sporadically if at all. Nevertheless, the available evidence suggests that the temporal joint component, at least in growing animals, undergoes remodelling that complements and augments condylar changes that serve to restore functional equilibrium.

It is the purpose of this report to 1. identify and describe microanatomical adaptations taking place in the temporal joint component of the rhesus monkey, *Macaca mulatta*, in response to increased protrusion of the lower jaw during function; and 2. compare and contrast the characteristics of the response in growing (juvenile) and young adult animals.

Materials and methods

Twenty-eight juvenile and 19 young adult

rhesus monkeys (*Macaca mulatta*) were included in this study. Morphological adaptations taking place at the mandibular condyle in these animals have been reported elsewhere (McNamara and Carlson, 1979; McNamara *et al.*, 1982). At the start of the experiment, all animals classified as juveniles had a complete deciduous dentition and erupted first permanent molars, and were judged to be from 18 to 24 months of age based on standards of dental eruption (Hurme and van Wagenen, 1961). In the juvenile sample, all animals were male, whereas only females were included in the young adult sample. Since young adult male monkeys continue to grow at a rate that is several times that in young adult females (McNamara and Graber, 1975), males were excluded in an effort to minimize growth changes not associated with experimental intervention. Although the exact ages of the young adult animals were unknown, all animals were physiologically mature with third molars in occlusion, making them at least 5.5 to 6 years of age (Hurme and van Wagenen, 1961). All animals were fed a normal Purina Monkey Chow diet.

For all experimental procedures, the animals were sedated with Ketamine HCl (7–15 mg/kg, IM) and Rompun (Xylazine) (1–2 mg/kg, IM). From mandibular and maxillary alginate impressions taken on each animal, a mandibular appliance was constructed so as to produce a protrusive centric occlusal relationship in the animals constituting the experimental groups (see McNamara and Carlson, 1979 for details). The appliance resulted in a vertical (inferior) mandibular displacement of 2–3 mm and a horizontal (anterior) displacement of 5 mm. The experimental (protrusive appliance) animals were studied for 2, 4, 6, 8, 10, 12 and 24 week periods. Prior to sacrifice, a radiograph was obtained and the animal was heparinized (300–500 units/kg, IV) to facilitate tissue preparation for histological sectioning and staining. The animal was then anaesthetized with Sernylan (phencyclidine HCl, 1–2 mg/kg, IM) and sodium pentobarbital (8–10 mg/kg, IV),

sacrificed by catheterization of the left ventricle or the carotid artery, and perfused with an AFA fixative (acetic acid, formalin, 95% ETOH).

After sacrifice, the head was placed into 10% neutral buffered formalin prior to the removal of the TMJ. The left and right temporomandibular joints were removed, immersed in Bouin's fixative for 72 hours, and then decalcified in Warshawsky's EDTA (Ethylenediamine Tetraacetic Acid). Decalcification was usually complete in 3 to 6 weeks and was verified radiographically. Tissue preparation followed our routine laboratory dehydration and infiltration protocol. The tissues were embedded in paraffin, sectioned at 18–22 μm , and stained with a hematoxylin and eosin (H and E) stain.

Results

The monkey temporomandibular joint resembles the human TMJ in overall form. The primary differences relate to the much shallower mandibular fossa (or much less pronounced articular eminence) and the relatively large postglenoid spine which are noted in the monkey (Fig. 1). The postglenoid spine, which is variably present in humans in reduced form, is a prominent feature in lateral and central parts of the monkey TMJ. Viewed from the anterior aspect of the joint, the postglenoid spine has a roughly triangular shape with its long side sloping medially. As a result, the spine is usually not visible in parasagittal sections in the medial part of the joint. All joint surfaces, including the anterior aspect of the postglenoid spine, are lined with a fibroelastic connective tissue, usually designated the articular layer in analogy to its counterpart on the condylar surface. Deep to this layer but superficial to the bony surface, a thin band of small, flattened cells that resembles the proliferative (prechondroblastic) zone of the mandibular condyle can be seen, especially on the lower posterior slope and crest of the articular eminence.



Figure 1 Overview of the posterior part of the temporomandibular joint in a control juvenile monkey. Note the prominent postglenoid spine (Mag. $\times 7$).

Juvenile Control Sample

Scattered chondrocytes were typically present deep to the proliferative layer on the crest and posterior slope of the articular eminence. In central and medial sections, the chondrocytes were more numerous and often constituted a distinct layer of cells interposed between the more superficial layers and the underlying bony cortex. Usually this cartilage layer was most prominent and thickest in the medial part of the joint (Fig. 2), where it appeared to extend back toward the roof of the mandibular fossa (see Hinton and Carlson, 1983). The anterior surface of the postglenoid spine was characterized in nearly every animal by some amount of resorption. This varied



Figure 2 Articular eminence in a juvenile control monkey, medial part of joint. Note the layer of cartilage cells lying deep to the fibrous articular tissue and a thin layer of mesenchymal cells (Mag. $\times 28$).



Figure 3 Overview of the posterior part of the temporomandibular joint in two juvenile monkeys sacrificed 2 weeks after placement of a functional protrusive appliance. Note the active deposition of new bone on the anterior surface of postglenoid spine and in the roof of the mandibular fossa (Mag.; A, $\times 7$; B, $\times 7$).



from small isolated foci of resorption (Fig. 1) to numerous patches all along the spine, giving the cortex a 'moth-eaten' appearance. Small resorptive areas were also frequently noted in the roof of the mandibular fossa, extending as far forward as the upper part of the posterior slope of the articular eminence, especially in lateral sections.

Juvenile Experimental Sample

Two and Four Week Animals: Active deposition of new bone was observed on the entire anterior surface of the postglenoid spine and in the roof of the mandibular fossa in both 2-week (Fig. 3) and 4-week animals (Fig. 4). The spicules of new bone were mostly oriented perpendicular to the articular surface and were separated from the fibrous articular layer by a zone of flattened mesenchymal cells that was thickened relative to controls (Fig. 5). Chondrocytes still

Figure 4 Overview of the posterior part of the temporomandibular joint in a 4-week juvenile monkey. Note the deposition of new bone along the anterior surface of the postglenoid spine and roof of the mandibular fossa (Mag. $\times 7$).



Figure 5 High-power view of the anterior surface of the postglenoid spine in the 2-week juvenile monkeys shown in Figure 3, with control juvenile for comparison. A: control animal.



Figure 5 B and C 2-week experimental animals. Note the insertion of the posterior fibres of the articular disc into the periosteum of the postglenoid spine (Mag.; A, $\times 28$; B, $\times 28$; C, $\times 28$).

persisted on the articular eminence deep to the articular layer. In more central and especially medial sections these comprised an extremely thick layer that was situated directly adjacent to a more posteriorly-located area of bone deposition (Fig. 6). Hypertrophic cells were noted in several

animals far forward on the eminence, almost on its anterior slope, and the cartilage layer in this area in the 2-week animals appeared to be encased in a matrix resembling that seen in the condylar cartilage.

Six Week Animals: Although a proliferative



Figure 6 Overview of the posterior part of the temporomandibular joint (medial aspect) in a 2-week juvenile. Note the newly-deposited bone in the mandibular fossa which grades relatively abruptly into a thick layer of cartilage lining the more anterior part of the temporal joint surface. Also note the deposition of considerable new bone along the posterior border of the ramus inferior to the condylar cartilage (Mag. $\times 7$).

layer was still quite evident, consolidation of the new bone formed on the anterior postglenoid spine appeared to have begun in the 6-week animals (Fig. 7). This was especially evident on the spine itself, and was characterized by the interposition between spicules of connecting islands of bone parallel to the articular surface. Some new bone formation continued in the mandibular fossa. The layer of fibrocartilage on the eminence seemed thinner and less pronounced in both animals than in their 2 and 4-week counterparts, but the greatest density of cells, especially those hypertrophic in appearance, continued to be far forward on the eminence crest.



Figure 7 Overview of the posterior part of the temporomandibular joint in a 6-week juvenile animal. Note the consolidation of new bone beginning on the anterior aspect of the postglenoid spine (Mag. $\times 7$).

Eight, Ten, and Twelve Week Animals: Animals in these three experimental groups displayed an increasing consolidation of the newly-formed bone on the anterior postglenoid spine and mandibular fossa into compact layers. This process was considerably advanced in the 8-week animals (Fig. 8), and was nearing completion in the 10 and especially the 12-week animals (Fig. 9). Like the 6-week animals, all four animals in the 8 and 10-week groups exhibited a relatively modest layer of fibrocartilage, even medially, while the 12-week animals showed a relatively thicker fibrocartilage layer.

Twenty-Four Week Animals: Like the 12-week animals, only more so, the single



Figure 8 Overview of the posterior part of the temporomandibular joint in an 8-week juvenile animal. Note: consolidation of new bone in the roof of the mandibular fossa and upper postglenoid spine; evidence of resorptive activity on the *posterior* surface of the postglenoid spine; attachments of the posterior fibres of the disc to the roof of the mandibular fossa and posterior part of the condyle, merging there with the fibrous articular tissue (Mag. $\times 7$).

24-week animal strongly resembled the morphology in the control animals. The anterior surfaces of the postglenoid spine and mandibular fossa were mostly quiescent, with consolidation of new bone essentially complete (Fig. 10). Articular eminence morphology was very similar to the controls, with a thick layer of fibrocartilage centrally and medially.

Young Adult Control Sample

The adult temporomandibular joint showed a somewhat contrasting morphological picture to that in juveniles. Cartilage cells were



Figure 9 Overview of the posterior part of the temporomandibular joint in a 10-week juvenile animal. Note the extensive consolidation of newly-deposited bone (Mag. $\times 7$).

occasionally still visible as a layer on the articular eminence, especially in younger adults. However, in general, they were more sporadically distributed, and were often noted singly or in clusters in the fibrous articular layer. The proliferative zone of cells was often less apparent, or even not present at all. The mandibular fossa and postglenoid spine typically presented a virtually unbroken surface of thin concentric layers of lamellar bone (Fig. 11). Resorption, if present at all, was usually confined to the lower half or tip of the anterior surface of the postglenoid spine.

Young Adult Experimental Sample

Compared to the juveniles, response in the



Figure 10 Overview of the posterior part of the temporomandibular joint in a 24-week juvenile animal. The postglenoid spine is very similar in appearance to control morphology (Mag. $\times 7$).

young adults was reduced in magnitude, delayed in timing, and much more infrequent in occurrence. This pattern and extent of tissue response was very similar to that noted for the condyle (McNamara *et al.*, 1982). Three of the animals developed a crossbite in response to appliance placement, and thus no functional protrusion was effected. Of the remaining nine who functioned anteriorly, distinct tissue responses in the temporal component of the joint were noted in four animals. However, with the exception of responses in the crossbite animals, no responses reminiscent of juveniles were observed in the 2, 4, or 6-week animals. In both 8 week animals, deposition of new bone was detected on the anterior aspect of the postglenoid spine and posterior part of the fossa roof (Fig. 12). Similar

patterns of deposition were present in one 12-week and both 24-week animals. However, in these animals, especially in one of the 24-week animals, the new bone appeared to be partly or mostly consolidated into layers (Fig. 13). The articular eminence appeared basically unchanged from controls, although some animals seemed to have very thick articular tissue on the crest of the eminence, and foci of resorption were noted on the crest of the eminence in one or two animals.

Although one of the crossbite animals (a 2-week animal) displayed no apparent TMJ response, the other two animals displayed distinct patterns of response that are explicable in terms of the developed malocclusion. In the crossbite animal sacrificed at 4 weeks, the left temporomandibular joint displayed a relatively thick condylar cartilage together with evidence of new bone formation on the anterior aspect of the postglenoid spine, while the right postglenoid spine contained foci of resorption along its anterior border (Fig. 14). The 6 week crossbite animal showed little difference in condylar morphology from that seen in controls, but distinct areas of resorption were present on the anterior surface of the postglenoid spine in both joints. As we have argued elsewhere (McNamara *et al.*, 1982), these responses are consistent with what would be expected for the persistent distraction of one condyle from the mandibular fossa and the retrusion of the other condyle, or for the retrusion of both condyles. Behaviours that would result in such patterns of habitual condylar positioning were observed for the 4 and 6 week crossbite animals, respectively.

Discussion

There is no doubt that the osteogenic response noted in the posterior region of the mandibular fossa of the experimental animals was a consequence of the appliance. In control juvenile animals, such remodelling was never observed and, in fact, the charac-

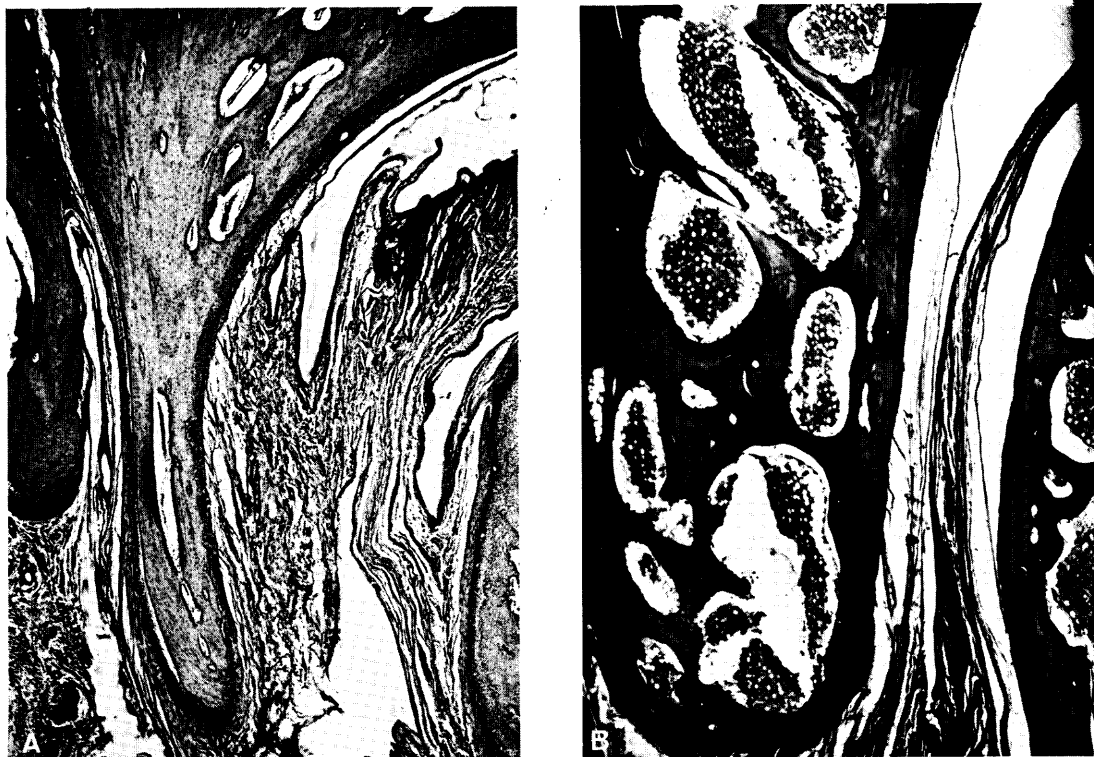


Figure 11 Postglenoid spine in two representative control adult animals (Mag. $\times 7$).

teristic pattern of remodelling in nearly all controls was resorptive. Moreover, Joho (1973) effectively demonstrated that the pattern of remodelling in the posterior region of the fossa can be 'reversed' from resorption to deposition and back again to resorption by changing the direction of the applied extrinsic forces from retrusive to protrusive and back again to retrusive. The experimental design of this study permits examination not only of the nature of the microanatomical adaptations, but also their temporal sequence and relations to changes occurring simultaneously in other regions of the TMJ and craniofacial skeleton.

These data also provide an opportunity to examine the notion of a mesial repositioning of the mandibular fossa in response to forced protrusion of the lower jaw, as suggested by Breitner (1930, 1933, 1940). Following application of intermaxillary elas-

tics to exert anterior traction on the lower jaw, Breitner (1940) observed deposition in the posterior region of the fossa and resorption on the posterior slope of the articular eminence. He interpreted this to mean that a 'migration forward of the fossa' (Breitner, 1940: p. 524) had taken place. In our study, no resorption on the posterior slope of the articular eminence was observed in the experimental sample in conjunction with bone deposition in the posterior region of the fossa. Rather, a certain amount of resorption on the upper posterior slope of the eminence was characteristic of *normal* growth in juvenile animals (see also Zimmermann (1971) for similar observations). It is possible that the differing presence of resorption on the anterior wall of the fossa in our experimental animals and those of Breitner may reflect differences in the way in which protrusion was



Figure 12 Postglenoid spine in an 8-week adult protrusive animal showing deposition of new bone along the anterior surface of the postglenoid spine (Mag. $\times 7$).

achieved – i.e., by alteration of muscular postural activity or by elastic traction – or in the duration and cumulative effect of the two treatments. However, mesial migration of the mandibular fossa, in the sense of Breitner (1940), was not observed in our material, since deposition of new bone on the posterior aspect of the fossa was *not* accompanied by resorption on its anterior aspect.

Adaptive Response in Juveniles

In the juvenile experimental sample, a specific sequence of tissue responses was associated with increasing duration of treatment with the protrusive appliance. The

most striking feature involved deposition of new bone on the anterior surface of the postglenoid spine and roof of the mandibular fossa. This was first noted in 2-week animals, continued in 4-week animals, and began to undergo consolidation into layers by 6 to 8 weeks. By 10–12 weeks, new deposition of bone had ceased and that which had been recently deposited had been largely assimilated into the cortical surface. The relevant morphology in the 24-week animal was virtually indistinguishable from controls. Although a more subjective judgment, there appeared to be associated with this bone deposition an early increase in fibrocartilage hypertrophy and thickening on the crest of the articular eminence, especially medially, in the 2 and 4-week animals, followed by a reduced thickness and cell density in weeks 6–10, with a return to normal-appearing morphology in 12–24 week animals.

An analogous sequence of responses has been documented for the condyle, with increased proliferation in the posterior and posterosuperior regions of the condylar cartilage in 2–6 week animals, followed by a gradual return to normal levels by 12–24 weeks (McNamara, 1972, 1973; McNamara and Carlson, 1979). It has been suggested that the variation in condylar proliferation is associated with the re-establishment of functional homeostasis in response to the changed occlusal relationships induced by the appliance: i.e., with time, the condyle becomes re-positioned in the mandibular fossa, thus eliminating the necessity for continued neuromuscular adaptations to the altered occlusion. In the present study, the timing of the transition from active deposition of new bone on the postglenoid spine and mandibular fossa to the beginnings of consolidation of this new bone into a layered cortex is of interest. The changeover from deposition to consolidation, which begins in the 6-week animals and is mostly accomplished by 8–10 weeks, coincides with alterations in two other components of the adaptive system. For example, McNamara (1973, 1980; see also Carlson *et al.*, 1980)

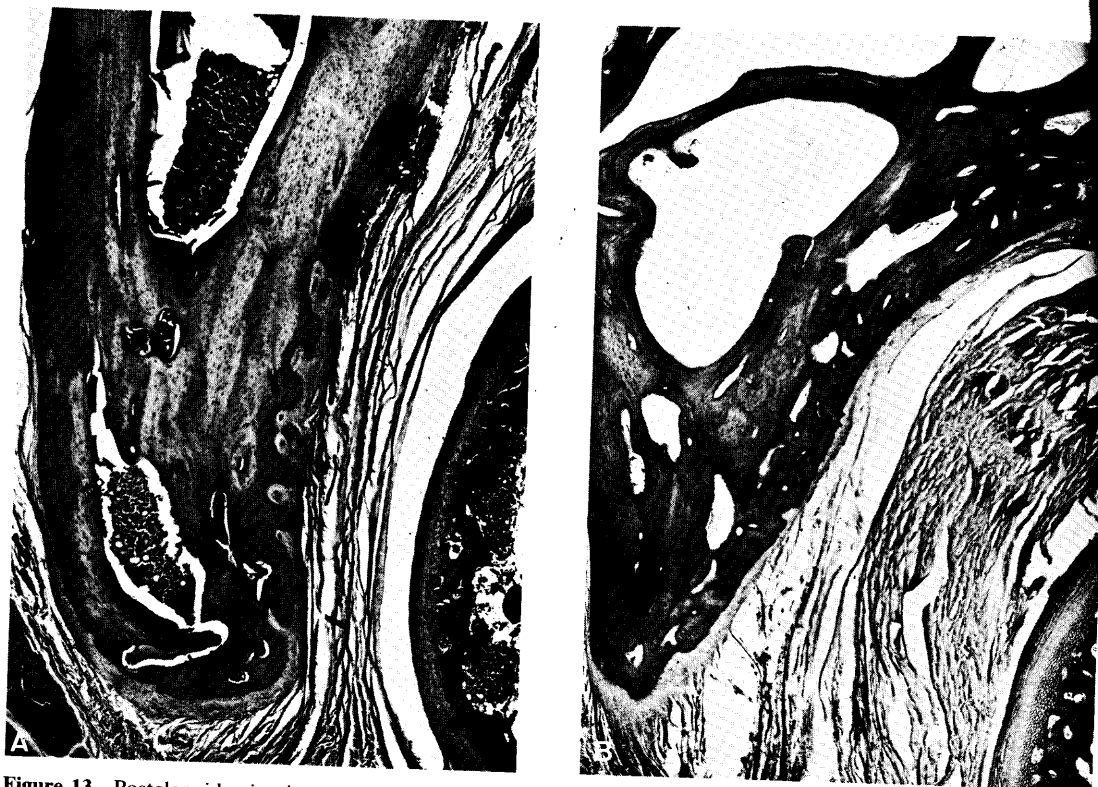


Figure 13 Postglenoid spine in two 24-week adult protrusive animals showing new bone deposition on the spine, consolidated to varying extents (Mag. $\times 7$).

observed that tonic discharges in the lateral pterygoid muscle, which increase dramatically with appliance placement and reach a maximum around 4–8 weeks, began to return to normal levels after about 8 weeks. Moreover, the greatest increments of increased condylar growth were noted from 4 to 8 weeks (Elgoyhen *et al.*, 1972; McNamara, 1980) and declined thereafter. Thus, it is likely that tissue responses in the temporal joint component, like those in the condyle, are part of a process of adaptation in which short-term neuromuscular adaptations to the altered occlusion are first augmented and then replaced by long-term skeletal adaptations at the TMJ and dentition.

Adaptive Response in Young Adults

Temporal component adaptations in the

adult sample were not as readily categorized as a sequence of distinct tissue responses. Part of the reason for this lay in the fact that several animals exhibited no response at all to the appliance, while several others displayed unique TMJ adaptations to development of a crossbite. However, in the four animals which did show temporal adaptations to anterior function there can be discerned the same overall sequence of new bone deposition followed by consolidation seen in juveniles (Figs 12 and 13). It is of some interest that, with the exception of a single crossbite animal, no depository adaptations to protrusion were noted in adults until 8 weeks. Both 8 week animals show new bone deposition, with spicules oriented perpendicular to the articular surface – a tissue first observed in juveniles at 2 weeks (compare Figs 3 and 12). In the same way, one 24-week adult animal shows par-

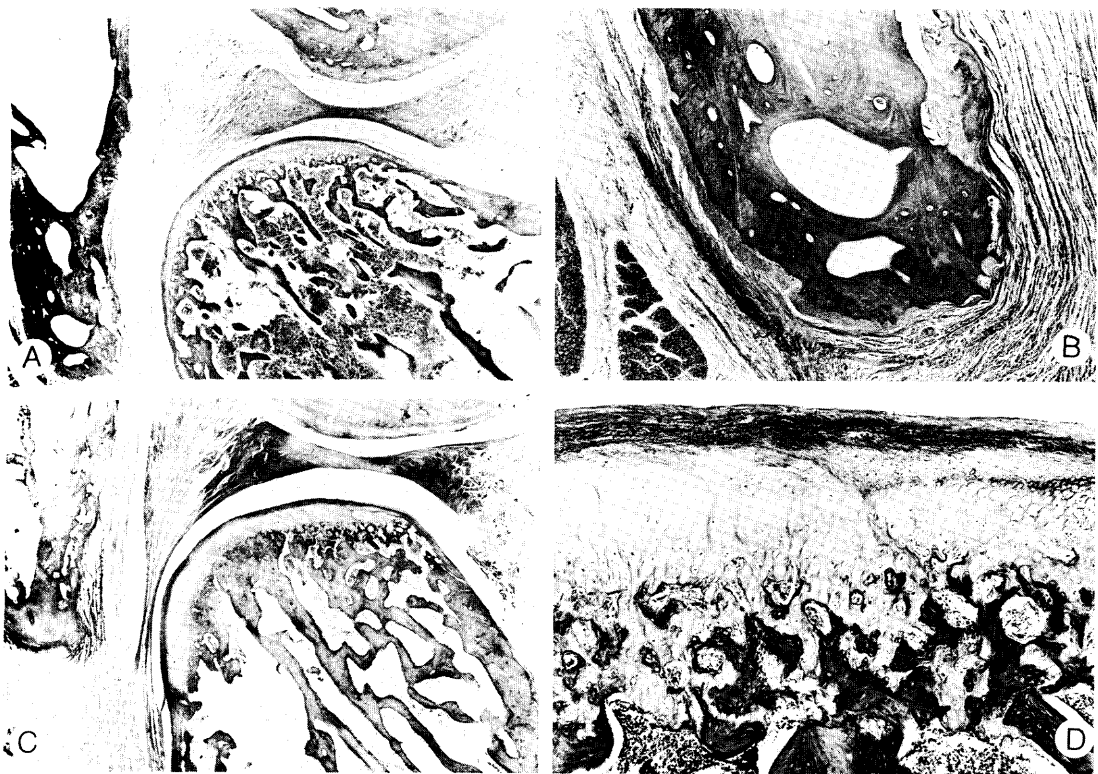


Figure 14 Temporomandibular joint adaptation in a 4-week adult protrusive animal with the development of a crossbite in which the mandible deviated to the right. A: Right temporomandibular joint region with resorption of bone along the anterior border of the postglenoid spine. Note the lack of cartilage proliferation along the posterior border of the mandible. B: High-power view of resorption of bone along the anterior surface of the postglenoid spine. C: Left temporomandibular joint region in same animal. Note deposition of new bone along the postglenoid spine and the proliferation of the condylar cartilage. D: Proliferation of condylar cartilage along the superior surface of the left condyle (Mag.; A and C, $\times 7$; B and D, $\times 26$).

tial but not complete consolidation of new bone that is strongly reminiscent of the response at 10–12 weeks in juveniles (compare Figs 9 and 13). This suggests that not only is the adaptive potential of the adult TMJ lower than that of growing animals (McNamara *et al.*, 1982), but that the speed at which adaptations take place may be considerably slower in adults.

We have suggested (McNamara *et al.*, 1982; Hinton and McNamara, 1984) that relative chronological age among the young adult sample may account for some of the variability in TMJ response: i.e., those animals showing little or no condylar response appear to be relatively older than the

rest of the sample, based on occlusal and interproximal attrition. Moreover, those animals exhibiting the greatest degree of condylar cartilage hyperplasia in response to the appliance, including two of the three crossbite animals, are among the youngest in the sample. Although the inverse association between relative age and adaptive response generally holds for the temporal component tissues, a perfect one-to-one correspondence between the presence of condylar and temporal adaptive responses was not observed. Part of the reason for this is that several of the youngest adult animals with considerable condylar hyperplasia were in the 2–6 week periods, during which no

temporal adaptations were noted, perhaps because of a diminished speed of temporal component response relative to condylar response. However, presence of a temporal response was also inconsistently associated with condylar response in two of the animals in the 8–24 week groups. Although the meaning of this is not clear, it may indicate that the nature of the mechanism eliciting condylar response differs somewhat from that initiating the temporal bone response. Whatever the case, the imperfect correlation between condylar and temporal component responses suggests that the temporal response is not contingent on some aspect of condylar response, but rather on one or more external stimuli that may affect either or both.

Possible Factors Promoting the Adaptive Response

The time-dependent nature of the temporal adaptation suggests the action of some sort of negative feedback or deviation-reducing system, an idea that has received its fullest elaboration in the work of Petrovic and associates on condylar growth (cf., Petrovic *et al.*, 1975; Petrovic and Stutzmann, 1977, 1981). At its most basic level, this notion postulates that an occlusal imbalance of such magnitude as to interfere with optimal intercuspation will initiate a neuromuscular response that restores a proper occlusal relationship on a short-term basis and that triggers a skeletal response at the TMJ (and dentition) which provides a long-term adaptation to the new occlusal configuration. The exact nature of the 'signal' which provokes the adaptive response at the condyle remains controversial (Petrovic *et al.*, 1975; Petrovic and Stutzmann, 1976, Carlson *et al.*, 1980). However, it seems clear that the tissue reactions in both condylar and temporal components are prompted by the anterior posturing of the condyle (and the concomitant distraction of the condyle from the mandibular fossa), and that the subsequent diminution of the tissue re-

sponse to normal levels is associated with restoration of the condyle back in the mandibular fossa.

A consideration of certain aspects of temporomandibular joint anatomy and of the articular disc in particular suggests a possible mechanism by which the temporal component response takes place. The most posterior region of the disc is designated as the bilaminar zone, because it is composed of two strata of fibres (or laminae) separated by loose areolar connective tissue. In humans, fibres of the superior lamina are attached to the squamo-tympanic fissure and tympanic plate (Rees, 1954; Griffin and Sharpe, 1960; Kreutziger and Mahan, 1975; Mahan, 1981), while fibres of the inferior lamina are attached to the inferior margin of the posterior articular surface of the condyle (Griffin and Sharpe, 1960). Whereas fibres of the inferior lamina are mostly ligamentous (collagenous) in nature, the superior lamina is composed primarily of thick fibres of elastin (Griffin and Sharpe, 1960; Dixon, 1962; Keith, 1979; Mahan, 1981). Since the disc is attached to the medial and lateral poles of the condyle, it translates forward with the condyle during functional movements. The composition and arrangement of fibres in the bilaminar zone presumably allows stretching of the superior lamina fibres to accommodate condylar translation. Since the posterior region of the disc is thought to rotate posteriorly with condylar translation (Mahan, 1981), less tension is produced in the fibres of the inferior lamina, thereby perhaps explaining the fewer number of elastic fibres in this region. While these features of joint anatomy are not easily examined in most histological preparations, they are more readily visible in sections prepared with the condyle situated forward on the articular eminence – e.g., the early stage protrusive animals. Inspection of Figs 3 and 5 from a 2-week protrusive monkey indicates that fibres from the posterior region of the disc appear to insert into the articular tissue (fibrous periosteum) lining the anterior surface of the postglenoid spine. In addition, the

uppermost fibres of the superior lamina of the disc appear to be reflected back upon the articular layer of the mandibular fossa, finally merging with the fibrous articular layer on the upper posterior slope of the articular eminence.

The correspondence between the areas of attachment of the fibres of the superior lamina of the disc and the presence of osteoblastic activity (cf., Fig. 8) is striking. The point of transition between active deposition of new bone and presence of fibrocartilage occurs almost precisely at the location where the superior lamellar fibres merge with the fibrous articular tissue - i.e., on the upper posterior slope of the articular eminence. It is generally believed that the condylar cartilage is the product of a modified periosteum (Enlow, 1975), and that the cells of the articular and prechondroblastic layers are homologous with the fibrous and osteogenic layers, respectively, of the periosteum in the remainder of the mandible (Petrovic, 1972; Wright and Moffett, 1974; Carlson *et al.*, 1978; Koski, 1981). This is very probably also true of the temporal component, as witnessed by the modulation of the tissue on the articular eminence into chondroid tissue and fibrocartilage during growth (Hinton and Carlson, 1983). If so, it is possible that the bony proliferative response in the posterior region of the mandibular fossa observed in the protrusive experiments may be the result of tensile forces from the posterior fibres of the disc acting on the osteogenic layer of the periosteum. Since the fibrous articular tissue of the temporomandibular joint contains a considerable number of elastic fibres, most parallel but some perpendicular to the articular surface (Miles and Dawson, 1962; Keith, 1979), it is not unreasonable to expect that tensile forces would be transmitted to this tissue from the posterior fibres of the disc during condylar translation.

Although the role of the periosteum in regulating the growth rate of long bones has only recently been investigated (cf., Crilly, 1972; Harkness and Trotter, 1978; Warrel and Taylor, 1979; Houghton and Dekel,

1979), the osteogenic potential and response of the periosteum has long been considered similar to that of sutures and periodontal ligament (Enlow, 1975; Azuma *et al.*, 1975; Koski, 1981). Sutures are now generally regarded as sites of adaptive growth that are chiefly responsive to local functional demands (Koskinen, 1976; Koskinen *et al.*, 1976; Linge, 1976; Evans, 1978; Oudhof, 1982). Moreover, bone deposition at sutural margins is generally thought to be initiated in response to tensile stresses of some sort (Enlow, 1975), although the exact manner by which such forces stimulate a tissue response is still unclear (cf., Meikle *et al.*, 1979, 1980).

Much less is known of the response of the periosteum to mechanical forces. Experimental removal of masticatory muscles has long been known to result in reduced development of bony processes and ridges (cf., Washburn, 1947; Horowitz and Shapiro, 1951, 1955; Avis, 1959, 1961), thus implying the importance of functional forces (presumably tensile) on periosteal bone deposition in these areas. However, the response of periosteum on free, relatively flat bony surfaces has been less well documented. It has been proposed that deposition of subperiosteal bone in the shaft of growing long bones is stimulated and oriented by periosteal tension, perhaps due to the force of the elongating growth cartilage (Lufti, 1964; Pritchard, 1972). More recently, transplantation studies using periosteal grafts have shown that the bone-forming capacity of calvarial periosteum, normally much less than that of tibial periosteum, increases five-fold when transplanted to a bone defect in the tibia (Udstromer and Ritsila, 1978). This finding, which parallels similar results for cranial sutures (Ryoppy, 1965), suggests that environmental factors may play a major role in the expression of osteogenic potential of the periosteum (see also Ritsila *et al.*, 1972 for further indications). In a related vein, the subperiosteal implantation of a haemostatic cellulose mesh has been shown to enhance deposition of new bone in repair of con-

genital clefts of the maxilla (Skoog, 1967; Thilander and Stenstrom, 1970). Although the clinical merits of this procedure have since been questioned (Engdahl, 1972; Uddstromer, 1978), the separation of the periosteal layer and the passive tension placed on it by the implanted material are of interest. Perhaps a more relevant study is that performed by Donnelly *et al.* (1973), who applied tensile forces directly to a tantalum mesh implanted beneath the buccal alveolar mucoperiosteum in adult female monkeys. They reported bone deposition exceeding control values, and noted that the histological appearance of the new bone 'showed either an areolar architecture, like that seen normally in areas of rapid deposition or consisted of trabeculae pointing toward the overlying wire mesh' (Donnelly *et al.*, 1973: p. 63). Experiments described by Harvold (1975) also suggest that bone deposition can be induced by tension applied to periosteal tissue.

The relatively rapid deposition of fibrous or woven bone is generally regarded as a response of pluripotent mesenchymal cells to local environmental factors (Frost, 1972). If deposition of new bone on the postglenoid spine and mandibular fossa occurs via a periosteal response to tension exerted by the posterior fibres of the disc, the cyclic nature of the adaptive response becomes readily explicable. It can be hypothesized that a transient osteogenic response would be stimulated by the greater-than-normal stretch of the posterior disc fibres, which in turn was prompted by the forced positioning of the condyle forward on the eminence to avoid occlusal trauma (2-6 weeks). As dentoalveolar and condylar responses combine to restore functional equilibrium and in so doing re-establish the condyle back within the mandibular fossa, tension in the posterior disc fibres would presumably decline to habitual levels encountered during normal jaw excursions and no further osteogenesis would be initiated (8-12 weeks). Such a process of tension-induced osteogenesis provides an interpretative framework for indications that greater

amounts of bone deposition in the mandibular fossa appear to occur in response to greater displacements of the condyle from the temporal bone (Sprinz, 1970). A similar process involving fibres of the inferior lamina of the disc may also account for the deposition of new bone on the posterior aspect of the condylar neck and ramus (Fig. 6) noted previously in protrusive experiments (Breitner, 1940; Petrovic, 1972; Petrovic *et al.*, 1975; McNamara, 1973; McNamara and Carlson, 1979). Since periosteal response has been shown in long bones to decline with age (Tonna, 1961; Tonna and Cronkite, 1962), this may account for the slower speed and possibly reduced magnitude of the adaptive response in young adults relative to juveniles.

An alternative explanation for the observed tissue response in the temporal joint component may be that bone deposition is in some way stimulated in response to loss of functional contact, or at least of proximity, between the condyle and temporal bone. In view of the possibility that functional contact may occur in monkeys between the condyle and the mandibular fossa and postglenoid spine (Carlson *et al.*, 1980; Hinton and Carlson, 1983; Zimmermann, 1971), this view cannot be dismissed. Also, at least until attachments of the articular disc to the squamosal bone are better understood, the loss of functional contact cannot be discounted as an explanation for bone deposition in the mandibular fossa of rodents and monkeys that have undergone condylectomy (Sarnat and Engel, 1951; Hayes, 1961) or condylotomy (Heurlin *et al.*, 1961; Gilhuus-Moe, 1969; Sprinz, 1970). However, flattening and remodelling of the mandibular fossa has been documented radiographically in human patients in response to condylar fractures and condylar displacements resulting from surgery (Thomson *et al.*, 1964; Hollender and Ridell, 1974; Hollender and Lindahl, 1974; Lindahl and Hollender, 1977), and the incidence and amount of remodelling of the fossa seems to increase with the extent of condylar dislocation (Lindahl and Hollender,

1977). Since the mandibular fossa and retrocondylar area are generally assumed to be non-functioning regions in the human TMJ (Sicher and DuBrul, 1970), deposition due to loss of functional contact or proximity would seem to be unlikely to account for the observed remodelling response.

Elucidation of the precise mechanism responsible for the adaptive responses documented in this study must await further investigation. The apparent association of experimentally-induced osteogenesis in the posterior region of the mandibular fossa with the position of the condyle within the mandibular fossa suggests that similar factors operating on a more subtle level may perhaps account for changes in patterns of remodelling on the postglenoid spine and mandibular fossa during normal growth and development of the rhesus monkey. Since there is evidence that joint reaction forces at the monkey TMJ become progressively more anteriorly directed with age (Carlson *et al.*, 1978; Hinton and Carlson, 1983), it is conceivable that the transition from a largely resorptive postglenoid spine and fossa in juveniles to a largely depository surface in adolescents and young adults may result from subtle changes in the biomechanical environment of the posterior region of the joint. In addition, the suggestion in this study that posterior fibres of the articular disc may exert an influence on temporal bone remodelling and response to extraoral forces requires further investigation in light of similar suggestions for the condyle (Petrovic and Stutzmann, 1977). Finally, it should be noted that the adaptive responses described histologically in growing rhesus monkeys in response to condylar distraction closely resemble changes observed radiographically in human children who have suffered condylar fractures involving dislocation of the condyle from the fossa (Thomson *et al.*, 1964; Lindahl and Hollender, 1977). Descriptions of the remodelling process note the development on the fracture side only of a 'double contour' of concentric layers of bone in the fossa within 1-6 months of fracture (Lindahl and Hollen-

der, 1977; Hollender and Lindahl, 1974). This is followed by a gradual disappearance of the original fossa roof and its eventual replacement (in 2-3 years) by the 'new' layer of bone, thereby flattening the mandibular fossa. In addition, what appears to be new bone deposition on the posterior wall of the mandibular fossa has been noted in a young patient undergoing forced anterior posturing of the lower jaw to correct a Class II malocclusion (Panherz, 1979). Thus, an awareness of the existence and ultimately the mechanism responsible for such a response is important from the standpoint of the clinician.

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References

- Adams C D, Meikle M C, Norwick K W, Turpin D I 1972 Dentofacial remodeling produced by intermaxillary forces in *Macaca mulatta*. *Archives of Oral Biology* 17: 1519-1535
- Avis V 1959 The relation of the temporal muscle to the form of the coronoid process. *American Journal of Physical Anthropology* 17: 89-104
- Avis V 1961 The significance of the angle of the mandible: an experimental and comparative study. *American Journal of Physical Anthropology* 19: 55-61
- Azuma M, Enlow D H, Fredrickson R G, Gaston L G 1975 A myofibroblastic basis for the physical forces that produce tooth drift and eruption, skeletal displacement at sutures, and periosteal migration. In: McNamara James A Jr (ed.). *Determinants of Mandibular Form and Growth*. Monograph Number 4, Craniofacial Growth Series, Center for Human

- Growth and Development. The University of Michigan, Ann Arbor, p. 179-208
- Baume L J, Derichswiler H 1961 Is the condylar growth center responsive to orthodontic therapy? An experimental study in *Macaca mulatta*. Oral Surgery, Oral Medicine, Oral Pathology 14: 347-362
- Breitner C 1930 Experimentelle Veränderung der mesiodistalen Beziehungen der oberen und unteren Zahnreihen. Zeitschrift für Stomatologie, 28: 343-356
- Breitner C 1933 Experimental change of the mesiodistal relations of the upper and lower dental arches. Angle Orthodontist 3: 67-76
- Breitner C 1940 Bone changes resulting from experimental orthodontic treatment. American Journal of Orthodontics and Oral Surgery 26: 521-547
- Breitner C 1941 Further investigation of bone changes resulting from experimental orthodontic treatment. American Journal of Orthodontics and Oral Surgery 27: 605-632
- Carlson D S, McNamara J A Jr, Jaul D H 1978 Histological analysis of the growth of the mandibular condyle in the rhesus monkey (*Macaca mulatta*). American Journal of Anatomy 151: 103-118
- Carlson D S, McNamara J A Jr, Graber L W, Hoffman D L 1980 Experimental studies of the growth and adaptation of the temporomandibular joint. In: Current Advances in Oral Surgery, Volume III, Chapter 4, C. V. Mosby, St Louis, pp 28-81
- Charlier J P, Petrovic A, Hermann-Stutzmann J 1969 Effects of mandibular hyperpropulsion on the prechondroblastic zone of young rat condyle. American Journal of Orthodontics 55: 71-74
- Crilly R G 1972 Longitudinal overgrowth of chicken radius. Journal of Anatomy 112: 11-18
- Dixon A D 1962 Structure and functional significance of the intra-articular disc of the human temporomandibular joint. Oral Surgery 15: 48-61
- Donnelly M W, Swoope C C, Moffett B C 1973 Alveolar bone deposition by means of periosteal tension. Journal of Dental Research 52: 63 (IADR Abstract-Feb)
- Elgoyhen J C, Moyers R E, McNamara J A Jr, Riolo M L 1972 Craniofacial adaptation to protrusive function in young rhesus monkeys. American Journal of Orthodontics 62: 469-480
- Engdahl E 1972 Bone regeneration in maxillary defects. Scandinavian Journal of Plastic and Reconstructive Surgery, Suppl. 8
- Enlow D H 1975 Handbook of Facial Growth. Saunders, Philadelphia
- Evans C A 1978 Facial growth. Section A: mechanisms. In: Textbook of Oral Biology, Shaw, J H, Sweeney E A, Cappuccino C C, Meller S M (eds) pp 55-109, W. B. Saunders, Philadelphia
- Folke L E, Stallard R E 1966 Condylar adaptation to a change in intermaxillary relationship. Journal of Periodontal Research 1: 79-89
- Frost H M 1972 The Physiology of Cartilaginous, Fibrous, and Bony Tissue. C C Thomas, Springfield, Illinois
- Griffin C J, Sharpe C J 1960 The structure of the adult human temporomandibular meniscus. Australian Dental Journal 5: 190-195
- Gilhuus-Moe O 1969 Fractures of the mandibular condyle in the growth period. Universitetsforlaget, Oslo
- Harkness E M, Trotter W D 1978 Growth of transplant of rat humerus following circumferential division of the periosteum. Journal of Anatomy 126: 275-289
- Harvold E P 1975 Experiments on mandibular morphogenesis. In: Determinants of Mandibular Form and Growth, McNamara J A Jr, (ed.), pp 155-178, Monograph Number 4, Craniofacial Growth Series, Center for Human Growth and Development, The University of Michigan, Ann Arbor, Michigan
- Häupl K, Psansky R 1939 Experimentelle Untersuchungen über Gelenktransformation bei Verwendung der Methoden der Funktionskieferorthopaedie. Deutsche Zahn-, Mund-, und Kieferheilkunde 6: 439-448
- Hayes A M 1961 Changes in the mandibular fossa of the rat following unilateral condylectomy. Journal of the Canadian Dental Association 27: 647-657
- Heurlin R Jr, Gans B, Stuteville O 1961 Skeletal changes following fracture dislocation of the mandibular condyle in the adult rhesus monkey. Oral Surgery, Oral Medicine, Oral Pathology 14: 1490-1500
- Hinton R J, Carlson D S 1983 Histological changes in the articular eminence and mandibular fossa during growth of the rhesus monkey (*Macaca mulatta*). American Journal of Anatomy 166: 99-116
- Hinton R J, McNamara J A Jr, 1984 Effect of age on adaptive response of adult temporomandibular joint. A study of induced protrusion in *Macaca mulatta*. Angle Orthodontist. 54: 154-162
- Hollender L, Lindahl L 1974 Radiographic study of articular remodeling in the temporomandibular joint after condyle fractures. Scandinavian Journal of Dental Research 82: 462-465
- Hollender L, Ridell A 1974 Radiography of the temporomandibular joint after oblique sliding osteotomy of the mandibular rami. Scandinavian Journal of Dental Research 82: 466-469
- Horowitz S L, Shapiro H H 1951 Modifications of mandibular architecture following removal of temporalis muscle in the rat. Journal of Dental Research, 30: 276-280
- Horowitz S L, Shapiro H H 1955 Modification of skull and jaw architecture following removal of the masseter muscle in the rat. American Journal of Physical Anthropology 13: 301-318
- Houghton G R, Dekel S 1979 The periosteal control of long bone growth. An experimental study in the rat. Acta Orthopaedica Scandinavica, 50: 635-637
- Hurme V O and van Wagenen G 1961 Basic data on the emergence of permanent teeth in the rhesus monkey (*Macaca mulatta*). Proceedings of the American Philosophical Society, 105: 105-140
- Ingervall B, Freden H, Heyden G 1972 Histochemical study of mandibular joint adaptation in experimental

- posterior mandibular displacement in the rat. *Archives of Oral Biology* 17: 661-671
- Joho J-P 1973 The effects of extraoral low-pull traction to the mandibular dentition of *Macaca mulatta*. *American Journal of Orthodontics* 64: 555-577
- Jolly M 1961 Condylectomy in the rat, an investigation of the ensuing repair process in the region of the temporomandibular articulation. *Australian Dental Journal* 6: 243-256
- Keith D A 1979 Elastin in the bovine mandibular joint. *Archives of Oral Biology* 24: 211-215
- Koski K 1981 Mechanisms of craniofacial skeletal growth. In: *Orthodontics: The State of the Art*. Barrer, H G (ed.), pp 209-222, University of Pennsylvania Press, Philadelphia
- Koskinen L 1977 Adaptive sutures. *Proceedings of the Finnish Dental Society* 73: Suppl. X
- Koskinen L, Isotupa K, Koski K 1976 A note on craniofacial sutural growth. *American Journal of Physical Anthropology* 45: 511-516
- Kreutziger K L, Mahan P E 1975 Temporomandibular degenerative joint disease. Part I. Anatomy, pathophysiology and clinical description. *Oral Surgery, Oral Medicine, Oral Pathology* 40: 165-182
- Lindahl L, Hollender L 1977 Condylar fractures of the mandible. II. A radiographic study of remodeling processes in the temporomandibular joint. *International Journal of Oral Surgery* 6: 153-165
- Linge L 1976 Tissue reactions in facial sutures subsequent to external mechanical influences. In: *Factors Affecting the Growth of the Midface*. McNamara J A Jr, (ed.) pp 251-276. Monograph No. 6, Craniofacial Growth Series, Center for Human Growth and Development, The University of Michigan, Ann Arbor
- Lufti A M 1974 The role of cartilage in long bone growth: a reappraisal. *Journal of Anatomy* 117: 413-417
- Mahan P E 1980 Anatomic, histologic, and physiologic features of temporomandibular joint. In: *Current Advances in Oral Surgery*, Vol. III, Irby W B (ed.), C. V. Mosby: St Louis, pp 1-9
- McNamara J A Jr, 1972 Neuromuscular and Skeletal Adaptations to Altered Orofacial Function. Monograph No. 1, Craniofacial Growth Series, Center for Human Growth and Development, The University of Michigan, Ann Arbor
- McNamara J A Jr, 1973 Neuromuscular and skeletal adaptations to altered function in the orofacial region. *American Journal of Orthodontics* 64: 578-606
- McNamara J A Jr, 1980 Functional determinants of craniofacial size and shape. *European Journal of Orthodontics* 2 (3): 131-160
- McNamara J A Jr, Graber L W 1975 Mandibular growth in the rhesus monkey (*Macaca mulatta*). *American Journal of Physical Anthropology* 142: 15-24
- McNamara J A Jr, Carlson D S 1979 Quantitative analysis of temporomandibular joint adaptations to protrusive function. *American Journal of Orthodontics* 76: 593-611
- McNamara J A Jr, Hinton R J, Hoffman D L 1982 Histological analysis of temporomandibular joint adaptation to protrusive function in young adult rhesus monkeys (*Macaca mulatta*). *American Journal of Orthodontics*, 82: 288-298
- Meikle M C, Heath J K, Reynolds J J 1979 Rabbit cranial sutures *in vitro*: New experimental model for studying the response of fibrous joints to mechanical stress. *Calcified Tissue International* 28: 139-144
- Meikle M C, Sellers A, Reynolds J J 1980 Effect of tensile mechanical stress on the synthesis of metalloproteinases by rabbit coronal sutures *in vitro*. *Calcified Tissue International* 30: 77-82
- Miles A E W, Dawson J A 1962 Elastic fibres in the articular fibrous tissue of some joints. *Archives of Oral Biology* 7: 249-252
- Oudhof H A J 1982 Sutural growth. *Acta Anatomica* 112: 58-68
- Pancherz H 1979 Treatment of Class II malocclusions by jumping the bite with the Herbst appliance. *American Journal of Orthodontics* 76: 423-442
- Petrovic A 1972 Mechanisms and regulation of mandibular condylar growth. *Acta Morphologica - Neerlandica Scandinavica* 10: 25-34
- Petrovic A G, Stutzmann J J, Oudet C L 1975 Control processes in the postnatal growth of the condylar cartilage of the mandible. In: *Determinants of Mandibular Form and Growth*, J A McNamara Jr, (ed.), Center for Human Growth and Development, Ann Arbor, Craniofacial Growth Series, Monograph No. 4, pp 101-154
- Petrovic A, Stutzmann J J 1977 Further investigations into the functioning of the "comparator" of the servosystem in the control of the condylar cartilage growth rate and of the lengthening of the jaw. In: *The Biology of Occlusal Development*, J. A. McNamara Jr, (ed.), Craniofacial Growth Series, Monograph No. 7, Center for Human Growth and Development, The University of Michigan, Ann Arbor, pp 255-292
- Petrovic A, Stutzmann J J, Gasson N 1981 The final length of the mandible: Is it genetically predetermined? In: *Craniofacial Biology* (D. S. Carlson, ed.), Craniofacial Growth Series, Monograph No. 10, Center for Human Growth and Development, The University of Michigan, Ann Arbor, pp 105-126
- Pritchard J J 1972 The control of trigger mechanisms induced by mechanical forces which causes responses of mesenchymal cells in general and bone apposition and resorption in particular. *Acta Morphologica Neerlandica-Scandinavica* 10: 63-69
- Rees L A 1954 The structure and function of the mandibular joint. *British Dental Journal* 96: 125-133
- Ritsila V, Alhopuro S, Rintala A 1972 Bone formation with free periosteum. *Scandinavian Journal of Plastic and Reconstructive Surgery* 6: 51-56
- Ryppy S 1965 Transplantation of epiphyseal cartilage and cranial suture. *Acta Orthopaedica Scandinavica* Suppl 82

- Sarnat B G, Engel M B 1951 A serial study of mandibular growth after removal of the condyle in the macacus rhesus monkey. *Plastic and Reconstructive Surgery* 7: 364-380
- Sicher H, DuBrul E L 1970 *Oral Anatomy*, St Louis, C. V. Mosby, 5th edition
- Skoog T 1967 The use of periosteum and Surgicel for bone formation in congenital clefts of the maxilla. *Scandinavian Journal of Plastic and Reconstructive Surgery* 1: 113-130
- Sprinz R 1970 Healing in fractures of the neck of the mandible in rats with detachment of the lateral pterygoid muscle. *Archives of Oral Biology* 15: 1219-1229
- Stöckli P W, Willert H G 1971 Tissue reactions in the temporomandibular joint resulting from anterior displacement of the mandible in the monkey. *American Journal of Orthodontics* 60: 142-155
- Thilander B, Stenstrom S J 1970 Bone healing after implantation of some hetero- and alloplastic materials: An experimental study on the guinea pig. *Cleft Palate Journal* 7: 540-549
- Thomson H G, Farmer A W, Lindsay W K 1964 Condylar neck fractures of the mandible in children. *Plastic and Reconstructive Surgery* 34: 452-463
- Tonna E A 1961 The cellular complement of the skeletal system studied autoradiographically with tritiated thymidine ($^3\text{HTdR}$) during growth and aging. *Journal of Biophysical and Biochemical Cytology* 9: 813-824
- Tonna E A, Cronkite E P 1962 Changes in the skeletal cell proliferative response to trauma with aging. *Journal of Bone and Joint Surgery* 44-A: 1557-1568
- Uddstromer L 1978 The osteogenic capacity of tubular and membranous bone periosteum. *Scandinavian Journal of Plastic and Reconstructive Surgery* 12: 195-205
- Uddstromer L, Ritsila V 1978 Osteogenic capacity of periosteal grafts. *Scandinavian Journal of Plastic and Reconstructive Surgery* 12: 207-214
- Warrell E, Taylor J F 1979 The role of periosteal tension in the growth of long bones. *Journal of Anatomy* 128: 179-184
- Washburn S L 1947 The relation of the temporal muscle to the form of the skull. *Anatomical Record*, 99: 239-248
- Wright D M, Moffett B C 1974 The postnatal development of the human temporomandibular joint. *American Journal of Anatomy* 141: 235-250
- Zimmerman H I 1971 The normal growth and remodeling of the temporomandibular joint of *Macaca mulatta*. Unpublished Master's Thesis, University of Washington, Seattle