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SIMON, Mark Robert, 1941-
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MOVEMENTS IN THE RAT.

The City University of New York, Ph.D., 1974
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AN EXPERIMENTAL INVESTIGATION OF MANDIBULAR MOVEMENTS IN THE RAT

by

MARK ROBERT SIMON

A dissertation submitted to the Graduate
Faculty in Anthropology in partial fulfillment
of the requirements for the degree of Doctor
of Philosophy, The City University of New York

1974

This manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

AN EXPERIMENTAL INVESTIGATION OF MANDIBULAR MOVEMENTS IN THE RAT

by

Mark Robert Simon

Adviser: Professor Alphonse Riesenfeld

A multidimensional approach, using cinefluorography of mandibular movements during chewing, histology of the mandibular joint, and comparison of muscle fiber direction of the masseter and temporalis muscles was employed in an attempt to separate and study the functioning and plasticity of the various components of the masticatory system. Three experimental situations were utilized: bilateral removal of the temporalis muscle in one group of rats, bilateral removal of the upper and lower incisors in a second group, and bilateral condylectomy in a third group. The observed modifications in arrangement of muscle fibers, structure of the mandibular joint, and pattern of chewing cut across the three experimental groups in a complex way. The experimental results were categorized in two ways, based on mandibular movements during the closing phase of chewing. First, some of the animals from which the temporalis muscle was removed were similar to the control animals in mandibular movement and in the thinness of the meniscus of the mandibular joint. In these temporalis removal animals muscle fiber direction of the masseter changed indicating a compensatory realignment of muscles. Secondly, the remaining temporalis removal animals and the

condylectomized animals showed a change in movement during closing and a thick central area of the meniscus indicating a significant reduction in compression at the mandibular joint. The group in which incisors were removed demonstrated an even more extreme reduction in compressive forces at the mandibular joint. Mandibular movement was similar to that in condylectomized animals, but maturation of the entire mandibular joint was abnormal. This suggests that incisor utilization is for more significant in the normal maturation of the mandibular joint than was previously recognized. The results of this study attest to the desirability of a multidimensional approach. In this way, inferences based on each component may be tested against those based on others, and the mutually corroborative results obtained here attest to the usefulness of the approach.

ACKNOWLEDGEMENTS

I wish to express my thanks to the people who offerred their assistance during the preparation of this thesis:

To Professor A. Riesenfeld, and to Professor E. Hunt Jr., and to Professor W. Kinzey for their help and advice while supervising

To Professor W. Bock for his advice and time generously given

To Ms. D. Sena who prepared the histologic material

To Mr. L. Wexler for his help in photographing the muscles of mastication

and to my friend Dr. I. Tattersall for his advice, help, and unwavering encouragement.

CONTENTS

LIST OF ILLUSTRATIONS

INTRODUCTION

Beginning with Washburn's (1947) study of the relationship between the temporalis muscle and the shape of the skull, experimental physical anthropology has been attempting on the one hand to elucidate biomechanically advantageous situations which might be selected for; and on the other hand to test hypotheses empirically. The masticatory apparatus, comprised of muscles, teeth, and bone, has been a fertile area for investigation on several levels of observation. The literature is replete with studies on the relationship between the teeth and bone, teeth and muscle, and muscle and bone (Avis 1955; Crompton and Hiiemae 1969; Moss 1960; Dullemeijer 1959; Riesenfeld 1965; Washburn 1947; a.m.o.).

It is believed that many human biomechanical processes may usefully be studied experimentally in other mammals, e.g., the laboratory rat (Rattus norvegicus). In this instance, the system under study is that of mastication, which appears to be of importance in the study of the evolutionary divergence of the hominids from their pongid forebears (Jolly 1970). It is the intent of this study to separate and study the various components which comprise this system, i.e., the main muscles of mastication, the histology of the mandibular joint, and the functioning of the system as seen through the movements executed by the mandible; and to investigate the plasticity of each component. The results will, it is hoped, be of value in understanding factors influencing the morphology of the mandibular joint and the facial complex.

Cinefluorography was used initially to determine mandibular movements in the normal, control rat, and the results compared to those reported by Hiiemae (1966). Surgical techniques were then applied to determine whether or not jaw movements would change as a result of such interference, and whether such changes would occur in a constant, predictable pattern.

Experimental alterations included the following: removal of the incisors in one group of rats, bilateral extirpation of the temporalis muscles in another group of rats, and bilateral condylectomy in a third group.

After cinefluorography, the animals were sacrificed and fixed by ventricular perfusion. The area of the mandibular joint was removed and serially sectioned to determine if the experimental procedure had produced changes in the histology of the joint. The heads were hemisected and photographs taken in the lateral view from which were determined the fiber orientation of the deep masseter and the anterior and posterior portions of the temporalis muscle. This was to ascertain if possible changes in jaw movements could be correlated with changes in the histology of the joint and the orientation of muscle fibers.

Cinefluorography affords a dynamic approach to the study of jaw movements as opposed to the more static one of hypothesizing from dissections or matching dental wear facets. Cinefluorography and electromyography have both contributed to an understanding of jaw movements. I hope to have enlarged upon the data accumulated for man by employing experimental interference.

METHODOLOGY

Introduction -

The conclusions reached from the observed data depend, in any study, upon the conceptual basis or philosophy supporting each decision made throughout the study. The philosophy, school of thought, or method should not be confused with the technique, or modus operandi, e.g., comparative anatomy or experimental animal surgery.

This study uses a holistic approach to functional morphology. The holistic approach, as opposed to an atomistic approach, was utilized as a starting point by van der Klaauw (van der Klaauw 1948-51; Dullemeijer 1968; Gans 1969). He considered function (biological role of Bock and von Wahlert) as a property and so introduced the concept of "functional components," by which he meant a part of an organism which performs a biological role and has a restricted individuality. Restricted individuality means that while it is possible to discern a particular part of an organism which is associated with a specific function (biological role), this particular part does not have an existence apart from the organism of which it is a part. Also, its size and shape may be determined in part by the other functional components surrounding it. Finally, the organism is, in essence, the totality of all the functional components.

Van der Klaauw restricted the term functional component to skeletal parts; Dullemeijer (1956, 1958) and Moss (1960) applied the term to soft parts. Moss's construct "the functional matrix" refers to all those tissues and functioning spaces, e.g., the oral cavity, necessary to carry out a given function (biological role) while the skeletal unit is synonymous with the "functional component" of van der Klaauw. Van der Klaauw did not apply his concept of "functional component" to dynamic morphology or to problems of growth and development. Moss has attempted this and has suggested a causal relationship among the elements comprising a functional component: he states that the growth of the "functional matrix" is primary and the growth of the "skeletal unit" is secondary, compensatory, and mechanically obligatory (Moss 1960; Moss and Simon 1968; Simon and Moss 1973).

In a holistic approach, one attempts to formulate the interrelation of the elements. There is a mutual influence of the elements since the elements together constitute a functional totality - the organism. The mutual influence is experienced through the properties of the elements: presence, position, size, shape, structure, and function (biological role). Dullemeijer (1958) has shown that there are 36 possible interactions in the influence of one element on another. Since the configuration of any particular feature is determined to some extent by other features which impinge upon it, the feature under study might not have the most desirable configuration. Also, if a particular feature participates in more than one activity, then the resultant configuration would be a compromise between the variousforces (Bock and von Wahlert 1965; Bock, Balda, van den Wall 1973).

The consequence of this holistic approach to experimental animal surgery is that each experimental group must be looked upon as a different animal from the control, and one should not expect modifications back towards the control but towards the final product of the mutual interactions of the structures. In each case there is the expectation that the principle of optimal design will obtain for the particular set of interacting features resulting from the operation and that the organisms can adjust to changes imposed upon them during their life. The ability of tissues of an organism to modify favorably their phenotype in response to stimuli, either from the environment or imposed upon it as in the case of experimental surgery, is termed physiological adaptation. A variable form and function (activity) to a selected feature affords a greater capacity for the organism to cope with a changing environment. The application of this to experimental surgery is that the supposition that there is only one response possible for the tissues is untenable.

Functional morphology, as opposed to descriptive morphology, attempts to explain form within the context of a functioning organism in its environment. Bock and von Wahlert (1965) state:

> "A morphology based upon pure form - isolated from function and from the interaction between the form-function complex and environmental factors - does not provide a broad enough foundation on which to analyze the phenomenon of biological adaptation...the inadequacy of this foundation is revealed by continued discussions, even recently, of whether the form of a feature is adapted to its function or whether the form of a structure is adapted to environmental factors without considering its function, or whether the form or the function of a structure changes first during evolution."

Much of the controvercies in the literature of functional morphology can be traced to different uses of the term "functional" to mean action, demand, biological role, and historical significance. To avoid such confusion, the terminology advocated by Bock and von Wahlert (1965) is adopted (because of their importance, I quote them in their entirety):

a) Feature - Any part or attribute of an organism will be referred to as a feature if it stands as a subject in a sentence describing the organism.

b) Form - In any sentence describing a feature of an organism, its form would be the class of predicates of material composition and the arrangement, shape, or appearance of these materials, provided that these predicates do not mention any reference to the normal environment of the organism. It must be emphasized that a feature may possess a range of forms, such as modifications of the lens of the eye, or change in length and diameter of a muscle fiber as it contracts and shortens, or the shape of a flight feather because of changing air pressures as the bird flies.

c) Function - In any sentence describing a feature of an organism, its functions would be that class of predicates that include all physical and chemical properties arising from its form (i.e., its material composition and arrangement thereof) including all properties arising from increasing levels of organization, provided that these predicates do not mention any reference to the environment of the organism. It should be emphasized that features possess many functions that are never utilized by the organism, yet these are valid functions and are worthy of being studied. Moreover, as the form of a feature changes, its function automatically changes. This definition of biological function is free, as it should be, of any form of teleology, Aristotelian or otherwise, or of any form of teleonomy; it does not involve any aspect of purpose, design or goal. A feature generally possesses a number of functions simultaneously even if it has only one form. Not all of the functions of a particular feature need be investigated by an anatomist, especially if it is clear that the functions are not pertinent to the problems at hand.

d) Faculty - A faculty is defined as a combination of a form and a function of a feature. Or more formally, in any sentence describing a feature of an organism, its faculties would be that class of predicates each of which includes a combination of a form (material composition and arrangement) and a function (physical and chemical properties) of the feature, provided that these predicates do not mention any reference to the normal environment of the organism. The faculty, comprising a form and a function of the feature, is what the feature is capable of doing in the life of the organism and is the unit that bears a relationship to the environment of the organism. The faculty is the unit acted upon by selection and is the aspect of the feature adapted to the environment.

e) Biological role - In any sentence describing a feature of an organism, the biological roles would be that class of predicates which includes all actions or uses of the faculties (the form-function complexes) of the feature by the organism in the course of its life history, provided that these predicates include reference to the environment of the organism. Essential to the description of a biological role is the observation of the organism living naturally in its environment. The descriptive adjective "biological" stresses this fundamental property of the biological role. A biological role cannot be determined by observations made in the laboratory or under other artificial conditions. This is the basic distinction between study of functions and study of biological roles; in morphology, the former would be functional anatomy while the latter would be biological anatomy." (See Bock and von Wahlert, 1965, for a more detailed explanation and a description of further terms relating the organism to the environment.)

The conclusions one can draw in a study depend upon the level of observation. Great care should be taken in extrapolating from one level of observation to another, because each of the elements that comprise a complex of features possess certain properties when studied individually; however, the properties resulting from the organization of the individual units to form a particular complex can be very different. For example, a muscle can be excised and its degree of shortening tested or its power output in contraction. This does not provide information regarding its degree of shortening or power output while functioning in the living organism. Any study using the physiological cross-section of a muscle as a parameter to determine the actual power output of the muscle while functioning in the organism is basing results upon an erroneous assumption. How the muscle functions in a laboratory apparatus and how the muscle functions in the intact organism are different phenomena (Gans and Bock 1965). The application of this to the numerous studies on the muscles of mastication in primates (especially man) is obvious, and will be discussed in greater detail in the section "Comparison of Muscle Fiber Direction."

The methodology employed in this study reflects a holistic approach to functional morphology. Using the technique of experimental animal surgery, the form of a feature was changed with the assumption that this would produce concomitant changes in the elements. A change in the morphology of a form of the complex will change its function and hence how the animal can perform its biological roles. Mastication was abstracted from the total picture as the role to be examined. This role is carried out by the same form-function complex responsible for speech, breathing, fighting, etc. Since the experimental animal surgery produces individual animals with different morphological patterns it is not relevant to ask if the various experimental groups will attempt to retain the control faculty; but rather, to try to explain the features as they appear in the experimental groups, assuming that in each case the optimal design was reached for the mutual interactions between the experimentally modified features and "untouched" features in the total morphological complex of each individual animal.

Operational procedures -

The animals used in this study were male and female rats of a mixed Wistar and Long Evans strain. Limiting the study to animals of one sex was considered unnecessary as Cabrini and Erausquin (1944), Cunat et al. (1956), and Hiiemae (1966) did not specify the sex of the rats used in their studies on the growth and morphology of the mandibular joint in the rat. Also, Hiiemae and Houston (1971) state: "as far as can be ascertained there is no sexual dimorphism in the arrangement or form of the muscles in the rat."

It was decided that, due to budgetary limitations, several experimental procedures would be performed, each one on a small sample of rats. The alternative, one experimental procedure performed on a single large sample of rats, would not shed as much light on the mechanisms of mandibular movements and morphology of the mandibular joint as would several experimental situations. Three experimental situations were employed, each one on a different group of rats. All operations were performed on animals anesthetized with ether. Survival after operations was 100%. After weaning, the animals were fed a diet of Purina rat pellets. The animals that underwent incisor removal were fed Purina meal, as they were unable to gnaw at regular rat pellets.

In one group, the upper and lower incisors were removed bilaterally at ten days of age. Four animals were used for this group.

In a second group, the temporalis muscle was excised bilaterally at twenty-one days of age. A few slips of the muscle, the most anterior ones directly behind the eye, were not removed as it was thought advisable not to chance disrupting the animals' vision. Cautery was used to prevent regeneration. Since the purpose of excising the temporalis muscle was to examine the effect of removing the main element responsible for retracting the mandible, the few anterior fibers remaining could not deter the effect of the operation. Five animals were used for this group.

In a third group, bilateral condylectomy was performed at five days of age. At this age, the bleeding that follows a removal of the condyle can be controlled by pressure. Three animals were used.

The control group consisted of three rats.

Cinefluorography was employed when the animals had attained an age of 105 days. This age was chosen because Hiiemae (1966) states that at this age the adult morphology of the mandibular joint is reached in the rat. The equipment used consisted of a Philips Image Intensification unit with a Plumbicon TV Howell 16 mm unit. The speed of the 16 mm unit was 32 frames per second. The KV was 70 and the MA was 2.5; minimum filtration was used. The film used was Kodak no.7276 reversal 16 mm film.

The animals were deprived of food for 24 hours prior to cinefluorography to ensure their performing well. Each animal was placed, in turn, in an empty, narrow cardboard box. A narrow cardboard box restricts lateral movements of the body and thereby keeps the animal better positioned; the cardboard causes no distortion of x-rays. The cinefluorography was undertaken in the lateral view only; analysis of this material was therefore restricted to movements of the jaw in the sagittal plane, i.e., elevation and depression.

Mandibular implants were not utilized as any irritation to the muscles of mastication would have introduced an additional factor; also, an initial trial showed that the upper and lower molar ridge and incisors are clearly visible in the developed film and could be used as reference lines.

A frame by frame analysis was executed for each animal to determine mandibular movements during the chewing cycle. The film was fed through a Kodak slide projector and the image of the skull and mandible traced separately onto paper. A minimum of 25 single frames were traced for each individual.

Immediately following cinefluorography each animal was sacrificed, fixed by ventricular perfusion with 10% formalin, decapitated, and the head skinned and hemisected midsagittally. A still x-ray was taken of each hemisected head and superimposed upon the tracings from the frame by frame analysis using the outline of the molar ridge and incisors as reference lines. The position of the mandible and thereby the determination of mandibular movements during the chewing cycle, in the control and experimental situations was obtained by superimposing the tracings from successive frames for each individual. The basicranial axis and maxillary incisors served as constant planes of reference.

After the hemisected heads had been x-rayed, the area of the mandibular joint was removed from the left side of each animal and decalcified in 5% formic acid. Histologic sections were prepared; the material was sectioned sagittally at intervals of 10 , and stained with hematoxylin and eosin. The slides were reviewed and a representative midsagittal cut through the mandibular joint was photographed.

The right side of each hemisected head was utilized to study muscle fiber direction. Each hemisected head was photographed, cut surface down, using Kodak TRI-X pan 35 mm film. Some muscle fibers were removed from the temporalis and deep masseter to create more contrast which would give greater detail. The prints were processed by hand, allowing manipulating for finer detail. The prints were enlarged so that the distance from the superior point of the orbital surface of the malar process to the posterior surface of the occipital condyle was held constant in all animals. A line connecting these two points was used as a base line, and the mean fiber direction of the masseter and temporalis muscles was measured relative to this line. It was assumed that the neurocranium will remain constant in the several experimental situations; by using reference points that are substantially neurocranial to determine the mean fiber direction a change in direction of the muscles attaching to the face becomes more apparent.

CINEFLUOROGRAPHY

Introduction

The earlier studies of normal mandibular movements in the Rodentia were based on examination of the teeth, the morphology of the dried skull, or the muscles of mastication (Ryder 1878; Stark and Wehrli 1935; Becht 1954; Smith and Savage 1959; Fox 1965). In these studies, mandibular movements in the Rodentia were described as being propalinal, i.e., movement in the antero-posterior direction. Simpson (1936) advocated three terms to define mandibular movement: "orthal, produced by the mandible sweeping as a radius over a sector in the vertical plane with the glenoid articulation as the center; propalinal, in the antero-posterior direction produced by the backwards and forwards movement of the condyles on an elongated glenoid fossa; and ectental, a transverse movement produced by lateral movements of the condyle coupled with some circular swinging or orthal movement of the jaw." These are, however, idealized abstractions and mandibular movements must be a combination of two or three of the idealized types. For example, in man depression of the mandible is not a simple orthal movement. As the mandible is being depressed, an orthal movement, the condyle moves forward onto the articular eminence, a propalinal movement (Moss 1959).

The usual description of mandibular movements in the Rodentia has been propalinal. This is because an examination of the articulated skull and mandible demonstrate that when the molars are in occlusion, the mandibular incisors are well behind the maxillary incisors. Gnawing would necessitate an extreme forward movement of the mandible, which is a propalinal movement. Hiiemae (1966) suggests "predominantly propalinal" as a more appropriate term since the mandible must be depressed for the mouth to open and that is an orthal movement.

Cinephotography and radiography were first combined in an attempt to study mandibular movement in a living animal by Klatsky (1939) who examined mandibular movements in man. Cineradiography was employed for the study of mandibular movements in mammals other than man first by Ardran, Kemp, and Ride (1958) in their study "Mastication and swallowing in the domestic rabbit, Oryctolagus cuniculus". Hiiemae's (1966) study and together with Ardran (1968) were the first studies of mandibular movements in the rat using cinefluorography. In both these studies, Hiiemae reported that:

> "the chewing cycle in the rat as seen in lateral projection consists of three smoothly sequential movements. The first brings the mandible downwards and backwards from its anterior position where the first lower molar is in front of the upper, the second, upwards and backwards movement, brings the third lower molar behind the third upper molar so that the lower molars are moved posteriorly through a distance approximately equivalent to the length of the first molar. The third movement carries the mandible forwards in linear protraction so that the lower teeth are moved across the uppers. When the cycle is considered in relation to the grinding action, it is seen that the first two strokes form a continuum. The first is a 'recovery stroke' to bring the mandible downwards and backwards into position for the upward and backwards 'preparatory stroke'. The third grinding or 'power stroke' is the protrusive movement completing the cycle." (Hiiemae 1966, 1968)

These mandibular movements describe an inverted triangle (see fig. 1). For the purpose of this study, mandibular movements during chewing (grinding food between the molars) were divided into two phases: first, forwards, then down and backwards; second, upwards and backwards. The first phase will be referred to as "opening" and the second phase as "closing".

Results

Control animals

When the tracings of successive frames were superimposed the path of the chewing cycle became apparent. In the case of the control animals there was no observable variation; the path executed by M_1 (first mandibular molar) in a normal chewing cycle did not differ from the description given by Hiiemae (1966) and Hiiemae and Ardran (1968). Opening consisted of a forwards and downwards motion; closing consisted of a backwards and upwards motion (see figs. 2,3,4). It described an inverted triangle.

A more comprehensive account of mandibular movements necessitates a consideration of the mandibular molars as a unit and as an occlusal plane together with the change in angulation of its occlusal plane relative to the maxillary molars as a unit and to the maxillary occlusal plane. An elevation or depression of M_3 (third mandibular molar) relative to M_1 during the chewing cycle would result in a completely different position of the several ramal processes during the chewing cycle, regardless of the path described by M_1.

As the mandible moves forward just prior to depression, in the opening phase of the chewing cycle, M_3 is lowered relative to M_1. This results in the condylar, coronoid and angular processes moving downwards and forwards. At the same time, the mandibular incisors move forwards and upwards. As the opening phase proceeds, M_3 undergoes a small excursion relative to that of M_1, which causes the mandible to pivot. This results in the condyle moving upwards and forwards, the coronoid process moving forwards, upwards and then down, the angular process moving upwards and backwards, and the incisor moving down and backwards.

As the mandible begins to move through the closing phase of the chewing cycle, the mandible moves backwards and M_1 is elevated relative to M_3. This brings the condylar, coronoid and angular processes backwards and down. The mandibular incisors move upwards and backwards. The mandible is elevated obliquely backwards without pivoting until the mandible is about to occlude, at which point M_1 moves upwards relative to M_3. The condylar, coronoid, and angular processes move upwards and backwards; the mandibular incisors move upwards.

The complete cycle can be depicted by employing a diagram (see fig. 2). From the diagram it can be seen that the sequence of normal mandibular movements in chewing is as follows:

1) the mandible moves forward as the ramus is depressed,
2) the mandible pivots, the incisor moving down and the ramus moving up, while the mandible as a whole moves down and back,
3) the mandible moves backwards and upwards without pivoting,

4) the mandible pivots, the incisor moving upwards bringing M_1 to the same level as M_3, and the mandible moves forwards.

Incisor-removal animals

No notable variation in mandibular movements was observed among the four animals comprising this group. The path described by M_1 during the opening phase of chewing was similar in general direction to that of the control animals, the only exception being an exaggerated backwards movement (see figs. 5,6,7,8). M_1 moved forwards and upwards during the closing phase of chewing. Because M_3 did not change its position, it remained relatively stable throughout most of the chewing cycle. The movement was, for the most part, a hinge-like action. Whenever a backwards movement was observed during the closing phase of chewing, it was just before the mandible occluded.

During the closing phase of the chewing cycle, M_3 again remained relatively stable while M_1 executed an upwards swing. This caused the several ramal processes, coronoid, condylar, and angular, to move downwards. They moved upwards just prior to the forwards movement of the mandible when occluding.

Temporalis-removal animals

The five animals in this group exhibited two distinct patterns of mandibular movements. Three of the animals, numbers 1,4,5, showed mandibular movements identical to those of the control animals; two of the animals, numbers 2,3, showed mandibular movements that were similar to those in the incisor removal group except that the pivoting that the incisor-removal group had demonstrated during the closing phase of chewing was not seen (see figs. 9, 10, 11, 12, 13). The opening phase of chewing in temporalis-removals numbers 2 and 3 was identical to that seen in the controls and in the incisor-removal group. The closing phase of chewing involved a forwards and upwards movement of the molar ridge as a unit, with little change in angulation relative to the maxillary occlusal plane. A backwards movement of the mandible occurred just prior to occlusion. In summation, then, the closing phase of the chewing cycle involved the mandible maintaining an angulation relative to the maxillary occlusal plane that was similar to that of the control, but moving through a path similar to the incisor-removal animals.

Bilateral-condylectomized animals

No notable variation in mandibular movements was observed among the three animals comprising this group. The opening phase of the chewing cycle did not differ from that seen in the control animals. The closing phase of the chewing cycle was a series of forwards and upwards movements describing an arc. It was a hinge-like action with no perceptible backwards movement of the mandible, except just prior to occlusion (see figs. 14, 15, 16).

Discussion

The results from the data suggest that the process of modifying to the various experimental interferences effected changes in mandibular movements in most cases. There was no instance among any of the animals of a change in the opening phase of the chewing cycle, in that in all cases it involved a forwards and downwards and backwards movement of the mandible. In animals showing a hinge-like movement, the opening phase included an exaggerated backward movement. It was in the closing phase of the chewing cycle that two modes of change became apparent. In one group, including the control and the temporalis-removal animals numbers 1,4,5, the closing phase of the chewing cycle described and upwards and backward movement. In the second group, including temporalis-removal animals numbers 2,3, the incisor-removal animals, and the condylectomized animals, the closing phase of the chewing cycle described an upwards and forwards movement.

Axis of Rotation

An examination of the dried skull and mandible of the rat would show that when the incisors are occluded for gnawing, the molars are out of occlusion, the mandibular molars being anterior to the maxillary molars. Conversely, when the molars are in occlusion for chewing, the incisors are out of occlusion. Each situation resulted in the condyle being in a different position.

It was noted in this study that, in the control, the opening phase of the chewing cycle involved a forwards and downwards movement of the mandible with M_1 undergoing a greater translation than does M_3. The condyle is, therefore, moving forward as well as rotating. The axis of rotation, in the lateral view, for this phase of the chewing cycle would lie behind the molar row (see figs. 2,3,4) and may lie near the mandibular foramen. Moss (1959) has suggested that this is the case in man.

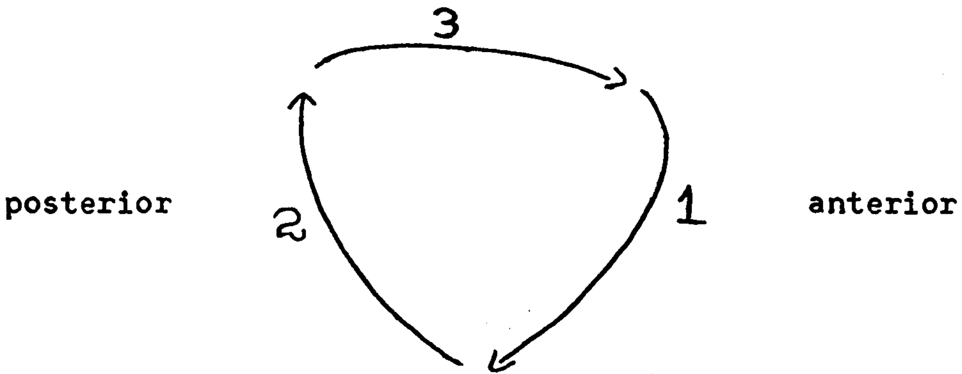
The closing phase of the chewing cycle involved a backwards and upwards movement of the mandible without a change in the angulation of the mandibular occlusal plane. It described a curved projectory: there was no rotation. This agrees with Hiiemae (1966): "a similar sequence of events is responsible for condylar movement during chewing. The recovery stroke is a combined translation and rotation on the posterior area of the fossa, the translation of the condyle backwards continues into the preparatory stroke. It is not accompanied by a rotation moving up in preparation of the simple translation of the power stroke."

The incisor-removal animals in this study demonstrated a rotation during the closing phase of the chewing cycle which suggests, in the lateral view, an axis of rotation near that in the opening phase of the chewing cycle. This presents a situation analogous to that found in man. It is noteworthy that a situation analogous to that in man occurred in the group which had undergone incisor removal, which produced an experimental shortening of the face, roughly analogous to the evolutionary shortening of the face in man (Jolly 1970).

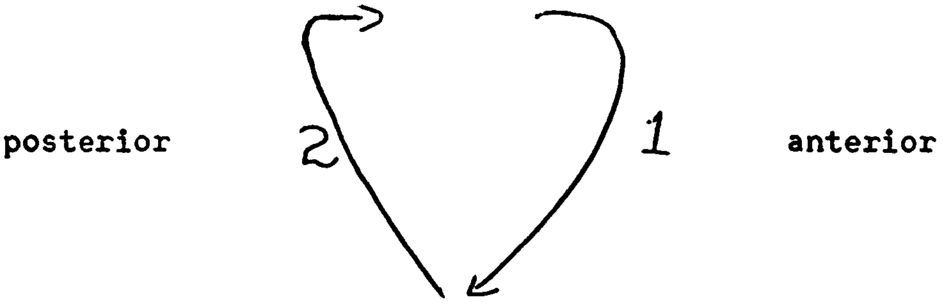
Since the mandible moves in three planes, a comprehensive study of the axis of rotation of the mandible would necessitate cinefluorography undertaken in three planes (see Huson 1961, for a similar approach applied to the ankle joint: to my knowledge no study of this kind has been undertaken on the jaw). Any study not taking the tridimensionality of mandibular movements into account must be incomplete. Since this study utilized cinefluorography in the lateral view only, no attempt was made to determine precise axes of rotation.

Fig. 1

A diagramatic representation of the chewing cycle in the rat. The line represents the path executed by the first mandibular molar.



After Hiiemae



For this study

Fig. 2

Positions of the mandible during several stages of the chewing cycle in Control animal number 1. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

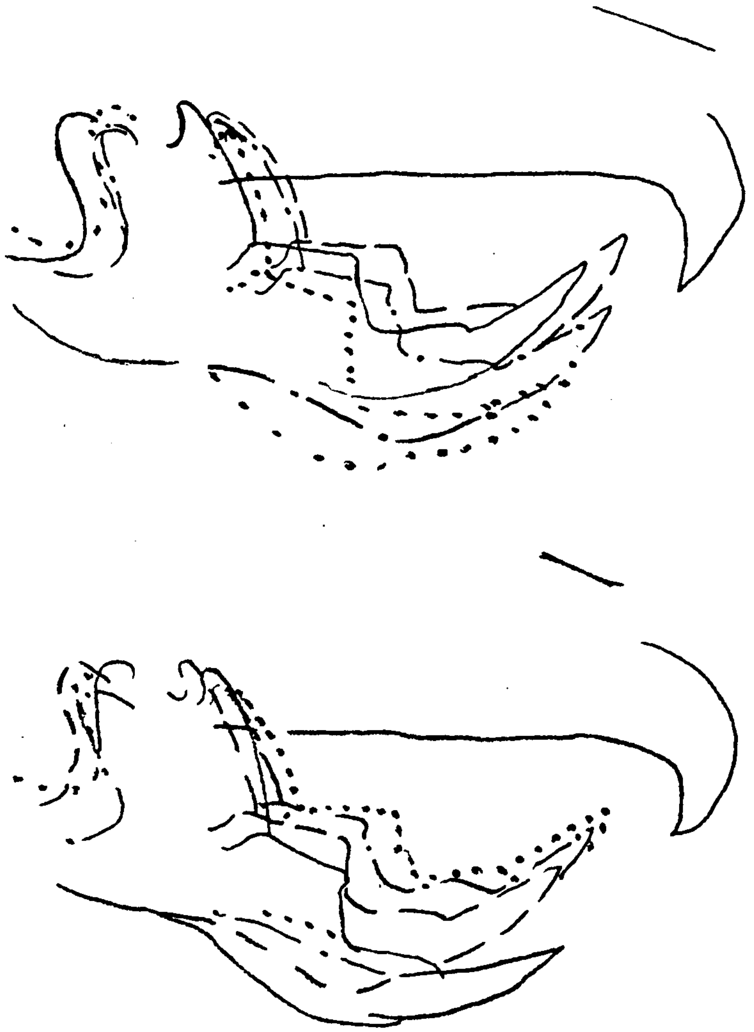


Fig. 2

Fig. 3

Positions of the mandible during several stages of the chewing cycle in Control animal number 2. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

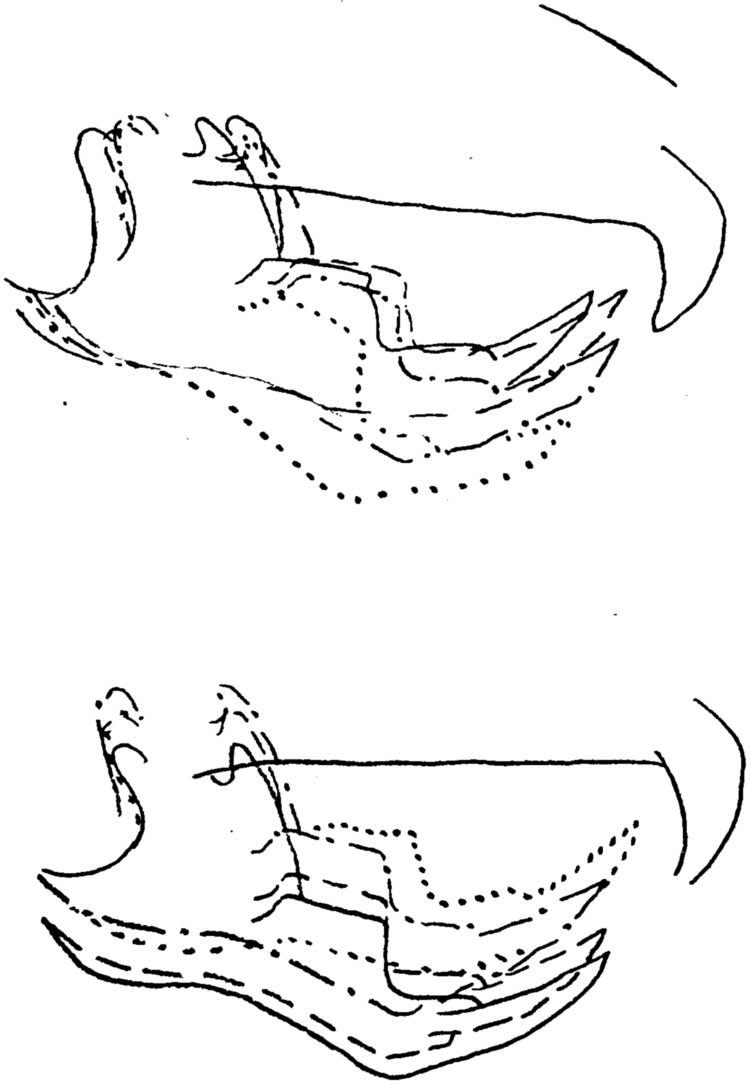


Fig. 3

Fig. 4

Positions of the mandible during several stages of the chewing cycle in Control animal number 3. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

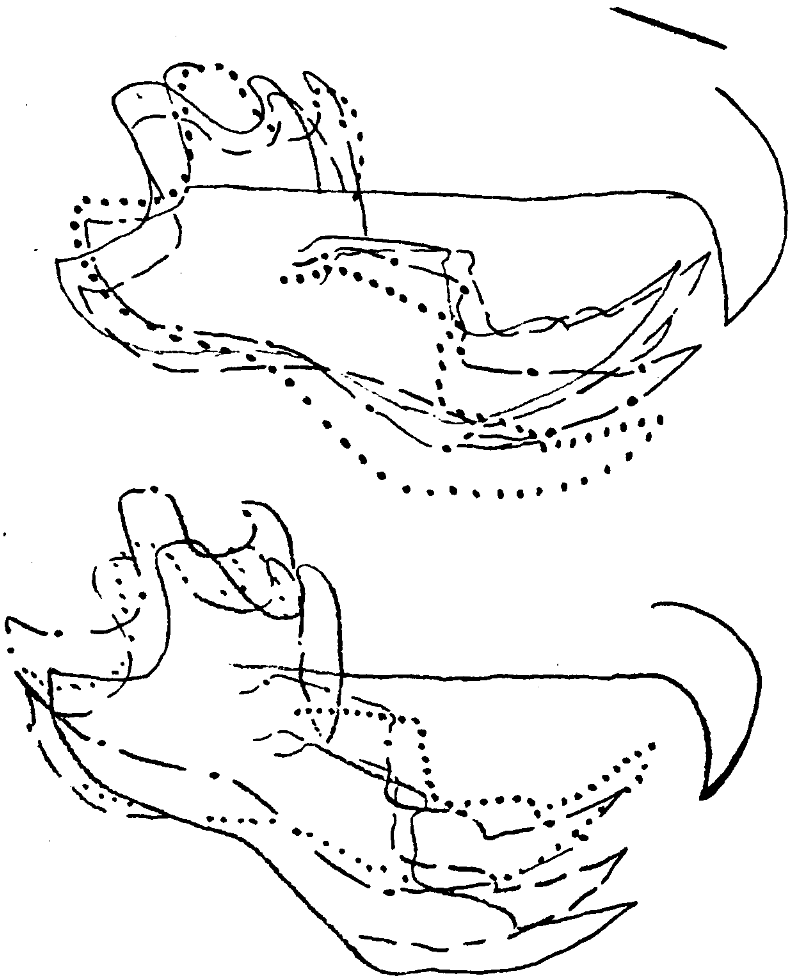


Fig. 4

Fig. 5

Positions of the mandible during several stages of the chewing cycle in Incisor-removal animal 1. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

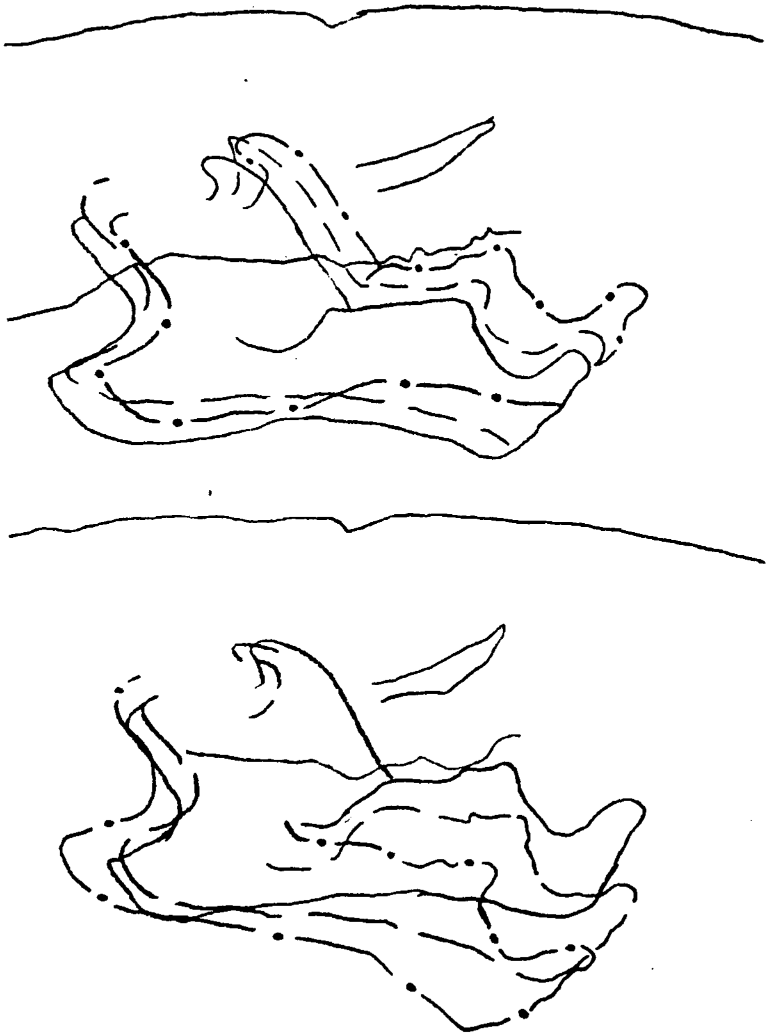


Fig. 5

Fig. 6

Positions of the mandible during several stages of the chewing cycle in Incisor-removal animal 2. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

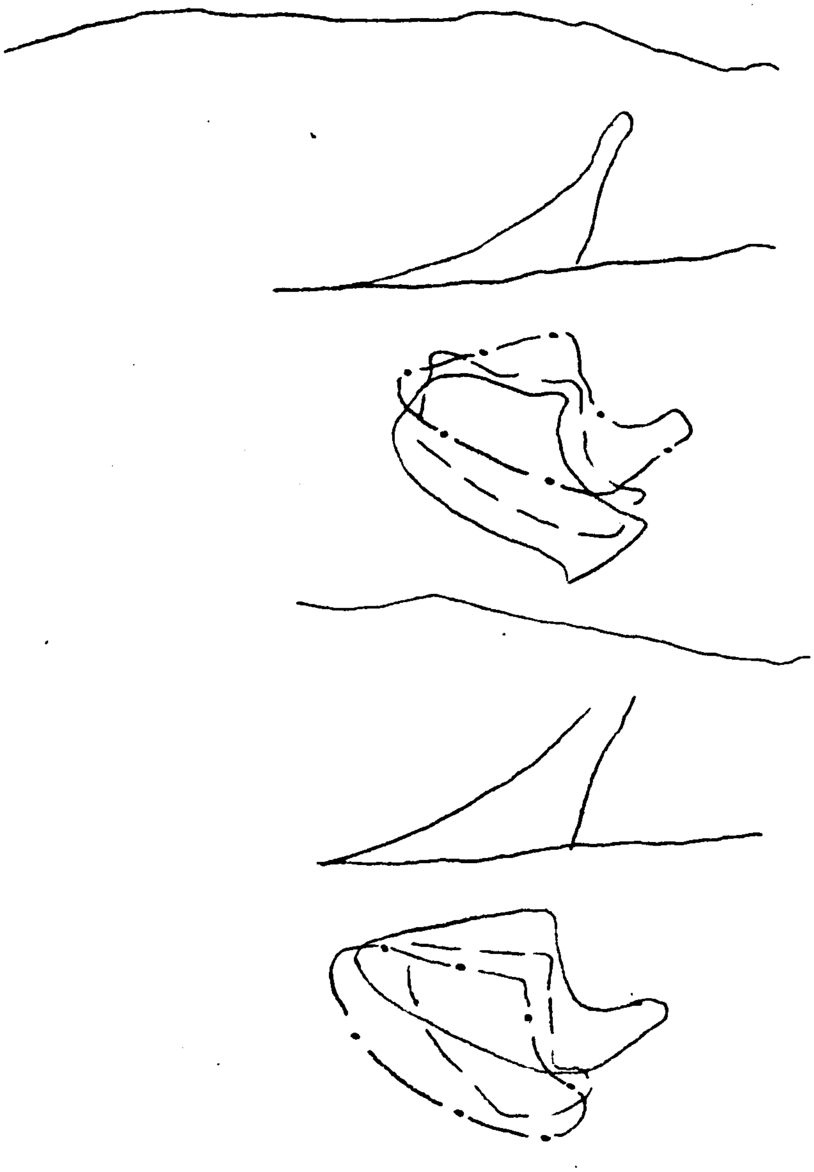


Fig. 6

Fig. 7

Positions of the mandible during several stages of the chewing cycle in Incisor-removal animal 3. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

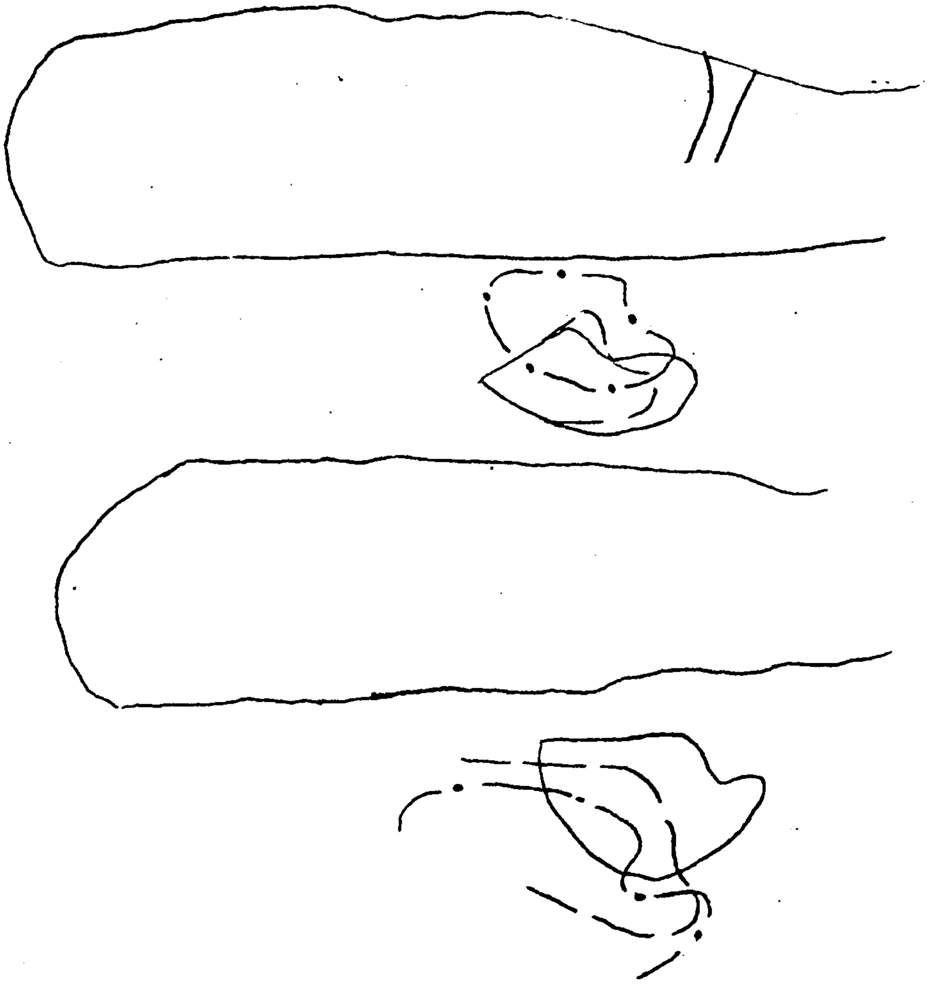


Fig. 7

Fig. 8

Positions of the mandible during several stages of the chewing cycle in Incisor-removal animal 4. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

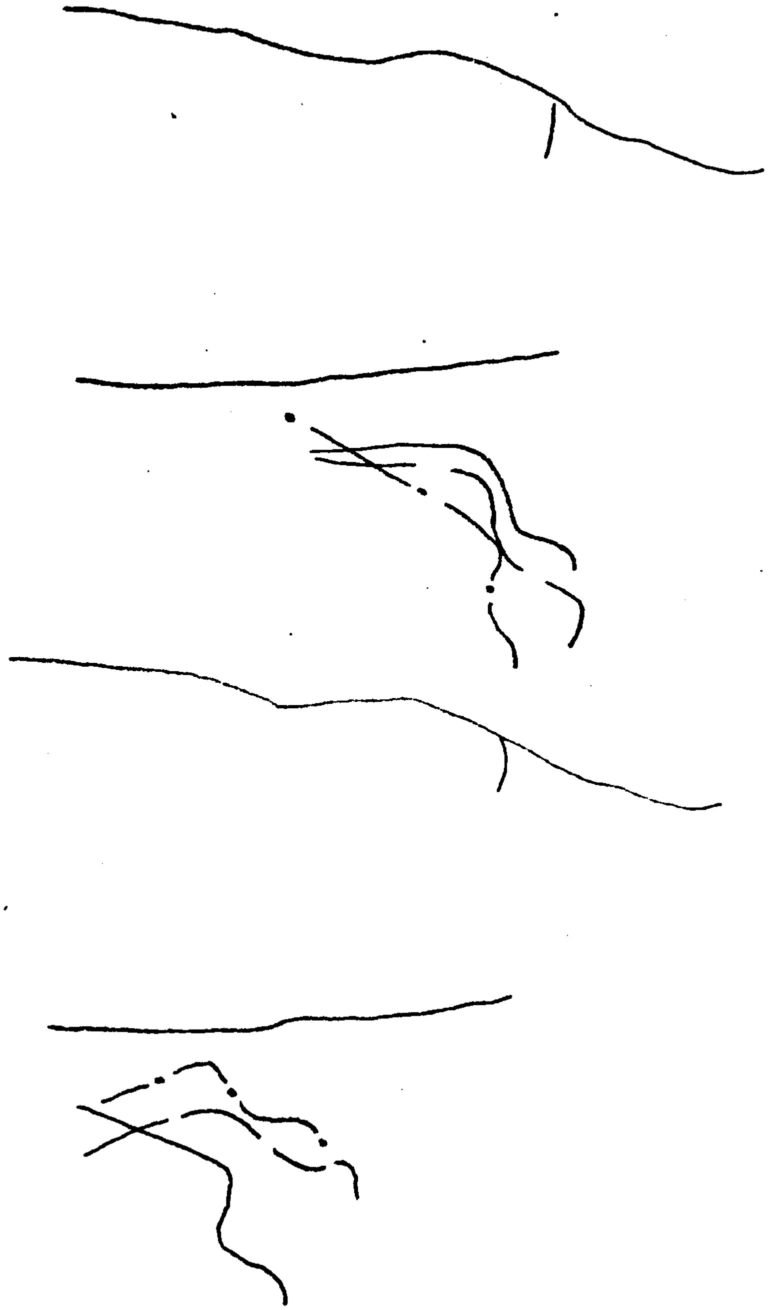


Fig. 8

Fig. 9

Positions of the mandible during several stages of the chewing cycle in Temporalis-removal animal 1. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

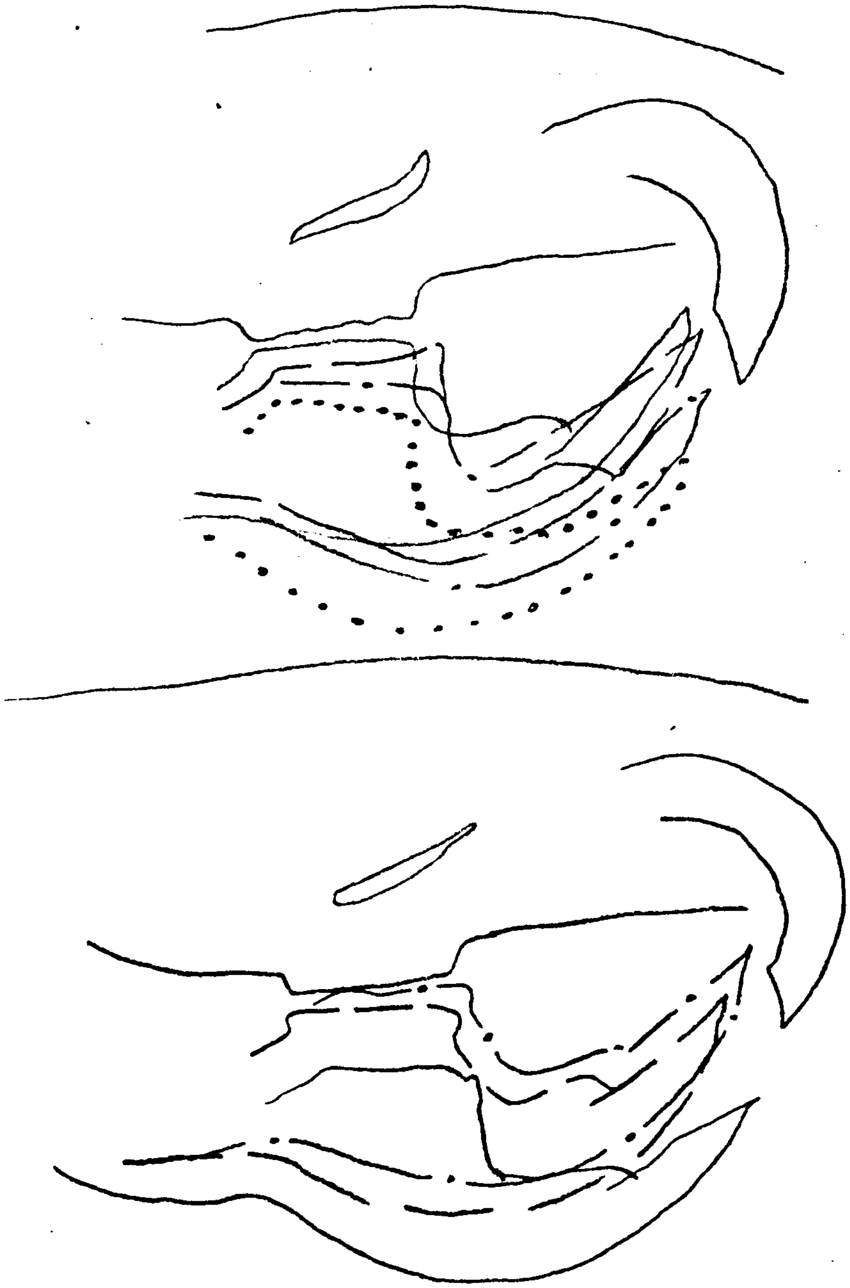


Fig. 9

Fig. 10

Positions of the mandible during several stages of the chewing cycle in Temporalis-removal animal 2. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

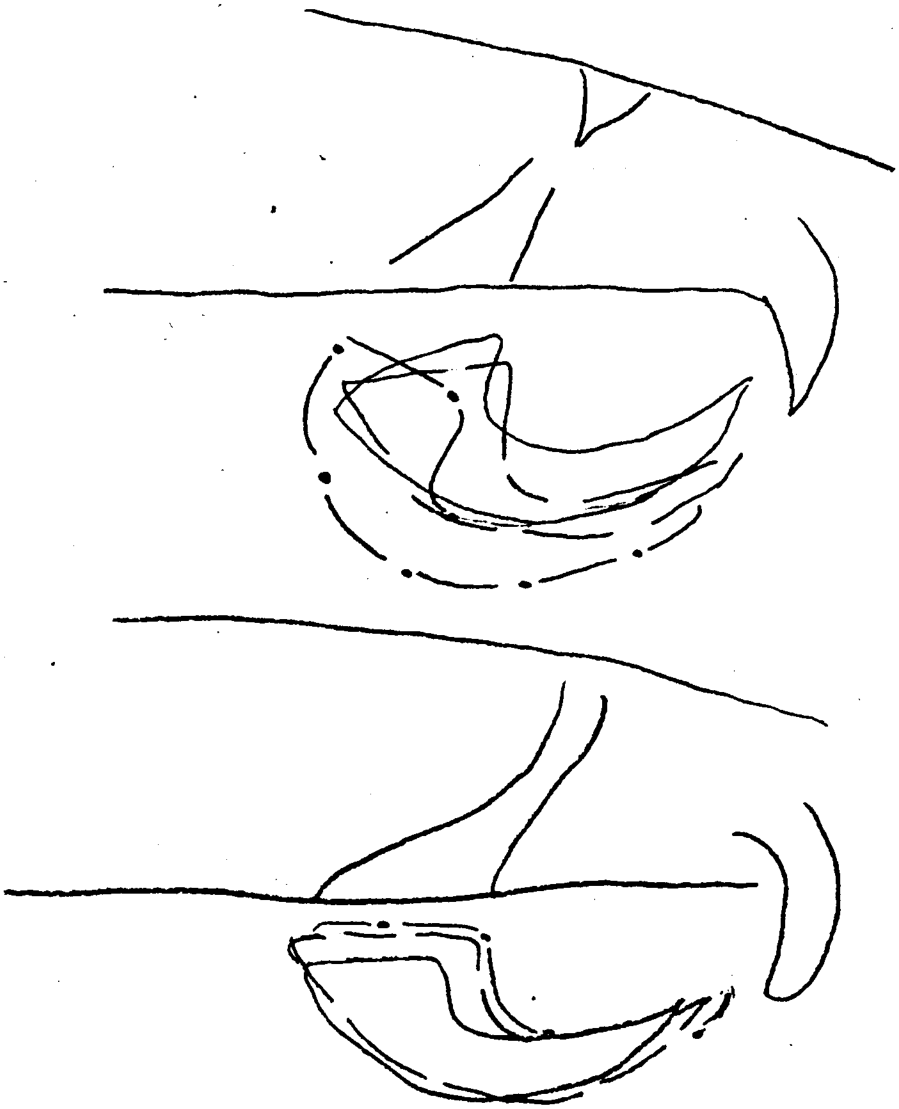


Fig. 10

Fig. 11

Positions of the mandible during several stages of the chewing cycle in Temporalis-removal animal 3. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

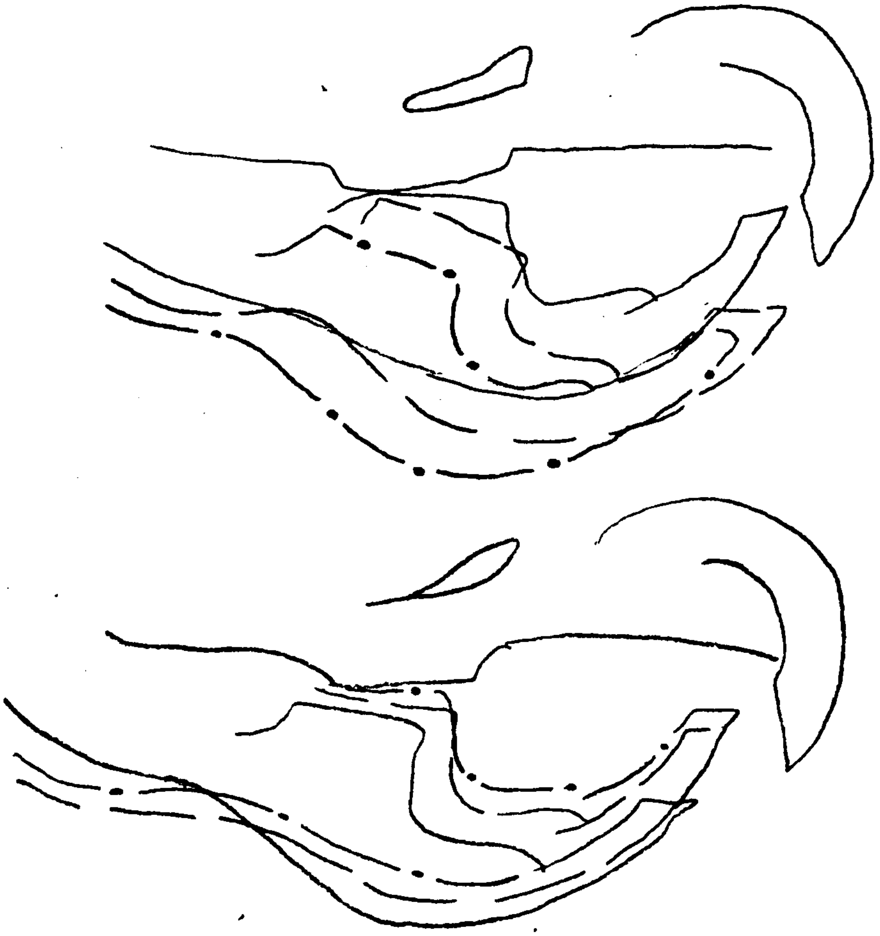


Fig. 11

Fig. 12

Positions of the mandible during several stages of the chewing cycle in Temporalis-removal animal 4. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

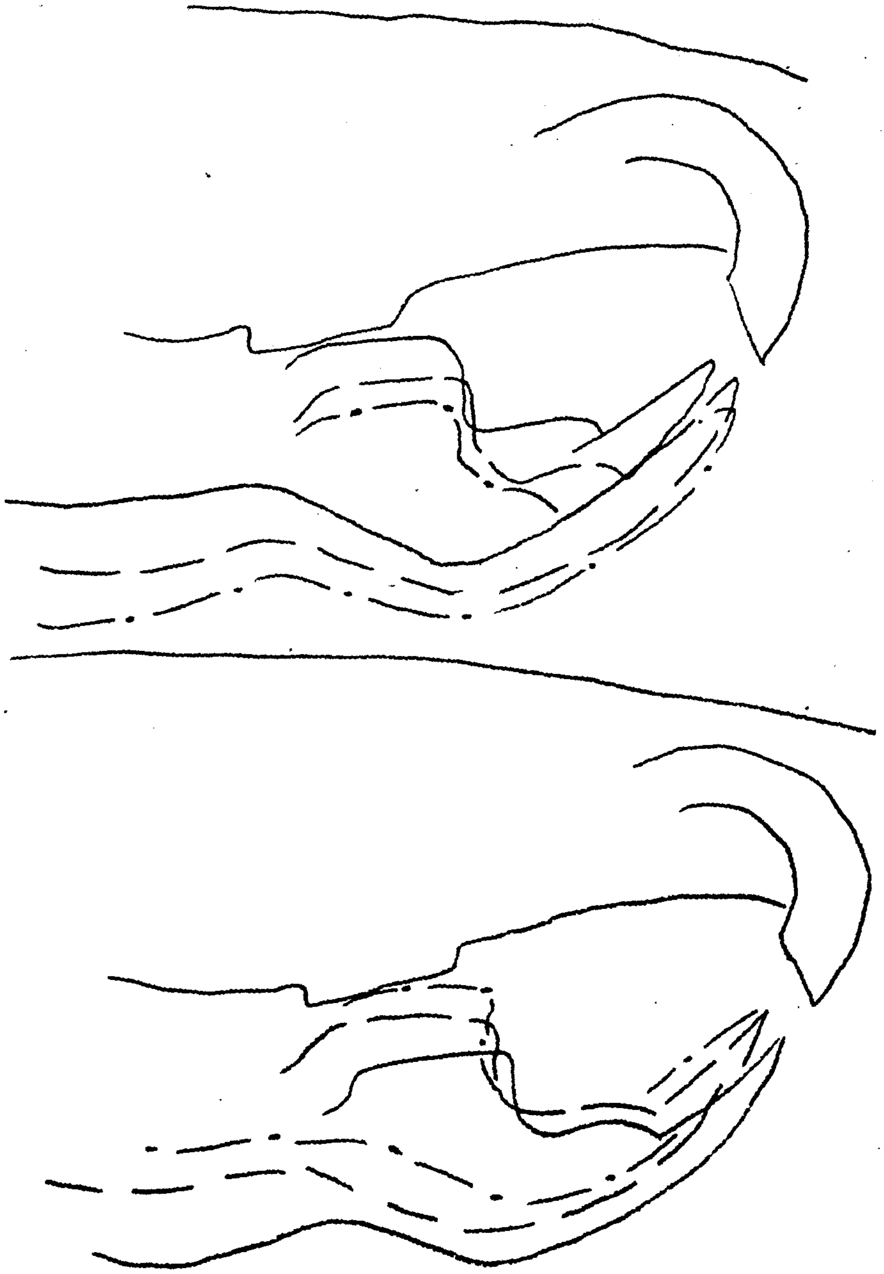


Fig. 12

Fig. 13

Positions of the mandible during several stages of the chewing cycle in Temporalis-removal animal 5. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

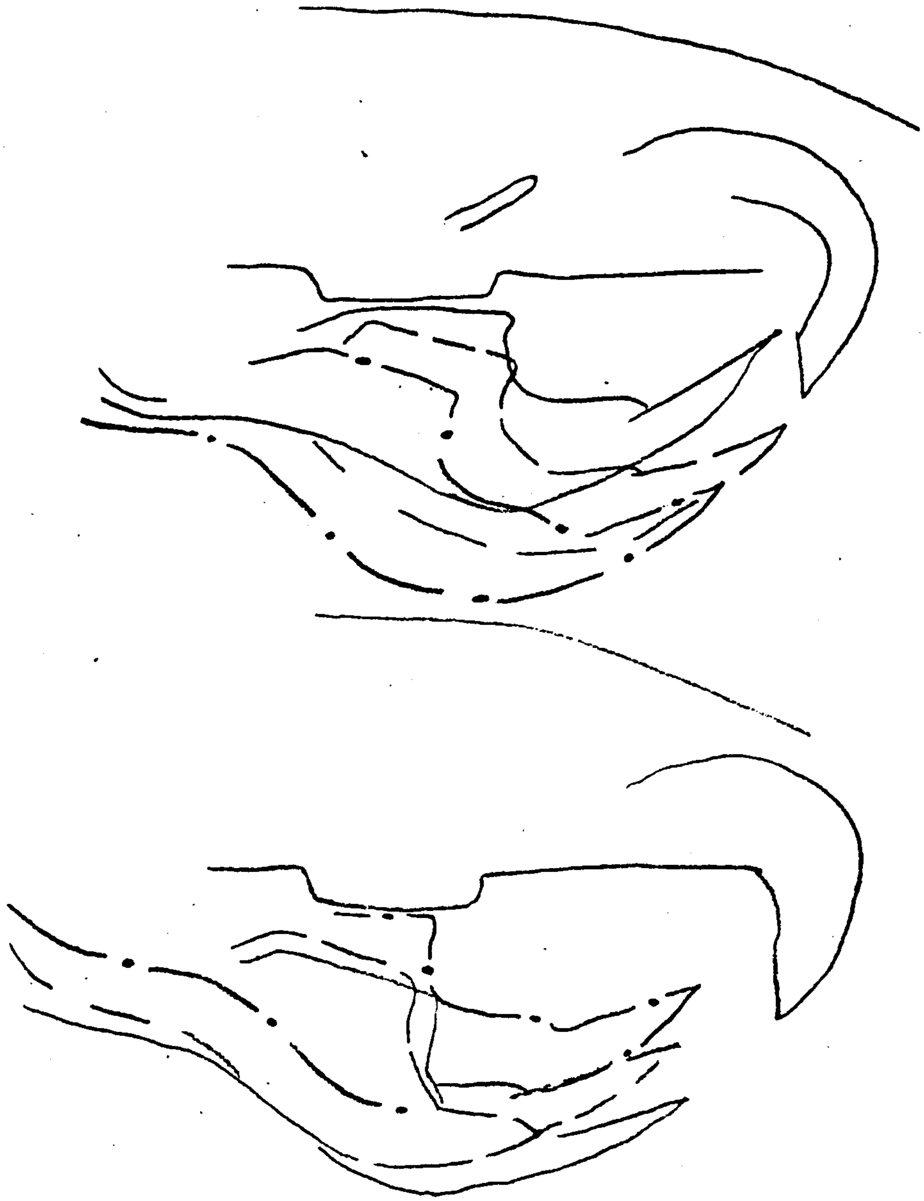


Fig. 13

Fig. 14

Positions of the mandible during several stages of the chewing cycle in Condylectomized animal 1. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

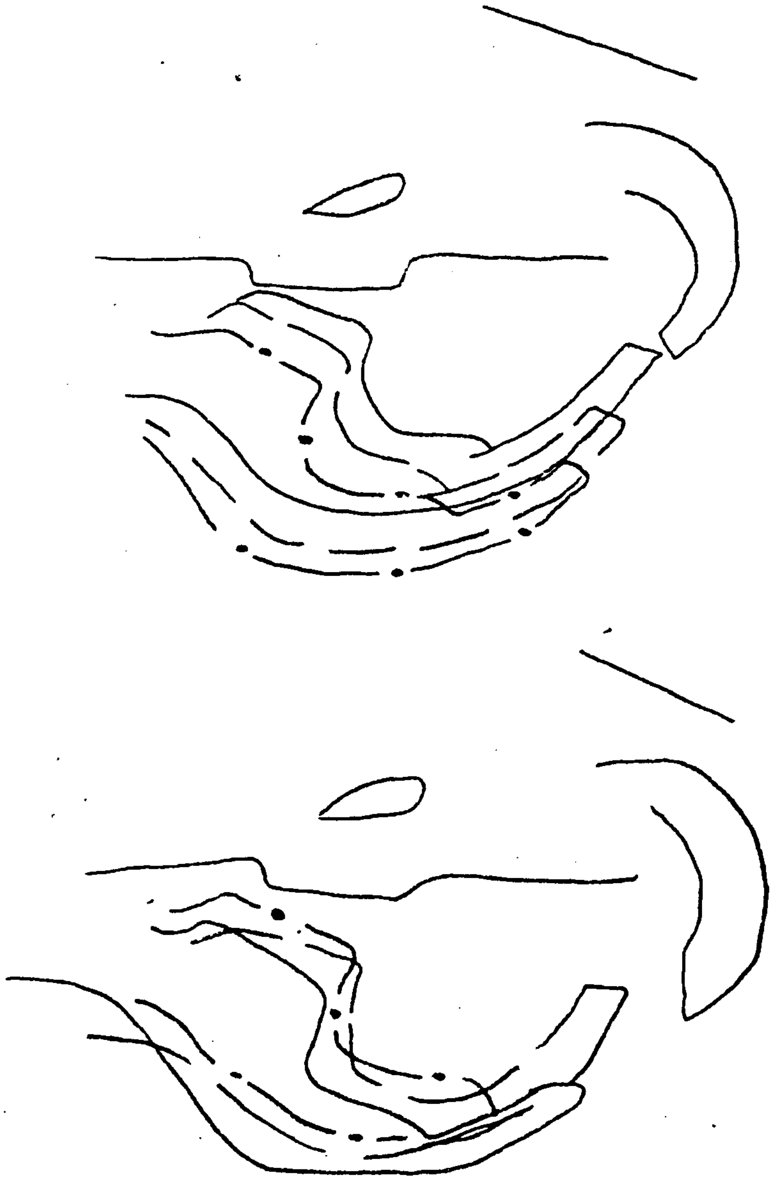


Fig. 14

Fig. 15

Positions of the mandible during several stages of the chewing cycle in Condylectomized animal 2. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

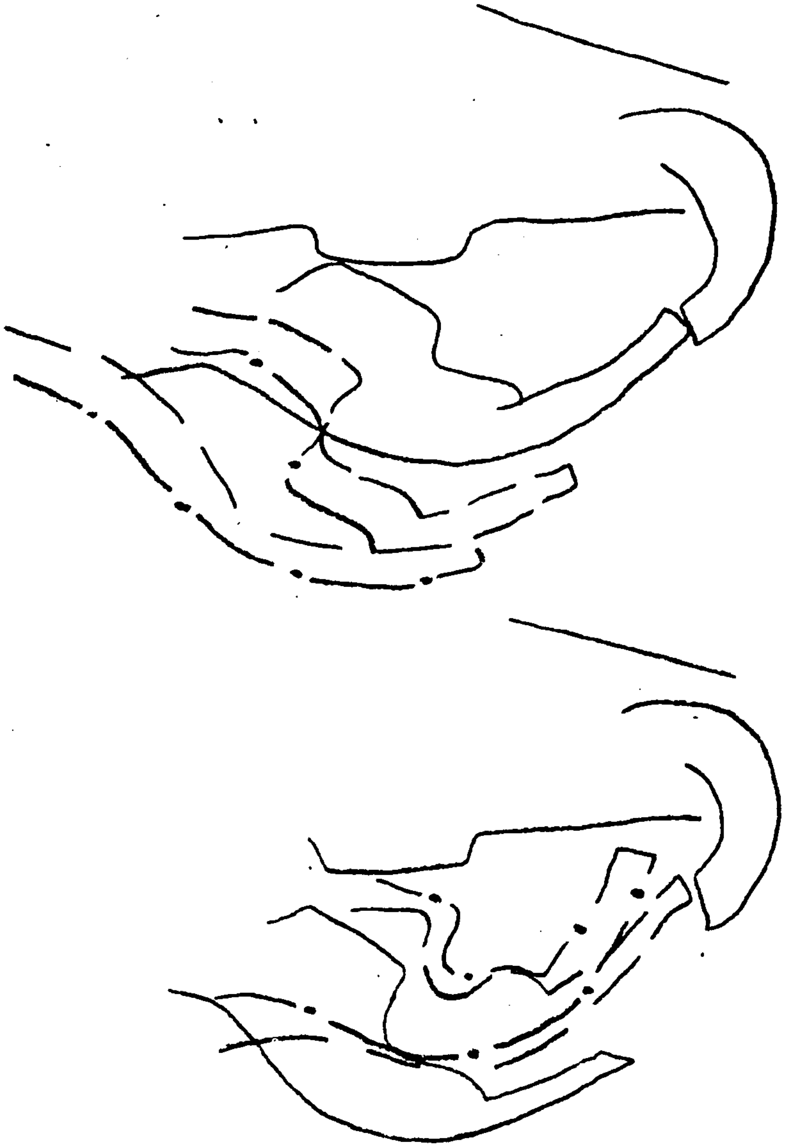


Fig. 15

Fig. 16

Positions of the mandible during several stages of the chewing cycle in Condylectomized animal 3. The unbroken line represents position 1, the broken line position 2, alternating dots and dashes position 3, and the dotted line position 4.

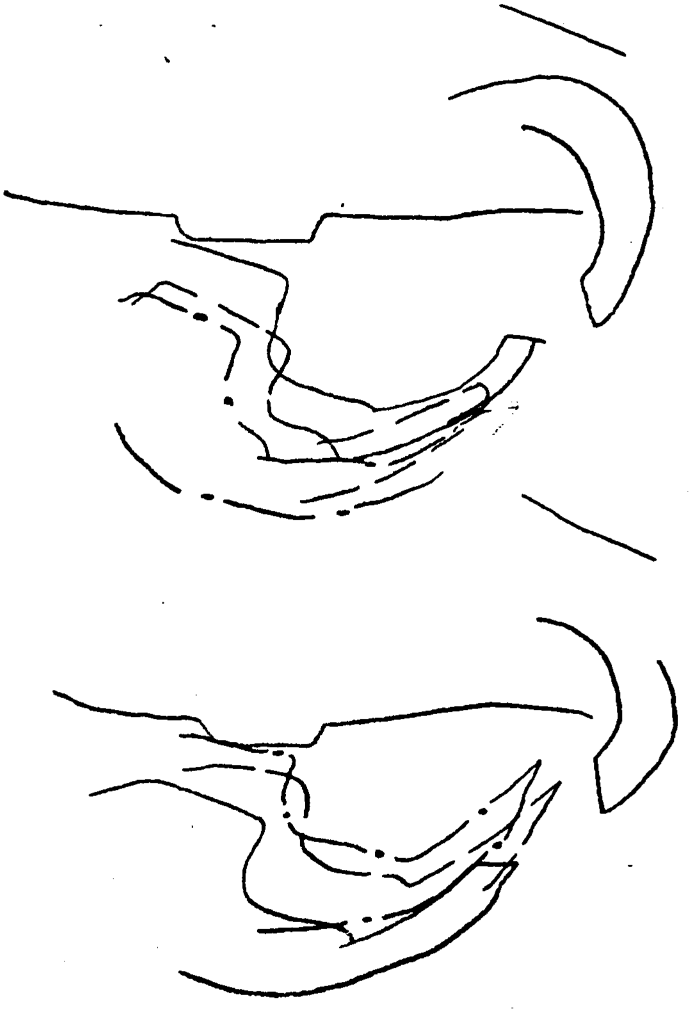


Fig. 16

HISTOLOGY

Introduction

Several aspects of the development of the mandibular joint morphology, as well as the modifications seen among the various orders of mammals, suggest a close correlation between the morphology of the joint and the functioning of the facial complex in mastication (Lindblom 1960). The articular eminence does not exist at birth, in man, but develops gradually during the suckling stage. The fossa is shallow at birth, gradually deepening during growth (Angel 1948; Lindblom 1960; Moffett 1957; Symons 1952; Biegert 1956; Sarnat 1964).

An examination of the histology of the mandibular (squamoso-dental in the rat) joint of the several groups of rats used in this study was undertaken because a close correlation between the morphology of the mandibular joint and the functioning facial complex implies that a change in the form-function complex produced by experimental interference could cause an alteration in the morphology of the mandibular joint. Such physiological adaptations might reflect the forces and movements at the mandibular joint in each experimental situation, and a comparison of the histology of the mandibular joint in the several experimental groups would demonstrate adaptations to changes in forces at the mandibular joint.

Review of the literature

The mandibular joint is a diathrosis; it is a complex joint because an articular disc is interposed between the cranial and mandibular articular cartilage, dividing the synovial capsule into separate upper and lower compartments (Cunningham 1943; Sarnat 1964). In synovial joints, the bones forming the articulation are covered by articular cartilage, typically being hyaline cartilage (Ham 1969). The mandibular and sterno-clavicular joints in man are exceptions to this in that "the articulating surfaces of the bones are not covered by hyaline cartilage but by an avascular fibrous tissue which may contain a variable number of cartilage cells and then can be designated as fibrocartilage" (Sarnat 1964). Moss (1959) suggests that the fibrous covering in the mandibular joint is due to the forces of shear:

> "Cartilage is an excellent material for the articulating surfaces of a joint because, in addition to the intrinsic smoothness of its surface, this tissue is greatly resistant to the forces of compression. On the other hand, cartilage is not very resistant to the forces of shear. The temporomandibular joint, it must be remembered, is not just a single joint, but in function really two coupled joints, a left and a right joint which must work in unison. In the lateral movements of the mandible from one side to another, there must invariably be considerable components of shear imposed on the joint surfaces. Fibrous connective tissue is particularly well-suited to withstand exactly this type of force."

Bock and Morioka (1971) reported the presence of fibrocartilagenous pads on the articular surfaces of an ectethmoid-mandibular articulation in two Meliphagidae (Aves). The authors stated that "because of the position and shape of the articular surface, the probable direction of the compressive force on the brace, and the lack of sliding movement of the two articular surfaces on each other, it seems reasonable to suggest that the articular cartilages of this joint experience little shearing stress."

Since the functional significance of the presence of fibrous connective tissue or fibrocartilage in the mandibular joint is as yet uncertain, the presence of the fibrous tissue is referred to, in this study, only as a distinguishing morphological feature.

The most comprehensive description of the development and morphology of the mandibular joint in the rat was given by Hiiemae (1966). Prior to Hiiemae's thesis, the only detailed description of the histology of the mandibular joint in the adult rat was that of Cabrini and Erausquin (1941). Other papers have considered the morphogenesis of the tissues of the joint (Collins *et al* 1946; Cunat *et al* 1956; Levy 1948).

For a detailed account of the histology of the mandibular joint for the normal adult rat, the reader is referred to Hiiemae (1966) and Cabrini and Erausquin (1941). A description of only those aspects of mandibular joint histology pertinent to this study will be undertaken here.

Results

Normal Mandibular Joint Histology (from the literature and from the results of the control animals in this study) - See figs. 17, 18, 19.

Glenoid Fossa

In the rat the glenoid fossa is on the squamosal bone (Cabrini and Erausquin 1941; Hiiemae 1966). The fossa is described as a canal with the long axis directed anteroposteriorly (Cabrini and Erausquin 1941). The fossa is divided into anterior and posterior compartments by a convex eminence that is continuous with the zygomatic arch (Collins *et al* 1946). The condyle articulates with the anterior compartment when the incisors are in occlusion; the condyle articulates with the posterior compartment when the molars are in occlusion.

The squamosal bone is composed of an inner and an outer table, separated by a marrow cavity. Hiiemae (1966) states that the marrow cavity decreases with age. The control rats in this study exhibited islands of cartilage rest among the bony trabeculae of the marrow cavity. This is typical of young bone (Ham 1969).

The bone of the squamosal is covered by a fibrous connective tissue. Hiiemae (1966) referred to this layer as fibrocartilage; however, in this sample, no lacunae of cartilage cells were discerned. The layer of fibrous connective tissue is in intimate contact with the squamosal and Cabrini and Erausquin (1941) traced collagen fibers from the squamosal into the fibrous layer. It was noted that, in the sample used in this study, the fibrous layer adhering to the squamosal bone is thicker posteriorly.

Anterior to the bone, the fibrous layer thickens and continues anteriorly as an "aponeurotic vault" (Cabrini and Erausquin 1941). It has no bony support. It is suggested that the condyle articulates with this extension of the glenoid fossa when the animal is sharpening the lower incisors. This activity was observed in an adult rat and recorded on cinefluorographic film as a part of this study.

The lower incisors are sharpened by bringing them anterior to and against the upper incisors which move against the lingual surface of the lower incisors. Such a protrusion of the mandible would bring the condyle to lie against the "aponeurotic vault."

The Condyle

The condyle has its long axis running antero-posteriorly and Collins et al (1946) and Cabrini and Erausquin (1941) state that the length of the condyle is approximately twice its width. Whereas there is a layer of fibrous connective tissue in intimate contact with the squamosal bone; a layer of fibrous connective tissue, identical to that found on the squamosal bone, caps a layer of hyaline cartilage which is continuous with the bone of the condyle. The innermost layer of hyaline cartilage is hypertrophic.

The Meniscus

The meniscus is composed of the same fibrous connective tissue which covers the roof of the glenoid fossa and the condyle. Both the superior and inferior surfaces are articular surfaces; the inferior surface is concave, conforming to the shape of the condyle, and the superior surface is convex to fit the glenoid fossa (Cabrini and Erausquin 1941; Hiiemae 1966). The disc is thicker at its ends where it is continuous posteriorly with the fibrous layer covering the squamosal and anteriorly with the "aponeurotic vault," forming the upper compartment of the mandibular joint. Inferiorly, it is thicker where it joins the fibrous layer covering the condyle, forming the lower compartment of the mandibular joint. It is thinner and avascular in the center. It can be assumed that this is caused by compression as the condyle is moved against the roof of the glenoid fossa.

<u>Incisor-removal animals</u> - See figs. 20, 21, 22, 23.

All four animals demonstrated similar changes in the histology of the mandibular joint.

The squamosal bone had no islands of cartilage rest as seen in the control animals. The bone had the appearance of old bone when compared to the control. There was just a very thin layer of fibrous connective tissue covering the squamosal bone. The aponeurotic vault was not always present.

The bone of the condyle was narrow. There was a very thin cap of hyaline cartilage, covered by a thin layer of fibrous connective tissue.

The meniscus was generally thin throughout its length, thicker at the ends.

<u>Temporalis-removal animals</u> - See figs. 24, 25, 26, 27, 28.

The five animals in this group can be divided into two groups based on similarity in histology of the mandibular joint: numbers 1, 4, and 5 form one group, and numbers 2 and 3 form the second group.

The squamosal bone of the animals in the first group (numbers 1, 4, and 5) maintained an oval shape and had islands of cartilage rest. There was a thicker lining of connective tissue covering the squamosal bone and, in each case, the buildup was most prominent on the anterior aspect of the squamosal, forming an articular eminence. The condyle and meniscus were normal.

The squamosal bone of the animals in the second group (numbers 2 and 3) was reduced to a small oval. Animal number 2 exhibited a strip of cartilage that was continuous from the superior to the inferior border. There was an extreme buildup of connective tissue covering the squamosal bone. The meniscus was thick throughout its length. The condyle appeared normal.

Condylectomized animals - See figs. 29, 30, 31.

The three animals comprising this group demonstrated similar changes in histology. The squamosal bone exhibited areas of cartilage rest. The bone was reduced in size and there was a buildup of connective tissue. The joint cavity was filled with connective tissue. The remnants of the meniscus showed extreme thickening.

Discussion

Similarity of histologic changes suggest that the animals could be grouped according to histologic changes instead to according to the specific experiment performed. Three groups became apparent. The criteria used were the thickness of the central area of the meniscus, and the distribution of the buildup of connective tissue on the squamosal bone. The choice of the thickness of the central area of the meniscus as a criterion was justified by the fact that the thin, avascular central area is the result of compressive forces produced when the condyle is against the roof of the glenoid fossa, the meniscus intervening between the two. The distribution of the buildup of connective tissue on the squamosal bone would indicate direction of forces.

The animals exhibiting a meniscus with a thin central area included the controls and numbers 1, 4, and 5 of the temporalis-removal group. It was these three animals of the temporalis-removal group which demonstrated normal mandibular movements in the chewing cycle. Temporalis-removal animals 1, 4, and 5 showed a buildup of connective tissue on the anterior part of the squamosal bone. This suggests that a coordination between the temporalis and masseter muscles during the power stroke was disrupted so that the vector of forces at the condyle (and teeth) was more anterior than it would otherwise have been.

The animals exhibiting a meniscus with a thick central area were numbers 2 and 3 of the temporalis-removal group and the entire condylectomized group. These animals demonstrated a hinge-like action during the closing phase of the chewing cycle.

Since the mandible in these animals did not move posteriorly during the closing phase of chewing, I have suggested that the posterior movement of the mandible, necessary to bring the mandibular molars behind the maxillary molars prior to the power stroke, was effected by the suprehyoid muscles during the opening phase of the chewing cycle. The backward component of the downward and backward movement comprising the opening phase of the chewing cycle was exaggerated. Among these animals the connective tissue on the squamosal bone was more or less evenly distributed; whereas, among the control animals the posterior component of the glenoid fossa had a thicker covering of connective tissue. Together with a thickened central area of the meniscus, the uniformly thick fibrous connective tissue suggests that there were no appreciable forces against the meniscus and glenoid fossa, in these two groups of experimental animals.

With reference to the condylectomized animals, removal of the condyle changed the morphology of the joint but not its ability to function as a joint. "The words 'articulation' (articulare - to connect) and 'joint' (jungere - to join) are used synonymously to refer to those structural arrangements that exist to connect two or more bones together at their site of meeting" (Ham 1969). In each of the condylectomized animals, connective tissue was found to be continuous between the mandible and the glenoid fossa. Therefore, there was a functioning articulation. A diarthrosis is only one of the several possible articular types found in jaws (Bock 1960, 1970); and, "the permitting of movement is not essential for a connecting structure to be termed a joint; indeed some joints become as solid as the bones they connect" (Ham 1969). It is not to be construed that, in this study, the joint was removed: only the mandibular condyle was removed.

Studies dealing with experimental condylectomy were concerned with the regenerative power of the condylar process (Das _et al_ 1965; Jarabak and Vehe 1952; Jolly 1961; Poswillo 1972) or the effect of condylectomy on occlusion patterns (Sarnat 1964). A regenerated duplicate condyle was not observed in the experimental studies; but rather, a growth of bone was observed which provided a functioning knob.

Poswillo (1972) reported an excessive growth of a bony knob producing a protrusion of the mandible.

The third group is composed of the animals which had undergone incisor removal. The histologic reaction among the animals of this group was a degenerative one. The bone had the appearance of belonging to a much older animal.

The groups demonstrated a relationship between forces due to mandibular movements and the resulting histology of the mandibular joint. The plasticity of the tissues of the mandibular joint, allowing an adaptation to changes in external forces upon them warrents a discussion of the possible role of the condylar cartilage in mandibular growth (For a review of the literature, see Koski 1968, and Moss 1964, 1971). Hiiemae (1966) concluded that: "it is largely the progressive growth and transformation of the condylar cartilage that is responsible for the development and maturation of the mandibular joint." The conclusion that the condylar cartilage is a growth center is based on the early work done in _in vivo_ staining or metallic implants which invariably showed an increase in the bone laid down by the condylar cartilage. The authors supporting the view that the growth and transformation of cartilage is controlled intrinsically depict the cartilage as a "Samson at the pillars" pushing apart the roof of the glenoid fossa and the neck of the condyle, thereby causing the mandible to move obliquely downwards (See Brodie _in_: Sarnat ed., The Temporomandibular Joint, 1964).

Opposed to this concept, Moss (1964, 1971) considers the role of the mandibular cartilage as compensatory in nature. As the mandible is carried down and forwards by the growing functional matrix (Moss's term), bone deposition occurs at the condylar cartilage to maintain the integrity of the mandibular joint. The works of Koski (1963, 1964, 1965) and Rönning (1966) on transplanted mandibular condyles support Moss's view. "The results showed that the growth cartilage of the mandibular condyle apparently lacks the kind of independent growth potential possessed by the epiphyseal cartilages of long bones" (Koski and Mäkinen 1963).

On a histologic level, there are significant differences between epiphyseal cartilage and condylar cartilage, a fact which lends further support to Moss's and Koski's view. Proliferation of cartilage in an epiphyseal growth plate is achieved by interstitial growth in the first zone of the growth plate. Condylar cartilage is not capped by bone, as is epiphyseal cartilage but by fibrous connective tissue, the innermost layer of which deposits new layers of cartilage. Therefore, growth of the mandibular cartilage is by appositional growth. The cartilage cells in an epiphyseal growth plate form regular straight lines continuous through the four zones of the cartilage. There are no regular straight lines of cartilage cells in the condylar cartilage (Sarnat 1964).

On the basis of her experimental studies, Hiiemae (1971) concluded that the mandibular articulation was not loaded in compression during incising. In the incisor removal group the compression forces at the mandibular articulation would presumably be reduced below that found in the normal rat.

Reduction in the thickness of the condylar cartilage in this experiment provides support for Moss's and Koski's view that external forces (in my view, compression forces) are necessary for the normal maturation of the mandibular condylar cartilage in the rat.

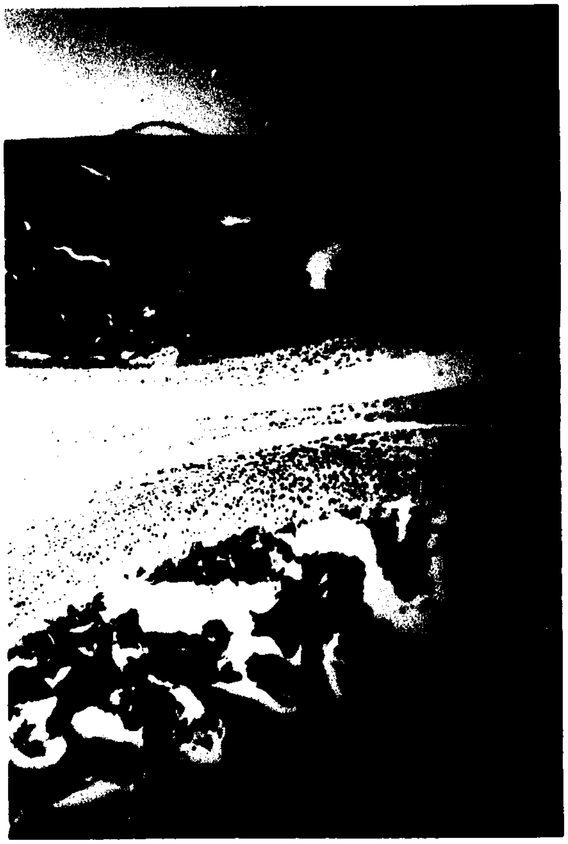


Fig. 17

Mid-sagittal section through the mandibular joint of Control animal 1.

Fig. 18

Mid-sagittal section through the mandibular joint of Control animal 2.

Fig. 19

Mid-sagittal section through the mandibular joint of Control animal 3.

Fig. 20

Mid-sagittal section through the mandibular joint of Incisor-removal animal 1.

Fig. 21

Mid-sagittal section through the mandibular joint of Incisor-removal animal 2.

Fig. 22

Mid-sagittal section through the mandibular joint of Incisor-removal animal 3.

Fig. 23

Mid-sagittal section through the mandibular joint of Incisor-removal animal 4.

Fig. 24

Mid-sagittal section through the mandibular joint of Temporalis-removal animal 1.

Fig. 25

Mid-sagittal section through the mandibular joint of Temporalis-removal animal 2.

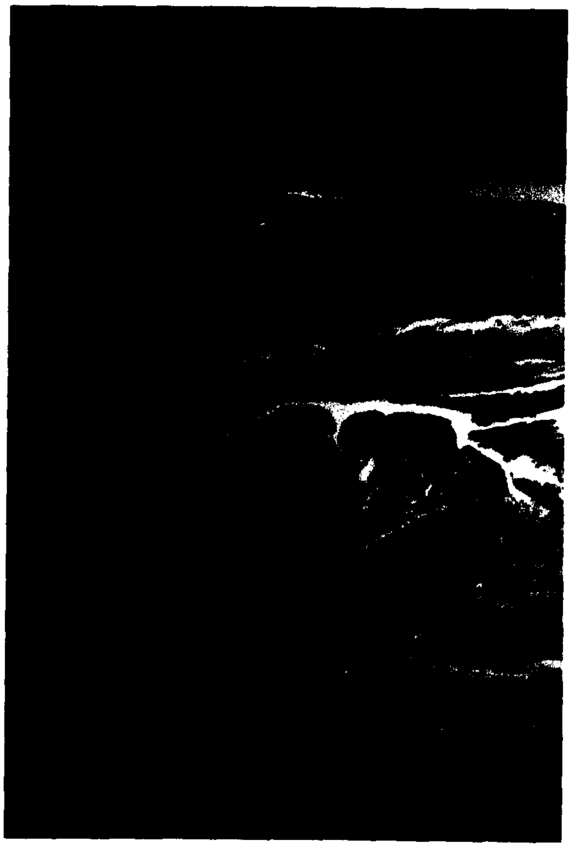


Fig. 26

Mid-sagittal section through the mandibular joint of Temporalis-removal animal 3.

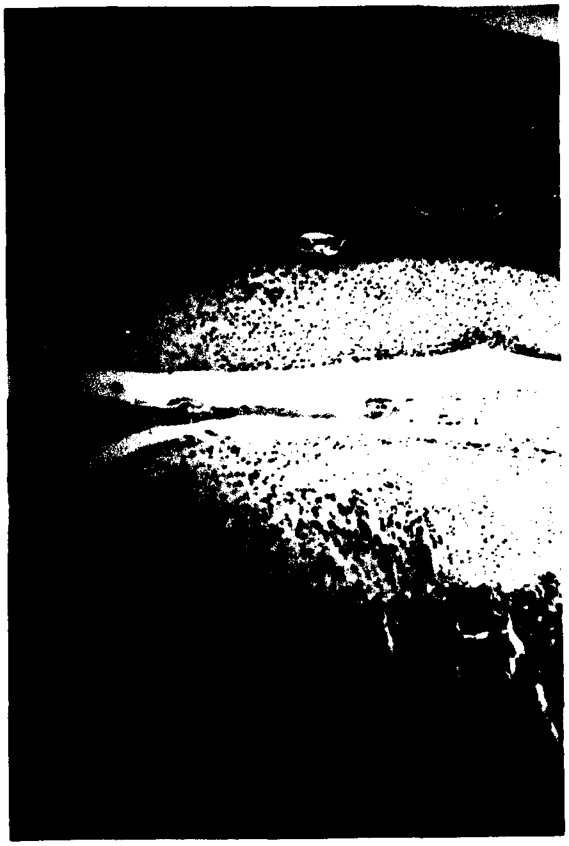


Fig. 27

Mid-sagittal section through the mandibular joint of Temporalis-removal animal 4.

Fig. 28

Mid-sagittal section through the mandibular joint of Temporalis-removal animal 5.

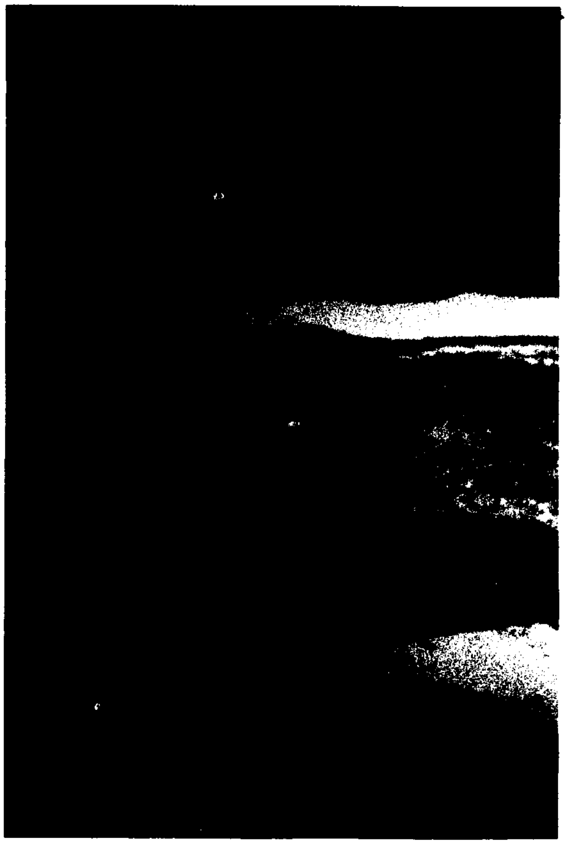


Fig. 29

Mid-sagittal section through the mandibular joint of Condylectomized animal 1.

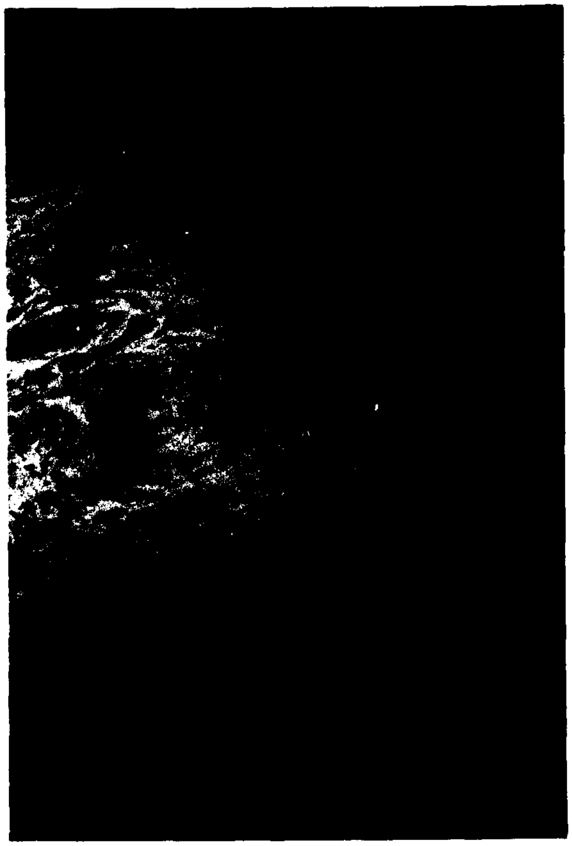


Fig. 30

Mid-sagittal section through the mandibular joint of Condylectomized animal 2.

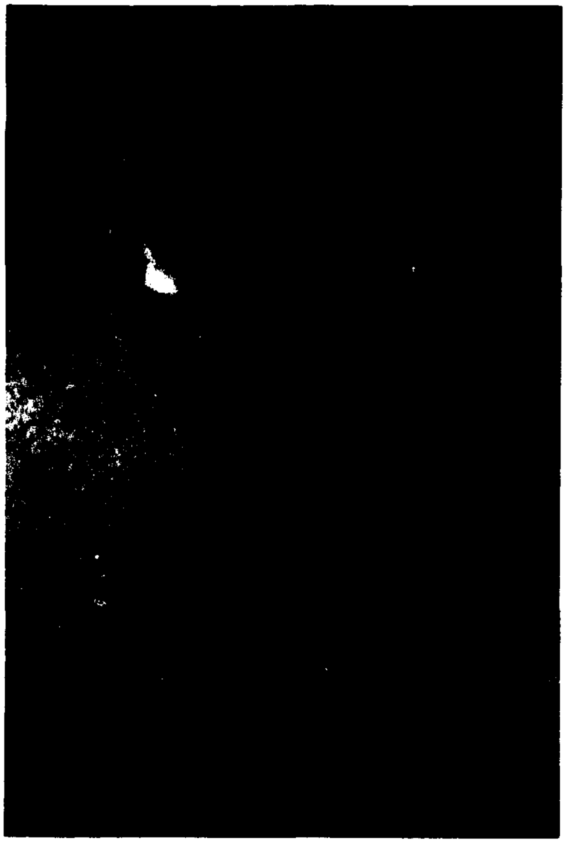


Fig. 31

Mid-sagittal section through the mandibular joint of Condylectomized animal 3.

COMPARISON OF MUSCLE FIBER DIRECTION

Introduction

A description of the muscles of mastication of several rodents has been given by Schumacher (1962), Greene (1935), Hiiemae (1966), Parsons (1896), Howell (1926), and Vendeloo (1953). The discussion in the literature, as respects the muscles of mastication, was most often concerned with the possible number of functionally or morphologically independent components of the masseter and temporalis muscles.

Greene's (1935) treatise was the first comprehensive study of the anatomy of the rat. Although Hiiemae and Houston (1971) attempted a more detailed survey of the muscles of mastication, their study was largely histological; anatomy of the muscles of mastication was confined to a verbal description of the areas of insertion and a general indication of muscle fiber direction, e.g., horizontal or oblique. There was no attempt to quantify, to treat the muscles of mastication as Schumacher (1962) had done for man; i.e., the angle of the fiber direction of the muscles of mastication and the change in the angles during growth. Such a study would afford at least a baseline for studies of changes in fiber direction in either comparative or experimental work.

In this part of the study, an attempt was made to quantify possible differences in muscle fiber direction to see if there was a relation among mandibular movements, histology of the mandibular joint, and muscle fiber direction.

The technique employed in this part of the study, however, proved unsatisfactory except for recording gross changes in muscle orientation.

Results

The results are tabulated (see fig. 32). Obviously, the samples were too small for meaningful statistical analysis; therefore, only major changes are discussed. No apparent major changes were observed in deep masseter and anterior temporalis.

The animals which underwent bilateral condylectomy exhibited an upward migration of the origin of the posterior temporalis relative to the control animals; it came to lie above the baseline. There was a concomitant change in muscle fiber direction of the posterior temporalis (see figs. 45, 46, 47).

The animals which underwent temporalis removal again comprised two groups. Animals numbered 2 and 3 had deep masseter angulations of 94° and 91° respectively (see figs. 41, 42), values near those of the control animals (see figs. 33, 34, 35). Animals numbered 1, 4, and 5 had deep masseter angulations of 78°, 98°, and 100° respectively (see figs. 40, 43, 44), values below or above the control animals. This change in angulation extends the range in value seen in the control, and may represent simply the result of a small sample size of the control.

The results of the animals which underwent incisor removal is inconclusive as yet (see figs. 36, 37, 38, 39).

Discussion

Based on the results from mandibular movements, histology of the mandibular joint, and comparison of muscle fiber direction, three separate groups can be distinguished.

The first group consists of temporalis-removals numbers 1, 4, and 5; the group most similar to the controls as respects mandibular movements. These animals exhibited an upwards and backwards movement of the mandible during the closing phase of the chewing cycle, movements similar to those of the control animals. The histology of the mandibular joint in these animals showed a meniscus with a thin central area, similar to that found in the control animals. The fiber direction of the deep masseter of the animals in this group was different from that found in the control animals. As there was no perceptible change in mandibular movements, a compensatory change in the orientation of the deep masseter might be expected.

The second group consisted of temporalis-removal numbers 2 and 3, and the condylectomized animals. The closing phase of chewing among these animals was an upwards and forwards hinge-like motion with no backwards movement. The histology of the mandibular joint among these animals showed a thickened meniscus. Animals numbers 2 and 3 of the temporalis removal group had deep masseter fiber orientations that were similar to that of the control animals. There was no compensatory reorientation of the muscle fiber direction in these two animals; this might account for the mandibular movements observed in this group, movements which were different from those observed in the control animals. The three animals which underwent bilateral condylectomy exhibited a change in orientation of the temporalis muscle; the muscle mass was positioned superior and anterior to the temporalis in the control animals.

The third group consisted of the incisor removal group. During the closing phase of the chewing cycle the mandible pivoted so that the condyle was depressed. This group demonstrated the greatest change in the histology of the mandibular joint. The squamosal bone was almost devoid of fibrous connective tissue. There were no islands of cartilage rest. The meniscus was thin throughout its length. The condyle had little hyaline cartilage. The results from the study of muscle fiber direction were inconclusive.

The observed modifications in arrangement of muscle fibers, structure of the mandibular articulation, and pattern of chewing cut across the three experimental groups in a complex way.

The technique for investigating the forces acting on the mandible and skull, most often found in the literature, is to examine either dried muscle weight or count muscle fibers from a histologic cross section. Papers relying on the outdated works of Weber, Fick, and Phuhl base their results on such erroneous concepts as "as striated muscle fibers within an animal are equal in contractile properties (and can thus be compared by volumetric or weight methods)" and "the several fibers attaching to a tendon must with insignificant exceptions all exert equal forces on the tendon." (Gans and

Bock 1965. The reader is referred to this paper for an excellent review of the subject). The results of such studies as Becht (1954), Smith and Savage (1959), Schumacher and Rehmer (1962), Hiiemae (1971) must, by the nature of the technique employed, arrive at misleading conclusions.

Generally speaking, there are three main reasons why such studies as the above mentioned must be inconclusive. First, studies employing fiber count or muscle weight are assuming the two previously quoted concepts as being correct. Secondly, muscles tend not to work in isolation, e.g., the suprahyoids can retract the mandible; the posterior temporalis is not the sole retractor of the mandible. In temporalis-removal animals numbers 1, 4, and 5, there was posterior movement during closing of the jaw. Also, in condylectomy, no posterior movement was observed even though the temporalis was intact. Thirdly, in extrapolating from either a physical or chemical property of a muscle as discerned in a laboratory apparatus to how the muscle functions together with other muscles in the living animal is to go from one level of observation to another. These limitations are discussed to some extent by Hiiemae (1971).

The application of the free body diagram to study the forces acting on the jaws has been advocated by Dempster (1961), Dempster and Duddles (1964), and Bock (1966, 1968). When using the free body diagram all external forces acting on the body must be included in the analysis. The analysis by Smith and Savage (1959) is by itself inherently incorrect according to the method of analyzing forces as shown by

Dempster and by Bock in the use of the free body diagram. Also, Smith and Savage's method of placing forces affords only one single, unique solution. This places erroneous restraints on the forces of the whole system. It follows that any study using Smith and Savage's technique will be incorrect.

MUSCLE FIBER ORIENTATION[1]

Animal Group	Animal no.	Deep Mass.	Ant. Temp.	Post. Temp.[2]
Control	1	93	50	25
	2	91	64	25
	3	89	70	19
Incisor removal	1	92.5	52	20
	2	85	61	14
	3	86	51	5
	4	85	55	12
Condylectomized	1	91	55	24
	2	88	59	13
	3	98	52	27
Temporalis removal	1	78		
	2	94		
	3	91		
	4	98		
	5	100		

1 - numbers in each muscle column show angulation, in degrees, of muscle mass relative to base line.

2 - angles shown in this column represent position of muscle below base line; angles for condylectomized animals represent position of muscle above base line.

fig. 32

Fig. 33

Skinned and hemisected head of Control animal 1 in lateral view, showing the masseter and temporalis muscles. The baseline, for measuring the angle of muscle fiber direction, is drawn in.

Fig. 34

Skinned and hemisected head of Control animal 2 in lateral view, showing the masseter and temporalis muscles. The baseline, for measuring the angle of muscle fiber direction, is drawn in.

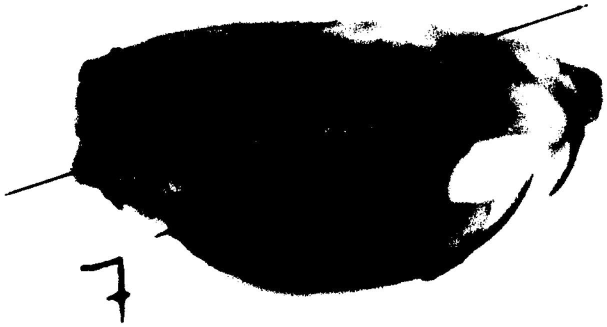


Fig. 35

Skinned and hemisected head of Control animal 3 in lateral view, showing the masseter and temporalis muscles. The baseline, for measuring the angle of muscle fiber direction, is drawn in.

Fig. 36

Skinned and hemisected head of Incisor-removal animal 1 in lateral view, showing the masseter and temporalis muscles. The baseline, for measuring the angle of muscle fiber direction, is drawn in.

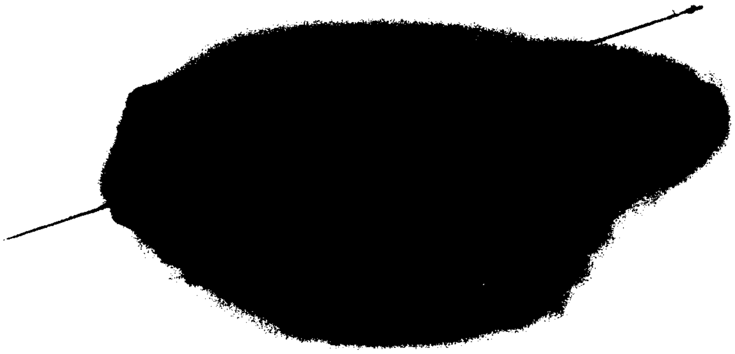


Fig. 37

Skinned and hemisected head of Incisor-removal animal 2 in lateral view, showing the masseter and temporalis muscles. The baseline, for measuring the angle of muscle fiber direction, is drawn in.

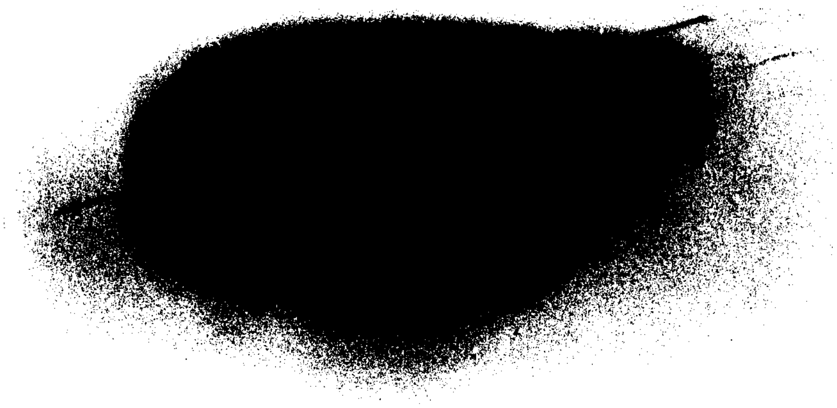


Fig. 38

Skinned and hemisected head of Incisor-removal animal 3 in lateral view, showing the masseter and temporalis muscles. The baseline, for measuring the angle of muscle fiber direction, is drawn in.

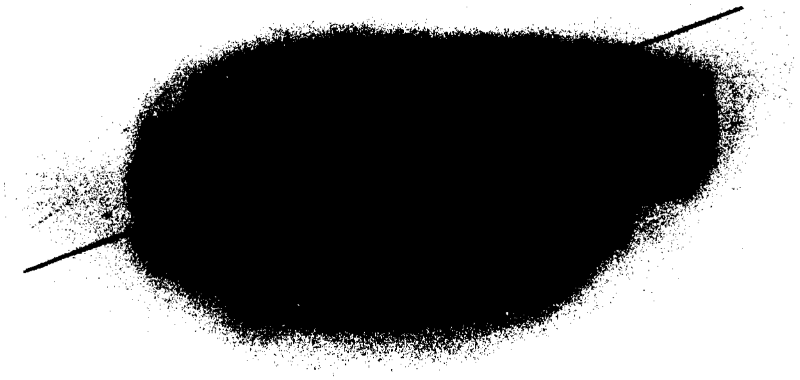


Fig. 39

Skinned and hemisected head of Incisor-removal animal 4 in lateral view, showing the masseter and temporalis muscles. The baseline, for measuring the angle of muscle fiber direction, is drawn in.

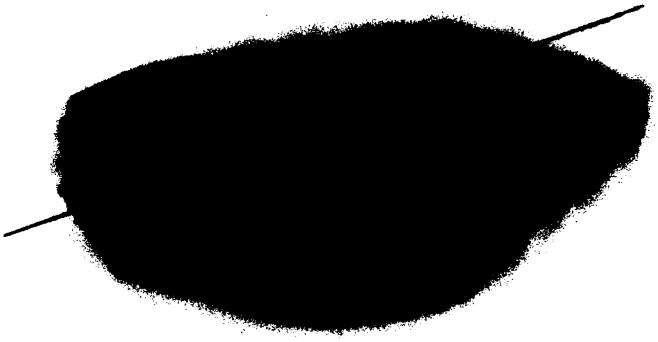


Fig. 40

Skinned and hemisected head of Temporalis-removal animal 1 in lateral view, showing the masseter muscle. The baseline for measuring the angle of muscle fiber direction is drawn in.

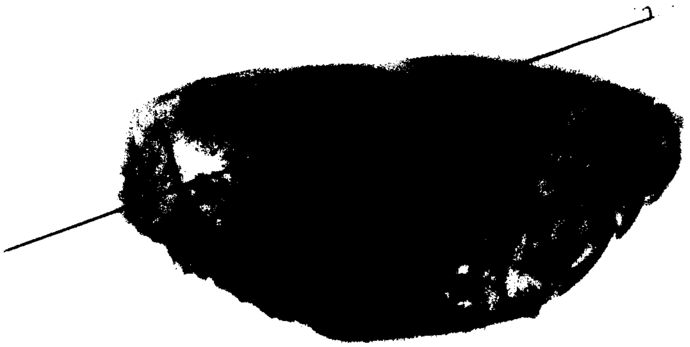


Fig. 41

Skinned and hemisected head of Temporalis-removal animal 2 in lateral view, showing the masseter muscle. The baseline for measuring the angle of muscle fiber direction is drawn in.

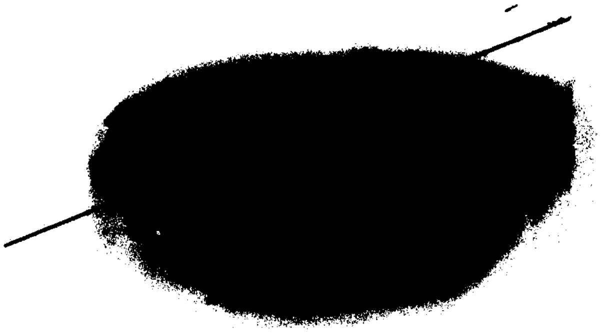


Fig. 42

Skinned and hemisected head of Temporalis-removal animal 3 in lateral view, showing the masseter muscle. The baseline for measuring the angle of muscle fiber direction is drawn in.

Fig. 43

Skinned and hemisected head of Temporalis-removal animal 4 in lateral view, showing the masseter muscle. The baseline for measuring the angle of muscle fiber direction is drawn in.

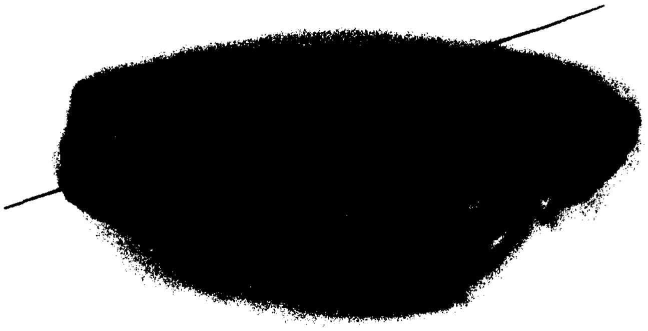


Fig. 44

Skinned and hemisected head of Temporalis-removal animal 5 in lateral view, showing the masseter muscle. The baseline for measuring the angle of muscle fiber direction is drawn in.

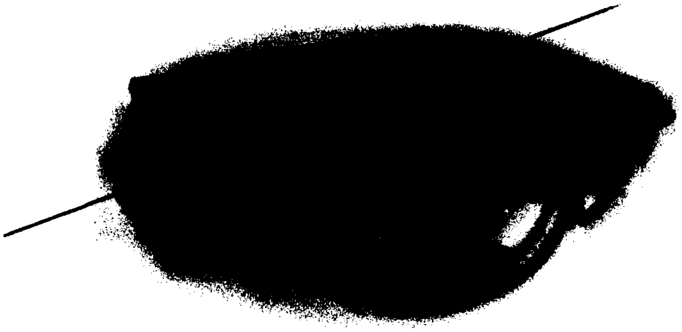


Fig. 45

Skinned and hemisected head of Condylectomized animal 1 in lateral view, showing the masseter and temporalis muscles. The baseline for measuring the angle of muscle fiber direction is drawn in.

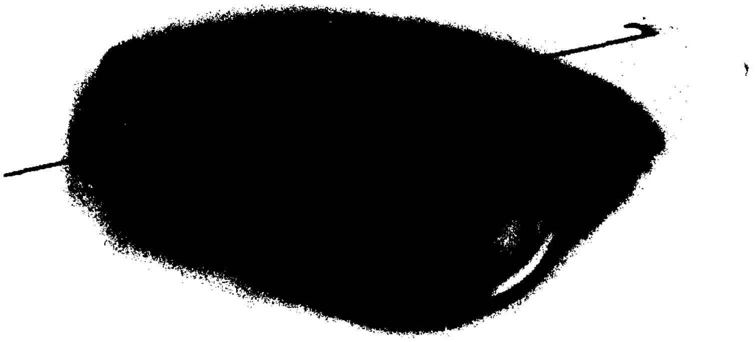


Fig. 46

Skinned and hemisected head of Condylectomized animal 2 in lateral view, showing the masseter and temporalis muscles. The baseline for measuring the angle of muscle fiber direction is drawn in.

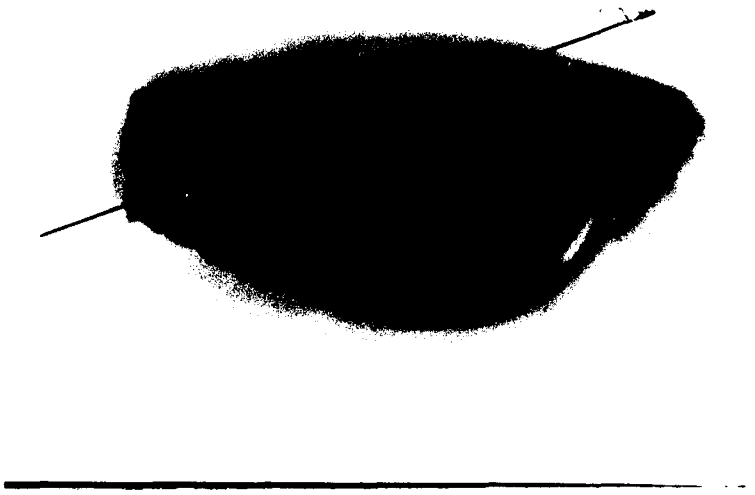


Fig. 47

Skinned and hemisected head of Condylectomized animal 3 in lateral view, showing the masseter and temporalis muscles. The baseline for measuring the angle of muscle fiber direction is drawn in.

SUMMARY AND CONCLUDING STATEMENTS

Among the control, incisor removal, bilateral temporalis removal, and bilateral condylectomy groups, it was in the closing phase of the chewing cycle only that differences were manifested in mandibular movements.

Based on the results from mandibular movements, histology of the mandibular joint, and comparison of muscle fiber direction, three separate groups were distinguished among the experimental animals.

The first group consisted of temporalis-removals numbers 1, 4, and 5. These animals exhibited an upwards and backwards movement of the mandible during the closing phase of the chewing cycle, movements similar to those of the control animals. The histology of the mandibular joint in these animals of the first group showed a meniscus similar to that found in the control animals; a meniscus with a thin central area. A meniscus with a thin, avascular central area suggests a posteriorly directed force exerted against the meniscus as the mandible is closed (Sarnat 1959).

The fiber direction of the deep masseter, in the animals of the first group, was different from that in the control animals. As there was no perceptible change in mandibular movements, a compensatory change in the orientation of the deep masseter might be expected.

The second group consisted of temporalis-removals numbers 2 and 3, and the condylectomized animals. The closing phase of chewing was an upwards and forwards motion, hinge-like with no backwards movement. The histology of the mandibular joint among these animals showed a thickened meniscus which would corroborate the findings from the cinefluorography. Animals numbered 2 and 3 of the temporalis removal group had deep masseter fiber orientations that were similar to that of the control animals. There was no compensatory reorientation of the muscle fiber direction; this might account for the mandibular movements observed in this group, movements which were different from those observed in the control animals.

The third group consisted of the incisor removal group. During the closing phase of the chewing cycle the mandible pivoted so that the condyle was depressed. This group demonstrated the greatest change in the histology of the mandibular joint. The squamosal bone was almost devoid of fibrous connective tissue. There were no islands of cartilage rest. The meniscus was thin throughout its length. The condyle had little hyaline cartilage. The results from the study of muscle fiber direction were inconclusive. The observed modifications in arrangement of muscle fibers, structure of the mandibular articulation, and pattern of chewing, cut across the three experimental groups in a complex way. No simple correlation exists between the three experimental interferences and the observed modifications.

The studies on the functioning temporomandibular joint in man are largely confined to the dental and orthodontic literature; the studies on the comparative morphology of the glenoid fossa and condyle in primates are found in the anthropological and dental literature. The most important of these works are included in the bibliography.

The studies on mandibular movement in man form part of the orthodontic literature and invariable are concerned with mapping the movements, not of the mandible as a whole, but of a point on or a process of the mandible (Bjork 1955; Boman 1948; Gibbs _et al_ 1969, 1971; Hall 1929; Hickey _et al_ 1963; Hildebrand 1931; Hjortsjo 1953, 1959; Koivumaa 1961; Lord 1937; Nevakari 1956; Posselt 1952; Rees 1954; Scully 1959; Sonstebo 1961; Thompson 1941). Moss (1959) described the probable movements of the mandible in man as a whole through an analysis of movement at the mandibular joint. He restricted his study to movements while opening the mouth and concluded that the mandible rotates about the lingula, above the mandibular foramen. The path executed by M_1 in his study is similar to that seen in the opening phase of the chewing cycle in the rat. Gibbs _et al_ (1971) state "paths of motion in the sagittal plane show that the central incisor usually closes in a retrusive movement and opens in a protrusive movement." The chewing cycle which has been described for the normal rat is forwards and down, then upwards and back. This type of mandibular movements in mastication, bringing the lower molars to a position behind their corresponding upper molars prior to a forwards crushing motion, has been attributed by Crompton and Hiiemae (1969) as a mandibular movement typical of primitive mammals.

The application of electromyography to the study of mandibular movements (Algren 1966; Moyers 1950; Møller 1966;

Munro 1972; Perry 1955) afforded a more dynamic approach, as the question of how the various mandibular movements are effected could be more readily studied. Møller's (1966) study showed that the external pterygoids contract during closing as well as opening of the jaw. The external pterygoids are, therefore, opposing posteriorly directed forces at the mandibular condyle, a fact that is not accounted for in diagrams attempting to depict mechanics of the mandible (Hiiemae 1971; Lord 1937; Robinson 1946; Scott 1955; Smith and Savage 1959; a.m.o.).

The above mentioned studies suffer from the same basic shortcoming: each is unidimensional, i.e., concerning itself with only the effect of one variable on another. But systems are complex integrated functioning units. The isolation of one component from the system will not necessarily reveal the dynamics of the system as a whole. What is needed is a multidimensional approach; one which studies simultaneously as many aspects as possible of a system. Kallen and Gans (1972) combined cinephotography, electromyography, and cusp patterns of the teeth in their study "Mastication in the little brown bat, *Myotis lucifugus*." They conclude that "on the other hand our results support the earlier conclusions that the best that descriptive anatomy may offer the functional morphologist is a statement of possibilities. The present methods permit decision of which among a spectrum of possible actions actually occur."

The results of this study attest to the desirability of a multidimensional approach. Instead of investigating the effects of excising the temporalis muscle on the bony structure to which it attaches, I have tried to understand the interrelations of some of the components within the system as a whole; i.e., the main muscles of mastication, the histology of the mandibular joint, the functioning of the system as seen through the movements executed by the mandible. In this way, inferences based on each component may be tested against those based on others, and the mutually corroborative results obtained here attest to the usefulness of the approach, and augur well for its use in the future.

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