

SINGLE MOTOR UNIT ACTIVITY
OF THE HUMAN LATERAL PTERYGOID MUSCLE
DURING DEFINED TASKS

by

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DECLARATION

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person nor material which to a substantial extent has been accepted for the award of any other degree or diploma of the university or other institute of higher learning, except where due acknowledgement has been made in the text.

(Signed) *Intira Phomachet*

ABSTRACT

There is a limited understanding of the normal functions of the human lateral pterygoid muscle (LP). The aims of this study were (a) to develop a methodology for standardising command jaw movements in the horizontal plane (*i.e.*, anteroposterior and mediolateral) and (b) to clarify the normal functions of the superior (SHLP) and the inferior heads (IHLP) of the LP. The hypotheses were that an important function of the LP is in the fine control of horizontal jaw movement, and the LP is functionally heterogeneous; that is subcompartments of the muscle are selectively activated. Single motor units (SMUs) were recorded from the SHLP (18 recordings) or IHLP (27 recordings) simultaneously with standardised and non-standardised jaw movements. The locations of electrodes were verified by computer tomography. Jaw movements were standardised by having subjects track a target during single- and multiple-step displacements at different rates and magnitudes of movement.

Within the medial part of the SHLP, SMUs exhibited activity during contralateral movement, protrusion, submaximal jaw-opening (maximal not tested) and jaw closing, while different SMUs from the middle and the lateral part of the SHLP exhibited activity during different combinations of tasks. All IHLP SMUs were active during contralateral movement and protrusion, and a majority of units were active during submaximal jaw-opening. None was active during maximal ipsilateral or retrusive jaw movements nor on jaw closing/clenching in the intercuspal position. None of the total of 181 units from the SHLP and IHLP was active at postural jaw position.

The lowest threshold of the IHLP SMUs was <0.2 mm of contralateral or protrusive displacements. Successively recruited SMUs could be recruited at small increments in displacement. Recruitment thresholds of some of the IHLP units were rate dependent with thresholds significantly decreasing with increasing rate of horizontal jaw movement in protrusion (25%) and contralateral movements (34%).

There was a statistically significant overall increase in firing rate of most IHLP units as the magnitude of jaw displacement increased in small increments. There was a significant correlation between jaw displacement and mean firing frequency. The correlation coefficients at the fast rate during the contralateral step task and the protrusive step task were significantly higher than those at the slow rate.

After dividing IHLP into four regions, the SMUs recorded in the superior-medial part exhibited significantly lower mean threshold values than the SMUs recorded in the other parts. In addition, significantly fewer units were related to the protrusive task in the superior-medial part. The SMUs recorded in the superior part (*i.e.*, superior-medial and superior-lateral) showed significantly greater mean firing rate changes per unit displacement during protrusion than for the SMUs recorded in the inferior part. Significantly fewer units were related to the protrusive task in the superior-medial part.

The present findings support previously proposed notions of functional heterogeneity within SHLP and IHLP. The data do not support a previous notion of reciprocal activity between the 2 heads of the muscle. Rather, the data suggest

that specific regions of the SHLP and IHL P are capable of selective activation in a finely controlled manner to allow the application of the appropriate force vector (magnitude and direction) to effect the required condylar movement needed for the generation and control of horizontal jaw movements.

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LIST OF ABBREVIATIONS

ATPase	Adenosine triphosphatase
CT	Computer tomography
EMG	Electromyographic
FF	Fast contracting and fatigue susceptible
FG	Fast twitch glycolytic fibres
FHP	Frankfort Horizontal Plane
FOG	Fast twitch oxidative glycolytic muscle fibres
FR	Fast contracting and intermediate fatigue resistant fibres
IHLP	Inferior head of the lateral pterygoid muscle
LED	Light-emitting diode
LP	Lateral pterygoid muscle
LSFF	Least sustainable firing frequency
MHC	Myosin heavy chain
MIPT	Mid-incisor point
PCS	Physiological cross-sectional area
S	Slow contracting and fatigue resistant fibres
SD	Standard deviation
SHLP	Superior head of the lateral pterygoid muscle
SMU	Single motor unit
SO	Slow twitch oxidative muscle fibres

TMD

Temporomandibular disorders

PUBLICATIONS

PAPERS

Part of this thesis has been published in the first 3 of the following 4 papers.

1. Phanachet, I., Wanigaratne, K., Whittle, T., Uchida, S., Peeceeyen, S., and Murray, G.M. A method for standardizing jaw displacements in the horizontal plane while recording single motor unit activity in the human lateral pterygoid muscle. *J.Neurosci.Methods* 105: 201-210, 2001.
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The following papers have arisen from research projects under taken during the author's period as a PhD candidate but are not included in this thesis.

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2. Phanachet, I., Murray, G.M., Chan, J.Y., and Wanigaratne, K. Human lateral pterygoid muscle is involved in fine jaw movement control. *Soc.Neurosci.Abstr.* 25: 1147, 1999.

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CHAPTER I

REVIEW OF LITERATURE

1. INTRODUCTION

The muscles of mastication are one of the components of the masticatory system. The masseter, temporalis, medial pterygoid, lateral pterygoid (LP) and digastric muscles are involved in jaw movements, such as jaw opening, jaw closing, lateral jaw movements, and stabilising the temporomandibular joint as well as maintenance of mandibular posture. The LP is one of the least understood jaw muscles. The LP has been studied in several aspects such as morphology, histology, biomechanics and physiology in an attempt to clarify the normal function of the muscle. Although there have been many electromyographic (EMG) studies involving the function of jaw muscles, LP muscle activity has not been widely investigated due partly to the difficulty of electrode placement and the deep location of the muscle.

An understanding of the anatomy and neurophysiology of the LP is essential since this muscle has been implicated as playing a role in the aetiology of temporomandibular disorders (TMD), a major cause of non-dental orofacial pain. However, we have a very limited understanding of its role in TMD and indeed its role in normal function. The LP generally consists of two heads: a superior or upper head (SHLP) and an inferior or lower head (IHLP). In TMD, a number of theories of LP disturbance have been proposed, including muscle hyperactivity, muscle hypoactivity, poor coordination between the two heads of the muscle, and/or a disturbance in the normal role of the muscle in the control or

stabilisation of the temporomandibular joint (Porter 1970; Farrar and McCarty, Jr. 1979; Johnstone and Templeton 1980; Mahan et al. 1983; Koole et al. 1983; Juniper 1984; Gibbs et al. 1984; Koole et al. 1984; Carpentier et al. 1988; Dahlström 1989; Liu et al. 1989; Okeson 1998; Hiraba et al. 2000). These notions have been partly the basis for unproven irreversible therapies, such as occlusal grinding and restorative treatments as well as reversible treatments with occlusal splints or jaw exercises. The occlusal splint, for example, is thought to reduce muscle activity, improve muscle coordination, reduce temporomandibular joint loading and/or aid in joint stabilisation, and thereby alleviate TMD symptoms in addition to a well-accepted placebo affect (Ash 1995; Stohler 1997; Hiraba et al. 2000). Present knowledge, however, provides little scientific basis for current treatment recommendations.

There have been many studies that have attempted to elucidate the normal function of the LP in animals and in the human. In general, many EMG studies suggest that the IHLP plays a role in jaw opening, protrusion and contralateral jaw movements, whereas the SHLP plays a role in jaw closing, retrusion and ipsilateral jaw movements (Kamiyama 1961; Gross and Lipke 1979; Mahan et al. 1983; Klineberg 1991; Miller 1991; Hannam and McMillan 1994; Hiraba et al. 1995; Hiraba et al. 2000). However, there is a lack of agreement as to the normal function of the LP among previous studies. Some investigators have claimed that both heads always act independently (Grant 1973; McNamara 1973; Mahan et al. 1983; Gibbs et al. 1984; Wood et al. 1986; Hiraba et al. 1995; Hiraba et al. 2000), whereas others have claimed that both heads can be active concomitantly

during some task performances (Sessle and Gurza 1982; Miller 1991; Hannam and McMillan 1994).

There are a number of possible reasons for the lack of agreement and limited understanding of normal LP function. First, there was the absence of reliable verification of electrode location within the muscle in most previous human studies. Some of these earlier recordings may have been from the adjacent jaw muscles, such as the deep temporalis or the medial pterygoid, or from the LP but incorrectly attributed to a particular head of the muscle (Widmalm et al. 1987; Hannam and McMillan 1994; Hiraba et al. 1995; Orfanos et al. 1996). Second, with the exception of a few studies (Sessle and Gurza 1982; Hiraba et al. 1995; Hiraba et al. 2000), most previous human studies have not accurately recorded jaw movement to correlate with LP activity and this has undermined the ability to identify the task relations of the LP. Third, most previous recordings have been made of multi-unit activity where it is more difficult to draw conclusions as to the relative levels of activity in each head of the LP.

Another possible explanation for the conflict in the literature could relate to the possibility of functional heterogeneity within the LP. Functional heterogeneity, that refers to the ability of the central nervous system to selectively activate different subcompartments of a muscle, has been well characterised in the masseter and temporalis muscles. If the LP is functionally heterogeneous, then recording at different sites within the muscle would yield different functional properties. This may well be an explanation for the inconsistencies between studies as to the task relations of the LP.

The normal function of the LP has been revisited by recording single motor units (SMUs) at computer tomography (CT)-verified sites within the muscle (Murray et al. 1999a). However, studies of the physiological properties of motor units during isometric or isotonic contractions, require standardisation of the dynamic parameters of the movement since motor unit properties are dependent on such parameters. For example, the rate of a contraction affects the recruitment threshold and the pattern of motor unit activity. Recruitment threshold of a motor unit in the masseter muscle and limb muscles is lower during rapid contractions than that during slow ramp contractions (Desmedt and Godaux 1979; Yoneda et al. 1986), abductor digiti minimi motor units have higher initial frequencies and increase their firing rates more quickly with faster isometric contractions (Tanji and Kato 1973a), and SMUs in forelimb muscles are directionally tuned (Herrmann and Flanders 1998).

A standardised methodology has never been developed for the study of SMUs in the human LP during isotonic contraction. A recent study (Hiraba et al. 2000) has developed a methodology for standardising vertical jaw displacements in humans during recordings of multi-unit EMG from unverified locations considered to be the LP. There was no indication in this study as to how accurate or reproducible were these displacements.

In order to understand the normal function of the LP, and how it functions in the patients with TMD, it is therefore necessary to develop a method that standardises jaw movement rate and amplitude so that the properties of SMUs can be characterised in relation to defined dynamic measures. Such an approach will allow a detailed description of SMU task relations and firing properties in

relation to defined dynamic features of jaw movement. These data will provide a basis for future studies of the muscle activity in patients with TMD to identify whether, during the same standardised movements, there are differences in activity patterns such as hyperactivity and lack of coordination between the two heads (Mahan et al. 1983; Juniper 1984; Gibbs et al. 1984; Juniper 1987; Okeson 1998; Hiraba et al. 2000). The method should also have general applicability to the study of SMUs from other jaw muscles.

Given the limitation inherent in previous studies and the uncertainties of the function of the LP, the overall aim of the present study is to clarify the normal function of the human LP at verified sites by SMU recording. The following review of literature summarises available data on anatomical, histological and physiological features of the LP as well as the other jaw muscles that point towards possible roles of the LP in horizontal (*i.e.*, mediolateral and anteroposterior) jaw movement control and a possibility of selective activation in the LP. The remainder of the review will deal with mechanisms employed by motor units for force and movement generation.

2. STRUCTURAL ORGANISATION OF JAW MUSCLES

It is generally accepted that the masseter, temporalis and medial pterygoid muscles are jaw elevator muscles, and the other muscles are jaw depressors. Many studies also suggest that individual jaw muscles do not necessarily activate homogeneously during a motor task (McMillan and Hannam 1992; Blanksma et al. 1992; Hannam and McMillan 1994; Blanksma and van Eijden 1995; Blanksma et al. 1997; Murray et al. 1999b). Therefore, activity at one site does not

necessarily reflect activity at other sites in a jaw muscle. The notion that individual muscles might be functionally subdivided is not new, especially in muscles with large attachments. Data from a number of studies in animal and human muscles have supported this notion (English and Weeks 1984; ter Haar Romeny et al. 1984; Herring et al. 1989; English and Timmis 1991; English et al. 1993). In a functionally heterogeneous muscle, selective regions within a particular muscle become active preferentially during specific tasks. However, in most previous EMG studies of the LP, there appears to be the implicit assumption that there is a uniform distribution of activity throughout each head of the LP, although notions of functional heterogeneity within the LP have been proposed based on anatomical features, muscle architecture and preliminary multi-unit findings (Hannam and McMillan 1994; Foucart et al. 1998; Murray et al. 1999b). The selective activation of muscle regions gives a muscle the potential to have numerous lines of action that differ in orientation and position. It is considered that the complex internal organisation of the jaw muscles is a reflection of the functionally heterogeneous nature of these jaw muscles. This is supported by data from histological, anatomical, electrophysiologic and EMG studies.

2.1 Skeletal Muscle Architecture

There is a wide variation in size, shape, complexity and fibre architecture of muscles. Muscle fibres usually attach to bones or tendons, but in complex muscles, which are composed of internal aponeuroses (*i.e.*, flat sheets of densely arranged collagen fibres), muscle fibres also attach to aponeuroses. Where there are several layers of aponeuroses in each muscle, fasciculi are parallel within a layer, and the arrangement of the fasciculi with respect to the aponeuroses may

take several patterns, varying from layer to layer (Tortora and Grabowski 1993). According to the orientation of fasciculi, muscles are generally classified as parallel or oblique and both of these types are found in jaw muscles.

Parallel muscles refer to a muscle in which the fibres lie parallel to the line of action of the entire muscle. The shape of the fasciculi varies from flat, short and quadrilateral to long and straplike. The individual muscle fibres often run almost the whole length of the muscle. Alternatively, where the fibres are oblique to the line of action, they are grouped as triangular or pennate (feather-like) and this pennate structure varies in complexity, and has been categorised as unipennate, bipennate and multipennate. Figure I-1 (b-d) shows examples of these pennate muscle fibre arrangements. The fibres of parallel-fibred muscles generate purely translational motion, while the fibres of pennate-fibred muscles can rotate about their origins, increasing their pennation angle as they shorten (Gans 1982) and the attached tendon or tendon sheet translates in the same direction. In the latter muscle type, only a proportion of the total force and range of action possible from individual muscle fibres is seen at the translating tendon sheet.

The force produced by a pennate fibre can be resolved into two components: one acting along the tendon and another at 90° to the line of the tendon (Fig. I-2). Only a portion of force ($\cos\theta$) is transmitted to the tendon (Fig. I-3). In bipennate (Fig. I-1c) or multipennate (Fig. I-1d) muscles, the vector at 90° is counterbalanced by the fibres on the other side of the tendon, however in unipennate muscles there is a tendency for the tendon to deviate (Fig. I-1b). Likewise, the range of movement is more limited in a pennate muscle than in a parallel-fibred muscle. The range of movement is in fact proportional to the

length of muscle fibres multiplied by the cosine of the angle of attachment of the muscle fibres to the tendon, which in the human masseter averages about 20°.

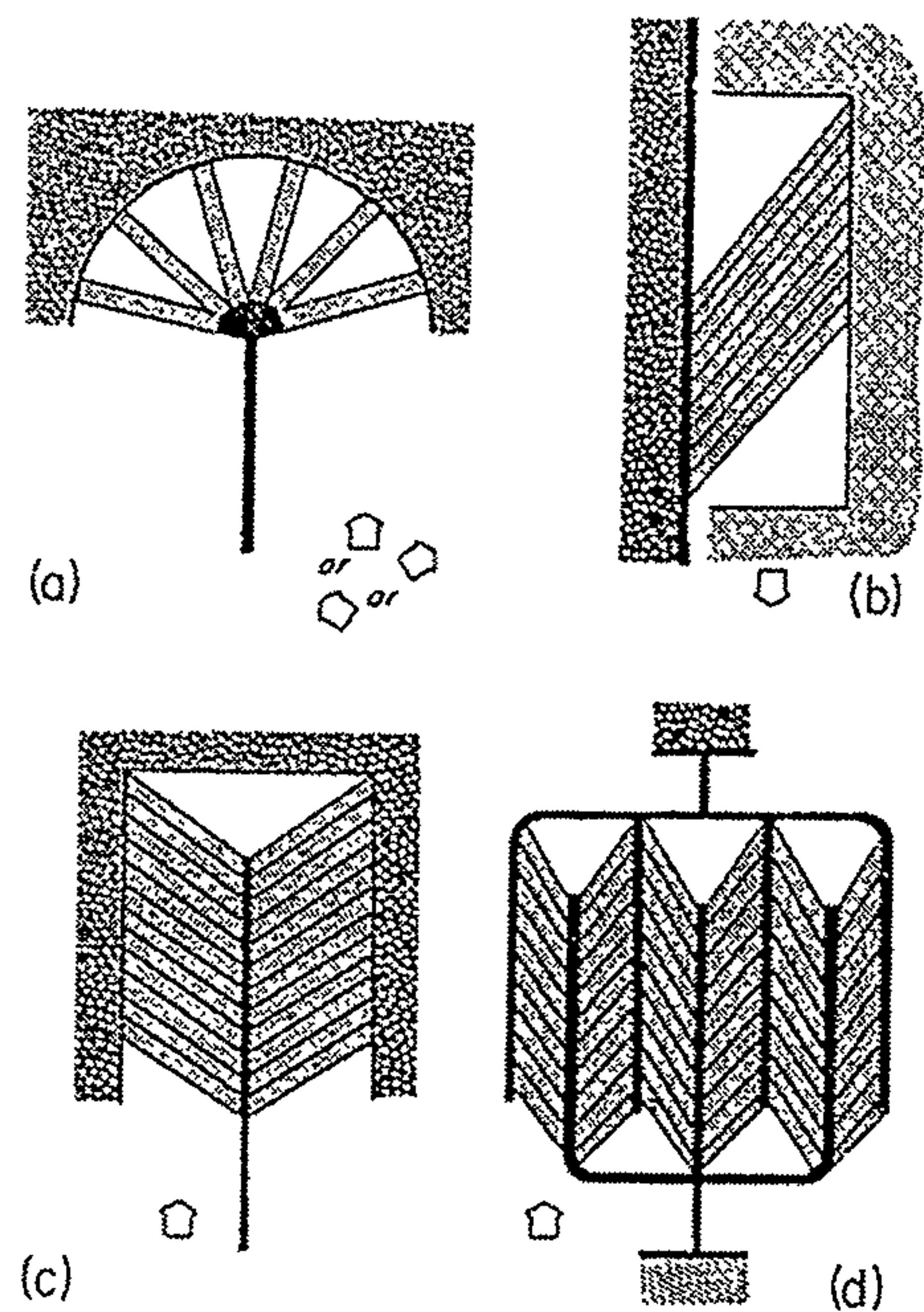
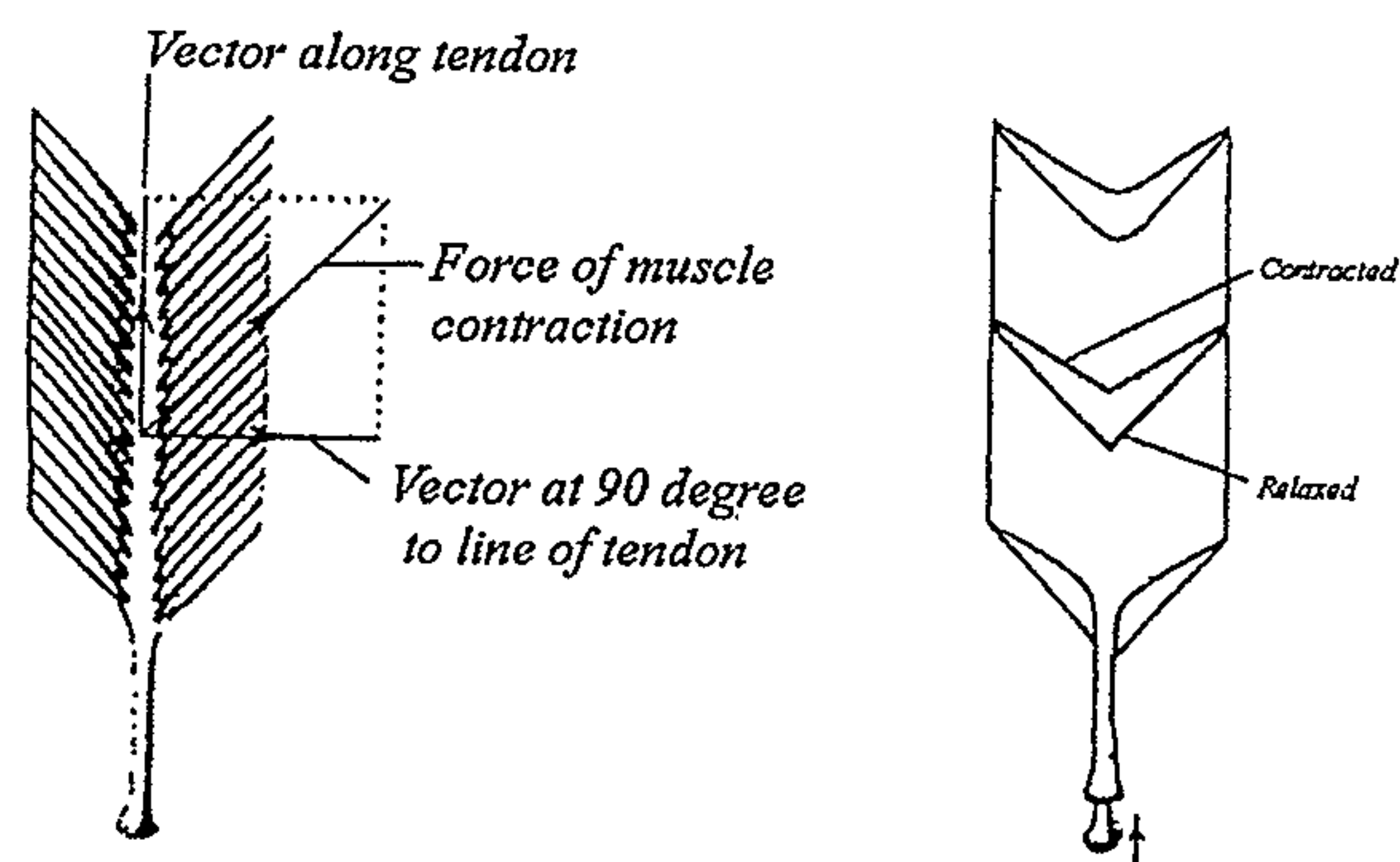


Fig. I-1 Permutations of muscle fibre arrangements. The hatched areas represent origin sites and the arrows show the movements of the insertion sites. (a) Radial arrangement of fibres. Activation of the different fibres can shift the position of the tendon off the centre line. (b) Unipennate muscle. The surface of origin and insertion are maintained in parallel by mechanical stops (eg., bones, fascia and other active muscles). (c) Bipennate muscle. (d) Multipennate muscle. In (c) and (d), symmetrical contraction shifts the tendons centrally. (From Gans 1982)

Fig. I-2 Simple mechanical considerations relating to the actions of bipennate muscles. (Modified from Williams and Warwick 1980)



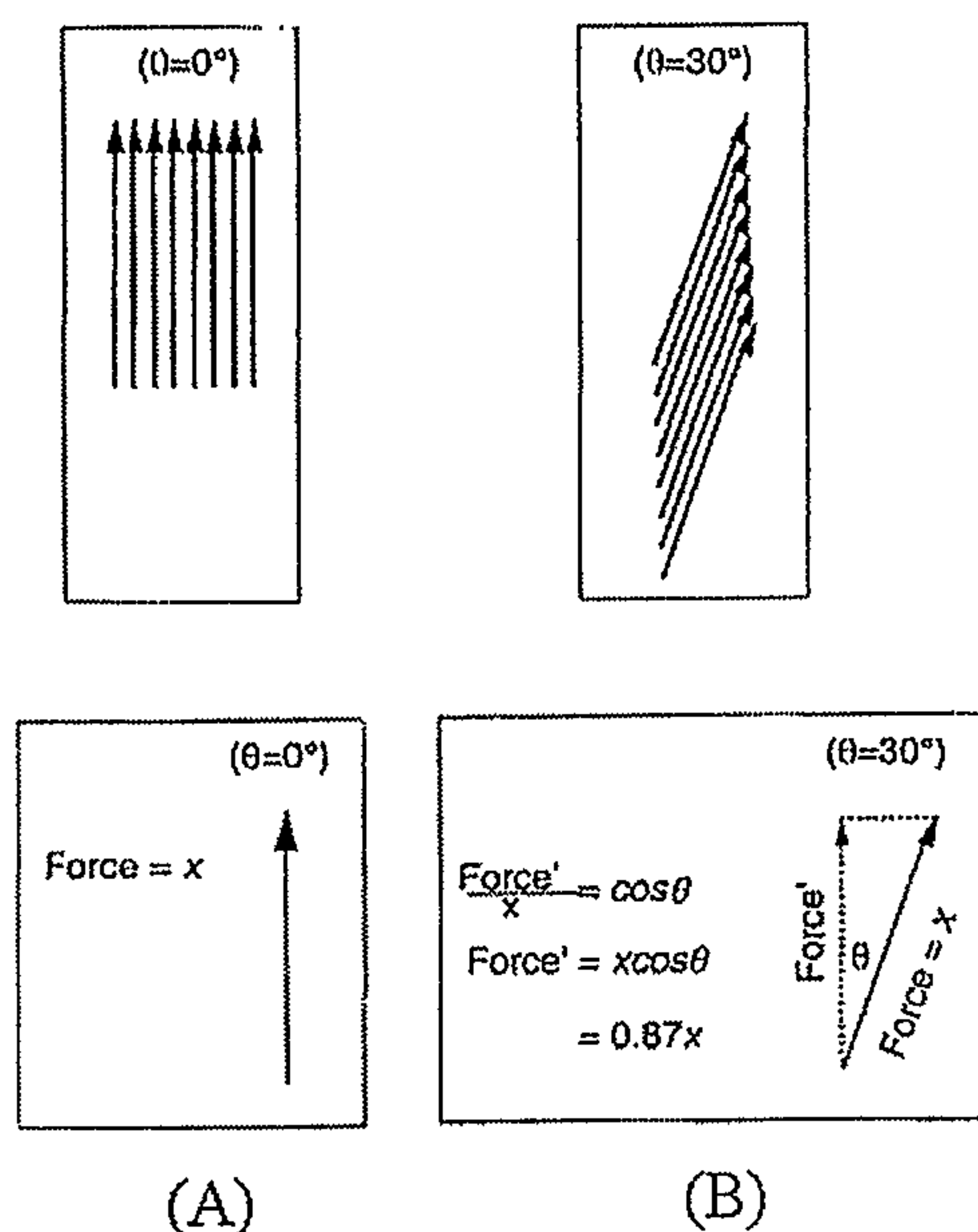


Fig. I-3 Schematic illustration of the effect of pennation. (A) Muscle fibres oriented parallel to the axis of force generation transmit all of their force to the tendon. (B) Muscle fibres oriented at a 30° angle relative to the force-generating axis transmit only a portion of their force ($\cosine\ 30^\circ = 0.87$, or 87%) to the tendon. Although only 87% of the force is transmitted to the tendon, pennation permits packing of a larger number of fibres into a smaller cross-sectional area. (Modified from Lieber and Friden 2001)

As implied in the above description, fascicular arrangements influence the power of a muscle and the range of motion over which a muscle can act. The power of a muscle depends on the total number of sarcomeres in parallel as well as an axial component of the force produced, which is inversely correlated with the angle of pennation. In contrast, the range of motion depends on the length of the muscle fibres or the number of sarcomeres in series. When a muscle fibre within a group of muscle fibres contracts, it attempts to shorten to a length just slightly greater than half of its resting length. Therefore, the longer the fibres in a muscle, the greater the potential range of motion. Muscle fibre orientation in relation to tendon architecture represents a compromise between power and range of motion, because a muscle can contain either a smaller number of long fibres or a larger number of short fibres. Muscles designed for producing maximal force have a relatively large number of short fibres arranged in pennate array. Conversely, muscles suited for generating a large amount of excursion have a relative large

number of long muscle fibres arranged in parallel (van Eijden and Brugman 1997). Parallel-fibred muscles, for instance, have longer fasciculi and a large number of sarcomeres in series, and these contribute to a greater range of motion and higher movement velocities during contraction. Thus, the parallel-fibred muscles can produce large and rapid movements. Pennate muscles, on the other hand, have shorter muscle fibres, resulting in a small range of movement. However, more fibres can be packed into the muscle because of space provided by pennation. Near-parallel groups of short fibres are arranged at acute angles to their tendinous insertion site. Consequently, pennate muscles can generate larger forces than parallel-fibred muscles of identical dimensions. Pennation is useful in muscles, such as the masseter and the medial pterygoid muscles, which generate power when the range of motion is not the most critical aim for contraction (Hannam 1994). Both muscles have relatively small areas of attachment and can produce considerable force. Nevertheless, the power of a muscle also depends on the size of the muscle and pennation angle; the greater the pennation angle, the lower could be the force transmitted to the bone. Therefore, pennate muscles are not necessary to produce larger force than that of parallel-fibred muscles. Further, the range of movement and the amount of muscle fibre length change also depend on the muscle moment arm. That is, the greater the moment arm, the greater the muscle fibre length change. As a result, the range of movement for the muscle-joint system with the larger moment arm is smaller compared with the system with the shorter moment arm length. Hence, muscles with longer fibres are not necessarily associated with the larger ranges of motion (Lieber and Friden 2000, 2001).

Many muscles often consist of more than one of the above morphological types, allowing multiple functional roles for these muscles. The different anatomical compartments of the muscle can exert different mechanical actions. Thus, in some actions, only one part of a muscle may be activated, while other parts are largely inactive.

2.2 Gross Anatomy and Architecture of Jaw Muscles

Many studies of internal muscle architecture have been carried out, including studies of fibre orientation, angulation, cross-sectional fibre area and fibre and sarcomere length. Anatomical observations suggest that masticatory muscles have irregular shapes, large attachment areas and a complex internal architecture.

2.2.1 Masseter Muscle

The masseter is a rectangular muscle composed of three parts: a superficial, an intermediate and a deep part. The fibres of masseter have a wide area of attachment. The superficial part arises from the maxillary process of the zygomatic bone and anterior two thirds of the inferior border of the zygomatic arch, and it inserts onto the lower posterior half of the lateral surface of the ramus out to the angle of the mandible. The intermediate part extends from the medial aspect of the anterior two thirds of the zygomatic arch and the lower border of its posterior third and inserts at the central part of the ascending ramus and the coronoid process. The origin of the deep part is the deep surface of the zygomatic arch and its insertion is the upper part of the ascending ramus and the coronoid process.

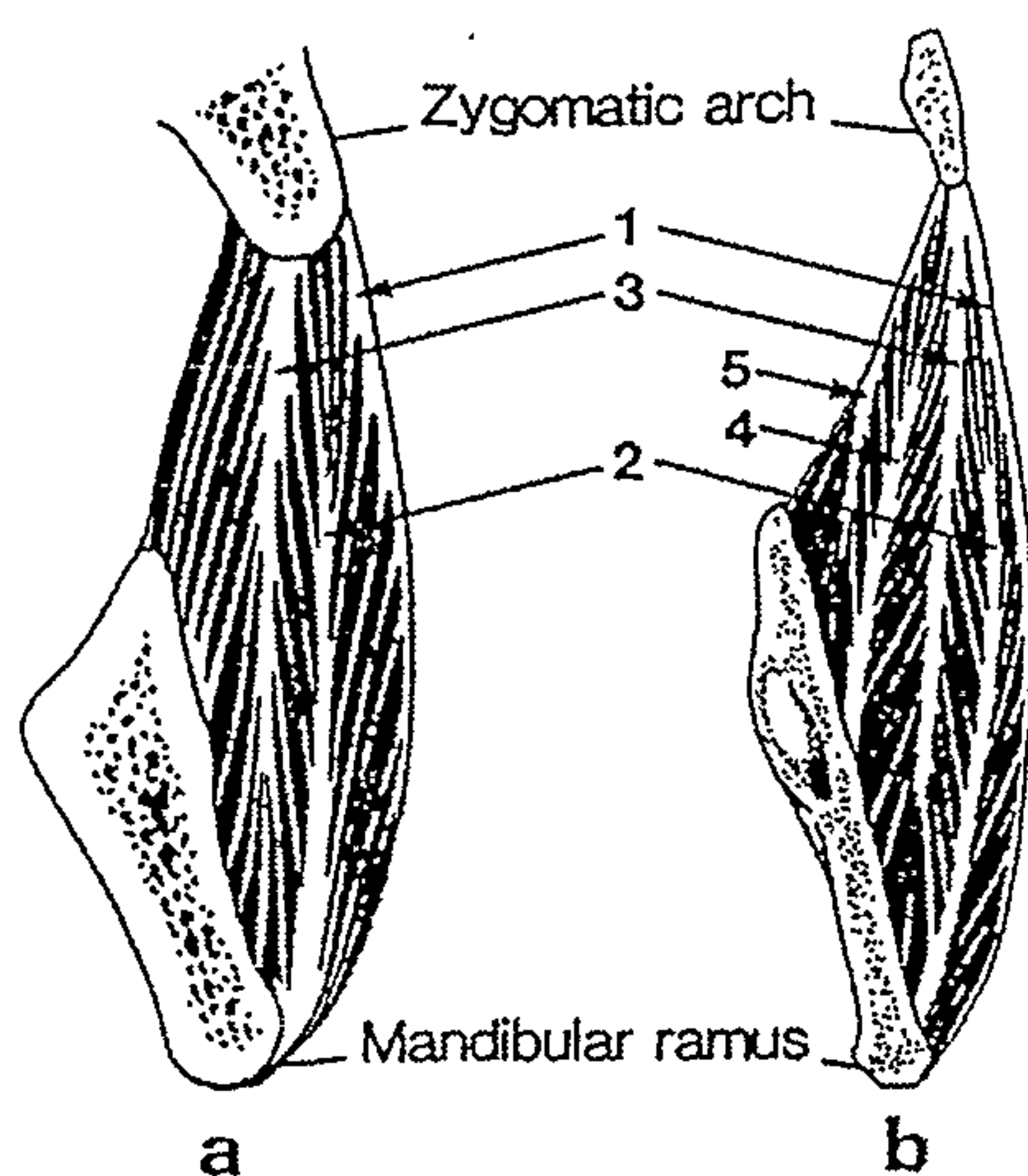


Fig. I-4 Longitudinal section from a frontal view of the human masseter muscle. Muscle fibres are black and tendinous tissues white. (a) Ebert's version (1939) and (b) Schumacher's version (1961). Both have been redrawn. (From Stålberg and Eriksson 1987)

The masseter is a multipennate muscle. It has at least four internal aponeuroses (Lam et al. 1991) which run in parallel, alternately from the zygomatic arch and the mandible, and these aponeuroses provide anchorage for most of the muscle fibres. This arrangement organises muscle fibres to separate parts, which can generate internal force vectors that differ from adjacent parts of the muscle. This anatomical arrangement contributes to graded activation and the capacity of fine jaw movement control. Between these layers, muscle fibres are arranged in a multipennate form, and insert into the interleaved aponeuroses. However, some fibres, particularly those radiating from the ends of the aponeuroses insert directly into the ramus or the zygomatic arch (Fig. I-4). Differences in fibre orientation within the masseter have been noted. In the sagittal plane, the angle of the muscle fibres varies with respect to the vertical, from about 15° (deep posterior portion) to 35° (superficial anterior portion) (van Eijden and Raadsheer 1992). These differences in morphology suggest that the masseter is organised into functionally separate compartments. For example, fusion of the superficial and the deep layers in the anterior part of the muscle might indicate that it

functions as a single unit, while the posterior deep part, which has a different orientation of fibres from the other fibres, might be functionally separate. Indeed, EMG studies have provided evidence for selective activation within the masseter (see Review of Literature: section 3.2.2.1).

2.2.2 Temporalis Muscle

The temporalis, a fan-shaped muscle, originates from the temporal fossa, between the inferior temporal line and the infratemporal crest. The majority of fibres converge into a flat tendon which is attached to the upper, the anterior and posterior border and the medial aspect of the coronoid process. Some fibres insert directly onto the medial side of the mandibular ramus. There is an internal central aponeurosis extending from the tendon and dividing the temporalis into a superficial and a deep part. Principal tension can be produced by synergistic contraction of both superficial and deep fibre groups. However, differential activation of the superficial and deep fibres can occur, depending on the tasks (Wood 1986). Laterally, muscle fibres have different inclinations. The fibres run increasingly obliquely with the anterior fibres having a nearly vertical orientation, while the most posterior fibres are almost horizontal. The differences in orientation of the action lines of the muscle fibres suggest a variety of functions. The anterior portion elevates the jaw vertically, whereas the middle portion elevates and retrudes the mandible. The selective activation provides advantages for the muscle; for instance, if all fibres within the muscle are activated simultaneously, the tendon is lifted vertically. However, if only some fibres are active, the position of the tendon is shifted away from the centre line and some of the fibres on the opposite side may be stretched (Fig. I-1d). When viewed

frontally, the anterior part of the temporalis is bipennate and the fibres diverge at low pennation angles to the central aponeuroses (Hannam and McMillan 1994).

2.2.3 Medial Pterygoid Muscle

The medial pterygoid muscle, a thick quadrilateral muscle, has its origin at the medial aspect of the lateral pterygoid plate, the palatine bone and the maxillary tuberosity. It descends posterolaterally to form a strong tendinous lamina attached posteroinferiorly to the medial surfaces of the mandibular ramus and angle. The muscle is heavily pennated with short fibres (Fig. I-5). At least six aponeuroses in the muscle have been observed, and they form interleaved septa (Schumacher 1961). The septa are not always parallel and not all of them run through the whole muscle; some extend about two-thirds of the way. From the lateral aspect, fibre angulations are sufficiently variable to suggest different actions due to the more anteroposteriorly disposed and wide mandibular insertion (Hannam and McMillan 1994).

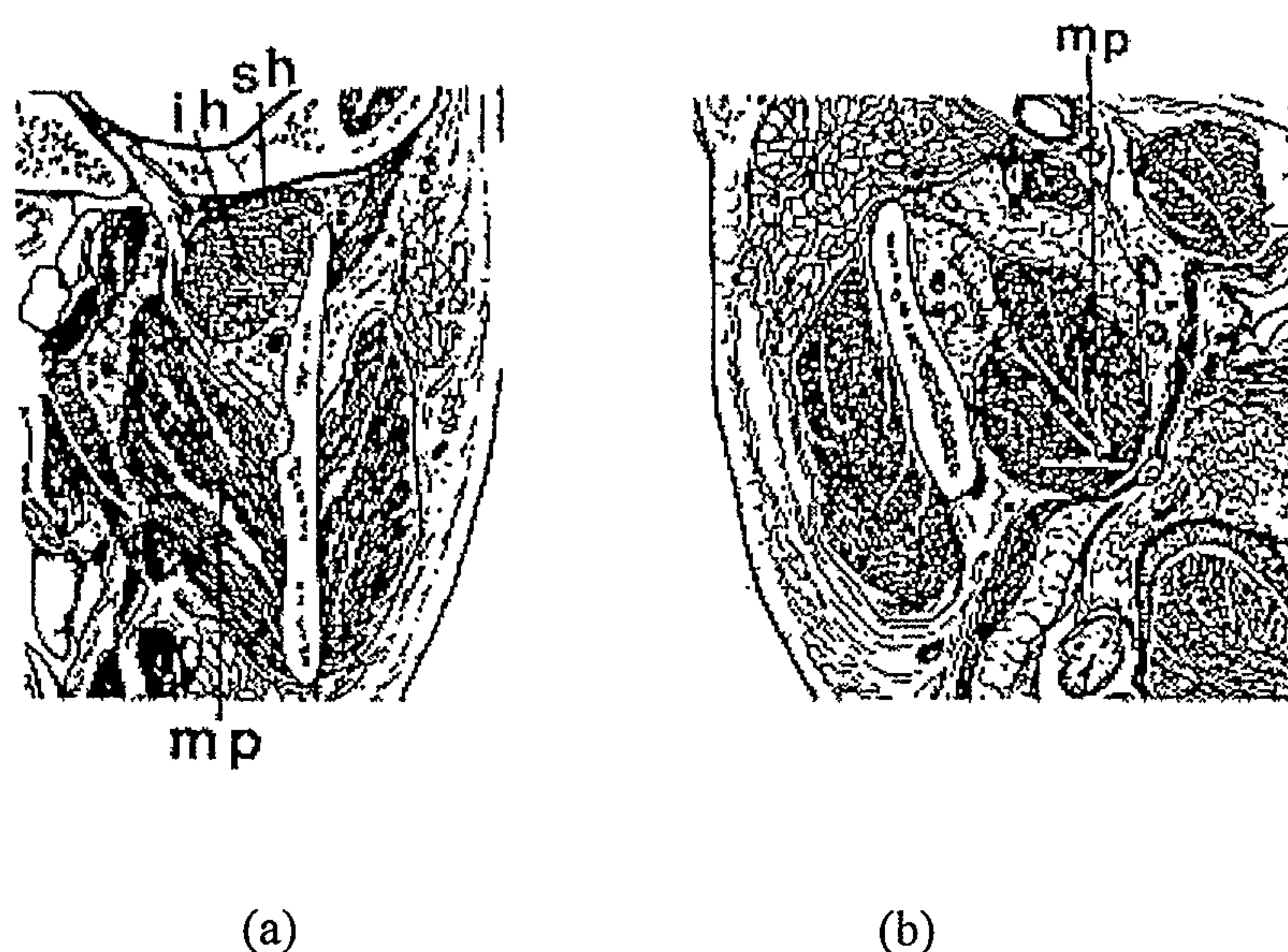


Fig. I-5 Sections illustrating tendons and pennation of the human medial pterygoid muscle: (a) frontal section and (b) horizontal section. Medial pterygoid muscle (mp), superior head (sh) and inferior head (ih) of the lateral pterygoid muscle are labelled. (Modified from Widmalm et al. 1987)

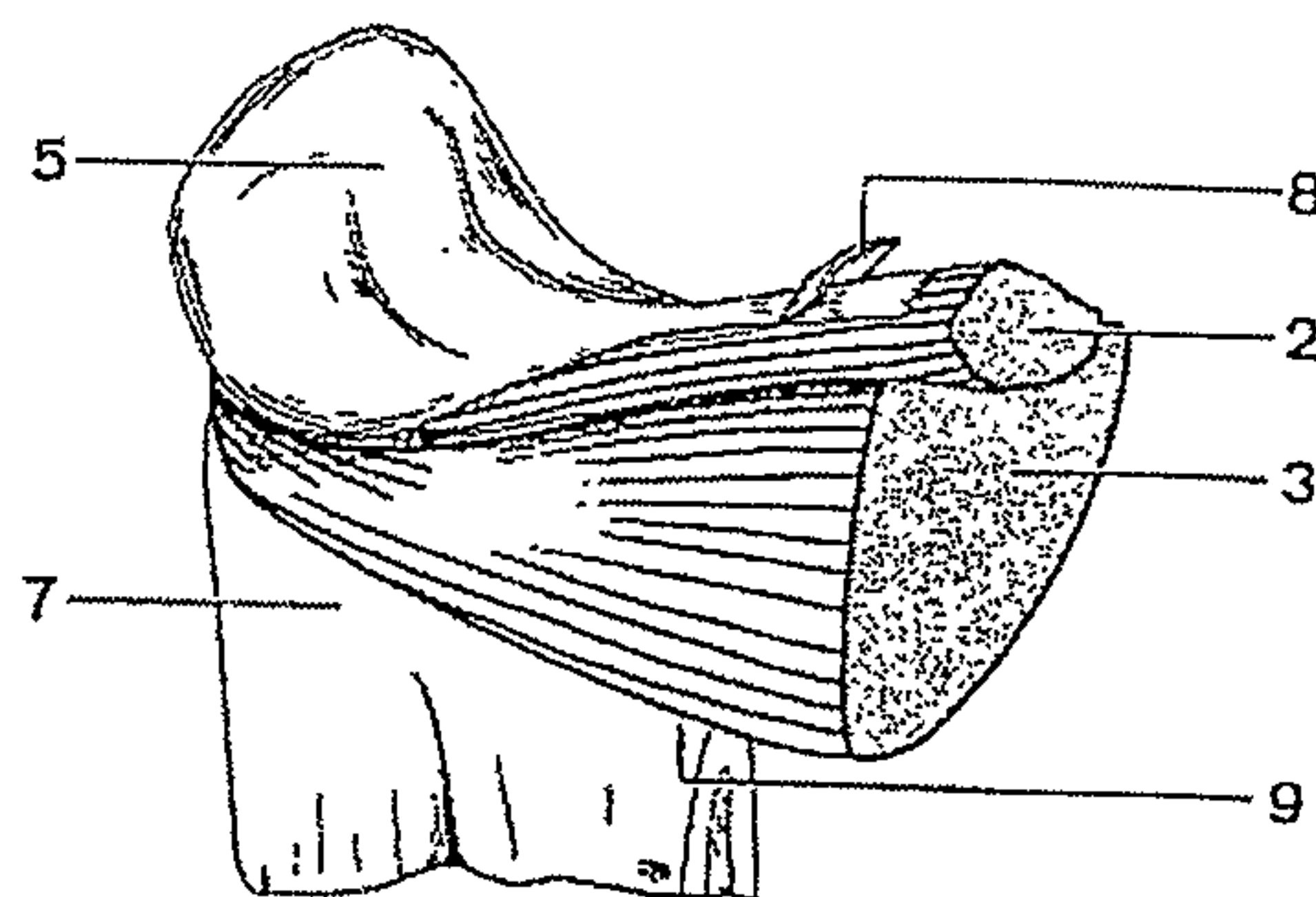
2.2.4 Lateral Pterygoid Muscle

The LP is classically considered to consist of two heads, a superior and an inferior head (Fig. I-6). The SHLP is small and flat in cross-section, whereas the IHLP is belly-shaped and is almost three times larger than the SHLP (Grant 1973; Wilkinson and Chan 1989). Both heads are separated at their origins by fibrous and adipose tissues and blend together to form a central pterygoid tendon at the point of insertion on the condylar neck (Hónee 1972; Wilkinson 1988). Although generally the LP appears to consist of two heads, the muscle is frequently composed of one or three heads (Troiano 1967; Birou et al. 1991; Ögütçen-Toller and Juniper 1994; Fujita et al. 2001). According to Bertilsson and Ström (1995), 65% of 89 original articles, published from 1879 to 1994, indicated that the LP is organised in two separate parts, 20% of articles stated that the muscle is a single

unit with a unipennate structure, while 15% of articles demonstrated three parts of the muscle: a SHLP consisting of two slips, named a superior and an inner or deep slips, a medial head and an IHLP (Fig. I-7).

The SHLP originates from the upper one-third of the pterygoid plate and from the infratemporal fossa which is made up of the greater wing of the sphenoid bone and the squamous part of the temporal bone, whereas the IHLP arises from the outer surface of the lateral pterygoid plate of the sphenoid bone and inserts on the neck of the condyle.

Fig. I-6 Medial view of left temporomandibular joint and the LP. 2 = SHLP; 3 = IHLP; 5 = disc; 7 = neck of condyle; 8 = disc attachment to the articular eminence; 9 = mandibular notch. (From Meyenberg et al. 1986)



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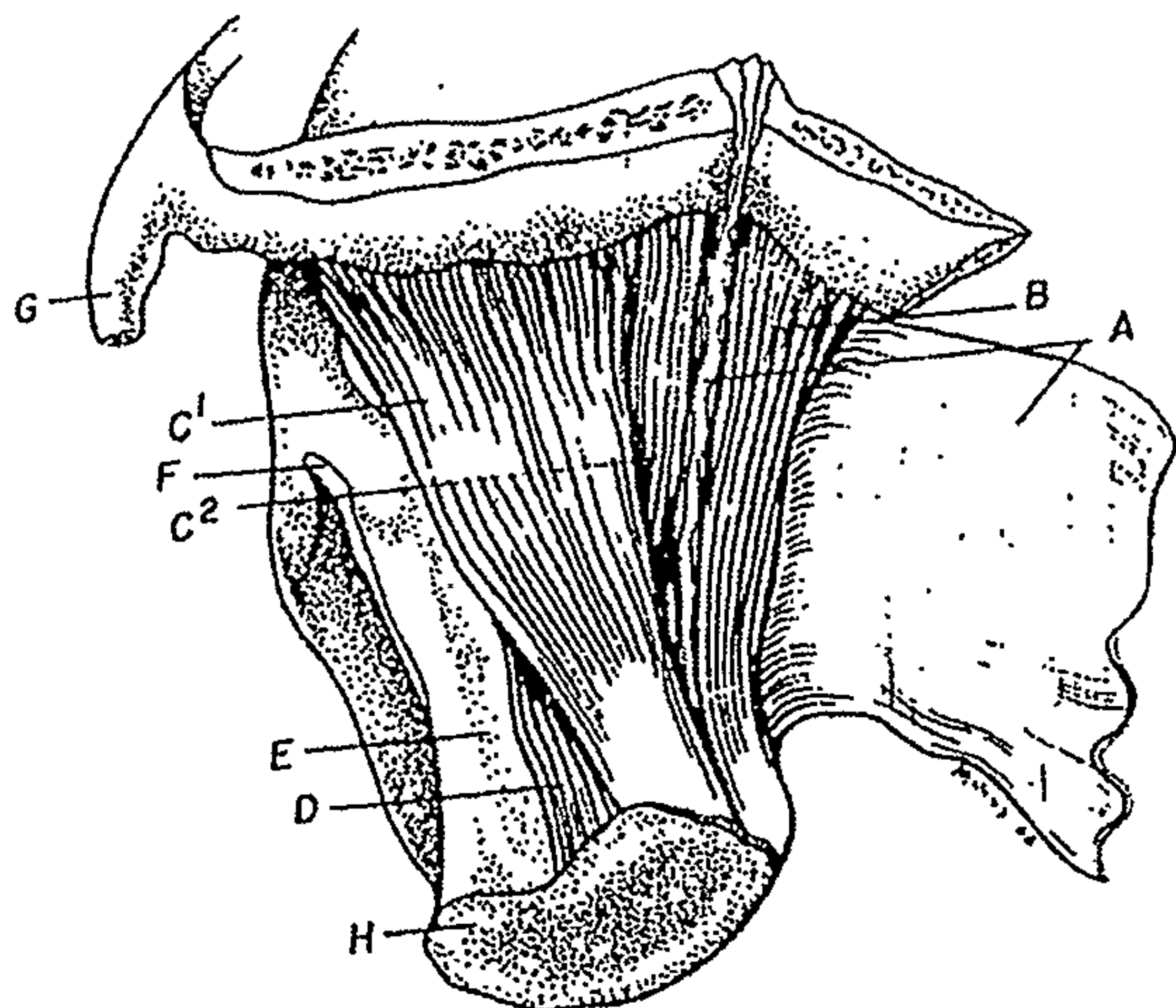


Fig. I-7 Superior view of the LP illustrating three parts of the muscle: (A) vascular fascia, (B) medial head, (C¹) superficial slip of SHLP, (C²) deep slip of SHLP, (D) IHLP, (E) ascending ramus of mandible, (F) coronoid process, (G) zygomatic process, and (H) articular capsule. (From Troiano 1967)

The exact attachment of the SHLP is controversial. Some studies showed that the SHLP fibres in all cases were attached mainly into the joint capsule and the disc (Porter 1970; Hónee 1972). The finding of attachment onto the joint capsule and disc led to the suggestion that this muscle is primarily involved in the positioning and stabilisation of the condyle and the disc (Hónee 1972). Many anatomical studies, however, have revealed that the majority of the SHLP fibres inserted to the pterygoid fovea of the condyle either directly or indirectly by fusing with tendons of the inferior part of the muscle, whereas a smaller portion of the SHLP fibres, only 20% of the uppermost fibres (Wilkinson 1988), insert into the antero-medial part of the disc-capsule complex (Mahan et al. 1983; Flatau and Klineberg 1985; Widmalm et al. 1987; Wilkinson 1988; Wilkinson and Chan 1989; Bittar et al. 1994; Schmolke 1994; Heylings et al. 1995; Naidoo 1996). It has also been reported that the SHLP muscle fibres interdigitating into the disc constituted only 2.4% - 6.3% of total LP insertion length (Bittar et al. 1994). A review by Bertilsson and Ström (1995) showed that a majority of the original articles (60%) indicated that the LP had three attachments and inserted into the disc, the temporomandibular joint capsule and the condyle (*i.e.*, McNamara, 1973). However, 30% of articles concluded that the majority of the LP muscle fibres inserted into the condyle, whereas only a few muscle fibres attached to the temporomandibular joint disc (*i.e.*, Wilkinson and Maryniuk 1983; Meyenberg et al. 1986; Wilkinson 1988) (Fig. I-8), and 10% of articles revealed that the LP conclusively inserted into the condyle.

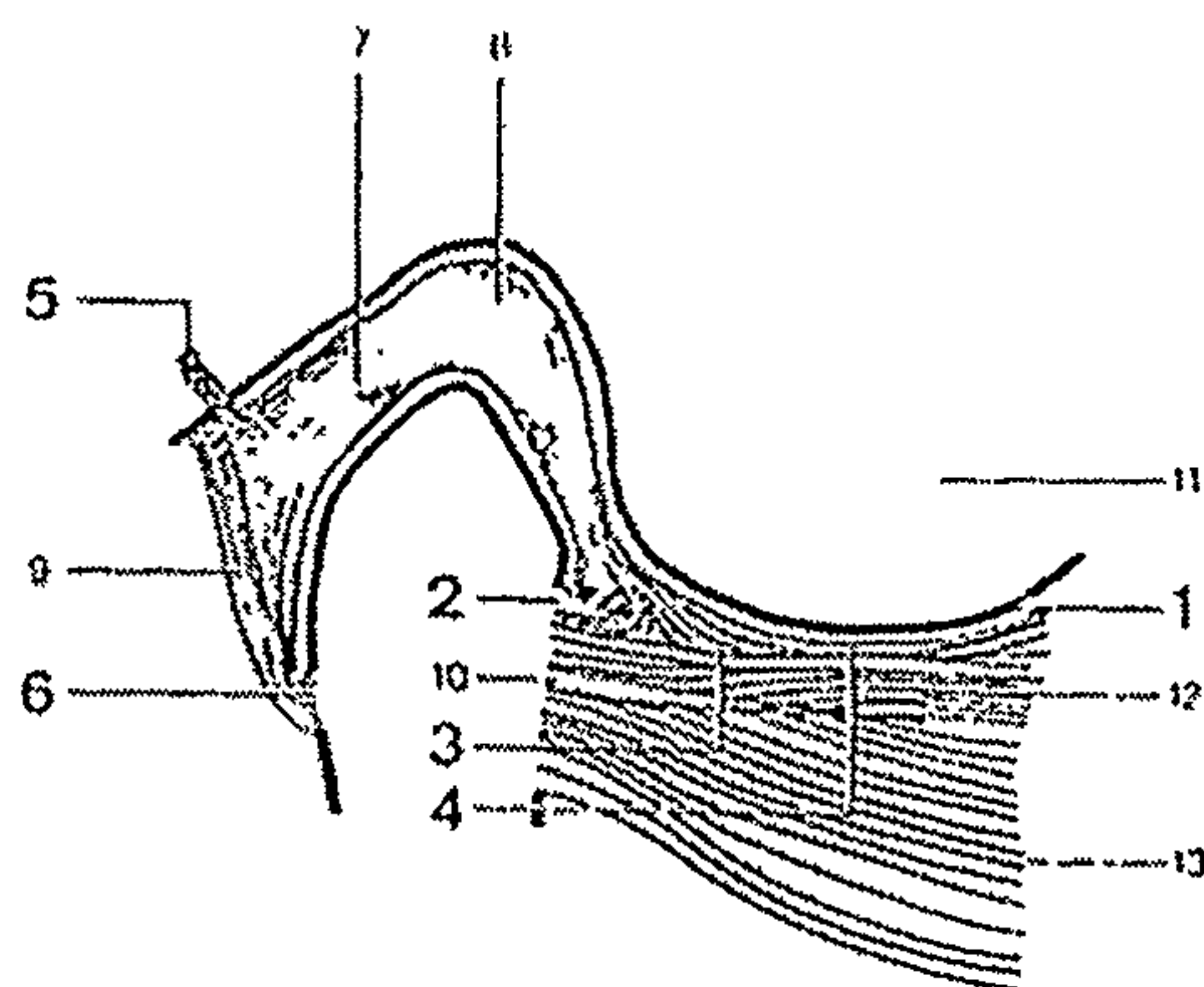


Fig. I-8 Sagittal section through the temporomandibular joint illustrating LP and disc attachments. The upper SHLP fibres are attached to the disc and the remaining fibres are inserted into the condyle. Most IHLP fibres are inserted into the condyle. 1 = disc attachment to the condyle; 2 = anterior disc attachment to the condyle; 3 = disc attachment to the LP; 4 = zone of insertion of the LP; 5 = attachment to the petrotympanic fissure; 6 = posterior attachment of the disc to the condyle; 7 = bilaminar zone; 8 = disc; 9 = posterior wall of the capsule; 10 = middle tendon of the LP; 11 = articular eminence; 12 = SHLP; 13 = IHLP. (From Meyenberg et al. 1986)

The preponderance of differing results might be caused by the different methodological approaches (Meyenberg et al. 1986; Bittar et al. 1994; Bertilsson and Ström 1995; Heylings et al. 1995; Naidoo 1996) and biologic factors (Bertilsson and Ström 1995). According to the study of Heylings et al. (1995), on a macroscopic level, the SHLP muscle fibres appeared to attach directly to the disc. However, in a microscopic study, the muscle fibres did not have their primary attachment directly to the disc but rather to the pterygoid fovea and the anterior aspect of the joint capsule. In addition, the thickness of the sections for histological examination has been taken into account in considering the varying conclusions (Heylings et al. 1995; Naidoo 1996). Since the fibres of the SHLP run posteriorly, inferiorly and laterally toward the condyle and the disc, it is impossible to follow the individual muscle fibres from its origin to the ultimate point of attachment if the serial sections of the specimens are thick (Heylings et

al. 1995; Naidoo 1996). Moreover, the biologic factors including remodelling, sex differences, or age changes (Osborn 1985) could contribute to the lack of consensus regarding the configuration of the disc-muscle interface.

The morphological features of insertion of both heads are important for understanding possible mechanisms of TMD. Based on anatomical findings, such as location of LP insertion and muscle orientation, theories of muscle hyperactivity, hypoactivity and incoordination between two heads of the LP have been proposed as possible mechanisms of internal derangement of the temporomandibular joint (Porter 1970; Farrar and McCarty, Jr. 1979; Johnstone and Templeton 1980; Mahan et al. 1983; Juniper 1984; Gibbs et al. 1984; Carpentier et al. 1988; Dahlström 1989; Liu et al. 1989; Okeson 1998; Hiraba et al. 2000). However, a study by Wongwatana and coworkers (1994) showed that the SHLP contributed to the anteromedial displacement of the disc only in cases of prior damage to the disc. If the SHLP is inserted entirely or predominantly into the foot of the disc, and the IHLP is inserted into the neck of condyle, dysfunction could be brought about by incoordination in onset and/or duration of activity between these muscles (Klineberg, 1991). Since it appears that the SHLP is mainly attached into the condyle, although there is a part of the muscle inserting to the disc, it seems unlikely that this small proportion of the fibres would cause the disc to shift independently from the condyle (Meyenberg et al. 1986; Wilkinson 1988; Bittar et al. 1994; Heylings et al. 1995). Indeed, manual traction on the SHLP in cadavers has been reported to bring both condyle and disc forward together (Meyenberg et al. 1986; Widmalm et al. 1987; Wilkinson 1988; Heylings et al. 1995), which would occur if there is always a uniform distribution

of activity throughout SHLP as in functionally homogeneous muscle. However, the possibility of selective activation of those SHLP fibres inserting into the disc could occur if the SHLP is a functionally heterogeneous muscle.

The LP has a unique architectural feature that its muscle fibre alignment allows a major vector component of the total force output from the muscle to be generated in the horizontal plane (van Eijden and Brugman 1997). The LP is therefore ideally suited to generating horizontal movements.

The SHLP and IHLP are however oriented in different directions. In the horizontal plane, the SHLP fibres are aligned 26° to the sagittal plane, while the fibres of the IHLP run laterally and posteriorly to the condyle at an angle of 45° to the sagittal plane (Hónee 1972). The SHLP fibres, in the sagittal plane, run downward and develop an angle of 23° to the Frankfort Horizontal Plane (FHP), while the IHLP fibres are aligned at an average angle of approximately 10° upward (Hónee 1972). The differences in angulation of fibres lead to the proposal of functional differentiation between the heads. Further, the direction of the action lines of the SHLP and IHLP are different (van Eijden et al. 1995). The action lines in this latter study have been estimated by registering spatial coordinates of origins, insertions of the SHLP and IHLP, and several skull markers of cadavers for computer model simulations. Table I-1 summarises the direction of action lines in angles. The sagittal angle is defined as the angle between the action line and the vertical axis in the sagittal plane; the frontal angle is defined as the angle between the action line and vertical axis in the frontal plane; and the transverse angle is defined as the angle between the action line and the anteroposterior axis in the transverse plane.

Table I-1 Direction of action lines in angles of the superior and the inferior heads of the lateral pterygoid. (Modified from van Eijden et al. 1995)

	Mean	SD
<i>Inferior head</i>		
sagittal angle	120.7	11.7
frontal angle	28.4	8.4
transverse angle	47.4	7.3
<i>Superior head</i>		
sagittal angle	76.4	7.8
frontal angle	16.7	11.5
transverse angle	41.7	8.0

See text for definition of angles.

Within the SHLP and IHLP, there is a marked convergence of muscle fibres onto a small insertion site on the condylar fovea, capsule and disc from a broad origin at the roof of the infratemporal fossa and lateral pterygoid plate. This marked change in fibre alignment from the uppermost to the lowermost muscle fibres, and from the medial to the lateral side of the muscle provide the opportunity for a range of force vectors capable of moving the condyle at the appropriate rate, and for the appropriate range and direction to effect the desired horizontal jaw movement. Further, in some cases where the SHLP is composed of two slips (Fig. I-7), the deep slip has a more acute angle to the condyle than the superior slip and inserts mainly into the medial portion of the articular capsule (Troiano 1967).

These differences in angulation of different components of the SHLP suggest the capability of producing different force vectors with differential activation within the head.

The SHLP is composed of parallel-arranged fibres with a few small fields of tendinous tissues (Hónee 1972; Sato et al. 1992). The IHLP appears to contain tendinous strips invading the muscle belly, especially at its origin (Widmalm et al. 1987; Sato et al. 1992) and these may provide some anatomical basis for different functional compartments within the muscle (Fig. I-9). A recent study (van Eijden and Brugman 1997) reported that the pennation angle of the IHLP was $1.3 \pm 3.3^\circ$, whereas there was no evidence of pennation in the SHLP.

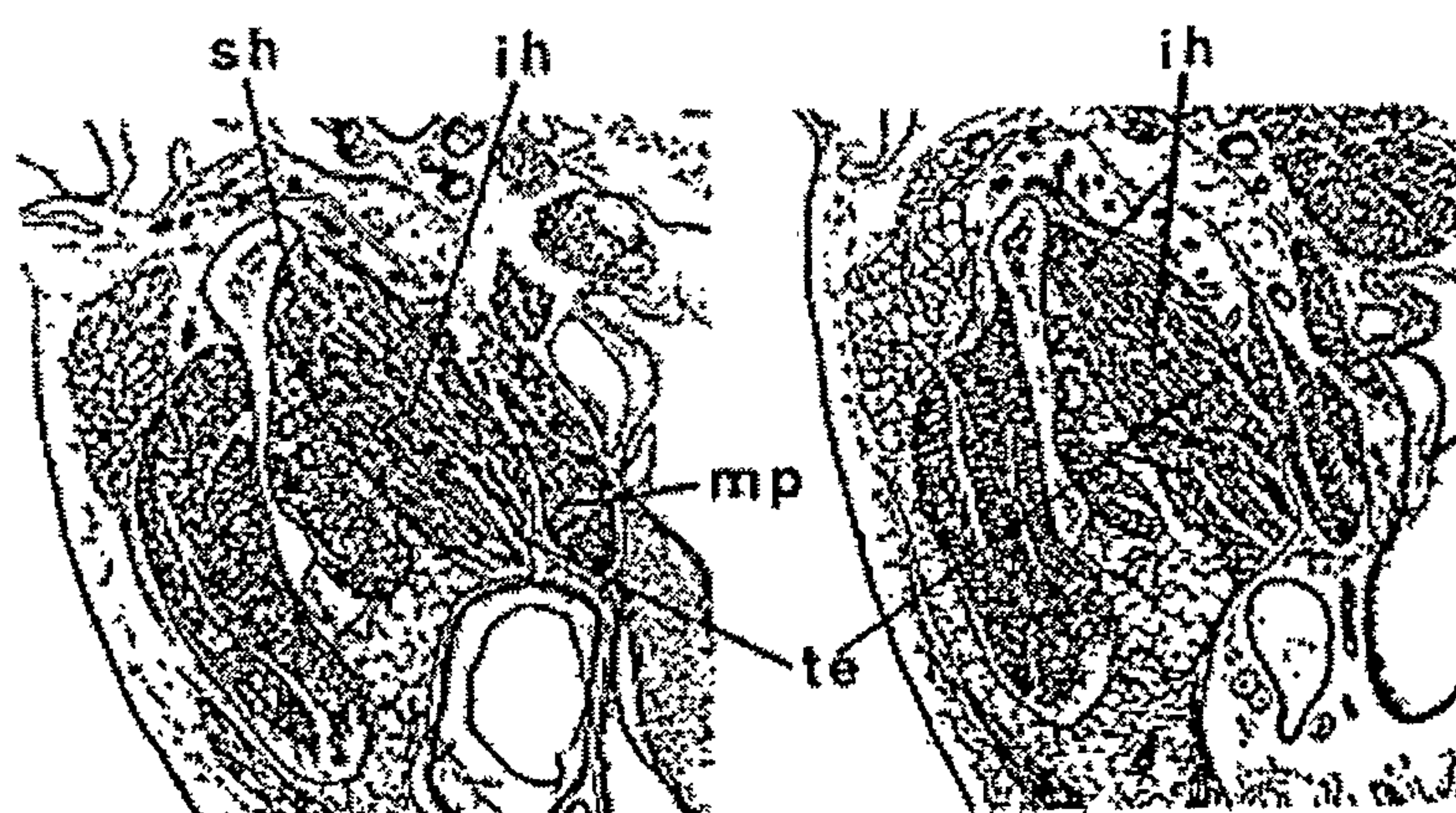


Fig. I-9 Horizontal sections through the right half of the head showing tendons within the inferior head: (sh) superior head, (ih) inferior head, (te) tendon within the inferior head, (mp) medial pterygoid muscle. (Modified from Widmalm et al. 1987)

The internal architecture of the LP (*eg.*, the pennation) is rather simple compared to other jaw muscles, such as the masseter. However, the LP constitutes a system

of fibres which could allow the differential activation. Hannam and McMillan (1994) have proposed that the

“lateral pterygoid is partitioned anatomically in a very simple fashion and seems to be designed to function differentially more by virtue of its separate origins than by any complex internal arrangement of septa” and

“.....the system of fibres acts as one muscle, with varying amounts of evenly graded activity throughout its entire range, with the distribution shaded according to the biomechanical demands of the task.”

2.2.5 Digastric Muscle

The digastric muscle consists of two bellies, an anterior and a posterior belly, separated by a cylindrical intermediate tendon connected with the hyoid bone via a sling. The anterior belly arises from the digastric fossa while the posterior belly arises from the digastric notch on the medial surface of the mastoid process and both of them insert into the intermediate tendon. Both bellies are active simultaneously during all mandibular movements, chewing and swallowing (Munro 1974). Nevertheless, they may occasionally be activated non-synchronously (Widmalm et al. 1988), and there is evidence for functional heterogeneity within the rabbit digastric muscle (Tsuruyama et al. 2002).

2.3 Physiological Cross Section, Fibre and Sarcomere Length

As well as the complex muscle fibre orientation, there is different total cross-sectional fibre areas (the physiological cross-sectional area = PCS) and fibre length between different jaw muscles and even within the same muscle. The PCS

is directly proportional to the maximum tetanic tension generated by the muscle, whereas fibre length is proportional to muscle velocity. The PCSs of the jaw closers are larger than those of the jaw openers (van Eijden and Brugman 1997). Of the jaw closers, the temporalis has the largest PCS ($13.25 \pm 3.30 \text{ cm}^2$) and the medial pterygoid has the smallest PCS ($6.00 \pm 1.24 \text{ cm}^2$) (van Eijden and Brugman 1997). Within the muscles, the PCSs in the superficial masseter, anterior temporalis and posterior medial pterygoid are larger than in the deep masseter, posterior temporalis and anterior medial pterygoid, respectively (van Eijden et al. 1996; van Eijden and Brugman 1997).

Of the jaw openers, the LP has a larger PCS than the digastric muscle. The IHLP is approximately 3 times greater in PCS than the SHLP (van Eijden and Brugman 1997). Thus, the expected maximal force which can be produced by the IHLP is about 3 times greater than that produced by the SHLP on the assumption of similar internal architectures. There is no difference in PCSs between the posterior and anterior bellies of the digastric muscle (van Eijden and Brugman 1997).

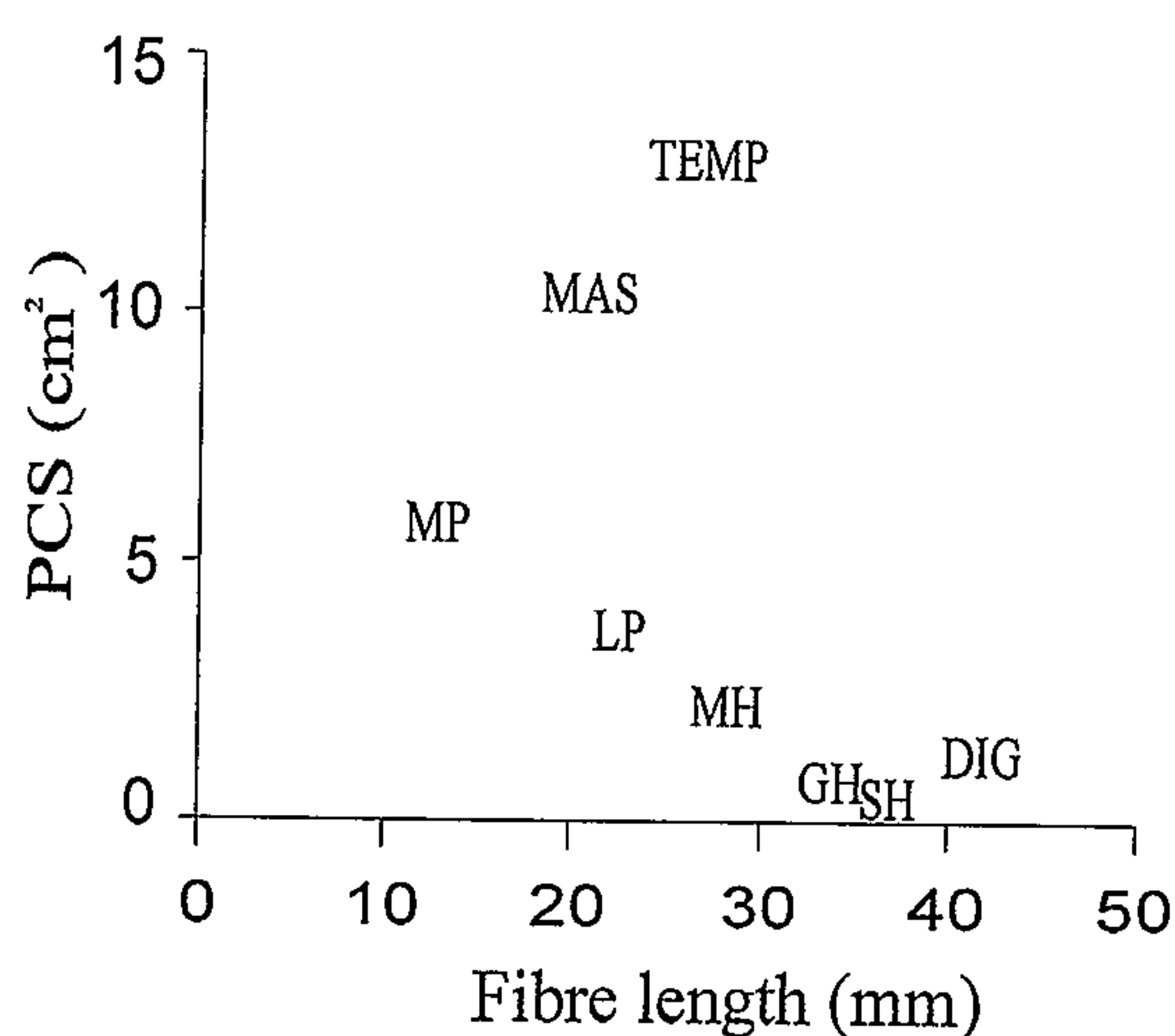
The jaw closers have shorter sarcomeres and fibre lengths than the jaw openers. The digastric muscle has the longest fibre length (van Eijden and Brugman 1997). Regional differences in fibre, tendon and sarcomere length have also been demonstrated. The fibre, tendon and sarcomere length in the masseter muscle decreases with depth in the muscle. An earlier study (van Eijden and Raadsheer 1992) revealed that the longest fibres in the masseter muscle were in the anterior part and these were 35% longer than those in the posterior portion. The fibres in the deeper parts were 5% shorter than those in the superficial part. In addition,

sarcomeres in the deep layer were shorter than those superficially, and the posterior deep part had shorter sarcomeres than the anterior deep part. In the temporalis, the fibre length of the anterior part was significantly larger than in the posterior temporalis (van Eijden et al. 1996; van Eijden and Brugman 1997). However, there was no regional difference in sarcomere length within the LP (van Eijden et al. 1995).

Differences in PCS, fibre and sarcomere length contribute to differences in function. As stated above, muscle force is proportional to the PCS, and muscle velocity and excursion are proportional to the fibre length. These two parameters are summarised for human jaw muscles in a scatter plot (Fig. I-10), and can be used to make general comparisons among the jaw muscles. For example, the LP is characterised by relatively long fibres and a small PCS, whereas the medial pterygoid muscle has relatively short fibres and a large PCS. Accordingly, the LP can generate 1.7 times greater range of motion and velocity than the medial pterygoid muscle (ratio of fibre lengths: 1.7), whereas the medial pterygoid muscle is capable of producing 1.6 times (ratio of PCSs: 1.58) greater force (van Eijden et al. 1995; van Eijden and Brugman 1997). Therefore, the medial pterygoid appears suited for the generation of relatively larger forces, whereas the long fibres in the LP mean that this muscle is most suited for (a) shortening over long distances and (b) providing support for near-isotonic rather than near-isometric conditions requiring power (Hannam and McMillan 1994). However, Honée (1972) proposed that the LP is primarily involved in the positioning and stabilisation of the disc-condyle complex that is, it is involved in near-isometric conditions rather than being a muscle having a better propensity for near-isotonic

conditions. Indeed, there are diverging opinions as to the normal functional activities of the LP. According to Bertilsson and Ström (1995), 75% of original articles reported that the muscle had three main functions: to produce lateral mandibular movements, to move the disc and condyle in a forward direction, and to stabilise the disc-condyle complex. The second opinion (20% of articles) was that the muscle has only two functions: to stabilise the disc during rotation and translation and to produce lateral jaw movements, and the other suggestion (5% of references) was that the muscle acts as a jaw opener without producing lateral forces. Thus, the function of this muscle is still disputed. The present study will provide data on its activities during defined jaw movements.

Fig. I-10 Scatter plot of the fibre length and physiological cross-sectional areas (PCS) of muscles in human masticatory muscles. Fibre length is proportional to muscle excursion, and cross-sectional area is proportional to maximum muscle force. DIG = digastric; GH = geniohyoid; LP = lateral pterygoid; MASS = masseter; MH = mylohyoid; MP = medial pterygoid; SH = stylohyoid; TEMP = temporalis. (Figure adapted from data from van Eijden et al. 1997)



In summary, the jaw closers are characterised by relatively large PCSs, large percentages of tendinous tissue, short fibres and large pennation angles, whereas the jaw openers have relatively small PCSs, small percentages of tendinous tissue, long fibres and small pennation angles. Therefore, the jaw closers can be

expected to produce larger force than the jaw openers, and the jaw openers can produce larger excursions and higher shortening velocities than the jaw closers. The fact that different muscles contain such different designs suggests that architecture of the muscle fibre is under tight control. Physiological studies will provide insight into the rationale for muscles in which the functions are not clear.

The available information about intramuscular architecture supports the concept that different regions of the jaw muscles can be activated independently. Internal aponeuroses establish anatomical compartments, and different orientations of muscle fibres allow muscles to have various directions of pull. In addition, different cross-sectional fibre areas, as well as different sarcomere and fibre lengths within a muscle, add a further level of complexity to the internal jaw muscle architecture and provide ample basis for functional heterogeneity in the jaw muscles.

The biomechanical effects of jaw muscles depend not only on their capabilities of generating force or movement, determined primarily by muscle architecture, but also on their three-dimensional position relative to the temporomandibular joints.

The amount of sarcomere lengthening/shortening during jaw movement is determined by the ratio between the length of the fibre and the moment arm.

With a long moment arm, fibre excursion is larger than with a short moment arm.

Since the LP has relatively large attachment areas (see Review of Literature: section 2.2.4), different muscle regions have different moment-arm lengths.

Hence, during jaw movement, muscle fibres in the various muscle regions will undergo different length changes. The model simulation during jaw opening

showed that the amounts of sarcomere shortening in the SHLP (0.87 μm) and IHLP (0.70 μm) were different (van Eijden et al. 1995). Due to an absence of intramuscular differences in fibre lengths, different sarcomere excursions within the muscle are primarily due to different moment-arm lengths. The model also predicted that during jaw movement the distribution of active tension is not uniform but will vary continuously throughout the muscle, due to differential lengthening/shortening of sarcomeres. The suggestion of differential activation of the LP through the differences in fibre alignment is in agreement with the proposal by Hannam and McMillan (1994).

2.4 Muscle Fibre Types

Not all skeletal muscle fibres have the same physiological and histochemical properties. Different types of fibres are classified on the basis of the contractile and fatigue properties of motor units as well as reactions of the intracellular proteins, mitochondrial enzymes and metabolic substrates of the muscle fibres to the histochemical enzymes. Various systems have been proposed. Table I-2 presents some of the popular classifications of muscle fibres.

On the basis of histochemistry, human muscle fibres have been divided into five groups: ATPase (adenosine triphosphatase) type I, type IIA, type IIB, type IIC and type IM fibres. The different histochemical types of muscle fibre appear to correspond to specific physiological types. Thus, type I corresponds with S fibres (slow contracting and fatigue resistant or predominantly aerobic fibres), type IIA with FR fibres (fast contracting and fatigue resistant fibres), type IIB with FF fibres (fast contracting and fatigue susceptible or predominantly anaerobic fibres)

and type IM with FI fibres (fast contracting and intermediate fatigue resistant fibres). There are few numbers of type IIC fibres, and they appear to have no physiological correlation. The characteristics of the three main skeletal muscle fibre types, type I, type IIA and type IIB fibres, are summarised in Table I-3.

Table I-2 Nomenclature of mammalian skeletal muscle fibres.

ATPase histochemistry	MHC immunohistochemistry	Physiological properties	Metabolic properties
Type I	Type I	S	SO
Type IIA	Type IIA	FR	FOG
Type IIB	Type IIX	FF	FG

SO = slow twitch oxidative muscle fibres	S = slow contracting and fatigue resistant fibres
FOG = fast twitch oxidative glycolytic muscle fibres	FR = fast contracting and intermediate fatigue resistant fibres
FG = fast twitch glycolytic fibres	FF = fast contracting and fatigue susceptible.

Table I-3 Comparison of histochemical skeletal muscle fibre types. (Modified from Schaaf et al. 1990)

Characteristics	Type I	Type IIA	Type IIB
<i>Metabolic</i>			
Capillaries	Abundant	Intermediate	Sparse
Glycolytic capacity	Low	Intermediate	High
Oxidative capacity	High	High	Low
Myoglobin content	High	Intermediate	Low
Glycogen content	Low	Intermediate	High
<i>Physiological</i>			
Function	sustained force as in posture	- powerful, phasic movements –	
Fibre diameter*	Small	Intermediate	Large
Rate of fatigue	Slow	Intermediate	Fast
Motor unit size	Small	Intermediate	Large
Recruitment order	Early	Intermediate	Late
Power output	Low	Intermediate	High
Contraction velocity	Slow	Fast	Fast
Twitch duration	Long	Short	Short
Myosin ATPase	Slow	Fast	Fast
Ca ⁺⁺ sequestration	Slow	Rapid	Rapid

* In jaw muscles, Type I fibres have larger diameters than Type II.

In the last decade, immunohistochemical techniques have been widely used to classify muscle fibre types, especially in masticatory muscles, since the ATPase histochemistry does not give a complete image of the myosin heavy chain (MHC) contents of muscle fibres, which largely determines the speed of contraction of muscle fibres. Based on the immunohistochemical techniques, at least three different isoforms of MHC are expressed in limb muscles: MHC-I, MHC-IIA, and MHC-IIX (or MHC-IID). In human, MHC-IIB is said to be absent. These three isoforms demonstrate an increasing speed of contraction. Adult human masticatory muscles contain five muscle fibre types: MHC-I, IIA, IIX, fetal and cardiac α (Butler-Browne et al. 1988; Korfage and van Eijden 1999; Korfage et al. 2000; Korfage and van Eijden 2000; Korfage et al. 2001). The two latter types are not expressed in limb and trunk muscles. MHC-fetal and cardiac α are normally expressed in developing muscle fibres and in the myofibrils of the atrium, respectively (Butler-Browne et al. 1988; Bredman et al. 1991; Korfage and van Eijden 1999; Monemi et al. 1999; Korfage et al. 2000; Korfage and van Eijden 2000; Korfage et al. 2001). In the masseter, MHC-fetal isoform has been shown to increase during aging (Monemi et al. 1999). The significance of MHC-fetal and MHC-cardiac α in masticatory muscles is not known. Muscle fibres can contain either one single MHC isoform (pure fibres) or a combination of different ones (hybrid fibres) (Pette and Staron 2000). MHC-fetal and MHC-cardiac α are always expressed in combination with other MHCs.

ATPase-classified fibre types I, IIA, and IIB are found to correlate with the immunohistochemically classified MHC-I, MHC-IIA and MHC-IIX fibre types. The ATPase technique cannot distinguish between MHC-IIX and MHC-IIB and

is unable to detect MHC-fetal and MHC-cardiac α , which could contribute to different physiological properties of fibres.

Myosin heavy chain largely determines the speed of contraction of the muscle fibre. It has been shown in the rabbit masseter that the contractile speeds of fibres increased in the order of MHC I, α , IIA, IIX (Kwa et al. 1995). However, the contractile speed of MHC-fetal is not known. The contractile speed of hybrid fibres lies between the contractile speed of the MHC isoforms they contain (Schiaffino and Reggiani 1994; Kwa et al. 1995). Hybrid fibres indicate fibre type transformation as a result of an overall increase or decrease of activity in a muscle. The following transformation pathway has been suggested: $I \leftrightarrow I/IIA \leftrightarrow IIA \leftrightarrow IIA/IIX \leftrightarrow IIX \leftrightarrow IIX/IIB \leftrightarrow IIB$ (Gorza 1990; DeNardi et al. 1993). The coexpression of different MHC isoforms provides a continuous range of physiological properties and facilitates a greater variance in shortening velocities and force generation than is possible in pure fibres (Kwa et al. 1995). It could also allow a smooth transition of force regulation needed in movements of the jaw muscles.

Compared to limb and trunk muscles, masticatory muscles have more hybrid fibres and many of them coexpress MHC-fetal and/or MHC-cardiac α (Korfage and van Eijden 1999; Korfage et al. 2000; Korfage and van Eijden 2000; Korfage et al. 2001). Furthermore, jaw muscle fibres have smaller cross-sectional areas than limb muscle fibres. It has been reported that in human masticatory muscles, type I fibres are larger than type II fibres, and this contrasts with limb and trunk muscles where type I fibres have smaller diameters than those of type II fibres (Ringqvist 1974; Eriksson and Thornell 1983).

Different muscles are responsible for different functions and have different contractile properties. Finger and eye muscles, for instance, contract rapidly and become fatigued easily, whereas postural muscles contract slowly and can maintain contraction for long periods. Differences in muscle functions are due to different numbers of each muscle fibre type. The jaw closers have architectural features (*i.e.*, short sarcomeres and large PCSs) that suit them for force production, whereas the jaw openers are better equipped for generating velocity and displacement. The difference in function of these two groups of muscles is also reflected in the fibre-type composition. According to Korfage et al. (2000, 2001), the jaw closers (which they classify as: temporalis, masseter, medial pterygoid, SHLP and IHLP muscles) have more MHC-I fibres, whereas the jaw openers (their classification: digastric, mylohyoid, geniohyoid and styloid muscles) contain more MHC-IIA fibres. This suggests that the jaw closers are suited for more tonic or prolonged activity, whereas the jaw openers are involved in phasic activity. Moreover, the jaw closers contain more hybrid fibres than the jaw openers (Korfage et al. 2000; Korfage et al. 2001). The higher proportion of hybrid fibres in the jaw closers provides a greater variance in shortening velocity and force generation, which may contribute to the better force-regulating ability of the jaw closers. In these studies, the LP was included among the group of jaw closers, since the proportions of pure and hybrid fibres of the LP had more similarities with the jaw closers than with the jaw openers.

Each masticatory muscle has different proportions of the different muscle fibre types. Within each muscle, the proportion of fibre types also varies when comparing anterior to posterior regions and superior to deep areas of the same

region. Variation in muscle fibre composition clearly points towards functional heterogeneity within the muscle. Thus, different parts of a muscle may be better suited for specific tasks. For example, the deep part of the temporalis muscle which is rich in type I fibres is most suited to producing fine movements and postural activity rather than gross movements (Eriksson and Thornell 1983).

2.4.1 Masseter Muscle

The masseter contains approximately 62% of MHC-I fibres (pure and hybrid), 20% of MHC-IIA and 30% of MHC-IIX. The deep masseter contains more MHC-I fibres and less fibres expressing MHC-fetal than the superficial masseter (Korfage et al. 2000). Further, the posterior portion of the superficial masseter contains less MHC-I (Monemi et al. 1999; Korfage et al. 2000) and more MHC-IIX fibres than the anterior portion (Korfage et al. 2000). This is consistent with the ATPase study by Eriksson and Thornell (1983) which reported that the anterior parts contained more ATPase type I fibres (range 64-72%) than the posterior part (range 47-62%). The large proportion of type I fibres suggests that the muscle is related to precise movements and the maintenance of jaw posture. The anterior parts of the muscle are also responsible for finer movements, and the posterior parts contribute to rapid jaw closing and coarser functional movements. Mao et al. (1992) postulated that by being closer to the application point of the bite force, that is the first molar teeth, and by containing more type I motor units, the anterior parts have more precise control over bite force, whilst the posterior parts have the capacity for rapid jaw closing as they are nearer to the jaw joint and consist of more fast contracting fibres. However, Nordstrom and Miles (1990) suggested that the physiological properties of human masseter motor units are

poorly related with histochemical type. They reported that the human masseter was composed predominantly of fast-twitch motor units with a broad spectrum of fatigability, and very few physiological type S units were found, while a substantial population of type I fibres in the masseter have been reported.

2.4.2 Temporalis Muscle

The highest proportion of fibres in the temporalis is the MHC-I fibre (45%). The muscle also contains MHC-IIA (14%), IIX (11%) and hybrid fibres (31%) (Korfage and van Eijden 1999). Fibre composition differs within the muscles. The anterior part contains more pure MHC-I fibres than the middle and posterior parts, although the number of MHC-IIA and MHC-IIX fibres are not significantly different among the muscle portions (Korfage and van Eijden 1999). However, this study did not investigate the difference between the deep and superficial temporalis. A histochemical study (Eriksson and Thornell 1983) showed that, in the deep part of the temporalis, ATPase type I fibres predominate and they represent approximately 81% of the total fibre content. The difference in muscle fibre composition within the temporalis suggests functional heterogeneity in this muscle and this is supported by EMG studies (see Review of Literature: section 3.2.1.2). It is likely that the anterior and deep temporalis is better suited for regulating the magnitude of the chewing or biting force, supporting jaw posture and for fine jaw movements.

2.4.3 Medial Pterygoid Muscle

The MHC-I fibres are the predominant fibre type in the medial pterygoid muscle (32%) (Korfage and van Eijden 2000). The muscle contains 5% of MHC-IIA,

11% of MHC-IIX and 52% of hybrid fibres. There are more MHC-I fibres in the anterior and lateral parts than in the posterior and medial parts respectively, and more MHC-II fibres, including type IIA and IIX, are found in the posterior and medial parts than in the anterior and lateral parts (Korfage et al. 2000; Korfage and van Eijden 2000). The anterolateral part has the highest proportion of MHC-I, while the posteromedial part has the highest proportion of MHC-II (Korfage et al. 2000). Eriksson and Thornell (1983) also found a predominance of ATPase type I fibres in the anterior part. Thus, the anterior part appears to be responsible for precision of jaw movement.

2.4.4 Lateral Pterygoid Muscle

The LP is composed of 33% and 36% of MHC-I fibres in the SHLP and IHLP respectively. More MHC-IIA fibres have been found in the SHLP (23%) than in the IHLP (15%) (Korfage et al. 2000; Korfage and van Eijden 2000). There is a relatively large proportion of hybrid fibres containing a great variety in the expression of MHC (40% in the SHLP and 45% in the IHLP) (Korfage et al. 2000; Korfage and van Eijden 2000). Compared to the other jaw closing muscles, the LP contains more MHC-IIA (pure and hybrid fibres) and less MHC-IIX fibres (Korfage et al. 2000).

Within the IHLP more MHC-I fibres were found in the lower than the upper part, whereas there was no significant difference in the distributions of fibre types among the muscle parts of the SHLP (Korfage et al. 2000; Korfage and van Eijden 2000). The difference in fibre composition may reflect different functions within the IHLP.

2.4.5 Digastric Muscle

The MHC-IIA fibres are the predominant fibre type in the digastric muscle (44%), followed by MHC-I (30%), MHC-IIX (18%), and hybrid fibres (8%) (Korfage et al. 2000). The anterior belly contains more MHC-IIX fibres, whereas the posterior belly contains more MHC-IIA fibres. The large proportion of MHC-II fibres in both anterior and posterior bellies suggests that the digastric muscle contributes to rapid jaw opening which is rather imprecise. Both IHLP and digastric muscles are strongly active in jaw opening, but their roles in jaw opening are distinct with the digastric being thought as a prime mover (Munro 1972), while the LP is thought to have a stabilising role (Carlsöö 1956). These different functions are consistent with the different fibre type compositions.

2.5 Muscle Spindles

Muscle spindles have a complex organisation, are spindle-shaped, are composed of intrafusal or modified muscle fibres and have independent sensory and motor innervations from the main body of the muscle. Muscle spindles are arranged in parallel with the extrafusal or main muscle fibres. They are sensitive to changes in muscle length, and are associated with refinements of movement. Muscles with high spindle density, such as the small muscles of the hands, allow the generation of fine finger and hand movements or maintenance of posture, whereas muscles with low spindle density provide more gross movements. Slow contracting muscles have higher spindle density than fast contracting muscles.

Muscle spindles have a non-uniform distribution in the jaw muscles, and vary in number between muscles. Kubota and Masegi (1977) found 114 spindles in the

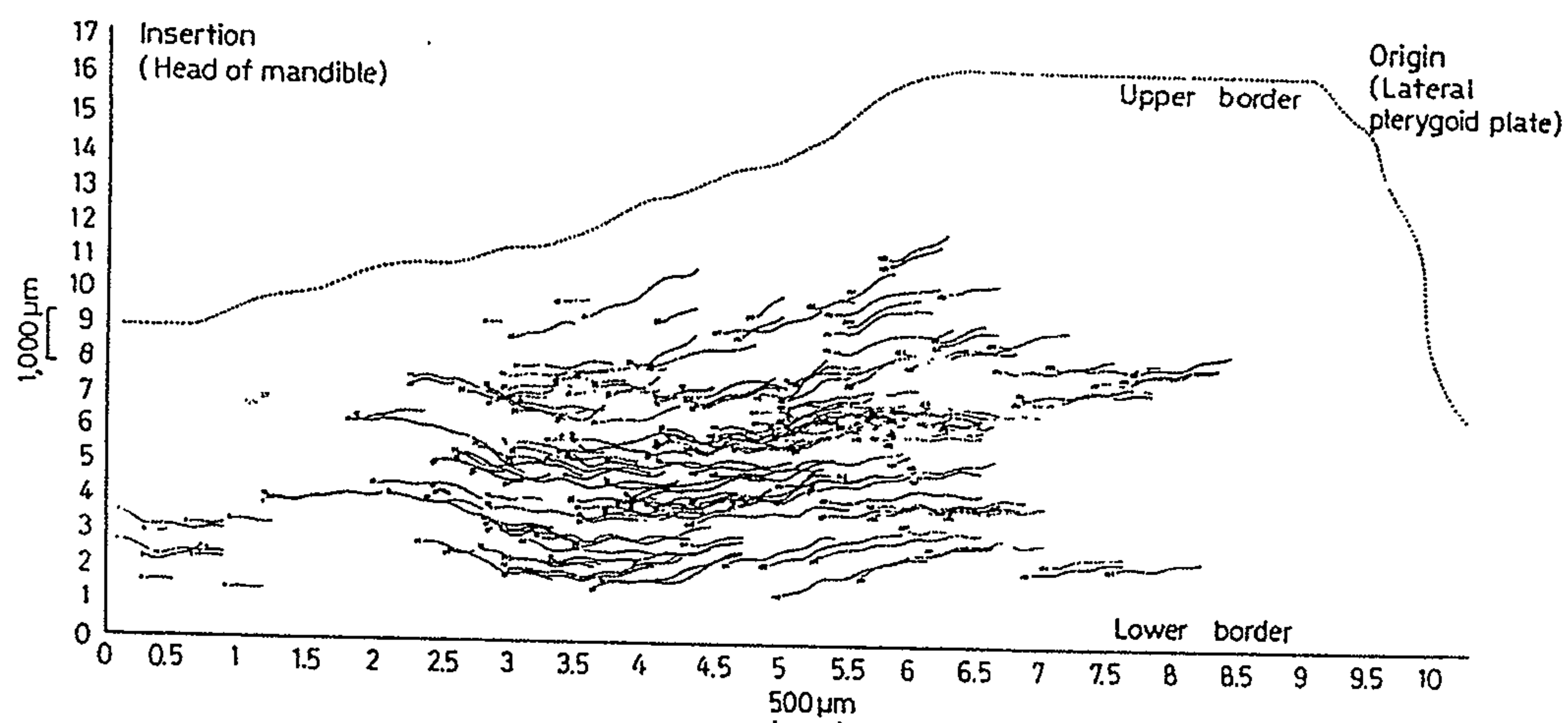
masseter: 80% in the superficial part and 20% in the deep part. In contrast, Eriksson and Thornell (1987) observed that most muscle spindles lay in the deep part of the masseter which contains a predominance of type I extrafusal fibres. This study suggests that spindle density relates directly to the proportion of type I fibres. Differences in the density of muscle spindles are often associated with differences in fibre type composition. Muscle spindles tend to be concentrated in muscle regions rich in type I fibres (Eriksson and Thornell 1987; Windhorst et al. 1989), and muscle spindles provide the sensory feedback needed for fine and precise movements, while type I fibres provide the refinement of motor control. Furthermore, it has been suggested that muscle spindles play a major role in sensing the spatial location of the mandible and the interdental dimension (Broekhuijsen and van Willigen 1983). Since the deep masseter contains large numbers of type I fibres and high concentrations of spindles, and its fibres are oriented vertically in a favourable direction to sense changes in stretch, the deep masseter would be well adapted for mandibular postural control at rest and locomotion (Eriksson and Thornell 1987).

In the temporalis muscle, Kubota and Masegi (1977) found 342 spindles, and the majority of them (208) were in the posterior part of the muscle. This high number of muscle spindles suggests that the temporalis may play an important role in maintaining the anteroposterior condylar position during mandibular movement.

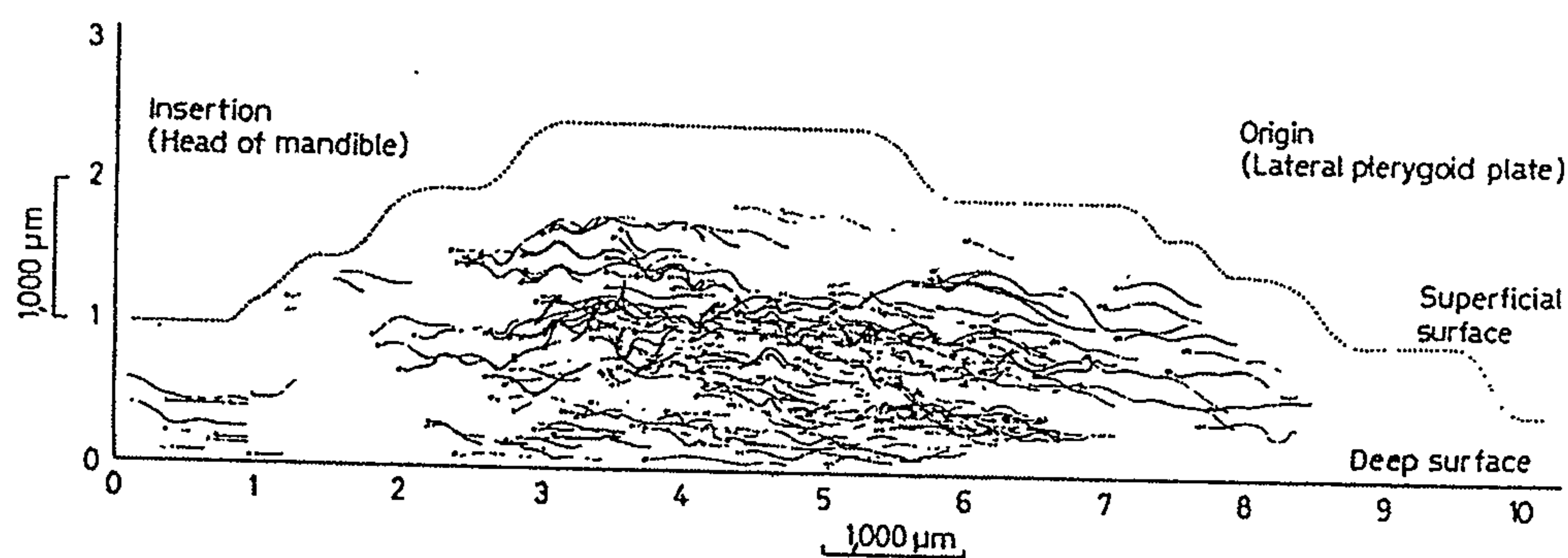
The number of muscle spindles identified in the LP varies from study to study. While Smith and Marcarian (1967) did not find any muscle spindles in the LP, Gill (1971) found that spindles (range of 2-18) were present and the majority were located in the middle third of the muscle with few in the anterior and none in the

posterior part. Kubota and Masegi (1977) found a few spindles ($n=6$) in the muscle, four in the SHLP and two in the IHLP. Ranges from 1-184 and 1-15 were reported in the muscle by Rakhawy and coworkers (1971) and Hónee (1966), respectively. Most were seen in the middle part of the muscle, whereas a small number of spindles were found at the origin and the insertion of the muscle. The above data suggest an uneven spindle distribution in the anteroposterior direction. In relation to the upper and the lower borders of the muscle, in some specimens, spindles were distributed throughout the whole muscle, while in others they were only at one side of the muscle (Fig. I-11).

Irregularity in the distribution of muscle spindles within the jaw muscles together with the apparent preferential location of type I or predominantly aerobic fibres in the regions of spindle distribution, indicates that different regions of a muscle have specialised functions. Thus, muscle spindles provide information about mechanical events in a muscle particularly in the region with the greatest spindle density, which in the case of the LP appears to be the central part of the IHLP of the muscle. If there is a preferential distribution of type I fibres in regions of high spindle density, then this supports the role of these regions of the IHLP in the fine control of condylar movement. The surrounding spindle-poor areas of the IHLP may therefore be less concerned with fine control.



(A)



(B)

Fig. I-11 Graphic reconstruction illustrating muscle spindles in the human lateral pterygoid muscle. (A) The distribution of muscle spindles in relation to the upper and lower borders and to the length of the muscle. (B) The distribution of the muscle spindles in relation to the superficial and the deep surfaces of the muscle. (From Rakhawy et al. 1971)

3. FUNCTIONAL ORGANISATION

3.1 Neuromuscular Compartment

The regions of muscle innervated by the branches of the primary afferent muscle nerve as it enters the muscle, are referred to as neuromuscular compartments or partitions. Figure I-12 illustrates a schematic diagram of the relationship between divisions of a muscle nerve and the target muscle fibres innervated. In some muscles, such as the ankle extensor muscles of cats and rats, the primary nerve branches are compartment branches, but in other muscles such as the cat hamstring muscles, the primary branches are not compartmental but rather supracompartmental branches (English et al. 1993). In animal studies, innervation territories can be mapped with the glycogen-depletion method, where a neuron is stimulated until the muscle fibres it innervates are depleted of glycogen. The anatomical organisation of neuromuscular compartments suggests a substrate for a localised function. The central nervous system controls a movement as subsets of muscles, not whole muscles.

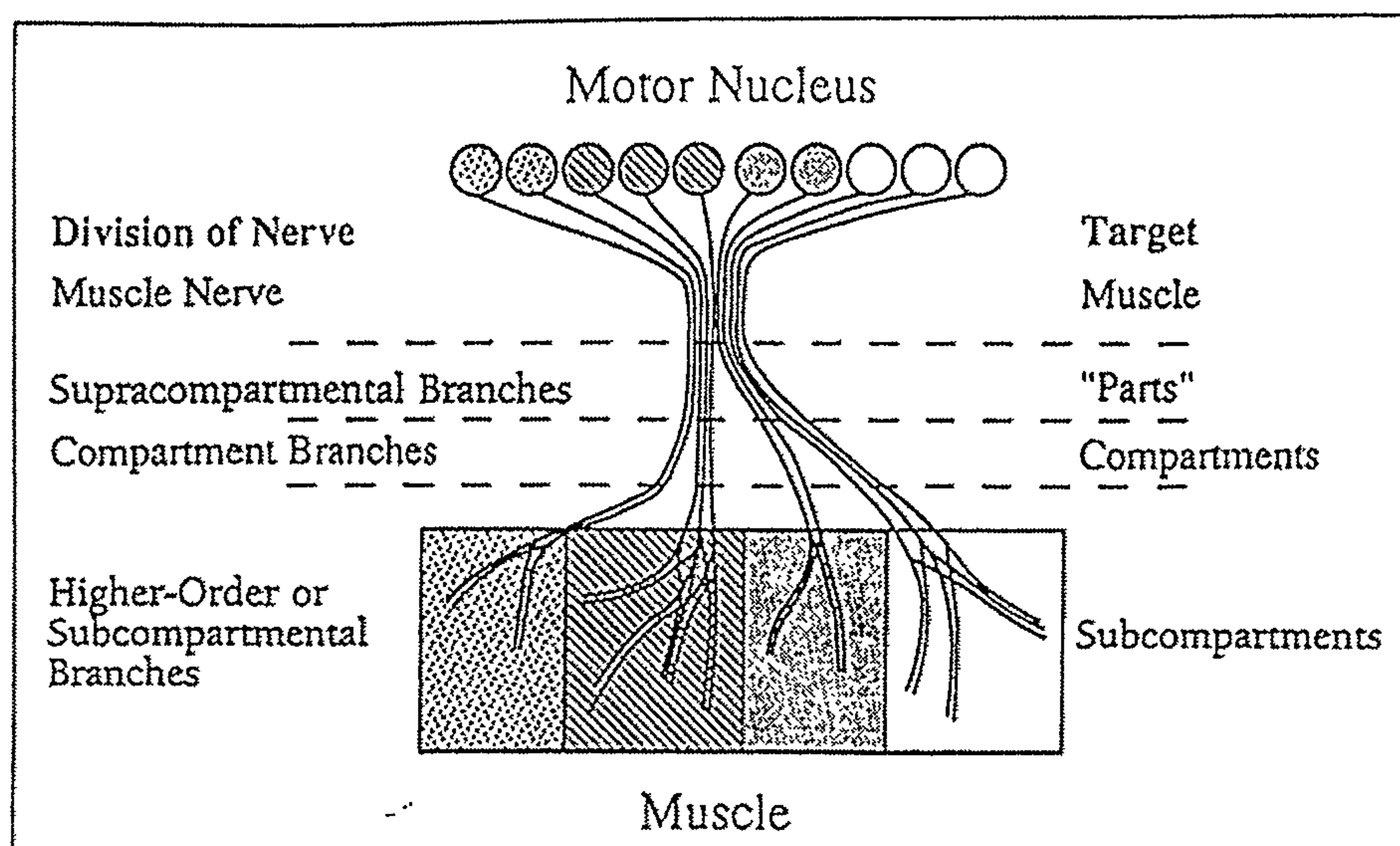


Fig. I-12 Schematic diagram illustrating the relationship between divisions of a muscle nerve and the target muscle fibres innervated. The different shaded circles at the top of the figure represent the motoneurons which innervate muscle compartments, represented by the corresponding shaded boxes at the bottom of the figure. The continuous line originating from each motoneurone represents its axon. The horizontal dashed lines indicate levels of nerve branching. (From English et al. 1993)

The innervation pattern of each jaw muscle is specific. In the human masseter, for example, which is reported to have a highly compartmentalised neuromuscular organisation, there are at least three primary or first-order nerve branches (Schumacher 1989) which supply the anterior, inferolateral and deep regions. It has been suggested that differential contraction may be possible on either side of central tendons which contain separate territories (Tonndorf and Hannam 1994). Lau (1972) also reported two trunks of the masseteric nerve, which enter the muscle medially at the posterior upper part. One of the trunks innervates the upper part, and the other supplies the lower two thirds of the muscle. The latter trunk ramifies into five branches at the middle of the muscle. There may be up to five primary nerve branches supplying the temporalis muscle (Schumacher 1989).

Because these branches, penetrating the internal aponeuroses before reaching the superficial layers, are oriented in an anteroposterior direction, it has been postulated that the compartmentalisation would also be most likely to occur in an anteroposterior direction (Hannam and McMillan 1994). This concurs with the EMG evidence for differential activation between the anterior, middle and posterior fibres (see Review of Literature: section 3.2.1.2). In the medial pterygoid muscle (Schumacher 1989), it has been found that there are two or three primary nerve branches which suggests that the muscle is compartmentalised. The first branch innervates the superior third of the muscle. The second supplies the inferior two thirds of the muscle as well as the middle and anterior sections, viewed in the sagittal plane. The third branch innervates the posterior part of the inferior two thirds of the muscle (Lau 1972).

The division of the LP into functional units is unclear. Patterns of nerve distribution in the LP vary from study to study. Some studies suggest that each head of the LP is innervated separately (Schumacher 1989); many studies however found that there were connections between nerves supplying the SHLP and IHLP (Aziz et al. 1998; Akita et al. 2000). It has been reported that the SHLP and the lateral half of the IHLP are each innervated by a nerve branching from the buccal nerve. The medial half of the IHLP is directly innervated by a branch of the anterior trunk of the mandibular nerve (Lau 1972). This supports the possibility of neuromuscular compartments in each head. Foucart and coworkers (1998) suggested that the LP is composed of five to six independent functional musculo-aponeurotic layers based on nerve distribution findings. This finding does not support the concept of independent functions between the two heads of

the LP since there is no independent nerve supply to the two heads (Fig. I-13). However, the information supports the possibility of graded activity in the LP, at least in the superior-inferior direction. The data led the authors to propose that the LP should be considered as a single unit made up of independent functional musculo-aponeurotic layers and EMG studies should be done using several vertical analysis levels and not just one or two recording points. Further, a recent study (Akita et al. 2000) indicated that according to the nerve distribution, the SHLP and IHLP were not clearly divided, especially in the posterior half of the muscle where some twigs to the IHLP from the anterior deep temporal nerve also supplied the SHLP and vice versa (Fig. I-14).

A recent anatomical study (Aziz et al. 1998) has shown three innervation patterns for the LP. In the two most frequently observed patterns (75%), each head of the muscle received a branch from a common nerve source that originated either from the long buccal or mandibular nerve or from a loop that arose between the long buccal and lingual nerves. Each head also received additional independent branches from the mandibular, long buccal or deep temporal nerve. In a third pattern, the common nerve source and the relative exclusivity of their nerve supply to both heads were not seen. Each head was innervated by independent branches which arose from the mandibular, long buccal or anterior deep temporal nerve. They concluded that the independent innervation of the SHLP and IHLP appears to support Juniper's (1981) proposal that the two heads are entirely separate muscles. Although they did acknowledge that without information of the exact functional components in each nerve branch, this conclusion is tentative. However, the data do not provide strong evidence to support the separate

neuromuscular partitioning of the LP. If the motoneurons or primary afferents that innervate each head belong to the same motoneurone pool within the trigeminal motor nucleus, both heads may be more likely to function simultaneously as a single unit. On the other hand, if the motoneurons belong to a different motoneurone pool, each head may be able to function separately. It is recognised however that descending suprabulbar inputs can be distributed to alpha-motoneurons irrespective of whether the neurones are grouped together or distributed throughout the motor nucleus.

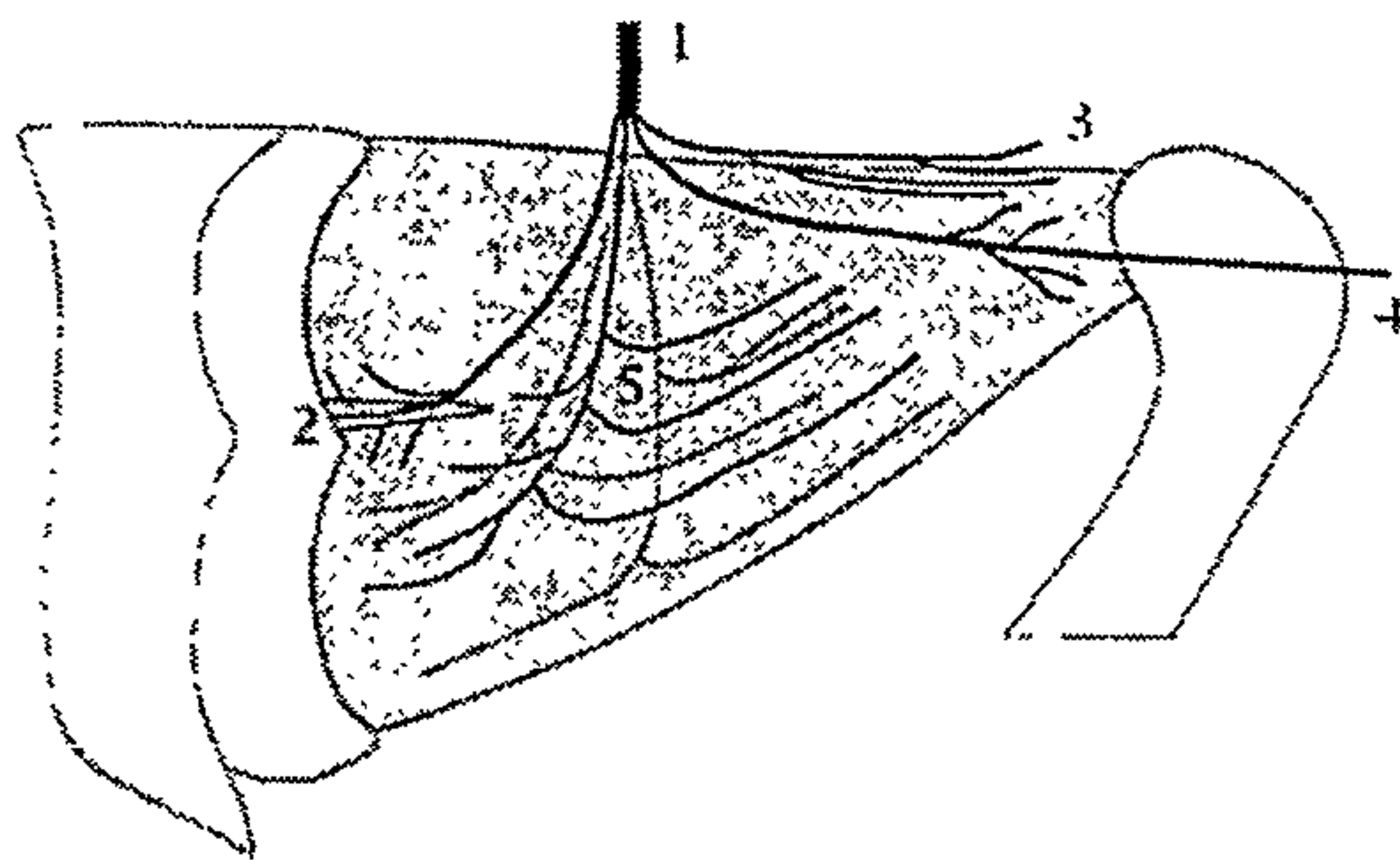
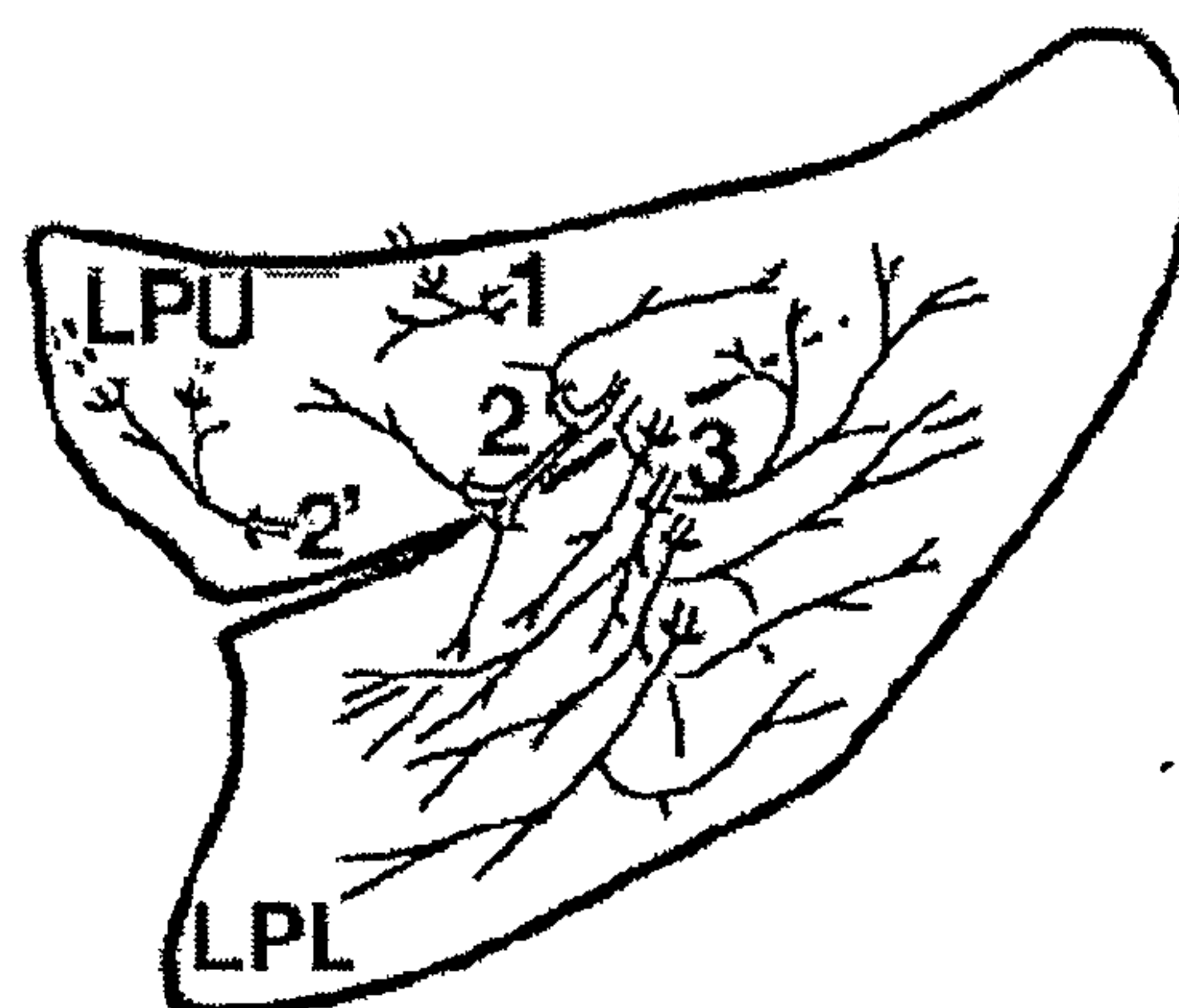


Fig. I-13 Intramuscular nerve branches distribution in a right LP. (1) Mandibular nerve, (2) the buccal nerve and its hiatal fibres, (3) the temporo-masseteric nerve, (4) the auriculotemporal nerve, and (5) the vertical lateral pterygoid nerve and their horizontal branches in anteroposterior direction. (From Foucart et al. 1998)

Fig. I-14 Schematic representation of intramuscular nerve distribution of a right LP from the medial aspect. (1) A branch of the middle deep temporal nerve, (2) and (3) branches of the anterior deep temporal nerve. The upper head is also innervated by some twigs supplying the inferior head from these branches, and vice versa. (2') a branch of the anterior deep temporal nerve pierces the upper head to distribute to the region between the parts innervated by the anterior and middle deep temporal nerves. LPU, upper head of the lateral pterygoid; LPL, lower head of the lateral pterygoid. (From Akita et al. 2000)



It seems that neuromuscular compartments do not necessarily follow anatomical compartments (Hannam and Sessle 1994). For example, the rat anterior digastric and the rabbit digastric are partitioned into several functionally distinct neuromuscular compartments (English and Timmis 1991; Tsuruyama et al. 2002), but this muscle is not a multipennate muscle as might be expected if it was divided into different compartments. Likewise, the architecture of the SHLP and the IHLP are much more like a simple muscle compared to the other jaw muscles; that is, their muscle fibres are near-parallel. This might give the impression that each head of the LP functions as a single unit. However, based on the neural distribution described above, there is the possibility of selective activation within the SHLP and IHLP. The importance of studying the functional partitioning at finer levels than the gross anatomy of muscles has been pointed out by English and coworkers (1993) that "most studies of human muscle have not taken into account the possibility of partitioning beyond the grossly visible anatomical heads."

3.2 Electromyographic Studies

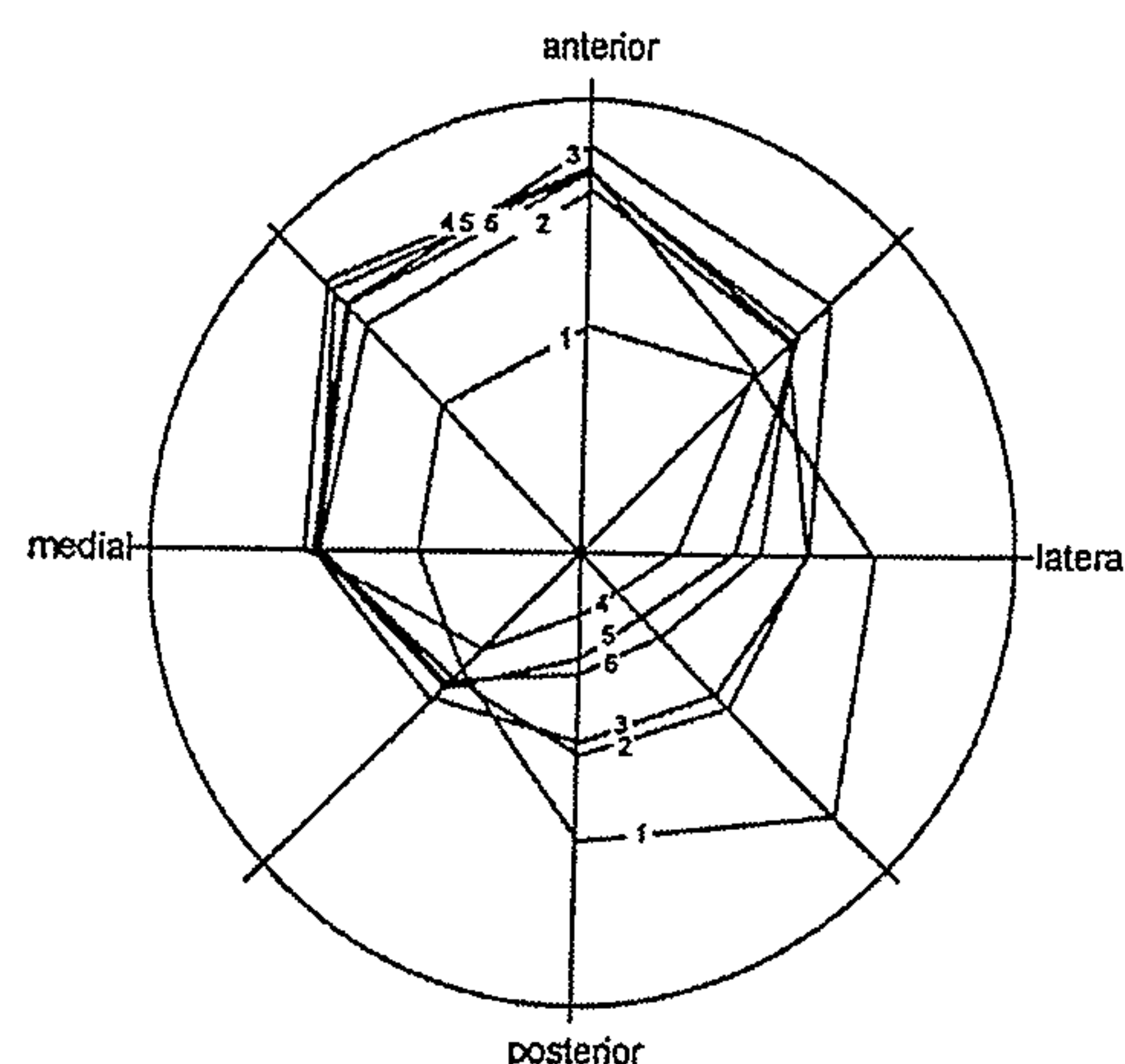
3.2.1 Multi-unit Studies

3.2.1.1 *Masseter Muscle*

In general, the masseter can be divided functionally into a superficial and a deep part. Electromyographic studies suggest that each part of the masseter can be activated independently during different motor tasks (Belser and Hannam 1986; Wood 1987; Blanksma et al. 1992; van Eijden et al. 1993; Blanksma and van Eijden 1995; Blanksma et al. 1997). The deep masseter, for example, showed a

high peak activity during retrusion, whereas the superficial masseter was almost silent (Blanksma et al. 1997). Furthermore, there is evidence that functional partitions into more than two parts might exist. At least three functionally different parts (a posterior deep, an anterior deep and a superficial part) have been proposed (Blanksma et al. 1992). In this study, six bipolar fine-wire electrodes were used to record EMG activity from six different sites, in the anterior, middle, and posterior regions of the superficial and deep layers of the human masseter muscle, during different static bite tasks at a constant bite force (Fig. I-15). It was found that the posterior deep part had a unique behavioural pattern. This part had its highest EMG activity during posterolateral bites and had its lowest activities for opposite bite force directions, while the other deep parts had their highest EMG activity during anteriorly and anteromedially directed bites, and their lowest activities were in the opposite directions. The activity patterns of all superficial parts were roughly similar to one another with activity during anteriorly, anteromedially and medially directed bites. Functional heterogeneity in the deep masseter has later been confirmed by van Eijden et al. (1993) who reported that there was no significant differential activity within the superficial masseter, but that activity within the deep masseter was either homogeneous or heterogeneous, depending on the motor tasks. For example, during incisal clenching EMG activity levels in the middle and anterior deep masseter were significantly larger than in the posterior deep part.

Fig. I-15 Polar plot of the mean masseter EMG of five subjects during biting in different directions with bite forces of 150 N. Scaled EMG activity is in the radial direction (ring represents 100% activity) and the direction of the bite force is in the angular direction. Curves of the six muscle regions (1-6) are depicted. 1 = posterior deep, 2 = middle deep, 3 = anterior deep, 4 = posterior superficial, 5 = middle superficial, 6 = anterior superficial. (From Blanksma et al. 1992)



3.2.1.2 Temporalis Muscle

The EMG studies of the temporalis have shown that the superficial and deep parts of the muscle can function simultaneously or separately depending on the task. For example, the deep part of the anterior temporalis is more active than the superficial part during clenching in intercuspal position with a posteriorly directed force (Wood 1986).

There is also evidence supporting the existence of regional differences in activation of the temporalis in the anteroposterior direction. The temporalis muscle fibres are capable of generating force in different directions since the muscle is fan-shaped. For example, the anterior temporalis showed significantly higher peak EMG activity than the posterior region during jaw open/close excursion, whereas the anterior region demonstrated lower peak EMG activity than the posterior region during protrusion/retrusion movement (Blanksma et al. 1997).

The posterior temporalis exhibited EMG activity during the rest position, whereas the middle part showed minimal activity and the anterior part was inactive (Ahlgren et al. 1985). This suggests that the posterior temporalis is the main postural muscle and gives the joint a better stabilisation than the anterior part since the posterior part is closer to the joint axes. The finding is also substantiated by the existence of high number of muscle spindles in the posterior region of the temporalis (Kubota and Masegi 1977).

3.2.1.3 Medial Pterygoid Muscle

The medial pterygoid muscle is active during clenching in intercuspal position, protrusion and contralateral jaw movements, while it exhibits low activity during wide jaw opening, ipsilateral jaw movement and clenching in the retruded position (Gibbs et al. 1984). The existence of differential contraction within the muscle is not known since this muscle is difficult to access for recordings. It is impossible to compare muscle activity recorded from different regions across studies due to the different tasks that have been used in these studies.

3.2.1.4 Lateral Pterygoid Muscle

The available studies do not necessarily agree as to the normal functions of the SHLP and IHLP. The activity of the SHLP and IHLP reported in the literature is summarised in Table I-4. Some of the earliest studies did not distinguish between the two heads of this muscle; however, it is likely that these recordings were obtained from the IHLP. In some studies, it is difficult to interpret whether the observed activity was real activity or background noise since the terms of 'very little', 'little' 'slight' or 'negligible' used in the literature were not defined. Data

from most studies were derived from multi-unit EMG recordings, where it is difficult to draw a conclusion as to a relative level of muscle activity due to limitations inherent in multi-unit EMG recording, such as variations in electrode physical properties. Further, it is impossible to classify muscle activity into different levels because of the variation in terminology and methods used in these previous studies. Therefore, Table I-4 lists a presence or an absence of EMG activity during certain tasks whether the presence or absence of activity was clear. Where activity was defined as very little, little, slight or negligible, it is labelled $\pm$.

In general, the IHLP and SHLP is considered to function independently or nearly reciprocally (Grant 1973; McNamara 1973; Mahan et al. 1983; Gibbs et al. 1984; Wood et al. 1986; Klineberg 1991; Hiraba et al. 1995; Hiraba et al. 2000). Thus, the SHLP is said to be active during closing, clenching, retrusion and ipsilateral jaw movements, while the IHLP is active during jaw opening, protrusion and contralateral jaw movements. However, this reciprocity of activity may not be true for all actions (Sessle and Gurza 1982; Widmalm et al. 1987; Miller 1991; Hannam and McMillan 1994). In a multi-unit study with CT-verified sites, both SHLP and IHLP were active during protrusion and contralateral jaw movements (Murray et al. 1999c). Further, a study from the LP in monkeys, verified by dissecting recording sites, demonstrated that both SHLP and IHLP could be active in both closing and opening, although the level of activity would depend on the amount of both vertical and horizontal jaw movements (Sessle and Gurza 1982). The SHLP, for instance, was more active during jaw closing, and was particularly active when the jaw opening was combined with contralateral deviation of the mandible. These data suggest that the SHLP and IHLP do not function completely

independently, but the activity recorded depends upon mandibular position. The study pointed out that it is essential to record jaw movement simultaneously with the EMG recording. Most studies, with the exception of some (Hiraba et al. 1995; Murray et al. 1999a; Murray et al. 1999b; Murray et al. 1999c; Phanachet and Murray 2000; Hiraba et al. 2000) have not recorded jaw movement simultaneously and therefore have not been able to clarify the nature of the association between jaw movement and LP EMG activity.

There is also an inconsistency concerning whether there is activity of the LP at rest or postural jaw position. The LP has been reported to be constantly maintained in a mild state of contraction, resulting in a slight anterior and medial force on the disc when the jaw is at the postural jaw position (Okeson 1998) (see also Table I-4), whereas others found an absence of SHLP and IHLP activity in asymptomatic subjects (eg., Mahan et al. 1983). However, the SHLP was tonically active in subjects with pain on palpation of the temporomandibular joints and masticatory muscles (Mahan et al. 1983). In contrast, some TMD patients exhibited hyperactivity of the IHLP, but not in the SHLP at resting posture (Lafreniere et al. 1997). Nonetheless, these data suggest that there was a relationship between TMD and activity in the LP; however, it was impossible to make a conclusion that the hyperactivity of the LP was a cause or an effect of the TMD.

Table I-4 Summary of EMG activity of the LP reported in literature during tasks.

	Rest	Clench	Open	Close	CL	Ipsi	Pre	Ret
<i>Superior head</i>								
Kamiyama (1961)	Nd	Nd	-	+	-	+	-	+
Sessle & Gerza (1983)**	Nd	Nd	+	+	Nd	Nd	Nd	Nd
Mahan et al. (1983)	-	+	±	Nd	±	+	±	Nd
Gibbs et al. (1984)	Nd	+	±	+	±	+	±	Nd
Widmalm et al. (1987)	±	+	+	Nd	+	±	+	±
Koole (1998)	+	+	+	+	+	+	+	+
Murray et al. (1999)	Nd	Nd	Nd	Nd	+	Nd	+	Nd
Hiraba et al. (2000)	-	+	+	+	+	-	+	-
Wang et al. (2001)	±	+	+	Nd	Nd	Nd	Nd	Nd
<i>Inferior head</i>								
Kamiyama (1961)	Nd	Nd	+	-	+	-	+	-
Sessle & Gerza (1983)**	Nd	Nd	+	±	Nd	Nd	Nd	Nd
Mahan et al. (1983)	-	+	+	Nd	+	+	+	Nd
Gibbs et al. (1984)	Nd	+	+	Nd	+	±	+	Nd

	Rest	Clench	Open	Close	CL	Ipsi	Pro	Ret
Wood et al. (1986)	-	-	+	Nd	Nd	Nd	Nd	Nd
Widmalm et al. (1987)	±	+	+	Nd	+	±	+	+
Koole (1998)	+	+	+	+	+	+	+	+
Murray et al. (1999)	Nd	Nd	Nd	Nd	+	Nd	+	Nd
Hiraba et al. (2000)	+	+	+	+	-	+	-	+
Wang et al. (2001)	±	+	+	Nd	Nd	Nd	Nd	Nd
<i>Lateral pterygoid*</i>								
Moyers (1950)	Nd	Nd	+	-	+	-	+	-
Carlsöö (1956)	+	Nd	+	-	+	±	+	Nd
Woelfel et al. (1960)	Nd	+	+	Nd	+	-	+	-
Griffin & Munro (1969)	Nd	+	+	-	Nd	Nd	Nd	Nd
Molin (1973)	+	+	+	Nd	+	+	+	Nd
Lehr & Owens (1986)	Nd	+	+	Nd	+	+	+	+

* Without differing heads, but most probably recording from the IHLP

** Study carried out in non-human primates

- = no activity observed, + = activity observed, ± = very little, little, slight or negligible activity, Nd = no data

Rest = postural jaw position, Clench = clenching in intercuspal position, Open = jaw opening, Close = jaw closing, CL = contralateral jaw movement, Ipsi = ipsilateral jaw movement, Pro = protrusion, Ret = retrusion.

One explanation for the inconsistency of these findings regarding the functions of both heads is that in many previous studies the locations of the EMG electrodes were not verified with a possible exception of a study by Kamiyama (1961). In this study, a cephalography was used for assigning electrode locations in either upper or lower part of the LP. However, there were no details of criteria for assigning location. It is possible that some of the previous recordings may have been obtained from other adjacent muscles, such as the deep temporalis or medial pterygoid, rather than from the LP, or may have been incorrectly attributed to a particular head of the LP (Widmalm et al. 1987; Hannam and McMillan 1994). Anatomical studies have demonstrated that the deep temporalis frequently adjoined the lateral part of the SHLP (Widmalm et al. 1987; Akita et al. 2000) and the IHLP shared a common origin with part of the medial pterygoid muscle at the antero-inferior part of the lateral aspect of the lateral pterygoid plate (Widmalm et al. 1987; Naidoo 1996). The interlacing between the LP and the adjacent muscle fibres could therefore confound selective recording from the SHLP in the lateral region and from the IHLP in the inferior-medial region. Further, the SHLP fibres often mingled with the muscle bundle of the IHLP (Fujita et al. 2001). This intermingling of the fibres of both heads was observed more frequently on the medial side than on the lateral side of the IHLP near the disc.

Another possible explanation could relate to the possibility of functional heterogeneity within the LP. Recording at different sites within the muscle would yield different functional properties if the LP is functionally heterogeneous. This

may well be an explanation for the inconsistencies between studies as to the task relations of the LP.

Given that there is a possibility of functional heterogeneity within each head of the LP, verification of electrode location is crucial not only to confirm that muscle activity is recorded from the LP, but also to provide information of the different patterns of LP activity, if any, at different locations within each head. If the muscle is capable of selective activation, it is not possible to rely on EMG patterns as the sole basis for verifying that electrodes are correctly located within the LP. Recently, CT scans have been introduced as a reliable method for verification of the location of the electrode in the LP (Orfanos et al. 1996) and this technique has been employed in the present study.

Since the LP inserts directly into the condyle, the muscle can apply direct force vectors to the temporomandibular joints. The muscle can also produce major force vectors in the horizontal plane. There is EMG evidence also supporting the role of the LP in horizontal jaw movement control. Multi-unit studies demonstrated that the magnitude of the smoothed SHLP and IHLP EMG activity was closely correlated with the magnitude of condylar translation during contralateral or protrusive jaw movements, especially during the outgoing phase (Murray et al. 1999c; Phanachet and Murray 2000). During the outgoing phase of contralateral movement and protrusion, the correlation coefficients for SHLP and IHLP were statistically significantly greater than from the correlation coefficients for the masseter, anterior temporal, posterior temporal and digastric muscles treated as a group (Murray et al. 1999c). Nonetheless, during the return phase of contralateral and protrusive jaw movements, the SHLP presented a much lower

correlation between condylar displacement and the rectified and smoothed EMG activity than that of the IHLP (Phanachet and Murray 2000). The data suggested that the IHLP also plays an important role in movement of the condyle back into the glenoid fossa; however, the SHLP did not appear to play the same role as the IHLP in the return phases of these movements. The high correlation with IHLP activity during the return phase supports the proposal by Wilkinson (1988) that a "lengthening contraction" of the IHLP "has the effect slowly letting out the rope to control the condyle as it travels back into the fossa." Moreover, Hiraba and coworkers (2000) demonstrated monotonic relationships between LP EMG activity and some kinematic parameters of jaw movement. The data suggest that the LP controls anterior condylar position and support a role of the muscle in the control of horizontal jaw movements. There was also a close relation between the fluctuations in condylar movement and those in the activity of both heads during the outgoing phase of contralateral or protrusive jaw movements (Murray et al. 1999c). The data suggest that both heads of the LP also play an important role in the precise positioning of the jaw and the condyle in the horizontal plane, such as mastication and speech. However, roles for other jaw muscles in these horizontal jaw movements cannot be ruled out. For example, the masseter, medial pterygoid and posterior temporalis muscles contain fibres capable of generating force vectors with horizontal components.

3.2.1.5 Digastric Muscle

The anterior and posterior bellies of the digastric muscle are synchronously active in all jaw movements, including chewing and swallowing, but are silent or have minimal activity during rest position and clenching (Munro 1972; Munro 1974;

Widmalm et al. 1988). Both bellies show high activity during jaw opening and moderate to high activity during protrusion, retrusion and lateral movements (Widmalm et al. 1988). The EMG activity continuously increases during the movement from the rest position to the fully open position, and decreases during closure to the rest position. These results indicate that the digastric muscle assists in jaw opening. There is no strong evidence supporting differential activation in the two bellies of human digastric muscle.

3.2.2 Single Motor Unit Studies: Task-related Behaviour of Motor Units

Studies of the task-relations of motor units have revealed that some motor units may participate in more than one task, and are defined as 'multitask' or 'polymodal' units. Within some muscles, different groups of motor units can exhibit specific task relations and these groupings are called motor unit task group (ter Haar Romeny et al. 1982; Nardone et al. 1989; Howell et al. 1995). For instance, at least two task groups have been identified among the extensor digitorum communis motor units (Riek and Bawa 1992). One was activated for middle finger and wrist extension, and the other group fired for ring finger and wrist extension. The selective activation may be caused by a different distribution of the input activity over the motoneurone pool for each task and therefore, different motor units would receive a different amount and/or type of input (ter Haar Romeny et al. 1982).

A study of 50 masseter SMUs at verified regions during 13 different intraoral tasks indicated that all motor units were capable of participating in more than one

task and some motor units could be activated by five or six tasks (McMillan and Hannam 1992). Nonetheless, even the multitask ones, that could be activated by more than one motor task, were not active in all the tasks performed, and comparable observation has been made in limb muscles (Thomas et al. 1986; Thomas et al. 1987). Likewise, most motor units in the anterior superficial temporalis are associated with multiple tasks and in some cases up to three or four. Most of them are activated by tasks involving the generation of bite force, and only a small number of the motor units are associated with postural tasks (McMillan 1993). This supports the hypothesis that the anterior superficial temporalis, mainly consisting of type II fibres (Eriksson and Thornell 1983), has a significant role in the generation of bite force. However, it has been reported that some motor units are task-specific units, although they appear to be less prevalent than multitask motor units. Eriksson and coworkers (1984) and McMillan (1993) found a mixture of task-specific and multitask units in the masseter and the temporalis, respectively.

Similar to multi-unit EMG findings, SMU studies have also demonstrated regional task-dependent behaviour. The task profiles of masseter motor units appeared to vary regionally (McMillan and Hannam 1992). For example, motor units that could be activated by anteriorly directed effort were preferentially located in the superficial part where the orientation of the fibres is most favourable for the task. Similarly, there were more units activated by tasks such as jaw retrusion with and without tooth contact in the deep part. Further, motor units in the posterior superficial part of the muscle were most commonly associated with tasks which involved tooth contact such as clenching with

different directions of effort. Therefore, this region may be responsible for the generation of bite force and may play a less important role in maintaining jaw posture. This concurs with previous histochemical studies of fibre composition which revealed that type II fibres, responsible for high contractile forces, are represented in the posterior superficial part more than any other parts of the masseter muscle (Eriksson and Thornell 1983). Differences in motor unit behaviour and the restricted motor unit territories within the human masseter (Stålberg and Eriksson 1987) strongly suggest that this complex jaw muscle displays regional and functional specialisation.

3.3 Motor Unit Organisation

As described earlier, muscle fibres are organised into motor units which are classified physiologically into three basic groups: slow (S), fast fatigable (FF) and fast fatigue-resistant (FR) motor units. Different motor unit types contain different types of muscle fibre. Type I fibres belong to slow-twitch motor units, Type IIB to FF units and type IIA to FR units. Therefore, each type of muscle fibre is responsible for different functions. The myosin heavy chain (MHC) content of motor unit fibres has also been correlated with their physiological properties (Kwa et al. 1995). The S units were associated with MHC-I, FR units with MHC-IIA and FF units with MHC-IIX. Slow-twitch motor units have long contraction times and are highly resistant to fatigue, whilst FF motor units contract and relax rapidly but fatigue rapidly. The FR units have contraction times slightly slower than FF units but are almost as resistant to fatigue as are slow units. Slow-twitch type I motor units, consisting of fewer fibres than fast-twitch motor units, are recruited first at low force levels, while FR and FF units become activated in an

orderly sequence according to motor unit size when the muscle force is raised (Burke 1981; Tansey and Botterman 1996). Since fine movements can be produced by the activation of different combinations of small motor units, slow-twitch type I motor units are responsible for precise movements which can be achieved with low forces. Larger, fast-twitch type II motor units, in contrast, have the capability for more rapid and less precise movements, but generate greater force. Type I muscle fibres, found in the greatest number in postural muscles such as the long muscles in the back, produce 10 grams of force per square centimetre of muscle cross-sectional area, whereas type II fibres generate more than 100 grams of force per square centimetre of muscle cross-sectional area. FF motor units produce much larger force than slow units because of two major factors: 1) the innervation ratio (*i.e.*, the number of muscle fibres per motor unit) is greater and 2) the cross-sectional areas of individual muscle fibres are larger in type IIB fibres than in type I fibres (Ghez 1991).

3.3.1 Motor Unit Territories

The number of motor units and the innervation ratio vary greatly within each muscle and especially between different muscles. The innervation ratio is roughly proportional to the size of the muscle. A low innervation ratio indicates a greater capacity for finely grading the muscle's total force. Motor unit size may vary between only two to three muscle fibres to over a thousand muscle fibres. In the extraocular muscles, for example, one motoneurone innervates only about 13 muscle fibres, and this results in the ability to produce very delicate eye movements. On the other hand, a motor unit in the large calf muscle of the leg, which produces mainly coarse movements, contains approximately 1700 muscle

fibres. In jaw muscles, the temporalis motor units are larger than those of the masseter, 936 and 640 fibres per unit, respectively (Carlsöö 1958). Although each motoneurone supplies several muscle fibres, each muscle fibre is innervated by only one motoneurone, so there is little or no polyneuronal innervation of adult human muscle fibres.

In human jaw muscles, the size of motor units and motor unit territories, *i.e.*, the area over which the fibres of one motor unit are distributed, have not been extensively investigated. Generally, motor unit territories in the masseter muscle were smaller than those in limb muscles. The scanning EMG technique was used to measure motor unit territories in the human masseter muscle (Stålberg and Eriksson 1987). A single monopolar needle electrode was inserted into the muscle and was moved through the muscle during biting until the motor unit activity disappeared. It was found that the motor unit territory width in the masseter muscle was 3.7 ± 0.6 mm compared with 7.0 mm in the biceps muscle and 7.3 mm in the tibialis anterior. Similarly, the mean territory width in the masseter studied by Tonndorf and Hannam (1994) was 3.7 ± 2.3 mm. Apart from the differences in the size of motor units between muscles, the dimensions of motor unit territories also vary from individual to individual, depending on the size of whole muscles. The mediolateral masseter motor unit dimensions depended on whole muscle widths (Tonndorf and Hannam 1994). The subject with the largest muscle had the largest motor unit territories, and vice-versa. It has been hypothesised that large motor units might belong to wide muscle compartments such as the anterior superficial part of the masseter muscle (Stålberg and Eriksson 1987). However, some large territories have been found in narrower muscle

regions, such as the middle and deep parts of the masseter muscle (Tonndorf and Hannam 1994).

The functional significance of the different sizes of the jaw-muscle motor-unit territories is unclear. It has been suggested that an arrangement with small motor unit territories may permit differential control of separate motor regions (Stålberg and Eriksson 1987). Selective recruitment of motor units within anatomical compartments within the muscle could allow small variations in the direction of pull which would favour fine modulations of jaw movements such as in mastication and speech. In contrast, large territories may indicate widespread motor actions, beneficial in bite force development where fine movement control is less important, as in biting through hard or tough foods, clenching in the intercuspal position or opposing gravitational force such as stabilising the mandibular position during movements. It has also been proposed that larger territories may generate adequate internal tendon stiffness when only a few compartments are activated, thus minimising internal tendon deformation when internal force vectors change (Tonndorf and Hannam 1994).

It has been suggested that the distribution of motor unit territories may be somewhat localised. For instance, each motor unit territory occupies only 5-10% of the total muscle volume in the pig masseter and usually lies within tendinous boundaries (Herring et al. 1989). The motor unit territories in the human masseter may also be focal and the restriction may provide the capability of selective regional motor control of the masseter (McMillan and Hannam 1991). The majority of motor units are confined to compartments, lying well with tendinous sheets, rather than randomly dispersed throughout the muscle, and only a small

number were distributed throughout the muscle layer (Tonndorf and Hannam 1994). In addition, SMU signals from 32 paired-needle recording sites throughout the human masseter muscle were recorded as time-locked events to investigate motor unit territories. Recording sites were located stereotactically with an optical system, magnetic resonance imaging and a common reference. The motor unit territories appeared to be related to anatomical compartments, and the preferred orientation of SMU territories of the masseter was anteroposterior because the mean distances between the 32 pairs of recording sites measured along the anteroposterior axis (6.1 ± 4.0 mm) were approximately double those measured along a superior-inferior (3.8 ± 2.5 mm) or mediolateral axis (3.2 ± 2.3 mm). The preferred orientation of SMU territories corresponds with the anatomical compartments described by Schumacher (1961). Additionally, layers of muscle fibres in the masseter were separated from superficial to deep, so that the aggregations within these layers were more likely to be in the anteroposterior direction than others.

Nevertheless, muscle compartments may not be defined strictly by the internal anatomical features of the muscle. In the human masseter, for example, a minority (10%) of motor unit territories extended across tendons (Tonndorf and Hannam 1994). It is therefore possible that functional compartmentalisation in the masseter may be less than that inferred by the internal anatomical architecture alone (Hannam and McMillan 1994). Localisation of motor unit territories between intramuscular tendons suggests that it is possible for the muscle to have a differential contraction on either side of central tendons, while the presence of

large territories which extend across tendons suggests that muscle fibres on either side of tendons must be active whenever these units are activated.

In summary, the localisation of motor units within certain muscle compartments provides the potential for selective activation of discrete muscle regions (Stålberg and Eriksson 1987; Herring et al. 1989; McMillan and Hannam 1991). Nevertheless, the restriction of motor unit activity is not always within the anatomical compartments provided by aponeuroses, and this may lead to a greater complexity of muscle function.

4. SINGLE MOTOR UNITS

4.1 Recruitment of Motor Units

4.1.1 Recruitment Order and Threshold

It has been known that the gradation in force produced by human muscle is regulated by two main strategies: recruitment of motor units and firing rate modulation of recruited motor units (or 'rate coding'). Motor units are thought to be recruited in the order of size, known as the 'size principle' (Henneman and Mendell 1981). That is, the excitability of a motoneurone is a function of its input resistance which varies inversely with cell size. Excitatory inputs to the motoneurone pool are distributed homogeneously; therefore, small motoneurons are recruited earlier than large ones (Henneman 1981). With a decrease in excitatory input, the motoneurons are de-recruited in the reverse sequence. The smaller type S motor units are recruited first, and with increase of force the larger type F motor units are recruited. Since the type S units produce less force and are more fatigue resistant than type F motor units, this orderly recruitment provides

for a fine control of muscle force gradation. Orderly recruitment also simplifies the task of modulating force and higher centres do not have to decide particular combinations of motor units to generate the desired amount of force. Only the overall level of synaptic input needs to be determined.

Findings from many studies in various muscles confirm the mechanism of orderly recruitment (Milner-Brown et al. 1973a; Freund et al. 1975; Desmedt and Godaux 1977a; Thomas et al. 1986; Thomas et al. 1987; Riek and Bawa 1992; Jones et al. 1993; Stotz and Bawa 2001). In almost all types of contraction, motor units with lower twitch tensions are recruited earlier than those with higher twitch tensions. A similar pattern of motor unit recruitment has also been reported in jaw muscles of human (Goldberg and Derfler 1977; Yemm 1977; Desmedt and Godaux 1979; Scutter and Türker 1998) and non-human primates (Clark et al. 1978). Studies of the contractile properties of the human masseter and temporalis motor units during voluntary isometric contraction showed orderly recruitment of the units with a nearly linear relationship between the voluntary force at which units were recruited and their measured twitch tensions (Goldberg and Derfler 1977; Yemm 1977).

Recruitment threshold, *i.e.*, muscle force at which a motor unit first begins to fire, is a parameter commonly used to characterise motor unit recruitment. Motor units with low twitch tensions tend to have lower thresholds than those with higher twitch tensions. The SMU twitch tension is positively correlated with recruitment threshold (Milner-Brown et al. 1973a; Thomas et al. 1987). Further, thresholds of motor units in jaw muscles seem to be correlated with the force

outputs, which confirms the size principle (Goldberg and Derfler 1977; Yemm 1977; Nordstrom and Miles 1990).

4.1.1.1 Threshold, Rate of Contraction and Motor Tasks

Recruitment threshold of a given motor unit is not always fixed, but depends upon the speed of contraction and the motor tasks being performed. The rate of muscle force change at isometric contraction is a parameter having the strongest influence on recruitment threshold. That is, threshold decreases with increasing rate of contraction. This phenomenon has been observed in limb (Freund et al. 1975; Büdingen and Freund 1976; Desmedt and Godaux 1977a; Desmedt and Godaux 1977b; Desmedt and Godaux 1978; Desmedt and Godaux 1979; Tanji and Kato 1981; Masakado et al. 1995; Christova and Kossev 2000) and jaw muscles (Desmedt and Godaux 1978). These observations suggest that recruitment of motor units is of importance for modification of speed of contraction. Studies in jaw muscles, however, have been restricted to isometric conditions.

Recruitment threshold also varies with the motor task performed, *eg.*, direction (McClellan 1984). Biceps motor units, for instance, exhibited considerably lower threshold for isotonic flexion and extension than for isometric contraction (Tax et al. 1989). Furthermore, there are changes in threshold with changes in muscle lengths. Thus, recruitment threshold of the masseter units during isometric contraction increased as the jaw was progressively opened (Miles et al. 1986). The data strongly suggested that the change in threshold was a consequence of the length-tension properties of the muscle. Many mechanisms responsible for

the modulation of recruitment threshold have been proposed, including changes in excitability of the motoneurone pool (Romaiguere et al. 1989), inhibition mediated by Golgi tendon organs, pre-synaptic inhibition and Renshaw inhibition (Calancie and Bawa 1990).

Generally, motor units preserve their ranks of recruitment, although their recruitment thresholds vary with rate of contraction and motor tasks (Büdingen and Freund 1976; Desmedt and Godaux 1977b; McClean 1984; Thomas et al. 1987; Masakado et al. 1995; Christova and Kossev 2000). However, there are studies showing that recruitment reversal can occur during rapid contraction (Tanji and Kato 1973b; Grimby and Hannerz 1981). Slow units, which may have been recruited first, may fire after some of the larger units. Nonetheless, these reversals of recruitment were often observed among units having nearly the same thresholds (Tanji and Kato 1973b; Thomas et al. 1987; Christova and Kossev 2000). Reversals of recruitment order among such units are not considered physiologically important nor examples of true reversals.

Even though the recruitment order of motor units is relatively fixed, it may be altered under certain conditions. Order of recruitment can be changed consistently by changing task and direction of exerted force in multifunctional muscles (Thomas et al. 1978; Desmedt 1981; Schmidt and Thomas 1981; ter Haar Romeny et al. 1982; Thomas et al. 1987). For example, recruitment order of the human first dorsal interosseous motor units was dependent on whether the muscle was being used as prime mover or synergist; that is, it depended on the direction of index finger movement (Fig. I-16). This muscle is a bifunctional muscle, which can function either as a prime mover in index finger abduction or

as a synergist to the long flexor muscle in index finger flexion. Several later findings also demonstrate recruitment order changes when a studied muscle acts as a synergist rather than as a prime mover (ter Haar Romeny et al. 1982; Thomas et al. 1986). One possible explanation is that the prime mover commands might be affected by excitatory synapses that are evenly distributed throughout the motoneurone pool, which would bring about a normal recruitment order of units. However, the command to the synergist might use a different group of synapses which are preferentially distributed to certain units (Fig. I-17) (Desmedt and Godaux 1981). That is, the synapses are less numerous on some of the smaller motoneurons; therefore, the smaller motoneurons could be activated later than the larger ones when a muscle acts as a synergist.

Another exception to the orderly recruitment occurs when synaptic inputs to motoneurone pools act selectively on specific types of motor units. Cutaneous stimulation, for example, has a predominantly inhibitory effect on low threshold motor units while an excitatory effect on high threshold ones (Garnett and Stephens 1981). The effect leads to less descending drive to the lower motoneurone pool being necessary to produce a given force, resulting in less required voluntary effort. Moreover, reversal of recruitment order has been observed during lengthening contraction (Nardone et al. 1989). There are, however, some studies reporting no recruitment reversal during this type of contraction (Søgaard 1995; Kossev and Christova 1998; Stotz and Bawa 2001).

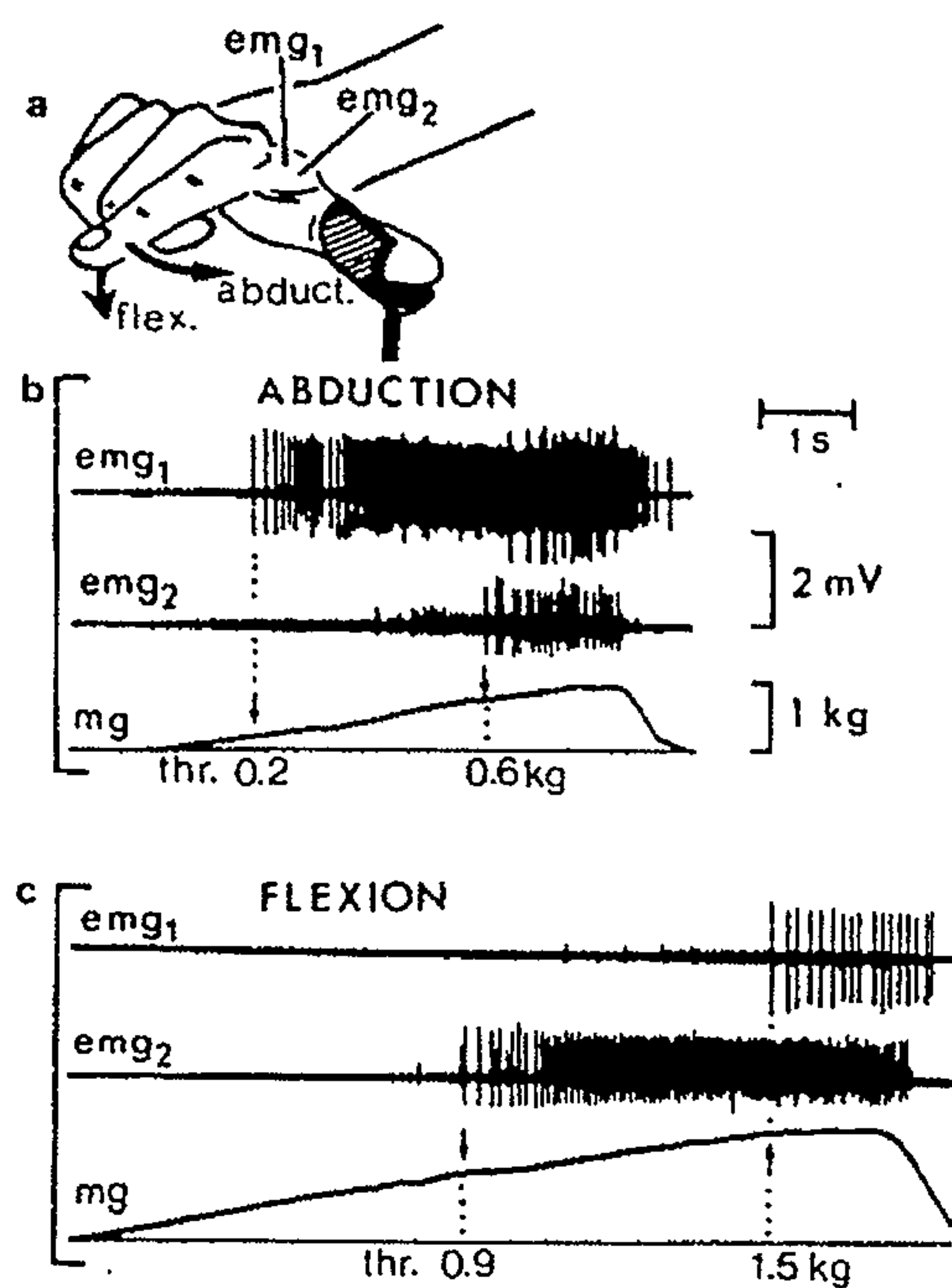
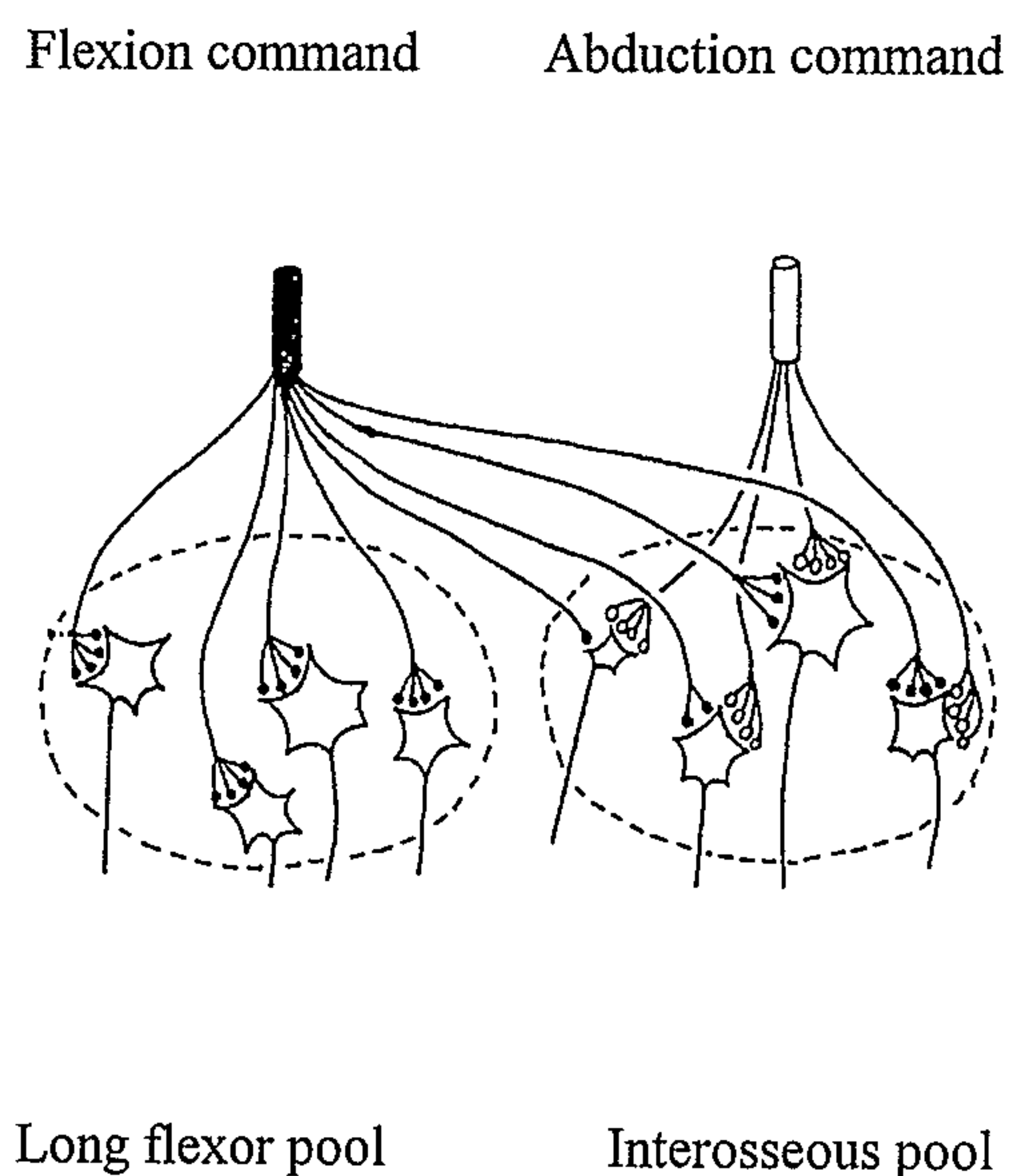


Fig. I-16 Recruitment reversal of a motor unit pair of the first dorsal interosseous muscle in relation to the direction of the movement of an index finger: abduction and flexion. (a) The motor units are recorded at two different sites (emg_1 and emg_2), and the hand is fixed. (b) For finger abduction, the single motor unit of emg_1 starts firing at 0.2 kg while the motor unit of emg_2 is active at 0.6 kg. The lower trace represents the isometric force ramp. (c) For finger flexion, the threshold of the unit of emg_1 is 1.5 kg while the unit of emg_2 is active at 0.9 kg. The recruitment thresholds of both units increases in flexion, but the threshold of the unit recorded at emg_1 increases much more than that of the other unit; therefore, both units are deordered. (From Desmedt 1981)

Fig. I-17 Diagram illustrating proposed mechanism of recruitment reversal in the first dorsal interosseous muscle (bifunctional muscle). Only four excitatory synaptic terminals per motoneurone are depicted. The excitatory synapses are equally distributed throughout the prime mover, the interosseous and long flexor, motoneurone pools. In contrast, the synapses for flexion commands are distributed unevenly throughout the synergic interosseous pool. This is shown by a smaller number of synapses on some smaller motoneurons. (From Desmedt and Godaux 1981)



There appears to be no evidence of recruitment reversal in the jaw muscles. One study in the human masseter muscle showed that the rank ordering of the masseter motor units was identical in slow and brisk voluntary clenches, and there was no evidence indicating the reversal of the recruitment order over a wide range of contraction speeds (Desmedt and Godaux 1979).

4.2 Firing Rate

As mentioned above, there are two mechanisms, recruitment and rate coding, that control force gradation. Studies in limb (Tanji and Kato 1973a; Freund et al. 1975; Seki and Narusawa 1996) and jaw muscles (Derfler and Goldberg 1978; Uchida et al. 2001) have shown that the firing rates of motor units increased as force increases during isometric contraction. The study in the IHLP during horizontal force gradation demonstrated that the muscle plays an important part in the generation and fine control of contralateral directed, horizontal isometric force (Uchida et al. 2001). There have been studies of the relation between firing rate modulation and isotonic tasks in other muscles, but have never been in jaw muscles. The study of saccadic eye movements that involve the rotation of a body (the eyeball) against low loads showed a linear change in the firing rates of SMUs from the human medial or lateral rectus muscles during horizontal stepwise movements (Sindermann et al. 1978). Also, recordings from motoneurons in the inferior rectus muscle in monkeys have shown progressive increases in the firing rates of units in a stepwise fashion during saccades in one direction (Henn and Cohen 1972). The new firing rate level was maintained until the next shift in eye position. Firing rate modulation permits a finer grade of control, which is essential for muscles involved in precise control.

Different muscles can employ different strategies for force generation. For example, during linearly varying contractions, the deltoid and the first dorsal interosseous muscles used different strategies to increase force output above 40% MVC: the deltoid relied primarily on recruitment, the first dorsal interosseous on rate coding (De Luca et al. 1982). It has been proposed that the number of motor units relative to the size of an individual muscle and its function, gross or fine movement, are influential factors in determining the major mechanism for force gradation (De Luca et al. 1982; Seki and Narusawa 1996). The first dorsal interosseous, for instance, is a small muscle with approximately 120 motor units; each unit thus produces a relative large amount of force to the total force output of the muscle. However, producing small and precise movements of the index finger is the function of the muscle. If recruitment were a principal means responsible for force gradation, the muscle would tend to exert force in step-like fashion and would be incapable of producing a smooth contraction. To achieve these fine movements, the muscle has to rely on rate coding to generate fine force gradation. In contrast, the deltoid is a large muscle composed of 1,000 motor units. Each unit contributes a relatively small amount of the total force output. Since the primary function of the deltoid is generating large and powerful contractions, finely controlled firing-rate activity is unnecessary during normal voluntary effort. Each newly recruited unit can provide a sufficiently small force increment to produce functionally smooth contractions.

It has been proposed that muscle fibre type composition is a possible factor influencing the strategy for force gradation. Kukulka and Clamann (1981) suggested that rate coding played an important role in force modulation in the

adductor pollicis, while recruitment was more prominent in the biceps brachii. It has been concluded that a factor underlying the different strategies in different muscles was the proportion of muscle fibres because the adductor pollicis was comprised mainly of type I fibres, whereas the biceps brachii was composed of mixed type I and II fibres. However, research conducted by Seki and Narusawa (1996) indicated that other factors, such as the number of motor units and the function of a muscle, rather than muscle fibre composition were more important factors in determining the main strategy. The rate coding of motor units in the first dorsal interosseous and the biceps brachii, which was comprised of a similar proportion of muscle fibre types, was compared. It was found that isometric force control of the first dorsal interosseous depended more on rate coding. If muscle fibre proportion did play a role in determining the relative importance of rate coding and recruitment, a similar strategy should have been observed.

The LP has been suggested to be concerned with precise condylar positioning (Murray et al. 1999c). Electromyographic activity of the human LP was recorded at verified sites simultaneously with condylar movement during protrusive and contralateral jaw movements. There was a high correlation between fluctuations in rectified and smoothed EMG activity and condylar displacement, suggesting an important role for precise condylar positioning for this muscle. As indicated above that rate coding plays a role in muscles involved in fine movements, the LP should employ this strategy to generate jaw displacement. The present study examined firing rate changes of human LP motor units as the jaw displacement increased in very small increments. The firing rate of a given unit among different

displacement levels should be significantly different if this muscle is associated with precise movement control.

4.2.1. Firing Rates in Slow and Fast Contractions

Apart from recruitment, rate coding also plays a role in modifying the speed of contractions. The rise of firing rate is greater when the contraction is faster (Tanji and Kato 1973a). The initial firing rate of a motor unit is higher (Tanji and Kato 1973a; Milner-Brown et al. 1973b), and the peak value of frequency is also higher at contractions with greater speed (Tanji and Kato 1973a).

The discharge pattern of motor units during different speed of contractions is also different. The study in the abductor digiti minimi showed different strategies used in contractions requiring slow and fast rates of force production (Tanji and Kato 1981). When the tension was raised slowly, the firing rate gradually increased as the tension reached its maximum. On the other hand, when the tension was increased as rapidly as possible, the firing rate rose sharply and immediately declined, even though the maximum contraction was maintained. It has been concluded that the central nervous system drives spinal motoneurons in a different manner depending on the speed of contraction. A transient initial peak in firing rate observed in fast contractions suggests that alpha-motoneurons were receiving a great deal of transient excitatory inputs from descending control systems at the onset of the rapid contraction to drive motoneurons at higher rates as well as to recruit more motoneurons to fire closer to the onset of contraction.

4.2.2 Firing Rate of Low and High Threshold Motor Units

There is a tendency for lower threshold motor units to have larger firing rate changes per unit of force change. Indeed, the lower threshold motor units tend to increase their firing rates more rapidly than the larger ones. This has been reported in SMU studies of human limb (Person and Kudina 1972; Freund et al. 1975) and jaw muscles (Derfler and Goldberg 1978). Different amounts of firing rate change may be a consequence of the same factors that underlie the size principle of recruitment order (Derfler and Goldberg 1978). If the excitatory input is distributed equally through a motoneurone pool, any increase in the input will produce a proportionally greater increment of depolarising current in small motoneurons than in large ones, resulting in a greater amount of firing rate change in the smaller units.

4.2.3 Least Sustainable Firing Frequency (LSFF)

The range of firing rate of human motor units is very small, 6-35 impulses/sec (imp/s), compared to that in sensory systems which can vary continuously between 0-300 imp/s or more. The LSFF at which units discharge continuously is 6-8 imp/s for limb muscle motor units (Tanji and Kato 1973a; Milner-Brown et al. 1973b; Freund et al. 1975), whilst the LSFF for facial motor units is greater, 10 imp/s (Petajan 1981). Nordstrom and coworkers (1989) have indicated that the masseter motor units could be driven without pauses between 8 and 10 imp/s, although Eriksson and coworkers (1984) have shown that they may be driven continuously between 5 and 8 imp/s. The lowest continuously maintainable firing rate of the LP was 8-10 imp/s, and it was more easy for subjects to control at ~15

imp/s (McMillan and Hannam 1989). The factors responsible for the low frequency limit are not clear, although Renshaw-type recurrent inhibition has been suggested. The firing probability of Renshaw cells is very high at low discharge rates of motoneurons, and decreases rapidly at higher rates. It is likely that the inhibition is so profound as to limit the LSFF. However, the motoneurons of the jaw muscles are considered to lack of the Renshaw inhibition; hence, this mechanism is unlikely to be responsible for the lower frequency limit in the jaw muscle motor units, but it is a possible mechanism for limb muscle motor units.

The LSFF has been used as a parameter to investigate task-related behaviour of motor units. In studies of the masseter and temporalis (McMillan and Hannam 1992; McMillan 1993), SMU activity was recorded and the LSFF was achieved by slow increases and decreases in firing rate, then firing was maintained at the lowest possible rate without significant pauses. There were statistically significant differences between LSFFs for the tasks performed by units of both jaw muscles, unlike limb muscle where the mean interspike intervals recorded for different tasks were similar (Thomas et al. 1987). Thus, the LSFF of the masseter and temporalis seems to vary with the motor task and are sensitive to the jaw position, the location of tooth contact and the direction of effort. Descending neural drive to the masseter and temporalis motor units, therefore, seems to be highly task dependent. Selective activation of the units during specific intraoral tasks suggests that different populations of motoneurons were activated within the trigeminal motoneurone pool, and supports the concept that a level of motor control is more specific than whole muscle control.

5. SUMMARY

It is clear that a fine level of contraction occurs within the jaw muscles to achieve force gradation and movement. This is facilitated by the internal anatomical and physiological organisation of the muscles. The muscle architecture, fibre type composition, innervation pattern, muscle spindle distribution, and motor unit organisation all contribute to the possibility of regional activation within the jaw muscles. A number of EMG studies have provided evidence supporting the concept that different parts of some muscles may be activated separately. However, extensive EMG studies from different muscle regions are required to provide more specific information about muscular compartments and functional differentiation.

6. HYPOTHESIS

One of the anatomic features of the LP that is unique to the jaw motor system is its muscle fibre architecture, which allows a vector component (*i.e.*, force magnitude and direction) of the total force output from the muscle to be generated in the horizontal plane. The LP, therefore, is ideally suited to generating horizontal jaw movements. The LP consists predominantly of muscle fibres expressing MHC-I that appear to be suited to low forces and prolonged contraction times, and this points toward an important role for the LP in the generation of fine horizontal force vectors, as is required during speech and mastication. The magnitude of the smoothed IHLP and SHLP multi-unit EMG activity was closely correlated to the magnitude of condylar translation during contralateral or protrusive jaw movements. Taken together, the data allow the

hypotheses that *the human LP plays an important role in fine control of horizontal jaw movements* to be made.

The muscle fibres of the SHLP and IHLP run from a broad origin at the roof of the infratemporal fossa and the lateral surface of the lateral pterygoid plate and converge onto the pterygoid fovea of the condyle and disc-capsule complex. The marked divergence of the muscle fibre alignment from the uppermost to the lowermost muscle fibres and from the medial to the lateral side of the muscle provides the possibility of directional pull over a wide angulation if there were selective activation within the muscle. That is, different parts of the SHLP and IHLP may have different contributions to jaw movement.

The internal architecture of the muscle suggests the possibility of separate anatomic compartments, selective activation, and the possibility of a range of force vectors on the condyle. Thus, the presence of some internal tendon lamellae within the IHLP, the grouping of fibres within the SHLP into nonparallel slips, and the complex innervation pattern of the LP, all provide anatomic structure consistent with functional heterogeneous zones within the LP. Histologically, muscle spindles can be concentrated in specific regions of the IHLP, and histochemically, the LP consists of groups of muscle fibres that are predominantly aerobic. Since there is also evidence that muscle spindles are concentrated in regions rich in predominantly aerobic fibres, it may be, therefore, that the spindle-rich regions of the IHLP contain predominantly aerobic fibres and represents functionally distinct zones. Although it is useful to represent the force output from each head of the LP as a single average vector, functional heterogeneity indicates that a range of force vectors are possible. Each of these

vectors would be capable of applying a different magnitude and direction of force on the condyle to effect the desired horizontal jaw movement.

There is preliminary data (Murray et al. 1999b) indicating that IHLP activity simultaneously recorded from two sites exhibited a significant difference of the time to peak during protrusion, but not during contralateral movement. The data suggest that there is a task-dependent change in the relative pattern of recruitment of motor units at the two sites, and further raise the possibility of independent control of subpopulations of motor units within the IHLP.

Based on these anatomical features and EMG evidence, it is proposed that *specific regions of the SHLP and IHLP are capable of selective activation in a finely controlled manner to allow the application of the appropriate force vector to effect the required condylar movement needed for the generation and control of horizontal jaw movements.*

7. AIMS

The aims of the present study were as followings:

1. to develop a method for standardising the horizontal plane command jaw movements recorded with the JAWS3D jaw-tracking system;
2. to demonstrate that human subjects can move their jaws in the horizontal plane to accurately track mid-incisor point (MIPT) targets at different rates, magnitudes and directions of displacement;
3. to show that SMU activity can be reliably recorded throughout task-defined jaw movements;

4. to identify unequivocally the task relations of individual SMUs verified to be located within SHLP and IHLP;
5. to identify whether there were different patterns of activity in different parts of the SHLP;
6. to identify thresholds of the IHLP SMUs in standardised horizontal jaw movement tasks and to determine whether these thresholds vary with the rate or direction of movement as would be expected if these units were involved in the fine control of these tasks;
7. to identify whether there is a relation between CT-verified location and threshold consistent with a proposal for functional heterogeneity within IHLP;
8. to determine whether there is an association between the firing rates of SMUs within IHLP and horizontal jaw movement tasks;
9. to identify whether there was a relation between CT-verified location and firing rate consistent with a proposal for functional heterogeneity within IHLP; and
10. to identify LSFFs of IHLP SMUs during horizontal jaw movements and to determine whether these LSFFs vary with the direction of movement.

CHAPTER II

MATERIALS AND METHODS

The study was performed on 31 subjects (age 18-63 years; mean 25.5 ± 8.1 years; 22 males, 9 females), in 45 recording sessions. Eighteen subjects (18 sessions) and nineteen (27 sessions) subjects participated in the SHLP and IHLP recordings, respectively. The SMU recordings from the SHLP and IHLP were carried out in different sessions when subjects participated in both experiments. The subjects were dental students and staff of the University of Sydney. All subjects did not exhibit signs and symptoms of TMD following history taking and comprehensive examination, including jaw and cervical muscle palpation, measurement of mandibular movements and occlusal assessment, and did not have a history of chronic pain or neuromuscular disorders. Experimental procedures were approved by the Western Sydney Area Health Service Ethics Committee of Westmead Hospital and the Human Ethics Committee of the University of Sydney. All subjects gave informed consent and subjects were informed of any possible complications. The total experimental recording period lasted 3-4 hours.

1. IMAGING SESSIONS

The technical procedures were similar to those used by Orfanos et al. (1996). The SHLP was approached extraorally through the sigmoid notch. For all subjects, two computer tomographic (CT) imaging sessions were conducted. The first was obtained to calculate the trajectory of insertion of the fine-wire electrodes into the

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SHLP. The second was used for verification of the fine-wire electrode placement in the SHLP or IHLP. An initial CT was not used prior to IHLP placement.

The trial insertion point was located in each subject. The following features were marked on the facial skin by a marker pen: (a) the palpated lateral pole of the mandibular condyle (b) the lower border of the zygomatic arch, and (c) the Frankfort Horizontal Plane (FHP) which is the plane of best fit to four points on the skull: the lowermost border of the infraorbital rim bilaterally and the uppermost border of the bony external auditory meatus bilaterally. All points were located by palpation or inspection. The trial insertion point was marked with radiopaque gutta percha on adhesive tape at the point which was 6-7 mm inferior to the lower border of the zygomatic arch and 15 mm anterior to the palpated lateral pole of the condyle.

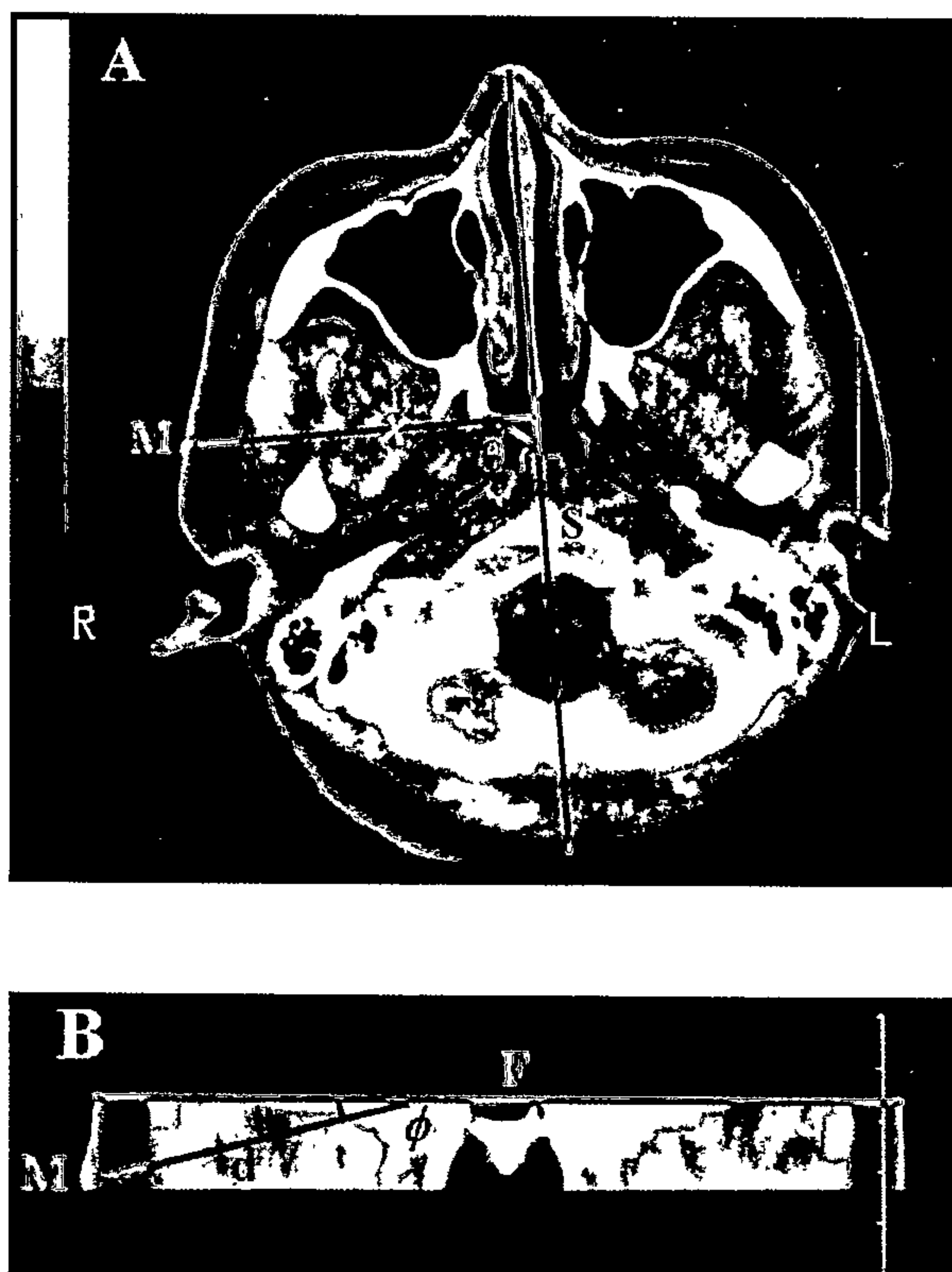


Fig. II-1 Computer tomographic images for craniometric measurement in the coronal plane (A) and reformatted image in the frontal plane (B). t = the target point in the SHLP; M = marker (gutta percha); S = mid-sagittal plane; F = the line parallel to the Frankfort Horizontal Plane; θ = angle to mid-sagittal plane; ϕ = angle to the Frankfort Horizontal Plane; d = depth from the marker to the roof of temporal fossa.

Computer tomographic images were obtained from each subject (General Electric High Speed Advantage CT scanner, Milwaukee, USA). Several contiguous axial slices were taken from each subject (normally 6-8 slices, 3-mm thick). The most superior slice was at the FHP and the most inferior was below the trial insertion point. If the reformatted coronal image demonstrated the roof of the infratemporal fossa, which is one of the landmarks (see below), no further CT scans were taken, but if the coronal image did not show the roof of the infratemporal fossa, a few slices superior to the uppermost slice were obtained until the roof was seen on the coronal image. This procedure provided all required landmarks and the subjects were exposed to the smallest radiation dose.

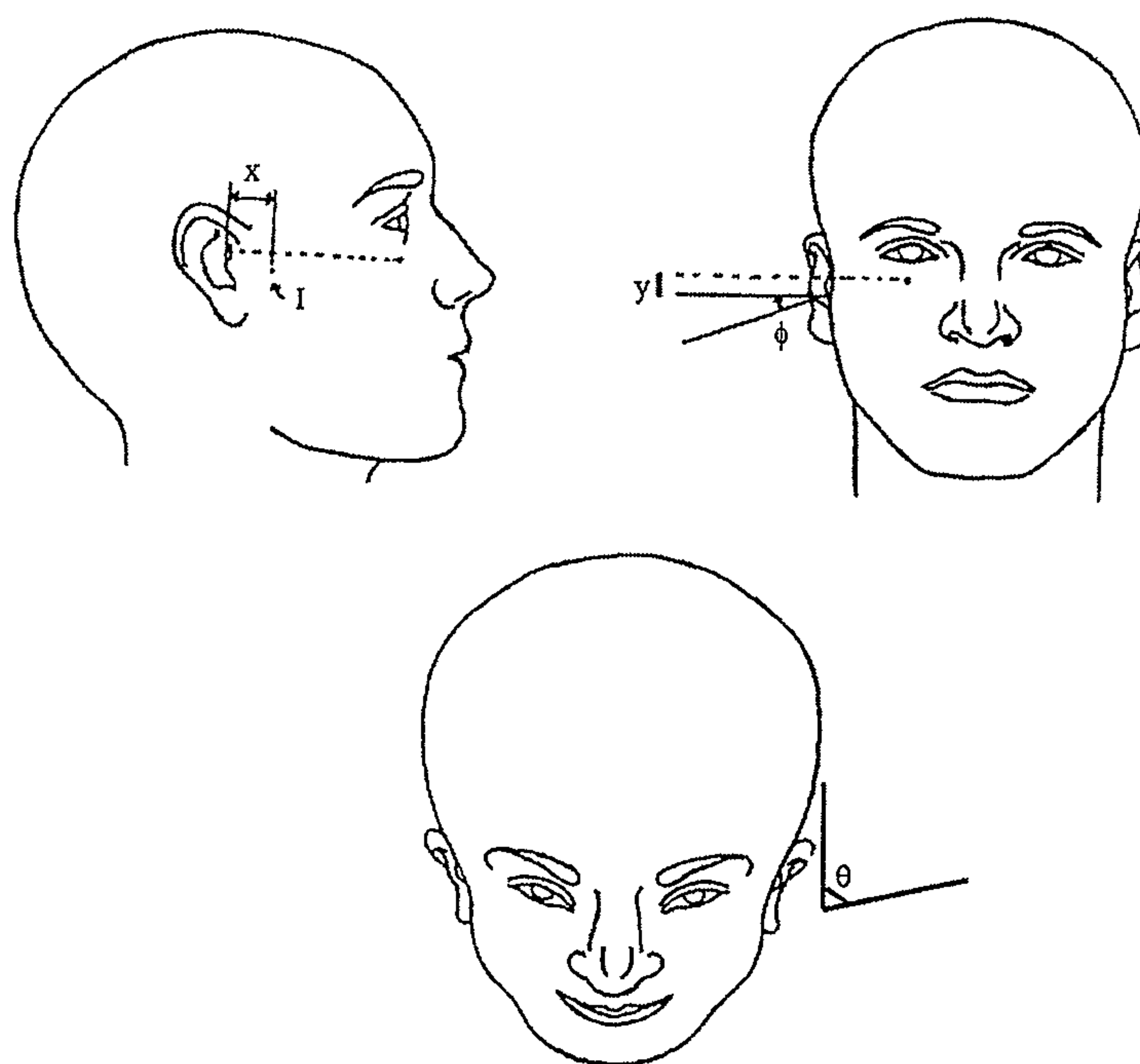


Fig. II-2 Measurements for electrode placement into the SHLP. Measurements were taken of trajectory of electrode into the approximate mediolateral and anteroposterior centre of the SHLP. θ° (*lower* drawing) = angle to the mid-sagittal plane directed forward or backward in the Frankfort Horizontal Plane (FHP) (dashed line in *top* drawings); x = distance (mm) anterior to the tragus of the ear; y = distance (mm) of insertion point below the FHP; ϕ° = upward angulation from the FHP; I = insertion point. (Modified from Orfanos et al. 1996)

Tracings were made on the axial and reformatted coronal images. The landmarks on the CT scan used to determine the final trajectory of insertion included the mandibular condyle, the infratemporal region anterior to the condylar head, the roof of the infratemporal fossa and the zygomatic arch. From the axial slices, a slice level with the trial insertion point was selected. The angle to the mid-sagittal plane (θ°) was measured on the slice. In the coronal plane, the measurements included the angle to the FHP through the gap between the coronoid process and the lower border of the zygomatic arch toward the roof of the infratemporal fossa (α°) and the depth (mm) of needle insertion (d) (Fig. II-1). The distance (mm) anterior to the tragus of the ear (x) and the distance (mm) inferior to the FHP (y) were modified as necessary to avoid adjacent structures such as the capsule of the temporomandibular joint and the mandibular nerve exiting the foramen ovale (Fig. II-2).

2. ELECTRODE PLACEMENT

Bipolar fine-wire electrodes were prepared by passing two teflon-insulated stainless-steel fine wires (Medwire®, New York, USA; 75 μm dia., total dia. with teflon coating 110 μm) through a disposable spinal needle (50-mm long, 25 gauge, Becton-Dickson, USA). The last 40 mm of the fine wires was bent backwards over the end of the spinal needle.

An extraoral approach was used to position the sterile electrode within the SHLP. The area around the insertion point was swabbed with alcohol and topical anaesthetic (EMLA® 5%, Astra, Australia) was placed over the insertion point to provide some anaesthesia. A modified dental facebow, adapted from Koole and

coworkers (1990), was placed on each subject, parallel to the FHP and mid-sagittal plane (Fig. II-3). Ear rods were fixed bilaterally in the external auditory meatus on both sides. A needle carrier was attached to the facebow and oriented according to the measurement obtained from the CT images. The wires were cut immediately with sterile scissors before insertion of the electrode, and left ~2-3 mm of the wire bent back from the tip of the needle. This technique provides a fresh metal exposure at the end of the wires. The distance between the bare ends was ~1-2 mm. The spinal needle was then directed extraorally along the carrier and was inserted (Fig. II-4). When the required depth had been reached, the needle was carefully retracted, leaving the wires within the SHLP.

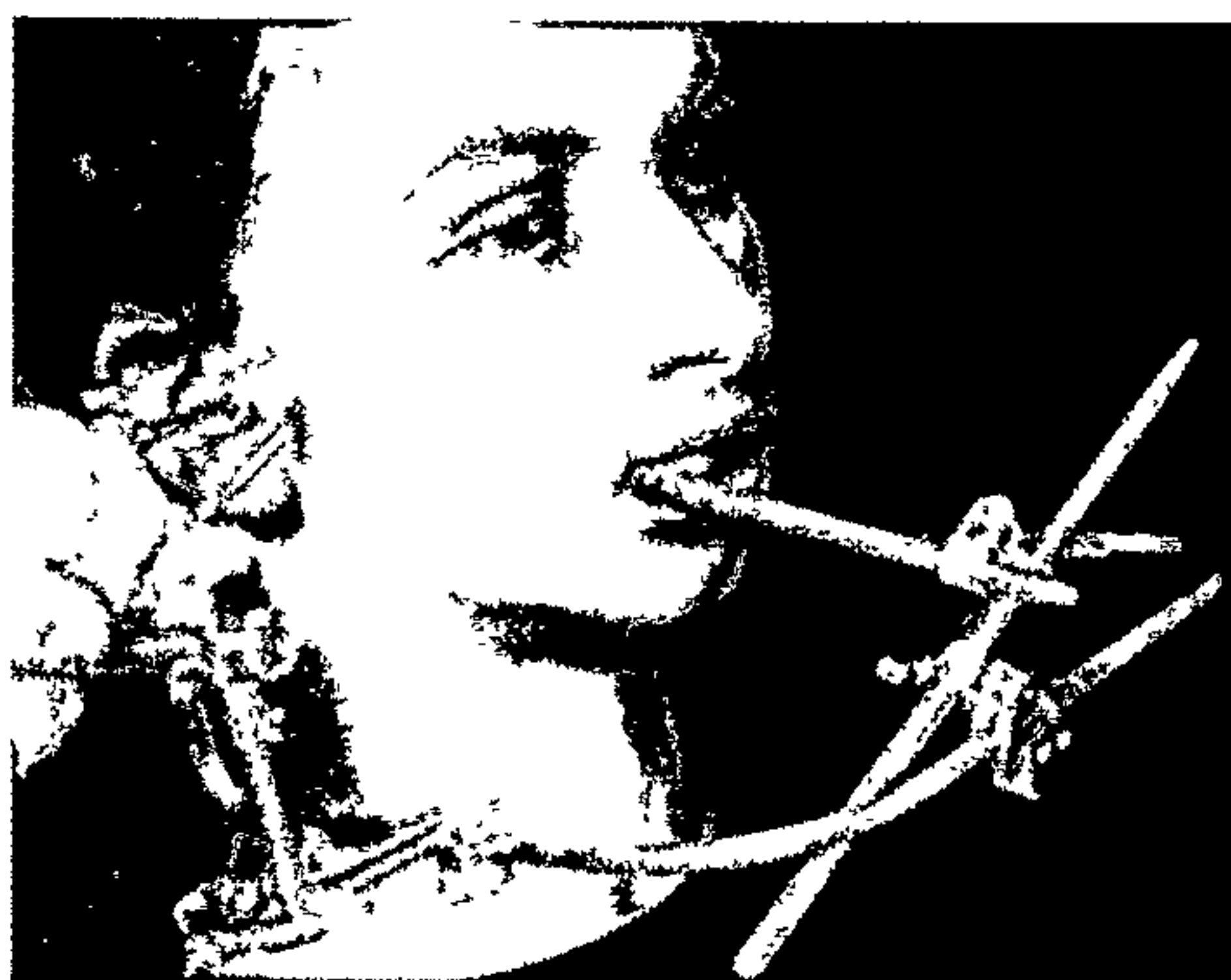


Fig. II-3 The modified facebow with the needle carrier for an electrode placement of the SHLP.



Fig. II-4 Extraoral approach for the SHLP electrode placement. The needle was placed along the carrier supported by the modified facebow; F = Frankfort Horizontal Plane; Z = the lower border of the zygomatic arch.

The method for electrode placement within the IHLP was modified from Wood and coworkers (1986). To place the electrode within the IHLP, and intraoral

approach was used. Topical anaesthetic cream (EMLA® 5%, Astra, Australia) was applied on an insertion point prior to the needle insertion. The insertion point was the depth of the posterior vestibular sulcus at about the gingival level of the upper second molar. The needle was inserted in an upward, medial and posterior direction until the needle was contacted the lateral aspect of the lateral pterygoid plate (Fig. II-5). The needle, then, was carefully retracted, leaving the wires within the IHLP. The wires were secured to the buccal surface of the upper first molar tooth with a small piece of Stomahesive® wafer (Convatec, Victoria, Australia) and led out through the angle of the mouth. Adhesive tape was used to secure both electrodes to the skin and the terminal ends were connected to the recording device.

At the end of each recording session, 5-9 CT-axial slices (1-3-mm thick) were taken inferior to and parallel with the clinically approximated FHP. An example of verification data in the IHLP is shown in Fig. II-6. The horizontal CT slice (1-mm thick) in Fig. II-6A showed the electrode fine-wire tips (arrows: fine-wire tips) in the IHLP. The electrode tips were 7 mm below the roof of the infratemporal fossa. The reformatted images in Fig. II-B and C were taken through the fine-wire tips in the plane of section indicated in the inset figurines on the right side. These data confirmed electrode location within the IHLP. An example of electrode verification in the SHLP is shown in Fig. II-7 in the same format as Fig. II-6.

The data-acquisition equipment was the micro1401 from Cambridge Electronic Design (CED; Cambridge, England) and the sampling rate was 10,000 or 20,000 samples/s, and bandwidth 100Hz – 10 kHz. Single motor units were discriminated

with Spike2® software from the CED. Power spectral analysis revealed that the highest frequency component of the SMU spike train was <4,000 Hz.

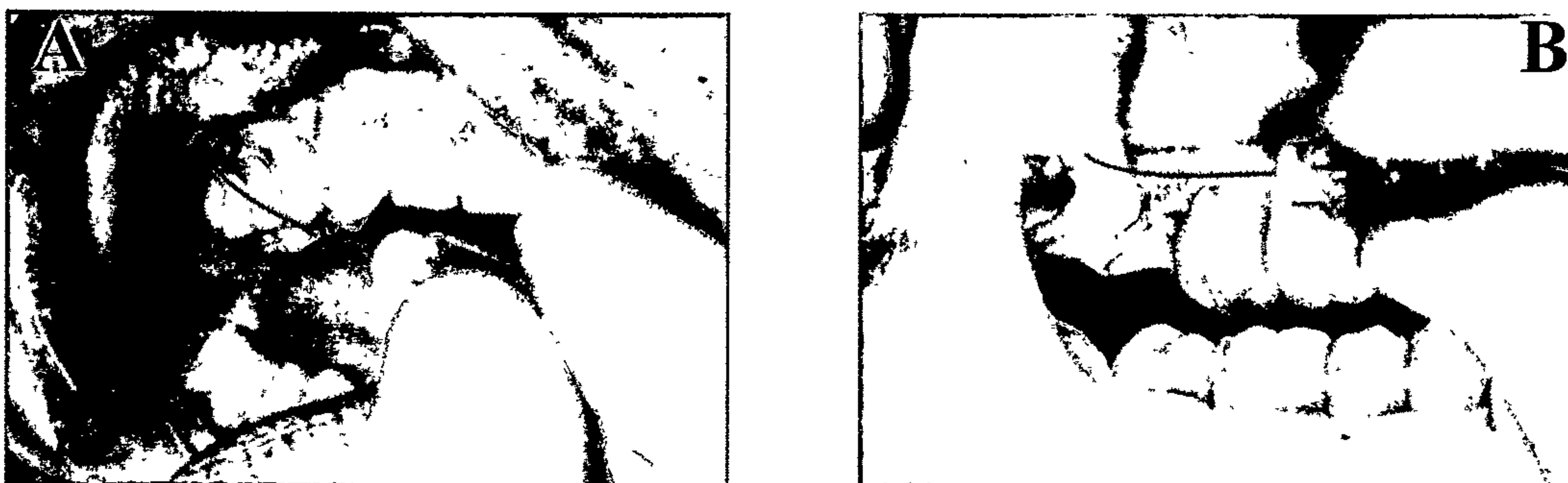


Fig. II- 5 Intraoral approach for the IHLP electrode placement. (A) The curved needle was inserted at the gingival level of the upper second molar. (B) The trajectory of the needle, aiming to contact the lateral pterygoid plate.

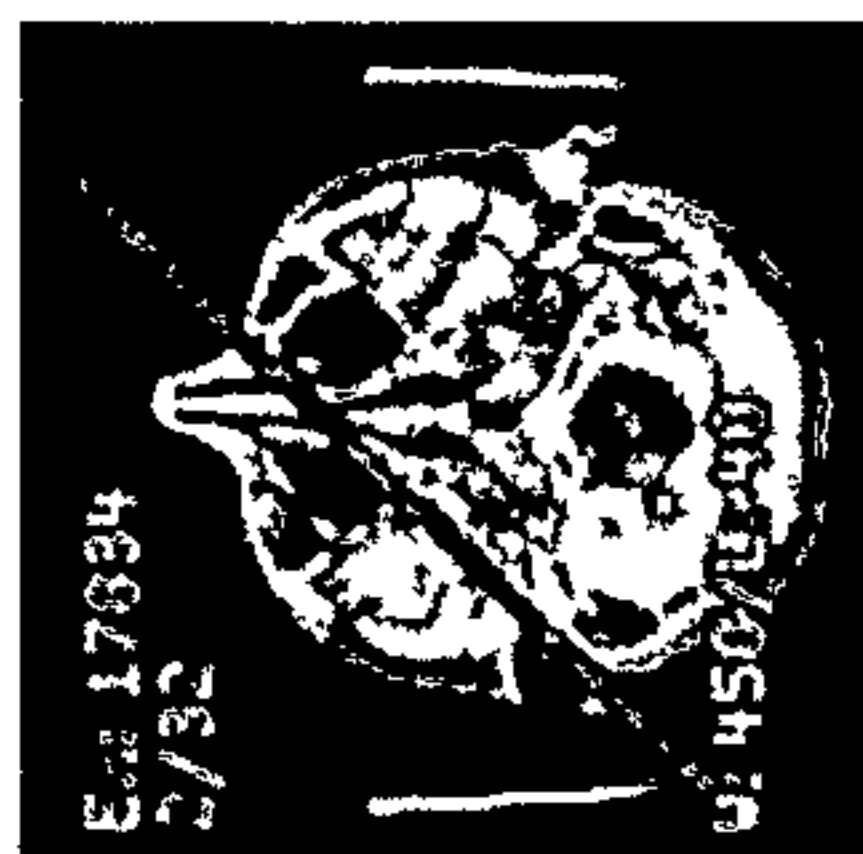
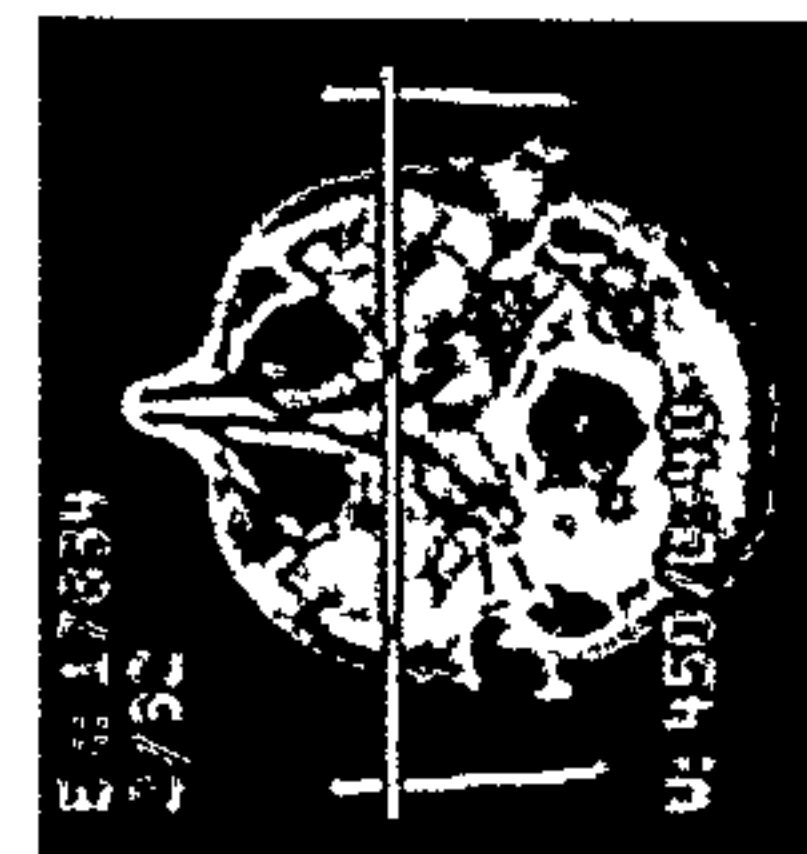
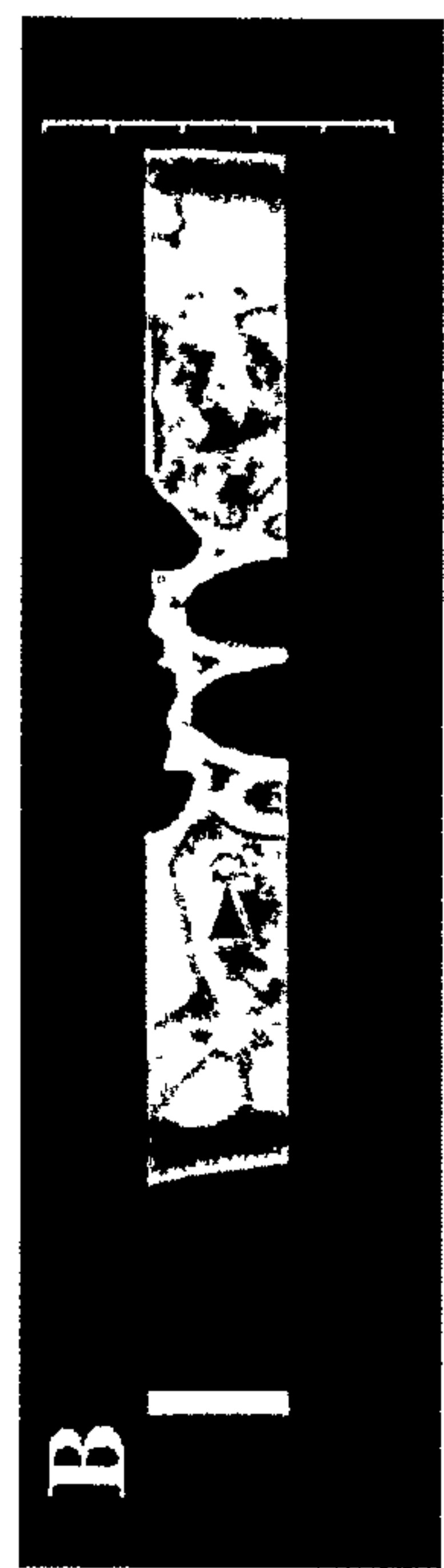
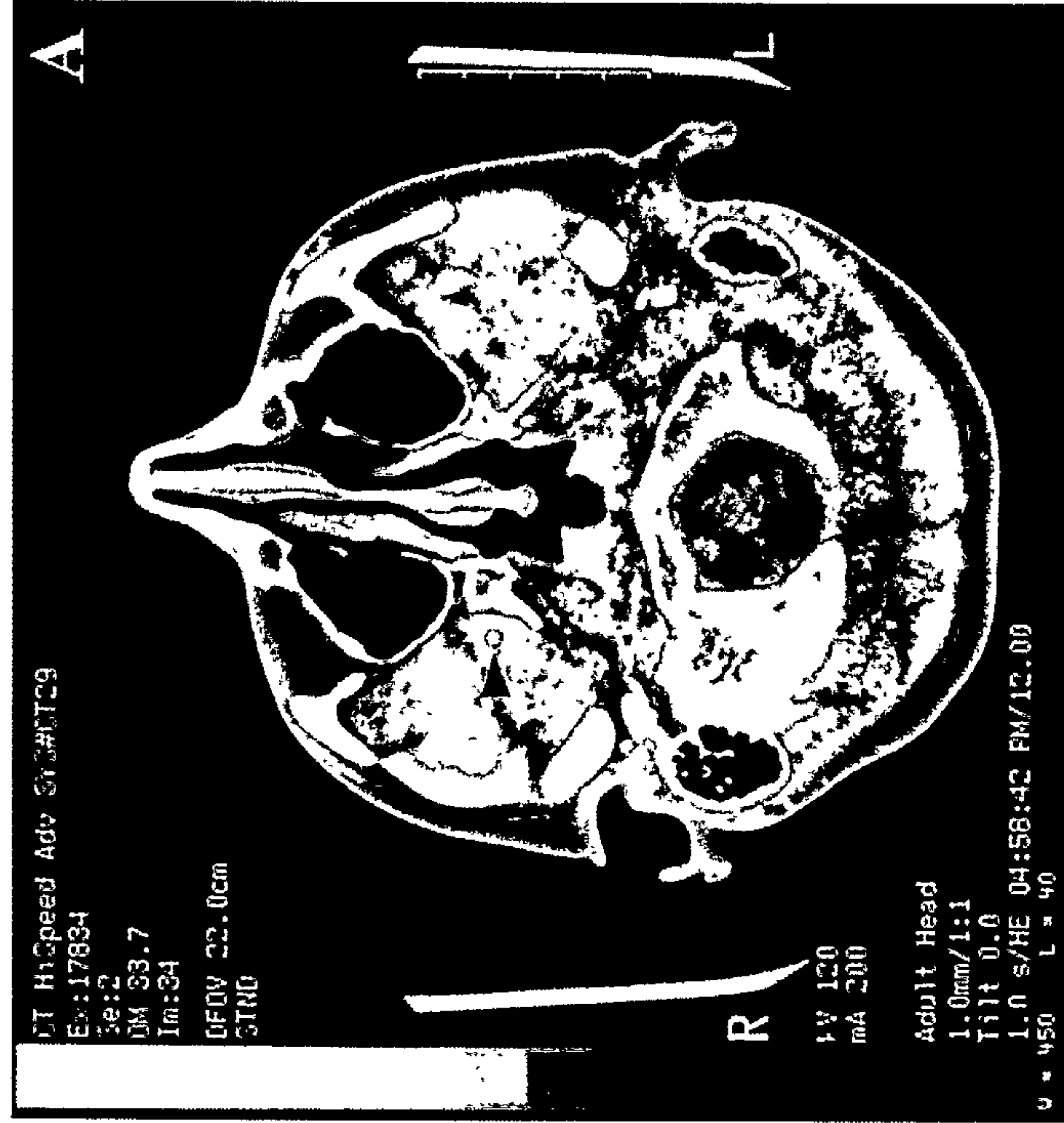


Fig. II-6 Verification of electrode placement within IHLP by CT imaging. (*A*) A horizontal slice (1-mm thick) showing electrode fine-wire tips (black arrow) within the IHLP in one subject. This slice was ~7 mm inferior to the roof of the infratemporal fossa. (*B*) and (*C*) Reformatted images taken through the fine-wire tips (black arrows) in the plane of section indicated in the figurines on the right. *B* was reformatted in the frontal plane and *C* represents an oblique plane parallel to the long axis of the IHLP. Calibration bar: each division = 10 mm.

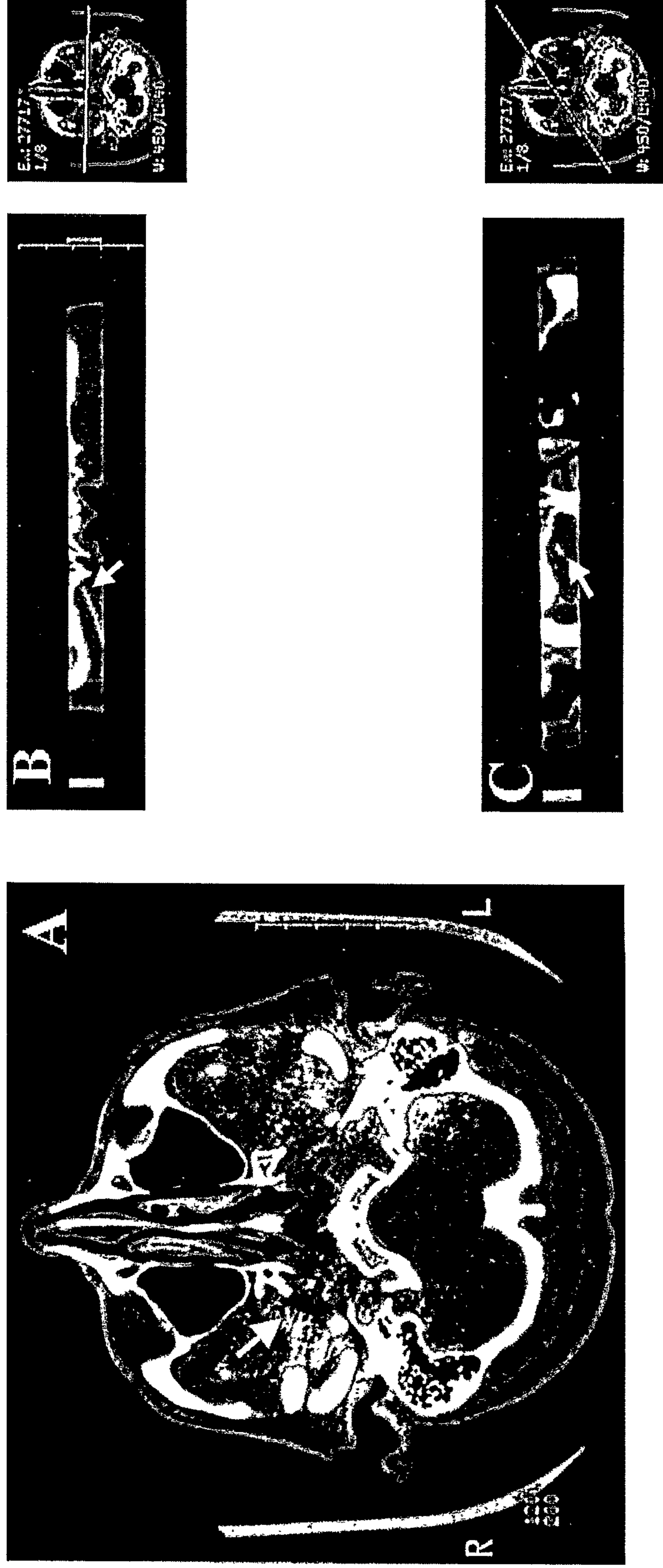


Fig. II-7 Verification of electrode placement within SHLP by CT imaging. The horizontal slice in *A* was ~ 2 mm inferior to the roof of the temporal fossa. The format is the

same as Fig. II-6. Calibration bar: each division = 10 mm.

3. RECORDING OF CONDYLAR AND MID-INCISOR POINT MOVEMENT DURING NON-STANDARDISED AND STANDARDISED TASKS

The movement of the palpated lateral condylar pole and mid-incisor point (MIPT, the point between the incisal edges of the lower central incisor teeth) was recorded with an optoelectronic jaw tracking system (JAWS3D, Metropoly AG, Zurich, Switzerland; Mesqui and Palla 1985) with a sampling rate of 67 samples/s. The position of the mandible was recorded with six degrees of freedom. The system uses three one-dimensional optosensor cameras to measure the spatial locations of six light-emitting diodes (LEDs) attached to two lightweight plastic triangular target frames. One target frame was attached to the maxilla and the other to the mandible at the anterior teeth by custom-made metal clutches with a rigid rod that projected out of the mouth. The clutches minimally interfered with lip movement and lip seal, and were free from occlusal contact in intercuspal position and during excursive movements of the jaw. The target frames were positioned on the side of the face near the area of the temporomandibular joint with their longest sides parallel with the FHP and each target frame lay in a plane parallel with the mid-sagittal plane. Cameras monitored the spatial locations of the LEDs. During all recordings, the subjects sat upright without head support. Since mandibular jaw movement was recorded in relation to the maxilla, any associated head movement did not influence the lower jaw motion measurement. In the present study, the coordinate system for jaw displacement was the MIPT. The experimental set up is shown in Fig. II-8.

The position of the subject's MIPT in the horizontal plane was displayed as a dot (termed MIPT dot) on the video screen for the subject to track and this was derived from the JAWS3D system on-line. The JAWS3D tracking system recorded the motion of the target frames and then, off-line, could also calculate the motion of any point subsequently selected. All jaw movements were performed with the teeth apart, and movements started from the postural jaw position. Subjects were instructed to swallow and relax their jaws with their lips lightly touching to achieve the postural jaw position. The error of the JAWS3D system bench tested was 0.1 mm (Airolidi et al. 1994). For the purposes of the present study, the spatial resolution was conservatively estimated to be ~ 0.2 mm for threshold estimation (Peck et al. 1997).



Fig. II-8 Experimental set up. JAWS3D tracking system, target frames and the LED bank placed over the video screen in front of the subject.

3.1 Non-standardised Tasks

Before the standardised tasks were performed (see Materials and Methods: section 3.2), EMG activity from the SHLP and the IHLF were studied during non-standardised contralateral, ipsilateral, protrusive, and retrusive jaw movement,

submaximal jaw-opening, jaw closing and clenching in intercuspal position. These movements were termed the non-standardised tasks, as there was no visual feedback to the subject of the movement. A contralateral movement was defined as a movement of the jaw from postural jaw position to the side opposite to the SMU recording side followed by a return of the jaw to postural position. An ipsilateral movement was a movement to the same side as the SMU recording side and back. A protrusive jaw movement was defined as a movement of the jaw from postural jaw position forward followed by a return to postural position. A retrusive jaw movement was a movement backward from postural jaw position and forward again. Jaw movement was performed without tooth contact to minimise periodontal contribution to EMG activity. Although subjects were instructed to move the jaw in protrusion, some subjects displayed a deviation to one side or the other. However, these protrusive movements were always distinctly different from the contralateral movements in the same subjects. Wide jaw opening in both standardised and non-standardised movements was avoided to minimise the danger of losing units.

These non-standardised tasks were performed to provide an overall assessment of the motor activity to which the units at the site were related. Further, the SHLP and IHLP activities during the postural jaw position, achieved by instructing subjects to swallow and relax their jaws with their lips lightly touching, were recorded at the beginning, during and at the end of the experiment. All SMUs recorded during non-standardised tasks, standardised single-step and/or multiple-step displacements were included in the analysis as to the tasks to which the SMUs were related. Before experimental recordings were carried out, the

maximum lateral, protrusive, retrusive jaw displacement and maximum jaw opening were measured in each subject.

3.2 Standardised Tasks

Jaw movement was standardised by having the subject move the position of the MIPT dot, so as to track a computer controlled target (Fig. II-9A). This target was an illuminated LED as part of a linear bank of 15 LEDs positioned over the video screen and to the side of the trajectory of the MIPT dot. The trajectory of the MIPT dot in the horizontal plane was displayed on the video screen. The LEDs were controlled by scripts written in Spike2 software (CED) and run on the CED system that was also used to record SMUs. In Fig. II-9B the sequence and timing of LED illumination is shown on the right of the figure. Only one LED was illuminated at any one time. Movement of the MIPT dot from the location at one illuminated LED to the location at the next illuminated LED corresponded to 0.33, 0.65 or 1.3 mm of movement at the subject's MIPT depending on the display gain on the video screen. Figure II-9 shows LEDs numbered 1 through 9. For ease of viewing small displacements, the display on the computer screen was magnified 3×. In the example illustrated in Fig. II-9, movement of the MIPT dot from the location at one illuminated LED to the location at the next illuminated LED corresponded with 1.3 mm of movement at the subject's MIPT.

The subject was initially instructed to perform a few trials of lateral or protrusive jaw movement to become accustomed to the task. The linear bank of LEDs was then oriented along the direction of movement of the MIPT dot, which was displayed on the screen in the horizontal plane. The Spike2 software illuminated

the LEDs in sequence and the subject was instructed to move the jaw so the MIPT dot on the screen followed the illuminated LED as smoothly as possible. This program allowed adjustment to the rate of jaw movement by changing time-off duration between each LED (*eg.*, *a* in Fig. II-9B), and time-on duration of each LED (*b* in Fig. II-9B), and also allowed control of the desired amount of displacement by varying the highest LED in the bank that was illuminated.

3.2.1 Single-step Displacements

The single-step tasks were performed by 8 subjects (13 sessions) and 13 subjects (13 sessions) during the IHLP and SHLP SMU recordings, respectively. Each movement started with the jaw in postural position for 3 s (Fig. II-9B). The subject was instructed to move the MIPT dot smoothly and track the target at the rate and magnitude of displacement controlled by the Spike2 software during standardised protrusive, lateral excursion or jaw opening. The amount of jaw displacement during each task was determined by the experimenter's ability to discriminate one or more SMUs throughout the task. Then the LEDs were aligned along the trajectory of MIPT movement, and the LED corresponding to the required displacement was programmed. During jaw movements, subjects were required to track the target by moving the dot to any point within the diameter of an LED (*eg.*, centre or the boundary of the LED). Each subject was required to hold the MIPT dot as much as possible within the boundaries of the LED that was illuminated for the holding phase period of each step displacement. The jaw was then returned to the postural position again following the return targets, and this concluded the trial.

To study the effects of rate of jaw movement on the SMU properties (*eg.*, threshold), the subject was instructed to track the target at fast, intermediate, and slow rates (see below). Each task was repeated five to eight times with a rest period of ≥ 1 min between trials. By changing the alignment of the linear bank of LEDs, it was possible to change the direction along which the subjects moved their jaw. Thus, subjects tracked the targets so as to move the jaw to the side contralateral or ipsilateral to the side of SMU recording, or with a change in the orientation of the LEDs, in protrusion or jaw opening. Standardised retrusive jaw movement has not been carried out due to very small displacement where the jaw could be retracted.

Figure II-9B is an example of single-step jaw movement. The shaded areas on the left reflect the diameter (2.8 mm) of each LED. The continuous line (—) in the centre of each shaded area was termed the target line and was obtained by plotting timing against distance and represents the ideal trajectory of MIPT movement. After the subject kept the jaw at postural position for 3 s the first LED was turned off (Fig. II-9B, right). After 200 ms (a in Fig. II-9B) the next LED was lit up for 100 ms. This cycle (200 ms off, next LED 100 ms on) was repeated until the jaw had displaced to a position requiring holding of the jaw for 5 s which was achieved by illuminating the assigned target LED for 5 s (No. 9 in the example in Fig. II-9B). Then, the same cycle started again from the target LED back to the first LED. For trials at slower rates of movement, the light-off duration (a in Fig. II-9B) was changed from 200 ms to 600 ms or 1 s. These durations corresponded with rates of movement of 6.5 mm/s (fast, f in Fig. II-9B), 2.2 mm/s (intermediate, i in Fig. II-9B) or 1.3 mm/s (slow), respectively.

The fastest rate of movement was about the fastest that our subjects found comfortable to perform. Although subjects could move slower than the slowest rate of movement, this rate was comfortable for the subjects. This range of rates of movement, therefore, provided a wide range of rates of displacement that was suitable for characterising associated SMU firing properties. A range of target displacements was possible with this method, from 0.33 mm to ~18.0 mm. The latter covered the maximum lateral and protrusive displacements possible.

3.2.2 Multiple-step Displacements

Fourteen subjects (18 sessions) and 15 subjects (15 sessions) also performed lateral and protrusive jaw movements in a step-like manner during IHLP and SHLP SMU recordings, respectively. Each trial contained 2-3 dynamic and holding phases. A holding phase was defined as the period (3-5 s) where the MIPT plot showed little or no fluctuation from a stable level. A dynamic phase was defined as the period to the onset of the first holding phase (D1 in Fig. II-10B) or from the end of one holding phase at one target to the next holding phase at the next assigned target (D2 or D3 in Fig. II-10B). In this experiment, the holding phases at the first, second and third steps were named H1, H2 and H3, respectively. Figure II-10 displays an example of a trial where the target was tracked by moving the jaw to the first assigned target (H1; *i.e.*, LED No. 3 in Fig. II-10B). The jaw was maintained in that position for 3 s. The jaw was then moved a further small amount laterally to the next assigned target (*i.e.*, LED No. 5 in Fig. II-10B) and again maintained in that position for 3 s. The subject then moved the jaw to the final target (LED No. 7) for 3 s. Each subject was required to hold the MIPT dot as much as possible within the boundaries of the LED that

was illuminated for the holding-phase period of the step displacement. To conclude the trial, the jaw was moved back to the postural position by following a pre-set target LED sequence (R in Fig. II-10B). In some subjects, only 2-step displacements were performed due to the difficulty of SMU discrimination at the larger magnitudes of displacement. The tasks were termed the contralateral (or ipsilateral or protrusive) 2-step (or 3-step) tasks. Trials for different rates of movement were repeated 5-8 times.

3.3 Tasks for Least-sustainable Firing Frequencies

Least-sustainable firing frequency for each SMU of the IHLP and SHLP was studied during contralateral, ipsilateral and protrusive movements in 14 and 10 subjects, respectively. The subjects were instructed to move the jaw in one direction to activate a SMU that was clearly distinguishable from other units, and to maintain the unit firing continuously at the lowest firing rate possible by visual feedback. Each task was repeated at least 5 times for each direction.

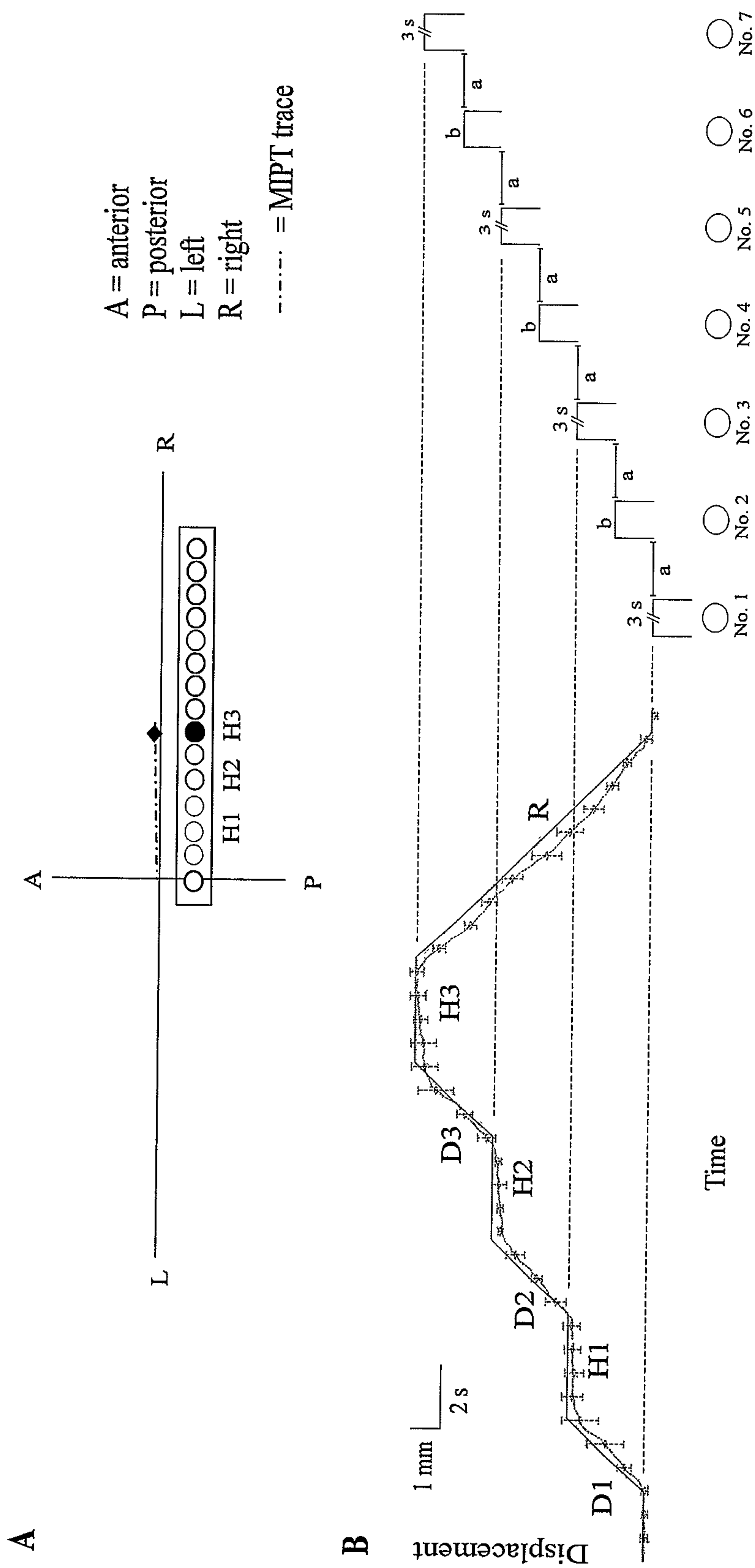


Fig. II-10 Diagrams illustrating the target lines and corresponding mid-incisor point (MIPT) displacements during right multiple-step jaw movement. *A*: a diagram representing the LED bank (row of open circles) and a display of the MIPT dot (filled diamond) on the video screen. The filled circle indicates an illuminated LED at the holding level 'H3'. *B*: multiple step displacement. *Left*: averaged MIPT displacement (dashed lines) with SD bars every 750 ms together with target lines (solid lines). Shaded area indicates diameter of LED (2.8 mm). *Right*: diagrams of actual time and sequence of illuminated LEDs. Each circle represents an LED. a = time-off duration (200 ms, 600 ms or 1 s) and b = time-on duration (100 ms). Tracings on the left-hand side correspond to the timing sequence on the right-hand side at time-off duration of 1 s which correspond to rate of movement of 1.3 mm/s. D1, D2 and D3 = dynamic phase 1, 2 and 3. H1, H2, H3 = holding phase 1, 2 and 3. R = return phase.