FUNCTIONAL PROPERTIES OF SINGLE MOTOR UNITS DURING ISOMETRIC CONTRACTION IN THE SUPERIOR HEAD OF THE HUMAN LATERAL PTERYGOID MUSCLE

by

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DECLARATION

I hereby declare that the work described herein is, to the best of the knowledge, original and is entirely the work of the author, except where due acknowledgements have been made. The work was conducted while the author was pursuing a Master degree program at the Faculty of Dentistry, the University of Sydney and carried out at the Jaw Function and Orofacial Pain Research Unit, Westmead Hospital under the supervision of Professor Greg Murray and Associate Professor Chris Peck. I certify that this thesis has not already been submitted, wholly or in part, for the award of the higher degree to any other university or institution that all help received in preparing this thesis, and all sources used have been acknowledged.

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ABSTRACT

Despite the considerable interest in the function of the superior head of the human lateral pterygoid muscle (SHLP) for many decades, there is still limited information and controversy as to the normal function of the SHLP. The aims of the present study were (1) to determine the isometric tasks for which single motor units (SMUs) from computer tomography-verified sites within the SHLP were active and whether SHLP SMUs were preferentially active for specific horizontal isometric tasks, (2) to determine whether different SMUs were selectively active for different horizontal isometric tasks of the SHLP as would be expected if the SHLP is functionally heterogeneous, (3) to determine whether the firing rates of the SHLP SMUs increase with the gradation of isometric force as would be expected if the SHLP is crucial for a fine control of horizontal isometric force. The hypotheses were that (1) the SHLP delivers force to the condyle in a range of directions similar to those for which the IHLP is involved and (2) different SMUs recorded from the SHLP are selectively active for specific isometric tasks and are active or inactive for other isometric tasks, (3) the SHLP plays an important role in the gradation of horizontal isometric forces through the increment of firing rate as the magnitude of force increases.

SMU activities from 11 healthy subjects were recorded from SHLP unilaterally with fine-wire electrodes and during the generation of horizontally directed isometric jaw forces in the ipsilateral (IL, i.e., jaw force to the same side as the recording side for SHLP), protrusive (P) and contralateral (CL) directions and in two intermediate directions [ipsilateral-protrusive (IL-P), contralateral-protrusive (CL-P)]. Assessment of activity within the SHLP was also made when the jaw was at the rest or postural jaw position in all subjects and during maximum clenching in nine subjects. Force
was exerted on a transducer, attached to an upper bite-block, by a rod attached to a bite-block on the lower jaw. Subjects tracked a target on a screen where the force increased by 100 gwt (0.98 N) increments from 400 gwt (3.92 N) to 800 gwt (7.84 N). A total of 48 SHLP SMUs were discriminated and each of them was active during at least one of the horizontal isometric tasks. None of the SMUs were active when the jaw was at rest or postural jaw position. Of the 48 SMUs, 34 (71%) SMUs were active at CL, 33 (69%) at CL-P, 32 (67%) at P, 17 (35%) at IL-P and 6 (13%) SMUs were active at IL. Electrode locations of all subjects, after verification by computer tomography (CT), were plotted on two-dimensional grids representing the SHLP in the supero-inferior and antero-posterior directions and in the medio-lateral and antero-posterior directions. No activity was observed for any horizontal isometric tasks at the two lowermost and lateralmost recording sites within the SHLP. The SMUs from most of the subjects that were active during CL, CL-P, P, IL-P with or without IL were mostly scattered throughout the SHLP both vertically and horizontally. There was EMG activity present in SHLP during 100% maximum clench in five of nine subjects.

Qualitatively, SHLP EMG activity increased with increases in isometric force. Quantitatively, the mean firing rates of 48 SMUs recorded from SHLP of all subjects significantly increased with force from 400-800 gwt in one or more directions \[F_{\text{force}} (4, 1650) = 55.512, P = 0.000\] with the mean firing rates being 7.4, 9.9, 12.8, 13.9 and 17.8 impulses/s in relation to 400, 500, 600, 700 and 800 gwt, respectively. The pairwise comparisons between possible pairs of tasks indicated that CL, CL-P and P have comparable firing rates (e.g., 13.3, 12.6 and 12.6 impulses/s, respectively).
The data suggest that (1) the SHLP plays an important role in delivering graded horizontal forces to the condyle in a range of directions and (2) SMUs within SHLP contribute to the generation of contralateral and protrusive forces on the condyle just as has been proposed for the inferior head of the lateral pterygoid (IHLP), and also contribute to the generation of forces to the ipsilateral condyle. The proposed evidence provided for selective activation of subcompartments within the SHLP may be associated with specific fibre bundle orientations and/or lengths that may be best suited to specific horizontal isometric forces. Taken together these data are not consistent with previous notions that these two heads function reciprocally but are consistent with Hannam and McMillan’s proposal (Crit. Rev. Oral Biol. Med., 5: 55-89; 1994) that both SHLP and IHLP should be regarded as part of one muscle with the distribution of activity shaded depending on the biomechanical demands of the task.
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ABBREVIATIONS

CL : Contralateral
CL-P : Contralateral protrusion
CT : Computer tomography
EMG : Electromyographic
FR : Fast contracting and intermediate fatigue resistant fibres
FF : Fast contracting and fatigue susceptible fibres
gwt : Gram weight (unit of measuring force)
IHLP : Inferior head of lateral pterygoid muscle
IL-P : Ipsilateral protrusion
IL : Ipsilateral
MHC : Myosin heavy chain
MRI : Magnetic resonance imaging
MTFR : Minimal tonic firing rate
MVC : Maximum voluntary contraction
P : Protrusion
PCSA : Physiological cross sectional area
S : Slow contracting and fatigue resistant fibres
SHLP : Superior head of lateral pterygoid muscle
SMU : Single motor unit
TMDs : Temporomandibular disorders
TMJ : Temporomandibular joint
PUBLICATIONS

PAPER

PUBLISHED ABSTRACT
CHAPTER I
REVIEW OF LITERATURE

1. INTRODUCTION

The lateral pterygoid muscle is an important masticatory muscle and is recognized as being divided into the upper or superior head (SHLP) and the lower or inferior head (IHLP). However, there is a limited understanding and lack of consensus as to the normal function of the human lateral pterygoid muscle (for reviews see, Hannam and McMillan, 1994; Murray et al., 2001; Murray et al., 2004). Further, the clinical view that this muscle may be dysfunctional in patients with temporomandibular disorders (TMDs) is still widely accepted (Mahan et al., 1983; Juniper, 1984; Okeson, 2003; Hiraba et al., 2000). This clinical view has contributed to the development of irreversible and reversible therapies for TMD patients. Poor coordination between the two heads, or muscle hypoactivity or hyperactivity, for example, have been hypothesized as possible disturbances in the activity of the lateral pterygoid muscle in TMD patients (Porter, 1970; Mahan et al., 1983; Juniper, 1984; Okeson, 2003; Hiraba et al., 2000).

The SHLP muscle is of special interest given that it has long been thought to play an important, although controversial role in temporomandibular joint (TMJ) function and also in the aetiology of TMD (Juniper, 1984; Klineberg, 1991; Heylings et al., 1995; Fujita et al., 2001; Murray et al., 2001, 2004). Further, recent evidence points to anatomical, histological and functional complexity within the muscle. For example, three functionally distinct zones have recently been described within the SHLP (Phanachet et al., 2003). Given the very limited information available on the function of the SHLP together with the emerging evidence for functional complexity within the lateral pterygoid, this study focused on the functional activities of the SHLP.
There has been considerable controversy as to the nature of the insertion of the SHLP into the condyle. For example, some studies have concluded that the SHLP inserts exclusively into the anterior part of the joint capsule and the disc (Hónee, 1972) as well as into the medial portion of the disc (Porter, 1970), while others maintain a predominant insertion into the condyle with a variable insertion into the disc (Grant, 1973; Widmalm et al., 1987; Wilkinson, 1988; Wilkinson and Chan, 1989). There is also a range of functions that have been proposed for the SHLP. For example, some studies report that the SHLP mainly stabilizes the head of the condyle and disc against the articular eminence during jaw closing (Widmalm et al., 1987; Osborn, 1995), while others claim that the SHLP controls the angular relationship between the disc and condyle (Hiraba et al., 2000), or acts only as a jaw closer (Juniper, 1981). Further, other studies report that SHLP is active in a reciprocal manner to the IHLP during ipsilateral movement (Van Eijden et al., 1995), jaw closing and retraction (Mahan et al., 1983; Gibbs et al., 1984; Hiraba et al., 2000), whereas other studies propose that it may be active during jaw opening, protrusion or contralateral movement (Sessle and Gurza, 1982; Murray et al., 1999). Its function at the postural jaw position is also a conflicting issue. A number of studies (Mahan et al., 1983; Wood et al., 1986; Murray et al., 2001) reported that activity in the SHLP was absent at resting or postural jaw position in asymptomatic subjects, whereas Juniper (1981), Okeson (2003) and Hiraba et al. (2000) reported that the SHLP is maintained in a mild state of contraction at postural jaw position and proposed therefore that the SHLP exerts an anterior and medial force on the disc when the jaw is at postural position.

Fujita et al. (2001) investigated the macroanatomy and histology of the human lateral pterygoid muscle and supported the hypothesis that uncoordinated activity between
the muscle bundles of the SHLP and IHLP could cause unstabilized movement of the disc and disc displacement. This could occur because their data suggested that the SHLP inserted into the disc-capsule complex and the IHLP onto the pterygoid fovea (Fujita et al., 2001), although most recent data indicate that the SHLP inserts predominantly into the neck of the condyle (see below). This notion of uncoordinated activity between the SHLP and IHLP as a possible cause of disc displacement is in agreement with Juniper (1984), Okeson (2003) and Hiraba et al. (2000) and added weight to the broadly accepted clinical viewpoint that the lateral pterygoid muscle is dysfunctional in patients with TMD. The deep location of the lateral pterygoid muscle, however, means that electrode placement within the muscle for the purpose of studying lateral pterygoid muscle function is difficult. Few previous studies have described the activity of the SHLP in non-TMD subjects and TMD patients but most of the studies lack a reliable method to verify the electrode location within the SHLP except some recent studies (e.g., Orfanos et al., 1996; Murray et al., 1999; Phanachet et al., 2003). The earlier lack of verification could be a reason for the variability between studies as to the normal function of the SHLP. Therefore, a reliable verification of electrode placement is a significant factor for any electromyographic study of SHLP.

Many studies have attempted to investigate the normal function of the lateral pterygoid muscle during various mandibular movements (i.e., during contralateral and protrusive jaw movements). A number of recent studies (Phanachet et al., 2001, 2002, 2003) have clarified the normal function of the lateral pterygoid muscle through recordings of IHLP and SHLP activity during standardized isotonic movements. Isotonic muscle contraction results in a change in length of the muscle through either shortening or lengthening; however, the muscle tension remains
constant. Muscles may also contract isometrically. That is, muscles contract with no change in length. Even though muscle length is unchanged, there is still shortening of the sarcomeres to allow internal tension to be generated and the muscle becomes rigid without shortening.

Several isometric contraction studies in limb muscles have clarified the normal function of these muscles through single motor unit (SMU) recordings (Büdingen and Freund, 1976; De Luca et al., 1996; Herrman and Flanders, 1998). Similar approaches have been applied to the jaw closing muscles (Desmedt and Godaux, 1979; Stålberg et al., 1987; Hannam and McMillan, 1994; Miles, 1995). In masticatory muscles, isometric contractions could occur during the parafunctional jaw activities of tooth grinding and clenching, which can be directed horizontally or vertically. Though isometric contraction in masticatory muscles is the result of the activation of many muscles (Freund, 1983), the predominantly horizontal arrangement of fibres that characterizes the lateral pterygoid muscle has led to the suggestion that the lateral pterygoid muscle plays a major role in the generation and fine control of horizontal force in mastication and in parafunctional grinding (Uchida et al., 2001; Uchida et al., 2002; Murray et al., 2004).

Isometric contraction of the masticatory muscles has been studied extensively in the masseter muscle during isometric clenching (e.g., Manns et al., 1979; Scutter and Turker, 1998; Rodrigues and Ferreira, 2004). There is little information on the isometric contraction in the lateral pterygoid muscle despite evidence for the involvement of the lateral pterygoid muscle in the development of horizontal force vectors towards the end of the intercuspal phase of chewing (Wood et al., 1986) as well as the proposal by Widmalm et al. (1987) that the lateral pterygoid muscle is
active during voluntary tooth grinding or gnashing. In light of the current view that the SHLP inserts predominantly or exclusively into the condyle (Schumacher, 1961; Wilkinson, 1988; Naidoo, 1996), it is hypothesized that a major function of the SHLP is in the generation and control of horizontally directed jaw forces and movements. This proposal is consistent with the recent findings of activity in SHLP during isotonic contralateral and protrusive jaw movements (Phanachet et al., 2003) and is in contrast to the previous dogma of activity in SHLP during jaw closing, retraction and ipsilateral jaw movement (e.g., Van Eijden et al., 1995; Hiraba et al., 2000). Recent studies focusing on multi-unit and SMU electromyographic activity of the IHLP during isometric tasks has provided evidence that the IHLP plays a major role in the generation and fine control of larger horizontal forces especially in the contralateral direction as required in masticatory and parafunctional activities (Uchida et al., 2001; Uchida et al., 2002).

Since knowledge about the function of lateral pterygoid muscle is essential for the understanding of the function of the TMJ (Frank, 1965; Ramford and Ash, 1983) and given the uncertainties described above as to the normal function of the SHLP, the general aim of this present study was to clarify the normal function of the SHLP during standardized isometric horizontal tasks and to do this by recording SMU activity from verified sites within the SHLP. The following review of the literature summarizes anatomical, histological, radiological and functional information relating to the SHLP and in terms of a possible role of the SHLP in isometric horizontal force production.
2. ARCHITECTURE OF THE SHLP

In contrast to the jaw closing muscles, namely the masseter, temporalis and medial pterygoid, the lateral pterygoid muscle has been classified as a jaw opening muscle. The lateral pterygoid muscle has been the subject of many anatomical studies of, for example, the nature of the insertion to the TMJ, and the complex fibre and neurovascular organization. This muscle, however, remains controversial from an anatomical, histological, and physiological point of view.

2.1 Anatomy

2.1.1 Origin and Insertion

The lateral pterygoid muscle is generally divided into 2 heads: the upper or SHLP and the lower or IHLP (Hónee, 1972; McNamara, 1973; Grant, 1973; Meyenberg et al., 1986; see Fig. I-1). The origins of both heads have by far not been studied as extensively as the insertions. Although there is agreement regarding the separation of the two heads at their origins, the degree of separation at their insertion is in dispute (Aziz et al., 1998). Generally speaking, the SHLP originates widely from the upper one-third of the lateral pterygoid plate and from the roof of the infratemporal fossa, at the base of skull; the roof of this fossa is made up of the greater wing of the sphenoid bone and the squamous part of the temporal bone. The IHLP arises broadly from the lower two-thirds lateral surface of the lateral pterygoid plate of the sphenoid bone. Anatomically, there are adipose and fibrous connective tissues which keep the SHLP and IHLP isolated in the vicinity of the origin but both heads intermingle at the point of insertion on the condylar neck (Hónee, 1972; Wilkinson, 1988). The IHLP fibres are directed posteriorly, laterally and superiorly and insert onto the condylar neck with varying degrees of attachment (Grant, 1973). The SHLP fibres are directed posteriorly, laterally and inferiorly and however, have a more complex
insertion in relation to the condylar head and the disc-capsule complex (Wilkinson and Chan, 1989; Heylings et al., 1995; Naidoo, 1996).

Fig. 1-1 A medial sectional view through the left TMJ representing the classical two-headed anatomy of the lateral pterygoid. Part of the SHLP fibres insert to the articular disc. The remaining fibres insert to the condylar fovea. The IHLP fibres insert onto the condylar head. 1=Articular disc, 2=Attachment to articular eminence, 3=Fascia, 4=SHLP, 5=IHLP, 6=Attachment to petrotympanic fissure, 7=Capsule, posterior wall, 8=Posterior condylar attachment (From Meyenberg et al., 1986).

Most authorities currently view the SHLP as being partly attached to the capsule of the TMJ and to the anterior part of the disc (Hónee, 1972) with, however, most of its fibres being inserted into the mandibular condyle either directly or via tendons within the IHLP (Wilkinson and Maryniuk, 1983). Nonetheless, the precise attachment of the SHLP is still controversial and varies from study to study and this may relate to the variety of methodological approaches between studies (Meyenberg et al., 1986; Bittar et al., 1994; Bertilsson and Ström, 1995; Heylings et al., 1995, Naidoo, 1996) for example, the capability of the dissector or different methods of dissection either through the lateral, medial or superior approach. Moreover, variations between individual and variations of muscle attachment to the surrounding structures, and
deep localization of the lateral pterygoid makes it difficult to access and determine the muscle both clinically and experimentally (Bertilsson and Ström, 1995).

It is also important to know that there are close interlacing fibres of deep temporalis into the SHLP fibres particularly at the anterior portion of the infratemporal fossa or medial to the temporal crest. This could have bearing on the difficulty in distinguishing these two groups of fibres (Schumacher, 1961; Widmalm et al., 1987; Akita et al., 2000) and the recordings obtained from this area could be contaminated by crosstalk from the deep temporalis.

The anatomical configuration of the disc-muscle insertion is debatable. Table I-1 summarizes the area of insertion of the SHLP. There are, however, two different opinions regarding the insertion of the SHLP. The first view proposes the idea that the SHLP has no attachment to the disc even though a small proportion of fibres are proposed to attach to the anterior part of the capsule (Mahan et al., 1983; Wilkinson, 1988; Wilkinson and Chan, 1989). The second view is that the SHLP attaches directly to the disc and capsule (Porter, 1970; Hónée, 1972; Carpentier et al., 1988; Widmalm et al., 1987). There is also evidence that a few supero-medial bundles of fibres of the SHLP insert at the medial half of the disc (60% of the specimen) but it was not considered that these fibres could cause direct anterior displacement of the disc (Meyenberg et al., 1986), and similar observations were made by with Wilkinson and Maryniuk (1983) who proposed the majority of the SHLP inserts to the condyle and few muscle fibres to the disc. While numerous studies reported that only part of the upper head inserted into the disc with the remaining parts of the muscle being connected to the pterygoid fovea (Meyenberg et al., 1986; Carpentier et al., 1988), a number of studies have raised the idea that the SHLP inserted solely
into the disc and anterior capsule (Porter, 1970; Hónee, 1972). Heylings et al. (1995) also proposed that only a part of the SHLP is attached to the anterior portion of the capsule, with varying degrees of attachment, and the capsule in turn is firmly attached to the disc. Despite the conflicting evidence, the view is still widespread that the SHLP and the disc are directly connected and this has perpetuated the view that the lateral pterygoid muscle plays a critical role in disc displacement. Thus, it has been proposed, as indicated above, that some disturbance in the normal coordination between the SHLP and IHLP leads to the disc being pulled forward ahead of the condyle by the SHLP and this possibly is a factor in the aetiology of disc displacement and TMD (Porter, 1970; Mahan et al., 1983; Juniper, 1984; Wilkinson, 1988; Hiraba et al., 2000; Okeson, 2003). However, several studies have argued against this proposal (Meyenberg et al., 1986; Carpentier et al., 1988) for example, the SHLP contributes to anterior-medial disc displacement only in cases of prior damage to the disc from trauma but is not a primary cause of disc displacement in normal disc (Wongwattana et al., 1994).

### Table I-I Summary of the insertion of SHLP reported in the literature.

<table>
<thead>
<tr>
<th>SHLP</th>
<th>Meniscus/Disc of TMJ</th>
<th>Articular capsule of TMJ</th>
<th>Pterygoid fovea of the condyle</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Schumacher (1961)</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>-</td>
</tr>
<tr>
<td>Möller (1966)</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>-</td>
</tr>
<tr>
<td>Troiano (1967)</td>
<td>Y, Superficial slip</td>
<td>Y, Superficial slip, deep slip, medial head</td>
<td>Y, Inferior head</td>
<td>3 heads (superior heads-2 slips; superficial and deep, medial head, inferior head)</td>
</tr>
<tr>
<td>Porter (1970)</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>-</td>
</tr>
<tr>
<td>Hónee (1972)</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>2 separate muscles Positioning and stabilization of the condyle and disc</td>
</tr>
<tr>
<td>Grant</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>2 separate muscles</td>
</tr>
<tr>
<td>(1973) McNamara (1973) (in monkey)</td>
<td>Most of the fibres</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Wilkinson and Maryniak (1983)</td>
<td></td>
<td>Y</td>
<td>0</td>
<td>Y</td>
</tr>
<tr>
<td>Meyenberg et al. (1986)</td>
<td></td>
<td>Y</td>
<td>0</td>
<td>Y</td>
</tr>
<tr>
<td>Widmalm et al. (1987)</td>
<td></td>
<td>Y</td>
<td>0</td>
<td>Y</td>
</tr>
<tr>
<td>Carpentier et al. (1988)</td>
<td>Only few fibres to medial</td>
<td>Y</td>
<td>0</td>
<td>Y</td>
</tr>
<tr>
<td>Wilkinson (1988)</td>
<td></td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Gray (1989)</td>
<td>Small portion to the central part of disc and capsule</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Bittar et al. (1994)</td>
<td>Few fibres (2.4-6%), Disc attaches to the roof of SHLP</td>
<td>Y</td>
<td>0</td>
<td>Y</td>
</tr>
<tr>
<td>Ögütten-Toller and Juniper (1994)</td>
<td>Superiorly and medially</td>
<td>Y</td>
<td>N</td>
<td>N</td>
</tr>
<tr>
<td>Wongwattana et al. (1994)</td>
<td>Anterior band</td>
<td>Y</td>
<td>0</td>
<td>Y</td>
</tr>
<tr>
<td>Heylings et al. (1995)</td>
<td>Partly to anterior portion</td>
<td>Y</td>
<td>Y</td>
<td>0</td>
</tr>
<tr>
<td>Naidoo (1996)</td>
<td></td>
<td>Y</td>
<td>0</td>
<td>Y</td>
</tr>
<tr>
<td>Fujita et al. (2001)</td>
<td>Upper head, inner head</td>
<td>Y</td>
<td>Upper head, inner head</td>
<td>Y</td>
</tr>
</tbody>
</table>

Y = inserted, N = not inserted, 0 = no data
There has also been controversy as to the number of heads of the lateral pterygoid. Classically, the lateral pterygoid has been divided into two heads (Hönée, 1972; McNamara, 1973; Grant, 1973; Meyenberg et al., 1986). However, it has been found from some studies that it is frequently composed of one to three heads (Troiano 1967; Ögütçen-Toller and Juniper 1994; Fujita et al., 2001). Troiano (1967) described diagrammatically the lateral pterygoid consisting of three portions: a superior head consisting of superior and deep slips, a medial head, and an inferior head (Fig. I-2).

Fig. I-2 Superior approach to the lateral pterygoid muscle (three-headed model). A=Vascular fascia, B=Medial head, C¹=Superficial slip of the SHLP, C²=Deep slip of SHLP, D=IHLP, E=Ascending ramus of mandible, F=Coronoid process, G=Zygomatic process, H=Articular capsule (From Troiano, 1967).

2.1.2 Physiological Cross Section, Fibre Length and Angulation

The SHLP is small and flat in cross-section with parallel-arranged fibers, whereas the IHLP is a robust belly-shaped muscle. According to van Eijden et al. (1995), the physiological cross-sectional area of the IHLP (i.e., $2.82\pm0.66 \text{ cm}^2$) is approximately three times larger than that of the SHLP (i.e., $0.95\pm0.35 \text{ cm}^2$) (see also Grant, 1973; van Eijden et al., 1997). The largest cross-sectional area of the SHLP is approximately 0.5-1.5 cm from its origin (Widmalm et al., 1987). At this point deep
fibres of temporalis lie immediately lateral to the muscle and branches of the mandibular nerve also lie close to the SHLP as they enter the infratemporal fossa through the foramen ovale (Widmalm et al., 1987). As the physiological cross-sectional area of the muscle is proportional to force production, the expected maximal force that can be produced by the IHLP is thus about three times greater than that produced by the SHLP on the assumption of similar internal architectures.

Muscle velocity and excursion is proportional to the fibre length of a muscle (Freund, 1983). The lateral pterygoid muscle has relatively long fibres (SHLP 21.4±2.2 mm, IHLP 23±2.7 mm; van Eijden et al., 1997). Hence this muscle is more suited for shortening over long distances and providing support for near-isotonic contractions rather than near-isometric contractions requiring power (Hannam and McMillan 1994) as is demanded of other jaw muscles, such as the masseter and medial pterygoid muscles.

In addition, the long axes of the SHLP and IHLP have different angulations. On average, the SHLP makes a medially directed angle of 26° with the sagittal plane through the condyle, while the fibres of the IHLP run laterally and posteriorly to the condyle at an angle of 45° to the sagittal plane (Hónee, 1972). With respect to the Frankfort horizontal plane, the SHLP fibres are oriented downwards at an average angle of 23° whereas the IHLP aligns at an average angle of approximately 10° upward (Hónee 1972). Differences in physiological cross sectional area (PCSA) and fibre angulation possibly point towards differences in function between the two heads.
Moreover, lateral ptergoid muscle fibre alignment in the horizontal direction is a unique architectural characteristic which allows a major vector component of the total force output from the muscle to be generated in the horizontal plane (van Eijden et al., 1997). Therefore, the lateral pterygoid muscle is ideally suited to play a role in generating horizontal force and movement.

2.1.3 Tendinous Architecture and Pennation

Unlike other powerful masticatory muscles (i.e., masseter and medial pterygoid), the lateral pterygoid muscle has a quite different internal organization in terms of pennation and presence of internal aponeuroses. The origin of the IHLP appears to show some limited internal tendon lamellae (Fig. I-3) consistent with a pennate structure (Widmalm et al., 1987) and the SHLP is composed of a few small sections of tendinous tissues (Hónee 1972; Sato et al., 1992). However, van Eijden et al. (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. Moreover, Foucart et al. (1998) proposed that the lateral pterygoid is composed of independent functional musculo-aponeurotic layers which separate the muscle in to strata according to its nerve innervation.

2.1.4 Power of Muscle and Range of Motion

As previously reviewed concerning the fibre angulation of the lateral pterygoid muscle, Hónee (1972) proposed the potential force from both heads from the calculation according to the force vectors. It was proposed that the SHLP can generate a force of 3.5 kg in a forward direction, 0.3 kg in an inferior direction and 3.6 kg in medial direction whereas the IHLP, the potential force is 9.2 kg anteriorly, 0.7 kg inferiorly and 6.9 kg medially.
The differences of fibre alignment of the SHLP and the IHLP determine the range of horizontal movements and horizontal force vectors. There is a marked convergence of muscle fibres of both heads onto a small insertion site on the condyler fovea, capsule and disc from a broad origin at the roof of the infratemporal fossa and lateral pterygoid plate. This distinct diversion of muscle fibre alignment from the most superior to the most inferior, and from the medial to the lateral side 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. The fibre alignment of SHLP is more controversial due to the fact that Troiano (1967), Ögütcen-Toller and Juniper (1993) and Fujita et al. (2001) have proposed that there are at least two-slips within the SHLP. 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. These data suggest the capability of different force vectors being capable of being exerted on the condyle from these different slips if these different slips were able to be independently activated.

According to Bertilsson and Ström (1995), 75% of original articles reported that the lateral pterygoid 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, whereas 20% of articles proposed that the muscle has only two functions: to stabilise the disc during rotation and translation and to produce lateral jaw movements. Only 5% of references suggested that the muscle acts as a jaw opener without producing lateral forces. Hence, the normal function of the lateral pterygoid is disputed and worthy of further investigated.
Fig. 1-3 Horizontal section through the right TMJ illustrating the presence of tendon lamellae within the IHLP. sh=SHLP, ih=IHLP, mp=medial pterygoid, te=tendon within the IHLP (From Widmalm et al., 1987).

2.1.5 Nerve and Blood Supply

Patterns of nerve distribution into the lateral pterygoid have been conflicting from study to study. Many investigators have, quite reasonably, proposed an association between the function of lateral pterygoid and its neural organization. As the SHLP approaches its insertion, it becomes flattened in the superoinferior dimension and this area is surrounded by the large vascular pterygoid venous plexus (Wildmalm et al., 1987). The view of the prevalence of an anterior gap between the two heads as well as different angulations between the upper and lower head fibres, accentuated the two-head model in the lateral pterygoid muscle. This model was reinforced by biomechanical and physiological (e.g., electromyography) data that ostensibly showed reciprocal activity of the two heads (Gibbs et al., 1984; Juniper, 1981; Kamiyama, 1961; McNamara, 1973: Mahan et al., 1983; Widmalm et al., 1987) and which suggested the two heads should be regarded as two separate muscles (Møller, 1966; McNamara, 1973; Mahan et al., 1983).
Nevertheless, the lateral pterygoid has been proposed to consist of independent functional musculo-aponeurotic layers with separate nerve supplies (Foucart et al., 1998). According to Foucart et al.'s findings (1998), the lateral pterygoid muscle is divided into 5-6 oblique sagittal planes separated into horizontal layers by several nerve branches. This neural organization could not support the two-head conceptual theory as there is no independent nerve running to each head. As a result of the complex neural distribution to each partition of the lateral pterygoid, EMG studies could have recorded different activity patterns according to the position and depth of the needle and this may have contributed to the conclusion of the reciprocal functions between the two heads.

**Fig. I-4** Schematic representation of the intramuscular nerve branch distribution in the right lateral pterygoid muscle. 1=Mandibular nerve, 2=Buccal nerve and its hiatal fibres, 3=Temporomasseteric nerve, 4=Auriculotemporal nerve, 5=Vertical lateral pterygoid nerve and its horizontal branches (from Foucart et al., 1998).

Figure I-5 illustrates an example of the neural distribution of the lateral pterygoid (Flatau, 2000). Aziz et al. (1998) have shown that the two heads were supplied by a common lateral pterygoid nerve derived from the long buccal or the mandibular nerve or from the ansa pterygoidea bridging the long buccal and lingual nerves. However, there are reports of independent branches that innervated each head from
sources such as the deep temporal, long buccal and/or mandibular nerves. Hence, the conclusion that the two heads function as a single unit (Foucart et al., 1998) was still as enigmatic as the two heads functioning separately (Juniper, 1981). If there is evidence that the motoneurones or primary afferents that supply each head belong to different populations within the trigeminal motor nucleus and/or one or more of the trigeminal somatosensory nuclei, there would be stronger data in support of the proposal of Juniper who suggested that the two heads of the human lateral pterygoid should be regarded as two separated muscles (Aziz et al., 1998). Currently there is no strong evidence to support the notion of separate neuromuscular partitioning of the lateral pterygoid muscle.

Fig. I-5 Neural distribution in the lateral view of the right lateral pterygoid after removal of the antero-lateral part of the SHLP. 2=Mandibular nerve in foramen ovale, 6=SHLP, 8=IHLP, 18=Temporobuccal nerve trunk, 19=Nerves to lateral pterygoid muscle (From Flatau, 2000).

Even though the vascular organization has not been as extensively studied as the neural organization, Foucart et al. (1998) have evaluated the maxillary artery ratio (The ratio of the proportion of the medial part of the SHLP supplied by the maxillary artery to the proportion of the lateral portion of the muscle supplied by maxillary
artery) of the lateral pterygoid from lateral to medial which was 1:2 and 2:3 respectively in the two-head and one-head patterns. Moreover, the maxillary artery either crossed the IHLP in the two-head pattern (Fig. I-6) or ran between the cranial base and lateral pterygoid muscle in the one-head pattern. The SHLP is reported to have close proximity to the maxillary artery and pterygoid venous plexus (Wildmalm et al., 1978) that is, at the SHLP insertion, it becomes flattened in the supero-inferior dimension and this region of the SHLP is surrounded by large vessel of pterygoid venous plexus.

Because of the intimate topographic relationships of the lateral pterygoid heads to the TMJ and adjacent nerves and blood vessels, this muscle has been implicated as playing a role in TMDs (Juniper, 1981; Koole et al., 1984; Juniper, 1984; Klineberg, 1991). For example, as described above it has been proposed that SHLP could be involved in anterior disc displacement by virtue of the incoordination between two heads (Fujita et al., 2001).

![Figure I-6 Anatomical distribution of the maxillary artery crossing the IHLP. 4=Lateral ligament of TMJ, 6=Condylar neck of the mandible, 17=Maxillary artery, 56=SHLP, 57=IHLP (From Flatau, 2000).](image)
2.1.6 Mechanoreceptors: Muscle Spindles, Golgi Tendon Organs

Muscle contains specialized receptors that sense different features of the state of muscle. Muscle spindles are sensitive to muscle stretch whereas Golgi tendon organs are sensitive to change in muscle tension (Gordon and Ghez, 1991). These two receptors transmit proprioceptive information to the central nervous system. Muscle spindles are complex mechanoreceptors which lie in parallel with the extrafusal fibres. A number of researchers have attempted to identify the number of muscle spindles in the lateral pterygoid muscles either in human and non-human masticatory muscles. In non-human studies (Kubota et al., 1979; Lennartsson, 1980; Kubota et al., 1983; Rokx et al., 1984; Rokx and van Willigen, 1988), the histological examinations of the lateral pterygoid muscles confirm the notion that the lateral pterygoid muscle is devoid of muscle spindles. However, a histological study of muscle spindles within the human lateral pterygoid muscle has identified 6 muscle spindles, four in the upper head and two in the lower head (Kubota and Masegi, 1977). In addition, Hónee (1966) and Gill (1971) reported that the number of muscle spindles in the lateral pterygoid muscles ranged from one to 15 and two to 18, respectively. Most of these spindles were situated parallel with the extrafusal muscle fibres and found chiefly in the middle third while there were only a few in the anterior region and none in the posterior region. Nevertheless, there was also a report of absence of muscle spindles in the human lateral pterygoid muscle (Smith and Marcarian, 1967). The sparse distribution in numbers of the muscle spindles in the lateral pterygoid may contribute to a different feedback mechanism or may not require the same degree of proprioceptive control as is required to contribute to fine movement control for postural jaw muscles, and especially the deep masseter muscle (Klineberg, 1991).
Klineberg (1991) commented on the proprioceptive control of the SHLP. As the SHLP is devoid of muscle spindles or they are few in number and are simple in structure, Klineberg (1991) suggested that other mechanoreceptors may provide feedback to the SHLP during jaw and joint movement. For example within the posterior attachment tissues there is a rich innervation and a high population density of articular mechanoreceptors which could serve as proprioceptive feedback to modulate SHLP activity during jaw closing and to facilitate the return of condyle and disc during the end phase of jaw movement. This proposal has been supported by the study of the reflex excitation of masticatory muscles induced by algesic chemicals applied to the temporomandibular joint of the cat (Broton and Sessle, 1988) which confirmed the presence of continuous feedback from articular mechanoreceptors in the control of jaw movement.

2.2 Histology and Physiology of Muscle Fibres

Jaw muscle is skeletal muscle which contains many motor units. Each motor unit consists of a single α-motoneurone that innervates a homogenous population of muscle fibres; fibres may differ in type from unit to unit. The physiological classification of muscle fibres is S (slow contracting and fatigue resistant fibre), FR (fast contracting and fatigue resistant fibre) and FF (fast contracting and fatigue susceptible fibre). Similarly, ATPase histochemical properties (Type I, Type IIA, Type IIB) have also been used for muscle fibre classification. It seems that Type I, IIA and IIB fibres make up motor units that are defined physiologically as S, FR and FF fibres, respectively (Mao et al., 1992). Type I or S fibres are equivalent to red muscle fibres which in jaw muscles are larger in diameter and produce sustained low-level force. Their colour comes from myoglobin and they are aerobic fibres consisting of many mitochondria and are rich in mitochondrial enzymes (Mao et al.,
1992). On the other hand, Type IIB or FF fibres are smaller in diameter and are white fibres. They lack the red myoglobin, are anaerobic, have fewer mitochondria and quickly fatigue. The intermediate group (FR or Type IIA) is distinct due to its intermediate properties (Mao et al., 1992). Immunohistochemical techniques have revealed different isoforms of the heavy chain of the myosin molecule; myosin heavy chain (MHC) within muscle. At least 3 MHC isoforms can be distinguished in human limb muscles namely, MHC type I, IIA and IIX. There is also a direct correlation between the ATPase histochemically defined fibre types and MHC isoforms (Korfage and van Eijden, 2000) with MHC type I corresponding with ATPase histochemically defined Type I muscle fibres, MHC type IIA corresponding with defined Type IIA fibres and MHC Type IIX corresponding with defined Type IIB fibres. Motor units with a predominance of Type I fibres gain powerful influences from muscle spindle afferents and provide finely graded force output. On the other hand, motor units with a predominance of Type II fibres are high threshold, and thereby contribute to high contraction forces and powerful force output with relatively coarse movement (Burk, 1981). In addition, in jaw muscles, Type I fibres are supplied by small diameter motoneurones and are first to be activated when the muscle contracts. However, Type II fibres are supplied by larger diameter motoneurones and become activated when muscle force increases in magnitude and after there are no additional type I fibres available for recruitment (Mao et al., 1992).

Histochemically, Eriksson et al. (1981) reported a high proportion of Type I fibres (81%) in the lateral pterygoid muscles while Korfage et al. (2000) and Korfage and van Eijden (2000) have proposed that 33% and 36% of MHC-I fibres were located in the SHLP and IHLP respectively. More MHC-IIA fibres have been found in the SHLP (23%) than in the IHLP (15%). Compared to the other jaw closing muscles,
the lateral pterygoid muscle contains more MHC-IIA (pure and hybrid fibres) and fewer MHC-IX fibres (Korfage et al., 2000). This distribution of fibre types may influence different functional properties between the SHLP and IHLP e.g., 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).

2.3 Radiology

2.3.1 Computer Tomography (CT)

In evaluating the functional activities of masticatory muscles, electromyography has been successfully used, for example, surface electromyography in masseter and intramuscular electromyography in temporalis muscles. In some muscles, especially the lateral pterygoid, even though many methods and equipment have been introduced, it has not been easy to access the muscle due to its deep location and small muscle size relative to some of the other jaw muscles (Mahan et al., 1983; Orfanos et al., 1996; Hiraba et al., 2000). In the past, verification of electrode placement by dissection was important in animal studies but it is impossible in living human subjects. Thus, computer tomography (CT) has been recently used to allow verification of electrode placement, and has allowed a study of the morphology of the lateral pterygoid muscle (Birou et al., 1991). Since the lateral pterygoid is often completely covered by the temporalis muscle laterally and by the medial pterygoid muscle medially, the precise placement of recording electrodes in the lateral pterygoid is problematic and may result in misleading data. For this reason, CT has been introduced to enhance an accurate and verify electrode location and could therefore minimize the chance of incorrect electrode placement.
In addition, CT may also provide advantageous information in assessing the masticatory muscles (Raustia et al., 1996, 1998). For example, functional and structural changes can alter the density detected in CT. Density changes in the lateral pterygoid muscle have been reported to be more significant than in other masticatory muscles in relation to TMD (Raustia et al., 1998). However the CT scan still has a limitation when visualizing the orientation of the muscle fibres (Birou et al., 1991) and the patient or subject is inevitably exposed to an amount of radiation.

The use of CT has been favorably applied to EMG studies particularly in the lateral pterygoid muscle by Orfanos et al. (1996) in order to measure the trajectory of electrode placement into the SHLP and to verify that electrodes were correctly located within the SHLP or IHLP and not other jaw muscles. This reliable verification technique has been employed as the principal basis for verification of the location of fine wires in a number of studies (e.g., Murray et al., 1999; Phanachet et al., 2001, 2002, 2003; Uchida et al., 2001).

2.3.2 Magnetic Resonance Imaging (MRI)

MRI is a non-invasive imaging technique which uses a strong magnetic field and high-frequency radio waves for high-quality soft tissue imaging without exposure to ionizing radiation (van Spronsen et al., 1989). A series of frontal, horizontal, sagittal and angulated MRI scans can be made without modification of the patient’s position, facilitating reconstruction of the jaw muscles (van Spronsen et al., 1989). The normal structure of the lateral pterygoid muscle as well as hypertrophy and atrophy of the masticatory muscles can be demonstrated with the use of MRI (Yang et al., 1992). The normal lateral pterygoid structure was observed in oblique sagittal MRIs as a fan-like muscle radiating from the neck of the mandibular condyle to the lateral
pterygoid plate (Yang et al., 2001). Recent MRI investigations of the structural and pathological alterations involved in the lateral pterygoid muscle in temporomandibular joint hypermobility patients reported that significantly more pathological changes (e.g., hypertrophy) were found in the SHLP rather than the IHLP (Yang et al., 2001). Nevertheless, van Spronsen et al. (1989) reported that after comparing the MRI of the cross-sectional areas of jaw muscles in the same subject with the cross-sectional images from CT, there was low correlation between the CT and MRI cross sections of the lateral pterygoid muscle.

3. MOTOR UNIT ORGANIZATION AND FUNCTION

Each jaw muscle consists of several hundred motor units. As mentioned earlier the motor unit has been considered as the basic unit of motor activity since it is the smallest unit which can be recruited and controlled by the central nervous system (van Eijden and Turkowski, 2001). It contains an α-motoneurone and the group of muscle fibers innervated by this neuron. Each muscle fiber is innervated by only one motoneurone, but each motoneurone may innervate tens to thousands of muscle fibres (Van Eijden and Turkowski, 2001). When a motoneurone is excited, the action potentials will be propagated along the Aα nerve fibre to muscle fibres and the muscle fibres consequently contract to generate the force.

The properties of the motor units for example, contraction speed, fatigability and force output, vary due to morphological and physiological characteristics. Based on the physiological properties (contraction velocity and fatigability), motor units have been classified into 3 groups, namely slow-fatigue resistant motor unit (S), fast fatigue-resistant motor unit (FR) and fast fatigable motor unit (FF) (Burke et al., 1973, 1974). Fast motor units i.e., FF units have fast twitch contraction times of less
than 40 ms and fatigue rapidly, whereas slow motor units have longer twitch contraction times and are highly resistant to fatigue. The FR units have contraction times slightly slower than FF units but are more resistant to fatigue. Different motor units are composed of different types of muscle fibres which are, therefore responsible for different functions due to the fact that Type I fibres, Type IIA fibres and Type IIB fibres belong to S, FR and FF motor units, respectively. In addition to the physiological classification, the classification by histochemistry of the MHC content in the motor unit fibres has also been studied. Kwa et al. (1995) have associated the types of myosin heavy chain with the physiological properties accordingly: MHC-I have been associated with S motor units, MHC-IIA with FR motor units and MHC-IX with FF motor units.

Since Type I muscle fibres belong to slow motor units, these muscle fibres are located in the postural muscles such as the long muscles in the back, they 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. Fast motor units produce a much larger force than slow motor units because of two major factors: 1) the innervation ratio which has been defined as the number of muscle fibres per motor unit for example, there is higher innervation ratio in fast motor units, and 2) the cross-sectional areas of individual muscle fibres (Ghez, 1991) which are larger in Type IIB fibres than in Type I fibres. In other words, the greater the innervation ratio and the cross-sectional area of muscle fibres, the larger the force produced. 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.
3.1 Motor Unit Size and Motor Unit Territories

Motor unit size is proportional to the numbers of muscle fibres innervated. The 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 10-20 muscle fibres. This results in the ability to produce very delicate eye movements. However, a motor unit in the limb muscle might contain approximately 1700 muscle fibres. This enables extraocular muscles to exert muscle force more finely than that of limb muscles (van Eijden and Turkawski, 2001). In masticatory muscles, motor units of the temporalis muscle are composed of an average of 936 muscle fibres per unit while only 640 fibres per unit are present in the masseter muscle (Carlsöö, 1958).

Motor unit territory has been defined as the area over which the fibres of one motor unit are distributed. There have been few investigations regarding the motor unit sizes and motor unit territories. Stålberg and Eriksson (1987) used the scanning EMG technique to measure motor unit territories in the human masseter muscle by inserting a single monopolar needle electrode into the muscle and moving the needle along the whole muscle during biting until the motor unit activity disappeared. They suggested that the motor unit territory width in masseter muscle was 3.7±0.6 mm and this agreed with the findings from Tonndorf and Hannam (1994) who reported 3.7±2.3 mm. Since motor unit territory in masticatory muscles appears to be smaller than in limb muscles (e.g., 7.0 mm in biceps muscle), this suggests a more localized organization of motor control in masticatory muscles (van Eijden and Turkawski, 2001). It was said that the localisation of motor units within certain muscle compartments provides the potential for selective activation of the distinct regions in muscle (Stålberg and Eriksson, 1987; Herring et al., 1989; McMillan and Hannam,
1991). Localization 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.

It has been suggested that an arrangement with small motor unit territories may allow differential control of separate motor regions (Stålberg and Eriksson, 1987). The large motor unit territory may reflect extensive motor actions and could help to develop large bite forces for mastication. This is in contrast to the fine movement control required during, for example, jaw closing along cuspal inclines or controlling opposing gravitational force such as stabilizing the mandibular position during movements and biting through hard or tough objects.

3.2 Task Related Behavior

A single preferred direction of SMU firing has been previously identified in limb muscles (Theeuwen et al., 1994; Herrmann and Flanders, 1998) and these researchers discriminated subpopulations of the SMUs with their different preferred directions of firing. Previously, concepts of SMU activation have proposed that units of the same muscle or at least of the same neuromuscular compartment are activated homogenously with activity peak in the best direction or the most preferred direction. However, more recent studies have suggested a more complex rule of SMU activation in which it is proposed that neighboring motor units could have significantly different preferred directions. This provides the possibility of multiple directions of force production from the muscle (Herrmann and Flanders, 1998). It is thus proposed that various SMUs within each portion of each muscle have different
best directions (Herrmann and Flanders, 1998). The best directions of units could change continuously with their locations in the muscle and not cluster into distinct groups. 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 (Haar Romeny et al. 1982).

In the jaw muscles, McMillan and Hannam (1991) have proposed that all SMUs from verified regions in the masseter muscle show activity in more than one task and they termed these multi-task units. However, there were reports of task-specific motor units (a specific motor unit for a specific task) which were less prevalent than the multi-tasks units (a motor unit is active for more than one tasks) (Eriksson et al., 1984; McMillan, 1993).

SMU studies have provided evidence for regional task-dependent behaviour in masticatory muscle. For example, the task profiles of masseter motor units appeared to vary regionally within the muscle (McMillan and Hannam, 1991). 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 suitable for the task while the units activated by tasks such as jaw retrusion with and without tooth contact were located in the deeper part. Moreover, units in the posterior superficial part, which consisted of a high proportion of Type II fibres (Eriksson and Thornell 1983), were also associated with tasks that involved tooth contact such as clenching and this region may be responsible for generation of bite force and may not be suited for controlling jaw posture.
Recent studies of SMU recordings in the lateral pterygoid muscle have provided evidence of functional complexity within both heads of the muscle (Phanachet et al., 2001, 2002). For instance, preliminary evidence suggests that the superomedial part of the IHLP appears to be important in initiating contralateral jaw movement whereas the inferomedial part appears to exhibit fine control in continuing movement (Phanachet et al., 2001). The SHLP has been proposed to be more complex than suggested by a simple reciprocal function to the IHLP. This is because recent and earlier evidence has shown activity in the SHLP in opening, protrusion and contralateral jaw movements, similar to those patterns identified for IHLP. These functions also appear to vary regionally through the SHLP and accordingly the SHLP has been divided tentatively into 3 regions (Phanachet et al., 2003). The medial zone shows patterns of activity very similar to the classic function of the IHLP. The lateral zone can be active on closing, ipsilateral and retrusion whereas, the middle zone presents the combination of activities found in the medial and lateral zones. These data reflect the task-related behaviors of the lateral pterygoid and provide further suggestive evidence for functional heterogeneity that is a regional activation of the muscle, thereby, increasing motor control by facilitating changes in the muscle’s force vector during loading of mandible.

3.3 Recruitment Gradation and Rate Gradation

Recruitment order during a continuing contraction can be determined by motoneurone size as proposed by Henneman et al. (1965). The size-ordered recruitment has subserved smooth generation and control of graded force with minimal fatigue development (Herrmann and Flanders, 1998), since the motor units that are activated follow the size principle. For example, small motor units principally are active for posture and large motor units are involved in movement.
(Ghez, 1991; Flanders and Herrman 1992). At low levels of force, for example in controlling posture or fine movement, Type S motor units, consisting of fewer muscle fibres, are continuously recruited but if the force is increased and the movement is less precise, FR and FF motor units will become activated in an orderly fashion according to motor unit size (Burke, 1981; Tansey and Botterman, 1996). Therefore, slow-twitch units are responsible for precise movement at low force whereas, large and fast-twitch motor units are more involved in fast and less precise movement at higher force.

There are two mechanisms of force production in muscle and which can be modulated by the central nervous system. These are 1) recruitment gradation which refers to the recruitment of different numbers of motor units, and 2) rate gradation (or rate coding) which refers to the variation in the discharge rates of action potentials of each motor unit in order to control the force. It was however, suggested that for force modulation, masticatory muscles rely mostly on recruitment gradation at low force levels and on rate gradation at high force levels (Herrmann and Flanders, 1998). For example, at approximately 0-20% of MVC, between 50% (Hannam and McMillan, 1994) and 87% (Scutter and Türker, 1998) of the masticatory motor units are recruited.

3.3.1 Recruitment Gradation

The excitability of a motoneurone is inversely related to motoneurone cell size. Small motoneurones achieve their activation threshold and start firing earlier than large motoneurones as proposed by the size principle from Henneman et al. (1965). Since the size of motoneurones is closely related to the size of the motor unit, i.e., small motor units are innervated by small motoneurones and large motor units by
large motoneurones, the recruitment of motor units is also assumed to occur in the same orderly sequence (van Eijden and Turkawski, 2001). Studies of the contractile properties of the human masseter and tempolaris 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).

Generally, because the force produced by the individual masticatory muscles cannot be measured directly, there is a parameter used to characterize motor unit recruitment as a function of motor unit size, and this is the so-called recruitment threshold, that is, the force or activation threshold. Recruitment threshold is defined as the muscle force level at which a motor unit first starts to fire. The sizes of the motor units can be estimated from the amplitudes of the motor unit action potentials. A motor unit action potential could be defined as the summation of all action potentials propagated by the muscle fibres that belong to that motor unit (Stålberg et al., 1996). As the action potentials of the single fibres that make up a motor unit differ in amplitude and frequency, motor unit action potentials hence, differ in shape. The amplitude of action potentials is associated with differences in motor unit size (van Eijden and Turkawski, 2001). Moreover, muscle length (Miles et al., 1986), distance between active fibres and electrode location are crucial factors contributing to the changes in size and shape of the motor unit action potential. Importantly, it becomes increasingly difficult to discriminate SMU action potentials in the interference EMG recordings if the force levels are larger than 30% of the maximum force (van Eijden and Turkawski, 2001).
3.3.2 Rate Gradation

Studies in limb (Tanji and Kato, 1973; 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 increased during isometric contraction. Eriksson et al. (1984) reported firing rates for human temporalis motor units during voluntary isometric contractions, when force increases from slight to moderate. The lowest rate of firing was between 5 and 8 imp/s and the highest rate was between 20 and 25 imp/s. Beyond this force, other units often disturbed the recordings, and therefore motor unit firing rates at higher force levels could not be investigated (van Bijden and Turkawski, 2001). This suggestion should be taken into consideration in the study of the SMUs that can be reliably discriminated. For example, in SMU recordings of the IHLP during horizontal isometric contraction, the levels of force of 400-800 gwt were chosen to facilitate the discrimination of SMUs (Uchida et al., 2001, 2002).

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, the deltoid and the first dorsal interosseous muscles used varying strategies to increase force output above 40% MVC during linearly different contractions. The deltoid basically relies on recruitment, the first dorsal interosseous on rate coding (De Luca et al., 1982). It has been suggested that the number of motor units according 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). Further, muscle fibre type composition could also be a possible factor influencing this mechanism.
However, the study of Seki and Narusawa (1996) indicated that the number of motor units and the function of a muscle were more important factors than muscle fibre composition. 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 the rate coding.

3.4 Firing Rate

Previous studies in limb muscles (Tanji and Kato, 1973; Freund et al., 1975) and jaw muscles (Uchida et al., 2001, 2002) have characterized the muscle functional properties in terms of firing rate which is defined as numbers of motor units firing (or the presence of action potentials) for one second (impulses/second). They suggested that the firing rates of motor units increased as the force increased during isometric contraction. Firing rate modulation allows a finer grade of control that is essential when muscles are involved in precise and smooth contraction.

Many previous studies have investigated the minimal tonic firing rate (MTFR) of SMUs in limb (e.g., Tanji and Kato, 1973; Freund et al., 1975) and in masticatory muscles (e.g., Eriksson et al., 1984; McMillan, 1993). The MTFR is the lowest firing rate at which a motor unit fires at a regular rate. It has been used as a parameter to investigate the task related behaviour of motor units. Masseter and temporalis muscles were reported to have the MTFR of 5-8 imp/s (Eriksson et al., 1984) whereas there is limited information about the MTFR of the lateral pterygoid muscle except McMillan and Hannam (1989) reported that MTFR of IHLP was 8-10 imp/s. Recent findings suggested that the MTFR of the lateral pterygoid muscle is greater
than previously described and does not vary with the task within each muscle head (Phanachet et al., 2004).

4. ELECTROMYOGRAPHIC STUDIES OF THE SHLP

4.1 Multi-unit and SMU Studies in the Role of the Lateral Pterygoid in Movement and Isometric Force

Most studies of the masticatory muscles in the past were based on multi-unit EMG recordings (e.g. Gibbs et al., 1984; Wood et al., 1986; Widmalm et al., 1987) which make it difficult to draw a conclusion as to the comparable quantities of muscle activity among the studies because there were inconsistent methodologies (e.g., different EMG recording techniques) and terminology used in describing the magnitude of EMG activity. Further, accurate electrode placement in each particular head of the lateral pterygoid muscle was still equivocal.

Table I-2 summarized the task related activity of the SHLP and IHLP from previous literature. Many studies have suggested the reciprocal functions between the IHLP and SHLP (Grant 1973; McNamara 1973; Mahan et al., 1983; Gibbs et al., 1984; Wood et al., 1986; Hiraba et al., 1995; Hiraba et al., 2000). The SHLP is said to be active during closing, clenching, retrusive and ipsilateral jaw movements, while the IHLP is active during jaw opening, protrusive and contralateral jaw movements. However, there have been a few studies that have proposed that the SHLP may also be active concomitantly with the IHLP during opening, protrusion or contralateral jaw movements (Sessle and Gurza, 1982; Widmalm et al., 1987; Murray et al., 1999). Even though the level of EMG activity depends upon the amount of vertical and horizontal jaw movements, the data from EMG study of the lateral pterygoid in monkey (EMG electrode location verified by dissection) also demonstrated the
presence of EMG activity during jaw closing and opening in both heads (Sessle and Gurza 1982). The level of concomitant activity in the SHLP and IHLP does not only depend on mandibular position but also depends on the recording sites within the muscle, for example, the medially located SMUs in the SHLP showed activity during protrusive, opening and contralateral jaw movement as the classic function of the IHLP whereas SMUs of the middle and lateral region showed activity in relation to a mixed variety of jaw movements (Phanachet et al., 2003).

The activity of the lateral pterygoid at rest or postural jaw position related to the TMDs is also controversial. Many researchers have proposed dysfunction of the lateral pterygoid in association with the incidence of TMD. For example, Mahan et al. (1983) reported that the SHLP was tonically active in symptomatic subjects who reported pain on palpation of the temporomandibular joints and masticatory muscles, whereas there was an absence of tonic activity at rest in the SHLP and IHLP of asymptomatic subjects. Furthermore, the upper head of the lateral pterygoid muscle has been proposed to be 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 (Juniper, 1981; Okeson 2003; Hiraba et al., 2000). On the other hand, some studies reported that the activity in the verified site in the SHLP was absent at rest in asymptomatic subjects (Wood et al., 1986; Murray et al., 2001; Phanachet et al., 2003). According to these inconsistencies, it is not possible to conclude that the hyperactivity or hypoactivity of the lateral pterygoid muscle was a cause or an effect of the TMDs. One possible explanation for these inconsistencies is that the deep location of the lateral pterygoid muscle makes it difficult for reliable electrode placement unless a reliable verification method has been used as described by the
recent study of the normal function of the lateral pterygoid muscle (Orfanos et al., 1997; Murray et al., 1999; Phanachet et al., 2003). The earlier lack of verification could be a reason for the variability between studies. For example some previous recordings may have been obtained from the other adjacent muscles. Therefore, a reliable verification of electrode placement is a crucial factor for any EMG study of SHLP. Another possible explanation is the possibility of functional heterogeneity within the lateral pterygoid. This has been defined as a selective activation of specific regions of the muscle fibres for specific functional demands. Some evidence has been provided for functional heterogeneity in the masticatory muscles for example, in masseter and IHLP (Hannam and McMillan, 1994; Phanachet et al., 2001). Further, the SHLP has also been proposed to be functionally heterogeneous (Hannam and McMillan, 1994; Foucart et al., 1998; Phanachet et al., 2003). Therefore, recordings at different sites in the SHLP could yield different functional properties.

Table I-2 Summary of the task relations of the SHLP and IHLP reported in the literature

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- no activity reported; + activity reported; ± little activity reported; 0 no data.

Rest, postural jaw position; Clench, clenching in intercuspal position; Open, jaw opening; Close, jaw closing; CL, contralateral jaw movement; IL, ipsilateral jaw movement; Pro, protrusion; Ret, retraction.

5. ISOMETRIC CONTRACTION

Isometric contraction has been described as the contraction of the muscle when there is no change in length. Even though muscle length is unchanged, there is still shortening of the sarcomeres to allow internal tension to be generated and the muscle becomes rigid without shortening.

5.1 Motor Unit Activity during Isometric Contraction

Motor unit activation in controlling force production combines recruitment and rate coding gradation of motor units within the muscles. Generally speaking, in order to achieve the MVC, all SMUs must be recruited and driven at the appropriate rate. Functional characteristics of human motoneurones are determined by the graded excitability of motoneurones according to size (Freund et al., 1975). It has been well established that the recruitment of motor units during isometric contraction follows
the size principle as described by Henneman et al. (1965). The conduction velocity of the nerve fibre innervating the motor unit was used as an estimator for the size of the motoneurone (Freund et al., 1975). During slowly increasing contractions, the units were recruited at force levels which were closely correlated to conduction velocity. Therefore, the neurons with small slow conducting axons which innervate slowly contracting fatigue-resistant muscle fibres are recruited before neurons with large rapidly contracting fatigable muscle fibres (Milner-Brown et al., 1973; Freund et al., 1975; DeLuca et al., 1982). After the additional force primarily achieved by the increase of the firing rate from the active units, the new motor units start to recruit and continue up to 50-80% MVC (Milner-Brown et al., 1973; DeLuca et al., 1982). However, this strategy of force production entirely depends upon the muscles.

During small, stepwise force increments, the units first activated during the steps could become inactive during the subsequent plateaus. When the higher steady-force levels are reached, the unit remains continuously active. This steady force represents the tonic threshold of the unit (Freund et al., 1975). Tonic threshold is correlated with conduction velocity. This means high-threshold units have a large force range below the tonic threshold where they can be transiently activated whereas low-threshold units have a large force range above tonic threshold where they can be active tonically. Thus, the phasic or tonic appearance of recruitment reflects quantitative differences in tonic threshold between units of different size (Freund et al., 1975). However, all units could be activated phasically (below the tonic threshold) or tonically (above the tonic threshold).

The change in firing rate per unit force was inversely related to conduction velocity: the slower conducting units show larger changes in firing rate per unit force than
faster conducting units. This correspond to the larger excitability of the smaller units indicated by their earlier recruitment (Freund et al., 1975).

5.2 EMG Studies Related to Isometric Contraction in Jaw muscles

Several isometric contraction studies in limb muscles have clarified the normal function of these muscles by SMU recordings (e.g., Büdingen and Freund, 1976; De Luca et al., 1996; Herman and Flanders, 1998). Similar approaches have been applied to the jaw closing muscles (Desmedt and Godaux, 1979; Stålberg et al., 1986; Hannam and McMillan, 1994; Miles, 1995), for example, in temporalis muscle, it was reported that the deep part of the anterior temporalis muscle is more active than the superficial part during clenching in intercuspal position (Wood, 1986). Another example is the study of Gibbs et al. (1984). They found that the medial pterygoid is active during clenching in intercuspal position, protrusion and contralateral mandibular movement. However, it shows low activity during jaw opening, ipsilateral movements and clenching in retruded position.

5.3 Role of Lateral Pterygoid in Generation and Control of Isometric Force

In jaw muscles, isometric contractions could occur during the parafunctional jaw activities of tooth grinding and clenching, which can be directed horizontally or vertically. Though isometric contraction in masticatory muscles is the result of the activation of many muscles (Freund, 1983), the predominantly horizontal arrangement of fibres that characterizes of the lateral pterygoid muscle has been proposed to play a major role in the generation and fine control of horizontal force as in mastication and parafunctional grinding (Uchida et al., 2001; Uchida et al., 2002; Murray et al., 2004). Currently, there are few reports considering isometric contraction in the lateral pterygoid muscle despite evidence for the involvement of
the lateral pterygoid muscle in the development of isometric horizontal force vectors towards the end of the intercuspal phase of chewing (Wood et al., 1986) as well as the proposal by Widmalm et al. (1987) that the lateral pterygoid muscle is active during voluntary tooth grinding or gnashing.

The multi-unit and SMU studies in the IHLP by Uchida et al. (2001, 2002) support the role of the IHLP in generation and fine control of horizontal jaw forces by presenting data showing progressive increases in IHLP EMG activity with force increments and with changes in horizontal force direction from the same side to the contralateral or opposite side. This proposal was made even though the IHLP is considered more appropriate for isotonic than isometric contraction (Hannam and McMillan, 1994) because of the limited architecture of this muscle e.g., small physiological cross sectional area and limited pennation. It is possible that excessive demands on the IHLP, and indeed on the SHLP, for heavy mastication or parafunctional activities may produce localized muscle tenderness especially in TMD patients (Frank, 1965; Ai and Yamashita, 1992; Murray et al., 2004). There is limited information as to the role of the SHLP to isometric contraction. However, the SHLP could also be subject to similar excessive demands given that there is evidence that the SHLP is activated concomitantly with the IHLP in some horizontal directions (Sessle and Gurza, 1983; Miller, 1991, Hannam and McMillan, 1994; Murray et al., 1999).

6. HYPOTHESES

Despite the considerable interest in the function and anatomy of the SHLP for many decades, we still have very limited information on the normal function of the SHLP. Recent studies of the SHLP have suggested anatomical complexities of the SHLP in
terms of internal organization, for example, different orientation of muscle fibres in
different parts of the SHLP, and different innervation patterns, as well as functional
data pointing towards variations in activity depending on the location within the
SHLP and the possibility of functional heterogeneity within the SHLP. Recent data
supports a role for the SHLP in the fine control of horizontal jaw movements.
However, there is no information as to whether SHLP plays a role in the generation
and control of horizontal jaw force as would be expected from the distinct horizontal
alignment of the muscle fibres of the SHLP and as would be expected if the SHLP is
involved in parafunctional grinding and clenching. Therefore, the objective of the
present study was to obtain more specific information concerning the role of the
SHLP in the gradation of isometric force.

The SHLP has typically a horizontal orientation of SHLP muscle fibres arising from
a board origin at the infratemporal fossa and lateral surface of the lateral pterygoid
plate and converging onto a small insertion site on the condylar fovea, capsule and
disc. This broad orientation allows for the possibility of different force vector
components (i.e., magnitude) to be applied to the condyle in a range of horizontal
directions. A study of the SHLP during a range of isotonic contractions has
supported a role for the SHLP in generating fine horizontal jaw movements for
example, during contralateral, protrusive, ipsilateral and retrusive jaw movements
(Phanachet et al., 2003). However, there is little information regarding the functional
activity of the SHLP during isometric contractions. That is, different parts of the
SHLP may also have different contributions to generating horizontal force. The
complex neural distribution with in the SHLP has also supported the possible
selecting of specific compartment within the SHLP for specific demand. Based on the anatomy and evidence from previous studies, it is, therefore, hypothesized that:

1. One of the principal functions of the SHLP is to deliver horizontal isometric forces to the condyle in a range of directions similar to those for which the IHLP is involved (i.e., contralateral and protrusive jaw directions).

2. Different SMUs recorded from the SHLP are selectively active for specific isometric tasks and are active or inactive for other isometric tasks.

3. The SHLP plays an important role in the gradation of horizontal isometric forces through the increment of firing rate as the magnitude of force increases.

7. AIMS

The aims of this present study were as followings;

1. to determine the tasks for which the SHLP becomes active during isometric contraction whether there are preferential horizontal isometric tasks of the SHLP SMUs;

2. to determine whether different SMUs were selectively active for different horizontal isometric tasks of the SHLP as would be expected if the SHLP is functionally heterogeneous;

3. to determine whether the firing rates of the SHLP SMUs increase with the gradation of isometric force as would be expected if the SHLP is crucial for a fine control of horizontal isometric force.
CHAPTER II
MATERIALS AND METHODS

The study was carried out on 11 student volunteers (age 22-28 years; mean 24.4 ± 2.6 years; 8 males, 3 females) from the University of Sydney. Each of them completed a physical health screening questionnaire to determine the presence of any major medical problems which might have an effect upon the experimental procedures, for example those with rheumatic fever, congenital heart disease, and/or bleeding disorders, were excluded. After taking a dental history, jaw movements were examined (i.e., opening pattern, vertical range of motion, jaw excursion), as well as the jaw joints, jaw muscles and cervical muscles were palpated for tenderness. All volunteers did not reveal any signs or symptoms of TMDs nor any history of chronic pain or other neuromuscular problems. Those individuals with a deep overbite and any teeth missing (other than the molars) on the recording side were not recruited because of the difficulties in fabricating the upper and lower bite blocks in such individuals. All recruited subjects had intact natural dentition. Before the experimental procedures, the purposes of the study and any possible risks were clarified. Informed consent was obtained from each volunteer. Each volunteer was aware that he/she could withdraw from the experiment at any time. All 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. The experiment consisted of two sessions conducted on separate days. The total experimental recording duration was 4-5 hours. Most of the procedures have been previously described in detail (Orfanos et al., 1996; Murray et al., 1999; Uchida et al., 2001, 2002; Phanachet et al., 2003).
1. FIRST SESSION

1.1 Laboratory Procedures

Primary impressions of upper and lower dental arches and a face-bow transfer were taken. After upper and lower casts were mounted on an articulator (Denar® system), upper and lower self-cured acrylic bite blocks were fabricated and polished (Fig. II-1A, B). These bite blocks were extended to cover all anteriors and premolars and ground to a flat plane and as thin as possible to achieve the smallest jaw opening (3-8 mm from intercuspal position) when the flat surfaces of the acrylic bite blocks were in evenly smooth contact. Isometric horizontal force was measured with a force transducer (LM-5KA: Kyowa Dengyo, Japan) secured to a bar that projected from the upper bite block. A force rod was secured to the lower bite block. At the end of the force rod was a flat disc (9 mm diameter) which contacted a hemispherical projection (1 mm radius) on the disc-shaped transducer. The bar and rod were oriented parallel to the occlusal plane and could be swivelled horizontally (Fig. II-1B).

![Fig. II-1 Experimental apparatus. A force transducer is attached by a bar to an acrylic resin bite block secured to the upper anterior teeth and a force rod is attached to an acrylic resin bite block secured to the lower teeth](image-url)
1.2 Craniometric Measurement

Technical procedures were similar to those previously described by Orfanos et al. (1996). The electrode placement into the SHLP was an extraoral approach through the skin overlying the gap between the sigmoid notch and the most concave part of the zygomatic process. Craniometric measurements were required to calculate the trajectory of fine-wire electrode placement to the SHLP. These measurements were derived from craniofacial landmarks on computer tomographic radiographs. The total dose of radiation was within the limits recommended by The National Health and Medical Research Council of Australia (NHMRC) for volunteers.

A preliminary insertion point was initially marked with gutta percha on the facial skin. This insertion point was determined in the following manner.

1. The lower border of the zygomatic arch was identified by palpation on the side on which the electrode insertion was intended. This landmark was marked on the facial skin with a marker pen (Fig. II-2A, B, line labelled Z)

2. The lateral pole of the condyle was palpated by asking the volunteer to open and close the mouth. After located, this lateral pole was marked with the marker pen (Fig. II-2A, line labelled C)

3. The infraorbital rim was palpated and the straight line representing the Frankfort Horizontal Plane was traced from this position to the approximate location of the uppermost border of the bony external auditory meatus (Fig. II-2A, B, line labelled F).

4. The preliminary insertion point (arrow in Fig II-2A) was marked with gutta percha attached by adhesive tape at the point which was 6-7 mm inferior to the lower border of the zygomatic arch and 15 mm anterior to palpated lateral pole of the condyle (Fig. II-2B). This point should be within the sigmoid
notch and the most concave part of the zygomatic arch which would provide adequate space for electrode insertion.

5. The horizontal distance of the preliminary insertion point anterior to the posteriormost part of the tragus was noted as well as the length of the distance perpendicular to the Frankfort Horizontal Plane.

Fig. II-2 Determination of primary insertion point. (A) Primary insertion point has been defined. F = Frankfort Horizontal Plane, Z = zygomatic process and zygomatic arch, C = lateral pole of condyle, White arrow = primary insertion point (B) Gutta percha placement on the primary insertion point.

Computer tomographic scans (General Electric High Speed Advantage CT scanner, Milwaukee, USA) were taken parallel to the Frankfort Horizontal Plane and with the first scan 2-3 slices above the Frankfort Horizontal Plane and with the last scan 10-12 slices below the Frankfort Horizontal Plane. Each horizontal slice was 1 mm thick. After all slices were obtained, they were finally reformatted into a coronal image taken through the gutta percha landmark (Fig. II-3). The bony boundaries on the horizontal slice and reformatted coronal image were traced. The essential landmarks used to calculate the final trajectory of electrode insertion into the SHLP comprised
the roof of the infratemporal fossa, the infratemporal region anterior to the condylar head, the zygomatic arch and the mandibular condyle.

The following steps were carried out to measure the trajectory of insertion:

1. The horizontal slice containing the preliminary marker of gutta percha was selected.

2. The mid-sagittal line (S) on the horizontal slice was identified (Fig. II-3A). The line from the gutta percha marker was drawn in the estimated electrode insertion direction toward the mid-sagittal line (E).

3. Another straight line was drawn from the point where the mid-sagittal line and the line form the marker crossed together, toward the gutta percha marker (G) side and perpendicular to the mid-sagittal line. This line (P) was determined as 0°.

4. The angle from this 0° line to the angled line was measured. This angle (θ°) was the trajectory of the electrode either in the forward or backward direction.

5. The reformatted coronal image was used for measuring the trajectory of the electrodes in the upward direction (Fig. II-3B).

6. The line from the gutta percha marker through the gap between the coronoid process and lower border of zygomatic arch was drawn toward the roof of infratemporal fossa which was estimated as the region of the SHLP.

7. The angle of this line to the Frankfort Horizontal Plane, was the trajectory of the electrodes in upward direction (Φ°).

8. The length (d) of this line from the the gutta percha marker to the roof of the infratemporal fossa was calculated. This distance was the estimated depth of needle insertion.
Fig. II-3 Computer tomographic images for craniometric measurement in the horizontal plane (A) and the reformatted image in the coronal plane (B); x = estimated end point of the electrode placement, S = mid-sagittal line, G = Gutta percha marker, E = the line from the marker to mid-sagittal line which was the proposed trajectory of electrode insertion, P = the line perpendicular to the mid-sagittal line, F = Frankfort Horizontal Plane, d = the depth of the electrode placement (mm), $\theta^o$ = backward or forward angulation, $\phi^o$ = upward angulation.

2. SECOND SESSION (RECORDING SESSION)

2.1 Electrode Placement

2.1.1 Intramuscular Electrode Placement

Bipolar fine-wire electrodes were prepared by inserting two Teflon-coated stainless-steel fine wires (Medwire®, New York, USA; 75 µm dia., total dia. with Teflon coated 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 place the sterile bipolar fine-wire electrodes within the SHLP. The volunteer sat in a dental chair with a head rest. The area around the estimated insertion point was vigorously swabbed with alcohol, and a topical anaesthetic pad (EMLA® 5%, Astra, Australia) was placed over the estimated insertion point which was marked again by using the same procedure from the first session. This local anesthetic pad was left in place for at least 45 min to achieve a sufficient anesthetic effect. The volunteer was asked to bite on a softened thermoplastic compound attached to the fork plate of a modified dental facebow set (Fig. II-4).

![Fig. II-4 Modified dental face bow. The modified dental facebow is shown with the needle carrier for electrode placement within the SHLP. The horizontal arms of the face bow were adjusted parallel to the Frankfort Horizontal Plane. The vertical arms were adjusted parallel to the mid-sagittal plane.](image)

A modified dental facebow (Orfanos et al., 1996), adapted from Koole et al., (1990), was set up on the volunteer and the compound was used to stabilize the facebow (Fig. II-4). The horizontal arms and vertical arms of the facebow were adjusted parallel to
the Frankfort Horizontal Plane and mid-sagittal plane, respectively. Ear rods were fixed bilaterally and comfortably in the external auditory meatus on both sides. The upward and forward angulations were set up (Fig. II-5B). The needle carrier of the face bow was attached to the facebow and angled so that the needle trajectory corresponded to measurements obtained from the CT images. The sterile fine-wire electrodes were cut immediately with the sterile scissors so that ~2-3 mm of wire was bent back from the tip of the spinal needle to provide a small area of fresh metal exposure at the tip of the wire for recording. The distance between the bared ends was ~1-2 mm. The spinal needle carrying the bipolar electrodes was guided along the needle carrier (Fig. II-5A) and directed through the skin overlying the gap between the sigmoid notch and the zygomatic arch.

Fig. II-5 Electrode placement and angulation setting of modified dental face bow. (A) Extraoral approach for SHLP placement. (B) Upward (\(\Theta^o\)) and forward (\(\Theta^o\)) angulations were set up on the face bow.

The needle was inserted firmly and gently until it reached the predetermined depth as assessed from CT images and touched the roof of the infratemporal fossa. The fine-wire electrodes were then left in the muscle after the withdrawal of the spinal needle. The wires were secured to the facial skin with adhesive tape, leaving a small loop of
electrode wire between the adhesive tape and facial skin to prevent a sudden pulling of electrodes. The terminal ends were connected to the electrode panel.

2.1.2 Surface Electrode Placement

A bipolar surface patch electrode (Duo-Trode, Myo Tronics, Seattle, USA) was utilized for recording EMG activity from the masseter muscle. The masseter muscle was located during clenching and swabbed with alcohol to disinfect the area. The electrode was placed over the disinfected lower one-third of masseter ~10 mm from the anterior border unilaterally (Fig. II-6A). This electrode was secured with adhesive tapes following application of conductive electrolyte paste to the electrode disc and the terminal ends were connected to the electrode panel. A copper wrist collar served as ground.

2.2 Electromyographic Recordings

After electrode placement, the volunteers were asked to perform simple jaw movements (i.e., ipsilateral, contralateral, protrusive, open-close, clench) to determine whether the preliminary EMG activities from the SHLP could be discriminated into one or more SMUs. During the recordings, the volunteers sat in an upright position without head support. 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 100 Hz-10 kHz. SMUs 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-6 Surface electrode recording and force transducer. (A) Surface electrode recordings from unilateral masseter. (B) Force transducer projected from an acrylic bite-block surrounding the upper teeth. Force rod projected from the lower bite-block.

During the standardized isometric clenching, multi-unit EMG activity was also recorded with surface electrodes from unilateral masseter on the same side of the insertion (Fig. II-6A). The data-acquisition unit [Model micro1401; Cambridge Electronic Design (CED), Cambridge, England] was used with a sampling rate of 9,500 samples/s per channel and the bandwidth of 100 Hz-5 kHz were employed. Standardized isometric clenching was obtained by recording the rectified and smoothed EMG activity of masseter with 3 poles Paynter filter during 100% Maximum Voluntary Contraction (MVC). The masseter EMG activity at 100% MVC was set as the baseline target force for the subject to clench at this 100% MVC predetermined level.

2.3 Standardized Horizontal Isometric Tasks Recording

An isometric horizontal task was defined as a task when the volunteer exerted isometric horizontal force in one of the five horizontal directions without any movements of the mandible. Isometric horizontal force was measured by a force
transducer (LM-5KA; Kyowa Dengyo, Japan) secured to a bar that projected from an acrylic bite block surrounding the upper teeth (Fig. II-6B) when the force was exerted from a force rod that projected from lower bite block. At the end of the force rod was a flat disc (9 mm diameter) that contacted a hemispherical projection (radius 1 mm), the pressure sensor on the disc-shaped transducer. Since the end of the force rod lightly contacted a small button on the transducer, unbalanced vertical forces would result in the force rod slipping off the transducer button. The rod and button were both oriented parallel with the occlusal plane and could be swivelled horizontally for 5 directions of force exertion and these directions were labelled; protrusion (P), contralateral (CL), ipsilateral (IL), contralateral protrusion (CL-P) and ipsilateral protrusion (IL-P). Contralateral (opposite side) and ipsilateral (same side) refers to the side of insertion of the electrode into the SHLP. The latter two tasks were termed the intermediate tasks. Before electrode placement, these directions were measured on each subject by using a semi-circular protractor fixed to the upper bite block by silicone impression material (Formasil® Xact). The volunteers were guided to perform excursive movements to the ipsilateral or contralateral side to the recording side of the SHLP. The protrusive direction was set at 0° to the sagittal plane, and the contralateral and ipsilateral directions were ~60° to the sagittal plane. Contralateral protrusion and ipsilateral protrusion were ~30° to the sagittal plane (Fig. II-7).

Each volunteer performed a stepwise tracking task on a video screen (Fig. II-8) by exerting horizontal isometric force on the transducer at each horizontal direction (Fig. II-6B, 7). The force target was on the right hand side of the monitor whereas the exerted force was on the left hand side on the monitor. Each task consisted of a number of force steps, each of which was 5-s in duration. The force target was
increased 100 gwt for every force step from 400 gwt to 800 gwt. These force ranges were chosen by virtue of the feasibility in carrying out SMU discrimination and they were in the range of 10-20% of the horizontal maximum voluntary contraction [IHL horizontal MVC is \( \sim 37 \pm 8.3 \text{ N}, \text{ S. Uchida personal communication} \), 3.5-3.6 kg (\( \sim 35-36 \text{ N} \) from the calculation with respect to the force vector angulation of the SHLP which makes a medially directed angle of 26° with the sagittal plane and a supero-inferior directed angle of 23° to the Frankfort plane, Hönee, 1972]. Equivalent values in SI units of each force step are: 100 gwt (0.98 N), 400 gwt (3.92 N), 500 gwt (4.9 N), 600 gwt (5.88 N), 700 gwt (6.86 N) and 800 gwt (7.84 N).

\[\text{Fig. II-7} \text{ Horizontal angulation measurements using semicircular protractor fixed to the upper bite block; CL = contralateral, CL-P = contralateral protrusion, P = protrusion, IL-P = ipsilateral protrusion and IL = ipsilateral.}\]

Prior to the recording procedure, the force rod was set to be lightly contacting the transducer so that although contact was made, there was zero force output from the transducer at this position. The volunteers were given an opportunity to practice tracking the force target on the video screen at every direction before the recordings. The isometric force signal, derived from the transducer, was recorded using the AMLAB data-acquisition system (Associative Measurements, North Ryde, Sydney,
Australia) at a sampling rate of 1000 samples/s and bandwidth of 0-500 Hz. The target levels and timing markers were displayed by the CED system. Ten trials were performed for each isometric horizontal task. The first five trials of each task were consecutively recorded until all tasks were completed. The remainder of the trials of each task was then recorded. The orders with which the tasks were carried out were randomly assigned in each individual. Trials were separated by ≥1 min rest periods.

Fig. II-8 AMLAB video screen. The force target (yellow arrow) was on the right hand side of the volunteer whereas the exerted force (white arrow) was on the left hand side of the volunteer on the monitor.

2.4 CT Verification

At the end of the recording session, CT scans were taken for the second time to verify electrode location within the SHLP (see results, Fig. III-6). This involved taking 2-3 slices above the Frankfort Horizontal Plane and 10-12 slices (1 mm thick) below the Frankfort Horizontal Plane and parallel with the Frankfort Horizontal Plane. The reformatted images were then sectioned in the coronal plane through the fine-wire tips and also in an oblique sagittal plane through the fine-wire tips and along the long axis of the SHLP.
3. DATA ANALYSES

3.1 Location of Electrode Position within the SHLP

In all subjects, the superior border of the SHLP was clearly defined by the roof of the infratemporal fossa. In 3 subjects, the inferior border of the SHLP was clearly defined by a radiolucent band that was assumed to demarcate SHLP from the IHLP. In the remaining 8 subjects where the boundary between the SHLP and the IHLP were not clearly identified by a radiolucent band that was assumed to demarcate the SHLP from the IHLP, the supero-inferior dimension of the SHLP was assessed from previous histological studies (Meyenberg et al., 1986; Widmalm et al., 1987; R. Hawthorn, personal communication) and for the purpose of the present study was defined as ~5-mm.

The location of the electrode tips within the SHLP was evaluated by viewing the electrode tip in relation to muscle boundaries on the horizontal, reformatted coronal and oblique sagittal views through the electrode tips (see results, Fig. III-6). The location of the electrodes was therefore, considered in the supero-inferior, antero-posterior and medio-lateral views. The defined location of the electrodes in the SHLP in each CT image from each volunteer was normalised in proportion to 10x10 lattices and transferred into two dimensional maps (Fig. III-7, 8). The amount of bend back of the wires (2-3 mm) was taken into account when assessing the recording sites.

3.2 SMU Analysis

3.2.1 SMU Discrimination

Recordings containing discriminable SMUs were obtained from the SHLP in most subjects. SMUs were discriminated by using custom-written data management software with Spike® 2 data-capture analysis software from CED, and each action
potential was verified by visual inspection. The criteria for discriminating each SMU were similarities in amplitude and waveform and a regular time of occurrence of the SMU action potential.

3.2.2 Task Relations

All discriminated SMUs from 11 volunteers were studied to determine which SMUs were active for particular tasks. Further, the task relations were also considered in relation to the location of the electrodes in the SHLP. After the defined location in the SHLP from each volunteer was measured in proportion to 10x10 lattices and transferred into two dimensional maps, the task relations of each electrode location in the SHLP was defined.

3.2.3 Firing Rates of the SHLP Motor Units

After the SMUs were completely discriminated, SMUs from the most stable 2-s holding periods were analyzed for mean firing rates. The most stable period was chosen for SMU analysis and defined as the continuous 2 s period which contained the least number of fluctuations of the force trace and where the force level remained within the range of force of ± 30 gwt from each force step (400-800 gwt). After SMUs were discriminated, they were determined for which horizontal isometric tasks that each SMU was preferentially active (see Table III-2a, b, c).

The mean firing rate was defined as the number of action potentials counted in one second (impulse/s) at a particular force level. Inter-spike intervals >160 ms were discarded from the analysis. It was observed in early recordings that when the interspike interval went <160 ms for a tonically firing unit, this was associated with a reduction in applied force level. It was considered inappropriate to include these
greater inter-spike intervals in the firing rate analysis as they might excessively lower the firing rates at a particular force level. This inter-spike interval criterion was also implemented in the previous study (Phanachet et al., 2004) and was based on the minimal firing rate of temporalis muscle motor units which was reported as 6 imp/s (McMillan, 1993). It is also a more conservative approach for analysis of firing rate changes with force level increases. The mean firing rate was calculated from usually at least 5 trials of each task.

The analyses for firing rate properties during horizontal isometric contraction involved a Univariate Analyses of Variance (ANOVA) with least significant difference (LSD) as the post hoc adjustment for multiple comparisons. A significance level of 5% (P<0.05) was applied throughout the analyses. The statistical software SPSS (version 12) was used by defining the firing rate as a dependent variable, the tasks and force levels as fixed factors and the SMUs as random factors. Where a particular SMU was not active during a particular task trial but was active in other trials, a value of zero was included for that trial in the statistical analysis. However, the absence of SMU activity, for example, when there was no EMG activity of a particular SMU at 400-600 gwt, was included only when there was SMU activity of other force steps (e.g., 700-800 gwt).
CHAPTER III

RESULTS

1. SYNCHRONOUS RECORDINGS OF STANDARDIZED HORIZONTAL ISOMETRIC FORCE AND SHLP EMG ACTIVITY

Figure III-1A-E illustrates the superimposition of five force traces from representative subjects during isometric contraction in contralateral (subject H, see Table III-1), contralateral protrusion (subject E), protrusion (subject B), ipsilateral protrusion (subject H) and ipsilateral direction (subject A), respectively and shows the close matching of the average force traces from each of the directions with the exact target force (dotted, straight lines) in different subjects. Every subject was capable of exerting the force to the target level at a comparable level of accuracy. The ability of the subjects to track and hold the force for 5 s was less difficult at the lower forces, for example 400-600 gwt. However, some subjects experienced more difficulty in tracking and holding to the target at force levels of 700-800 gwt. Each subject was considered to have tracked the target satisfactorily if the tracking force during each force step was stable for at least a 2-s period and was steady, that is, the force variation was within ±30 gwt from the actual force step. Figure III-2A shows an overlay of average force traces from all tasks of subjects from Figure III-1. The averaged force indicates the capability of subjects to hold the force within ±30 gwt (shaded area, Fig. III-2B) for at least 5 s. In addition, we were able to record the SHLP EMG activity synchronously with the gradation of horizontal isometric force (Fig. III-4A, B).
**Fig. III-1** Left panel: superimposition of five force traces from representative subjects for each direction of isometric contraction, that is, contralateral (subject H), contralateral protrusion (subject E), protrusion (subject B), ipsilateral protrusion (subject H) and ipsilateral direction (subject A). Right panel: average force traces from each of the directions in relation to the target force and ±30 gwt of the actual target force (dotted straight line).
Fig. III-2 Association between exerted force and target force. (A) Superimposed mean force trace during CL- CL-P, P, IL-P and IL from representative subjects in Figure III-1. (B) Average force trace of the upper panel representing the close association with the target force (dotted line). Shaded area indicates the accepted ± 30 gwt from the exact force levels.

2. SYNCHRONOUS RECORDINGS OF STANDARDIZED ISOMETRIC CLENCH AND SHLP EMG ACTIVITY

Standardized isometric clenching was characterized by recording the rectified and smoothed EMG activity during 100% MVC of the masseter muscle of each subject. Figure III-3A shows Payneter filtered signals and three rectified and smoothed EMG traces at 100% MVC in one subject (subject D, see Table II-1). All subjects displayed difficulty in holding the force steady at a predetermined level. Figure III-
3B illustrates 3 trials of simultaneous recordings of the SHLP EMG activity during 5 s holding period. There were slight SHLP EMG activities observed during isometric clenching.

![Graph A](image1)

![Graph B](image2)

**Fig. III-3** An example of SHLP EMG activity during 100% MVC and Paynter filtered signals. (A) 3 trials of Paynter filtered signals during 100% MVC in relation to the target force during 5 s holding period. (B) EMG activity during isometric clenching.

3. **QUALITATIVE DESCRIPTION OF SHLP EMG ACTIVITY DURING HORIZONTAL ISOMETRIC CONTRACTION**

3.1 **Task relations of SHLP SMU Activity**

From the SHLP of 11 subjects, a total of 48 SHLP SMUs were discriminated: 15 units (3 sites) from the medial part, 25 units (5 sites) from the middle part and 8 units (3 sites) from the lateral part of the SHLP (Table III-2a, b, c). Forty eight SMUs were active during at least one of the isometric tasks. None of the SMUs were active with the jaw at the resting postural jaw position. A representative trial of protrusive isometric contraction is shown in Figure III-4. During the isometric task, four SMU
(Fig. III-4B, C) were discriminated from the filtered EMG (Fig. III-4A) from a verified electrode recording site within the SHLP (Fig. III-6). Table III-1a, b indicates whether at least one SMU was active at a site for each task and subject arranged in relation to the medio-lateral and supero-inferior view of the SHLP. In eight of the 11 participants, activity was apparent for CL, CL-P, and P. In seven participants, activity was present at IL-P and/or IL and in five, activity was present during clenching at intercuspal position. Of the 48 SMUs, 34 (71%) SMUs were active at CL, 33 (69%) at CL-P, 32 (67%) at P, 17 (35%) at IL-P and 6 (13%) SMUs were active at IL.

3.2 Association between SMU Activity and Horizontal Isometric Force

Qualitatively, there was a close association between SHLP activity and the magnitude of horizontal isometric force for all directions. An example of SHLP activity from a representative subject is shown in Figure III-4. Four SMUs were discriminated from a filtered EMG (Fig. III-4A) of a verified electrode recording site within the SHLP during a protrusive task. SMUs 1 and 2 were usually active throughout each force increment level while SMUs 3 and 4 were tonically recruited only at the highest force level and exhibited progressively larger bursts of SMU activity (* in Fig. III-4A) during the dynamic force fluctuations at successively higher force levels. The criteria that we considered for SMUs discrimination are amplitude, waveform and time of occurrence. Normally, we could determine this tentatively by the waveform and amplitude of the SMUs. However, sometimes when many SMUs including the SMUs that we can not discriminate, fired together at the same time, the original waveform and amplitude of the SMUs might alter and distort but we can tentatively determine the SMUs by its time of occurrence. For example,
the first spike of SMU 3 is slightly different from the later spikes but we believe that this first was just contaminated by another spike. The third occurrence of SMU 3 was also slightly contaminated by SMU 4. Similarly there was some contamination of the first occurrence of SMU 2 by other motor units or noise. The larger amplitude of SMU 3 reflects a slight drift in the amplitude of this single motor unit over time and that tended to occur with this SMU in association with the high protrusive forces exerted at this isometric step level. Therefore, we could interpret and believe that the SMU discrimination was correct.

3.3 Association between SMU Activity and Direction of Horizontal Isometric Task
The 48 SMUs exhibited a variety of combinations of directions in which activity was observed (Table III-2; medial, middle and lateral sites). Thus, 5 units in 2 subjects were active in all directions, while 15 units in 6 subjects were active in one direction only (4 units at CL only, 3 CL-P, 6 P, 2 IL-P). Eight units were active in 2 directions (5 CL and CL-P units; 1 IL-P and IL units; 1 IL-P and P unit; 1 CL-P and P unit), 14 units were active in 3 directions (12 CL, CP and P units; 1 C, P and IL-P unit; 1 CL, CL-P and IL-P unit), and 6 units were active in 4 directions, all of which were active for CL, CL-P, P and IL-P.

In 2 subjects, all SMUs recorded at a site exhibited the same directions of task relation while in 2 subjects there was no activity although a few SMUs were active at >800 gwt and EMG activity was present during isotonic contralateral and protrusive movements without the force transducer apparatus in place. In 7 subjects, each SMU recorded at each site exhibited a different pattern to the other SMUs at the site. There
were examples of SMUs with opposite patterns, for example, in one subject the patterns recorded were CL, CL-P, P (2 units), and IL-P, IL (1 unit).

The SMUs from the SHLP not only altered their activity in association with increasing force in one direction but also altered their activity with different directions of horizontal isometric force. Figure III-5 shows the variation of SMU activity with change in direction of isometric task in one subject. SMUs 1 and 3 were active for CL, CL-P and P except IL-P and IL. SMUs 2 and 4 were active for CL direction only. SMUs 5 and 6 were selectively activated for IL-P direction only. There was essentially no activation of any SMU for IL direction. Table III-1 summarizes the directional relations of SMU’s recorded at all recording sites. Only about 27% of sites exhibited activity for IL.
Fig. III-4 An example of SMU activity during protrusive isometric contraction from a verified electrode recording site within the SHLP. (A) force trace. (B) filtered EMG and spike train pulses of 4 discriminated SMUs. Each short vertical line is a spike train pulse indicated the time of occurrence of a SMU action potential. The period delineated by the vertical lines is the expansion of the filtered EMG and spike trains. * represents the bursting EMG activity in association with the fluctuation of force.
Fig. III-5 Force tracing and, filtered EMG and spike trains from 6 SMUs (waveforms on the right) from one representative trial of each direction in one subject.

CL = contralateral direction, CL-P = contralateral protrusion, P = protrusion, IL-P = ipsilateral protrusion, IL = ipsilateral direction
4. QUALITATIVE DESCRIPTION OF THE SHLP EMG ACTIVITY DURING VERTICAL ISOMETRIC CONTRACTION

4.1 Association between SMU Activity and Vertical Isometric Tasks

The activity of the SHLP at 100% MVC was studied in nine subjects (Table III-1a, b). There was EMG activity present in SHLP during 100% MVC in five of nine subjects where this task was studied. Of the five, two subjects had electrodes located in the medial part of SHLP while in three the electrodes were in the middle part of the SHLP. There was no detectable EMG activity during maximum clench in four subjects. The locations of the recording sites in these subjects were scattered medio-laterally throughout the SHLP (2 were lateral, 1 middle, 1 medial).

Table III-1a Task relation of the SHLP activity (mediolateral). SMUs of the SHLP from 11 subjects (A to K), were arranged in relation to the mediolateral location of verified electrode recording site and numbers of units recorded from each site.

<table>
<thead>
<tr>
<th>Subjects</th>
<th>CL</th>
<th>CL-P</th>
<th>P</th>
<th>IL-P</th>
<th>IL</th>
<th>Clench</th>
<th>Number of SMUs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medial</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>b</td>
<td>+</td>
<td>8</td>
</tr>
<tr>
<td>B</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>C</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>D</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>E</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>nd</td>
<td></td>
<td>7</td>
</tr>
<tr>
<td>F</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>G</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>H</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>I</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>J</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>K</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>nd</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Lateral</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Total 48</td>
</tr>
<tr>
<td>% of sites showing activity</td>
<td>73</td>
<td>73</td>
<td>82</td>
<td>64</td>
<td>27</td>
<td>56</td>
<td></td>
</tr>
</tbody>
</table>

a = +, at least one SMU active for this direction of task
b = -, not active
nd = no recording was made in clenching activity in these subjects
CL = contralateral direction, CL-P = contralateral protrusion, P = protrusion, IL-P = ipsilateral protrusion, IL = ipsilateral direction
Table III-1b Task relation of the SHLP activity (superoinferior). SMUs of the SHLP from 11 subjects (A to K), were arranged in relation to the superoinferior location of verified electrode recording site and numbers of units recorded from each site.

<table>
<thead>
<tr>
<th>Subjects</th>
<th>CL</th>
<th>CL-P</th>
<th>P</th>
<th>IL-P</th>
<th>IL</th>
<th>Clench</th>
<th>Number of SMUs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>8</td>
</tr>
<tr>
<td>I</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>8</td>
</tr>
<tr>
<td>F</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>6</td>
</tr>
<tr>
<td>G</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>5</td>
</tr>
<tr>
<td>B</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>3</td>
</tr>
<tr>
<td>D</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>H</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>5</td>
</tr>
<tr>
<td>C</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>4</td>
</tr>
<tr>
<td>E</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>nd</td>
<td>7</td>
</tr>
<tr>
<td>K</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>nd</td>
<td>0</td>
</tr>
<tr>
<td>J</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Inferior</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% of sites showing activity</td>
<td>73</td>
<td>73</td>
<td>82</td>
<td>64</td>
<td>27</td>
<td>56</td>
<td>48</td>
</tr>
</tbody>
</table>

Same format as in Table III-1a.

Table III-2a Task relation for each SHLP motor unit located in the medial site of the SHLP.

Medial Sites

<table>
<thead>
<tr>
<th>Subject</th>
<th>Task relation vs Force levels</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unit</td>
<td>CL</td>
</tr>
<tr>
<td>A</td>
<td>4</td>
</tr>
<tr>
<td>1</td>
<td>++</td>
</tr>
<tr>
<td>2</td>
<td>++</td>
</tr>
<tr>
<td>3</td>
<td>++</td>
</tr>
<tr>
<td>4</td>
<td>++</td>
</tr>
<tr>
<td>5</td>
<td>++</td>
</tr>
<tr>
<td>6</td>
<td>++</td>
</tr>
<tr>
<td>7</td>
<td>++</td>
</tr>
<tr>
<td>8</td>
<td>++</td>
</tr>
<tr>
<td>B</td>
<td>9</td>
</tr>
<tr>
<td>10</td>
<td>++</td>
</tr>
<tr>
<td>11</td>
<td>++</td>
</tr>
<tr>
<td>C</td>
<td>12</td>
</tr>
<tr>
<td>13</td>
<td>++</td>
</tr>
<tr>
<td>14</td>
<td>++</td>
</tr>
<tr>
<td>15</td>
<td>++</td>
</tr>
</tbody>
</table>
\(+\) = active, \(-\) = not active

4 = 400 gwt, 5 = 500 gwt, 6 = 600 gwt, 7 = 700 gwt, 8 = 800 gwt

CL = contralateral direction, CL-P = contralateral protrusion, \(P\) = protrusion, IL-P = ipsilateral protrusion, \(IL\) = ipsilateral direction

\(*\) = SMUs excluded for statistical analyses for the firing rates

**Table III-2b** Task relation for each SHLP motor unit located in the middle site of the SHLP.

**Middle sites**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Task relation vs Force levels</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Unit</td>
</tr>
<tr>
<td>D</td>
<td>16*</td>
</tr>
<tr>
<td></td>
<td>17*</td>
</tr>
<tr>
<td>E</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>24*</td>
</tr>
<tr>
<td>F</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>28</td>
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<tr>
<td></td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>30</td>
</tr>
<tr>
<td>G</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>35</td>
</tr>
<tr>
<td>H</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>39*</td>
</tr>
<tr>
<td></td>
<td>40</td>
</tr>
</tbody>
</table>

Same format as in Table III-2a.
Table III-2c Task relation for each SHLP motor unit located in the lateral site of the SHLP.

**Lateral sites**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Task relation vs Force levels</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CL</td>
</tr>
<tr>
<td>Unit</td>
<td>4</td>
</tr>
<tr>
<td>I</td>
<td>+</td>
</tr>
<tr>
<td>42</td>
<td>+</td>
</tr>
<tr>
<td>43</td>
<td>+</td>
</tr>
<tr>
<td>44</td>
<td>-</td>
</tr>
<tr>
<td>45*</td>
<td>-</td>
</tr>
<tr>
<td>46*</td>
<td>-</td>
</tr>
<tr>
<td>47</td>
<td>-</td>
</tr>
<tr>
<td>48</td>
<td>+</td>
</tr>
<tr>
<td>J</td>
<td>0</td>
</tr>
<tr>
<td>K</td>
<td>0</td>
</tr>
</tbody>
</table>

Same format as in Table III-2a.

5. **ELECTRODE LOCATION WITHIN THE SHLP**

All 11 subjects underwent a second CT scan for verifying the electrode tips in relation to the SHLP boundaries after the recordings. The horizontal slices, frontal reformatted and oblique sagittal reformatted CT images in all subjects were evaluated and the electrode fine-wire tips were shown to be reliably located in the SHLP. Figure III-6 shows an example of CT scan data in the horizontal plane (upper panel) and in a reformatted oblique sagittal plane (lower panel) taken along the long axis of the SHLP and showing the tips of the fine-wire electrodes within the SHLP. Table III-3 shows the normalized electrode locations in three dimensions. The relative locations of the electrode recording sites were plotted in the vertical plane (Fig. III-7) and in the horizontal plane (Fig. III-8, see also Table III-1) along the long axis of the SHLP. Each symbol represents the isometric task(s) for which the SMUs at that site were active.
Table III-3 The normalized electrode locations in three dimensions.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Antero-posterior</th>
<th>Medio-lateral</th>
<th>Supero-inferior</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>5.6/10</td>
<td>1.8/10</td>
<td>1/10</td>
</tr>
<tr>
<td>B</td>
<td>2.7/10</td>
<td>2.5/10</td>
<td>6/10</td>
</tr>
<tr>
<td>C</td>
<td>1.3/10</td>
<td>2.9/10</td>
<td>8.1/10</td>
</tr>
<tr>
<td>D</td>
<td>5/10</td>
<td>5/10</td>
<td>6.7/10</td>
</tr>
<tr>
<td>E</td>
<td>5.3/10</td>
<td>6.3/10</td>
<td>8.9/10</td>
</tr>
<tr>
<td>F</td>
<td>4.8/10</td>
<td>6.4/10</td>
<td>4/10</td>
</tr>
<tr>
<td>G</td>
<td>5.2/10</td>
<td>6.7/10</td>
<td>5/10</td>
</tr>
<tr>
<td>H</td>
<td>4.8/10</td>
<td>6.7/10</td>
<td>8/10</td>
</tr>
<tr>
<td>I</td>
<td>4.7/10</td>
<td>7.5/10</td>
<td>2.1/10</td>
</tr>
<tr>
<td>J</td>
<td>4.2/10</td>
<td>8.6/10</td>
<td>10/10</td>
</tr>
<tr>
<td>K</td>
<td>3.3/10</td>
<td>9.2/10</td>
<td>9/10</td>
</tr>
</tbody>
</table>

Fig. III-6 Example of CT images showing the electrode fine-wire tips located within the SHLP (blank circles). Upper panel: a horizontal slice (1 mm thick). Lower panel: a reformatted oblique sagittal image taken through the fine-wire tips along the long axis of the SHLP.

There was no activity for any of the horizontal isometric tasks at the two lowermost and lateralmost recording sites within the SHLP (Fig. III-7, III-8, Table III-1). The SMUs from most of the subjects were normally active during CL, CL-P and P. The
muscle fibres of the SHLP that were active during CL, CL-P, P, IL-P with or without IL were mostly scattered throughout the SHLP both vertically and horizontally. However, the muscle fibres in the upper part of the SHLP tended not to be active in any of the ipsilateral tasks. Thus, in one subject there was activity during CL, CL-P and P only and from another one subject there was activity only in protrusion in the upper part of the SHLP. While most of the recording sites showed activity during IL-P, the mediolateral middle portion of SHLP tended to be the only part of SHLP that was active in the IL tasks.

Fig. III-7 Two dimensional mapping of electrode locations within the SHLP and showing the antero-posterior and supero-inferior relationship in association with the task relations.

(Θ, SMUs were active during CL, CL-P, P, IL-P with or without IL; +, SMUs were active during CL, CL-P, P; P, SMUs were active during P only and - , no activity).
Fig. III-8 Two dimensional mapping of electrode locations within the SHLP and showing the antero-posterior and medio-lateral relationship in association with the task relations. The format of the figure is as in Fig. III-7.

6. FIRING RATE OF THE SHLP SMUs

Forty out of 48 SMUs discriminated from 8 out of 11 subjects were included in the firing rate statistical analysis. The remaining 8 SMUs were not included due to the difficulties of motor unit discrimination (symbolized with * in table III-2).

6.1 Firing Rate during the Increment of Force between 400-800 gwt

An overall analysis for the firing rate and force of each subject separately showed that the firing rate of all SMUs of each subject increased significantly with an increase in force from 400 to 800 gwt [Subject A; F(4,309)=17.457, P=0.000, Subject B; F(4,70)=8.320, P=0.000, Subject C; F(4,160)=6.678, P=0.003, Subject E; F(4,298)=13.633, P=0.000, Subject F; F(4,204)=10.245, P=0.000, Subject G;
F(4,164)=16.298, \( P=0.000 \), Subject H; \( F(4,168)=3.913, \ P=0.016 \), Subject I; \( F(4,264)=38.639, \ P=0.000 \). However, pairwise comparisons between force levels and between tasks showed variability of significant values from subject to subject. Table III-4 illustrates the mean firing rates and standard errors in association with the increase of force for each subject. The 95% confidence intervals for each force level indicates that the overlap between the force levels was greatest at the 700 and 800 gwt levels. As zero firing rate was included in the analyses, it can be seen in table III-4 that some firing rate values at 400 and/or 500 gwt were below 6 imp/s. Figure III-9 is a graphical representation of the means that clearly shows the tendency of mean firing rates of each subject to substantially increase from 400 to 800 gwt.

**Table III-4** Mean firing rates of all SMUs for each subject in relation to the isometric force increment.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Force</th>
<th>Mean</th>
<th>Std.Error</th>
<th>95% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Lower bound</td>
</tr>
<tr>
<td>A</td>
<td>400</td>
<td>8.6</td>
<td>.712</td>
<td>7.2</td>
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<tr>
<td></td>
<td>500</td>
<td>11.8</td>
<td>.703</td>
<td>10.4</td>
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<td>600</td>
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<td>.713</td>
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</tr>
<tr>
<td></td>
<td>700</td>
<td>16.6</td>
<td>.721</td>
<td>15.2</td>
</tr>
<tr>
<td></td>
<td>800</td>
<td>16.9</td>
<td>.723</td>
<td>15.5</td>
</tr>
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</table>

**Graph:**
- A
- B
- C
- E
- F
- G
- H
- I

**Axes:**
- Firing Rate (imp/s)
- Forces (gwt)
Fig. III-9 Mean firing rate of all discriminated SMUs in each subject (total eight subjects, A through I).

6.2 Determination of Preferential Tasks using Firing Rate of Force between 400-800 gwt

SMU firing rate values from all subjects were pooled and assessed by further statistical analyses. Primarily, it was found that there were significant effects of task, force and SMU [$F_{\text{task}} (4,1650)=9.679$, $F_{\text{force}} (4,1650)=48.710$, $F_{\text{SMU}} (39,1650)=5.136$, ($P=0.000$)] as well as two-way interactions among these variables (task by force, task by SMU, force by SMU) that showed statistically significant effects [$F_{\text{task}*force}} (16,1650)=3.283$, $F_{\text{task}*SMU}} (50,1650)=3.885$, $F_{\text{force}*SMU}} (154,1650)=1.760$, ($P=0.000$)]. However, a three-way interactions of task by force by SMU did not show a statistically significant effect [$F_{\text{task}*force}*\text{SMU}} (177,1650) = 1.093$, ($P=0.207$)]. Therefore, the three-way interactions of these three variables could be omitted from the analyses. The number of times that all SMUs occurred for each level of force and the direction of task were presented by Table III-5. The numbers of occurrence of SMUs represent all of the SMUs that were firing during each level of force and direction. These numbers have been included from every trial. It can be determined from the values that for IL-P and IL, not many SMUs were recruited and therefore a smaller sample size of SMUs was available at IL-P and IL than for other directions in the statistical analysis.

Table III-5 The occurrence of time of SMUs for each level of force (400-800 gwt) and direction of tasks used for the statistical analyses.

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<td>CL</td>
</tr>
<tr>
<td></td>
<td>CL-P</td>
</tr>
<tr>
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<td>P</td>
</tr>
<tr>
<td></td>
<td>IL-P</td>
</tr>
<tr>
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<td>IL</td>
</tr>
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</table>

There was a significant increase of firing rate with increase of force with the means being 7.4, 9.9, 12.8, 13.9 and 17.8 impulses/s in relation to 400, 500, 600, 700 and 800 gwt, respectively \((F_{\text{force}} (4,1650) = 55.512, \ (P=0.000))\). A pairwise comparison of all possible pairs of force levels indicated significant differences between the force levels \((P<0.05)\) (Table III-6). Furthermore, the analysis also showed that the firing rate changed significantly with direction with the marginal means being 13.3, 12.6, 12.6, 9.8 and 11.1 in relation to CL, CL-P, P, IL-P and IL, respectively \((F_{\text{task}} (4,1650) = 9.572, \ (P=0.000))\). Pairwise comparisons between each task indicated significant differences of firing rates only for CL with IL-P, CL-P with IL-P, P with IL-P and CL with IL \((P<0.05)\) (Table III-7). Table III-8 displays the mean firing rates and standard errors for all subjects in relation to the increase of force for each task and Figure III-10 plots the data of Table III-8.

**Table III-6** Pairwise comparisons of all possible pairs of each force level from 400-800 gwt showing standard errors and significant values \((P<0.05)\).
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Table III-7 Pairwise comparisons of all possible pairs of each direction showing standard errors and significant values (P<0.05).

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### Table III-8

Mean firing rates of all subjects in association to force (400-800 gwt) and task

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Fig. III-10 Mean firing rate of all subjects in association with the gradation of force and task (CL; contralateral, CL-P; contralateral protrusion, P; protrusion, IL-P; ipsilateral protrusion, IL; ipsilateral)

Although the mean firing rates in some tasks, for example CL, IL-P and IL, showed small decreases of firing rate between 600 and 700 gwt, the overall mean firing rate indicated a gradual increase of the SHLP SMU activity with increase of force.

The pairwise comparisons between the tasks mentioned above indicate that CL, CL-P and P have comparable firing rate (i.e., 13.3, 12.6, and 12.6 impulses/s, respectively) and were significantly higher than IL-P. The firing rate at the IL direction was significantly less than the CL direction but was not significantly different from the other directions. Therefore, it is suggested that CL, CL-P and P are preferential directions of firing for the SHLP.

Figure III-11 plots the variation in the mean firing rate at each force level in association with the different tasks. It seems that the firing rates at the 700 and 800
gwt were considerably different to the other force levels and did not fit the analyses model. This may be due to the substantially fewer discriminated SMUs at higher force levels. At these higher force levels, there were the pre-existing tonic SMUs which increased in firing rates as the force increased as well as the recruitment of new SMUs (high threshold units), which are just recruited and still maintained low firing rates (as can be seen in Fig. III-4). This may, therefore, result in the inconsistency of the marginal mean firing rates at these force levels.

![Graph showing firing rates for different force levels](image)

**Fig. III-11** Mean firing rate of all subjects in association with ranges of tasks and force levels (the same format as Figure III-10).

**6.3 Firing Rate during the Increment of Force between 400-600 gwt**

After omitting the force levels (700 and 800 gwt) from the statistical analysis (select case option from SPSS, version 12), it was found that there were no significant two-way interactions between force and task \( [F_{\text{force} \times \text{task}} (8,1023) = 1.818, (P=0.70)] \) nor between force and SMUs \( [F_{\text{force} \times \text{SMU}} (77,1023) = 1.217, (P=0.106)] \) in all subjects. There was, however a significant effect of the two-way interaction between task and SMUs \( [F_{\text{task} \times \text{SMU}} (50,1023) = 3.514, (P=0.000)] \) and a significant effect of the
individual variable of force, task and SMUs SMUs \( F_{\text{force}} (2,1023) = 20.983, F_{\text{task}} (4,1023) = 9.294, F_{\text{SMU}} (39,1025) = 5.070, (P<0.001) \). Therefore, these significant effects were taken into account in the subsequent statistical analyses. As the data now provided a better fit to the analysis model, the same process of statistical analysis was repeated. The numbers of times that all SMUs occurred for each task were consequently reduced (Table III-9) after removal of the data at force levels 700 and 800 gwt. It can be determined from the values that for IL-P and IL, not many SMUs were recruited and therefore a smaller sample size of SMUs was available at IL-P and IL than for other directions in the statistical analysis.

**Table III-9** The occurrence of time of SMUs for each level of force (400-600 gwt) and direction of tasks after omitting the data of force level 700 and 800 gwt.

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<th>Variables</th>
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</table>

6.4 Determination of Preferential Tasks using Firing Rate of Force between 400-600 gwt

There was a significant increase of firing rate for the increase of force with the marginal means \( F_{\text{force}} (2,1023) = 70.067, (P=0.000) \); **7.2, 10.1 and 12.6** in relation to 400, 500 and 600 gwt, respectively. A pairwise comparison of each pair of force levels also indicated significant differences between the force levels \( P<0.001 \) (Table III-10). Furthermore, the analysis showed a significant difference of the firing
rate for the change of direction with the means \( F_{\text{task}} (4,1023) = 9.275, \ (P=0.000) \);
11.5, 10.0, 9.5, 7.6 and 9.7 in relation to CL, CL-P, P, IL-P and IL, respectively. However, pairwise comparisons between each task indicated the significant differences of firing rates only for CL with CL-P, CL with P, CL with IL-P, CL-P with IL-P and P with IL-P (\( P<0.05 \)) (Table III-11). The ipsilateral direction showed no significant differences in firing rates when compared to other tasks. Table III-12 displays the mean firing rate and standard errors according to the increase of force for each task and Figure III-12 shows the plots of the values of Table III-12. An inspection of both the table and graph clearly shows that the CL direction exhibited the highest firing rate followed by CL-P, P and IL-P. The ipsilateral direction does not seem to conform to the trend of a progressive decrease of SMU activity from the contralateral to ipsilateral direction. This might be due to the small sample sizes obtained for this direction which resulted in a large difference between the upper and lower bound of the confidence interval than for any other tasks.

**Table III-10** Pairwise comparisons of all possible pairs of each force level from 400-600 gwt showing standard errors and significant values (\( P<0.05 \)).

<table>
<thead>
<tr>
<th>Force levels</th>
<th>Force levels</th>
<th>Std. Error</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>400</td>
<td>500</td>
<td>.457</td>
<td>0.000</td>
</tr>
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</tr>
<tr>
<td></td>
<td>500</td>
<td>.453</td>
<td>0.000</td>
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</table>
Table III-11 Pairwise comparisons of all possible pairs of each direction showing standard errors and significant values (P<0.05).

<table>
<thead>
<tr>
<th>Tasks</th>
<th>Tasks</th>
<th>Std. Error</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>CL</td>
<td>CL-P</td>
<td>.615</td>
<td>0.015</td>
</tr>
<tr>
<td>P</td>
<td>CL-P</td>
<td>.573</td>
<td>0.001</td>
</tr>
<tr>
<td>IL-P</td>
<td>CL-P</td>
<td>.783</td>
<td>0.000</td>
</tr>
<tr>
<td>IL</td>
<td>CL-P</td>
<td>1.400</td>
<td>0.204</td>
</tr>
<tr>
<td>CL-P</td>
<td>CL</td>
<td>.651</td>
<td>0.015</td>
</tr>
<tr>
<td>P</td>
<td>CL</td>
<td>.612</td>
<td>0.446</td>
</tr>
<tr>
<td>IL-P</td>
<td>CL</td>
<td>.812</td>
<td>0.003</td>
</tr>
<tr>
<td>IL</td>
<td>CL</td>
<td>1.416</td>
<td>0.840</td>
</tr>
<tr>
<td>P</td>
<td>CL-P</td>
<td>.573</td>
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<tr>
<td>IL-P</td>
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<td>.781</td>
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</tr>
<tr>
<td>IL</td>
<td>CL</td>
<td>1.399</td>
<td>0.897</td>
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<td>IL-P</td>
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<td>IL-P</td>
<td>CL-P</td>
<td>1.497</td>
<td>0.160</td>
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Table III-12 Mean firing rate in association with force (400-600 gwt) and task

<table>
<thead>
<tr>
<th>Task</th>
<th>Force</th>
<th>Mean Firing Rate</th>
<th>Std. Error</th>
<th>95% confidence interval</th>
</tr>
</thead>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Lower bound</td>
</tr>
<tr>
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<td></td>
<td>600</td>
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<td>.484</td>
<td>13.2</td>
</tr>
<tr>
<td>CL-P</td>
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<td>.543</td>
<td>6.1</td>
</tr>
<tr>
<td></td>
<td>500</td>
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<td></td>
<td>600</td>
<td>12.6</td>
<td>.527</td>
<td>11.6</td>
</tr>
<tr>
<td>P</td>
<td>400</td>
<td>6.7</td>
<td>.485</td>
<td>5.8</td>
</tr>
<tr>
<td></td>
<td>500</td>
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<td>12.2</td>
<td>.483</td>
<td>11.2</td>
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<td>IL-P</td>
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<td>1.366</td>
<td>9.7</td>
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</table>

**Fig. III-12** Mean firing rate of all subjects in association with the gradation of force (400-600 gwt) and task (CL; contralateral, CL-P; contralateral protrusion, P; protrusion, IL-P; ipsilateral protrusion, IL; ipsilateral)

The result of this process of analyses is therefore different from the process described in topic 6.2 in terms of the tasks for which the SMUs of SHLP exhibit the highest firing rates. Given, however, the issues associated with the smaller size of the IL task data, it may still be concluded that the contralateral task is the preferred direction of the SHLP which is significantly greater in firing rate from contralateral protrusion, protrusion and ipsilateral protrusion, respectively (Fig. III-13). The firing rate during contralateral protrusion and protrusion were comparable to each other and
significantly higher than ipsilateral protrusion. Similarly it is difficult to state the relationship of the ipsilateral direction to the other directions even though there was no significant effect of firing rate with any of the other directions because of the limitation of the sample sizes.

![Graph showing firing rate vs tasks and force levels](image)

**Fig. III-13** Mean firing rate in association with ranges of tasks and force levels (400-600 gwt). (the same format as Figure III-10)
CHAPTER IV
DISCUSSION

Amongst the masticatory muscles, the SHLP is one of the jaw muscles (e.g., medial pterygoid muscle) that is poorly understood as a result of the difficulty in accessing and locating recording electrodes during electromyographic investigations. The medial pterygoid muscle is another poorly understood jaw muscle. Moreover, reliable techniques for verifying that the electrodes are correctly located within the muscle have not always been employed in previous studies. Although there is currently considerable information on the anatomy, histochemistry and physiology of the human lateral pterygoid muscle (e.g., Eriksson et al., 1981; Foucart et al., 1998; Aziz et al., 1998; Korfage et al., 2000; Fujita et al., 2001, Akita et al., 2000), the normal function of the superior part of it, the SHLP, is still very limited. Indeed, there are inconsistencies between studies particularly in terms of the role of this muscle in controlling force delivery to the condyle. For example, there is some conflict in the literature as to when the SHLP becomes active, thus some studies (Mahan et al., 1983; Gibbs et al., 1984; van Eijden et al., 1995; Hiraba et al., 2000) have proposed that the SHLP becomes active in a reciprocal manner to that of the IHLP that is, the SHLP is only active during jaw closing, retraction and ipsilateral jaw movements while others propose that it may be active concomitantly with the IHLP during jaw opening, protrusion or contralateral movement (e.g., Sessle and Gurza, 1982; Murray et al., 1999; Phanachet et al., 2003). A recent study, that has employed a well-designed standardized task and reliable verification technique, has provided preliminary data for a role of the SHLP in delivering low amplitude forces to the condyle and therefore in the control of low-force jaw movements (e.g., Phanachet et al., 2003; Murray et al., 2004). These data have indicated an important role for the
SHLP in the generation and control of low-force contralateral and protrusive jaw movements and a less important role in the control of jaw closing, retrusive and ipsilateral jaw movements.

The role of the masticatory muscles at high-force as during parafunction is limited. Parafunctional clenching and grinding are frequently carried out in individuals (Klineberg, 1994; Baba et al., 1996; Rodrigues and Ferreira, 2004). Although the muscles contributing to these activities are known in general terms, the role of individual jaw muscles is unclear and specifically it is unknown whether the SHLP plays any role in these activities. The SHLP might be well suited to applying high forces to the condyle as would be required for parafunctional grinding activities since the muscle fibres have a predominantly horizontal orientation.

Given the inconsistencies of the SHLP normal function, the uncertain role of the SHLP in delivering force to the condyle and the possible role of this muscle during parafunction, the general aim of the present study was to determine the normal function of the SHLP during isometric contraction as would possibly occur during parafunctional grinding and clenching. Recent findings point to an important role for the SHLP in the control of low-force contralateral and protrusive jaw movements. Therefore, the general hypothesis was that an important role of the SHLP is in controlling the force delivered to the condyle in a range of horizontal directions.

The aims of the study were

1. to determine the tasks for which the SHLP becomes active during isometric contraction whether there are preferential horizontal isometric tasks of the SHLP SMUs;
2. to determine whether different SMUs were selectively active for different horizontal isometric tasks of the SHLP as would be expected if the SHLP is functionally heterogeneous;

3. to determine whether the firing rates of the SHLP SMUs increase with the gradation of isometric force as would be expected if the SHLP is crucial for a fine control of horizontal isometric force.

The present study employed a rigorous, standardized methodology including a standardized extraoral approach for electrode placement into the SHLP (Orfansos et al., 1996), pre- and post-CT scans for craniometric measurement and electrode verification after SHLP electrode placement, respectively, as well as studying SHLP activity during standardized isometric tasks. This superior methodology has allowed the general aim of the study to be satisfied, that is, to determine the normal function of the SHLP during isometric contraction. The present findings suggest that the reciprocal function between the SHLP and IHLP is not true for the normal function of the SHLP. Further, the data obtained support the proposal of an important role of the SHLP in the fine control of isometric force to the condyle in different directions as could be expected to the force during parafunctional activities. We have also provided preliminary data supporting the notion of functional heterogeneity which implies regional activation within the SHLP, thereby increasing motor control by facilitating changes in the muscle’s force vector during loading of the mandible. Given the similarities in activity patterns between SHLP, as reported in the present and a previous study employing CT verification of electrode recording sites (Phanachet et al., 2003), and previous descriptions of the activity of the IHLP (Uchida et al., 2001, 2002), the data are consistent with the notion that SHLP and
IHLP should be regarded as a single muscle with activities shaded according to the biomechanical demands of the task (Hannam and McMillan, 1994).

1. STANDARDIZED TASKS AND SYNCHRONOUS RECORDINGS OF SHLP MOTOR UNIT ACTIVITY WITH HORIZONTAL ISOMETRIC FORCE

Standardization of the jaw task is crucial given that we have provided evidence that SMU firing properties depend on dynamic parameters. Previous studies in the limb motor system have clarified the normal function of limb muscles during standardized isometric contractions (Büdingen and Freund, 1976; De Luca et al., 1996; Herrmann and Flanders, 1998). For example, the magnitude and direction of force have been controlled in the assessment of the directional preference of SMUs in limb muscles. Similar approaches have been applied to the jaw closing muscles (Desmedt and Godaux, 1979; Stålberg et al., 1986; Hannam and McMillan, 1994; Miles, 1995) and to the IHLP (Uchida et al., 2001; 2002). Given the prior successful standardized methodology in the IHLP (Uchida et al., 2001; 2002), it has also been applied to this present study of the SHLP. The data in the present study have shown that SMU activity could be reliably discriminated from the SHLP during the standardized isometric tasks (see Fig. III-4). Further, the subjects could be trained to track a force target in different horizontal directions and at different force levels (see Fig. III-1), that is, the subject could track the force target accurately and steadily within the acceptable range of ±30 gwt of the exact force level. The maximum force level employed in this study was 800 gwt as higher force levels precluded reliable discrimination of SMUs and represented ~10-20% of the horizontal maximum voluntary contraction (35-40 N, S. Uchida, personal communication). It is technically very difficult to record from SMUs that are recruited above about 40% of
the maximal contractile force in human limb or jaw muscles (Miles, 1995). Therefore, this method is well suited for the characterization of the activity of SHLP SMUs during horizontal isometric contraction.

2. TASK RELATIONS OF SHLP MOTOR UNITS DURING ISOMETRIC CONTRACTIONS

There is controversial data as to the jaw tasks for which the SHLP becomes active and delivers force to the mandibular condyle of the TMJ. In light of the current view that the SHLP inserts predominantly or exclusively into the condyle (e.g., Christo, Wilkinson, Townsend, in press, 2004; Möller, 1966; Mahan et al., 1983), it is hypothesized that a major function of the SHLP is in the generation and fine control of forces to the TMJ as required during the generation of contralaterally directed and protrusively directed jaw forces. This proposal is consistent with the recent findings of activity in SHLP during contralateral and protrusive isotonic contractions (Phanachet et al., 2003) and which pointed to a role for the SHLP in controlling horizontal jaw movements. As yet, it is unclear whether the SHLP also plays a role in controlling the force to the condyle during isometric contraction.

There is evidence for the involvement of the IHLP in the development of isometric horizontal force vectors towards the end of the intercuspal phase of chewing (Wood et al., 1986) as well as evidence that the lateral pterygoid muscle is active during voluntary tooth grinding or gnashing (Widmalm et al., 1987). A recent EMG study of the IHLP during isometric contraction (Uchida et al., 2001; Uchida et al., 2002) has provided evidence, consistent with previous studies (Miller, 1991; Hannam and McMillan, 1994), that the IHLP plays a major role in the generation and fine control
of horizontal forces, especially in the contralateral direction and as required in masticatory and parafunctional activities.

However, these data are not consistent with the conventional view that the SHLP functions in a reciprocal manner to that of the IHLP (Juniper, 1981, 1984; Gibbs et al., 1984; Hiraba et al., 1995, 2000). This view proposes that the SHLP is active only during ipsilateral jaw movements (van Eijden et al., 1995), jaw closing and jaw retrusion (Mahan et al., 1983; Gibbs et al., 1984; Hiraba et al., 2000), while the IHLP is active in jaw opening, protrusion and/or contralateral jaw movements. However, our present findings are consistent with some studies which propose that the SHLP may also be active concomitantly with the IHLP during opening, protrusion or contralateral jaw movements (Sessle and Gurza, 1982; Murray et al., 1999; Phanachet et al., 2003). Recent SMU studies of the SHLP during different jaw movements without tooth contact and therefore at a low level of force application have demonstrated activity at CT-verified sites within SHLP during combinations of contralateral, protrusive, ipsilateral, opening and/or closing jaw movements. Our present SMU study of SHLP activities at higher force levels (namely about 20% of the maximum horizontal force able to be exerted in the contralateral or protrusive directions) has therefore supported the capability of SHLP SMUs to be active for these directions of isometric tasks as demonstrated at the lower force level (Phanachet et al., 2003). There is abundant data pointing to IHLP activity during isometric and isotonic horizontal tasks in the contralateral and protrusive directions and in jaw opening (Phanachet et al., 2001, 2002; Uchida et al., 2001, 2002). The similarities in the task relations of SMU and multi-unit activity in the SHLP and IHLP supports the hypothesis supported above that both SHLP and IHLP should be
regarded as parts of one muscle with the distribution of activity shaded according to the biomechanical demands of the task (Hannam and McMillan, 1994).

2.1 Horizontal Isometric Contraction

In the present study, the SHLP in most subjects was found to be active during contralateral and protrusive isometric tasks and this indicates that the SHLP is well suited to deliver horizontal contralateral and protrusive forces to the condyle with the contralateral direction being the preferential task direction for the SHLP and similar findings have been made for the IHLP (Uchida et al., 2001, 2002). Moreover, the activity of the SHLP during protrusive function was also comparable to that observed during contralateral function and this conclusion derives from the quantitative analysis of the firing rate between these two tasks from 400-800 gwt which points toward the role of the SHLP in controlling the force in contralateral and protrusive directions (see Table III-7). The results of the present thesis and previous data (Phanachet et al., 2003) suggest that the SHLP and IHLP have similar functions. Previous data (Uchida et al., 2002) indicated that IHLP SMUs exhibited the greatest firing rate at CL and lower firing rates at P. However, SMUs in SHLP exhibited similar firing rates at CL and P (see Fig. III-11). This evidence may be well explained by the muscle fibre orientation of the SHLP. The SHLP is composed of groupings of muscle fibres with specific orientations which points towards the direction feasible for those specific muscle fibres to generate maximal force in the protrusive and contralateral direction. As the muscle fibres of the SHLP are oriented in a more acute angle (26°) to the midsagittal plane than the IHLP (45°) (Hónee, 1972), it is likely that the SHLP could be also suited in controlling the force in protrusive direction. The SHLP has additionally demonstrated activity during ipsilateral isometric force generation and clenching.
Further, the task-related activity of the SHLP showed that units located in different parts of the SHLP were active during different combinations of tasks. For example, the units in the lower part of the SHLP were active for contralateral, contralateral-protrusion, protrusion, ipsilateral-protrusion and ipsilateral, whereas, the units located in the upper part were active for other tasks except ipsilateral-isometric force. Moreover, there was evidence that the lateral-most and inferior-most part of the SHLP have no units active for any tasks despite the presence of units active for isotonic tasks. These data are not in accord with the previous reports that the SHLP was active only during ipsilateral movement, retrusion and jaw opening (e.g., Kamiyama 1961; Gross and Lipke, 1979) but are in accord with some previous studies (Sessle and Gurza, 1982; Murray et al., 1999) reporting that the tasks for which the SHLP demonstrates activity depend on the recording site in the SHLP. Therefore, whether it can be concluded that the SHLP and IHLP have reciprocal function or concomitant function is subject to the EMG recording site.

2.2 Isometric Clenching

There is also evidence that the SHLP SMUs were active in isometric clenching (100% MVC) in five of nine subjects. This presence of SHLP activity during isometric clenching is consistent with the conventional view that one of the functions of the SHLP is to stabilize the head of the condyle and disc against the articular eminence (Widmalm et al., 1987; Osborn, 1995) and to prevent the condyle from being displaced posteriorly and thereby exerting pressure on sensitive postcondylar structures. This supports the previous remark that *a muscle that is strongly engaged in this manner in taking place in a direction opposite to that for which it is mechanically qualified must serve either to stabilize the movement or to guide the articulate components* (Carlsöö, 1956). Therefore, we suggest the SHLP is primarily
a stabilizer (Widmalm et al., 1987) not primarily a closer of the mouth (Juniper, 1981, 1983).

Even though one study has demonstrated that the mid-medial bundle of temporalis inserts directly and laterally into the disc adjacent to the SHLP (Akita et al., 2000), we believe that the presence of activity during clenching in this study reflected a direct recording from the SHLP given that there was no clenching or ipsilateral activity in the lateral-most recording sites within SHLP (see Table 1). Presumably, there would be marked activity in the mid-medial bundle of the temporalis during clenching or ipsilateral activity. In addition, all of the recording sites that exhibited clenching activity were in the anterior-middle part of the SHLP which were well clear of interlacing with the deep temporalis muscle fibres adjacent to the disc. At the insertion of the SHLP, the muscle becomes flattened in the superior-inferior dimension and is surrounded by large vessels of the pterygoid venous plexus (Widmalm et al., 1987). Therefore, the electrode insertion in this present study was directed to avoid the insertion site of this muscle.

3. ROLE OF THE SHLP IN FINE CONTROL OF FORCE TO THE CONDYLE

The lateral pterygoid muscle has been suggested to be more suited for shortening over long distances and providing support for near-isotonic rather than near-isometric contractions requiring power (Hannam and McMillan, 1994) and this is by virtue of the limited pennation and relatively long fibres and small physiological cross-sectional area of the muscle (Van Eijden et al., 1995). However, previous data have suggested an important role for the IHLP in generation of horizontal isometric forces (Wood et al., 1986; Widmalm et al., 1987; Uchida et al., 2001, 2002) and the
role of the IHLP in generation of horizontal jaw movement (Phanachet et al., 2001). Our findings additionally support a role for the SHLP in the generation and fine control of horizontal isometric forces. For example, the SHLP is capable of applying forces to the condyle and thereby presumably stabilizing the condyle during ipsilateral isometric force generation and clenching, there were different SMUs activated for different isometric tasks and there were bursts of SMU activities during dynamic phases where force levels rapidly changed, and there was evidence for increases in activity levels at higher horizontal isometric forces. These horizontal forces may well be required in the power phases of chewing when the teeth are in contact or in parafunctional grinding. The present data of the SHLP suggest that the relevant motor centres are capable of activating the SHLP in a finely controlled manner.

This possible role of the SHLP in the generation and fine control of horizontal isometric forces to the condyle is consistent with the structural organization within the muscle. The SHLP (Korfage and van Eijden, 2000) is composed of a substantial proportion of MHC-I fibres (33%) that are suited to prolonged low-force contraction and fatigue resistance. Further, the SHLP contains more MHC-IIA fibres (23%) than in the IHLP (15%). The MHC-IIA fibres are well suited for higher force contraction. However, there was no significant difference in the distributions of muscle fibre types within the SHLP (Korfage et al., 2000; Korfage and van Eijden, 2000).

3.1 SHLP in Stabilizing the Condyle during Ipsilateral Isometric Forces and Clenching

In 5 subjects, SHLP EMG activity was present during maximum voluntary clenching. The presence of SHLP activity during clenching is consistent with the conventional
view that one of the functions of the SHLP is to stabilize the head of the condyle and disc against the articular eminence during intercuspal clenching (Widmalm et al., 1987; Osborn, 1995).

Moreover, there was also evidence that the SHLP was active during ipsilateral contraction. The lower fibres of the SHLP, which are long fibres, are not only active during contralateral and protrusive isometric tasks but are also active for ipsilateral tasks. However, the ipsilateral SHLP is not the principal muscle that generates a movement of the jaw to the ipsilateral side. Instead, the contralateral SHLP and IHLP are important for this movement. This is because the muscle fibre alignment of the SHLP on the side ipsilateral to a lateral jaw movement is not suited for ipsilateral function when the path of contraction from insertion to origin of the SHLP is considered (see Fig IV-1). The contralateral SHLP and IHLP are the principal muscles that move the jaw to the opposite side while the ipsilateral SHLP appears to function to stabilise and prevent the ipsilateral condyle from compressing excessively the posterior attachment. Therefore, the activity of the SHLP that was observed during ipsilateral tasks in this study might reflect the need for a contralaterally directed force vector derived from activity in the ipsilateral SHLP. This vector derived from ipsilateral (e.g., right side) SHLP activity during a contralateral (e.g., leftward) jaw movement might assist in preventing movement of the condyle further to the ipsilateral side because of the activity within the contralateral SHLP and IHLP. Activity in the ipsilateral SHLP may therefore provide an additional stabilizing function on the ipsilateral condyle. Another stabilizing function provided by activity in the ipsilateral SHLP might be to minimize force on and thereby protect the posterior attachment tissues which are highly innervated by nerves and blood vessels.
Fig IV-1 Diagram illustrating movement towards contralateral direction. The contralateral SHLP is the principle muscle that moves the jaw to the opposite (i.e., ipsilateral) side while the ipsilateral SHLP stabilizes and prevents the condyle to compress the posterior attachment tissues behind the temporomandibular joint.

The EMG activity of the SHLP during isometric clenching or maximum voluntary contraction of this present study was obtained from the rectified and smoothed EMG activity of the masseter muscle during maximum clench and this method has been employed given the evidence for a linear relationship between the EMG activity of the elevator muscles and bite force (e.g., Lippold, 1952; Hiraba et al., 2000; Ferrario et al., 2004). However, recently, new methods of force recording using an intraoral force transducer (e.g., Clark and Carter, 1985; Junge and Clark, 1993; Mäntyvaara et al., 1999; Proeschel and Mornenburg, 2002) or a novel sensor of bite force determination (e.g., Fernandes et al., 2003; Nickel et al., 2003) have been introduced to measure the force directly. Further study should either implement these new methods with either a study of isometric clenching or horizontal isometric force.
3.2 SHLP in Controlling Horizontal Force

Previous data (Uchida et al., 2001, 2002) have pointed towards the IHLP as an important generator of horizontal forces to the mandible in the isometric tasks used in the present study. The other jaw muscles, however were implicated in assisting to stabilize the jaw, for example, in the coactivation of the jaw opening and closing muscles to help prevent the jaw from slipping up or down on the force transducer (Uchida et al., 2001, 2002). The SHLP also appears to play a crucial role in the generation of horizontal forces to the condyle given the evidence provided in this present study together with the anatomical evidence that the SHLP inserts directly to the condyle. Therefore, the data from the previous studies (Uchida et al., 2001, 2002) together with the findings of the present study indicate that both the SHLP and IHLP are ideally suited to provide a range of force vectors to the condyle particularly in the horizontal plane.

3.3 Firing Rate and Increase of Force

The close relation between EMG activity and force was previously described in limb muscles (Lippold et al., 1952; De Luca et al., 1982) and jaw closing muscles (Garrett et al., 1964; Manns et al., 1979). In the present study, EMG recordings from tomographically verified sites within the SHLP demonstrated graded changes in SMU activity with an increase of force and with progressive changes of horizontal force direction. As the magnitude of force increased, there was an increase in frequency of firing of SMUs and an increase in the numbers of SMUs that were active. A qualitative evaluation and quantitative analysis of the data showed that the EMG activity of the SHLP increased as the isometric force increased from 400 to 800 gwt. These data support the hypothesis that the SHLP plays an important role in the generation and fine control of horizontal isometric forces. This close relation
between SHLP EMG activity and the active tension developed during voluntary isometric contraction suggests that the SHLP is a prime mover for the generation and fine control of horizontal isometric forces as required in mastication and parafunctional activities just as has been proposed for the IHLP (Uchida et al., 2001).

Human jaw muscles seem to rely more on rate coding than on recruitment of SMUs to increase contraction (Clark et al., 1978) but in limb muscles which are more powerful, motor units were recruited over the entire range of the contraction (De Luca, 1985). In this study, the force ranges allowed SMU discrimination over ~10-20% of the horizontal maximum voluntary contraction (horizontal MVC: 35-40 N, S. Uchida, personal communication). We were able to identify clearly the presence of SMUs that exhibited increased firing rates as force increased from a lower step level to higher force levels (low and high threshold units) and also SMUs that were recruited during the dynamic phases when the force levels rapidly increased at the higher force levels (i.e., at 700 and 800 gwt, higher threshold units). Therefore, the SHLP relies on both rate coding and recruitment to increase voluntary contraction (see Fig. III-4). In addition, there were differences in the firing rate among different subjects which provide the evidence for variation in motoneuron properties (e.g., the time course after hyperpolarization) or as a result of training or due to genetic factors (De Luca et al., 1982). However, these contentions await further investigation by more direct methods and cannot be discussed meaningfully here.

A presence of bursts of EMG activity during the dynamic phase when the force was abruptly increased from one level to another level also suggests that the SHLP is concerned with the generation of these dynamic phases. To facilitate SMU discrimination in this study, large horizontal forces were avoided, however, it is
interesting to observe motor unit activities in association with an increase of horizontal forces as similar horizontal forces could occur during parafunctional grinding. Our data support the proposal that both SHLP and IHLP participate in the generation of horizontal forces as required during mastication and parafunctional activities.

3.4 Firing Rate and Different Directions

There is evidence for a selective activation of specific SMUs for a specific direction. (see Fig. III-5). The SMUs of the SHLP not only altered their activity in association with increasing force in one direction but also altered their activity with different directions of horizontal isometric force. The firing rates of SMUs within SHLP altered with changes in the direction of horizontal isometric forces. Despite the small sample size, it is suggested from a quantitative analysis that the contralateral task is the preferred direction for the SHLP due to the significantly greater firing rate of SMUs in the contralateral direction in comparison with the other directions. A similar conclusion was also previously stated for the IHLP (Uchida et al., 2002) that the contralateral direction of horizontal isometric force is the single preferred direction of SMU firing for the IHLP. However, in this present study the firing rates at contralateral-protrusion and protrusion were comparable to contralateral and significantly higher than the firing rate at ipsilateral-protrusion. Therefore, it is suggested that protrusion is also a preferred direction of the SHLP. This could relate to the muscle fibre orientation of the SHLP being more closely aligned to the sagittal plane than the IHLP (namely 26° for SHLP compared with 45° for IHLP, Hónee, 1972). The force vectors generated by SHLP activation could, therefore, be more closely aligned with the protractive direction than from the IHLP. Nevertheless, the statistical analysis of the relationship of the ipsilateral direction with other directions
was unclear even though there was no significant effect of firing rate with other directions. It is difficult to imply that ipsilateral direction has a comparable activity to other directions as a result of the raw EMG activity obtained from the SHLP during ipsilateral isometric contraction was relatively small compared to other directions. Further studies with larger sample of trials are needed to determine whether a larger proportion of SMUs would result in a significant difference in firing rate of the ipsilateral direction with other directions.

A single preferred direction of SMU firing has been previously identified in limb muscles (Theeuwen et al., 1994; Herrmann and Flanders, 1998). Although there was evidence in the present study that some motor units showed a broad direction of firing, most units exhibited significantly greater firing rates in the contralateral direction and these same SMUs displayed different firing rates for different directions.

4. EVIDENCE FOR FUNCTIONAL HETEROGENEITY IN THE SHLP

The data from this present study are evidence that the SHLP is active during the generation of horizontal isometric forces in a range of directions. While most of the SMUs (≥64%) were active in the contralateral, contralateral-protrusive, and protrusive directions, eight SMUs were active in a range of directions including ipsilateral. Selective activation of some motor units for specific horizontal task directions within specific regions of the SHLP provides preliminary data consistent with previous findings (Phanachet et al., 2003) supporting functional heterogeneity within the SHLP.
Korfage et al. (2000) and Korfage and van Eijden (2000) reported that there was no significant difference in the distributions of muscle fibre types within the SHLP. This could possibly argue against the presence of functional heterogeneity within the SHLP. There are however, three lines of evidence established in the limb musculoskeletal system and support the notion of functional heterogeneity within a muscle. They are, first, the presence of a broad attachment (i.e., origin and insertion) within a muscle, second, the complexity of internal muscle architecture, and third the muscle fibre type and muscle sensory receptor distribution (Windhorst et al., 1989). The territory of a SMU (i.e., the region of muscle containing that motor unit's muscle fibres) is generally restricted to a portion of the whole muscle (Burke, 1981). These neuromuscular compartments, which are the regions of muscle innervated by the branches of the efferent muscle nerve that enters the muscle, may differ in their composition of muscle fibres and in their fibre architecture (Windhorst et al., 1989).

Similarly, the SHLP fulfills some of the criteria established within the limb musculoskeletal system for functional heterogeneity and summarized above. There are possible explanations for the central nervous system to selectively activate specific units of the SHLP for specific performance during horizontal isometric contraction or isometric clenching. First, the muscle fibre orientation of the SHLP of the SHLP is 26° to the sagittal plane and 23° downward to the Frankfort Horizontal Plane (Honné, 1972). Therefore, SHLP muscle fibres alter their alignment from a broad origin at the roof of the infratemporal fossa and lateral pterygoid plate and converge towards a small insertion site on the condylar fovea and disc-capsule complex (Mahan et al., 1983; Widmalm et al., 1987; Bittar et al., 1994; Heylings et al., 1995, Naidoo, 1996). This arrangement of muscle fibres changing superoinferiorly and lateromedially provides a capability of the muscle to generate
different force vector during selective activation (Troiano, 1967). Therefore, direction of force vectors varies according to which part of the muscle is activated. The non-parallel muscle fibre bundles that have been described within the SHLP (Troiano, 1967) and the complex neural distribution dividing the muscle into horizontal layers (Foucart et al., 1998) provide additional evidence to suggest the selective motor units control within the muscle and support of the second criterion above for functional heterogeneity. As yet there is little evidence for the third criterion above since the muscle sensory receptor of the SHLP (i.e., muscle spindles) is devoid in non-human studies (Kubota et al., 1979; Lennartsson, 1980; Rokx and van Willigen, 1988) and in human studies (Smith and Marcarian, 1967). However, Kubota and Masegi (1977) could identify four muscle spindles in SHLP and two in the IHLIP but the distribution of the muscle spindles within the SHLP has not yet identified.

We also have evidence suggesting the existence of functional heterogeneity within SHLP, that is, that there is the possibility of selective activation of specific regions within the SHLP for specific functional demands (Hannam and McMillan, 1994; Foucart et al., 1998; Phanachet et al., 2003). It was found from the present study that the muscle fibres of the lower region of the SHLP, which are long fibres, were active for contralateral, contralateral-protrusion, protrusion, ipsilateral-protrusion and ipsilateral isometric forces whereas the muscle fibres in the upper part of the SHLP (shorter fibres) were less likely to be active for ipsilateral forces.

In addition to the above lines of evidence for functional heterogeneity within SHLP, as has been shown recently for low-amplitude forces to the condyle (Phanachet et al., 2003), the distribution of activity patterns with the SHLP provide additional evidence
consistent with functional heterogeneity. While most fibres of the SHLP appear important for the generation of contralateral and protrusive forces, it is possible that the direction of force applied to the ipsilateral condyle needs to be more horizontally directed as applied through activation of the lower, more horizontally directed fibres of the SHLP than the upper fibres of the SHLP that are more vertically directed. It is possible that these lower fibres may play a more important role in stabilizing the condyle on the ipsilateral side. The inferior-most and lateral-most fibres of the SHLP may be inactive for isometric force at the level used in the present study although there were units active for isotonic horizontal movements. It is possible that the above three groups of activity patterns may be associated with specific fibre bundle orientations and/or lengths (e.g., see Troiano 1967) that may be biomechanically best suited to specific horizontal isometric forces. Therefore, the data support the hypothesis that SHLP fibres with specific orientations could be selectively activated and specific force vectors could be applied to the condyle to produce the desired horizontal movement (Murray et al., 2001).

5. ABSENCE OF ACTIVITY AT POSTURAL JAW POSITION

Our data supports previous studies (e.g., Mahan et al., 1983; Murray et al., 2001; Phanachet et al., 2003) indicating a lack of SHLP activity at postural jaw position in non-TMD subjects. This suggests that there is no anteriorly directed force in the condyle and disc from active muscle contraction of the SHLP that would maintain the condyle in close apposition with the disc and articular eminence at the resting postural position (Phanachet et al., 2003).

However, other studies and reviews of the lateral pterygoid muscle have reported a mild stage of contraction of the SHLP and IHLP with the jaw at the rest position and
such mild contraction could possibly influence the articular disc and/or condyle so as to maintain the condyle and disc-capsule complex in an anterior-medial position (Okeson, 2003; Hiraba et al., 2000; Møller, 2001). Nevertheless, none of these authors report on the use of a method to verify electrode placement within the SHLP and therefore there is the very real possibility of misplacement within other muscles, such as the anterior temporalis (e.g., Orfanos et al., 1996). In addition, since these earlier studies were all multi-unit EMG studies, at low levels of EMG activity it can be difficult to draw a conclusion as to whether there was activity clearly recorded from the SHLP and not from the noise background. Moreover, there has been a report of the presence of tonic EMG activity in the SHLP in symptomatic subjects (Mahan et al., 1983) but Lafreniere et al. (1997) found hyperactivity only in the IHLP at postural jaw position. Therefore, the relationship between hyperactivity of the lateral pterygoid muscle and TMDs is unclear and is another aspect of investigation.

There was a report of an effect of changes in vertical dimension on jaw closing muscle activity for example, the masseter EMG activity was high when there was 7 mm jaw opening during the constantly maintained bite force in comparison with biting at intercuspal position (Manns et al., 1979). This effect of an increase in vertical dimension may be playing a role in influencing SHLP EMG activity. However, there are 3 lines of evidence that argue against any systemic influence from changes in vertical dimension in this study. First, we did not recruit any subjects who had deep overbite in order to minimize variations in the amount of change in vertical dimension among subjects. Second, the bite-blocks used in this study did open the jaw from the intercuspal position about 3-8 mm however, there was no activity in the SHLP while the jaw was resting and with bite-blocks in place.
and prior to each task. Therefore, at least for postural position with the bite-blocks in place, the thickness of the bite-blocks did not contribute to the presence to the firing of the SHLP SMUs activity at postural jaw position. Third, there was no association between the amount of opening by bite-blocks and the different patterns of activity observed in this study. The average amount of mouth opening (in terms of vertical dimension) in every subject when they wore the bite-blocks compared with postural jaw position when they did not have bite-blocks was 5.7 mm (range 3-8 mm). The subject that showed only activity during protrusion (see table III-1) was one of the subjects where the amount of opening was 5 mm and this is very close to the average of 5.7 mm and yet this subject exhibited an unusual pattern of activity. Therefore for these 3 reasons it is not convincing that there was a systemic effect on the distribution of task-related activity in this study from any difference in vertical dimension among subjects. Note that the subjects were were requested not to apply force vertically during horizontal force tracking. Therefore, we believe that the EMG activities recorded from the SHLP during the horizontal force tasks only resulted from the generation of horizontal forces.

6. **SHLP IS MORE SUITED TO MOVEMENT RATHER THAN PRODUCE FORCE**

There was no task-related activity in two subjects of this study, although a few SMUs were active at >800 gwt and EMG activity was clearly present during isotonic movements. A possible explanation for this observation is that the recordings in these two subjects were made from an area of the muscle that may not contain SMUs that become active for isometric tasks but may be better suited for isotonic tasks. However, even if the rest of the subjects had SMUs that were active for isometric contraction, the EMG activities for isotonic contraction appeared to be qualitatively
greater. This was determined by observing the EMG activity of the SHLP when the subjects moved the jaw into range of directions (isotonic) and comparing this with the SHLP EMG activity when the subjects exerted the isometric force tasks in the present study. It is possible therefore that the SHLP might be more appropriate for shortening over long distances, that is, so called near isotonic rather than near isometric contraction and this has been previously proposed for SHLP and IHLP (Hannam and McMillan, 1994). The internal architecture of the lateral pterygoid is comprised of relatively long fibres [~22 mm (Schumacher, 1961)]. These fibres are not arranged in a multipennate structure as is found in other powerful muscles, for example, masseter and medial pterygoid but rather the muscle fibres within the lateral pterygoid muscle are arranged in the same line of action as the bulk of muscle.

7. POSSIBLE ROLE OF THE SHLP IN PARAFUNCTIONAL JAW ACTIVITIES

The data obtained from this present study of the SHLP as well as previous studies of the IHLP during isometric contractions (Uchida et al., 2001, 2002) have pointed towards an important role of these two heads in delivering force to the condyle especially in the contralateral horizontal direction. This direction is likely to be similar to the direction of jaw movement during lateral parafunctional grinding and also is likely to be similar to the direction of the lateral masticatory force generated near the end of intercuspal clenching.

Isometric contractions could occur in masticatory muscles during the parafunctional jaw activities of tooth grinding and clenching. Although the generation of isometric force in the masticatory system is the result of activity in more than one muscle, the predominantly horizontal arrangement of fibres that characterizes the lateral
pterygoid muscle has been proposed to play a major role in the generation and fine control of the horizontal forces generated in mastication or parafuncional grinding (Miller 1991; Hannam and McMillan 1994; Uchida et al., 2001, 2002; Murray et al., 2004).

Although the SHLP may not have a fibre composition that is highly appropriate to play a significant role in mastication (especially during heavy force) and parafunction, excessive demands on the SMUs activities to produce ranges of horizontal force may produce localized muscle tenderness in TMD patients (Frank, 1965; Ai and Yamashita, 1992). This tenderness could apparently be explained by the central and peripheral mechanisms of sensitization (Stohler, 1999; Sessle, 2000) for example, in peripheral sensitization, chemical mediators (e.g., bradykinin, histamine) released by damaged tissue are thought to sensitize nociceptive primary afferents and make them respond to non-noxious stimuli namely alodynia. Therefore, muscles may be painful at rest and during normal functional movements.

8. FUTURE STUDIES

We did not observe any systematic influence on SHLP EMG activity with changes in vertical dimension between subjects. For example, the only subject who had activity only during protrusion had an opening of 5.0 mm, close to the mean value of 5.7 mm. For this reason, it remains to be determined whether periodontal activation during masticatory movements leads to different patterns of SHLP EMG activity than those observed in the present study.

The present study provides the first detailed description of the functional properties of the SHLP during isometric contraction in non-TMD subjects. The standardized
methodology employed in this study is suitable for defining the firing properties of the SMUs of the SHLP in relation to isometric force tasks, and should be directly applicable to studying the functional properties of SMUs of these two heads in TMD patients. The present data may serve as a baseline for future comparative studies of the possible involvement of the SHLP and IHLP in patients with TMD.

Given the limitation in evaluating the size of the SMUs recorded from the SHLP, another electrode with Teflon®-coating and having a single-fibre recording port (Single Fiber Macro Electrode - SFME) could be additionally used together with bipolar fine-wire electrodes as a technique for Macro-EMG study in order to detect the size of the motor-unit potentials so that any recruitment reversal of SMUs could be well discriminated and could be interpreted to mean that these SMUs were located in separate neuromuscular compartments within which SMUs would be recruited according to the size principle of Henneman and Mendell (1981). Macro EMG is a method for analysing motor units quantitatively. It differs from other EMG systems by reflecting all the electrical activity of motor units. It is normally used for determining pathology quantitatively and in evaluating and following up diseases affecting motor units.

The data of the present study also suggested the possibility of functional heterogeneity within SHLP. Future studies could be directed towards the study of the functional properties of these different potential compartments within the muscle and could incorporate innovative magnetic resonance imaging techniques and three dimensional reconstruction to define the local internal architecture in the vicinity of the recording electrodes.
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Functional Activity of Superior Head of Human Lateral Pterygoid Muscle during Isometric Force

INTRODUCTION
Isometric contractions can occur in masticatory muscles during parafunctional jaw activities such as tooth-grinding and clenching. Although the generation of isometric force in the masticatory system is the result of activity in more than one muscle, the predominantly horizontal arrangement of fibers in the lateral pterygoid muscle indicates a major role for the lateral pterygoid in the generation and fine control of the horizontal forces generated in mastication or parafunctional grinding (Miller, 1991; Hannam and McMillan, 1994; Uchida et al., 2001, 2002; Murray et al., 2004). Jaw-closing-muscle isometric contractions have been studied extensively (Clark et al., 1988; van Eijden et al., 1990, 1993; Junge and Clark, 1993; Nickel et al., 2003). There is, however, little information about isometric contraction in the lateral pterygoid muscle, although there is evidence for the involvement of this muscle in the development of isometric horizontal force vectors toward the end of the intercuspal phase of chewing (Wood et al., 1986), as well as evidence that the muscle is active during voluntary tooth-grinding or gnashing (Widmalm et al., 1987).

A recent EMG study of the inferior head of the human lateral pterygoid (IHLP) during isometric contraction (Uchida et al., 2001, 2002) has provided data, consistent with data from previous studies (for review, see Miller, 1991; Hannam and McMillan, 1994), that the IHLP plays a major role in the generation and fine control of horizontal forces, especially in the contralateral direction, and as required in masticatory and parafunctional activities. There are controversial data, however, as to the jaw tasks for which the superior head of the human lateral pterygoid muscle (SHLP) becomes active and delivers force to the condyle and disc/capsule complex of the temporomandibular joint (TMJ) for review, see Murray et al., 2001, 2004). For example, most studies have concluded that the SHLP demonstrates reciprocal activity with the IHLP, and is active on closing, retraction, and ipsilateral jaw movements. In light of the current view that the SHLP inserts predominantly or exclusively into the condyle (e.g., Moller, 1966; Mahan et al., 1983; Christo, Wilkinson, Townsend, personal communication, 2004), it is hypothesized that a major function of the SHLP is in the generation and fine control of forces to the TMJ as required during the generation of contralaterally directed and protractively directed jaw forces, and to play a much less important role in intercuspal clenching and ipsilaterally directed jaw forces. This proposal is consistent with the recent findings of activity in SHLP during contralateral and protractive isotonic contractions with the teeth apart (Phanachet et al., 2003), which pointed to a role for the SHLP in controlling horizontal jaw movements.

Given the limited information available on the function of the SHLP, the aim of the present study was to describe the functional activity of SMUs recorded from the SHLP during isometric force tasks. Analysis of the data presented helps clarify the normal function of the SHLP. The new information is important in view of the controversial role of the SHLP in

ABSTRACT
There is controversy as to the jaw tasks for which the superior head of the human lateral pterygoid muscle (SHLP) becomes active. The aim was to describe the functional activities of SHLP single motor units (SMUs) during horizontal isometric force tasks. In 11 subjects, 48 SMUs were recorded from computer-tomography-verified SHLP sites during generation of horizontal isometric force in the contralateral (CL), protractive (P), and ipsilateral (IL) directions and intermediate directions (CL-P, IL-P). In eight subjects, SHLP SMUs were active in CL, CL-P, and P. Qualitatively, SHLP EMG activity increased with increased isometric force. Forty-two SMUs were active in directions other than IL; 6 exhibited activity at IL and other directions. The similarity of these data to previous human lateral pterygoid (IHL) data supports the notion that SHLP and IHL should be regarded as a single muscle, with activities shaded according to the biomechanical demands of the task.

KEY WORDS: isometric force, computer tomography, single motor unit, lateral pterygoid muscle, electromyogram.

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normal function and the frequent claim, although unsubstantiated, of a functional disturbance in the lateral pterygoid muscle in patients with temporomandibular disorders.

**MATERIALS & METHODS**

Eleven human volunteers (ages, 22-28 yrs; mean, 24.4 ± 2.6 yrs; eight males, three females), without history of chronic pain or neuromuscular condition, participated. All subjects gave informed consent, and experimental procedures were approved by the Western Sydney Area Health Service and University of Sydney Human Ethics Committees. Most procedures have been previously described (Orfanos et al., 1996; Murray et al., 1999a,b; Uchida et al., 2001, 2002).

**EMG Recording**

Computer tomography (CT) provided craniometric measurements for fine-wire electrode placement via a sterilized spinal needle directed below the zygomatic arch and retracted to leave the wires within the muscle. A CT scan at the end of the recording session verified electrode location within SHLP. Data were acquired at a sampling rate of 10,000 or 20,000 samples/sec and a bandwidth of 100 Hz-10 kHz. SMUs were discriminated with Spike2® software (Cambridge Electronic Design, Cambridge, England). Bipolar surface electrodes were placed over the anterior middle part of the right masseter muscle.

**Tasks**

An isometric horizontal task involved the subject exerting isometric horizontal force via a force rod secured to the lower teeth and onto a force transducer projecting from the upper teeth (Fig 1A). The apparatus could be swiveled horizontally in 5 directions—contralateral (CL), ipsilateral (IL), protrusive (P), CL-P, and IL-P directions—in relation to the SHLP electrode. Each subject monitored a video screen to perform a task that consisted of 5 five-second force steps, that increased by 100 gwt (0.98 N) at each force step. These force ranges allowed for SMU discrimination and represented ~10-20% of the horizontal maximum voluntary contraction (35-40 N; S. Uchida, personal communication). Equivalent values in SI units of each force step are: 100 gwt (0.98 N), 400 gwt (3.92 N), 500 gwt (4.9 N), 600 gwt (5.88 N), 700 gwt (6.86 N), and 800 gwt (7.84 N).

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Figure 1. Task apparatus, CT verification, and recording site location. (A) (Upper) Force transducer. The force bar and rod could be swiveled horizontally. (Lower) The custom-made upper acrylic bite block. Five isometric force directions were used: P, protrusive; CL, contralateral; IL, ipsilateral; CL-P, contralateral protrusive; and IL-P, ipsilateral protrusive. Ipsilateral refers to the side of the SHLP recording electrode. The average opening with the bite-blocks compared with postural jaw position was 5.7 mm (range, 3-8 mm). (B) Example of CT-verified electrode placement within the SHLP. (Upper) Horizontal slice (1 mm thick) and (lower) reformed oblique sagittal image through the long axis of the SHLP, showing electrode tip within the SHLP. (C) Two-dimensional mapping of electrode location in the SHLP in all subjects. Lower Fig. was taken along the long axis of the lateral pterygoid. Horizontal axis represents the long axis of the SHLP; the vertical axis represents the supero-inferior dimension of the SHLP. Task relations: CL, CL-P, P, and IL-P; with or without IL; +, SMUs were active during CL, CL-P, P, and IL-P, with or without IL; - , no activity. (D) Same data as in C, but plotted in the horizontal plane.
We are confident that the force vector generated was parallel with the intended force direction and perpendicular to the face of the force transducer at each direction, because the force rod (that projected from the acrylic block attached to the lower jaw) came into contact with a small hemispheric button (radius, 1 mm) that projected from the flat face of the transducer (9-mm diam.). If the force was not exerted perpendicular to the transducer’s face, the force rod would slip off the hemispheric button on the transducer. The force signal was sampled at 1000 samples/sec and at a bandwidth of 0-500 Hz. Each task was repeated 5-10 times, was undertaken in random order, and was separated by ≥ one-minute rest periods. In separate trials, nine subjects also clenched at 100% maximum voluntary jaw-closing contraction for 5 sec.

Data Analysis
Electrode tip location within SHLP was related to muscle boundaries on horizontal, reformatted frontal, and oblique-sagittal CT images. The supra-inferior dimension of the SHLP was defined as 5 mm (Mayenber et al., 1986; Widnalm et al., 1987). Electrode location was normalized to 20 x 20 lattices (see Figs. 1C, 1D). The criteria for discriminating among SMUs were similarities in amplitude and waveform, a regular time of occurrence, and firing within a continuous two-second period where the force level remained within a ± 30 gwt range at each force step.

RESULTS
Task Relations of SHLP SMU Activity
From the SHLPs of 11 subjects, 48 SMUs were active during at least 1 of the isometric tasks. None was active with the jaw at the postural jaw position. A representative trial of protrusive isometric contraction (Fig. 2) shows 4 SMUs (Figs. 2B, 2C) discriminated from the filtered EMG (Fig. 2A) from the SHLP (Fig. 1B). Whether at least 1 SMU was active at a site for each task and subject is shown (Table). In eight ([11] participants, activity was apparent for CL, CL-P, and P. In seven, activity was present at IL-P and/or IL, and in five of nine subjects, activity was present during incisal clenching. Of the 48 SMUs, 34 (71%) SMUs were active at CL, 33 (69%) at CL-P, 32 (67%) at P, 17 (35%) at IL-P, and 6 (13%) SMUs were active at IL.

Qualitatively, there was a close association between SHLP activity and the magnitude of horizontal isometric force. For example, SMUs 3 and 4 were tonically recruited only at the highest force level, and exhibited progressively larger bursts of SMU activity (* in Fig. 2A) during the dynamic force.

Table. Task Relations of SHLP Activity

<table>
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<tr>
<th>Subjects</th>
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<th>Task Relations at Each Direction</th>
<th>Number of SMUs</th>
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</table>

* SMU activity of the SHLP from 11 subjects (A-K), arranged in relation to the mediolateral location of the verified electrode recording sites and numbers of units recorded from each site.
+ at least one SMU was active for this direction of task.
- not active.
nd = no recording was made of clenching activity in these subjects.
CL = contralateral direction, CL-P = contralateral protrusive, P = protrusive, IL-P = ipsilateral protrusive, IL = ipsilateral direction.

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fluctuations at successively higher force levels.

**Association between SMU Activity and Direction of Horizontal Isometric Task**

The 48 SMUs exhibited a variety of combinations of directions in which activity was observed. Thus, 5 units in two subjects were active in all directions, while 15 units in six subjects were active in 1 direction only (4 units at CL only [e.g., units 2, 4, in Fig. 3], 3 CL-P, 6 P, 2 IL-P [e.g., units 5, 6 in Fig. 3]). Eight units were active in 2 directions (5 CL and CL-P units; 1 IL-P and IL units; 1 IL-P and P unit; 1 CL-P and P unit). 14 units were active in 3 directions (12 CL, CL-P and P units [e.g., units 1, 3 in Fig. 3]; 1 CL, P and IL-P unit; 1 CL, CL-P and IL-P unit), and 6 units were active in 4 directions, all of which were active for CL, CL-P, P, and IL-P. At any one site, units could exhibit different combinations of directional relations (e.g., Fig. 3).

In two subjects, all SMUs recorded at a site exhibited the same directions of task relation, while in two subjects there was no task-related activity, although a few SMUs were active at >800 gwt, and EMG activity was present during isotonic contralateral and protrusive movements without the force transducer apparatus in place. In each of seven subjects, there were at least 2 SMUs recorded at the site that were active for the same direction(s) of force, but not for the same distribution of range of force levels. For example, in subject D, 2 units were active at CL and CL-P at 600-800 gwt, while 1 unit was also active at CL and CL-P, but only at 800 gwt. Of the 25 units that were not active for the entire range of forces from 400 to 800 gwt in at least one force direction, 22 of these were inactive only at the lower force levels.

**Association between SMU Activity and Vertical Isometric Task**

In five of nine subjects, there was SHLP activity during 100% MVC. Of the five, two had electrodes in the medial part of SHLP, while in three, the electrodes were in the middle of the SHLP. There was no detectable EMG activity during maximum clench in four subjects. The medio-lateral locations of the recording sites in these subjects were scattered medio-laterally throughout SHLP (2 were lateral, 1 middle, 1 medial).

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**Electrode Location within the SHLP**

CT scan data in the horizontal plane (upper panel) and in a reformatted oblique sagittal plane (lower panel) along the long axis of the SHLP show the electrode tips within SHLP (Fig. 1B). The relative locations of the recording sites were plotted in the vertical (Fig. 1C) and horizontal (Fig. 1D, see Table) planes along the long axis of the SHLP. Each symbol represents the task(s) for which the SMUs at that site were active.

There was no activity for any of the horizontal isometric tasks at the 2 lowermost and lateralmost recording sites (Figs. 1C, 1D, Table). The muscle fibers of the SHLP that were active...
during CL, CL-P, P, and IL-P, with or without IL, were mostly scattered throughout the SHLP, both vertically and horizontally. However, there was some possible evidence for compartmentalization of activity patterns within the SHLP, in that the muscle fibers in the upper part of the SHLP tended not to be active in any of the IL tasks. Further, the mediolateral middle portion of SHLP tended to be the only part of SHLP that was active in the IL task.

**DISCUSSION**

The present study shows that the SHLP is active during horizontal isometric jaw forces in a range of directions. While most SMUs (40/48) were active in directions other than ipsilateral, 8 SMUs were active in a range of directions, including ipsilateral. Qualitatively, the EMG activity of the SHLP increased as the isometric force increased from 400 to 800 gwt. In five subjects (of nine studied), SHLP EMG activity was present during maximum clenching.

The presence of SHLP activity during clenching is consistent with the conventional view that one of the functions of the SHLP is to stabilize the head of the condyle and disc against the articular eminence (Widmalm et al., 1987; Osborn, 1995). Other data from the present study were not consistent with other conventional views, however—for example, that the SHLP functions in a manner reciprocal to that of the IHLP (Juniper, 1981, 1984; Gibbs et al., 1984; Hiraba et al., 2000). The present study demonstrates SHLP activities during contralateral and protractive directions of isometric force, and this is consistent with recent and earlier demonstrations of SHLP activity during lower-force isometric horizontal contralateral and protractive movements (Sessle and Gurza, 1982; Murray et al., 1999a; Phanachet et al., 2003). There are abundant data pointing to IHLP activity during isometric and isotonic horizontal tasks in the contralateral and protractive directions and in jaw opening (Phanachet et al., 2001, 2002; Uchida et al., 2001, 2002). The similarities in the task relations of SMU and multi-unit activity in the SHLP and IHLP support the hypothesis that both SHLP and IHLP should be regarded as parts of one muscle, with the distribution of activity shaded according to the biomechanical demands of the task (Hannam and McMillan, 1994).

The long muscle fibers of the lower region of the SHLP were active for contralateral, contralateral-protrusive, protrusive, ipsilateral-protrusive, and ipsilateral isometric forces, whereas the shorter muscle fibers in the upper part of the SHLP were less likely to be active for ipsilateral forces. While most of the SHLP appears important for the generation of contralateral and protractive forces, it is possible that the direction of force applied to the ipsilateral condyle needs to be more horizontally directed, as applied through activation of the lower, more horizontally directed fibers of the SHLP, than the upper fibers of the SHLP, which are more vertically directed. During an ipsilateral jaw movement, the lower fibers may play a more important role on the ipsilateral side in stabilizing the condyle and/or disc-capule complex, and preventing excessive posterior displacement and trauma to the highly innervated and vascularized posterior attachment tissues. The inferior-most and lateral-most fibers of the SHLP may be inactive for isometric force at the level used in the present study, although there were units active for isotonic horizontal movements. It is possible that the above three groups of activity patterns may be associated with specific fiber bundle orientations and/or lengths that may be biomechanically best-suited to specific horizontal isometric forces. It is possible that these groups of fibers could be selectively activated—that is, the SHLP is functionally heterogeneous (Hannam and McMillan, 1994; Fournet et al., 1999, 1998; Phanachet et al., 2003; Murray et al., 2001). This concept is consistent with SHLP muscle fiber anatomy, where fiber alignment changes from a broad origin, at the roof of the infratemporal fossa and lateral pterygoid plate, toward a small insertion site on the condylar head and disc-capsule complex (Mahan et al., 1983; Widmalm et al., 1987; Bittar et al., 1994, 1995; Heylings et al., 1995; Akita et al., 2000). The concept is also consistent with the presence of non-parallel fiber bundles within SHLP (Troiano, 1967), and a complex neural distribution within the SHLP (Fournet et al., 1998).

We did not observe any systematic influence on SHLP EMG activity from different changes in vertical dimension between and among subjects. For example, the only subject who had activity only during protrusion had an opening of 5.0 mm, close to the mean value of 5.7 mm. A related issue is that it remains to be determined whether periodontal activation during masticatory movements leads to SHLP EMG activity patterns different from those observed in the present study. Another issue is that it is unlikely that the lateral recordings from the SHLP recorded activity from the mid-medial bundle of the temporalis muscle (Akita et al., 2000) that inserts directly into the disc adjacent to the SHLP, because there was no clenching or ipsilateral activity at these most lateral recording sites (see Table). In addition, recording sites were in the anterior half of the SHLP (Figs. 1C, 1D), well clear of the insertion of the mid-medial bundle (Akita et al., 2000).

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**REFERENCES**


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