FOCUS ARTICLE

The Role of the Human Lateral Pterygoid Muscle in the Control of Horizontal Jaw Movements

Greg M. Murray, MDS, PhD (Tor), FRACDS

Associate Professor

Intira Phanachet, DDS Graduate Student

Jaw Function and Orofacial Pain Research Unit Faculty of Dentistry University of Sydney Westmead Centre for Oral Health Westmead, New South Wales Australia

Shinji Uchida, DDS, PhD

Visiting Research Scholar Jaw Function and Orofacial Pain Research Unit Faculty of Dentistry University of Sydney Westmead Centre for Oral Health Westmead, New South Wales Australia

Department of Removable Prosthodontics and Occlusion Osaka Dental University Osaka, Japan

Terry Whittle, BSocSci

Research Assistant Jaw Function and Orofacial Pain Research Unit Faculty of Dentistry University of Sydney Westmead Centre for Oral Health Westmead, New South Wales Australia

Correspondence to:

Dr G. M. Murray Jaw Function and Orofacial Pain Research Unit Faculty of Dentistry University of Sydney Level 3, Professorial Unit Westmead Centre for Oral Health Westmead, NSW 2145 Australia Fax: 61-2-9633-2893 E-mail: gregm@mail.usyd.edu.au

Portions of the data in this paper appear in the PhD thesis of Dr Phanachet.

There is a limited understanding of the normal function of the lateral pterygoid muscle (LP) and the role that this muscle plays in temporomandibular disorders. This article addresses the hypothesis that a major function of the LP is in the control of horizontal jaw movements. The range of fiber alignments suited to generating a major horizontal force vector (magnitude and direction), together with the likelihood of independent activation of subcompartments (that is, functionally heterogeneous zones) within each head, provide the possibility of a finely graded range of force vectors on the condule to effect the fine control of horizontal jaw movements. This level of control does not appear to extend to the control of resting jaw posture, as recent single motor unit (SMU) data indicate that the LP is inactive with the jaw in the postural jaw position. Available electromyographic data demonstrate graded changes in multiunit and SMU activity with small horizontal jaw displacements at low force levels, a single preferred direction of the SMU firing rate during horizontal isometric jaw tasks, and graded changes in the SMU firing rate with horizontal force magnitude and direction. The evidence suggests that a major function of the LP is in the generation and fine control of the horizontal component of jaw movement by the graded activation of a subset of SMUs within the LP. The data also suggest that the LP is involved in the generation of horizontal force vectors, as required in parafunctional activities and heavy mastication. J OROFAC PAIN 2001;15:279-305.

Key words: pterygoid muscles, single motor unit, jaw, computed tomography, electromyography

The clinical opinion that the lateral pterygoid muscle (LP) is dysfunctional in patients with temporomandibular disorders (TMD) is still widely accepted.^{1,2} Popular theories of LP disturbance include muscle hyperactivity, muscle hypoactivity, poor coordination between the 2 heads of the muscle, and/or a disturbance to the normal role of the muscle in the control or stabilization of the temporomandibular joint (TMJ).1-10 These and other claims are largely unsubstantiated, although many TMD patients report that the region of the LP is frequently very tender.^{11,12} Irrespective of whether this report is a valid measure of LP tenderness, this clinical sign, together with preconceived notions of LP dysfunction in TMD patients, has formed part of the basis for unproven irreversible therapies-such as occlusal grinding and restorative treatments-as well as reversible treatments with occlusal splints or jaw exercises. The occlusal splint, for example, is thought to reduce muscle activity, improve muscle coordination, reduce TMJ loading, and/or aid in TMJ stabilization and thereby alleviate TMD symptoms in addition to a well-accepted placebo effect.^{1,2,13–15} Despite the importance attributed to the human LP, we have a very limited understanding of its role in TMD and indeed of its role in normal function. Present knowledge provides little scientific basis for current treatment recommendations.

Many studies in animals and humans have attempted to elucidate the normal function of the LP, and there are a number of excellent reviews of the subject.^{10,16,17} In general terms, many electromyographic (EMG) studies suggest that the inferior head of the LP (IHLP) plays a role in opening, protrusion, and contralateral jaw movements, while the superior head of the LP (SHLP) plays a role in closing, retrusion, and ipsilateral jaw movements, and there is a reciprocal relationship between the activity of the SHLP and the IHLP.^{2,10,16-19} However, there is no consensus view among studies concerning the tasks to which each head is related. For example, some studies suggest that both heads of the muscle always act independently, while others suggest synchronous activity in both heads during certain jaw movements.¹⁷ Further, there is no consensus as to the special role that the SHLP is thought to play in the control of the TMJ. This lack of agreement between some previous EMG studies is due at least partly to a number of significant limitations in these studies. For example, a major limitation of previous human EMG studies is the absence of a reliable method for verification of electrode location within the LP. There is the very real possibility that some of these earlier recordings may have been from other jaw muscles or may have been from the LP but were incorrectly attributed to a particular head of the muscle.^{17,20,21}

Given these uncertainties, together with the clinical significance that has been attributed to the LP in TMD patients, it is timely to review our current understanding of the normal function of the LP in humans. This article will provide this review in the context of evidence that bears on our own hypothesis that an important function of the LP is in the generation and fine control of horizontal jaw movements. This account will also serve as a baseline for future studies of the possible involvement of this muscle in TMD and for the development of improved therapies.

Anatomic Complexity of the Lateral Pterygoid

One of the anatomic features of the LP that is unique to the jaw motor system is its muscle fiber

architecture, which allows a major vector component (ie, force magnitude and direction) of the total force output from the muscle to be generated in the horizontal plane²²; the LP is therefore ideally suited to generating horizontal jaw movements. Many investigators have studied LP anatomy $^{20,23-30}$; the muscle consists of an upper or superior head (SHLP) and a lower or inferior head (IHLP). While the IHLP inserts into the condylar neck and capsule (and has a broad origin at the lateral surface of the lateral pterygoid plate), the SHLP (origin at the roof of the infratemporal fossa) has a complex insertion into the condyle and the disk-capsule complex.^{26,29,31,32} Within the SHLP and IHLP, there is a marked convergence of muscle fibers onto a small insertion site on the condylar fovea, capsule, and disc from a broad origin at the roof of the infratemporal fossa and lateral pterygoid plate. This marked change in fiber alignment from the uppermost to the lowermost muscle fibers, and from the medial to the lateral side of the muscle,^{24,33,34} provides 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.

Functional Heterogeneity

The central nervous system could take full advantage of this wide range of fiber alignments if each head of the muscle were functionally heterogeneous. That is, if fiber groups with specific orientations could be selectively activated within each head, then specific force vectors could be applied to the condyle to produce the desired horizontal jaw movement.

In most previous EMG studies of the LP, there appears to be the implicit assumption that there is a uniform distribution of activity throughout each head of the LP, and that activity recorded at 1 site within 1 head reflects activity throughout the entire head. There is anatomic, histologic, histochemical, and preliminary EMG evidence suggesting that this is unlikely and that instead, the LP is functionally heterogeneous.³⁵ We have recently proposed that regions or subcompartments of each head can be differentially activated to produce the appropriate force vector to aid in generating the required jaw movement.³⁵ This is consistent with the hypothesis proposed by Hannam and McMillan¹⁷ that both heads of the LP constitute a system of fibers acting as a single muscle, "with varying amounts of evenly graded

activity throughout its entire range, with the distribution 'shaded' according to the biomechanical demands of the task" (see also Widmalm et al²⁰). Such a notion of functional heterogeneity is not new to the jaw motor system, as it has already been well characterized in the temporalis and masseter muscles.^{36,37}

The internal architecture of the muscle suggests the possibility of separate anatomic compartments, selective activation, and the possibility of a range of force vectors on the condyle. Thus, the presence of internal tendon lamellae within the IHLP consistent with a pennate structure,^{20,22,27} the grouping of fibers within the SHLP into nonparallel slips,^{24,33,34} and the complex innervation pattern of the LP ^{30,38–40} all provide an anatomic structure consistent with functionally heterogeneous zones within the LP. Histologically, muscle spindles are concentrated in the central part of the IHLP,^{41,42} and histochemically, the LP consists of groups of muscle fibers that are predominantly aerobic.^{43,44} Since there is also evidence that muscle spindles are concentrated in regions rich in predominantly aerobic fibers,⁴⁵ it may be, therefore, that this central, spindle-rich region of the IHLP contains predominantly aerobic fibers and represents a functionally distinct zone. Therefore, although it is useful to represent the force output from each head of the LP as a single average vector,²² functional heterogeneity indicates that a range of force vectors are possible. Each of these vectors would be capable of applying a different magnitude and direction of force on the condyle to effect the desired horizontal jaw movement.

There is recent preliminary EMG data from our laboratory that supports the above evidence for functional heterogeneity.35 Multiunit EMG recordings were made from 2 sites within IHLP. One recording site (IHLP-intra) was approached intraorally; the other (IHLP-extra) was reached via an extraoral approach.^{21,46} A total of 47 excursive jaw movements (26 protrusive and 21 contralateral) performed with the teeth together were recorded in 3 subjects. During each trial of protrusion in each subject, the time of occurrence of the peak in the Butterworth-filtered signal from IHLPextra was significantly different from that from IHLP-intra for all protrusion trials in each subject (P < .05, paired t tests). During a contralateral slide, however, there was no significant difference between the times of occurrence of the peak EMG between the 2 IHLP sites in each subject and when all subjects' data were grouped together (P > .05;n = 21; paired *t* test). The data suggest that there is a task-dependent change in the relative pattern of recruitment of motor units at the 2 sites, and further raise the possibility of independent control of subpopulations of motor units within the IHLP. These preliminary data support the hypothesis that the IHLP is functionally heterogeneous; that is, that differential activation could occur within the IHLP and, given the range of muscle fiber alignments, that different internal force vectors could be generated to effect the appropriate horizontal jaw movement. Further SMU studies are needed to confirm these preliminary data.

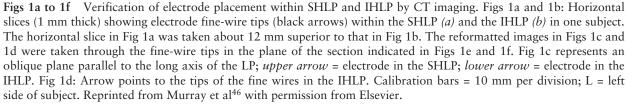
Given the range of fiber alignments in the SHLP,²⁴ it is likely that the SHLP is also functionally heterogeneous, and we have preliminary SMU data in support of this. Of 26 SMUs recorded from SHLP, 5 were shown by computed tomography (CT) to have been located in the medial part of SHLP. The general task relations of all 5 were identical to those of the IHLP, that is, these medial units were active only on contralateral, protrusive, and jaw-opening movements and not on ipsilateral, retrusive, or jaw-closing movements. Ten units recorded from the lateral part of the SHLP (see Figs 1a to 1f for sample verification data), were active on ipsilateral, retrusive, and jaw-closing movements; 1 additional unit from this lateral part was active in all horizontal movements as well as jaw-closing and jaw-opening movements. The remaining 10 units were recorded from the mediolateral middle part of the SHLP (Figs 1a to 1f), and these units were related to different combinations of tasks. These data suggest that the classically defined SHLP consists of more than 1 functional zone, each with characteristic functional properties, and the data thereby support the existence of functional heterogeneity within the SHLP.

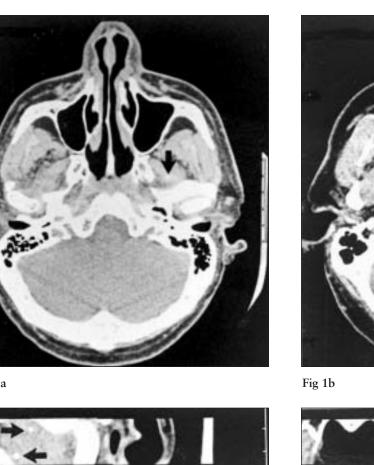
Another line of evidence that might support a role for LP in the control of horizontal jaw movements relates to the proposal that clicking and/or locking conditions arise in the TMJ through some disturbance in the horizontal positioning of the condyle in relation to the disc.^{2,47,48} Such a hypothesis necessitates an important role for the SHLP in horizontal disc and condyle position. Others consider that such a mechanism is unlikely given the insertion of the SHLP into both the disk and the condyle.^{27,28,30,31} Thus, if there is always a uniform distribution of activity throughout the SHLP, as in a functionally homogeneous muscle, then independent movement of the disc is unlikely; and, indeed, manual traction on the SHLP in cadavers has been reported to bring both disc and condyle forward together.^{20,25,27,49} However, the possibility of selective activation of those SHLP fibers inserting into the disc, as could occur in a Fig 1a



Fig 1c

Fig 1e

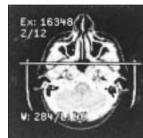














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functionally heterogeneous LP, points to the need to reevaluate some proposed mechanisms of the etiology of internal derangement. Further studies are clearly needed in which SMUs are recorded at spatially identified sites within the muscle and combined with imaging of disc position.⁵⁰

Absence of Spontaneous Activity in the Lateral Pterygoid at Postural Jaw Position

It has been claimed that the SHLP is constantly maintained in a mild state of contraction or tonus^{2,51} that results in a slight anterior and medial force on the disc when the jaw is in the postural jaw position.¹ Such a proposal of control of horizontal jaw posture would be consistent with the hypothesis of fine control of horizontal jaw movements. However, Mahan and coworkers⁴ reported that both SHLP and IHLP were silent at resting posture in normal asymptomatic subjects, and only SHLP was tonically active in 2 subjects with pain on palpation of the TMJs and masticatory muscles. Further, our recent data do not support such a role for the SHLP or the IHLP in this fine control of the jaw at the postural jaw position. A total of 108 SMUs have been recorded from the SHLP or IHLP in 1 or more recordings from 31 young adult subjects without signs or symptoms of TMD. The locations of most of the SMUs were verified by CT, and an example of verification data for electrode placement within SHLP and IHLP by CT imaging is shown in Figs 1a to 1f. This figure shows fine-wire electrode tips within the SHLP (arrow in horizontal slice in Fig 1a, upper arrow in reformatted section in Fig 1c) and the IHLP (lower arrow in Fig 1c, arrows in Figs 1b and 1d) in 1 subject and provides unequivocal verification of the correct location of recording electrodes.

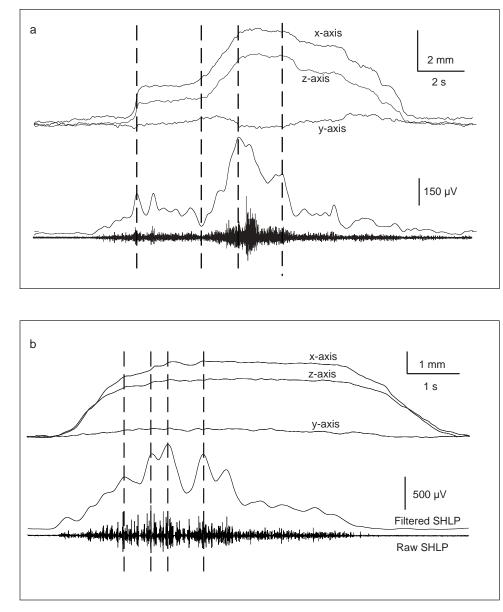
Of the 108 SMUs, 82 were recorded from the IHLP and 26 from the SHLP. None of the 108 were spontaneously active when the jaw was in the clinically determined postural jaw position. These data are unequivocal in that they are derived from SMUs and are not subject to the limitations inherent in multiunit EMG recordings, where it can be difficult to define absence of activity. This observation calls into question the claim that the SHLP is maintained in a mild state of contraction or tonus when the jaw is in the postural or "rest" position.^{1,2,51} However, the data are consistent with the findings of Mahan and coworkers⁴ and suggest that, in the postural jaw position, there is no anterior and medial force on the condyle and disc

derived from active LP contraction that would serve to maintain the condyle in close apposition with the disc and articular eminence. There may, however, be anterior force vector components from tonically active masseter and medial pterygoid motor units.

Role of the Lateral Pterygoid in Jaw Movements

Many muscle fibers in the LP appear to be predominantly aerobic (slow-contracting and fatigue-resistant, about 80%).44 The evidence that such fibers are suited to low forces and prolonged contraction times points toward an important role for the LP in the generation of fine horizontal force vectors, as is required during speech and mastication. If the LP is indeed important in horizontal jaw movements, then a close association would be expected between horizontal jaw movements and LP EMG activity. There are many studies that have concluded that the IHLP is active during protrusion, contralateral, and opening movements while the SHLP is active during retrusion, ipsilateral, and closing movements.^{10,16,17} With the exception of some studies,^{2,18,35,46,52} most have not recorded jaw movement simultaneously and therefore have been unable to clarify the nature of the association between jaw movement and LP EMG activity. Inspection of the EMG recordings in the studies that provide no record of jaw movement gives limited insight into the precise role that the LP is playing in these movements. Nonetheless, most of the studies appear to suggest that the level of IHLP activity is correlated with the magnitude of anterior condylar translation. In a study by Hiraba et al,² in which jaw movement was recorded, crucial electrode verification data were unfortunately not obtained, although monotonic relationships were observed between LP EMG activity and some kinematic parameters of jaw movement. These data led Hiraba et al to suggest that the IHLP controls anterior condylar position; this supports the hypothesis that the IHLP plays an important role in the control of horizontal jaw movements. Although these authors also concluded that the SHLP controls the angular relation between the disc and the condyle, confirmation of their conclusions requires CT verification of EMG electrode location, together with, in the case of the SHLP, imaging of disc position.⁵⁰

We have recent multiunit and SMU EMG data that clarify the nature of the association between kinematic parameters of jaw movement and LP EMG activity. In 8 human subjects, the magnitude



Figs 2a and 2b Close association between the activity of the LP and horizontal jaw movements. *(a)* Multiunit EMG activity from the IHLP during a trial of protrusion. *(b)* Activity from the SHLP during a contralateral jaw movement. The trial began and ended in intercuspal position. Subjects were instructed to keep the teeth lightly in contact at intercuspal position throughout the jaw movement. The upper 3 traces in each panel show displacement of the lateral condylar pole for the x-axis (anterior-posterior), y-axis (mediolateral), and z-axis (superior-inferior), and the lowermost trace plots raw EMG activity; the Butterworth-filtered signal (after rectification) is shown in the middle trace. Vertical dashed lines indicate the peaks of major fluctuations in filtered EMG activity levels. The target frames for the recordings in b were slightly angled to the midsagittal plane. Therefore, the contralaterally directed jaw movement exhibited only a small displacement along the mediolateral y-axis during the contralateral excursion.

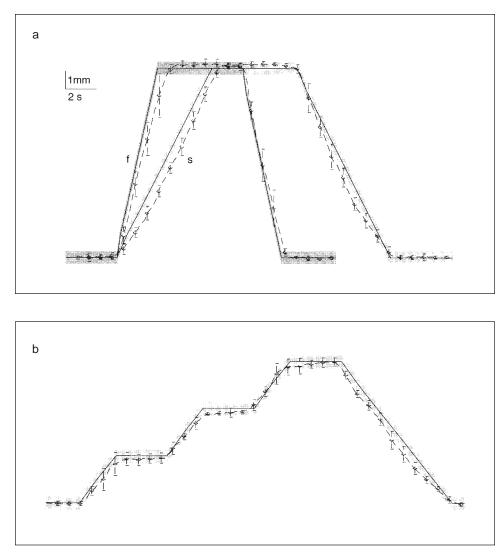
of the smoothed IHLP and SHLP multiunit EMG activity was closely correlated to the magnitude of condylar translation during contralateral or protrusive jaw movements,^{46,53} as would be expected if the LP is concerned with the details of control of horizontal jaw movements. Figure 2a shows multiunit EMG activity from the IHLP during a trial of protrusion, and Fig 2b shows activity from a CT-verified site in the SHLP during a contralateral jaw movement. Vertical lines show the peaks of major fluctuations in EMG activity (middle traces, Figs 2a and 2b) and condylar movement (upper traces). In all subjects there was also a high correlation between condylar displacement and smoothed EMG activity of the SHLP and IHLP on the outgoing phase. A high correlation with IHLP activity during the return phase supports Wilkinson's proposal that a "lengthening contraction" of the IHLP "has the effect of slowly letting out the rope to control the condyle as it travels back into the fossa."²⁵ The data suggest that, in addition to a role for the IHLP in the control of horizontal jaw movements, the SHLP also plays a role, at least where the teeth are slid past each other. These data do not discount roles for other jaw muscles in these horizontal movements, but rather point to the LP as being an important driver of these movements.

Of the 108 SMUs recorded from the LP in our recent studies, 61 were recorded from the IHLP and were studied during horizontal isotonic jawdisplacement tasks to a target. All 61 were active during contralateral and protrusive jaw movements as well as jaw-opening movements. In contrast to some previous findings,^{4,16,20} none were active during ipsilateral displacements or clenching. It is possible that the claims of IHLP activity on ipsilateral movement and clenching reflect recordings from units located in other muscles, such as medial pterygoid, which has an origin from the lower border of the lateral surface of the lateral pterygoid plate.²⁰

Figures 3a and 3b illustrate the time course of the target (shaded bands) and corresponding averaged mid-incisor-point displacements (dashed lines) during single-step (Fig 3a) and multiple-step (Fig 3b) contralateral horizontal jaw displacements. Figure 4 shows representative SMU data during a contralateral jaw movement. The upper line shows displacement, the center tracing shows spike-train pulses recorded from the IHLP, and the lower graph shows a sample of the original raw data where the unit labelled "1" is the unit discriminated in the center of Fig 4. Unit "1" exhibited increases in firing rate as displacement increased from time points a to b to c, a total of 1.4 mm. Of 25 IHLP units that were tonically firing and able to be discriminated, the firing rates of 17 (68%) showed a significant increase (P < .05, ANOVA repeated measures) over the 3-step range. Since rate coding is 1 of the methods of increasing force output from a muscle,⁵⁴ this evidence for rate coding in IHLP supports an important role in the generation and fine control of horizontal jaw movements. There was also evidence for recruitment of SMUs in association with fine horizontal jaw movements. The sample of 61 SMUs recorded from IHLP exhibited a range of displacement thresholds. In Figure 4, T indicates threshold. For the entire population of recorded units, thresholds ranged from 0.1 mm of displacement to a contralateral displacement of 6 mm.

This evidence for an association between SMU firing properties and horizontal jaw displacements at low loads is entirely consistent with the high proportion of predominantly aerobic fibers in the LP, which may correlate with fatigue resistance and low forces.44 The evidence is also consistent with the proposal that the LP's internal muscle architecture offers a better propensity for near-isotonic than near-isometric conditions requiring power.^{17,22,55} Thus, the presence of long fibers (about 22 mm),^{22,23,55} with many sarcomeres in series arranged in the same line of action as the bulk of the muscle and with small cross-sectional areas, provides an architecture most suitable for shortening over longer distances than that seen in the masseter and medial pterygoid muscles, which are more suited to high power generation over short distances. These data, together with the above multiunit data obtained from our own and other EMG studies and our recent SMU data, point to an important role for the IHLP and SHLP in the generation and fine control of horizontal jaw movements. These movements include not only contralateral and protrusive jaw movements, but also other movements where a component can be resolved in the horizontal plane. For example, masticatory jaw movements are usually associated with horizontal vector components.⁵⁶

The claim for a role for the SHLP in the control of horizontal jaw movements is indeed consistent with the anatomy of the SHLP. Thus, although there is a great deal of variability in the architecture of the insertion of the SHLP, there is nearly always a portion that inserts into the pterygoid fovea³⁰ and is therefore capable of applying anteriorly directed force vectors to the condyle.²⁰ Other studies might appear to come to different conclusions about the function of the SHLP. For example, some believe



Figs 3a and 3b Standardization of horizontal jaw movements. Diagrams illustrate the target lines (*solid lines*) and corresponding averaged mid-incisor point displacement (*dashed lines*) during a movement of the jaw to the left side with teeth apart. Standard deviation bars are located on the averaged displacements every 750 ms, together with a shaded area indicating light emitting diode diameter (2.8 mm). (*a*) Single-step displacements at 2 rates of movement: 2.2 mm/s (s) and 6.5 mm/s (f). (*b*) Multiple-step displacement at a rate of 1.3 mm/s.

that the SHLP plays a role in stabilizing the condylar head and disc against the articular eminence during jaw closing.^{20,25,47,57,58} The hypothesis of a role for the LP in the control of horizontal jaw displacements is indeed consistent with this notion of the SHLP as a stabilizer of the condyle and disc,^{47,57–61} as stabilization here implies control of horizontal jaw position. Another hypothesis proposes that the SHLP prevents the disc-capsule complex from being trapped or sprained during condylar movement,²⁷ another claims that SHLP controls the angular relationship between the disc and condyle,² while another views the SHLP as a jaw closer.⁵¹ Added to this variety of concepts is the lack of agreement between previous studies as to the relative task relationships between the SHLP and IHLP. For example, while many have reported that the SHLP and IHLP function independently and reciprocally,^{4,5,51,57} and this notion is widely accepted clinically,^{1,10} others report simultaneous activity, at least during some motor tasks.^{16,17,20,46,62}

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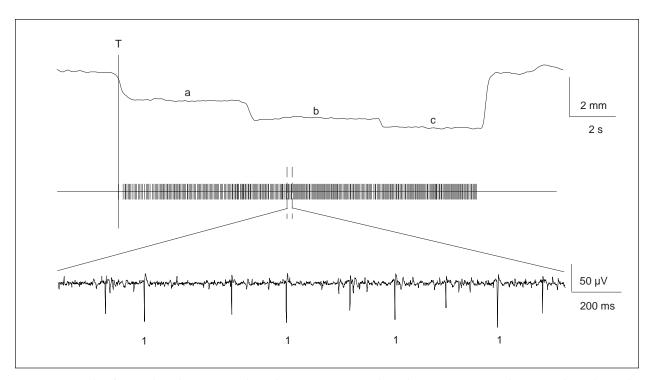


Fig 4 Example of SMU data during contralateral jaw movement with teeth apart. *(Top)* Displacement along the mediolateral axis (ie, y-axis) of the mid-incisor point during a 3-step jaw movement to the left side. The trial started and ended at postural jaw position. *(Center)* Spike-train pulses recorded from the IHLP during this trial. *(Bottom)* The period delineated by the dotted vertical lines is shown in expanded form as the original raw data, where the unit labelled "1" is the unit discriminated in the center graph. Another smaller unit could also be discriminated. Sampling rate for SMU recording = 10,000 samples/s; bandwidth = 100 Hz to 10 kHz; highest frequency component = 4 kHz.

There are a number of possible explanations for these inconsistencies and a variety of theories concerning the function of the SHLP and the relative task relationship between the SHLP and the IHLP. First, despite excellent anatomic evidence, 20,26-28 there is still a dedicated following for the view that the SHLP is inserted exclusively into the articular disc, and this erroneous concept underpins some current hypotheses of function and dysfunction.² Second, and as mentioned earlier, a major limitation of most previous human studies is that they have not verified that electrodes were correctly located within the LP and not other jaw muscles. In the absence of a reliable verification technique such as that outlined above (Figs 1a to 1f), conclusions about LP function drawn from these studies are questionable given the very real possibility of electrode misplacement.^{17,20,21} Therefore, despite recent claims to the contrary,² it is not possible to rely on EMG patterns as the sole basis for verifying that electrodes are correctly located within the LP. Third, there is uncertainty in many previous

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studies as to how the jaw was moving in relation to LP EMG activity, given that most previous studies did not record jaw movement together with LP EMG activity. The recording of condylar movement together with LP activity is essential, particularly in light of the observation of Sessle and Gurza⁶² from their verified primate recordings that jaw position appeared to be an important determinant of EMG activity in the LP. In our laboratory, standardized jaw movements are recorded with the JAWS3D tracking system (Metropoly AG, Zurich, Switzerland). (Figs 3a and 3b).63 The use of this standardized methodology allows clear definition of LP EMG activity patterns in relation to movement. Fourth, the possibility that both the SHLP and the IHLP are functionally heterogeneous provides a very reasonable additional explanation for the variety of theories that have been proposed in the past, as well as the inconsistencies between previous studies. Functional heterogeneity also underscores the importance of verification of electrode location within the LP. Thus, not only is it essential to verify that electrodes are located within the LP and not other jaw muscles,^{21,46} but, given the likelihood that each head of the LP is functionally heterogeneous, it appears that it is also necessary to define electrode location within each head of the muscle. This applies particularly to the SHLP, for which our recent SMU data point to multiple functional zones.

Despite these limitations and erroneous concepts, the SHLP may well play a role in performing some or all of the functions listed above, given the complexity and probable functional heterogeneity of the SHLP. However, a detailed understanding of the SHLP, particularly in relation to the interarticular disc, must await the outcome of carefully designed studies that employ SMU recordings at sites identified by CT and combined with accurate recording of standardized jaw movements and dynamic magnetic resonance imaging of disc position.⁵⁰

Role of the Lateral Pterygoid in Force Production

The data summarized above from previous investigations and our own recent studies point to an important role for the LP in the fine control of horizontal jaw displacements. However, there is also evidence for a role for LP in the generation of greater horizontal force vectors, as required during heavy chewing as well as parafunctional grinding activities, where large frictional resistance between the teeth has to be overcome. First, a significant proportion of fibers within the LP (about 20%) are predominantly anaerobic⁴⁴ and are therefore fast-contracting, fatigue-susceptible, and likely to correlate with higher force generation. This suggests that the muscle is involved in the generation of horizontal force vectors required during chewing of tough foods and during parafunctional motor activities involving protrusive and side-toside tooth grinding and clenching. Second, LP EMG activity has been shown to modulate in association with voluntary tooth gnashing²⁰ and also to show graded changes in multiunit EMG activity correlated with horizontal level of applied force.⁶⁴ Third, in an early elegant study, the IHLP was implicated in the development of isometric horizontal force vectors toward the end of the intercuspal phase of chewing and after jaw-closing muscle activity had declined significantly.65 These findings are consistent with the proposal that during clenching at intercuspal position, both heads act to prevent posterior condylar displacement and pressure on the sensitive tissues behind the condyle,²⁰ although our recent SMU recordings do not support the view of IHLP activity during intercuspal clenching. The findings also suggested that the IHLP plays a role in preventing posterior condylar displacement⁶⁵ during protrusive or contralateral clenching.

Fourth, recent SMU data from our laboratory support a role for the IHLP in the magnitude and direction of force generation in the horizontal plane. A total of 21 SMUs have been discriminated from the IHLP during isometric horizontal force tasks. Figure 5a shows 6 representative isometric force trials in the contralateral direction of applied force with the teeth held apart. The subject was required to track and hold force targets at 400, 500, 600, 700, and 800 gwt of applied force. Force traces are shown at the top and spike-train pulses are in the middle. The histogram at the bottom of Fig 5a and the graph in Fig 5b show that the EMG activity of the unit increased significantly (P < .05, ANOVA repeated measures) with increasing force levels at the contralateral direction of force application. The graphs in Fig 5b illustrate the progressive decrease (P < .05) in firing rate as the direction of applied force was changed from contralateral through to an intermediate force direction (contralateral-protrusion) to protrusion to a second intermediate force direction (ipsilateral-protrusion) and ipsilateral.

These preliminary data support the general hypothesis that the LP is involved in the generation of horizontal force vectors required in heavy mastication and parafunctional activities. Many parafunctional jaw movements, for example, are characterized by protrusive and/or side-to-side movements of the jaw, often with heavy jaw-closing muscle activity. Under these circumstances, large horizontal force vectors would be needed to overcome frictional resistance between the teeth, particularly during heavy parafunctional movements.

It should be pointed out that the overall hypothesis of this paper does not rule out a role for other jaw muscles in these movements. For example, the masseter, medial pterygoid, and temporalis muscles all contain fibers capable of generating force vectors with horizontal components.^{17,22,64,66} Further, the hypothesis does not address the role of the LP in other jaw movements, such as jaw opening and closing.^{2,16} Nonetheless, the observations of graded changes in activity with direction of horizontal jaw movement suggest that the generation of horizontal jaw movements requires the combined activation of a collection of SMUs WITHOUT WRITTEN PERMISSION FROM THE PUBLISHER. COPYRIGHT @ 2001 BY QUINTESSENCE PUBLISHING CO, INC. PRINTING OF THIS DOCUMENT IS RESTRICTED TO PERSONAL USE ONLY. NO PART OF THIS ARTICLE MAY BE REPRODUCED OR TRANSMITTED IN ANY FORM

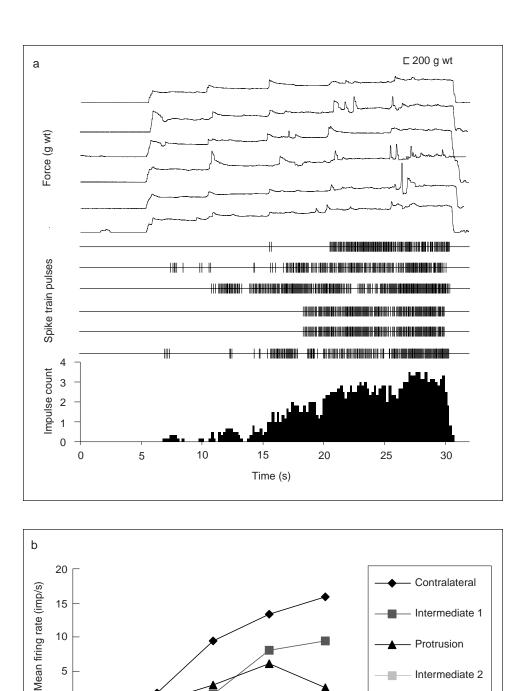
0

400

500

600

Force (g wt)



Figs 5a and 5b Single motor unit data during isometric force task. (a) Six isometric force trials in the contralateral direction of applied force. The subject was required to track and hold force targets at 400, 500, 600, 700, and 800 gwt of applied force. Force traces are shown at the top, spike-train pulses appear in the middle, and the histogram at the bottom summarizes the level of activity recorded for that direction of force. (b) Mean firing rates obtained during each force holding phase and at each direction of force application (contralateral, contralateral-protrusion, or intermediate 1, protrusion, ipsilateral-protrusion, or intermediate 2, and ipsilateral).

700

800

Intermediate 2

Ipsilateral

within the LP, each activated in a graded manner depending on the force vector required to be exerted on the condyle.

Conclusions

The clinical opinion that the LP is dysfunctional in patients with TMD is widely accepted and influential in the management of TMD. There is, however, little scientific basis for this opinion and, indeed, there are a number of significant limitations of previous studies that undermine our understanding of normal LP function. Nonetheless, there is sufficient reliable evidence to support the hypothesis that 1 of the major functions of the LP is in the control of horizontal jaw movements. The LP contains a range of fiber alignments suited to generating a major horizontal force vector. The LP also appears to consist of subcompartments within each head capable of independent activation that provide the possibility of a finely graded range of force vectors (magnitude and direction) on the condyle to effect the desired horizontal jaw movement. At the postural jaw position, however, there is no force on the condyle from active LP muscle contraction. A variety of EMG evidence is summarized that points toward an important role for the LP in the fine control of horizontal jaw movements. The data also support the general hypothesis that the LP is involved in the generation of the horizontal force vectors required in parafunctional activities and heavy mastication. Recent SMU data characterized during standardized tasks will serve as baseline data for future studies of comparable activity features from the LP in patients with TMD. If differences are identified, and if these features can be related to symptoms, then we will be in a more rational position to recommend improvements in therapy, rather than the ad hoc approach commonly adopted in clinical practice.

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Herring

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CRITICAL COMMENTARY $\mathbbm{1}$

THE ROLE OF THE HUMAN LATERAL PTERYGOID MUSCLE IN THE CONTROL OF HORIZONTAL JAW MOVEMENTS

Susan W. Herring, PhD Professor Department of Orthodontics University of Washington Box 357446 Seattle, WA 98195-7446 Fax: (206) 685-8163 E-mail: herring@u.washington.edu

The elegant studies on the lateral pterygoid muscle (LP) summarized in the focus article¹ by Murray and colleagues provide data that are both quantitatively (sample size) and especially qualitatively (single motor unit [SMU] recording) far superior to any previous work in this muchinvestigated area. With the inclusion of validated electrode position and simultaneous tracking of condylar movement and jaw force, these studies represent the state of the art for masticatory muscle function.

Dragonslayers

Armed with superior information, the authors have slain several of the dragons of misinformation that prey on the dental research countryside. The most thorough slaughter is of the notion that the LP maintains postural position. The authors also provide convincing evidence for functional heterogeneity within each head of the LP and suggest that the 2 heads are not distinct in their function but simply represent different parts of the continuum of muscle fiber directions in the muscle as a whole.

One dragon remains alive, although less healthy than before, and this is the question of whether the superior head (SHLP) is exclusively active during ipsilateral, retrusive, and closing movements, as reported by earlier workers. These movements are opposite to the muscle's direction of pull, so if the electromyographic (EMG) activity is real, the SHLP is strictly an eccentrically contracting antagonist and never an effector muscle, an unusual biologic situation. On this question, Murray and his colleagues bring the evidence of 26 SHLP SMUs, of which 10 lateral SMUs were indeed active during ipsilateral, retrusive, and closing movements. However, 5 medial SMUs showed the opposite activity pattern (contralateral, protrusive, and opening), which is expected on anatomic grounds and was also observed in all SMUs from the inferior head. The remaining 11 SMUs, all intermediately positioned, showed mixed activity patterns. Therefore, the claim that the entire SHLP has an "eccentric" contraction pattern is laid to rest, but the evidence seems to support the existence of some SMUs in the SHLP that do contract eccentrically part or all of the time. Murray et al use these data to reinforce their emphasis on functional heterogeneity within the LP and do not comment further on the strange activity pattern of the lateral SMUs.

Although I too believe in the functional heterogeneity of jaw muscles in general and the LP in particular, I am still not convinced that any LP SMUs are active in this counterproductive fashion. Murray et al do not give serious consideration to an alternate explanation: that of crosstalk from the deep temporalis. The deep temporalis and the lateral fibers of the SHLP are very near neighbors, sometimes sharing a common tendon of origin at the infratemporal crest. Even an electrode correctly situated in the lateral SHLP could easily pick up large SMUs from the adjacent deep temporalis. The value of the new data from Murray and his colleagues, in my view, is to localize the "eccentric" contraction pattern to the part of the SHLP most likely to experience crosstalk from the deep temporalis. To decide whether the activity pattern represents crosstalk or an eccentric contraction pattern will have to await a method for mapping individual motor unit territories in human jaw muscles.

Is the Lateral Pterygoid Unique?

One dragon that Murray et al have not tried to slay is the idea that the LP is a special muscle. In fact, the very existence of this excellent article, which focuses on the LP to the exclusion of other jaw muscles, strengthens this dragon. In defense of the other jaw muscles, however, I would like to point out that many characteristics discussed are not unique to the LP:

1. The LP is anatomically complex, with internal tendons and diverging muscle fibers, but it is much less tendinous than the masseter or medial pterygoid, and its fibers are less diverse than those of the temporalis.

- 2. Murray et al convincingly demonstrate that the LP is functionally heterogeneous, but so are the masseter,² the temporalis,³ and even the biceps brachii.⁴ Thus, if the criterion for functional heterogeneity is task-specificity of individual motor units, it is not clear that there are *any* homogeneous muscles in the body.
- 3. The surprising predominance of aerobic fiber types in the LP is also found in the masseter, medial pterygoid, and temporalis⁵ and may be related to the requirements of speech.
- 4. Like the LP, these adductor muscles show differential distributions of muscle spindles, and overall they are much richer in spindles than the LP.⁶
- 5. The fibers of the LP are indeed relatively long and thus suited for producing isotonic contractions, but they are much shorter than many fibers of the similarly adapted temporalis.⁷

In short, in most parameters the LP is a typical representative of the mandibular adductor musculature from which it develops.⁸ Within this group, its only unusual feature is the scarcity of muscle spindles, a characteristic shared by other jaw-opening muscles.⁶

Is the Major Function of the Lateral Pterygoid to Produce Horizontal Movements and Force?

Contralateral jaw movement in humans involves translation of the condyle and disc forward, downward, and medially on the articular eminence. The LP is unquestionably involved in this movement; both the superior and the inferior heads of the muscle pull exactly in this direction. Murray et al adduce additional evidence of SMU recruitment and rate coding to support this role. Although I am in basic agreement, I think there are some broader issues here. My arguments are: (1) the LP is actually more significant for protrusion than for lateral deviation, and in any case protrusion is an integral element of lateral deviation; (2) the LP's role in normal function is to produce horizontal movements and protrusion; and (3) the LP is probably not a major source of muscle force in any direction.

Protrusion or Horizontal Movement?

The major mechanism by which lateral jaw position is achieved is by the asymmetric positioning of the condyles along the anteroposterior axis. From resting or closed jaw positions, the condyles can

Herring

protrude a long distance but retrude only a little, if at all. Thus horizontal movements from rest feature a protrusive movement of the contralateral condyle, which brings it down the articular eminence. The LP is an absolute necessity for such movements because its fibers are the only ones anatomically capable of producing this protrusive movement. Other muscles with protrusive and/or medial actions (the superficial masseter and medial pterygoid) cannot substitute for the LP, because their strong adductive components prevent them from being able to pull the condyle down the eminence. The LP would not be necessary if one started from a position with both condyles already protruded; in this case, horizontal movement could be produced by retrusion of the ipsilateral condyle.

These arguments suggest that the LP is most important for protrusion. Its admittedly important role in horizontal movement arises not only from its medial component but even more from its unique protrusive component. Interestingly, computed tomographic scans indicate considerable variability in the relative size of the medial and protrusive components of LP angulation, suggesting that different individuals might have varying degrees or efficiencies of horizontal movement.⁹

Movements During Normal Function

The experiments described by Murray et al were exercises performed from rest position or intercuspation, and thus the LP was necessary for condylar translation. What about speech and mastication? Normal speech does not utilize horizontal movements,¹⁰ but horizontal movements are crucial for chewing. While there are numerous variations,¹¹ the mandible usually deviates toward the working side as it closes. This horizontal movement features retrusion of the working-side condyle and thus does not require the LP. The power stroke brings the mandible to the midline, primarily by retruding the balancing side condyle via the temporalis while the masseter/medial pterygoid are active on the working side.¹² After reaching maximal intercuspation, the mandible continues toward the balancing side and then opening begins. This latter part of the power stroke requires the working-side condyle to protrude and thus the LP. The onset of opening involves the protrusion of the balancing-side condyle as well and thus the recruitment of the balancing LP.13 In summary, the LP does serve an essential role in producing horizontal movements during mastication, but not all horizontal movements-only at the end of the power stroke and the beginning of opening.

Force

Although the argument of Murray and colleagues for the importance of the LP in horizontal movement is powerful, their evidence for a major role in horizontal force is less compelling. Their points are: (1) the presence of anaerobic fibers, (2) the modulation of activity with horizontal force, (3)masticatory activity, and (4) SMU data showing that firing rate increases fastest for the most contralateral forces. Points 2 to 4 do indicate that the LP generates horizontal force-but any muscle will generate force along its action line. With regard to the first point, the anaerobic fiber type is actually the default condition, not a specialization.¹⁴ As the authors mention, the long-fibered architecture of the LP is better suited to producing movement than force.

Man Among the Animals

The article by Murray et al is directed at the human condition, but it is interesting to consider an evolutionary context. The LP and the temporomandibular joint (TMJ) are unique to the mammals and apparently evolved at the same time. In contrast, the TMJ disc is absent in monotremes and some marsupials¹⁵; thus the attachment of the LP to the condyle is the original one. Two heads can be distinguished in most mammals, based on the area of origin. Anatomic complexity is therefore the rule.

The functional activity of the LP in other mammals is similar to that of humans. Except for carnivorans (dogs, cats, etc), most mammals use horizontal movements during chewing and show LP activity during the late power stroke and opening.¹² Thus, motor programming has been conserved during evolution.

The human LP is most remarkable in being relatively large, often contributing over 10% to the total masticatory muscle mass.¹⁶ This compares to less than 1% in carnivorans, which have little capacity for protrusive or horizontal movement, and 3% to 6% in other species with grinding mastication, such as ungulates and nonhuman primates, which have extensive protrusive and horizontal movements.¹⁶ Only in some very specialized feeders such as whales and anteaters is the LP relatively as large as in humans.

Why is the human LP so massive? Clearly not for speech, which uses only minor mandibular movement, and not for mastication, which is accomplished with smaller LPs in other species. Rather, the large LP may reflect the elongated pterygoid plates and steep articular eminence that accompany the evolutionary buckling of the human skull. This steep eminence makes the LP crucial for protrusion, a unique human problem that gives the LP a special importance in the masticatory system.

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CRITICAL COMMENTARY 2

THE ROLE OF THE HUMAN LATERAL PTERYGOID MUSCLE IN THE CONTROL OF HORIZONTAL JAW MOVEMENTS

Anne S. McMillan, BDS, PhD, FDSRCPS, FDSRCS Professor Oral Rehabilitation Faculty of Dentistry The University of Hong Kong 34 Hospital Road Hong Kong

Fax: +852-2858-6114 E-mail: annemcmillan@hku.hk

The focus article¹ by Murray and colleagues has addressed the role of the lateral pterygoid muscle (LP) in the control of horizontal jaw movements. The authors have identified the conundrum of the putative role of the LP in the clinical expression of temporomandibular disor-

ders (TMD) and have sought to clarify the issue by a rigorous, scientifically based study of LP activity during normal function that provides a rational basis for the understanding of the muscle's role during jaw dysfunction. This work is pertinent for clinicians and basic scientists, as it highlights the

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need to underpin clinical impressions with carefully controlled experiments in human subjects that disclose the mechanisms thought to be involved in normal as well as aberrant jaw movement.

There has been much speculation on the role of the LP in TMD.²⁻⁵ For example, "hyperactivity" of the superior head of the muscle has been cited in the progression of TMD from myalgia, through internal derangement, to arthritis of the temporomandibular joint (TMJ).⁴ Many theories have been based on erroneous anatomic detail and an imperfect understanding of the functional behavior of the muscle. To date, there is no compelling evidence that the LP behaves abnormally in TMD patients.⁴ The authors have reviewed some of the clinically based literature that seeks to link a dysfunctional LP with TMD. They comment on the general use of scientifically unproven management strategies, some of which are irreversible, that are based on the assumption that the biomechanical linkage between the LP and the TMJ is disturbed. What is insightful in the authors' commentary is the acknowledgment that the normal function of the LP is poorly understood, and yet assertions about LP dysfunction and TMD continue to be made.

The LP has been studied extensively in humans and animals, although it is less physically accessible than most other jaw muscles.⁶⁻¹⁰ The precise role of the LP in jaw movement continues to be contentious, with views ranging from discrete roles for the superior and inferior heads to a reciprocal arrangement between heads. The putative role of the superior head in the control of TMJ motion is also unclear. A major reason for the conflict is that almost all previous electromyographic (EMG) studies, both mixed-response and single motor unit (SMU), have used a random probe with no precise knowledge of the EMG recording location within the muscle.^{6-8,10,11} The studies described by the authors of this article have made a quantum leap in terms of EMG methodology by recording from verified sites within both heads of the muscle; thus the precise role of the LP in jaw motion can be addressed unequivocally, with no risk of inadvertent recording from adjacent muscles such as the deep temporalis.

Architecture

In their description of the anatomy of the LP, the authors have cited evidence for a major force component that is generated in the horizontal plane.

Moreover, the change in fiber orientation from superior to inferior and medial to lateral aspects, which curves from almost vertical to near horizontal, provides a potential substrate to effect horizontal movement. However, the authors do not make a strong case for pennation within the muscle. Although internal connective tissue has been described in the inferior head and non-parallel fiber groups in the superior head, the longer fibers and sarcomeres, the relatively uniform fiber length, and the very limited amount of tendinous tissue (5% to 6%) suggest, at most, only very limited pennation compared with other jaw muscles, notably the masseter, temporalis, and medial pterygoid muscles.^{12,13} Thus the LP appears more suited to isotonic than isometric operational conditions. Given the internal architectural arrangement within the LP, the likelihood of distinct anatomic compartments is less compelling compared with the multipennate jawelevator muscles. Nonetheless, the authors do dispel the notion that muscle tensions produced by the LP can be attributed to simple force vectors.¹⁴ The variation in fiber orientation in different muscle parts suggests a system of angled force vectors that effect horizontal jaw motion by controlled movement of the mandibular condyle through the grading of activity throughout the fibers as different lines of muscle action are required.9

Regional Electromyographic Activity

The authors present a well-reasoned case for functional heterogeneity in the LP muscle. The separate innervation of the inferior and superior heads of the muscle suggests neuromuscular compartmentalization.¹² Thus, there is the potential for more localized motor control. This could result in selective action of muscle regions or more widespread synergistic activity, depending on the motor task and the movement sequence.¹⁵ The multiunit study by the authors¹⁶ of the inferior head of the LP reveals evidence that selective activation occurs in discrete regions during jaw protrusion with tooth contact, whereas during contralateral jaw movement, there is more generalized activity throughout the inferior head. A meticulous method was used that involved simultaneous recording of jaw motion and EMG activity and verified sites. However, data were captured in only 3 subjects, and no SMU recordings were made; therefore, some caution should be exercised in data interpretation. Nonetheless, the data strongly suggest that there is regional task-related behavior in the inferior head of the LP.

The case for functional heterogeneity in the superior head of the LP is supported by SMU data. These data reveal that SMUs are associated with multiple tasks, but that task specificity varies regionally within the muscle head. Regional, taskrelated SMU behavior has been reported previously in the masseter and temporalis muscles.^{6,17} Moreover, masseter SMU thresholds have been observed to vary with the motor task, and this suggests "directional tuning" of units.18 The experimental paradigm used by the authors is already complex; however, it would be intriguing to also measure bite force and its direction, as this would potentially provide further evidence for the horizontal jaw movement hypothesis. The authors rightly suggest that, in the light of the new data on LP functional heterogeneity, present theories of TMJ derangement should be reviewed. An appropriate starting point would be the development of a computer model of condyle/disc/muscle relationships informed by data from the present studies and related work by Hiraba et al.7

Electromyographic Activity During Jaw Motion

Previous studies have often inferred links between jaw motion and LP EMG activity without conclusive data gleaned from the simultaneous recording of movement and EMG data. The combined recording of jaw motion and EMG activity at known recording sites in the recent studies of the authors has permitted clear associations to be established, notably during condylar translations. The data indicate that in addition to the acknowledged role of the inferior head in horizontal movements, the superior head is also involved. The authors present clear data for activity in the superior head during contralateral jaw movement involving tooth contact. Additional, simultaneous EMG recordings from other jaw muscles would permit the LP's contribution to horizontal jaw movement to be assessed more comprehensively.

The study of SMU recruitment characteristics over a range of motion revealed that the LP appears to depend predominantly on SMU firing rate modulation for the fine control of horizontal jaw movement. A comparable reliance on rate coding has been observed in the masseter muscle.¹⁹ Given that LP SMUs are associated with multiple motor tasks, it would be useful to determine whether SMU lowest sustainable firing frequency varies with the motor task, as noted previously in masseter and temporalis SMUs,^{6,17} and whether any putative differences are region-specific, as this would provide additional insight into the mechanisms of regional motor control.

The Lateral Pterygoid and Bite Force

Histochemical evidence is provided to support the role of the LP in the generation of bite force, particularly during vigorous chewing and tooth grinding activities. The distribution of type I and IIB fibers does vary between muscle heads, with mainly type I fibers in the inferior part and more type II fibers in the superior part, although overall the majority of fibers are type I. This suggests a prime role in the fine control of jaw motion rather than strong bite force.^{6,20} It is noteworthy that type I fibers are predominant in the jaw muscles generally and that previous data suggest that the physiologic characteristics of jaw muscle SMUs do not correlate well with their histochemical type.²¹

Previous EMG studies have provided supportive data for the LP's role in chewing and tooth clenching and grinding.^{11,22} However, these studies did not involve verification of the EMG recording site, and there was also the possibility of electrode movement during vigorous motor tasks; therefore, these data should be interpreted with care. The authors' SMU data recorded at known sites in the LP do suggest that the muscle is involved in force generation in the horizontal dimension and that there is precise motor control of the process, as observed in the modulation of the SMU firing rate with motor task. Simultaneous EMG recording from multiple jaw muscles would help reveal whether the LP is indeed the prime mover in the movement sequence.

Conclusions

The authors present a strong case for the role of the LP muscle in the generation of horizontal jaw movements based on clear data from known sites in the muscle. These data are pivotal to the understanding of the role of the LP in TMD. The experimental paradigm used in the present studies would be very effective in the exploration of reflex behavior of the LP. There is the potential for investigation of the horizontal jaw reflex²³ as well as the question of sensorimotor partitioning²⁴ within the muscle. Such studies would further elucidate the role of the LP in the generation of horizontal jaw movement.

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CRITICAL COMMENTARY 3

THE ROLE OF THE HUMAN LATERAL PTERYGOID MUSCLE IN THE CONTROL OF HORIZONTAL JAW MOVEMENTS

Eigild Møller, DDS, Dr Odont

Professor Emeritus School of Dentistry Faculty of Health Sciences University of Copenhagen 20 Nørre Allé DK-2200 Copenhagen N, Denmark Fax: +45-35-32-65-69

In their article, Murray et al¹ have stated that their chief aim is to demonstrate that generation and fine control of horizontal jaw movements is the major function of the lateral pterygoid muscle (LP). They succeed in this task by integrating an extensive review of anatomic and functional studies of motor unit activity recorded by bipolar wire electrodes, verified by computed tomography (CT) to be situated within the superior head. With meticulous efforts concerning the physical-

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anatomic aspects of electrode positioning, in their final conclusions they do not support the view of independent functions of the 2 heads, but suggest instead heterogeneity in the actions of either head. In addition, the authors, with remarkable certainty, reject the involvement of the LP in mandibular posture.

The present commentary on the action of the LP is based on a review, an early study of the right and left muscle of 36 subjects,² and new, unpublished data obtained from blockade of muscle activity, including that of the LP, with botulinum toxin A (Botox, Allergan).^{3,4} The LP was approached intraorally with concentric needles² and monopolar cannula electrodes^{3,4} without an attempt to differentiate the action of the 2 heads.

Electrodes

The activity of the LP in general has been assessed by concentric monopolar and bipolar needle electrodes and by bipolar wires inserted by a cannula that is subsequently removed. The bipolar electrode causes a differentiation of the single action potentials⁵ and results in a much more localized pickup than the other needle electrodes. Hence, in spite of identical placement and activity, for physical reasons the concentric and monopolar needle electrodes pick up more activity than the bipolar electrodes, and a priori it is a mistake to use this difference to support one concept or the other.

Attempts to distinguish between the action of the 2 heads of the LP have utilized bipolar wire electrodes with core diameters from 25 to 100 µm, with the core exposed for the last 1 to 2 mm from the tip or only at the tip and an intended distance of 1 to 2 mm between the 2 leads after withdrawal of the insertion needle. The pickup range of the diminutive recording surfaces include only a few muscle fibers, the number being the least and the possibility of signal extinction the greatest if the surfaces happen to be placed perpendicular to the direction of the fibers.^{6,7} If the 4 LP motor units presented in Fig 3 of Murray et al⁸ are looked upon pairwise for each head, the changes in polarity with time in one is a mirror image of the other, meaning that it could be the same motor unit recorded twice. This explanation is ruled out by the marked differences in firing patterns. Most likely the wires acted in a monopolar way, with the reversed changes in polarity with time a result of the position of the recording surfaces in relation to the motor end plates of each unit.

Electrode Positions

The conventional method of guiding and verifying electrode positions is via the electromyographic (EMG) activity pattern seen during deliberate tasks or functions for which the muscle under examination is mechanically well qualified, which in the case of the LP is usually during opening and protrusion. Other previous methods have involved cranial radiographs⁹ or the response to electrical stimulation through the recording electrode.¹⁰ With the EMG test indicating incorrect or uncertain placement, the electrode position is adjusted, but if the pattern of activity then remains unchanged, it must be accepted as correctly positioned for characterizing the action of the LP in the subject or patient under examination.

Adjustment or renewed insertion is easy with needle electrodes. Conversely, once they are inserted and the carrier needle is removed, the position of the wire electrodes cannot be adjusted. Therefore, if recordings are assumed to indicate failure in placement, the unbiased collection of data leaves no alternative but withdrawal and reinsertion. In 3 studies¹¹⁻¹³ cited by Murray et al, data from 2 to 4 subjects were discarded without reinsertion because the EMG test did not substantiate the preconceived view of the action of the superior^{11,12} or inferior¹³ head of the LP.

A system that includes 2 CT imaging sessions has been developed for placement of bipolar wire electrodes in the superior head of the LP and verification of their position¹⁴ while positions in the inferior head were tested via EMG recordings, eg, during full protrusive and contralateral effort.^{1,8,14-17} However, outcomes, conclusions, and possible consequences of these tests are not mentioned except for 1 subject,¹⁴ in whom no electrode reinsertion was reported. Irrespective of imaging efforts for placement and verification of electrode position, the interference pattern is a valuable parameter, eg, for normalization of data, to account for the possible variation by a factor of 2 between closely situated intramuscular sites,² or simply to ensure that the muscle is healthy. With respect to anatomy, placement and verification by EMG recordings and CT imaging seem equally biased.

Postural Activity

A number of multiunit EMG studies using concentric needles,^{2,18–20} bipolar needles,^{13,21} or bipolar wires²² have demonstrated postural EMG activity WITHOUT WRITTEN PERMISSION FROM THE PUBLISHER.

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in the LP. When quantitated, the level of activity was 4% to 6% of that of full effort,^{2,13,19} which is in keeping with the view that mandibular posture is not positional but spatial, including sagittal, vertical, and transverse movements of the mandible.²³ However, in agreement with Ekholm and Siriilä,9 Murray et al have noted that none of 82 motor units from the inferior head of the LP and 26 units from the superior head recorded on 1 or more occasions in 31 subjects were active in the "clinically determined postural jaw position."1 Isometric force trials have demonstrated that motor units in the inferior head have thresholds of 500 to 600 g wt or 5 to 6 N for loads opposing contralateral and protrusive movements.1 For comparison, we measured in a 52-year-old man maximal effort against resistance to 118 N toward the right, 107 N toward the left, and 113 N during protrusion (personal communication, M. Bakke, December 2000). This indicates that the isometric motor unit thresholds were probably in the order of 4% to 5% of full effort. Furthermore, irrespective of their location in the LP, the motor units in Figs 2 and 3 of Murray et al⁸ were recruited during vertical and horizontal movements of the condyle within the limits of the condylar fossa and had thresholds down to 0.1 mm. Motor units active in tasks with a very low demand for power belong to the slow oxidative or type I fibers²⁴ that occupy about 81% of the total cross-sectional area of the LP.25 Hence, although Murray et al¹ claim that none of their motor units were active in the postural jaw position, their findings appear to be in conflict with the motor unit thresholds in their studies,^{1,8} the predominant type of fibers in the LP,25 and previous quantitative multiunit EMG studies.^{2,13,19} In addition, it is difficult to imagine posture with condylar movements less than 0.1 mm.

Deliberate Tasks

The LP contributes with interference patterns of full effort during protrusion, opening, contralaterally directed force per se or during biting, and less vigorously during biting in the intercuspal position.^{2,9,11-13,18,20,21,26-30} It is to the credit of Murray et al¹ that the task-related activity of the LP has been proven at the level of single motor units by distinguishing between units recruited in accordance with the classical platform of the LP (ie, during contralateral and protrusive movements), units that are active during ipsilateral and retrusive movements in an antagonistic mode, and, finally, units that contribute to several different tasks. Hence, they have demonstrated the basis for modulation of the response of inputs to the motor neuron pool of the LP.

The Lateral Pterygoid and Horizontal Jaw Movement

All EMG studies of the LP unanimously support the view that the muscle is active in movements during which the condyles are shifted horizontally. With the attempts to distinguish between the 2 heads came the suggestions of an antagonistic-like action of the superior head,^{11,12,22,31,32} and in some biomechanical models³³ the 2 heads have been separated, with the superior viewed as a jaw-closing muscle and the inferior as a jaw opener. Mathematical modeling with dynamic simulation³⁴ has demonstrated the importance of the LP during opening, including the transition from true hinge movement to combined rotation and translation.

A block of activity of both LPs with injections of botulinum toxin A (Botox) reduced maximal activity to 10% and almost eliminated protrusive and lateral movements, while opening capacity measured in mm at the incisors was unchanged (Table 1). However, the track of incisor movement ran continuously to maximal opening without the normal break forward, corresponding to the transition into translation (Fig 1a). Since the subsequent closing movement, until about 10 mm below the intercuspal position (ICP), obviously followed a track 5 to 10 mm anterior to the opening path, the condyles must have slid forward on the tuberculum in the final phase of opening. At this time, masticatory movements in the frontal plane were narrow, with a maximal width of 6 mm halfway down. At repeated recordings 74 days later, lateral movements were almost restored, but protrusion was restored to only about 50% (Table 1). Nevertheless, the opening movements showed distinct transition from hinge to translation at the typical spot in the opening movement about 20 mm below ICP, and the width of the frontal envelope had increased to 10 mm (Fig 1b).

The concept of antagonism between the 2 heads may be a misinterpreted attempt to fit the LP into the conventional frame of jaw-openers and jawclosers due to co-contraction. Instead, the concept should be perceived in view of its unique qualifications to move the condyles horizontally, eg, as in a right-sided chewing cycle (Fig 2). With a phaseangle displacement of 90 degrees, the 2 LPs are almost continuously active, with the ipsilateral LP strongest in the last half of closing in a contralat-

Parameter	Time before/after block			
	-2 days	+35 days	+111 days	+169 days
Postural activity (µV)				
Right	98	8	20	43
Left	104	14	29	47
Maximal activity (μV)				
Right	388	27	238	298
Left	409	40	200	257
Overjet, relaxed posture (mm)	4.5*	2.5	2.5	2.5
Jaw opening (mm)	52	55	53	54
Laterotrusion (mm)				
Right	13	2	11	12
Left	13	1	11	11
Protrusion (mm)	11	0	6	12

Table 1EMG and Clinical Data Gathered Before and After EMG-Guided Blockof the Right and Left Lateral Pterygoid Muscles with Botulinum Toxin A in a 62-Year-Old Woman with Focal Dystonia of the Lateral Pterygoid Muscles

*ie, a mandibular overjet (negative overjet); all other numbers in row represent maxillary overjet.

Corresponding diagrams of jaw movements during mastication in Fig 1 are based on recordings from day +35 and day +111. Data were kindly provided December 2000 by the Danish National Group for the Treatment of Oromandibular Dystonia^{3,4} from an unpublished manuscript.

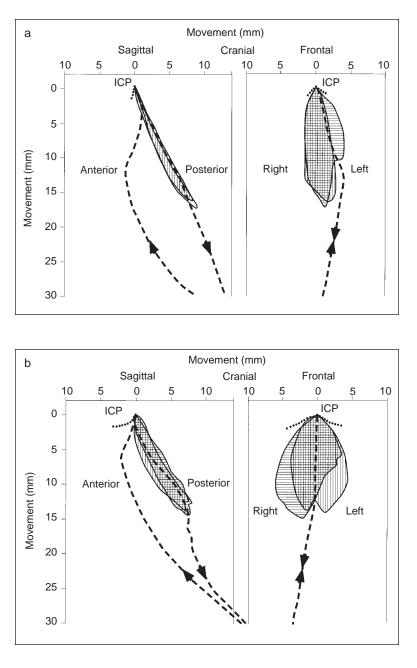
eral direction through ICP and during the first half of opening, and the contralateral LP dominating from half-open to half-closed. Hence, there is a close association between jaw position and EMG activity.³⁵

Murray et al¹ point to the crucial importance that the LP must have in the control of protrusive and/or side-to-side movements of the mandible occurring in time with vigorous elevator activity, eg, during heavy mastication. This notable statement implies precise synchronization of the LP and elevator muscles during the phases of closing and tooth contact (see Fig 2). With the 90-degree phase displacement angle of the LP in relation to open/close, the horizontal aspects of jaw movement could very well be managed by a single LP, but the 2 almost coherent bursts in each cycle may result in considerable strain. If the classical and antagonistic units¹ took turns according to the task-related preferences of their motor neurons, the strain would decrease. Since bipolar wire electrodes are able to distinguish and monitor the activity of single motor units almost to full effort,^{6,7} the authors of this focus article¹ should be able to solve this problem.

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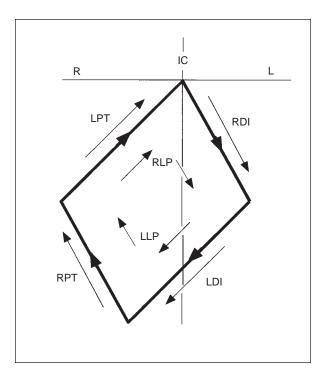
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Møller



Figs 1a and 1b Graphic assessment of mandibular movements of the mandibular incisors at 36 (a) and 114 (b) days after injection of botulinum toxin A into the right and left LPs (same subject as in Table 1). Movement envelopes of chewing: horizontal lines = right-side chewing, vertical lines = left-sided chewing; ICP = intercuspal position; dotted lines = contact movements; dashed lines = opening and closing movements; superimposed arrows = direction. Note restricted protrusive and lateral movements, narrow envelopes, and the straight track during opening at 36 days, and in contrast the larger horizontal movements, wider envelopes, and the opening track broken by the transition from hinge movement to combined translation and rotation at 114 days. Recordings²³ made with the Sirognathograph, Siemens AG, type D 3175. Data were kindly provided December 2000 by the Danish National Group for the Treatment of Oromandibular Dystonia^{3,4} from an unpublished manuscript.

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Fig 2 Phases of movement and muscle activity in a right-sided chewing stroke. The trapezoid represents movements of the mandibular incisors in the frontal plane (facing the subject). Superimposed arrows indicate direction of movement. R = right side; L = left side; IC = intercuspidation. Separate arrows indicate predominance of the different muscles moving the mandible: RDI/LDI = right and left digastric; RPT/LPT = right and left posterior temporal; RLP/LLP = right and left lateral pterygoid muscles. Note that RLP/LLP are activated with a phase angle displacement of 90 degrees relative to RDI/LDI and RPT/LPT. Diagram based on averaged data from Møller³⁵; reprinted with permission.

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Greg M. Murray, MDS, PhD (Tor), FRACDS Intira Phanachet, DDS Shinji Uchida, DDS, PhD Terry Whittle, BSocSci

The commentaries by Drs Herring,¹ McMillan,² and Møller³ have raised a number of very important points. The 3 authors were in general agreement with our fundamental hypothesis that one of the major roles of the lateral pterygoid muscle (LP) is in the generation and control of horizontal jaw movements. They also agreed that the available evidence supports functional heterogeneity within the LP.

Herring queried whether the single motor units (SMUs) that we attributed to the lateral part of the superior head (SHLP) of the LP could simply represent crosstalk from the adjacent deep temporalis. Although possible, this is unlikely in light of our recent recordings from the deep temporalis (verified by computed tomography [CT]) that show spontaneous SMU activity at postural jaw position; LP SMUs at CT-verified SHLP sites were never spontaneously active at the postural jaw position.

We agree with Herring that the LP shares characteristics in common with the other jaw muscles, for example, functional heterogeneity has been well described in other jaw muscles. Although the data from SHLP is quite convincing on this issue, the data from the IHLP is less so, being, as McMillan points out, from a limited number of subjects. However, we have recent SMU evidence of recruitment reversals in IHLP during different tasks, thus strengthening the evidence for IHLP.

The paper may not have been entirely clear in asserting that just *one* of the major functions of the LP is in the control of horizontal jaw movements; the LP is also involved in jaw opening. In addition, we used the term "horizontal" to embrace lateral or protrusive movements, and we agree entirely with Herring that the LP plays an important role in protrusion. Although McMillan suggested that the evidence points to firing rate modulation in LP in the fine control of horizontal displacements, further data are needed to examine the role of recruitment.

Herring also made the point that the LP is probably not a major source of muscle force in any direction, and McMillan mentioned the need to record from other jaw muscles. Recent multiunit electromyographic (EMG) data from the IHLP, masseter, temporalis, and the submandibular group of muscles during the same horizontal isometric tasks point to a closer association between changes in IHLP activity levels and changes in force than for the other jaw muscles. The data suggest an important role for the IHLP in the generation of horizontal forces.

Møller considered that the bipolar fine-wire electrodes acted in a monopolar way; however, the difference in firing patterns of all simultaneously recorded SMUs⁴ argues against this. Møller also felt that we were using this type of electrode to support our hypothesis. We wished to record SMUs to test our hypothesis, and the bipolar finewire electrode is well suited to recording the firing rates and recruitment patterns of SMUs in deep muscles during fine movements; in addition, it allows the unequivocal differentiation between EMG activity and background noise. Møller also commented that verification of electrode location by EMG and CT imaging seems equally biased. However, the functional complexity of the SHLP underscores the importance of avoiding the use of the EMG pattern alone to verify electrode location.

The lack of SMU activity in the clinically determined postural jaw position observed in our study was questioned by Møller. By comparing results from our study and a personal communication (Bakke), Møller considered that our isometric thresholds were probably 4% to 5% of full effort, that is, at the same level at which they and others had previously recorded postural activity. However, the results from our study and Bakke's study are probably not comparable, since the methods that Bakke used to record force were not specified and the methods are likely to influence the force output recorded at maximum effort. Further, SMU recordings allow the unequivocal discrimination of EMG activity from background noise. There was never any EMG activity in LP at

the postural jaw position that started each horizontal movement trial in our study. In addition, we have no difficulty reconciling the low thresholds of a few of our SMUs with the absence of spontaneous activity at postural jaw position. Indeed, the low thresholds of some of our units support the notion that the LP is involved in the early phases of these horizontal movements.

We would like to thank all 3 commentators for their critical commentaries and their excellent suggestions for further research. For example, McMillan suggested, among other things, the need to study LP activity during reflex behavior, lowest sustainable firing frequencies, different directions of bite force, and to develop a computer model of condyle/disc/muscle relationships.

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