Functional Properties of Single Motor Units in the Inferior Head of Human Lateral Pterygoid Muscle: Task Firing Rates

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Received 3 December 2001; accepted in final form 22 March 2002.

Phanachet, I., T. Whittle, K. Wanigaratne, and G. M. Murray. Functional properties of single motor units in the inferior head of human lateral pterygoid muscle: task firing rates. J. Neurophysiol. 88: 751–760, 2002. The precise function of the inferior head of the human lateral pterygoid muscle (IHLP) is unclear. The aim of this study was to clarify the normal function of the IHLP. The hypothesis was that an important function of the IHLP is the generation and fine control of horizontal (i.e., anteroposterior and mediolateral) jaw movements. The activities of 50 single motor units (SMUs) were recorded from IHLP (14 subjects) during two- or three-step contralateral movement (n = 36) and/or protrusion (n = 33). Most recording sites were identified by computer tomography. There was a statistically significant overall increase in firing rate as the magnitude of jaw displacement increased between the holding phases (range of increments: 0.3–1.6 mm). The firing rates during the dynamic phases for each unit were significantly greater than those during the previous holding phases but less than those during the subsequent holding phases. For the contralateral step task at the intermediate rate, the cross-correlation coefficients between jaw displacement in the mediolateral axis and the mean firing rate of each unit ranged from $r = 0.29$ to $0.77$; mean ± SD: $r = 0.49 ± 0.13$ (protrusive step task: $r = 0.12–0.74$, $r = 0.44 ± 0.14$ for correlation with anterior–posterior axis). The correlation coefficients at the fast rate during the contralateral step task and the protrusive step task were significantly higher than those at the slow rate. The firing rate change of the SMUs per unit displacement between holding phases was significantly greater for the lower-threshold than for the higher-threshold units during contralateral movement and protrusion. After dividing IHLP into four regions, the SMUs recorded in the superior part exhibited significantly greater mean firing rate changes per unit displacement during protrusion than for the SMUs recorded in the inferior part. Significantly fewer units were related to the protrusive task in the superior–medial part. These data support previously proposed notions of functional heterogeneity within IHLP. The present findings provide further evidence for an involvement of the IHLP in the generation and fine control of horizontal jaw movements.

INTRODUCTION

The human lateral pterygoid muscle (LP) has been implicated as playing an important role in the control of jaw movement and, by virtue of its direct insertion into the condyle and disk-capsule complex of the temporomandibular joint (TMJ), in the control of TMJ function (Dubner et al. 1978; McNamara 1973; Wilkinson 1988). However, there is limited and sometimes conflicting information as to the functions of the LP in jaw movements (Murray et al. 2001; Phanachet et al. 2001b). The LP has also been implicated in the etiology of temporomandibular disorders, a major cause of nondental orofacial pain, although there is very limited understanding of the role of this muscle in temporomandibular disorders.

Most previous studies appear to suggest that the level of activity of the inferior head of the LP (IHLP) is correlated with the magnitude of anterior condylar translation. For example, monotonic relationships between IHLP electromyographic (EMG) activity and some kinematic parameters of jaw movement have been demonstrated by Hiraba et al. (2000). Multi-unit and single motor unit (SMU) EMG studies have also revealed close associations between IHLP activity and small fluctuations in condylar movement and a high correlation between condylar displacement and smoothed EMG activity of IHLP during horizontal jaw movements (i.e., protrusion and contralateral movement) (Murray et al. 2001), and this is consistent with other studies (e.g., Hiraba et al. 1995, 2000; Kamiyama 1961; for reviews, Hannam and McMillan 1994; Klineberg 1991; Miller 1991). Further, our studies of SMU thresholds have provided evidence supporting a role for IHLP in the fine control of these horizontal jaw movements (Phanachet et al. 2001b). First, successively recruited IHLP SMUs could be recruited at small increments (<1 mm) of jaw displacement. Second, the lowest thresholds of the SMUs were <0.2 mm of horizontal jaw displacement, suggesting that the IHLP is involved in the initiation of the movement. Third, the recruitment thresholds of some units varied in association with different rates of jaw movement in the horizontal plane, suggesting that these units were concerned with subtle changes in the rate of jaw movement.

Suggestive evidence has also been recently provided supporting previously proposed notions of functional heterogeneity within IHLP (Foucart et al. 1998; Hannam and McMillan 1994; Murray et al. 1999c, 2001; Phanachet et al. 2001b). For example, SMUs recorded in the superior–medial part of the IHLP have been shown to exhibit significantly lower mean threshold values for contralateral movement and protrusion than for the SMUs recorded in the other parts. These data suggest that the units in this part were important in initiating these jaw movements. Anatomically, the IHLP has a broad origin at the lateral surface of the lateral pterygoid plate and converges onto the pterygoid fovea of the condyle. The fiber

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lines of action diverge mediolaterally and superoinferiorly from the mandibular condyle. This marked divergence would allow directional pull over a wide angulation if there were selective activation within the muscle. These data indeed allowed us to hypothesize that specific regions of the IHLP were capable of selective activation in a finely controlled manner to allow the application of the appropriate force vector to effect the required condylar movement needed for the generation and control of horizontal jaw movements.

Another SMU property that should correlate with small changes in the magnitude of horizontal jaw displacement is firing rate. In the present study, we use precise quantification of SMU firing rates at spatially identified sites during standardized tasks to address the hypothesis that the IHLP is concerned with the generation and control of horizontal jaw movements. These data will also provide baseline information on the firing rate properties of IHLP SMUs in asymptomatic individuals as a prelude to the study of patients with temporomandibular disorders.

The aims of this study therefore were 1) to determine whether there is an association between the firing rates of SMUs within IHLP and horizontal jaw movement tasks and 2) to identify whether there was a relation between CT-verified location and firing rate consistent with a proposal for functional heterogeneity within IHLP. Some of these data have been briefly reported (Phanachet et al. 2000).

METHODS

Fourteen human volunteers without signs and symptoms of TMD (age 20–41 yr; 11 males, 3 females) and without any history of chronic pain or neuromuscular condition participated in this study. All subjects gave informed consent and approval for experimental procedures was granted by the Western Sydney Area Health Service Ethics Committee of Westmead Hospital and the Human Ethics Committee of the University of Sydney. Most of the methods have been previously described in detail elsewhere (Murray et al. 1998a,b; Orfanos et al. 1996; Peck et al. 1997; Phanachet and Murray 2000; Phanachet et al. 2001a,b). and the following will review these methods and detail those methods not previously described.

Electrode placement within IHLP

Single motor units were recorded from the IHLP with bipolar Teflon-coated stainless-steel wire electrodes. A curved spinal needle carrying the fine wires was advanced through the oral mucosa (pretreated with topical anesthetic) above the level of the upper second molar tooth to contact the lateral surface of the lateral pterygoid plate. The needle was then withdrawn, leaving the wires within the IHLP. The wires were led out through the angle of the mouth. At the end of each recording session, five to nine computer tomographic (CT)-axial slices (1–3-mm thick) were taken inferior to and parallel with the Frankfort Horizontal Plane to confirm electrode placement. Verification data have been previously published for the subjects used in this paper (Phanachet et al. 2001b). The data-acquisition equipment was the micro1401 from Cambridge Electronic Design (CED, Cambridge, England) and the sampling rate was 10,000 samples/s and bandwidth 100 Hz to 10 kHz. Single motor units were discriminated with Spike2 software from CED. Power spectral analysis revealed that the highest frequency component of the SMU spike train was <4,000 Hz.

For the purposes of assessing the location of electrode recording site within IHLP, the muscle was arbitrarily divided mediolaterally into medial and lateral parts and superoinferiorly into superior and inferior parts. Location was assessed by viewing the electrode tip in relation to the muscle boundaries on a horizontal CT scan through the electrode tips. The amount of bend back of the wires (2–3 mm) was taken into account for assigning location. Previous histological studies (Meyenburg et al. 1986; Widmalm et al. 1987) have indicated that the superior head of the LP is approximately 5-mm-thick supero-inferiorly and we therefore adopted this criterion for identifying the upper boundary of the IHLP. The remainder of the LP extending inferiory to the lower border of the lateral pterygoid plate was considered to be IHLP.

Recording of condylar and midincisor point movement

The movement of the midincisor point (MIPT) was recorded with an optoelectronic jaw tracking system (JAWS3D, Metropoly AG, Zurich, Switzerland) (Mesqui and Palla 1985) with a sampling rate of 67 samples/s. Three charge-coupled devices (cameras) recorded the relative displacement of two target frames. One target frame, containing three light-emitting diodes (LEDs) arranged in a triangle, was attached to the maxilla and the other to the mandible by custom-made metal clutches. The plane of each target frame was oriented parallel to the sagittal plane, and the longer arm of each target frame was oriented parallel with the Frankfort Horizontal Plane. The origin of the coordinate system for jaw displacement display was the MIPT. During all recordings, the subjects sat in an upright position without head support. Any associated head movement did not influence the measurement of lower jaw motion since mandibular jaw movement was recorded in relation to the maxilla. The position of the subject’s MIPT in the horizontal plane was displayed as a dot (termed MIPT dot) on a video screen positioned in front of the subject. All jaw movements were performed with the teeth apart, and movements started from the postural jaw position after 2–3 s. Subjects were instructed to swallow and relax their jaws with their lips lightly touching to achieve the postural jaw position.

Standardized tasks

Jaw movements were standardized by having the subject move the position of the MIPT dot, so as to track a computer-controlled target (Fig. 1). The target was an illuminated LED as part of a linear bank of LEDs positioned over the video screen and to the side of the trajectory of the MIPT dot (Fig. 1A, filled diamond). The LEDs were controlled by scripts written in Spike 2 software (CED). Movement of the MIPT dot from the location at one illuminated LED to the location at the next illuminated LED corresponded to 0.33, 0.65, or 1.3 mm of movement at the subject’s MIPT, depending on the display gain on the video screen. After performing a few trials of contralateral or protrusive jaw movement to become accustomed to the task, the bank of LEDs was oriented along the direction of movement of the MIPT dot in the horizontal plane. The Spike2 software illuminated the LEDs in sequence and the subject was instructed to move the jaw so the MIPT dot on the screen followed the illuminated LED as smoothly as possible. This program allowed adjustment to the rate and magnitude of jaw movement by controlling LED illumination. Three rates were defined: 6.5 mm/s (fast), 2.2 mm/s (intermediate), and 1.3 mm/s (slow). The magnitude of displacement was controlled by the highest LED that was illuminated in the bank. The amount of jaw displacement and the increment of jaw displacement during each task were determined by assessing the magnitude of jaw displacement required to allow one or more SMUs to be recruited and still able to be discriminated throughout trials. The criteria for defining a SMU were similarities in amplitude and waveform between all representatives of an identified SMU.

Each trial contained two to three dynamic and holding phases. A holding phase was defined as the period (3–5 s) during which the MIPT plot showed little or no fluctuation from a stable level. A dynamic phase was defined as the period from the onset of jaw movement to the onset of the first holding phase (Fig. 1, D1) or from
the end of one holding phase at one target to the next holding phase at the next assigned target (Fig. 1, D2 or D3). In this experiment, the holding phases at the first, second, and third steps were named H1, H2, and H3, respectively. Figure 1 displays an example of a trial in which the target is tracked by moving the jaw to the first assigned target (H1; e.g., Fig. 1B, LED No. 3). The jaw was maintained in that position for 3 s. The jaw was then moved a further small amount laterally to the next assigned target (e.g., Fig. 1B, LED No. 5) and again maintained in that position for 3 s. The subject then moved the jaw to the final target (LED No. 7) for 3 s. Each subject was required to hold the MIPT dot as much as possible within the boundaries of the LED that was illuminated for the holding-phase period of the step displacement. To conclude the trial, the jaw was moved back to the postural position by following a preset target LED sequence (Fig. 1B, R). In some subjects, only two-step displacements were performed due to the difficulty of SMU discrimination at the larger magnitudes of displacement. The tasks were termed the contralateral (or protrusive) two-step (or three-step) tasks. Trials for different rates of movement were repeated five to eight times. The experimental recording period lasted 3–4 h. Before experimental recordings were carried out, the maximum lateral and protrusive jaw displacement were measured in each subject.

Data analysis

For each subject, MIPT displacement data for each task-defined movement were plotted along the anterior–posterior (x), mediolateral (y), and superior–inferior (z) axes for contralateral and protrusive jaw movement. For an analysis of firing-rate changes during the tasks, an assessment of firing rate was made for the units that fired continuously through at least two steps of displacement. Firing rate was calculated as the inversion of the average interspike interval during a holding or dynamic period. According to previous studies, the least sustainable firing frequency of facial motor units was /H110116 imp/s (Eriksson et al. 1984; McMillan 1993); therefore, an interspike interval /H11022160 ms was considered to be a pause and was excluded from the analysis. The General Linear Model (GLM) repeated-measures analysis was used to compare the firing rates of units during the holding phases and the firing rates during dynamic and holding phases.

A cross-correlation was performed between the amount of jaw displacement along the x- or y-axis and the mean frequency (100-ms binwidth, CED software) for each defined task. For each unit, jaw displacement and matched mean frequency were normalized to the same number of data points. Both jaw displacement and mean frequency from five to eight trials for each task were then concatenated, and cross-correlation analysis was performed. Correlation coefficients
at the slow and fast rates of movement for each SMU were compared by the paired t-test. A $P$ value of $< 0.05$ was considered a statistically significant difference.

RESULTS

A total of 50 SMUs were recorded from CT-verified sites in IHLP. Of these 50 units, 17 were studied only during the contralateral jaw task, 14 only during the protrusive jaw task, and 19 were studied in both contralateral and protrusive jaw tasks. Not all units were able to be discriminated in both tasks.

Firing rates and rates of movement

The firing rates at each holding phase during contralateral movement were studied for 36 SMUs (33 units in protrusion). For both contralateral movement and protrusion, the firing rates at each holding phase were not significantly different between the two or three rates of movement studied for each SMU ($P > 0.05$, Wilcoxon signed-rank test). Also, for each SMU, there was no statistically significant difference in the firing rates during the dynamic phases as the rate of movement changed ($P > 0.05$, Wilcoxon signed-rank test). Therefore, for each SMU, the data obtained from the different rates of movement were combined for the analysis of firing rate changes during the holding and dynamic phases.

Comparison of firing rates at different holding phases

There was a statistically significant overall increase in firing rate as the magnitude of jaw displacement increased between holding phases when the data from all SMUs were analyzed during the contralateral step task and the protrusive step task ($P < 0.001$, GLM repeated measures). The range of an increment in jaw displacement during the contralateral step task or the protrusive step task was 0.3–1.6 mm. Individual SMU analysis showed that 25 of 36 (70%) and 25 of 33 (76%) SMUs studied during the contralateral step task and the protrusive step task, respectively, showed a significant increase of firing rate with jaw displacement ($P < 0.05$, GLM repeated measures). Twelve of each group of 25 units, which showed a significant increase in firing rates during the contralateral and protrusive step tasks, were the same units. None of the units showed significant decreases in activity with increases in displacement.

Representative data for a unit showing a significant increase in firing rate during a three-step contralateral task is shown in Fig. 2. The firing rate of the unit, averaged from five trials (spike-train pulses in Fig. 2B), at a displacement of 2.9 mm (H1) was 19.2 imp/s, which then increased to 20.9 and 24.9 imp/s at 3.5 and 4 mm of jaw displacement (H2 and H3), respectively. Data from another representative unit that showed a significant increase in firing rate during protrusion are illus-
trated in Fig. 3. The pauses in SMU firing during the fifth trial were attributed to slight variations in jaw movement from trial to trial.

Figure 4 shows graphs of the firing rates of 25 units exhibiting significant increases in firing rate during the contralateral step task (Fig. 4A) and the protrusive step task (Fig. 4B). The nonsignificant units have been omitted for clarity. The displacement at the first holding phase for each unit was just above the threshold of firing. Therefore, the units could be recruited up to approximately 95% (i.e., 9 mm) of the average maximum contralateral jaw displacement (9.4 ± 1.7 mm, mean ± SD) or approximately 73% (5.7 mm) of average maximum protrusive displacement (7.8 ± 2.1 mm). The firing rates of the SMUs at the first step levels shown in Fig. 4 were >12 imp/s and these rates were just greater than the least-sustainable firing frequencies of the IHLP units observed in the present study (range: 11–24 imp/s). These values were greater than those reported for the other jaw muscles (i.e., 5–8 imp/s for the temporalis units) (Eriksson et al. 1984; Hannam and McMillan 1994).

Cross-correlation between mean firing rate and jaw displacement

An assessment was made of the closeness with which variations in SMU firing rates correlated with variations in the magnitude of jaw displacement. This was done by performing a cross-correlation between averaged SMU firing rates and jaw displacement (see METHODS). For the contralateral step task, the cross-correlation coefficients between jaw displacement in the y axis (mediolateral axis) at the intermediate rate and the mean firing rate of each unit ranged from $r = 0.29$ to $0.77$ ($r = 0.49 ± 0.13$; mean ± SD; $n = 36$). For the protrusive step task, the cross-correlation coefficients between jaw displacement in the x axis (anterior–posterior) at the intermediate rate and mean firing rate ranged from $r = 0.12$ to $0.74$ ($r = 0.44 ± 0.14$; $n = 33$).

For the contralateral step task and the protrusive step task, the correlation coefficients for each unit were compared between the fast and slow rates. This was done to determine whether changes of a parameter of jaw movement (i.e., rate) affected the closeness between the firing rate and displacement. The correlation coefficients at the fast rate during the contralateral step task ($n = 28$ units) and the protrusive step task ($n = 19$) were significantly higher than for the corresponding tasks at the slow rate ($P < 0.05$, paired $t$-test).

Comparison of firing rates during holding and dynamic phases

A study was made of the role of firing-rate modulation in IHLP in the control of the dynamic and holding phases during contralateral or protrusive horizontal jaw displacements. Firing rates were compared statistically for 36 SMUs studied during
A Contra lateral task

![Graph A](image)

B Protrusive task

![Graph B](image)

**Fig. 4.** Graphs demonstrating firing rates for the 25 IHLP SMUs that showed significant change in firing rate with an increase of jaw displacement to the contralateral side (A) and in protrusion (B). The firing rates increase with an increase of jaw displacement. Nineteen of the units were the same in A and in B. Note that the increment of jaw displacement varies for individual units.

Firing rate changes and thresholds

Previous studies in limb and jaw-closing muscles have demonstrated that the change in firing rates per unit force was greater for low- than for high-threshold units (Derfler and Goldberg 1978; Freund et al. 1975; Tanji and Kato 1973). To address this aspect in our data, the units showing a significant increase in firing rate between the holding phases (25 units for each contralateral and protrusive step task) were divided into two groups for each direction of movement: 1) the units that started firing continuously at an amount of displacement of <4 mm (arbitrarily termed “low-threshold” SMUs; n = 12 for contralateral task and 14 for protrusion) and 2) the units that started firing continuously at an amount of displacement of >4 mm (arbitrarily termed “high-threshold” SMUs; n = 13 for contralateral task and 11 for protrusion). The change in firing rate of the units per unit displacement between the first and second step was calculated. For example, the firing rate at H1 was subtracted from that at H2 and divided by the amount of the increment of the jaw displacement between these two holding phases. For the contralateral step task, the mean (±SD) firing-rate change for the low-threshold units was 3.9 ± 1.7 imp s⁻¹ mm⁻¹ (3.8 ± 1.7 imp s⁻¹ mm⁻¹ for protrusion) and 1.9 ± 0.9 imp s⁻¹ mm⁻¹ for the high-threshold units (1.6 ± 0.9 imp s⁻¹ mm⁻¹ for protrusion). There was a significant difference between the firing rate changes of low- and high-threshold units for the protrusive task (P < 0.05, one-tailed t-test), but not for the contralateral task (P = 0.06). The firing rate change of the units between the second and third step was tested in the same manner. The mean firing rate change for the low-threshold units during both contralateral movement and protrusion (1.8 ± 0.9 for contralateral movement and 1.9 ± 1.4 imp s⁻¹ mm⁻¹ for protrusion) was significantly greater than for the high-threshold units (0.8 ± 0.4 for contralateral movement and 1.1 ± 0.4 imp s⁻¹ mm⁻¹ for protrusion) (P < 0.05, one-tailed t-test).

Firing rate changes and recording-site locations: evidence for functional heterogeneity

The number of units studied for firing rate changes in relation to location is shown in Table 1. The firing rate change of units located in the superior part (3.3 ± 0.5 imp/s; mean ± SD) was greater than that of units in the inferior part (1.7 ± 0.4 imp/s) during the protrusive step task (P < 0.05, Mann–Whitney U test). For the contralateral step task, the comparison between the firing rate change of units located in the superior part (3.3 ± 0.5 imp/s) and the inferior part (1.7 ± 0.4 imp/s) was not significant (P = 0.1). The firing rate changes in both step tasks were also observed during D3 and H3 and during protrusion. Figures 2C and 3C show firing-rate changes during the contralateral step task for one SMU and the protrusive step task for another SMU.

TABLE 1. Units showing a significant increase in firing rates and total units in relation to location within the IHLP during contralateral and protrusive step tasks

<table>
<thead>
<tr>
<th>Location</th>
<th>Superior-Medial</th>
<th>Superior-Lateral</th>
<th>Inferior-Medial</th>
<th>Inferior-Lateral</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Contralateral task</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Significant increase in firing rates</td>
<td>8 (73)</td>
<td>8 (80)</td>
<td>3 (75)</td>
<td>ND</td>
<td>19*</td>
</tr>
<tr>
<td>Nonsignificant increase in firing rates</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>ND</td>
<td>6*</td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>10</td>
<td>4</td>
<td>ND</td>
<td>25</td>
</tr>
<tr>
<td><strong>Protrusive step task</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Significant increase in firing rates</td>
<td>2 (20)</td>
<td>10 (100)</td>
<td>8 (100)</td>
<td>ND</td>
<td>20*</td>
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<tr>
<td>Nonsignificant increase in firing rates</td>
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<td>0</td>
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<tr>
<td>Total</td>
<td>10</td>
<td>10</td>
<td>8</td>
<td>ND</td>
<td>28</td>
</tr>
</tbody>
</table>

Values in parentheses are percentages. ND, no units recorded in this part of the muscle. * Computer tomography was unavailable for 6 units (contralateral) and 5 units (protrusion). † Computer tomography was unavailable for 5 units (contralateral).
and inferior parts has not been carried out due to the small sample size for units in the inferior part. There was no statistically significant difference between the firing rate change of units located in the medial and lateral part (P > 0.05, Mann-Whitney U test) during the contralateral or protrusive step task.

The percentage of units showing a significant increase in firing rates during the protrusive step task (20%) was lower in the superior–medial part of the IHLP than that recorded in the two other regions of the IHLP (each 100%) (Table 1). Within the superior–medial part, the percentage was greater during the contralateral step task than during the protrusive step task and was comparable to those in the other two regions (Table 1).

**Discussion**

The present study extends our previous report of IHLP SMU thresholds that provided evidence for a role for the IHLP in the fine control of horizontal (i.e., anteroposterior and mediolateral) jaw movements (Phanachet et al. 2001b). The data demonstrate a significant association between IHLP SMU firing rates and horizontal jaw displacement and provide good evidence for an involvement of the IHLP in the generation and fine control of horizontal jaw movements. First, the firing rates of most IHLP SMUs increased as jaw displacement increased in small increments (i.e., as low as 0.3 mm of MIPT displacement) from one holding phase to the next. This suggests a role for IHLP in the holding phase of each task. Second, there was a significant correlation between jaw displacement and mean firing frequency. Third, firing rates were significantly greater during the dynamic in comparison with nearby holding phases, which suggests that IHLP is concerned with the generation of these dynamic phases. We attribute the absence of a significant effect on firing rates during different rates of horizontal jaw movement to methodological issues (see following text).

Previous limb (Freund et al. 1975; Seki and Narusawa 1996; Tanji and Kato 1973) and jaw muscle studies (Derfler and Goldberg 1978; Uchida et al. 2001) have shown that motor units increase firing rates as force increases during isometric contractions. Although there are no studies detailing jaw muscle SMU activity during standardized isometric tasks, there have been in other motor systems. For example, a linear change in SMU firing rates has been observed in the human medial or lateral rectus muscles during stepwise horizontal eye movements (Sindermann et al. 1978). Also, motoneurons in the inferior rectus muscle in monkeys exhibited progressive increases in firing rates during stepwise saccades in one direction (Henn and Cohen 1972). The new firing rate level was maintained until the next shift in eye position. Although force was not measured in these eye tasks or in the present study, the SMUs are most likely increasing their firing rates to overcome progressive increases in passive tensions associated with progressive horizontal displacement of the eye or jaw. Horizontal passive tensions have not been measured in the jaw motor system but have been assessed during jaw opening (e.g., Koolstra and van Eijden 1997; Peck et al. 2000).

Some units did not exhibit significant differences in firing rates at different displacement levels because some may have already reached their maximal firing rates at the second step level and/or the small number of trials may have reduced the possibility of identifying statistically significant differences.

**Role of the IHLP in jaw movement**

A role for the IHLP in the fine control of horizontal jaw movements concurs with previous multiunit IHLP EMG studies that demonstrated close associations between IHLP activity and small fluctuations in condylar movement during contralateral or protrusive jaw movements (Murray et al. 1999a). Linear changes in IHLP EMG activity have also been observed in studies from IHLP that have recorded anterior condylar translation during jaw-opening movements (Hiraba et al. 2000). We have also recently demonstrated small increments in horizontal displacement between successively recruited IHLP SMUs, and some SMUs had thresholds of <0.2 mm, suggesting a role in the initiation of these horizontal movements (Phanachet et al. 2001b). Further, the observation that some SMU recruitment thresholds were rate dependent points to an involvement of the IHLP in the control of subtle changes in the rate of jaw movement (Phanachet et al. 2001b).

This involvement of the IHLP in the fine control of horizontal jaw movements is also supported by histochemical evidence and the muscle’s internal architecture. Histochemically, IHLP consists predominantly of muscle fibers expressing myosin heavy chain type I (approximately 69% of pure and hybrid fibers) (Korfage and van Eijden 2000) that appear to be suited to fine control. The IHLP contains long fibers (approximately 22 mm) (Hannam and McMillan 1994; Schumacher 1961; van Eijden et al. 1995, 1997) with small cross-sectional areas and many sarcomeres in series. The fibers tend to be arranged along the same line of action with little pennation (Widmalm et al. 1987). This architecture is more suited to shortening over longer distances (and isotonic contractions) than for the heavily pennated architecture in the masseter and medial pterygoid muscles that are more suited for high-power generation over short distances and isometric contractions (Hannam and McMillan 1994; van Eijden et al. 1995, 1997).

The data therefore suggest a role for the IHLP in horizontal jaw positioning in mastication and speech. In the closing phase of the chewing cycle, it is necessary for the jaw to achieve a trajectory that results in the teeth shearing smoothly past each other. The IHLP would appear to be involved here and previous studies do show contralateral IHLP activity during the closing phase (Miller 1991). The IHLP may also play a role around the intercuspal phase during which much higher forces are generated as food is comminuted between the teeth (Wood et al. 1986). Although our data were derived from a low-force task and therefore do not bear on this issue, clear associations have been demonstrated between IHLP SMU firing rate and the magnitude of horizontally directed contralateral forces (Uchida et al. 2001). Further studies involving isometric tasks are needed to confirm this role of the IHLP in the generation of large horizontal forces.

The same precise control of horizontal jaw movements is also required during speech that involves movement of the jaw with the teeth apart in a manner similar to the protrusive task employed in the present study. For example, some fricative sounds require precise anteroposterior positioning of the lower jaw so that incisal edges are correctly positioned and nearly touching in relation to each other for the articulation of a clear “s” sound (Ladefoged 2001). Our data clearly support a function of the IHLP in this positioning.

We propose that the higher correlation coefficients between
jaw displacement and mean firing frequency at the fast rather than the slow rate of movement principally relates to differences in unit activity during the initial dynamic phase. Since the thresholds of units were lower at the fast rate of movement (Phanachet et al. 2001b), there would have been a longer early dynamic phase to correlate with the jaw displacement data at the fast rate. The higher thresholds at the slower rates mean that there is a shorter period over which correlations between displacement and firing rates can be obtained and could contribute to the reduced correlation coefficients at these slower rates of movement. The firing rates during the holding phases and during the dynamic phases between the holding phases were shown not to be different between the different rates of movement.

We nonetheless believe that the observations of a difference in correlation coefficients between rates as well as the significant difference between firing rates at the dynamic and holding phases (e.g., Fig. 2C) do indeed point to a relationship between rate of movement and firing rate. An explanation for the absence of a significant difference between firing rates with different rates of movement is that there was an inability to control precisely the rate of jaw movement over the smallest displacements employed in this study, that is from one holding-phase LED to the next holding-phase LED that was the next immediate LED in the sequence. This may also have reduced the likelihood of identifying a significant difference between rates.

The presence of units that increased their firing rates for both contralateral and protrusive step tasks (12/19 units; 63%) suggests that these units were responsible for generating displacement in both directions. However, the units may be more sensitive to protrusion than to contralateral movement, as two units were recruited at <1 mm during protrusion in comparison with none during contralateral movement, and none of the units was recruited after 6 mm of protrusive displacement in comparison with four units during contralateral movement (Fig. 4).

The IHLP is also clearly involved in jaw-opening movements (Miller 1991). However, in the present study, firing rates of IHLP SMUs were studied only during horizontal jaw movements. The relative contribution of the IHLP in horizontal jaw movements and jaw opening is a subject of future studies.

Firing rate change and threshold

The firing rate modulation of the IHLP units was significantly greater for the lower-threshold than for the higher-threshold units during contralateral movement and protrusion (Fig. 4). This is consistent with previous findings in human limb and jaw muscles during isometric contractions (Derfler and Goldberg 1978; Freund et al. 1975; Tanji and Kato 1973). The low-threshold units were most likely small motor units producing less force than the higher-threshold units (Freund 1983). It appears therefore that the lower-threshold units require greater firing rate changes than the higher-threshold units to generate the same amount of jaw displacement. This finding suggests the possibility for finer gradation of force output at jaw displacements closer to postural jaw position, at which many jaw movements are carried out, than for jaw positions displaced further from postural position. It also should be noted that, at greater magnitudes of horizontal jaw displacement, larger tensions are likely to be required to move the jaw the same amount of displacement given the larger passive tensions that would be exerted on the mandible and that have a tendency to pull the jaw back to postural jaw position.

These differences in firing-rate change with threshold are also consistent with the findings in limb muscles in which firing rates have been shown to increase nonlinearly as force increases (Bigland and Lippold 1954; Clamann 1970; Freund et al. 1975). The largest change in firing rate per unit force was observed to occur in the just-suprathreshold range, that is, at forces just above the threshold for firing of motor units recruited early in the task. The smallest change in firing rate was observed at the higher force levels tested during stepwise isometric contraction (Freund et al. 1975). The present findings show that firing rate changes per unit displacement were greater between the first and second steps than between the second and third steps, where the firing rates of some units exhibited a plateau.

In the gradation of force output it has been reported that, at low-force levels, masticatory muscles rely mostly on recruitment while, at high-force levels, they rely more on rate modulation (van Eijden and Turkawski 2001). While the present and our previous (Phanachet et al. 2001b) study do not specifically address this issue in the LP, the previous study demonstrated that IHLP SMUs could be recruited at jaw displacements ≤61–89% of the maximum contralateral or protrusive displacement. The present study suggests that firing rate modulation is also involved in gradation of force output over a large range of contralateral and protrusive jaw displacement. Comparable observations have also been made in previous studies in the human masseter and nonhuman primate temporalis during isometric tasks (Clark et al. 1978; Derfler and Goldberg 1978). Further studies are needed to allow definitive statements about the relative contributions of recruitment and rate-coding mechanisms for IHLP SMUs in the control of horizontal jaw movements.

Role of other jaw muscles

The present paper supports a role for IHLP in the fine control in horizontal jaw movements. Even though our previous multunit study indicated that the other jaw muscles appear to make lesser contributions than the IHLP in contralateral movement and protrusion (Murray et al. 1999a), these earlier data did not rule out contributions from other jaw muscles. For example, the masseter and medial pterygoid muscles are composed of muscle fibers capable of generating horizontal force vectors (Hannam and McMillan 1994; Miller 1991). Future studies are needed to clarify the relative contributions from these muscles to the horizontal movement tasks described in the present study.

Firing-rate change and location

During the protrusive task, the units located in the superior part of IHLP had significantly greater firing-rate modulation than that of the units located in the inferior part. Most of this modulation appeared to occur within the superior–lateral part, with few units in the superior–medial part exhibiting significant firing-rate change (Table 1). All recorded units in the inferior–medial part of the IHLP also exhibited significant changes in firing rate. These data suggest that the units in the
superior–medial part were less concerned with the fine control of the jaw during protrusion than the units in the other parts of the IHLP. During the contralateral step task, all three parts appeared equally concerned with the fine control of contralateral movements. These findings suggest a differential role for the superior–medial part of IHLP in horizontal movements as supported by our previous study (Phanachet et al. 2001b) in which the units located in the superior–medial part had significantly lower thresholds than those in the other parts of the muscle. We hypothesize therefore that the units in the superior–medial part of the IHLP are more important than those in the other parts of the muscle in initiating contralateral and protrusive movements but are less concerned with fine control during the protrusive task than the contralateral task once the movement has commenced. During the contralateral task, all three parts appear to make a similar contribution to the movement once the movement has been initiated by the superior–medial part.

In regard to assigning location, it should be noted that, since the territories of IHLP motor units have not been defined, it is possible that many or even most of the muscle fibers of a given unit may not be located in the part of the muscle to which the unit has been assigned. Nonetheless, the data indeed do provide suggestive evidence supporting previously proposed notions of functional heterogeneity within the IHLP (Foucart et al. 1998; Hannam and McMillan 1994; Murray et al. 1999c, 2001; Phanachet 2001b).

Anatomically, there is a marked convergence of the IHLP muscle fibers onto a small insertion site on the condylar fovea from a broad origin at the lateral surface of the lateral pterygoid plate. This marked change in fiber alignment from the uppermost to the lowermost muscle fibers (Hawthorn and Flatta 1990; Naohara 1989; Troiano 1967) provides the opportunity for a range of force vectors capable of moving the condyle at the appropriate rate, range, and direction to effect the desired horizontal jaw movement. The activation of specific regions within the IHLP would allow the application of an appropriate force vector to effect the required condylar movement, and this would provide a sophistication of delivery of different force vectors on the condyle to perform the desired jaw movements. More information regarding LP fiber architecture, i.e., muscle fiber alignment, together with computer simulations of jaw biomechanics are necessary to provide a better understanding of the functions of the LP.

We thank Associate Prof. Mark Onslow and Dr. Elise Baker of Faculty of Health Sciences, University of Sydney for comments. We also thank P. Sindhusake of Westmead Hospital for excellent statistical advice and T. Bowerman for secretarial assistance. We acknowledge the photographic and art services of Westmead Hospital and the Department of Radiology, Westmead Hospital for the CT scans.

This research was supported by National Health and Medical Research Council of Australia Grant 990460, the Australian Research Council Small Grants Scheme, the Australian Dental Research Foundation, Inc, the Dental Board of NSW, the Dental Alumni Society of the University of Sydney, and the University of Sydney Research Grants Scheme. Dr. Intira Phanachet is a Royal Thai Government Sponsored Scholar.

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