Functional Properties of Single Motor Units in Inferior Head of Human Lateral Pterygoid Muscle: Task Relations and Thresholds

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Phanachet, I., T. Whittle, K. Wanigaratne, and G. M. Murray. Functional properties of single motor units in inferior head of human lateral pterygoid muscle: task relations and thresholds. J Neurophysiol 86: 2204–2218, 2001. The aim of this study was to clarify the normal function of the inferior head of the human lateral pterygoid muscle (IHLP). The hypothesis was that an important function of the IHLP is in the fine control of horizontal jaw movements. The activities of 99 single motor units (SMUs) were recorded from IHLP (22 recordings from 16 subjects). Most recording sites were identified by computer tomography (CT). All 99 SMUs were active during contralateral jaw movements with the teeth apart, and protrusive jaw movements with the teeth apart, and 81% (48 of 59 units studied during all 3 tasks) were active during submaximal jaw-opening movements. None were active on maximal ipsilateral or retrusive jaw movements with the teeth apart nor on jaw closing/clenching in intercuspal position; nor were they spontaneously active when the jaw was at the clinically determined postural jaw position. Thresholds of SMUs ranged from <0.2 mm of contralateral or protrusive horizontal displacements to 61–89% of the maximum contralateral or protrusive displacement, respectively. For the 35 units continuously active during the contralateral task, 23 (66%) were recruited within 2 mm of contralateral displacement [25 (63% of 40 units) for protrusion]. Recruitment thresholds (mm) of some of the units were rate dependent with thresholds significantly decreasing with increasing rate of horizontal jaw movement in protrusion and contralateral movements. At eight recording sites where up to six SMUs were able to be discriminated, the average thresholds of successively recruited SMUs were within 1-mm increment of horizontal jaw displacement. After dividing IHLP into four regions, the SMUs recorded in the superior-medial zone exhibited significantly lower mean threshold values than for the SMUs recorded in the other zones (no units were recorded in the inferior-lateral zone). This provides suggestive evidence supporting previously proposed notions of functional heterogeneity within IHLP. Taken together, the data suggest that specific regions of the IHLP are capable of selective activation in a finely controlled manner to allow the application of the appropriate force vector (magnitude and direction) to effect the required condylar movement needed for the generation and control of horizontal jaw movements.

INTRODUCTION

The human lateral pterygoid muscle (LP) has been implicated as playing an important role in the control of jaw movements 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). The LP consists of two heads or bellies, an upper or superior head (SHLP) and a lower or inferior head (IHLP). In general terms, many electromyographic (EMG) studies suggest that the IHLP plays a role in opening, protrusion, and contralateral jaw movements, that the SHLP plays a role in closing, retrusion, and ipsilateral jaw movements, and that there is a reciprocal relationship between the activity of the SHLP and the IHLP (Hannam and McMillan 1994; Hiraba et al. 1995, 2000; Kamiyama 1961; Klineberg 1991; Miller 1991). However, there is a very limited understanding, and controversy between studies, as to the precise role that both heads of the muscle play in jaw and TMJ function. For example, some studies indicate activity in IHLP on clenching in intercuspal position (Mahan et al. 1983; Widmalm et al. 1987) while others suggest that IHLP is inactive in these circumstances (Murray et al. 1999a; Wood et al. 1986). Further, some previous studies suggest that both heads of the muscle always act independently (Grant 1973; Juniper 1984; Mahan et al. 1983; McNamara 1973) while others suggest synchronous activity in both heads during certain jaw movements (Sessle and Gurza 1982; Widmalm et al. 1987; for reviews, Hannam and McMillan 1994; Miller 1991).

There are a number of possible reasons for the uncertainty and limited understanding of normal LP function. First the absence of reliable verification of electrode location within the muscle in most previous human studies suggests that some of these earlier recordings may have been from other jaw muscles or from LP but incorrectly attributed to a particular head of the muscle (Hannam and McMillan 1994; Orfanos et al. 1996; Widmalm et al. 1987). Second, most previous human studies have not accurately recorded jaw movement to correlate with LP activity, and this has undermined the ability to identify the task relations of the LP. Third, recordings have been made of multi-unit activity where it is more difficult to draw conclusions as to the relative levels of activity in each head of the LP.

We have recently addressed some of the limitations of previous studies by recording multi-unit EMG activity from sites verified by computer tomography (CT) to be correctly located within the LP and from subjects in which jaw movements have been accurately recorded in 6 df (Murray et al. 1999a, 2001). These studies have supported the hypothesis that...
the LP plays an important role in the fine control of horizontal jaw movements. Close associations were observed between multi-unit LP EMG activity and condylar movement during contralateral and protrusive jaw movements (Murray et al. 1999a). In this previous study, most recordings from IHLP were not verified by CT, although the recordings from SHLP were verified. Given that the IHLP has a broad origin and converges onto a narrow insertion site, it is possible that different IHLP recording sites may yield different functional characteristics. We have recently provided evidence that the IHLP is functionally heterogeneous, that is, that selective activation of subcompartments within the IHLP can occur to allow the application of the appropriate force vector (direction and magnitude) to effect the required condylar movement (Murray et al. 1999c). This concept is also consistent with a previous proposal of LP function (Hannam and McMillan 1994). It is possible therefore that only part of the IHLP might exhibit a role in the fine control of horizontal jaw movements and that recordings at different sites might yield different functional characteristics. Evidence supporting the hypothesis of functional heterogeneity would be apparent, for example, if there were to be a preferential grouping to one part of the IHLP of single motor units (SMUs) with a low threshold to a particular task and a preferential grouping to another part of the IHLP of SMUs with a significantly higher threshold to the same task.

The LP has also been implicated as playing an important role in temporomandibular disorders (TMDs) (Hiraba et al. 2000; Lund 2000; Okeson 1998) that are a major cause of nondental orofacial pain. These disorders are characterized by pain in and about the TMJ, limitation of jaw movement, and TMJ sounds (DeBoever and Carlsson 1994). The view that there is hyperactivity or incoordination between the two heads of the LP is a widespread dental clinical opinion that at least partly underpins some current modes of treatment of TMD (Hiraba et al. 2000; Juniper 1984, 1987; Okeson 1998). However, our understanding of LP function in TMD patients is even less than our limited understanding of its normal function, with no reliable studies having ever been performed in TMD patients. It would be valuable therefore to have baseline information on the functional properties of SMUs from the LP during standardized tasks in control subjects without TMD. These data could provide the basis for the design of future studies of the possible involvement of the LP in TMD.

We have therefore initiated studies to provide rigorous baseline data on the normal function of the human LP. We chose to study the IHLP first given previous controversy as well as the uncertainty in our previous multi-unit EMG study (Murray et al. 1999a) as to the spatial location of recording sites within IHLP. In the present paper, we use precise quantification of SMU activity at spatially identified sites during standardized tasks to address the hypothesis that the IHLP is concerned with the generation and fine control of horizontal jaw movements. This hypothesis is proposed because of the following lines of evidence. First, our previous multi-unit EMG data (Murray et al. 1999a; Phanachet and Murray 2000) supported this hypothesis of fine control. Second, the arrangement of IHLP muscle fibers suggests that they are well suited to generating significant horizontal force vectors on the condyle. Third, the IHLP contains a relatively high proportion (~80%) of type I muscle fibers (Mao et al. 1992) that seem best suited to providing continuous work at low forces. Recruitment thresholds and firing rates are two common features of SMU activity that may be precisely quantified during tasks and both have been well described in the limb motor system (Freund 1983). For example, recruitment thresholds have been shown to decrease with increasing rate of limb movements (Freund 1983) and to vary with the direction of a limb movement (Herrmann and Flanders 1998). If IHLP is indeed concerned with the fine control of horizontal jaw movements, then thresholds should vary in association with different rates and/or directions of horizontal jaw movement.

The aims of this paper therefore are as follows: to identify unequivocally the task relations of individual SMUs verified to be located within IHLP; to identify SMU thresholds in standardized horizontal jaw movement tasks and to determine whether these thresholds vary with the rate or direction of movement as would be expected if these units were involved in the fine control of these tasks; and to identify whether there is a relation between CT-verified location and threshold consistent with a proposal for functional heterogeneity within IHLP. Some of these data have been briefly reported (Murray et al. 2001; Phanachet et al. 2000).

METHODS

Sixteen human volunteers without signs and symptoms of TMD (age 20–41 yr; 12 males, 4 females) and without any history of chronic pain or neuromuscular condition, participated in this study. All subjects gave informed consent and all experiment procedures were approved by the Western Sydney Area Health Service Ethics Committee of Westmead Hospital and the Human Ethics Committee of the University of Sydney. Most of the methods have been previously described in detail (Murray et al. 1999a,b; Orfanos et al. 1996; Peck et al. 1997; Phanachet and Murray 2000; Phanachet et al. 2001), and the following will review these methods and detail those methods not previously described.

Electrode placement within IHLP

The method for electrode placement within IHLP (modified from Wood et al. 1986) involved inserting a sterilized, precurved needle containing two Teflon-coated, stainless-steel fine wires through the oral mucosa above the level of the upper second molar tooth. Topical anesthetic was placed around the insertion site prior to needle insertion. The wires were cut with sterile scissors immediately prior to placement to provide fresh cut-wire ends for recording. The needle was advanced to contact the lateral surface of the lateral pterygoid plate. The needle was then withdrawn, leaving the wires within the IHLP, and the wires were secured to the buccal surface of the upper first molar tooth with a small piece of stomahesive wafer (ConvaTec, Victoria, Australia) and led out through the angle of the mouth. At the end of each recording session, five to nine CT-axial slices (1–3-mm thick) were taken inferior to and parallel with the clinically approximated Frankfort horizontal plane. The Frankfort horizontal plane is the plane of best fit to four points on the skull: the lowermost border of the infraorbital rim bilaterally and the uppermost border of the bony external auditory meatus bilaterally. An example of verification data is shown in Fig. 1. The horizontal CT slice (1-mm thick) in A is through the electrode fine-wire tips (black arrow) 7 mm below the roof of the infratemporal fossa. The reformatted images in B and C (arrows: fine-wire tips) were parallel to the long axis of the IHLP (B) or through the frontal plane (C) as indicated in the lowest CT images. These data confirmed electrode location within the IHLP and showed the location within the muscle relative to the boundary of the IHLP. The data-acquisition equipment was the microl401 from Cam-
bridge Electronic Design (Cambridge, UK), the sampling rate was 10,000 samples/s, and bandwidth was 100 Hz to 10 kHz. SMUs were discriminated with Spike2 software from Cambridge Electronic Design. Power spectral analysis revealed that the highest frequency component of the SMU spike train was <4,000 Hz.

Recording of condylar and mid-incisor point movement during standardized tasks

The movement of the mid-incisor point (MIPT, the point between the incisal edges of the lower central incisor teeth) was recorded with an optoelectronic jaw-tracking system (JAWS3D, Metropoly AG, Zurich, Switzerland) (Mesqui and Palla 1985) with a sampling rate limited to 67 samples/s. One lightweight 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 with a rigid rod that projected out of the mouth with minimal interference to lip competence. 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. Cameras monitored the spatial locations of the LEDs. For the data reported in this paper, the origin of the coordinate system for jaw displacement was the MIPT. During all recordings, the subjects sat in an upright position without head support. Since mandibular jaw movement was recorded in relation to the maxilla, any associated head movement did not influence the lower jaw motion measurement. 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. Subjects were instructed to swallow and relax their jaws with their lips lightly touching to achieve the postural jaw position. The error of the JAWS3D system bench tested was 0.1 mm (Airoldi et al. 1994)—for the purposes of the present study, the spatial resolution was conservatively estimated to be ~0.2 mm for threshold estimation (Peck et al. 1997).

Jaw movements were standardized by having the subject move the
position of the MIPT dot so as to track a computer-controlled target (Fig. 2A). The target in these standardized tasks was an 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. 2A). The trajectory of the MIPT dot in the horizontal plane was displayed on the video screen. The LEDs were controlled by scripts written in Spike2 software [Cambridge Electronic Design (CED)] and run on the CED system that was also used to record SMUs (see following text). Only one LED was illuminated at any one time. Movement of the MIPT dot from the location at one illuminated LED to the location at the next illuminated LED corresponded to 0.65 or 1.3 mm of movement at the subject’s MIPT depending on the display gain on the video screen. The subject was instructed to perform a few trials of contralateral or protrusive jaw movement to become accustomed to the task. A contralateral movement was defined as a movement of the jaw from postural jaw position to the side opposite to the IHLP recording side followed by a return of the jaw to postural position. A protrusive movement was defined as a movement of the jaw from postural jaw position forward followed by a return to postural position. Both movements were performed without tooth contact. Although subjects were instructed to move the jaw in protrusion, some subjects displayed a deviation to one side or the other. However, these protrusive movements were always distinctly different from the contralateral movements. The linear bank of LEDs was then oriented along the direction of movement of the MIPT dot, which was displayed on the screen in the horizontal plane. The Spike2 software illuminated the LEDs in sequence, and the subject was instructed to move the jaw so that 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 changing time-off duration between each LED (e.g., a in Fig. 2B), and time-on duration of each LED (b in Fig. 2B). Three rates were defined: 6.5 mm/s (fast, f in Fig. 2B), 2.2 mm/s (intermediate, s in Fig. 2B), and 1.3 mm/s (slow). The desired amount of displacement could be controlled by varying the highest LED in the bank that was illuminated.

**Standardized tasks**

Each movement started with the jaw in postural position for 2–3 s (Fig. 2). During standardized protrusive or contralateral excursion or jaw opening, the subject was instructed to move the MIPT dot smoothly and track the target at the rate and magnitude of jaw displacement controlled by the Spike2 software. The amount of jaw displacement during each task was determined by the experimenters’ ability to discriminate one or more SMUs throughout the task. The

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**FIG. 2.** Diagrams illustrating the target lines and corresponding mid-incisor point (MIPT) displacements during right jaw movement. A: a diagram representing the light-emitting diode (LED) bank and a display of the MIPT on the video screen. ● an illuminated LED at the holding level c. B: single-step displacement. Left: averaged MIPT displacement (- - -) with SD bars every 750 ms together with target lines (—). ○, diameter of LED (2.8 mm). Right: diagrams of actual time and sequence of illuminated LEDs. Each circle represents an LED. a, time-off duration (200 or 600 ms or 1 s); b, time-on duration (100 ms). Tracings on the left correspond to the timing sequence on the right at time-off durations of 200 ms (f) and 600 ms (s), which correspond to rates of movement of 6.5 and 2.2 mm/s.
criteria for defining a SMU were similarities in amplitude and waveform between all representatives of an identified SMU. Then the LEDs were aligned along the trajectory of MIPT movement, and the LED corresponding to the required displacement was programmed. 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. The jaw was then returned to the postural position again following the return targets, and this concluded the trial. This standardized task was termed the single-step task. To study the effects of rate of jaw movement on the threshold of SMUs, the subject was instructed to track the target at fast, intermediate, and slow rates (see preceding text). The fastest rate of movement was about the fastest that our subjects found comfortable to perform. Although subjects could move slower than the slowest rate of movement, this rate was also comfortable for the subjects. Each task was repeated five to seven times with a rest period of ≥1 min between trials. By changing the alignment of the linear bank of LEDs, it was possible to change the direction along which the subjects moved their jaw. Thus subjects tracked the targets so as to move the jaw to the side contralateral to the side of IHLP EMG recording, or with a change in the orientation of the LEDs, in protrusion or jaw opening. A multiple-step task involving two to three step levels was also performed in which the rate of illumination of the LEDs required subjects to move the jaw in the horizontal plane to two to three sequential holding phases or step levels (3–5-s duration) (Phanachet et al. 2001). The multiple-step task was not used for standardized jaw opening.

We have previously established criteria for successful performance of a task by subjects (Phanachet et al. 2001). Trials that did not meet these criteria were not included in further analysis. Figure 2R, for example, illustrates a close match between target lines (—) and averaged MIPT traces (- - -) during jaw movement without tooth contact in one subject. The diameter of each LED (2.8 mm) is represented as the shaded area and, during jaw movements, subjects tracked the target by moving the dot to any point within the diameter of an LED (e.g., center or the boundary of the LED). A MIPT trace was considered acceptable during the holding phases of a task when, from a minimum of five trials, at least part of the shaded target area fell within 1 SD of the mean MIPT displacement for at least two mean data points calculated at 750-ms intervals and in addition was always <2 SDs of the mean at any data point. The same criterion was used for each dynamic phase of each movement, that is, the outgoing phase and the return phase of a movement.

Before the standardized tasks were performed, EMG activity from IHLP was studied during nonstandardized maximal contralateral, protrusive, and retrusive jaw movement and submaximal jaw-opening movements, and clenching in intercuspal position (normal biting between the teeth). These tasks were performed to provide an overall assessment of the motor activity to which the units at the site were related. These movements were termed the nonstandardized tasks as there was no visual feedback to the subject of the movement. All except two SMUs were characterized during standardized horizontal isotonic displacements contralateral to the recording side and in protrusion. Some units were also studied during standardized jaw-opening movements although wide jaw opening in both standardized and nonstandardized movements was avoided to minimize the danger of losing units. The remaining two units were only studied during nonstandardized contralateral, ipsilateral, protrusive, and jaw-opening movements in which the subject was instructed to move the jaw as far as comfortable in each movement task. All SMUs recorded during single-step and/or multiple-step displacements were included in the analysis as to the tasks to which the SMUs were related.

In this paper, thresholds are reported in terms of MIPT displacement. To provide an indication of SMU thresholds in relation to condylar displacement, an assessment was made of condylar displacement at each 1 mm of MIPT displacement. During the contralateral movement in the horizontal plane, there was on average a 35° ± 5° difference between the average trajectory made by the MIPT and the average trajectory along which the condyle moved. The trajectory along which the condyle moved was determined on the axial CT scans as coincident with the long axis of the lateral pterygoid muscle. The MIPT trajectory was determined as the line of best fit through the MIPT displays on horizontal plots. The relative displacements in three dimensions were calculated at 1-mm intervals for both the MIPT and the clinically palpated lateral condylar pole in a representative trial of contralateral movement in each subject. The clinically palpated lateral condylar pole was included as an additional reference in each subject prior to recording. The mean ratio of lateral condylar pole displacement to MIPT displacement at each 1-mm interval of contralateral displacement was 0.67 ± 0.22, range = 0.21–1.02 mm [3-dimensional (3D) coordinates], which indicates that on average, the condyle moved ~70% of the displacement at the MIPT. Although both condyles ideally move forward symmetrically during a protrusive movement, many subjects MIPTs deviated with protrusion and the mean ratio of lateral condylar pole displacement to MIPT displacement at each 1-mm interval for protrusion was 0.70 ± 0.20 mm, range = 0.33–1.02 mm (3D coordinates).

For the purposes of assessing location of electrode recording site within IHLP, the muscle was arbitrarily divided mediolaterally into medial and lateral regions, and superior-inferiorly into superior and inferior regions. Location was assessed by viewing the electrode tip in relation to 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 when assigning location. Previous histological studies have indicated that the SHLP is ~5-mm thick superior-inferiorly (Meyenberg et al. 1986; Moritz and Ewers 1987; Widmalm et al. 1987; R. Hawthorn, personal communication), and we therefore adopted this criterion for identifying the upper boundary of the IHLP. The remainder of the LP extending inferiorly to the lower border of the lateral pterygoid plate was considered to be IHLP.

**Data analysis**

For each subject, MIPT displacement data for each task-defined movement were plotted along the anterior-posterior (x, + posteriorly), mediolateral (y, + to right), and superior-inferior (z, + superiorly) axes for lateral and protrusive jaw movement, respectively. An analysis of the general features of task relations was conducted for all SMUs recorded during single-step and/or multiple-step displacements. An assessment of threshold was made only for the units that fired continuously throughout the single-step task and without a significant interruption in firing rate (i.e., all interspike intervals <160 ms) for the duration of the holding phase. Threshold was defined as the magnitude of jaw displacement when the first action potential occurred (Fig. 3). An action potential was disregarded for threshold assessment if it occurred >160 ms before the next action potential. Threshold values were averaged over at least five trials. Jaw displacement was calculated as the shortest distance in three dimensions from postural jaw position to the position of the jaw at which the unit started firing. Threshold was also calculated along the y axis for contralateral movement, and x axis for protrusion. Most values are reported as the shortest distance in three dimensions unless specified along a particular axis. In this paper, thresholds are reported below in terms of MIPT displacement to provide IHLP data in relation to a commonly used reference point on the mandible. Thresholds of each SMU at different rates were compared by using the Kruskal Wallis test (KWT) for three rates and Mann-Whitney U test (MWU) for two rates, given that the threshold values were not normally distributed. For the analysis of the differences in displacement between successively recruited SMUs recorded at any one site, continuously active units were analyzed.
RESULTS

General features of task relations

A total of 99 SMUs were discriminated from the right IHLP in 22 recording sessions from 16 subjects. Verification by CT was obtained in 17 of the 22 recording sessions. All 99 SMUs were examined for activity at postural jaw position, and during clenching in the intercuspal position, and nonstandardized retraction and ipsilateral jaw movement. Of the 99 units, 97 were examined for activity during standardized (i.e., single-step and/or multiple-step displacements) protrusion and contralateral movement while two units were studied during nonstandardized protrusion and contralateral movements.

None of the 99 units was spontaneously active when the jaw was in the clinically determined postural jaw position whether assessed at the beginning, during, or at the end of a 4-h recording session. None of the units were active during the nonstandardized tasks of retraction, ipsilateral jaw displacements or clenching in intercuspal position. All 99 units were active during contralateral and protrusive jaw movements. Of these 99 SMUs, 59 were examined for activity during jaw opening. Of these 59 units, 48 (81%) were active during all three movements (contralateral, protrusion, and jaw-opening), and 11 (19%) were active on contralateral and protrusive movements only. Six of these 11 units only gave brief bursts of activity during the tasks while the other 5 were continuously active units with higher thresholds than the other units. Since the 59 units were tested for activity during jaw opening that ranged from 22 to 58% of maximum jaw opening, it is possible that these 11 units would become active at greater magnitudes of jaw opening.

Figure 3 shows representative SMU data of the 81% that were active during protrusion (A), a contralaterally directed jaw movement (B), and an open-close jaw movement (C). The
same three SMUs were recorded simultaneously during each movement. Each short vertical line is a spike-train pulse that indicates the time of occurrence of a SMU action potential. Raw data from the segment delineated by the dotted vertical lines in A are displayed at the bottom of B with the units labeled 1–3 corresponding to the appropriately labeled spike-train pulses. The top three traces in each panel show displacement. This subject consistently deviated the jaw to the ipsilateral side during protrusion (A, top; see METHODS). However, the SMU activity was considered to relate to protrusive jaw displacement because there was no activity during ipsilateral movement in any subject.

Threshold of firing of SMUs

For the study of SMU threshold, only the units that fired tonically during the holding phases of single-step displacements were analyzed. According to this criterion, 35 of 99 units were analyzed during contralateral displacements, 40 were analyzed during protrusive displacements, and 29 of the units were studied during both contralateral and protrusive displacements. The units not meeting this criterion, that is they were either not studied in the single-step task or exhibited a phasic and sporadic pattern of firing during the dynamic phase only, were however assessed for task relations, as indicated in the preceding text.

RANGE OF THRESHOLDS FOR FIRING. The sample of SMUs from IHLP exhibited a range of activation thresholds. The dotted line labeled T in Fig. 3 represents displacement threshold for unit 1. The threshold of firing of SMUs exhibited a broad range from <0.2 mm of displacement, the level of resolution of the JAWS3D tracking system (see METHODS) to a contralateral displacement of 6.2 mm or a protrusive displacement of 7.3 mm when assessed at the intermediate rate of movement (see following text). As the average maximum displacements of the MIPT of subjects in contralateral movement and protrusion were 10.2 ± 1.6 mm (range: 8–12 mm) and 8.2 ± 2.0 mm (range: 6–10.5 mm), respectively, the thresholds of the population of SMUs ranged from very low (supporting a role in fine control) to ~61 or 89% of the maximum possible range of contralateral or protrusive horizontal displacements.

Figure 3B shows two units that commenced firing near the onset of movement (units 1 and 2). It also shows a unit (3) commencing firing at the end of a 7-mm contralateral displacement. Figure 4 shows frequency histograms of the thresholds of the 35 IHLP units recorded in contralateral movement (A) and the 40 units in protrusion (B). Each graph exhibits a bimodal distribution with a peak at both low and high thresholds. Of the 35 units in A, 23 (66%) were recruited within 2 mm of contralateral displacement [25 (63%) for protrusion]. The remaining 12 units (34%) were recruited at >2 mm of contralateral displacement [15 units (37%) for protrusion]. This bimodal distribution probably reflects sampling bias toward more easily discriminable small, low-threshold units rather than the observed low frequency of higher-threshold units.

DEPENDENCE OF THRESHOLD ON RATE OF MOVEMENT. The strongest influence on recruitment is the speed of a movement (Freund 1983). Therefore another feature of SMU activity supporting a role for IHLP in the fine control of horizontal jaw movements would be a change in the threshold of recruitment with a change in the rate of horizontal jaw movement. The thresholds of each IHLP unit were therefore studied during two to three rates of movement. For the contralateral movement, analysis of individual units showed that the threshold of firing of 12 (34%) of 35 units was significantly different (KWT or MWU; P < 0.05) at different rates of movement. Figure 5A plots mean threshold values for these 12 units. For protrusion, the threshold of firing of 10 (25%) of 40 units were significantly different (KWT or MWU; P < 0.05) at different rates of movement (Fig. 5B).

Table 1 presents these data in a slightly different way by listing the total number of comparisons available between the three rates of movement for the population of 35 units in contralateral movement (A) and 40 units in protrusion (B). Sometimes data were not available for all possible comparisons. Of the 35 units, 71 (76%) of the 93 rate comparisons
demonstrated progressive increases in threshold with decreases in the rate of movement. The remaining 22 (24%) comparisons exhibited a decrease although the differences in threshold were small with a mean of 0.3 ± 0.4 mm; 11/22 differences were within the working error of the JAWS3D system of 0.2 mm (see METHODS). The presence of a greater number of comparisons exhibiting increases in threshold with decrease in the rate of movement is unlikely to occur by chance alone and with larger numbers of trials, most of these comparisons would likely be significant. In protrusion, 60 (71%) of the 84 rate comparisons demonstrated progressive increases in threshold with decreases in the rate of movement. The remaining 24 (29%) rate comparisons exhibited a decrease (mean differences in threshold: 0.3 ± 0.3 mm; 12/24 within JAWS3D error).

A previous study (Yoneda et al. 1986) in limb muscles demonstrated that the units that did not significantly alter their thresholds with speed of isometric force were the lower-threshold units of their recorded population while the higher-threshold units did significantly alter threshold. We wished to determine if a comparable dichotomy was present in our population of units. For the contralateral movement, the mean threshold of the 10 units, for which there was a significant difference between rates of contralateral movement, was 2.6 ± 1.2 mm. These values were assessed at the intermediate rate of movement, or, when unavailable, the mean of the slow and fast rates of movement. These thresholds were significantly greater (MWU; \( P < 0.05 \)) than the mean of 1.5 ± 1.3 mm for the units for which there was no significant difference between rates of contralateral movement. In a corresponding analysis for protrusion, there was no significant difference \( (P = 0.3) \); however, only two units were studied at the three rates of movement.

Representative data for 1 of the 10 units that was significantly affected by rate of movement is shown in Fig. 6 for an IHLP SMU studied at the fast rate (A) and the slow rate (B) of a contralateral movement. The subject tracked the target and held displacement for 10 s. The mean threshold for this unit (1.5 mm along the y axis; 1.9 mm, 3D coordinates) at the fast rate of movement (A) was significantly lower (KWT; \( P < 0.01 \)) than the threshold at the slow rate of movement (B; 4.5 mm, y axis; 5.2 mm, 3D coordinates). Data from one representative unit that was not significantly affected by rate are illustrated in Fig. 7.

CONTROL FOR EFFECTS OF JAW OPENING. It is considered that there was little or no effect of any slight jaw opening on the threshold values observed in the contralateral or protrusive jaw movement tasks. For the contralateral or protrusive tasks, the mean (±SD) threshold in the z axis (i.e., superior-inferior) for the nine units that were also studied during standardized jaw opening was 0.6 ± 0.4 mm for contralateral movement and 0.9 ± 1.2 mm for protrusion. However, the mean threshold of these units during standardized jaw opening was 4.8 ± 1.7 mm in the z axis. For example, in Fig. 3 during protrusion (A) and contralateral movement (B), the thresholds in the z axis for unit 1 were ~3 and 1 mm, respectively, while the threshold in the z axis during jaw opening (C) for this unit was ~7 mm.

THRESHOLD AND DIRECTION OF MOVEMENT. For 29 SMUs studied in both contralateral and protrusive tasks, the correlation between the recruitment thresholds in protrusion and cont-

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<tr>
<td>Total</td>
<td>29</td>
<td>18</td>
<td>35</td>
<td>93</td>
</tr>
<tr>
<td><strong>B. Protrusive task</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Increased threshold</td>
<td>27</td>
<td>16</td>
<td>17</td>
<td>60    (71)</td>
</tr>
<tr>
<td>Decreased threshold</td>
<td>11</td>
<td>7</td>
<td>6</td>
<td>24    (29)</td>
</tr>
<tr>
<td>Total</td>
<td>38</td>
<td>23</td>
<td>23</td>
<td>84</td>
</tr>
</tbody>
</table>

Parentheses enclose percentages.

TABLE 1. Number of threshold comparisons showing an increase or decrease in threshold as the rate of movement decreases during contralateral and protrusive tasks
Contralateral displacement was $r = 0.69$ ($P < 0.01$). The mean (±SD) threshold value of 2.1 ± 2.2 mm ($n = 29$) assessed at the intermediate rate of protrusive jaw movement was greater than but not significantly different ($P > 0.05$; Wilcoxon signed-ranks test) from the value of 1.5 ± 1.1 mm for contralateral movement.

Recruitment features of SMUs during tasks

An assessment was made of the differences in displacement thresholds of successively recruited SMUs to determine whether recruitment is involved in the generation of the small incremental forces required for small increments in jaw displacements. Table
2 shows the mean (±SD) differences in threshold values between successively recruited units. At any one site, the first unit recruited in the displacement was arbitrarily labeled unit 1, the second unit recruited was labeled unit 2, and so on. The data demonstrate the small displacements, close to the level of resolution of the jaw-tracking system, between successively recruited SMUs. For example, at each of the recording sites and over the first ∼2 mm of contralateral or protrusive displacement, up to five SMUs could be recruited in a staggered fashion. The small displacements with which units were recruited are also illustrated in Fig. 8, which shows on an expanded time scale the activity of five SMUs recorded during a single-step protrusive displacement. Units were recruited at small displacement increments.

**Locations of units within IHLP and threshold values**

Table 3 lists the mean thresholds of SMUs recorded according to site within IHLP during protrusion (A) and contralateral...
movement (B). Although sample size was small, the SMUs recorded in the superior-medial zone during protrusion and contralateral movement exhibited significantly lower mean threshold values than for the SMUs recorded in the other zones (KWT; \( P < 0.001 \)). No SMUs were recorded in the inferolateral zone of the IHLP. An assessment was also made as to whether units whose thresholds were affected by the rate or the direction of movement were localized to a specific region. There was no significant association between the location of units and the number of units showing differences of threshold at different directions (\( P = 0.2; \) Fisher’s exact test; Table 4) or rates (\( P > 0.05; \) Fisher’s exact tests; Table 5) of movement.

**DISCUSSION**

**Task relations of IHLP SMUs**

This paper provides the first detailed description of the activities of SMUs recorded from CT-identified sites within the human IHLP. The sample of units allows a clear definition of the task relations of the IHLP with all units being active during contralateral and protrusive jaw movements with the teeth apart. Although only a proportion of units tested were active during jaw opening, it is very likely that all units would be active at or before maximum jaw opening since the remaining 19% of units either gave brief bursts of activity (i.e., phasic units below their tonic threshold) (Freund 1983) or were relatively high-threshold tonic units in horizontal movement. The sampling of units from a broad distribution within the muscle suggests that no part of the IHLP makes an active contribution to ipsilateral and retrusive movements with the teeth apart nor on jaw closing/clenching in intercuspal position.

The data provide good evidence for an involvement of the IHLP in the generation of contralateral, protrusive and jaw-opening movements. These findings are generally consistent with the patterns of activity reported in the many previous human and experimental-animal multi-unit EMG studies (for reviews, Hannam and McMillan 1994; Klineberg 1991; Miller 1991; Murray et al. 2001). For example, the findings are consistent with previous conclusions that the IHLP is concerned with pulling the condyle forwards along the articular eminence during protrusion and contralateral jaw movements (e.g., Miller 1991; Wilkinson 1988). In a study where jaw

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**Table 2. Differences in threshold between successively recruited SMUs**

<table>
<thead>
<tr>
<th>Unit 2—Unit 1</th>
<th>Unit 3—Unit 2</th>
<th>Unit 4—Unit 3</th>
<th>Unit 5—Unit 4</th>
<th>Unit 6—Unit 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Threshold differences</td>
<td>0.3 ± 0.4</td>
<td>0.5 ± 0.6</td>
<td>0.8 ± 0.8</td>
<td>0.4 ± 0.7</td>
</tr>
<tr>
<td>n</td>
<td>16</td>
<td>11</td>
<td>9</td>
<td>5</td>
</tr>
</tbody>
</table>

Values are means ± SD in millimeters. SMU, single motor unit.
displacement was recorded but where electrode site verification data were not obtained (Hiraba et al. 2000), correlations were demonstrated between the level of EMG activity in IHLP and anterior condylar translation.

Not only do the data demonstrate the task relations of these units, but the data show these units exhibited a continuous spectrum of thresholds ranging up to contralateral or protrusive displacements of 61–89% of the maximum recorded in our subjects. Given that most functional movements would appear to lie well within the range of 61–89% of maximum (Lundeen and Gibbs 1982), these data implicate IHLP not only in the generation and control of these contralateral, protrusive, and jaw-opening movements but also most jaw movements requiring horizontal vector components. For example, chewing cycles are not simply open-close jaw movements but are usually associated with jaw movements containing significant horizontal vector components (Lundeen and Gibbs 1982). Previous studies have suggested that the IHLP is active during the late intercuspal phase and the opening phase of the chewing cycle (Dubner et al. 1978; Møller 1966; Wood et al. 1986). It is proposed that the IHLP is involved in the generation of those horizontal vector components evident in these phases of the chewing cycle.

In light of our present findings, it appears that the reports of IHLP activity on clenching in intercuspal position (Mahan et al. 1983; Widmalm et al. 1987; Wood et al. 1986) reflect recordings from units located in other muscles such as medial pterygoid that has an additional origin from the lateral surface of the lower border of the lateral pterygoid plate (Widmalm et al. 1987). Further studies are needed to determine whether the reports of IHLP activity during vertically directed clenches with the jaw positioned to the ipsilateral side or in protrusion (Mahan et al. 1983; Wood et al. 1996) reflect true IHLP activity or whether in fact these activities represent cross-talk from medial pterygoid motor units.

The absence of spontaneous activity in any of the SMUs when the jaw was in the clinically determined postural jaw position is consistent with previous descriptions (e.g., Mahan et al. 1983). The data suggest that at the postural jaw position there is no anteriorly directed force on the condyle and disk from active muscle contraction in the IHLP maintaining the condyle in close apposition with the disk and articular eminence.

**Role in fine control of jaw movements**

The data also suggest that the IHLP is involved in the fine control of these horizontal jaw movements since SMU activity features varied closely in association with the dynamic parameters of the movement. First, successively recruited SMUs could be recruited at small increments in displacement. Second, the lowest thresholds of the SMUs were <0.2 mm of horizontal jaw displacement, and this suggests an important role in the initiation of the movement. Third, recruitment thresholds of some SMUs were rate dependent, suggesting that these SMUs were intimately concerned with subtle changes in the rate of jaw movement. Not all SMUs exhibited significant rate-dependent features, although a high proportion of the total number of comparisons available between the three rates of movement illustrated decreases in threshold with increases in the rate of movement. Further studies are needed to determine whether, with a larger sample of trials for each SMU recorded, a higher proportion of SMUs would exhibit significant rate differences. Nonetheless, the data suggest that the relevant motor centers (e.g., face motor cortex) are capable of activating the IHLP in a finely controlled manner.

This role for the IHLP in the fine control of horizontal jaw movements is also consistent with previous descriptions where multi-unit IHLP EMG activity was shown to modulate in close association with small fluctuations in condylar movement that reflected variations in the rate of jaw movement as the teeth slid past each other during contralateral or protrusive jaw movements (Murray et al. 1999a, 2001). Other jaw muscles (masseter, anterior and posterior temporal muscles, submandibular group) demonstrated weaker associations with the con-
tralateral and protrusive movements (Murray et al. 1999a) (see following text).

There is also histochemical evidence supporting such a role for the IHLP. The SMUs within the IHLP appear to be predominantly aerobic (slow contracting and fatigue resistant, ~80%) (Mao et al. 1992) and suited to low forces and prolonged contraction times. There is also little evidence for pennation within IHLP that suggests that the IHLP is more suited to isotonic than isometric operational conditions (Hannam and McMillan 1994; van Eijden et al. 1995, 1997). Thus the presence of long fibers (~22 mm) (Schumacher 1961; van Eijden et al. 1995, 1997) 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 seen in masseter and medial pterygoid, which are more suited to high power generation over short distances.

This fine control may extend to the activation of specific regions within the IHLP given the suggestive evidence provided in this paper for functional heterogeneity that has been previously put forward by us and others (Foucart et al. 1998; Hannam and McMillan 1994; Murray et al. 1999c, 2001). Such a notion of functional heterogeneity is not new to the jaw motor system as it has already been well characterized in temporalis and masseter muscles (Blanksmna and van Eijden 1990, 1995). The activation of specific regions within IHLP would allow the application of the appropriate force vector (magnitude and direction) to effect the required condylar movement. This would provide the possibility of considerable sophistication of delivery of different force vectors on the condyle to perform the desired jaw movements. The present paper provides suggestive evidence supporting this notion in that, for each task, SMUs with lower thresholds tended to be grouped in the superior-medial zone within IHLP (see following text). Given possible sampling bias in different locations as well as the small sample size, the data are only suggestive of the possibility of differential activation within IHLP. Further SMU evidence is needed to confirm whether functional heterogeneity is a feature of IHLP. Good evidence for functional heterogeneity would be obtained, for example, by demonstrating reversals of recruitment order among SMUs with changes in task.

Role of other jaw muscles

The present paper studies the role of the IHLP as a contributor to horizontal jaw movements. The data do not rule out roles for other jaw muscles in these movements. For example, the masseter, medial pterygoid and posterior temporalis muscles contain fibers capable of generating force vectors with horizontal components, and this is in accord with previous descriptions of the patterns of recruitment of these muscles during horizontal jaw movements (for reviews, Hannam and McMillan 1994; Miller 1991). Although recent multi-unit EMG data suggest a less notable role than the IHLP for some of these other jaw muscles in horizontal jaw movement generation (Murray et al. 1999a), verified SMU recordings at the same resolution as done in the present study will be needed to determine the role of other muscles in these movements.

Dependence of threshold on rate and direction of movement

Motor units are recruited at successively lower force levels as the speed of a movement or isometric contraction increases (for reviews, Freund 1983; Henneman and Mendell 1981). There have been no detailed studies of such possible associations in the jaw-motor system. In accordance with the findings in the spinal motor system, the present study has demonstrated an association between the rate of horizontal jaw movement and recruitment threshold. Although we did not measure force in these tasks, we believe that faster rates of horizontal jaw displacement are associated with increases in the rate of force delivery required to effect the faster horizontal jaw movement. This increase in the rate of force delivery is needed given the viscoelastic nature of the tissues attaching the jaw to the skull (Peck et al. 2000). The rate data also showed that the higher threshold units modified their onset thresholds with rate of movement, but there was not as large an influence of rate of movement on the threshold of units that have lower overall threshold. These data are entirely consistent with the findings of Yoneda et al. (1986) with different speeds of isometric contraction in limb muscles.

In this study, movements started at the postural jaw position and all tasks were performed with the teeth apart. It is unlikely that the small amount of jaw opening from tooth contact in lateral movements (2–3 mm) would have had a major affect on the threshold values. This is because threshold for a given unit during jaw opening in the z axis was always much higher than the amount of jaw opening during the contralateral or protrusive jaw movements. Further studies are needed to determine the effect, if any, of horizontal displacement on the opening thresholds of IHLP units.

Directional effects on EMG activity have been observed in other jaw (Mao and Osborn 1994) and limb muscles (Hermann and Flanders 1998). The small sample size may contribute to the lack of significant effect of direction of movement on thresholds of firing of IHLP SMUs. Further studies are needed to determine whether significant directional relations are observed in the IHLP.

Verification

A major limitation of most previous studies of the human IHLP has been the absence of reliable verification that electrodes were correctly located within the IHLP and not other jaw muscles. In the absence of a reliable verification technique such as CT imaging (e.g., Fig. 1), conclusions about IHLP function drawn from these studies are questionable given the very real possibility of electrode misplacement in other jaw muscles or the electrodes may have been within IHLP but incorrectly attributed to a particular head of the muscle (Hannam and McMillan 1994; Orfano et al. 1996; Widmalm et al. 1987). Therefore despite recent claims to the contrary (Hiraba et al. 2000), it is not possible to rely on EMG patterns as the sole basis for verifying that electrodes are correctly located within the IHLP.

In our experiments, electrodes were clearly seen in relation to muscle outlines on the CT scans, and this allowed the confirmation of electrode location within the IHLP and not within nearby muscles such as medial pterygoid, temporalis, and SHLP. The separation between SHLP and IHLP was not,
however, always clear on the CT scans, and in such cases, the SHLP was assigned an arbitrary thickness of 5 mm from the roof of the infratemporal fossa, and this was based on previous anatomical studies (Meyenberg et al. 1986; Moritz and Ewers 1987; Widmalm et al. 1987; R. Hawthorn, personal communication). However, even using this arbitrary criterion, the task relations of SMU activity recorded in the superior part of the muscle were entirely consistent with those of SMUs recorded in the other zones of the muscle. For those few units at sites where verification was not obtained, we were still confident that our electrodes were correctly located within the IHLp as the patterns observed matched the reliable patterns that we consistently obtained at the verified sites. No EMG activity was ever recorded in IHLp at intercuspal position clenching in this and all our previous studies (for review, Murray et al. 2001). We therefore do not believe that any of our recordings were from SMUs within the medial pterygoid muscle or temporalis, nor indeed SHLP, the most likely muscles from which erroneously attributed recordings could have been made.

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