4. DATA ANALYSIS

4.1 Locations of Electrodes

According to previous histological studies, the SHLP is approximately 5-mm thick superior-inferiorly (Meyenberg et al. 1986; Moritz and Ewers 1987; Widmalm et al. 1987; R. Hawthorn, personal communication). This criterion therefore was adopted 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.

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. The SHLP was divided into 3 parts in the mediolateral direction; namely the medial, the middle and the lateral part. 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 SMU location.

4.2 Standardised Tasks

For each subject, MIPT displacement data for each non-standardised and standardised task-defined movement were averaged and plotted along the anterior-posterior (x, + posteriorly), mediolateral (y, + to right) and superior-inferior (z, + superiorly) axes for each direction of jaw movement. For standardised tasks, standard deviations (SDs) for MIPT displacement were calculated at points every 750 ms. The closeness with which the subject could track the target was assessed for the lateral excursion by superimposing the target line calculated for the y-axis (mediolateral axis) over the actual mean trajectory calculated along the y-axis. For protrusion, the target line calculated for the x-axis (anterior-posterior axis) was superimposed over the actual mean trajectory calculated along the x-axis. 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, representing the diameter of the LED, 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 less than 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.

4.3 Single Motor Unit Activity

Single motor units were discriminated by using custom-written data management software with Spike2 from CED, and were carefully checked by visual inspection. The criteria for defining a SMU were similarities in amplitude and waveform between all representatives of an identified SMU. For the present study, task relations and LSFFs of both SHLP and IHLP units were presented. However, only IHLP units were characterised for thresholds and firing rate properties during standardised tasks.

4.3.1 Task Relations

An analysis of the general features of task relations was conducted for SHLP and IHLP SMUs, recorded from 18 (18 sessions) and 16 subjects (22 sessions), respectively, during standardised single-step and/or multiple-step displacements and non-standardised tasks. The IHLP SMUs from an additional 3 subjects (5 sessions) were analysed for LSFFs, but were not included in the task relations analysis.

4.3.2 Thresholds of IHLP Motor Units

An assessment of threshold was made only for the IHLP 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. III-9). A given displacement presumably equates to a particular force required to overcome passive forces such as tissue viso-elasticity. 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 the present study, thresholds are reported below in terms of MIPT displacement in order 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 for three rates and Mann-Whitney *U* Test for two rates, given that the threshold values were not normally distributed (Shapiro-Wilk). For the analysis of the differences in displacement between successively recruited SMUs recorded at any one site, continuously active units were analysed.

Thresholds are reported in terms of MIPT displacement. Therefore, in order 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 LP. 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 to 1.02 mm (3D coordinates), which indicates that on average, the condyle moved ~70% of the displacement at the MIPT. Although both condyles ideally move forwards 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 to 1.02 mm (3D coordinates).

4.3.3 Least-sustainable Firing Frequencies

For LSFF analysis, the firing rates were calculated over the period that the jaw-displacement traces were stable (*i.e.,* <0.5 mm fluctuation along any axis), and averaged from at least 5 trials of contralateral movement and protrusion. The mean LSFFs of each SMUs for two directions, (*eg.,* contralateral movement and protrusion) were compared by paired t-test.

4.3.4 Firing Rates

For an analysis of firing-rate changes during the standardised multiple-step tasks, an assessment of firing rate was made for the IHLP units that fired continuously at least through two steps of displacement. According to previous studies, the LSFFs of masticatory motor units was ~6 imp/s (Eriksson et al. 1984); therefore, an interspike interval >160 ms was considered as a pause and excluded from the analysis. Firing rates were calculated for each dynamic and holding phase and averaged over at least 5 trials. The period of the dynamic and holding phases were determined on the basis of when the jaw was displaced from baseline or a holding phase or when the jaw reached a stable displacement level. Firing rates of units during each holding and dynamic phase were compared between the rates of movement by using Wilcoxon Signed Ranks Test. 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 bin width, CED software) for each defined task. For each unit, jaw displacement and matched mean frequency were normalised to the same number of data points. Then, both jaw displacement and mean frequency from five to eight trials for each task were concatenated, and cross-correlation analysis was performed. Correlation coefficients at the slow and fast rates of movement were compared by the paired t-test. In the present study, a P-value of <0.05 was considered to indicate a statistically significant difference.

CHAPTER III

RESULTS

1. ABILITY OF SUBJECTS TO TRACK TARGETS AT DIFFERENT RATES AND MAGNITUDES OF DISPLACEMENT

In all subjects, the MIPT target could be tracked during single- and multiple-step displacements at different rates and magnitudes of movement. For example, Figure II-9B and II-10B illustrate a close match between target lines (—) and averaged MIPT traces (---) during jaw movement without tooth contact in one subject. All subjects fulfilled the criterion (see Materials and Methods: section 4.2) for single-step and multiple-step displacements and for different directions of movement in the horizontal plane. For example, Figure II-9B is data from a single-step jaw movement showing that the subject could track the target at the desired rate of MIPT movement. The MIPT displacements were tracked at two rates of movement: 6.6 mm/s (f, fast) and 2.2 mm/s (i, intermediate). The SDs during the movement phase ranged from 0.27 to 1.18 mm. Although there were deviations of the MIPT traces from the target lines, especially during the outgoing phase of the MIPT displacement at a rate of movement of 2.2 mm/s, the traces fell within our criterion of acceptability. Additionally, the MIPT displacements at both fast and intermediate jaw movements were approximately parallel to the target lines, which indicates that the subject could track both targets at these desired rates of movement. Further, SDs during the stationary phase were small (range: 0.04 – 0.26 mm) and mean values were contained within the shaded area. That is, the subject was able to move the jaw very accurately to the same magnitude of displacement in repeated trials and the mean displacement was contained within the boundary of the target LED. Similar SD values were observed in the data from the other subjects.

Tracings from one subject of individual MIPT displacements along x- (anterior-posterior), y- (mediolateral) and z- (superior-inferior) axes during right (ipsilateral) jaw movement are illustrated in Fig. III-1. Five to six tracings were superimposed for each task-defined jaw movement. The consistency from trial to trial along the y-axis (centre panel of tracings) is clearly apparent for fast (upper tracings) and slow (middle) single-step movements, and for multiple-step displacements (lowest tracings). There appeared to be somewhat more variability in the amount of displacement from trial to trial during faster movements (Fig. III-1, upper tracing) than during slower movements (Fig. III-1, middle tracings), and this is reflected in the somewhat larger SD values for fast in comparison with intermediate movements in Fig. II-9B.

The close superimposition of the individual tracings (Fig. III-1) confirms the small SD values about the mean values presented in Fig. II-9A and Fig. II-10A. Although subjects only monitored MIPT displacement along the x- and y-axes during recordings, displacements along the z-axis were also remarkably consistent from trial to trial. The average SD values for fast and slow single-step movements, and for multiple-step right displacements in Fig. III-1 were 0.21, 0.27 and 0.24 mm, respectively, and 0.51, 0.30 and 0.23 mm for the same tasks during protrusion. The data indicate that it is only necessary to monitor one plane when standardising jaw movement in the horizontal plane. Comparable findings to the above were also obtained during protrusive jaw movements in the horizontal plane, again with the teeth apart. This supports the applicability of this methodology to the movement of the jaw to any direction in the horizontal plane.

2. SIMULTANEOUS RECORDINGS OF SINGLE MOTOR UNIT ACTIVITY AND STANDARDISED JAW MOVEMENT

We were able to record standardised jaw movements in the horizontal plane together with activity of LP SMUs in the subjects. For example, Figure III-2 shows simultaneous recordings of SMU activity from the right IHLP during right jaw movement without tooth contact. The trial commenced at the far left of the figure with the jaw in postural position for 2 s. The subject was then instructed to track the target at a rate of movement of 4.3 mm/s until the first assigned target was acquired and the jaw was held steady in that position for 7 s.

Average MIPT displacement (---) from 5 repeated trials is shown in the upper trace together with the target line (—). The activity of a SMU recorded in the IHLP during these 5 successive trials is illustrated. The same unit was reliably discriminated throughout each trial. Five superimposed SMU waveforms are shown on the right of each set of spike-train pulses and each group of five waveforms were taken from the raw data file that produced the associated spike-train trace on the left. The waveforms were virtually identical between all recordings thus confirming reliable SMU isolation.

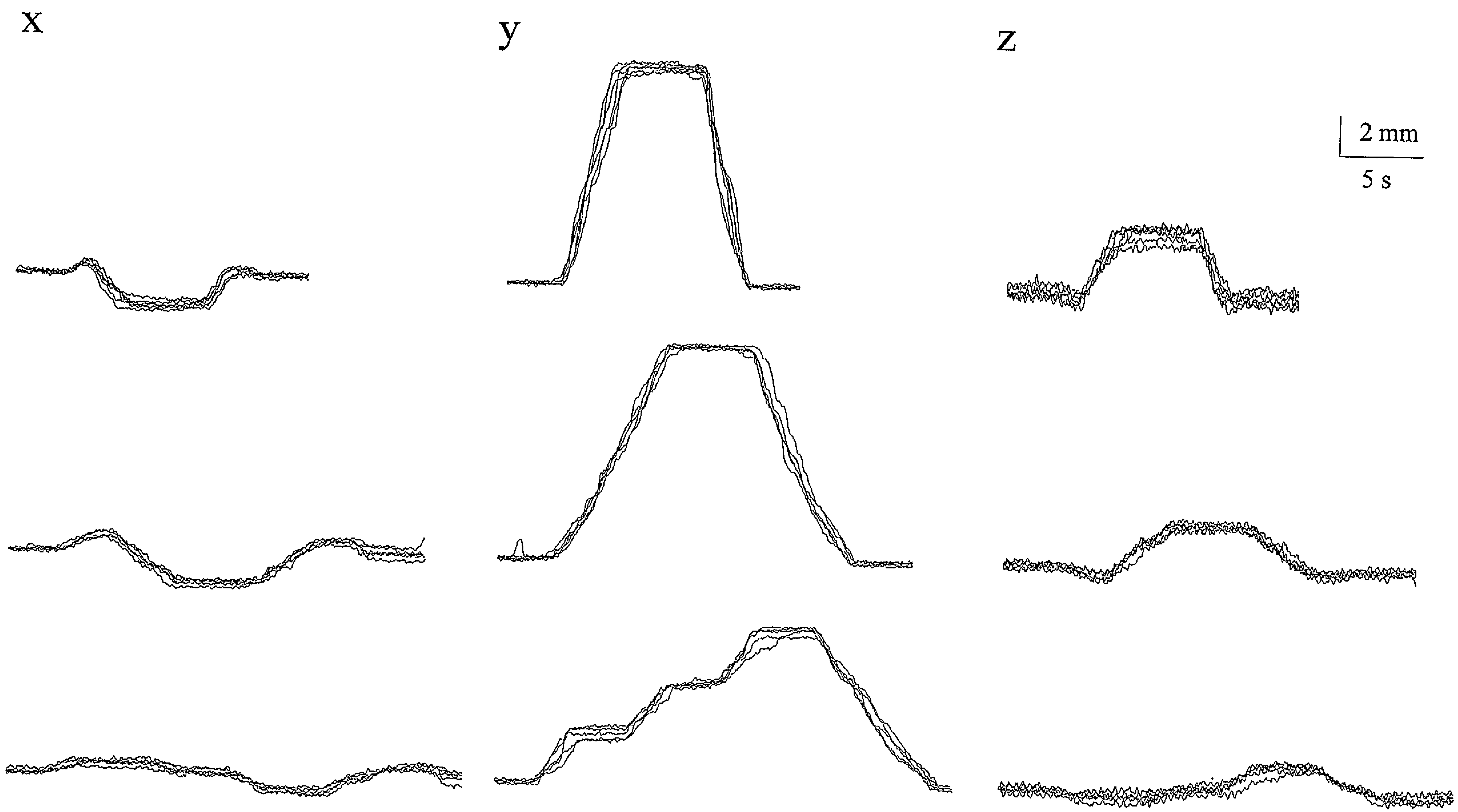


Fig. III-1 Superimposed individual MIPT displacements during right jaw movement. Tracings were plotted along x (anterior-posterior, *leftt* panel), y (mediolateral, *centre* panel) and z (superior-inferior, *right* panel) axes during single-step displacements at the rates of jaw movement of 6.5 (*upper* tracings) and 2.2 mm/s (*middle* tracings) and during multiple step displacements (*lowest* tracings) at the rates of jaw movement of 1.3 mm/s.

An assessment was also made of the consistency from trial to trial of the overall level of EMG activity in the IHLP and these data are shown qualitatively for one subject in Fig. III-3 and quantitatively for 6 subjects in Table III-1. Figure III-3A shows the mean (±SD) displacement trace along the y-axis during contralateral jaw movement and B shows the raw EMG signal from the IHLP together with the corresponding Butterworth-filtered (cut-off: 2 Hz) signal above each raw trace. There was no marked variation from trial to trial and this consistency from trial to trial was also a feature of all subjects where the area under the curve was calculated for all trials (see Table III-1).

Table III-1 Mean (±SD) filtered EMG level of the IHLP from 6 subjects during contralateral and protrusive jaw movements. Each data set is calculated from 5-8 individual values.

Subjects	Area under curve (arbitrary units)	
	Contralateral task	*Protrusive task*
S1	1.01 ± 0.08	0.77 ± 0.07
S2	0.25 ± 0.01	-
S3	1.06 ± 0.05	1.05 ± 0.14
S4	1.19 ± 0.09	1.04 ± 0.07
S5	0.66 ± 0.04	0.49 ± 0.03
S6	0.49 ± 0.03	0.48 ± 0.03

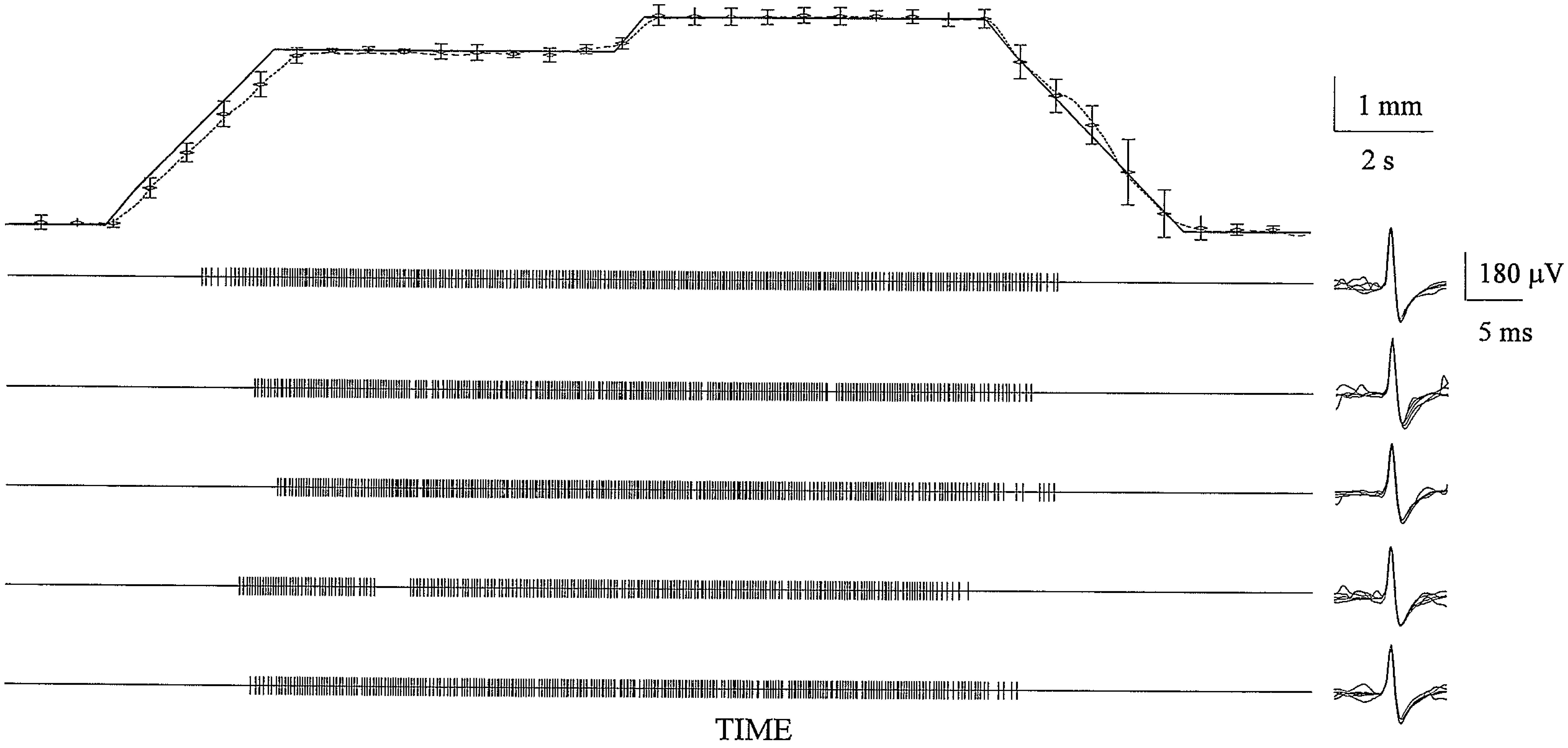


Fig. III-2 SMU recordings during repeated standardised jaw movements to the right side. Simultaneous recordings of SMU activity from the IHLP during multiple step displacement at a rate of movement of 4.3 mm/s. The uppermost trace shows averaged MIPT displacement with 1 SD bars (every 750 ms) superimposed on the target line. MIPT displacement is plotted along the mediolateral (y) axis. Activity of a SMU from the IHLP during these movements is shown in the 5 *lower* traces. Each vertical line indicates the time of occurrence of a SMU action potential and five superimposed traces of the waveform of the SMU are displayed to the *right* of each sequence of spike trains.

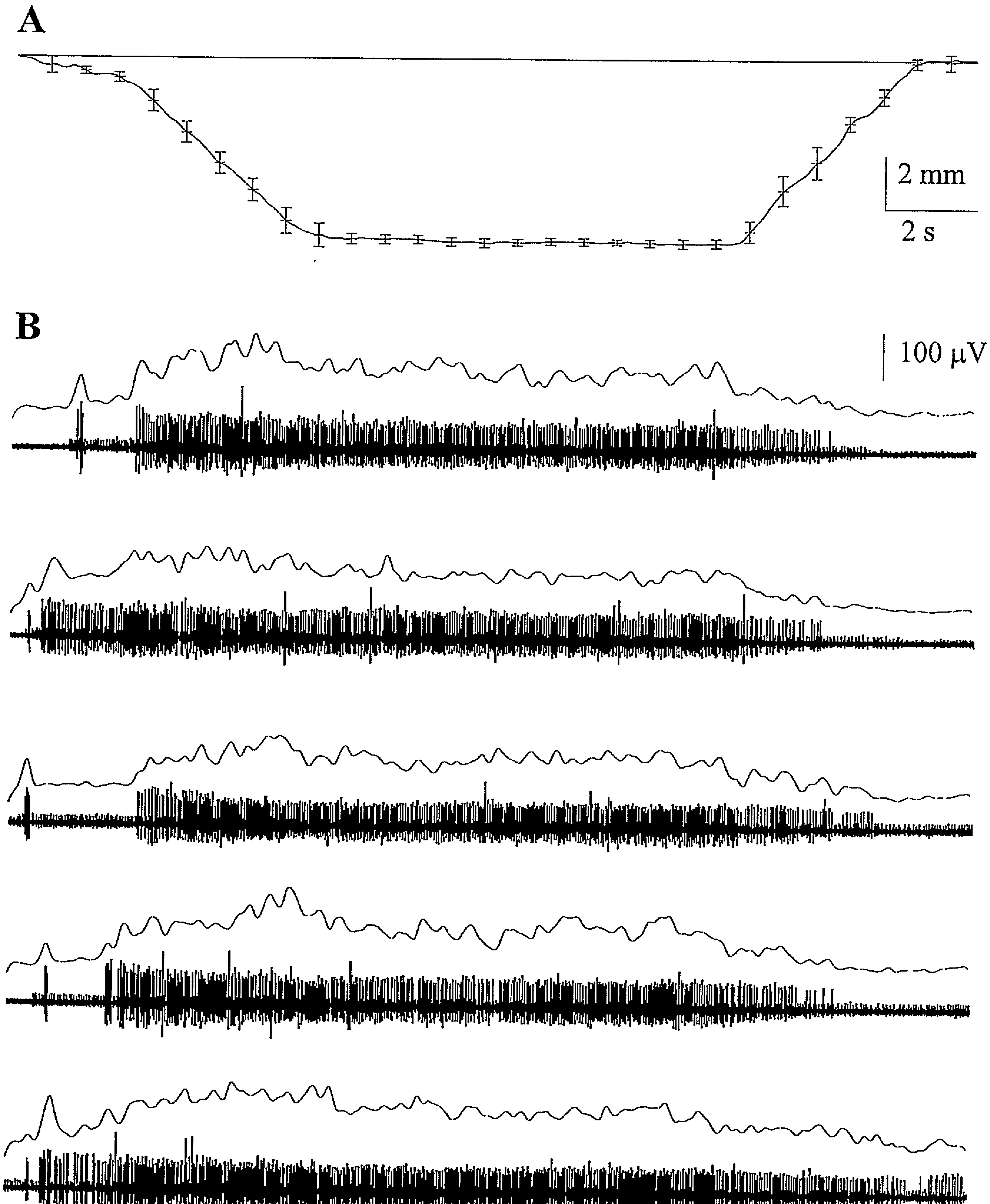


Fig. III-3 EMG activity of the IHLP during repeated standardised jaw movements to the left side. Simultaneous recordings of the IHLP activity during single-step displacement at a rate of movement of 2.2 mm/s. The uppermost trace shows averaged MIPT displacement with the same format as Fig. III-2. MIPT displacement is plotted along the mediolateral (y) axis. Raw EMG activity of the IHLP and the Butterworth-filtered signal during these movements are shown in the 5 lower traces.

3. GENERAL FEATURES OF TASK RELATIONS

3.2 Task Relations for the Superior Head

A total of 92 SHLP SMUs were recorded: 21 units (4 sites) from the medial part, 36 units (6 sites) from the middle part and 35 units (8 sites) from the lateral part of the SHLP. Of the 92 units, 77 were examined for activity during standardised tasks while 15 units (subject M, Q, R in Table III-2) were studied only for non-standardised tasks.

None of the units was active at postural jaw position. The muscle activity of the SHLP and the locations of each recording site are summarised in Table III-2, and the task relations for each unit are presented in Table III-3. The percentages of recording sites and percentages of units active in relation to each task are plotted for the medial, middle and lateral parts of the SHLP in the histograms illustrated in Fig. III-4 and Fig. III-5, respectively. In general, the SHLP could be active for any of the tasks performed, but the activity at a site within the muscle depended on the location of the electrodes. There were activities during contralateral movement, protrusion and jaw opening in >80% of the recording sites, while 38-39% of the recording sites exhibited activity during jaw closing, ipsilateral movement, retrusion and clenching (Table III-2). When the SHLP was divided into 3 parts, every recording site from the medial part showed activity during contralateral movement, protrusion and jaw opening. One of four sites (25%) showed activity during jaw closing. Units recorded from the medial part (Table III-3) showed activity during contralateral movement (86% of units), protrusion (95%), jaw opening (64%) and/or jaw closing (20%), and were silent during ipsilateral movement, retrusion and clenching in intercuspal position. In this medial part the percentage of units involved in jaw closing was less than those involved in the other tasks (Fig. III-5), and the units were active during the early closing phase and ceased activity before the teeth returned to intercuspal position.

Table III-2 Muscle activity of the SHLP from 18 subjects, in relation to electrode locations, and numbers of units recorded from each site.

Subject	Cl	Pro	Open	Close	Ipsil	Ret	Clench	Number of units
Medial								
A	+	+	+	-	-	-	-	5
B	+	+	+	-	-	-	-	5
C	+	+	+	+	-	-	-	5
D	+	+	+	-	-	-	-	6
Middle								
E	+	+	+	-	-	-	-	6
F	+	+	+	-	-	-	-	9
G	+	+	+	-	-	-	-	3
H	+	+	+	+	+	+	+	7
I	+	+	+	-	+	-	+	6
J	+	+	+	-	+	-	+	5
Lateral								
K	+	+	+	-	-	-	-	1
L	+	+	+	-	-	-	-	3
M	+	+	+	+	-	+	Nd	6
N	-	+	Nd	Nd	-	+	+	5
O	+	+	+	+	+	+	-	7
P	+	+	+	Nd	+	+	+	4
Q	-	-	-	+	+	+	+	7
R	-	-	-	+	+	+	Nd	2
% of sites showing activity	83	89	88	38	39	39	38	

Cl = contralateral movement; Pro = protrusion, Open = sub-maximal jaw opening, Close = jaw closing; Ipsil = ipsilateral movement; Ret = retrusion; Clench = clenching in intercuspal position.

+ , active; - , not active; Nd, no data available

Table III-3 Task relations for each SHLP motor unit.

Subject	Unit	Cl	Pro	Open	Close	Ipsil	Ret	Clench
Medial part								
A	1	+	+	-	-	-	-	-
	2	-	+	+	-	-	-	-
	3	-	+	-	-	-	-	-
	4	-	+	-	-	-	-	-
	5	+	+	-	-	-	-	-
B	6	+	+	+	-	-	-	-
	7	+	-	+	-	-	-	-
	8	+	+	+	-	-	-	-
	9	+	+	-	-	-	-	-
	10	+	+	+	-	-	-	-
C	11	+	+	+	+	-	-	-
	12	+	+	+	+	-	-	-
	13	+	+	+	+	-	-	-
	14	+	+	§	§	-	-	-
	15	+	+	+	+	-	-	-
D	16	+	+	§	-	-	-	-
	17	+	+	§	-	-	-	-
	18	+	+	§	-	-	-	-
	19	+	+	§	-	-	-	-
	20	+	+	§	-	-	-	-
	21	+	+	§	-	-	-	-

Subject	Unit	Cl	Pro	Open	Close	Ipsil	Ret	Clench
Middle part								
E	22	+	+	+	-	-	-	-
	23	+	+	+	-	-	-	-
	24	+	+	+	-	-	-	-
	25	-	+	+	-	-	-	-
	26	-	+	+	-	-	-	-
	27	+	-	§	-	-	-	-
F	28	+	+	-	-	-	-	-
	29	+	+	-	-	-	-	-
	30	+	+	-	-	-	-	-
	31	+	+	+	-	-	-	-
	32	+	+	+	-	-	-	-
	33	+	-	-	-	-	-	-
	34	-	+	-	-	-	-	-
	35	-	+	+	-	-	-	-
	36	-	-	+	-	-	-	-
G	37	+	+	§	-	-	-	-
	38	+	+	§	-	-	-	-
	39	-	+	§	-	-	-	-
H	40	+	+	+	+	+	-	+
	41	+	+	+	+	+	+	+
	42	+	+	+	+	-	-	+
	43	+	+	+	+	+	+	+
	44	§	+	§	§	+	+	+
	45	+	+	+	+	+	+	+
	46	+	-	§	§	-	-	-

Subject	Unit	Cl	Pro	Open	Close	Ipsil	Ret	Clench
I	47	-	-	-	-	+	-	-
	48	+	+	+	-	+	-	+
	49	+	+	+	-	+	-	+
	50	+	-	+	-	+	-	+
	51	+	+	+	-	+	-	+
	52	-	-	-	-	+	-	-
J	53	-	-	-	-	+	-	§
	54	+	+	+	-	+	-	§
	55	+	+	+	-	-	-	§
	56	+	+	§	-	-	-	§
	57	+	-	+	-	+	-	§
Lateral part								
K	58	+	+	§	-	-	-	-
L	59	+	+	+	-	-	-	-
	60	+	+	+	-	-	-	-
	61	+	+	+	-	-	-	-
M	62	+	+	+	+	-	+	Nd
	63	+	-	+	+	-	+	Nd
	64	-	+	-	-	-	-	Nd
	65	+	+	+	+	-	+	Nd
	66	+	-	-	-	-	-	Nd
	67	+	+	+	+	-	-	Nd
N	68	-	-	Nd	Nd	-	+	+
	69	-	+	Nd	Nd	-	+	+
	70	-	-	Nd	Nd	-	-	+
	71	-	+	Nd	Nd	-	-	-
	72	-	-	Nd	Nd	-	-	+

Subject	Unit	Cl	Pro	Open	Close	Ipsil	Ret	Clench
O	73	+	+	+	-	+	-	-
	74	+	+	+	+	+	+	-
	75	+	-	-	-	-	-	-
	76	+	+	+	-	+	-	-
	77	+	+	+	-	+	-	-
	78	+	+	+	-	+	-	-
	79	+	+	+	-	-	-	-
P	80	-	-	§	Nd	+	+	§
	81	+	+	§	Nd	+	-	§
	82	+	+	§	Nd	+	-	§
	83	+	+	§	Nd	+	-	§
Q	84	-	-	-	§	+	+	+
	85	-	-	-	§	+	+	+
	86	-	-	-	§	+	+	-
	87	-	-	-	§	+	+	+
	88	-	-	-	§	+	+	-
	89	-	-	-	§	+	+	-
	90	-	-	-	§	+	+	+
R	91	-	-	-	+	+	+	Nd
	92	-	-	-	+	+	+	Nd

Cl = contralateral movement; Pro = protrusion, Open = sub-maximal jaw opening, Close = jaw closing; Ipsil = ipsilateral movement; Ret = retrusion; Clench = clenching in intercuspal position.

+ , active

- , not active

§, there was activity during task performed, but unable to discriminate units

Nd, no data available

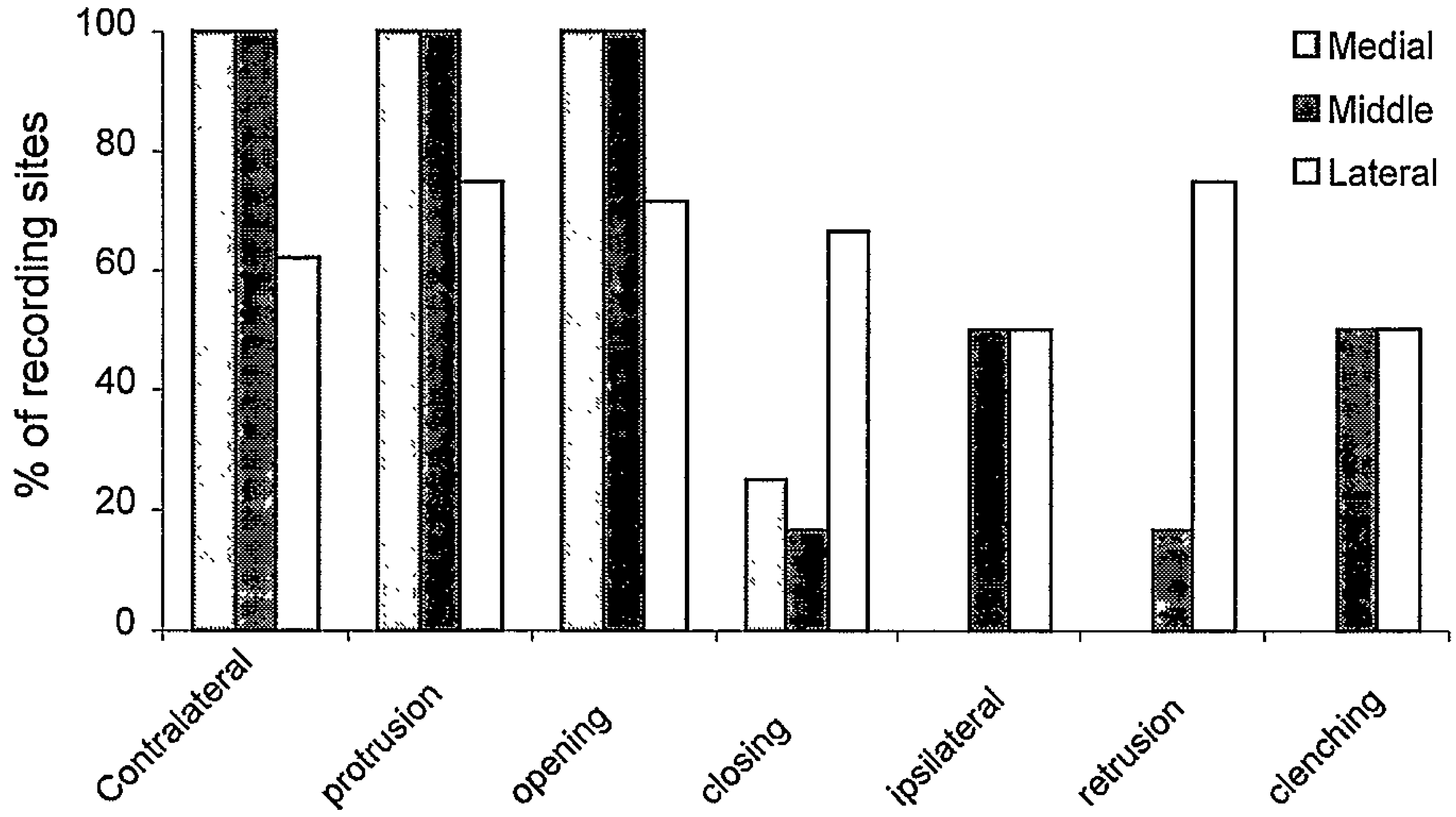


Fig. III-4 The percentages of recording sites in the medial, the middle and the lateral parts of the SHLP, and that exhibited activity during each task.

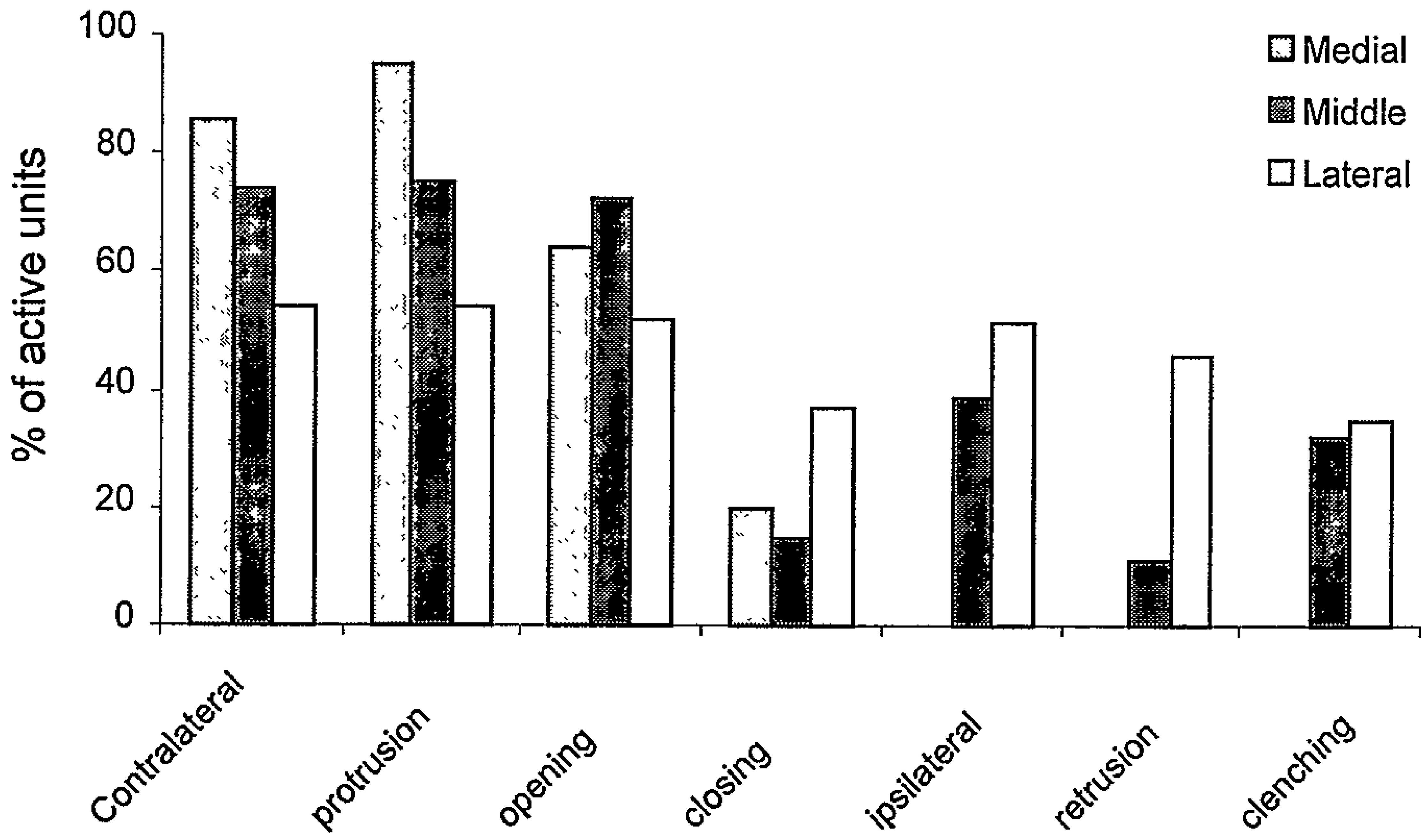


Fig. III-5 Percentages of units recorded from the medial, the middle and the lateral parts of the SHLP and that exhibited activity during each task.

Figure III-6 shows an example of SHLP SMUs recorded from the medial part of the muscle in subject B. Units were active during contralateral movement (A), protrusion (B) and sub-maximal jaw opening (C). Not all units were active during all tasks. Each short vertical line is a spike-train pulse that indicates the time of occurrence of a SMU action potential. The top three traces in each figure show displacement. The location of the electrode was verified by CT in the coronal and the frontal planes (Fig. III-6D).

Recordings from the middle part showed activity with different combinations of tasks in different subjects, including the same pattern as found in the medial part (3 of 6 sites) (Table III-2). In subject H, there was activity during all tasks performed, whereas in subjects I and J, there was activity during all tasks except jaw closing and retrusion. However, as a whole, the entire range of tasks was represented (Fig. III-5). Only a small percentage of units in the middle part were active during jaw closing and retrusion (11% and 14%), compared to those during the other tasks (range: 32% to 75%). Examples of SMU activity from the middle part, obtained from subject H is illustrated in Fig. III-7 in the same format as Fig. III-6. There was activity during ipsilateral (A) and contralateral (B) movement, retrusion (C), protrusion (D), submaximal jaw-opening and closing (E). The SMUs could not be reliably discriminated during jaw opening and closing. The units started firing at very small displacements during retrusion and protrusion.

In the lateral part, two (Q, R in Table III-2) of eight sites showed activity during ipsilateral movement, retrusion, jaw closing or clenching in intercuspal position, and two sites (K, L in Table III-2) demonstrated activity resembling those recorded from the medial part, while the other four sites (M, N, O, P in Table III-2) showed activity in various patterns. The percentages of units in the lateral part contributing to each task ranged from 35 to 54%. An example of units from the lateral part is shown in Fig. III-8 in the same format as Fig. III-6.

Not all units at each recording site contributed to all tasks labelled positive (Table III-2). Of the 92 units, 79 (86%) were involved in more than one task, and some units participated in up to 5-7 tasks, while the other 13 units (14%) were active during one task only.

The numbers of units activated during horizontal and vertical tasks were compared between the three regions of the SHLP to determine whether units active during vertical or horizontal tasks were localised to a specific region. The horizontal tasks included protrusion, retrusion, contralateral and ipsilateral movements. Jaw closing and clenching were defined as vertical tasks. The data from jaw opening were not included in the analysis because the subjects performed submaximal jaw-opening and it is possible that the units which were not active during submaximal jaw-opening would be active at maximal jaw opening. A total of 92 and 84 SMUs were included in this analysis for the horizontal and vertical tasks, respectively. The units that could not be distinguished during at least one of the vertical tasks were excluded from the analysis. Each unit was considered to be active in the horizontal tasks when the unit fired in at least one of the horizontal tasks, and the same method was applied for the vertical tasks analysis. The percentages of units active during the horizontal tasks in the medial, middle and lateral part were 100%, 97% and 94%, respectively, and were 20%, 17% and 45%, respectively during the vertical tasks

(Table III-4). There was no significant association between the location of units and the number of units active during the horizontal tasks (Pearson Chi-Square; $P = 0.05$). However, there was a significant association between the location of units and the number of units active during the vertical tasks (Pearson Chi-Square; $P < 0.05$). There was a greater percentage of units in the lateral part involved in the vertical tasks than those in the medial and middle parts.

Table III-4 Number of units active in horizontal or vertical tasks and the relation with location.

	Medial part	Middle part	Lateral part	Total
Horizontal tasks				
Active units	21 (100)	35 (97)	33 (94)	89
Inactive units	0	1	2	3
Total	21	36	35	92
Vertical tasks				
Active units	4 (20)	6 (17)	13 (45)	23
Inactive units	16	19	16	61
Total	20	35	29	84*

Parentheses enclose percentages.

Pearson Chi-Square: horizontal tasks, $P = 0.5$; vertical tasks, $P = 0.03$.

* 8 units were not distinguishable during one of the vertical tasks (jaw closing and clenching).

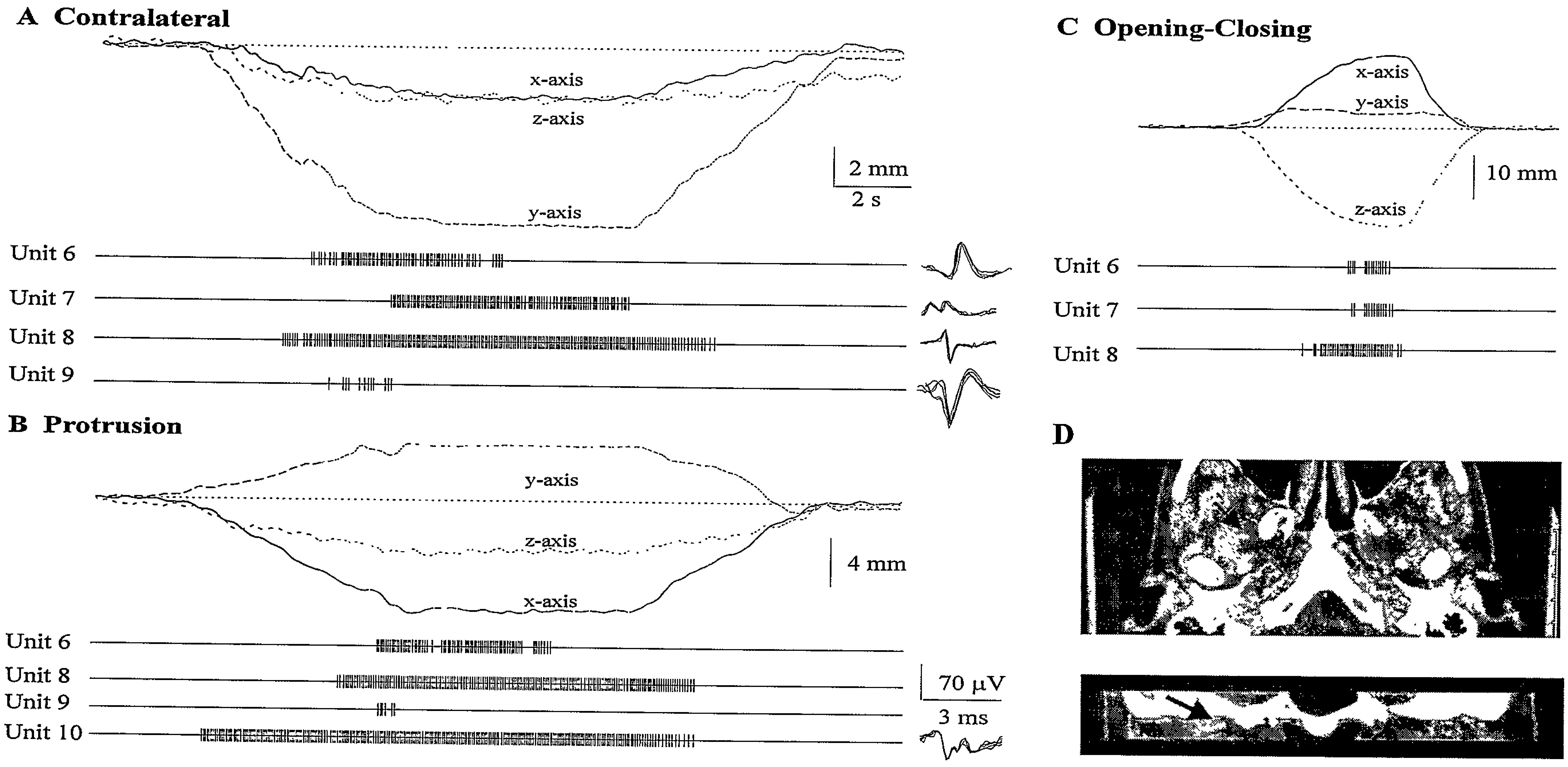


Fig. III-6 An example of SMU activity from the medial part of the right SHLP in subject B during contralateral movement (*A*), protrusion (*B*) and submaximal jaw-opening and closing (*C*). Traces at the top of each figure represent MIPT displacement in x (anterior-posterior; + posterior), y (mediolateral; + to right), and z (superior-inferior; + superiorly) axes. Spike-train pulses are at the bottom of each figure. Each short vertical line is a spike-train pulse that indicates the time of occurrence of a SMU action potential. All movements started and ended at postural jaw position. The CT imaging in the horizontal plane (top in *D*) and reformatted image taken through the fine-wire tips in the frontal plane (bottom in *D*) show the electrode fine-wire tips (black arrows).

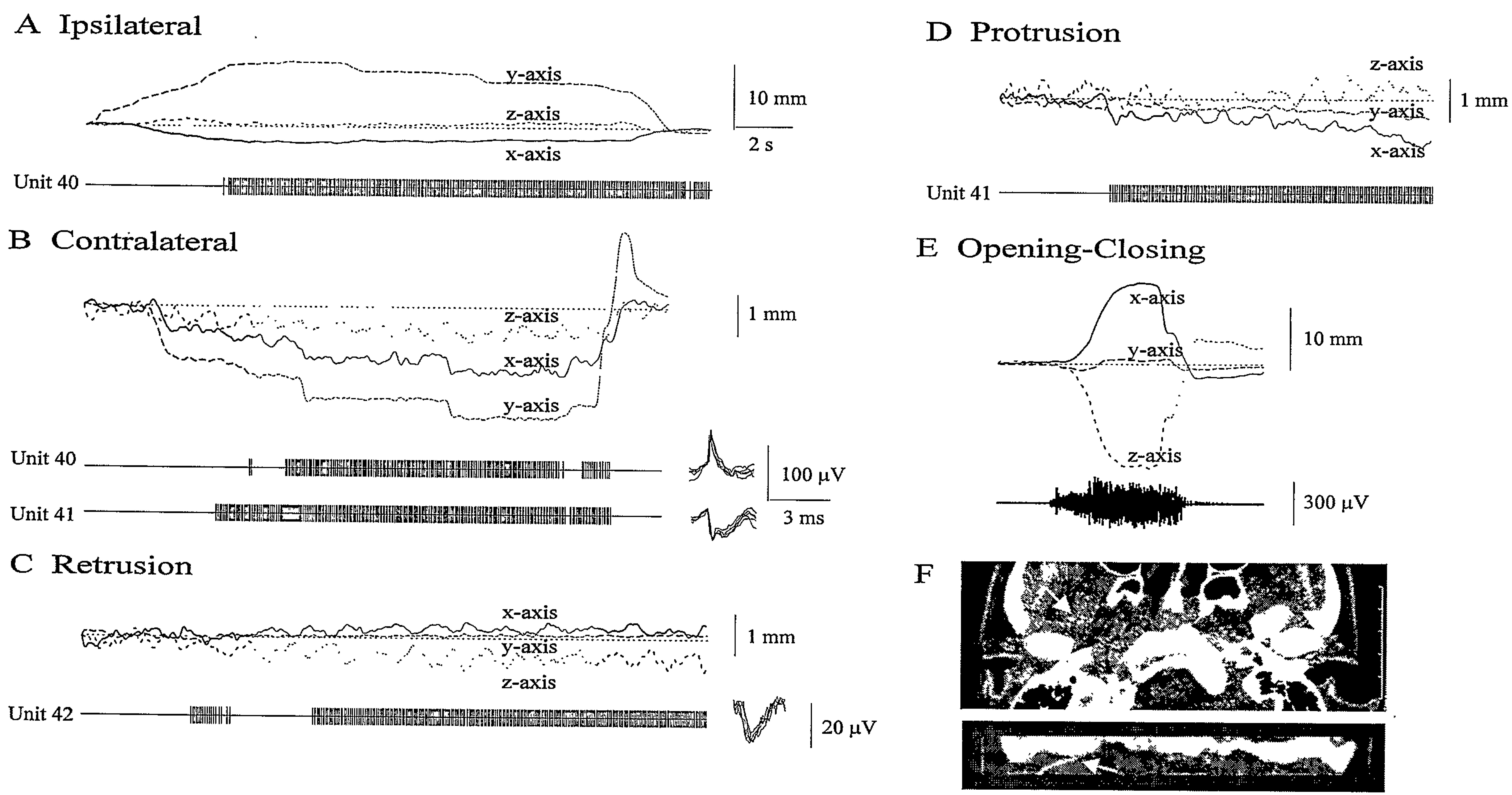


Fig. III-7 An example of SMU activity from the middle part of the right SHLP in subject H during ipsilateral (A) and contralateral movements (B), retrusion (C) and protrusion (D). Multi-unit activity during submaximal jaw-opening and closing, where the SMUs could not be reliably discriminated throughout the trial, is shown in E. The CT images are shown in F. The format of the figure is as in Fig. III-6.

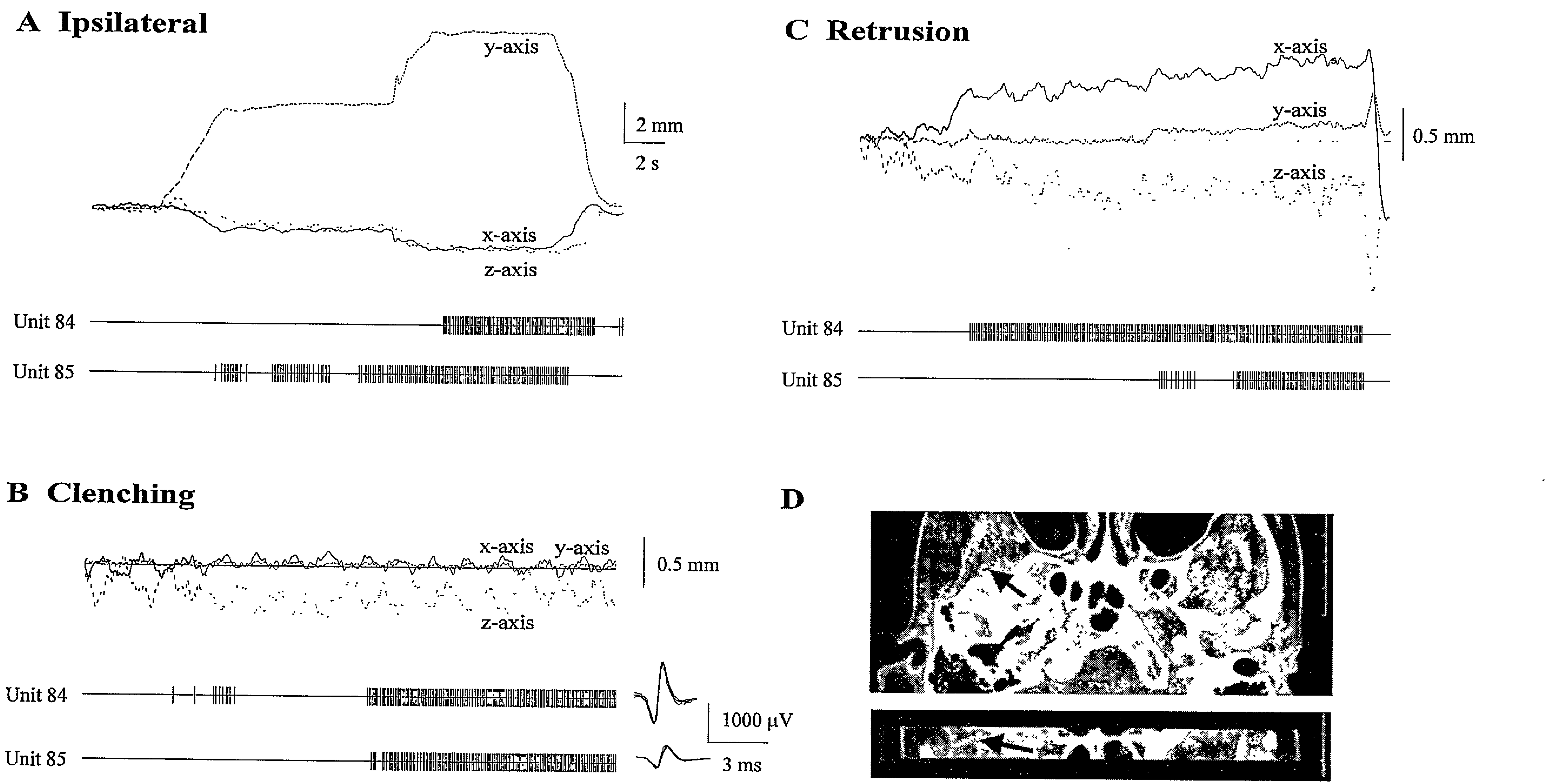


Fig. III-8 An example of SMU activity from the lateral part of the right SHLP in subject Q during ipsilateral movement (A), clenching in the intercuspal position (B) and retrusion (C). The format of the figure is as in Fig. III-6.

3.2 Task Relations for the Inferior Head

A total of 99 IHLP 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 intercuspal position, and non-standardised retrusion and ipsilateral jaw movement. Of the 99 units, 97 were examined for activity during standardised (*i.e.,* single-step and/or multiple-step displacements) tasks while two units were studied only during non-standardised 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-hour recording session. None of the units was active during the non-standardised tasks of retrusion, 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 five 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 III-9 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, is displayed at the bottom of A with the units labelled 1, 2 or 3 corresponding to the appropriately labelled spike-train pulses. The upper three traces in each panel show displacement. This subject consistently deviated the jaw to the ipsilateral side during protrusion (upper trace in B; see Methods: section 3.1). However, the SMU activity was considered to relate to protrusive jaw displacement since there was no IHLP activity during ipsilateral movement in any subject.

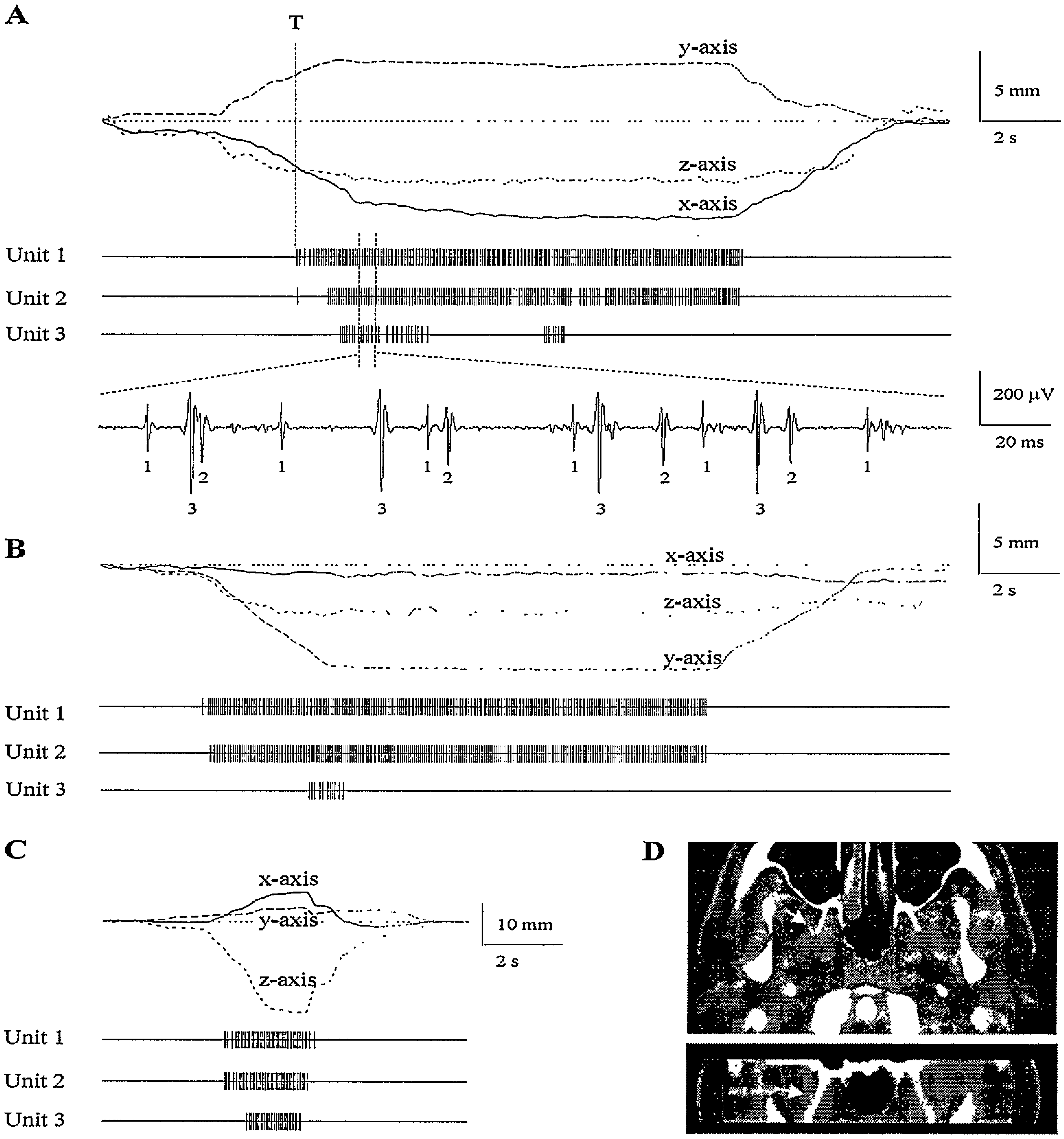


Fig. III-9 An example of SMU activity from right IHLP during contralateral and protrusive movements and jaw opening. The subject performed protrusive (*A*), and contralateral (to left side; *B*) jaw movements at the rate of 2.2 mm/s and non-standardised jaw opening (*C*). Traces at the top of each panel represent MIPT displacement in x (anterior-posterior; + posteriorly), y (mediolateral; + to right) and z (superior-inferior; + superiorly) axes. Spike-train pulses are at the *bottom* of each panel except for *A*, which is in the *middle*. The period delineated by the dotted vertical lines in *A* is shown in expanded form at the *bottom* as the original raw data where the units labelled 1-3 are the units discriminated. The dotted line labelled T represents displacement threshold for unit 1. All movements started and ended at postural jaw position with the exception of open-close which started and ended at intercuspal position. (*D*) CT scan of the electrode (arrow) in the IHLP.

4. THRESHOLDS OF THE INFERIOR HEAD MOTOR UNITS

For the study of SMU threshold, only the IHLP units which fired tonically during the holding phases of single-step displacements were analysed. According to this criterion, 35 of 99 units were analysed during contralateral displacements, 40 were analysed 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 not studied in the single-step task, they exhibited a phasic and sporadic pattern of firing during the dynamic phase only, or were studied in the single-step tasks but the first spike firing could not be reliably determined, were however assessed for task relations, as indicated above.

4.1 Range of Thresholds for Firing

The sample of SMUs from IHLP exhibited a range of activation thresholds. The dotted line labelled T in Fig. III-9 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: section 3), 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 below). 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 to about 61% or 89% of the maximum possible range of contralateral or protrusive horizontal displacements.

Figure III-9B 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 III-10 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 towards more easily discriminable small, low-threshold units, rather than the observed low-frequency of higher threshold units.

4.2 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 2-3 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 (Kruskal Wallis Test or Mann-Whitney *U* Test; $P < 0.05$) at different rates of movement. Figure III-11A plots mean threshold values for these 12 units. The non-significant units have been omitted for figure clarity. For protrusion, the threshold of firing of 10 (25%) of 40 units was significantly different (Kruskal

Wallis Test or Mann-Whitney *U* Test; $P < 0.05$) at different rates of movement (Fig. III-11B).

Table III-5 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). Data were sometimes 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: section 3). 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).

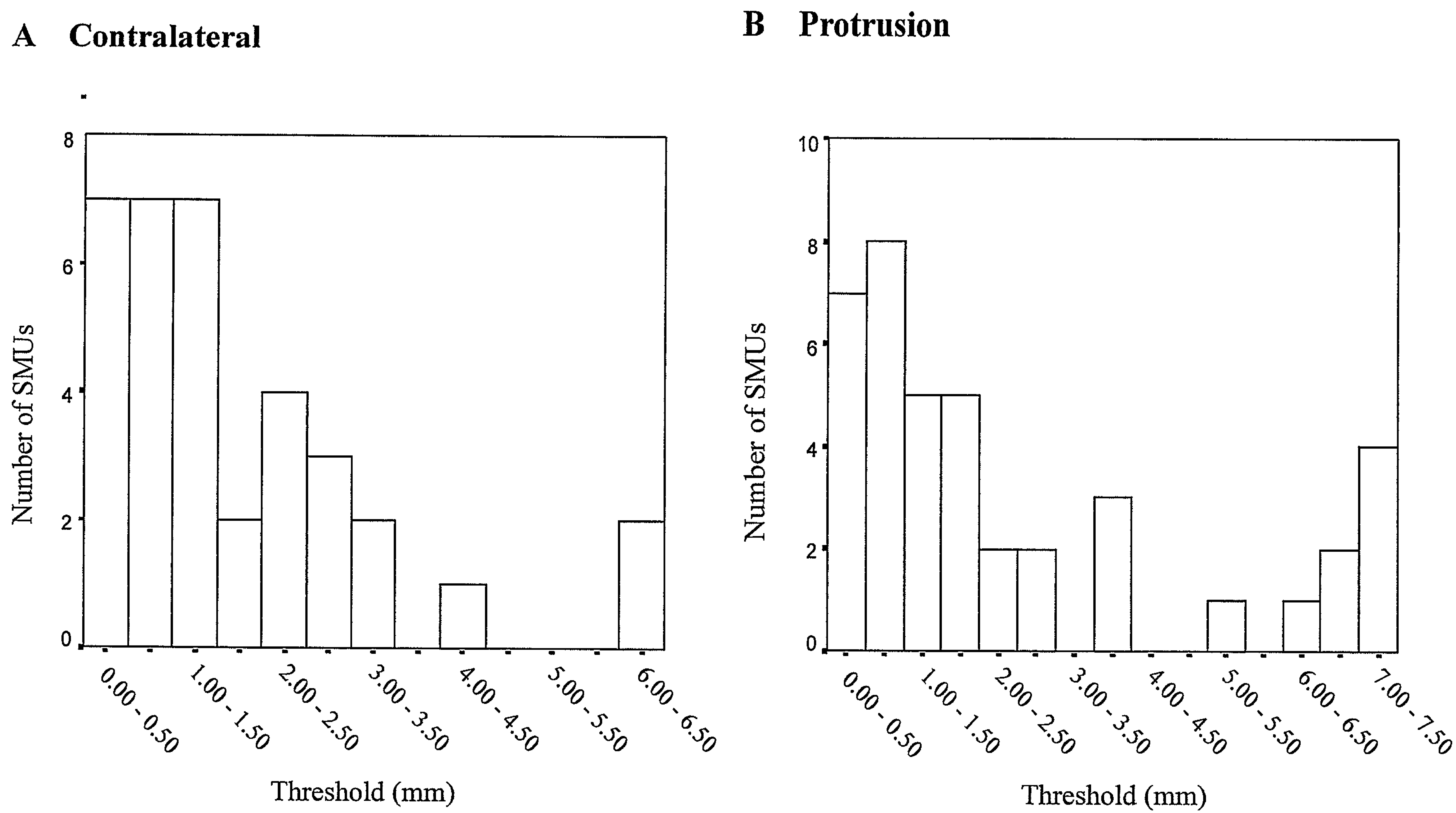


Fig. III-10 Frequency histograms of the range of thresholds of 35 IHLP units recorded in contralateral movement (*A*) and 40 units in protrusion (*B*).

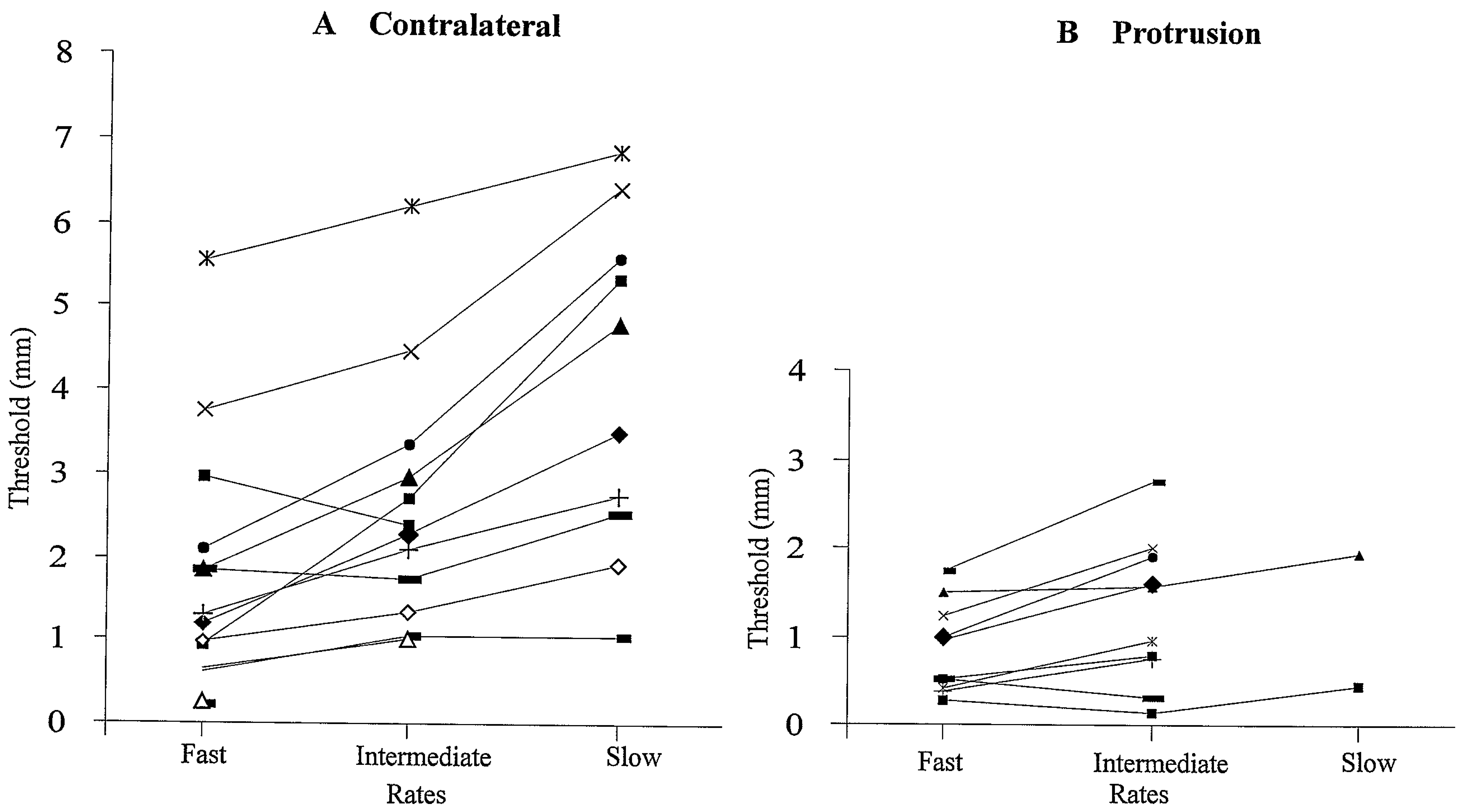


Fig. III-11 Graphs demonstrating threshold for the 12 IHLP SMUs that showed significant change in threshold with rate of movement to the contralateral side (*A*) and for the 10 units in protrusion (*B*). The thresholds increase with a decrease of rate. Three of the units were the same in *A* and *B*.

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. An analysis was carried out to determine if a comparable dichotomy was present in population of IHLP 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 (Mann-Whitney *U* Test; $P < 0.05$) 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 one of the 10 units that was significantly affected by rate of movement is shown in Fig. III-12 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 (Kruskal Wallis Test; $P < 0.01$) 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: III-13.

Table III-5 Number of threshold comparisons showing an increase or decrease in threshold as the rate of movement decrease during contralateral and protrusive tasks.

	Fast-Intermediate	Intermediate-Slow	Fast-Slow	Total
A. Contralateral task				
Increased threshold	25	20	26	71 (76)
Decreased threshold	4	9	9	22 (24)
Total				93
B. Protrusive task				
Increased threshold	27	16	17	60 (71)
Decreased threshold	11	7	6	24 (29)
Total				84

Parentheses enclose percentages.

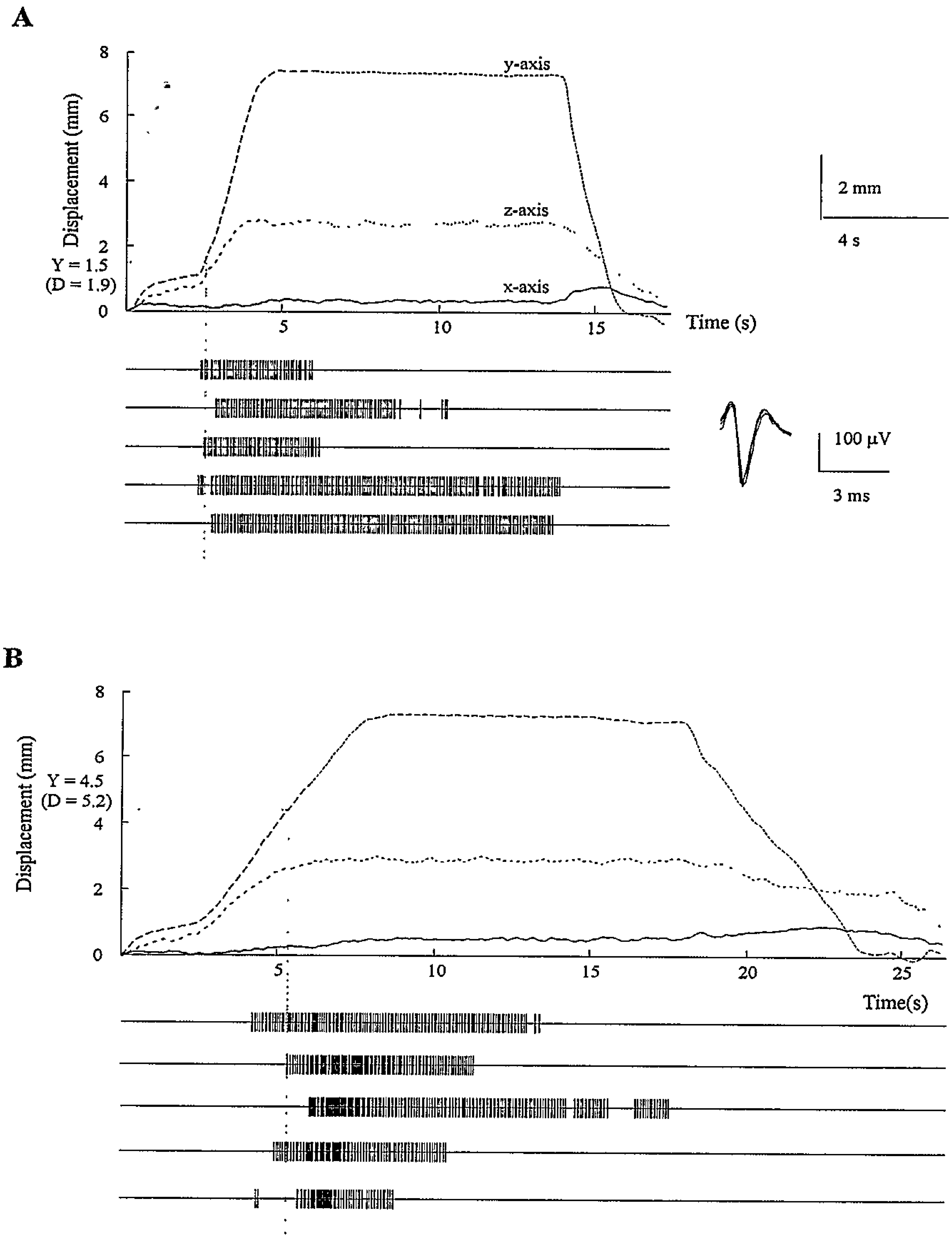


Fig. III-12 An example of an IHLP SMU demonstrating a significant decrease of threshold with a decrease of rate of jaw movement during contralateral movement. *Top 3 traces* in each panel represent MIPT displacement in x-(anterior-posterior; + posteriorly), y-(mediolateral; + to right) and z-(superior-inferior; + superiorly) axes for an average of 5 single-step trials. The subject tracked the target at the fast (*A*) and slow rate (*B*). Each short vertical line is a spike-train pulse that indicates the time of occurrence of an SMU action potential. The *bottom 5 traces* in each panel represent SMU activity during 5 trials. Five superimposed traces of the waveform are illustrated on the *right* in *A*. At the fast rate of movement in *A*, the threshold of this unit, indicated by the dotted vertical line, was significantly lower (Kruskal Wallis Test; $P < 0.05$) than during the slow rate in *B*. Mean thresholds assessed in 3 dimensions and along y-axis are shown. The slightly greater variability in threshold from trial to trial in *B* was a reflection of the greater variability in the rate of jaw movement from trial to trial in this subject.

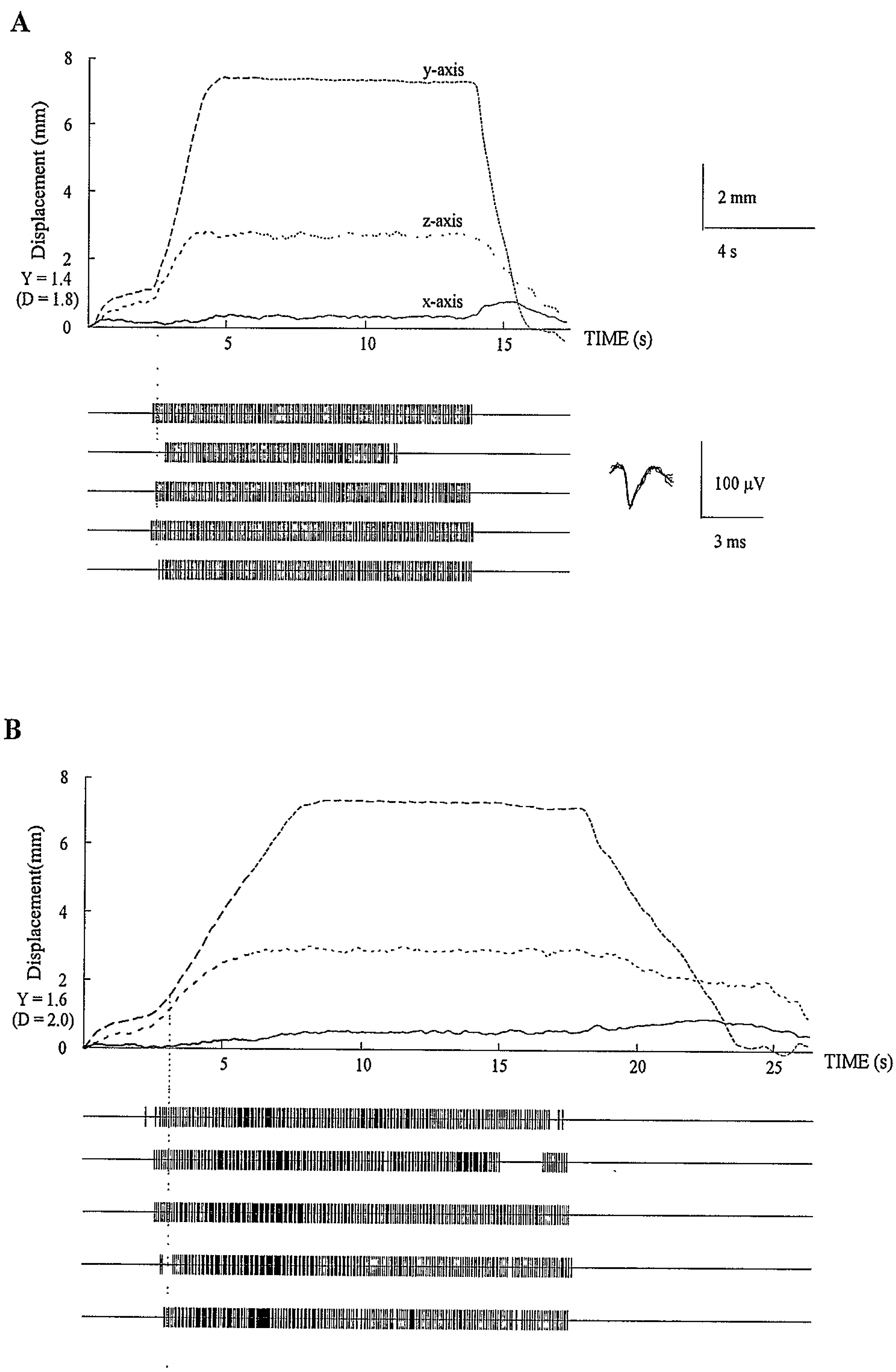


Fig. III-13 An example of an IHLP SMU demonstrating a no significant (Kruskal Wallis Test; *P* >0.05) effect on threshold of rate of contralateral jaw movement. The format of the figure is as in Fig. III-12.

4.3 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 standardised 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 standardised jaw opening was 4.8 ± 1.7 mm in the z-axis. For example, in Figure III-9 during protrusion (A) and contralateral movement (B) the thresholds in the z-axis for unit 1 were ~3 mm and 1 mm, respectively, while the threshold in the z-axis during jaw opening (C) for this unit was ~7 mm.

4.4. Threshold and Direction of Movement

For 29 SMUs studied in both contralateral and protrusive tasks, the correlation between the recruitment thresholds in protrusion and 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 (Wilcoxon Signed Ranks Test; $P > 0.05$) from the value of 1.5 ± 1.1 mm for contralateral movement. Figure III-14 demonstrates a scatter plot of thresholds of these 29 SMUs in contralateral movement and protrusion.

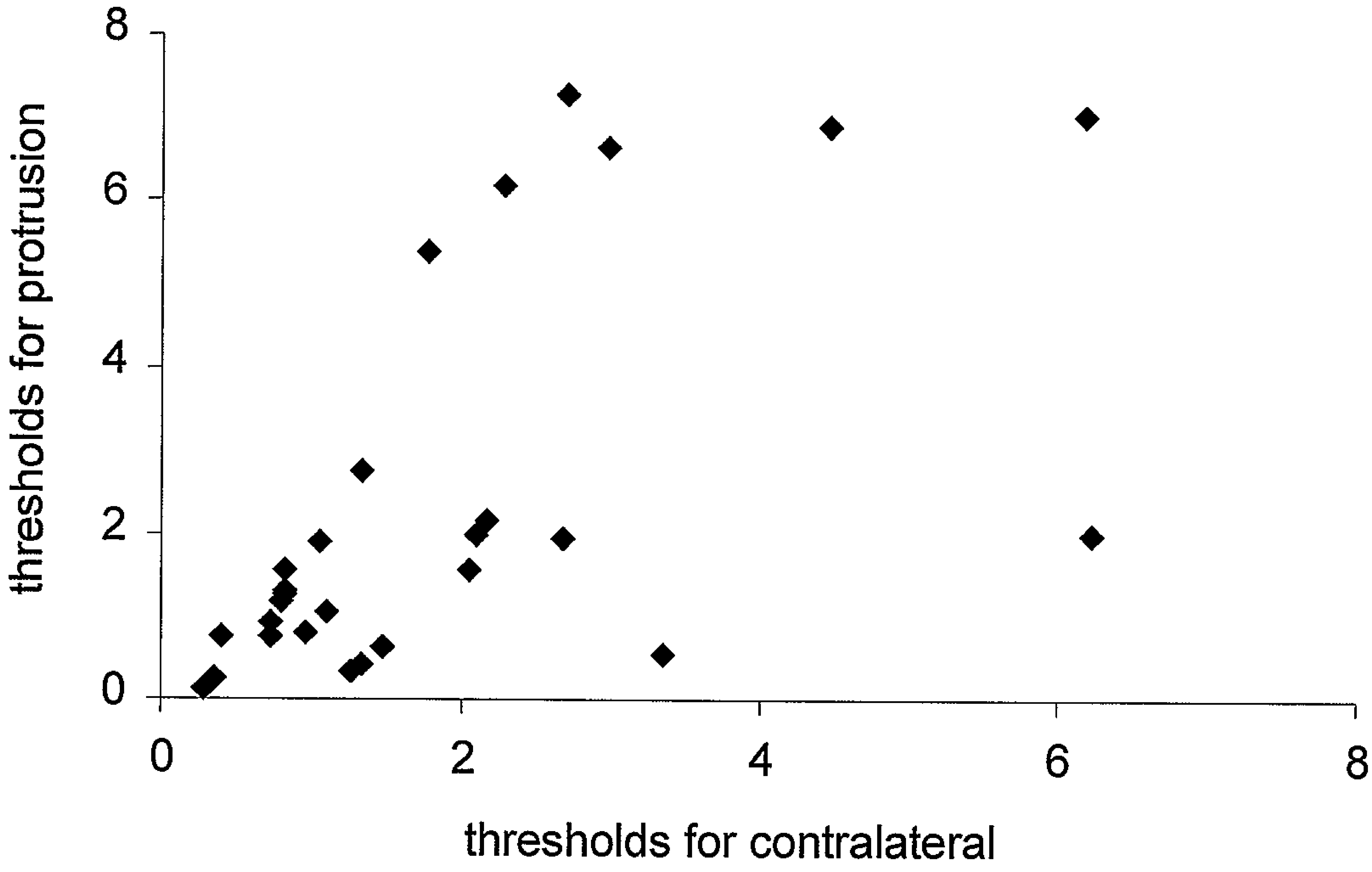


Fig. III-14 Thresholds of 29 IHLP units in contralateral and protrusive movements.

4.5 Recruitment Features of the Inferior Head Motor Units 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 III-6 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 labelled unit 1, the second unit recruited was labelled 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 5 SMUs could be recruited in a staggered fashion. The small displacements with which units were recruited are also illustrated in Fig. III-15 which shows on an expanded time scale the activity of 5 SMUs recorded during a single-step protrusive displacement. Units were recruited at small displacement increments.

Table III-6 Differences in threshold between successively recruited SMUs.

	Unit 2-Unit 1	Unit 3-Unit 2	Unit 4-Unit 3	Unit 5-Unit 4	Unit 6-Unit 5
Threshold differences	0.3 ± 0.4	0.5 ± 0.6	0.8 ± 0.8	0.4 ± 0.7	0.8 ± 1.1
n	16	11	9	5	3

Values are means ± SD in millimetres.

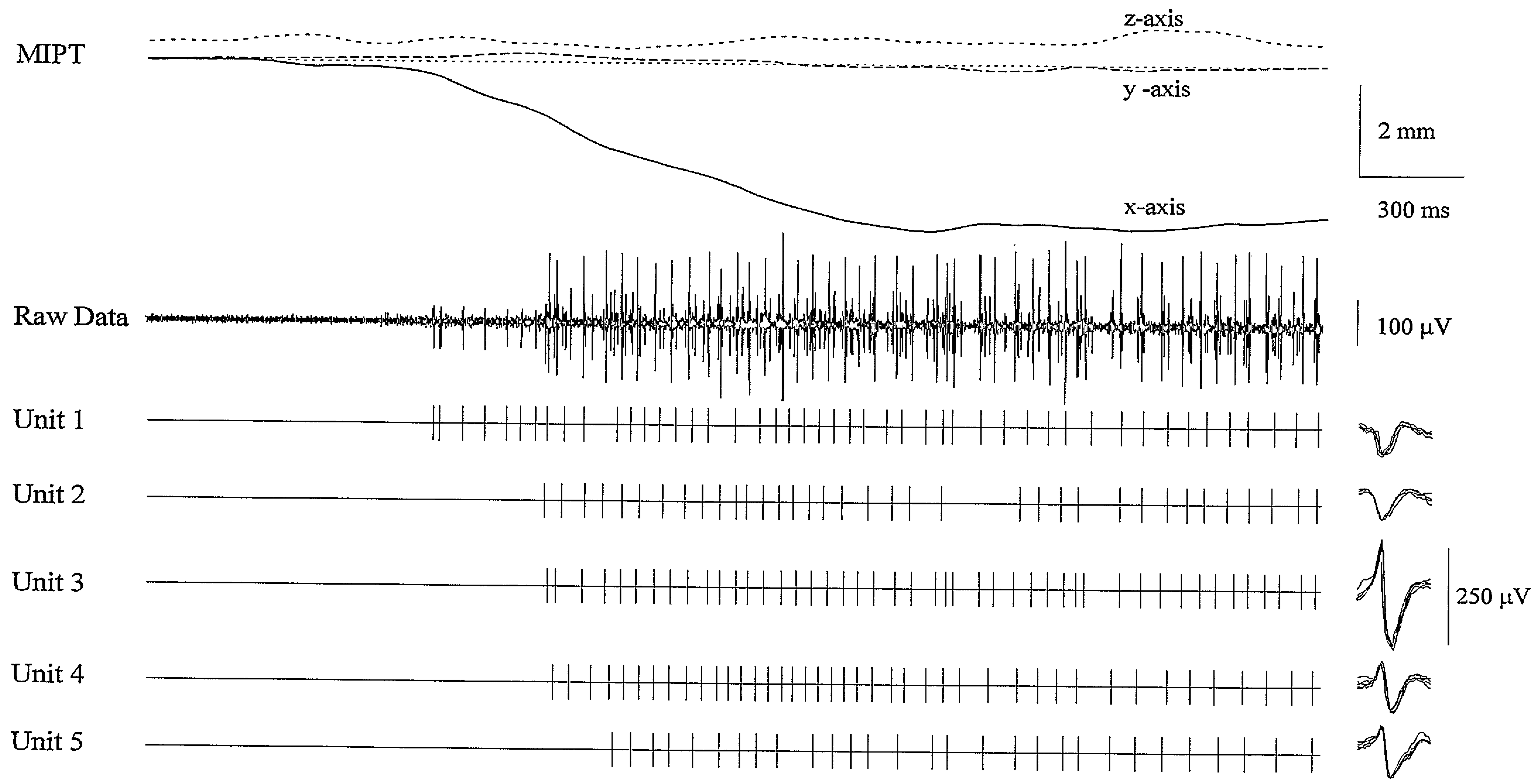


Fig. III-15 The closeness in displacement with which subsequent IHLP SMUs were recruited. The *upper* traces represent MIPT traces during single-step protrusion at the fast rate. Raw SMU activity is shown in the *middle*, and the five *bottom* traces represent spike-train pulses of 5 SMUs reruited successively and recorded with the one electrode. Five superimposed waveforms of the 5 SMUs are illustrated on the *right* of each spike train. The differences between the thresholds of subsequently recruited units were 0.7 mm, 0.03 mm, 0.1 mm and 0.6 mm.

4.6 Locations of Units within Inferior Head and Threshold Values

Table III-7 lists the mean thresholds of SMUs recorded according to site within IHLP during contralateral movement (A) and protrusion (B). Due to small sample size, the IHLP was divided into two parts (*i.e.,* medial and lateral part) in mediolateral direction, instead of three parts as in the SHLP. Although sample size was small, the SMUs recorded in the superior-medial part during protrusion and contralateral movement exhibited significantly lower mean threshold values than for the SMUs recorded in the other parts (Kruskal Wallis Test; $P < 0.001$). No SMUs were recorded in the inferior-lateral part 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 localised 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 (Fisher's Exact Test; $P = 0.2$; Table III-8) or rates (Fisher's Exact Tests; $P > 0.05$; Table III-9) of movement.

Table III-7 Thresholds (mm) in relation to location within IHLP

	Medial	Lateral	Total
A. Contralateral task			
Superior	0.9 ± 0.6	2.3 ± 2.1	1.8 ± 1.9
	(6)	(13)	(19)
Inferior	1.5 ± 0.9	Nd	1.5 ± 0.9
	(10)		(10)
Total	1.3 ± 0.9	2.3 ± 2.1	
	(16)	(13)	
B. Protrusive task			
Superior	0.7 ± 0.5	2.9 ± 2.5	2.2 ± 2.3
	(7)	(18)	(25)
Inferior	3.3 ± 2.3	Nd	3.3 ± 2.3
	(11)		(11)
Total	2.2 ± 2.2	2.9 ± 2.5	
	(18)	(18)	

Values are means ± SD. Number of units are in parentheses. Nd, no units recorded in this part; IHLP, inferior head of the lateral pterygoid muscles.

Table III-8 Number of units for the relation between location and thresholds in protrusive and contralateral tasks.

	Medial Location	Lateral Location	Total
Thresholds CL >Pro	8	2	10
Thresholds Pro >CL	7	8	15
Total	15	10	25*

Fisher's Exact Test, $P = 0.2$. CL, contralateral task; Pro, Protrusive task.

* Computer tomography was unavailable for 4 units studied in both CL and Pro.

Table III-9 Number of units for the relation between location and thresholds significantly affected by rate.

	Medial Location	Lateral Location	Total
A. Contralateral task			
Thresholds significantly affected by rate	4	6	10
Thresholds not significantly affected by rate	12	7	19
Total	16	13	29*
B. Protrusive task			
Thresholds significantly affected by rate	5	3	8
Thresholds not significantly affected by rate	13	15	28
Total	8	18	36*

Fisher's exact test: contralateral, $P = 0.3$; protrusion, $P = 0.7$.

* Computer tomography was unavailable or units were located in middle part for 6 units (contralateral) and 4 units (protrusion).

5. FIRING RATES OF THE INFERIOR HEAD MOTOR UNITS

A total of 50 SMUs were recorded from CT-verified sites in IHLP during multi-step displacements. 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 throughout the trials in both tasks.

5.1 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 (Wilcoxson Signed Ranks Test: $P > 0.05$). Also, for each SMU, there was no statistically significant difference in the firing rates during the dynamic phases as the rate of movement changed (Wilcoxson Signed Ranks Test: $P > 0.05$). 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.

5.2 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 analysed during the contralateral step task and the protrusive step task (GLM-repeated measures; $P < 0.001$). 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 (GLM-repeated measures; $P < 0.05$). Twelve of each group of 25 units, that 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 3-step contralateral task is shown in Fig. III-16. The subject tracked the target and held displacement for 4 s at each holding phase before moving to the next target (Fig. III-16A). The increment of jaw displacement was small at 0.6 mm. The firing rate of the unit, averaged from 5 trials (spike-train pulses in B), 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 illustrated in Fig. III-17. The pauses in SMU firing during the fifth trial were attributed to slight variations in jaw movement from trial to trial.

Figure III-18 demonstrates graphs of the firing rates of 25 units exhibiting significant increases in firing rate with jaw displacement during the contralateral step task (Fig. III-18A) and the protrusive step task (Fig. III-18B). The non-significant units have been omitted for figure clarity. Although the amount of displacement at the first firing rate plotted for each unit (*i.e.,* the first holding phase) was not the actual threshold of tonic firing of each unit, the displacement at the first holding phase was close to the actual threshold of firing. This was because the first holding levels were determined as being just above threshold of firing of each unit. On this basis, the graphs demonstrate that the units could be recruited up to ~95% (*i.e.,* 9 mm) of the average maximum contralateral jaw displacement (mean ± SD; 9.4 ± 1.7 mm) or ~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. III-18 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: 11-26 imp/s; see Results: section 6.1). 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).

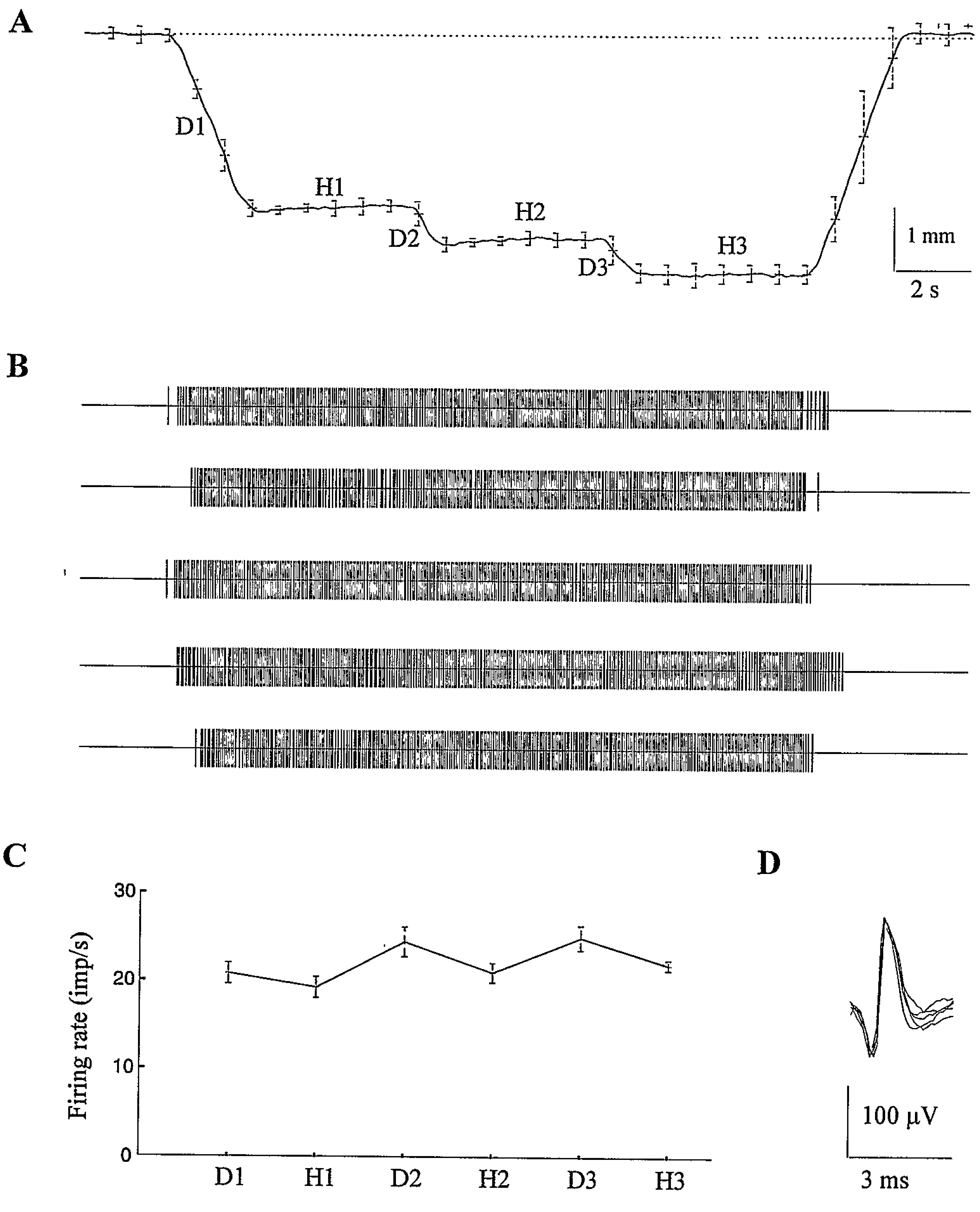


Fig. III-16 An example of an IHLP SMU demonstrating an increase of firing rate with an increase of jaw displacement during contralateral movement. (*A*) Traces represent averaged MIPT displacement in mediolateral (y) direction with SD bars every 750 ms for an average of five trials. (*B*) Each trace represents SMU activity during five trials. Each short vertical line is a spike-train pulse that indicates the time of occurrence of a SMU action potential. (*C*) A graph representing average firing rates with SD bars of the SMU from 5 trials during dynamic (D1, D2 and D3) and holding phases (H1, H2 and H3). (*D*) Five superimposed traces of the waveform.

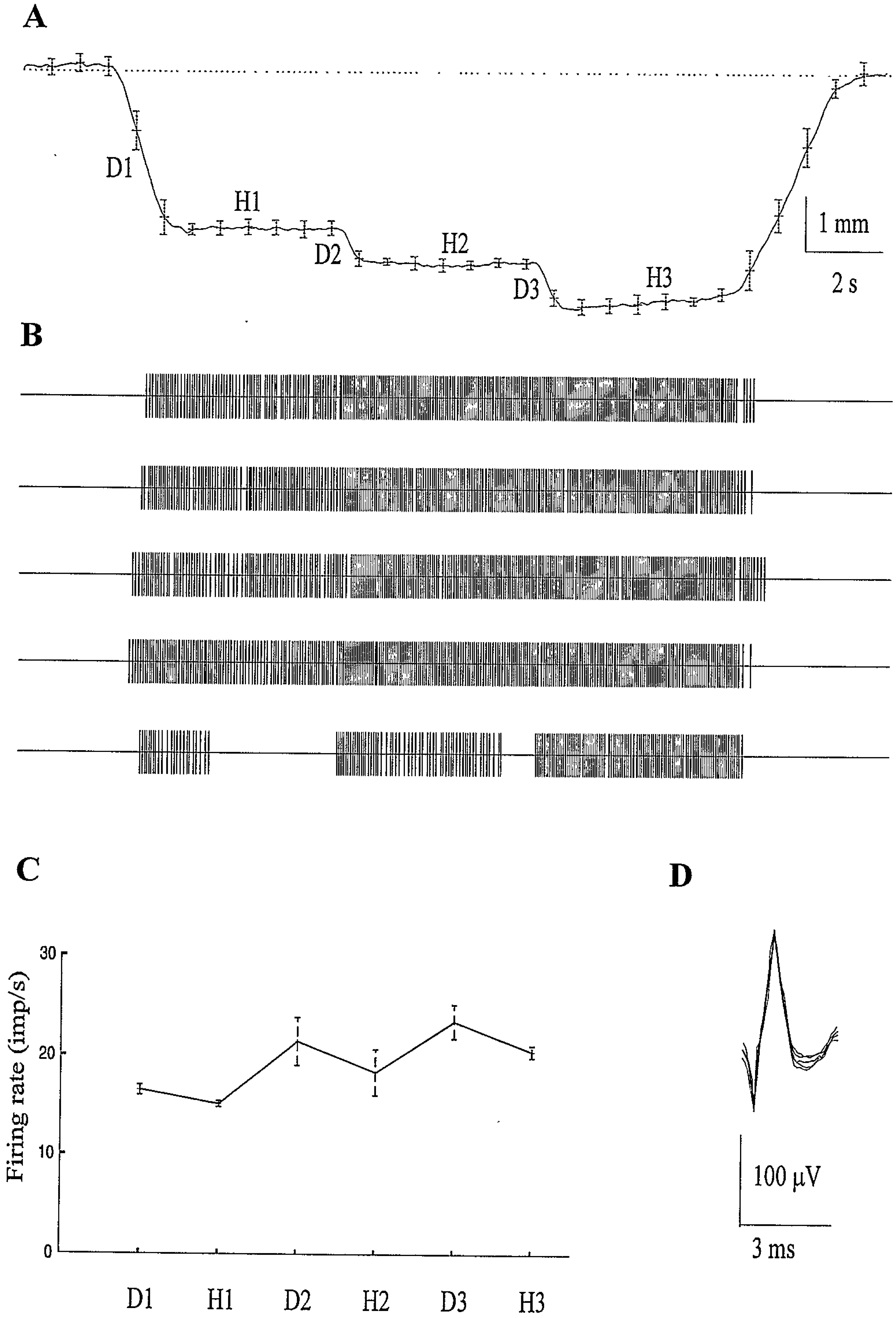
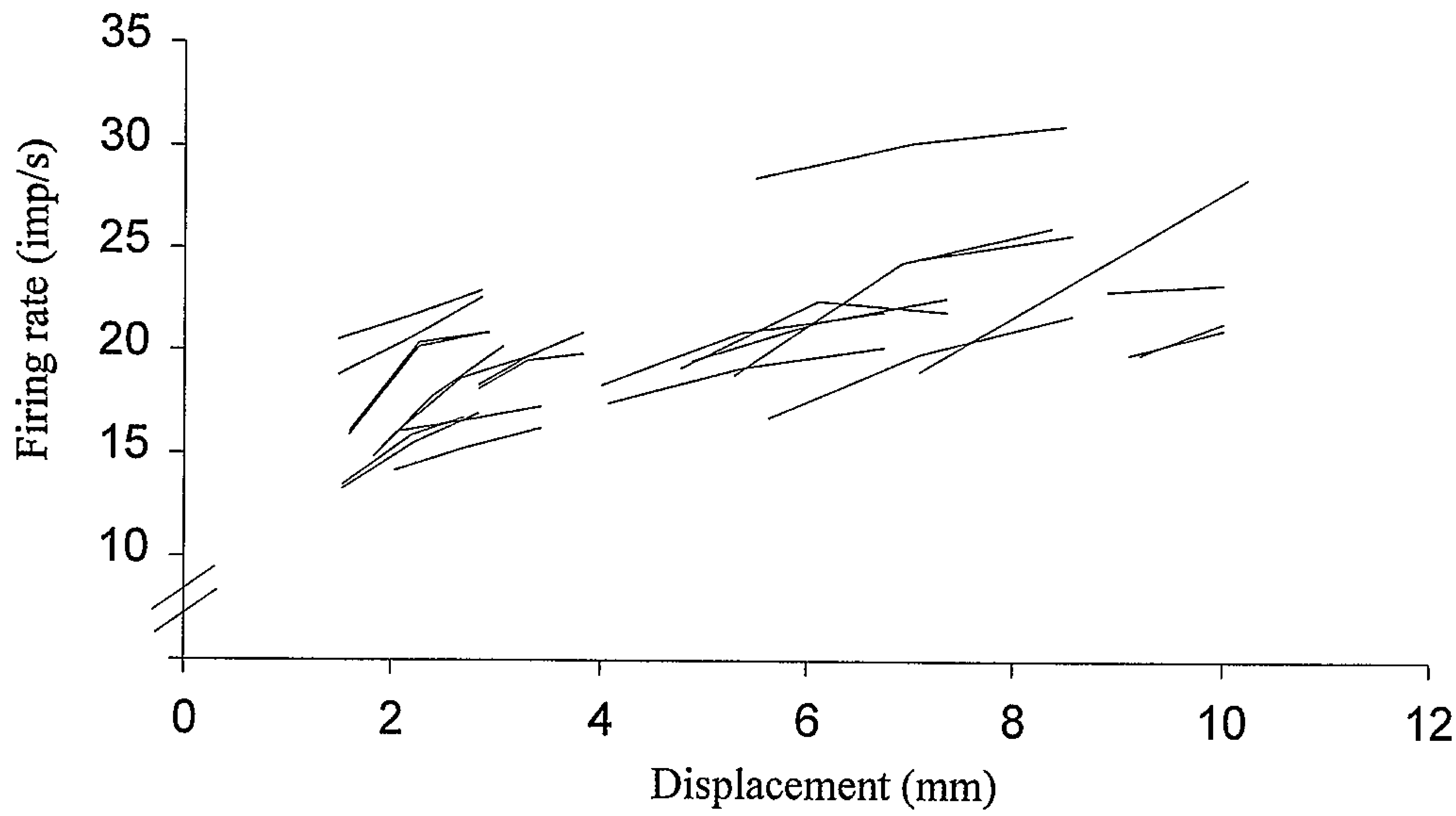


Fig. III-17 An example of an IHLP SMU demonstrating an increase in firing rates with an increase of jaw displacement during protrusion. The format of the figure is as in Fig. III-16 except traces in (*A*) represent MIPT displacement in antero-posterior (x) direction.

A. Contralateral task



B. Protrusive task

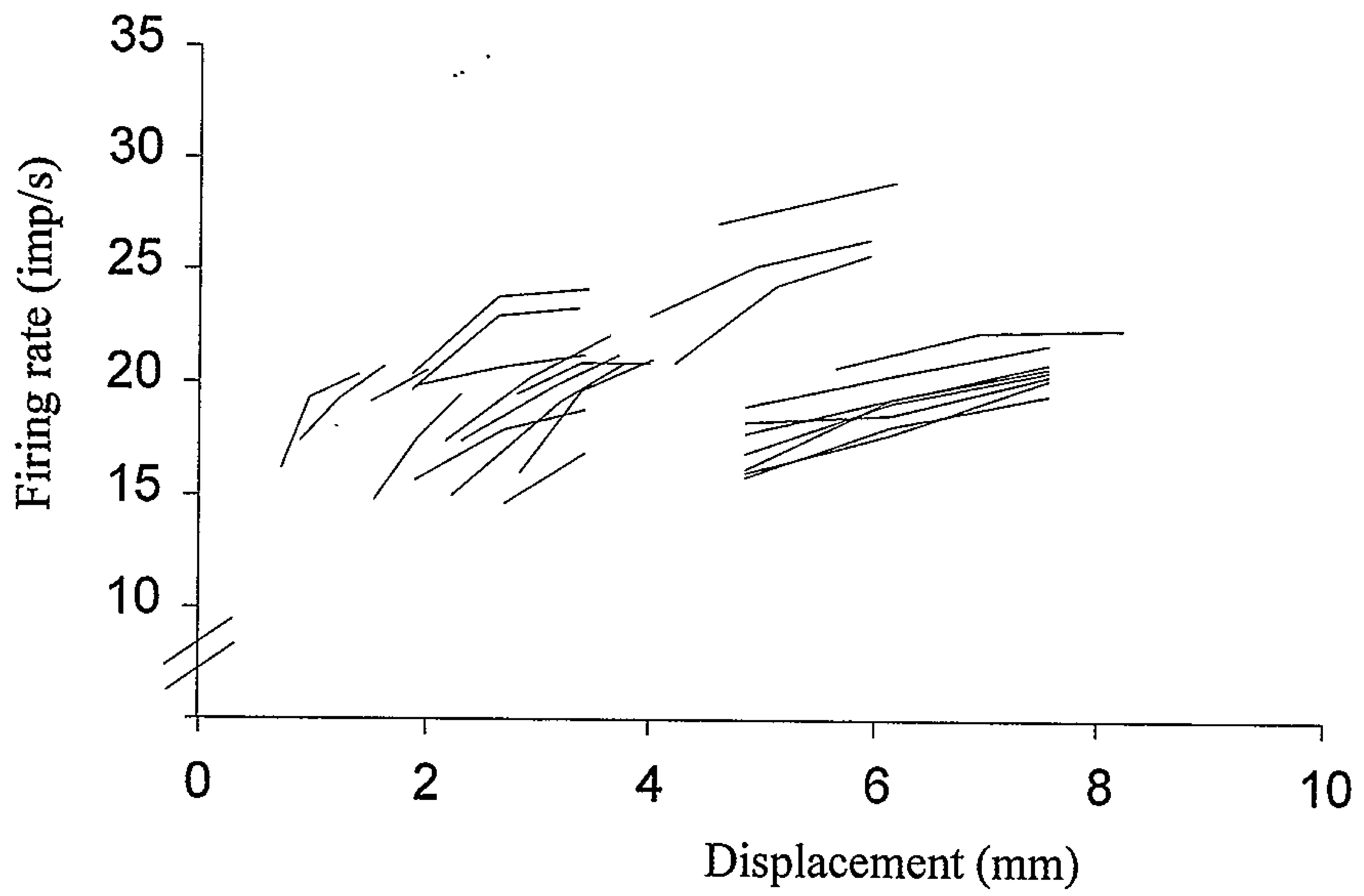


Fig. III-18 Graphs demonstrating firing rates for the 25 IHLP SMUs that showed significant change in firing rate with an increase of jaw displacement to the contralateral side (*A*) and in protrusion (*B*). The firing rates increase with an increase of jaw displacement. Nineteen of the units were the same in *A* and *B*. Note that the increment of jaw displacement varies for individual units.

5.3 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 Materials and Methods: section 4.3.4). 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 (mean ± SD; $r = 0.49 \pm 0.13$; 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 ($r = 0.44 \pm 0.14$; 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. Twenty-eight units and 19 units were available for this assessment during the contralateral step task and the protrusive step task, respectively. The correlation coefficients at the fast rate during the contralateral step task and the protrusive step task were significantly higher than for the corresponding tasks at the slow rate (paired t-test; $P < 0.05$).

5.4 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 the contralateral task and 33 SMUs during protrusion. Multiple comparisons of firing rates were performed between four pairs: H1-D2, D2-H2, H2-D3, and D3-H3 (see Fig. II-10B). For the contralateral step task, the firing rates during D2 and D3 were significantly greater than those during H1 and H2, respectively (GLM-repeated measures with Bonferroni multiple comparisons; $P < 0.001$), and the firing rates during H2 and H3 were significantly lower than those during D2 and D3, respectively. Similar significant increases and decreases in firing rates were also observed during D3 and H3 and during protrusion (Fig. III-17C).

Figures III-16C and III-17C show firing-rate changes during the contralateral step task for one SMU and the protrusive step task for another SMU. For the SMU whose data is displayed in Fig. III-16, the mean firing rate during D1 was higher than the mean firing rate during H1. During D2 when the jaw moved to the next target, the firing rate increased, and then, when the jaw was held at H2, the firing rate decreased, but was greater than the firing rate at H1.

5.5 Firing Rate Changes and Thresholds

Previous studies in limb and jaw-closing muscles have demonstrated an association between the threshold of units and whether or not their firing rate are modulated with force (Tanji and Kato 1973a; Freund et al. 1975; Derfler and Goldberg 1978). Thus the change in firing rates per unit force has been reported to be greater for low- than for high-threshold units. 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: (*a*) 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 (*b*) 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/mm (3.8 ± 1.7 imp/s/mm for protrusion) and 1.9 ± 0.9 imp/s/mm for the high-threshold units (1.6 ± 0.9 imp/s/mm for protrusion). There was a significant difference between the firing rate changes of low- and high-threshold units for the protrusive task (one-tailed t-test; P <0.05), 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 (1.8 ± 0.9 for contralateral movement and 1.9 ± 1.4 imp/s/mm 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/mm for protrusion) during each of contralateral movement and protrusion (one-tailed t-test; P <0.05).

5.6 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 III-10. The firing rate change of units located in the superior part (mean ± SD; 3.3 ± 0.5 imp/s) was greater than that of units in the inferior part (1.7 ± 0.4 imp/s) during the protrusive step task (Mann-Whitney *U* Test; $P < 0.05$). For the contralateral step tasks, the comparison between the firing rate change of units located in the superior and inferior part 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 (Mann-Whitney *U* Test; $P > 0.05$) 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 IHLP than that recorded in the two other regions of the IHLP (each 100%) (Table III-10). Within the superior-medial part, the percentage was greater during the contralateral step task than that during the protrusive step task, and was comparable to those in the other two regions.

Table III-10 Number of units showing a significant increase in firing rates and total number of units in relation to location within the IHLP during contralateral and protrusive step tasks.

	Superior-medial	Superior-lateral	Inferior-medial	Inferior-lateral	Total
A. Contralateral step task					
Significant increase in firing rates	8 (73)	8 (80)	3 (75)	Nd	19*
Non-significant increase in firing rates	3	2	1	Nd	6**
Total	11	10	4	Nd	25
B. Protrusive step task					
Significant increase in firing rates	2 (20)	10 (100)	8 (100)	Nd	20*
Non-significant increase in firing rates	8	0	0	Nd	8
Total	10	10	8	Nd	28

Parentheses enclose percentages.

*Computer tomography was unavailable for 6 units (contralateral) and 5 units (protrusion).

** Computer tomography was unavailable for 5 units (contralateral).

Nd, no units recorded in this part of the muscle.

6. LEAST-SUSTAINABLE FIRING FREQUENCIES

6.1 Least-sustainable Frequencies (LSFFs) for the Inferior Head Motor Units

An accurate assessment of LSFFs was difficult to obtain given the subjective reports of many subjects of the difficulty in maintaining the lowest firing rate of the IHLP units. For example, Figure III-19A-C shows an example of a unit visually controlled by the subject to fire at a LSFF of 14.3 ± 2.7 imp/s during protrusion. The LSFF was calculated over the period between lines ‘a’ and ‘b’ where the jaw displacement was relatively stable, although there were slight variations in horizontal displacement as indicated by the displacement along x-, y- and z-axes. Figure III-19C shows spike-train impulses on an expanded time-scale for the period delineated by the short vertical dotted lines.

An assessment of LSFFs was made during the contralateral task and the protrusive task, for 22 and 19 IHLP SMUs, respectively. Of these units, only 14 were available for analysis for both directions of movement, given that some units were clearly distinguished by subjects during one direction, but not in other directions. The mean (±SD) LSFF was 15.6 ± 2.3 imp/s (range: 11.3 to 20.6 imp/s) and 16.3 ± 3.4 imp/s (range: 11.9 to 25.6 imp/s) for contralateral movement and protrusion, respectively. There was a high correlation (r = 0.80) between the LSFF during contralateral movement and the LSFF during protrusion for the 14 units analysed for each direction of movement. Figure III-20 illustrates a scatter plot of the LSFFs of units during contralateral movement and protrusion. The LSFF during contralateral movement was not significantly different from that during protrusion (paired t-test; $P > 0.05$).

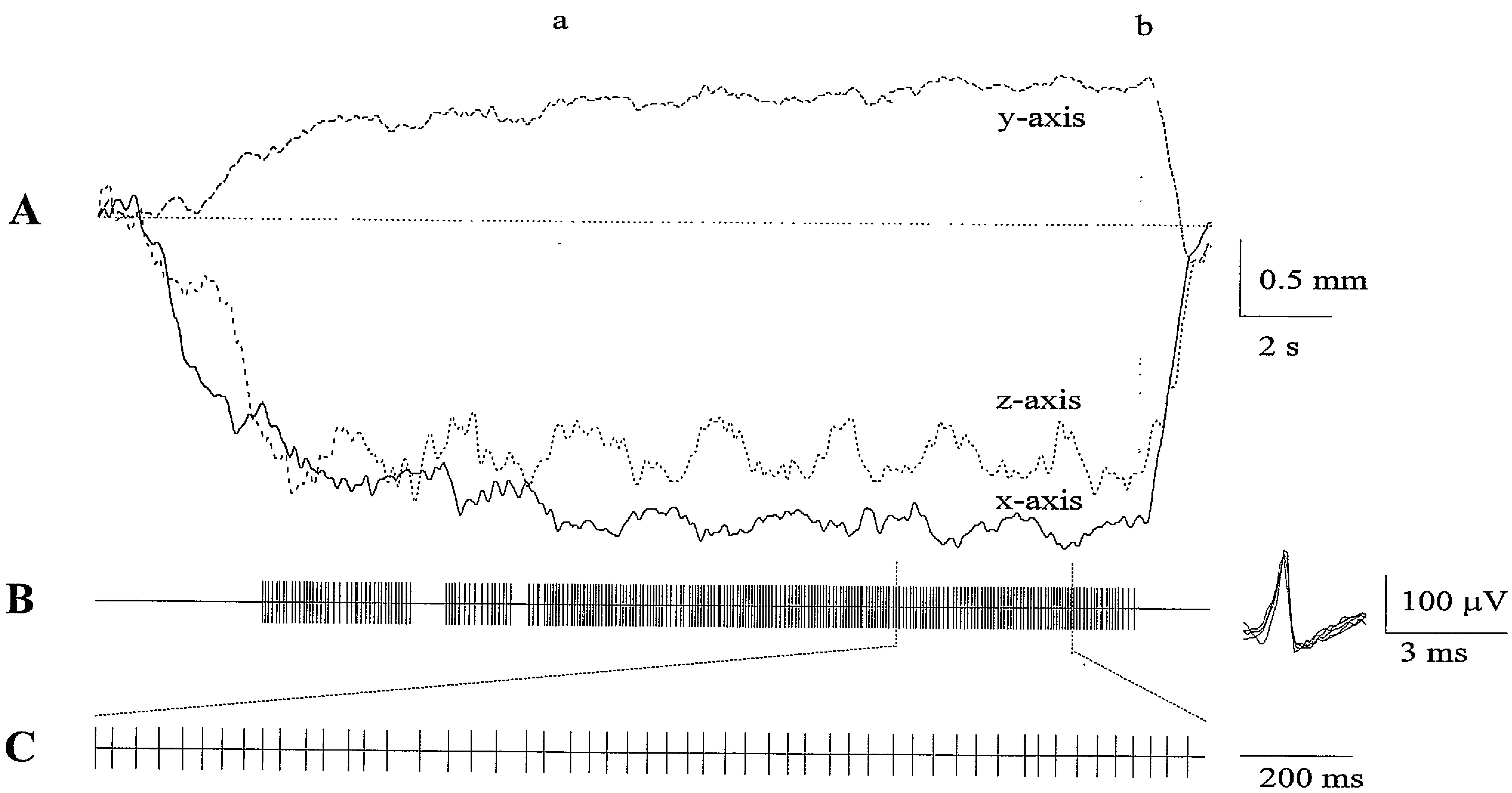


Fig. III-19 An example of IHLP SMU controlled by the subject at LSFF during protrusion. (*A*) Traces represent MIPT displacement in x-(anterior-posterior; + posterior), y-(mediolateral; + to right) and z-(superior-inferior; + superiorly) axes. (*B*) A trace represents SMU activity. Each short vertical line is a spike-train pulse that indicates the time of occurrence of an SMU action potential. The period delineated by the dotted vertical lines is shown in expanded form in (*C*). Line 'a' and 'b' indicate the period where the LSFF was calculated.

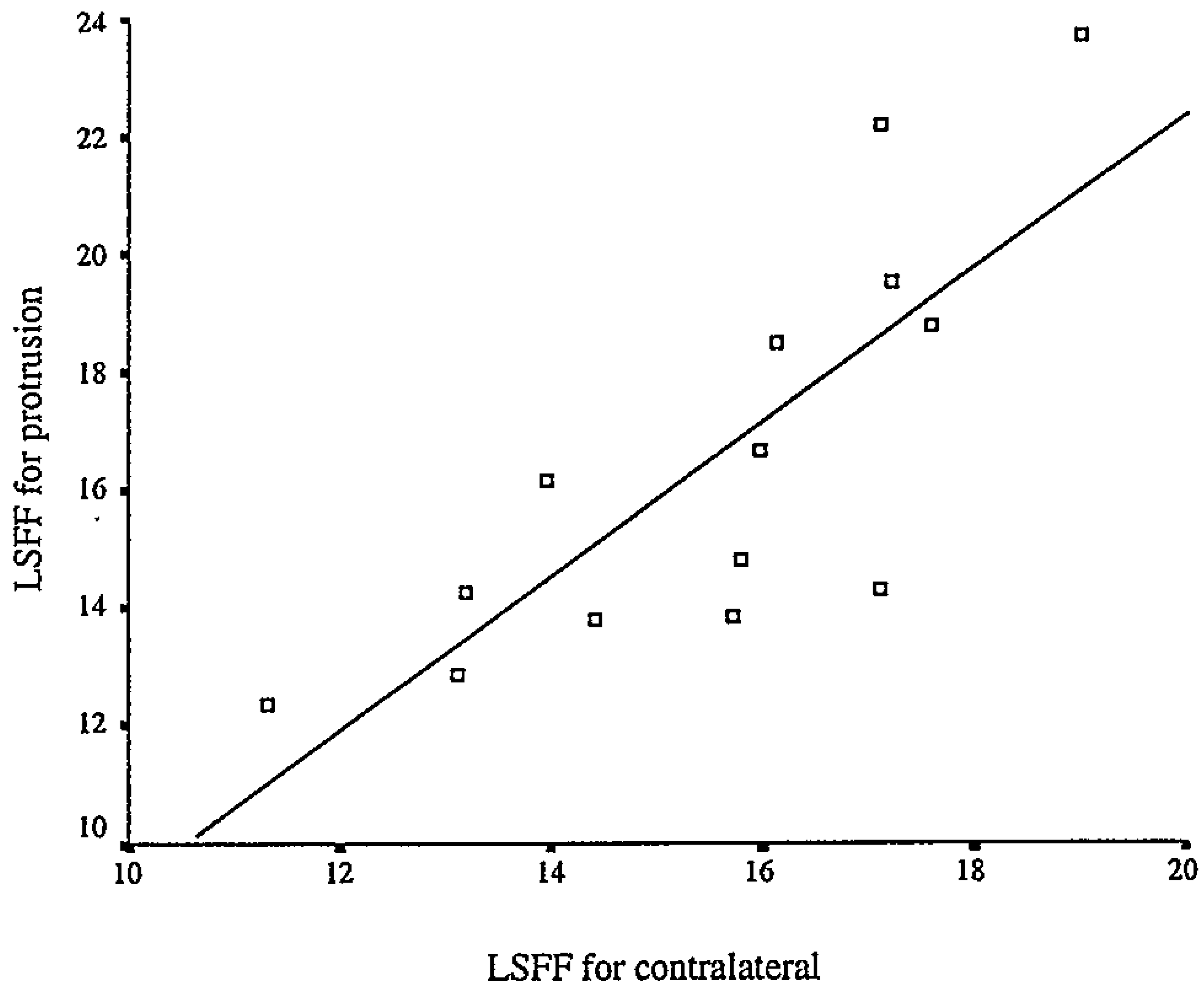


Fig. III-20 A scatter plot illustrating least sustainable firing frequencies (LSFFs) of 14 IHLP SMUs during contralateral movement and protrusion. Each open square represents a SMU. r = 0.80.

6.2 Least-sustainable Frequencies for the Superior Head Motor Units

The LSFFs of 10, 8 and 2 SHLP units were studied during contralateral, ipsilateral movement and protrusion, respectively. The mean (±SD) LSFF was 14.7 ± 2.5 imp/s (range: 10.6 to 17.8 imp/s), 13.2 ± 2.1 imp/s (range: 11.7 to 14.6 imp/s) and 16.2 ± 3.7 imp/s (range: 12.3 to 24.4 imp/s) for contralateral, ipsilateral movement and protrusion, respectively. A comparison between LSFFs for different tasks has not been carried out due to a small sample size of units available for more than one task.

CHAPTER IV

DISCUSSION

There is little information as to the normal function of the human LP, and there are some inconsistencies and uncertainties concerning the available data on the function of the LP. For example, some studies reported activity in IHLP on clenching while others showed an absence of IHLP activity; further, the nature of the reciprocal activity between IHLP and SHLP is unclear. These and other inconsistencies and uncertainties are partly due to limitations of previous studies, such as an absence of reliable electrode verification, and they were the impetus for the present study. The broad aims of the present study were (a) to develop a method for standardising command jaw movements in the horizontal plane and (b) to clarify the normal functions of the SHLP and IHLP. The hypotheses were that an important function of the LP is in the fine control of horizontal jaw movement, and that each head of the LP is capable of differential activation. The broad aims have been satisfied. The present study has shown that a method can be developed for standardising horizontal jaw movements, and human subjects can move their jaws in the horizontal plane to track targets accurately at different rates, magnitudes and directions of displacement. Novel data have also been provided on the task relations of individual SMUs at verified sites in the LP. Further, evidence was presented that supports the proposal of an important role of the IHLP in the fine control of horizontal jaw movements and supports notions of functional heterogeneity within the LP.

1. STANDARDISED TASKS

In the limb motor system, the standardisation of displacement and isometric force together with SMU recording has allowed valuable insights into the function of limb muscles (De Luca et al. 1996; Erim et al. 1996; Herrmann and Flanders 1998; van Groeningen et al. 1999). Similar methodologies have been successfully applied by some laboratories to the jaw motor system (for review, Hannam and McMillan 1994), including the LP during isometric contractions (Uchida et al. 2001). Although Hiraba and coworkers (Hiraba et al. 2000) partly standardised jaw-opening movements while recording multi-unit EMG activity from unverified sites, the accuracy and reproducibility with which subjects could track targets were not described and no study has developed a methodology for controlling jaw movements in the horizontal plane. Given that most jaw movements have horizontal movement vector components, a methodology for standardising jaw movements in the horizontal plane is necessary if the control of these movements is to be defined.

The present study describes a method for standardising jaw movements in the horizontal plane. It has shown that human subjects can be quickly trained to move their jaws in the horizontal plane to track a target, and has also shown that SMU activity can be reliably discriminated from the LP during these task-defined jaw movements. There have been other studies employing less sophisticated tracking of jaw movement that have assessed the closeness with which subjects were able to track targets (Caligiuri et al. 1988; Moon et al. 1993). The study of Moon and coworkers (1993), for example, showed that the subjects were able to perform reliably sinusoidal open-close jaw-tracking, and their data are generally consistent with the findings from our study that subjects were able to track the horizontal step tasks. However, given the difference between the tasks in the studies, it is not possible to make a more detailed comparison of the precision of the jaw tracking between these previous studies and the present study.

Subjects could accurately track a target in the horizontal plane at different rates and magnitudes of displacement, which is evidenced by the close match between the jaw displacements and the target lines as well as the small standard deviation values during the movement and stationary phases. Given the wide range of controlled displacements at different rates (range: 1.3 – 6.5 mm/s) and magnitudes (range: 0.65 – 12 mm) of movement possible with this methodology, as well as the ability to control jaw displacement along different directions of jaw displacement, this method provides a powerful tool to characterise SMU firing properties in the LP.

This method of standardisation of jaw movements in the horizontal plane is also readily applicable to jaw movements in any plane. For example, the rate and magnitude of open-close movements can be readily controlled by aligning the bank of LEDs along the trajectory of movement displayed in the frontal or sagittal plane on the screen. The rate and duration of illumination of the LEDs can be controlled by feeding in sine-wave signals of appropriate frequency into the scripts running on the CED data acquisition system. This method can also be readily adapted for studies of SMU activity from other jaw muscles during standardised tasks, for example, during isotonic displacements from the other jaw-opening muscle, the digastric muscle, and also during isometric force tasks from the jaw-closing muscles, masseter, temporalis and medial pterygoid.

2. SIMULTANEOUS RECORDING OF SINGLE MOTOR UNIT (SMU) ACTIVITY AND JAW MOVEMENTS

The present study also shows that SMU activity could be reliably discriminated during these standardised tasks. This method establishes a technique for defining jaw-muscle SMU firing properties, such as task relations of SMUs and threshold of firing, in relation to dynamic features of jaw movement. Since SMU properties depend on dynamic parameters, standardisation of movement to defined tasks is essential. For example, in limb muscles, directional preferences of SMUs have been studied in standardised task paradigms where the rates of force increase, the magnitude of target force, and the direction of force application were controlled (Herrmann and Flanders 1998). This standardisation allowed a detailed characterisation of the functional properties of SMUs within these limb muscles.

Several jaw muscles are likely to contribute to a given task. For example, jaw-closing force can be generated by the masseter, temporalis and medial pterygoid muscles. It has also been shown that the level of contribution of jaw openers and closers to a well-defined slow ramp force changes dramatically in repeated trials (Scutter and Türker 1998). There is a possibility therefore that other jaw muscles, such as the posterior temporalis, masseter and medial pterygoid could contribute to the horizontal jaw movement, and that the contribution of the SHLP or IHLP may alter in repeated trials. In general, however, the overall level of activity in the LP was similar in repeated trials and this is borne out by the similarity in the integrated EMG activity levels from trial to trial (Fig. III-3). Qualitatively, there was some variation in the onset time of the integrated EMG activity, as there was with SMU threshold. However, this variation in onset was considered to be related to the variation of jaw movement from trial to trial. Further, recent studies (Murray et al. 1999c; Phanachet and Murray 2000) showed that the LP was the principal muscle active during these stereotyped movements. The other jaw muscles recorded in these studies, namely the anterior and posterior tempolaris, masseter and digastric, did not play a major role in the performance of these horizontal jaw movements. However, the data from these previous and present studies do not rule out roles for other jaw muscles in these movements, since some jaw muscles contain fibres 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 review, Miller 1991; Hannam and McMillan 1994). Although 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. 1999c), 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.

3. TASK RELATIONS OF THE SUPERIOR HEAD MOTOR UNITS

The data provide evidence supporting the proposal of functional heterogeneity within the LP (Hannam and McMillan 1994; Foucart et al. 1998). The units located in different parts of the SHLP were active during different combinations of tasks. For example, the units in the medial part were silent during ipsilateral movement, retrusion and clenching, whereas the units in the other two parts could be active. Further, there was evidence that the units active in the vertical tasks (*i.e.*, jaw closing) were localised to the lateral part; however, there was no preferential location for units involved in the horizontal tasks (*i.e.,* lateral movement).

The SHLP is capable of participating in any of the tasks studied, which is not in agreement with some previous studies (*i.e.,* Kamiyama 1961; Gross and Lipke 1979) reporting that the SHLP was active only during ipsilateral movement, retrusion and jaw opening. The data suggest that the definition of reciprocal or simultaneous actively between the SHLP and IHLP depends on the recording site within the SHLP and the task being performed, and this is consistent with some previous studies (Sessle and Gurza 1982; Murray et al. 1999c).

The selective activation of each head of the LP is supported by anatomical features of the muscle. The SHLP and IHLP are oriented in different directions. In the horizontal plane, the SHLP fibres are aligned 26° to the sagittal plane, while the fibres of the IHLP run laterally and posteriorly to the condyle at an angle of 45° to the sagittal plane (Hónee 1972). The SHLP fibres, in the sagittal plane, run downward and develop an angle of 23° to the Frankfort Horizontal Plane, while the IHLP fibres are aligned at an average angle of 10° (Hónee 1972). The differences in fibre angulation support the notion of functional differentiation between the heads.

Within the SHLP and IHLP, there is a marked convergence of muscle fibres onto a small insertion site on the condylar fovea, capsule and disc from a broad origin at the roof of the infratemporal fossa and the lateral pterygoid plate. This marked change in fibre alignment from the uppermost to the lowermost muscle fibres, and from the medial to the lateral side of the each head of the muscle (Troiano

1967; Hawthorn and Flatau 1990) provides the capability of generating different force vectors with differential activation within each head.

It is possible that many or even most muscle fibres of a given unit may not be located in the assigned part of the muscle according to the CT images, since the territories of units have not been defined. It is also possible that the classic IHLP pattern observed in the medial part of the SHLP might simply be a reflection of cross-talk from the uppermost fibres of the IHLP since the SHLP fibres often mingle with the IHLP on the medial side near the disc (Fujita et al. 2001). However, all recording sites from the medial part in the present study were located in the anterior and antero-posterior middle part of the SHLP, where both heads are separated by fibrous connective and adipose tissues (Naidoo 1996). Further, the thickness of the SHLP varies from person to person and within individuals (Mahan et al. 1983) and the SHLP becomes thinner near its medial border. Nonetheless, it is most likely that the recordings from the medial part in the present study were from the SHLP, since there was a uniform pattern of activity in every recording.

Anatomical studies have demonstrated that the deep temporalis frequently adjoins the lateral part of the SHLP (Widmalm et al. 1987; Akita et al. 2000). The interlacing between the SHLP and the adjacent muscle fibres could confound selective recording from the SHLP in the lateral region. To date, the muscle activity of deep temporalis has not been studied in detail. However, spontaneous activity in the deep temporalis, observed in some subjects (unpublished observations), was never found in the SHLP in the present study.

In the present study, CT was used for electrode verification and the location was arbitrarily assigned into either SHLP or IHLP when the boundary of the two heads was not presented. As indicated above that the thickness of the SHLP varies from and within individuals, magnetic resonance imaging may provide better images of the muscle fibre alignment and possibly the boundary between the SHLP and IHLP. However, it has preliminarily been found that it was difficult to match the location of the electrode in CT images with the magnetic resonance images of the muscle. However, this could be achieved by using reference points during CT and magnetic resonance imaging sessions. Further, the boundary between the SHLP and IHLP were not always clearly apparent in the magnetic resonance images.

4. TASK RELATIONS OF INFERIOR HEAD MOTOR UNITS

This present study provides the first detailed description of the activities of SMUs recorded from CT-identified sites within the human IHLP (see also Results: section 4). 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, Klineberg 1991; Miller 191; Hannam and McMillan 1994). 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 (*eg.,* Wilkinson 1988; Miller 1991). In a study where jaw displacement was recorded but where electrode site verification data was not obtained (Hiraba et al. 2000), correlations were demonstrated between the level of EMG activity in IHLP and anterior condylar translation.

In light of our present findings, it appears that the reports of IHLP activity on clenching in intercuspal position (Mahan et al. 1983; Wood et al. 1986; Widmalm et al. 1987) reflect recordings from units located in other muscles such as the medial pterygoid that has an additional origin from the lateral surface of the lower border of the lateral pterygoid plate (Naidoo 1996). 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. 1986) reflect true IHLP activity or whether in fact these activities represent cross-talk from medial pterygoid motor units.

A major limitation of most previous studies of the human LP 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, conclusions about IHLP function drawn from these studies must be made with caution given the possibility of electrode misplacement in other jaw muscles or that the electrodes may have been within IHLP but incorrectly attributed to a particular head of the muscle (Widmalm et al. 1987; Hannam and McMillan 1994; Orfanos et al. 1996). 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; Widmalm et al. 1987; R. Hawthorn, personal communication). However, even using this arbitrary criterion, the task relations of IHLP motor unit activity recorded in the superior third of the muscle were entirely consistent with those of IHLP units recorded in the other parts of the muscle. For those few units at sites where verification was not obtained, it is likely that the electrodes were correctly located within the IHLP as the patterns observed matched the reliable patterns that were consistently obtained at the verified sites. No EMG activity was ever recorded in the IHLP at intercuspal position clenching in this study; therefore it is unlikely that any of the 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.

5. EVIDENCE FOR FUNCTIONAL HETEROGENEITY IN THE INFERIOR HEAD

5.1 Threshold and Location

The present study also provides suggestive evidence for the activation of specific regions which has been previously put forward (Hannam and McMillan 1994; Foucart et al. 1998; Murray et al. 1999b). Such a notion of functional heterogeneity is not new to the jaw motor system as it has already been well characterised in temporalis and masseter muscles (Blanksma and van Eijden 1990; Blanksma et al. 1992; Blanksma and van Eijden 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 findings provide suggestive evidence supporting this notion in that, for each task, SMUs with lower thresholds tended to be grouped in the superior-medial part within IHLP. 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.

5.2 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 III-10). All recorded units in the inferior-medial parts of the IHLP also exhibited significant changes in firing rate. These data suggest that the units in the superior-lateral and inferior-medial parts were more 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 the data that the units located in the superior-medial part had significantly lower thresholds for horizontal jaw movements than those in the other parts of the muscle. It is therefore proposed that the units in the superior-medial part of the IHLP are more important 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 some of the muscle fibres 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 (Hannam and McMillan 1994; Foucart et al. 1998; Murray et al. 1999b).

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 delivery of appropriate force vectors on the condyle to perform the desired jaw movements. More information regarding the LP fibre architecture, *i.e.,* muscle fibre alignment, together with computer simulations of jaw biomechanics are necessary to provide a better understanding of the functions of the LP.

6. ABSENCE OF ACTIVITY AT POSTURAL JAW POSITION

At the postural jaw position, the absence of SHLP and IHLP activity observed in the present study suggests that there is no anteriorly directed force on the condyle and disc from muscle contraction in the SHLP or IHLP maintaining the condyle in close apposition with the disc and articular eminence. This is contrary to some previous studies claiming that the SHLP and/or the IHLP are maintained in tonic contraction while the jaw was at the postural position (Okeson 1998; Koole 1998; Hiraba et al. 2000). However, most previous studies were multi-unit studies where it may have been difficult sometimes to draw a conclusion as to whether EMG activity was present. Although there appears to be no anteriorly directed force from LP SMUs, there may have been from units of other jaw muscles, such as the masseter and anterior temporalis, as SMUs in these muscles are known to be tonically active at the postural jaw position.

7. ROLE OF THE INFERIOR HEAD 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, a feature that is expected based on previous studies (for review, Freund 1983). 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 since a majority of units exhibited a tendency of decreases in threshold with increases in the rate of movement (Table III-5). Nonetheless, the data suggest that the relevant motor centres (*eg.,* face motor cortex) are capable of activating the IHLP in a finely controlled manner.

Further, the data regarding firing rates of IHLP SMUs during step-task jaw movements also 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.

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. 1999c). Other jaw muscles (masseter, anterior and posterior temporal muscles, and submandibular group) demonstrated weaker associations with the contralateral and protrusive movements.

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. III-19).

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

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.

7.1 Possible Roles of the Inferior Head during Chewing and Speech

The present study also shows that IHLP 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). There is the need for the control of horizontal jaw movements during these phases of the chewing cycle. Thus, in the closing phase of the chewing cycle, it is necessary for the jaw to be positioned to achieve a trajectory of movement that results in the teeth shearing smoothly past each other. The IHLP would appear to be involved here and previous studies provide data consistent with this view by showing that the contralateral IHLP is active during the closing phase to move the jaw to the side (Miller 1991).

The data of the present study were derived from a low-force task, and allow conclusions to be drawn about the role of the IHLP in the control of movement of the lower jaw under low loads. These movements occur throughout most of the chewing cycle except around the intercuspal phase where much higher forces are generated as food is comminuted between the teeth. Although our data cannot directly explain the generation of the horizontal components of jaw movements during the late intercuspal and early opening phases of the chewing cycle, an involvement of the IHLP in these phases of the chewing cycle has been previously suggested (Møller 1966; Dubner et al. 1978; Wood et al. 1986). Further, recent evidence has also demonstrated clear associations between IHLP SMU firing rate and the magnitude of horizontally directed contralateral forces (Uchida et al. 2001). This study suggests that the IHLP is a prime mover in exerting horizontal jaw force. The multi-unit data from the IHLP exhibited the steepest rate of increase during horizontal isometric force gradation, compared to the masseter, anterior temporalis and submandibular group. It is therefore proposed that the IHLP is involved in the generation of those horizontal vector components evident in the late intercuspal and early opening phase of the chewing cycle. It is important to note that other jaw muscles, such as the masseter, temporalis and submandibular group, also play a role in these phases of the chewing cycle, possibly in synergistically controlling jaw position to facilitate task performance. 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.

7.2 Dependence of Threshold on Rate and Direction

Motor units are recruited at successively lower force levels as the speed of a movement or isometric contraction increases (for reviews, Henneman and Mendell 1981; Freund 1983). 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 force in these tasks was not measured in the present study, it is likely 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 the present 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 (Herrmann 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.

7.3 Firing Rate and Jaw Displacement

A majority of IHLP units showed a significant increase in firing rates as the amount of jaw displacement increased in contralateral movement and protrusion. A small proportion of units did not exhibit significant differences in firing rates at different levels of displacement. This may be because some units had already reached their maximal firing rates at the second step of displacement and thus reducing the likelihood of a significant difference in firing rates being identified between step levels. Another reason could be the small number of trials performed; a larger number of trials may have resulted in statistically significant differences.

Previous studies in limb (Tanji and Kato 1973a; Freund et al. 1975; Seki and Narusawa 1996) and jaw muscles (Derfler and Goldberg 1978; Uchida et al. 2001) have shown that motor units increase their firing rates as force increases during isometric contractions. Although there are no detailed studies as to the relation between SMU activity and standardised isotonic tasks in jaw muscles, there have been in other motor systems, such as in the study of saccadic eye movements that involve the rotation of a body against low loads. Thus, a linear change in the firing rates of SMUs from the human medial or lateral rectus muscles has been observed as the eye was moved in horizontal stepwise movements (Sindermann et al. 1978). Also, recordings from motoneurones in the inferior rectus muscle in monkeys have shown progressive increases in the firing rates of units in a stepwise fashion during saccades in one direction (Henn and Cohen 1972). The new firing rate level was maintained until the next shift in eye position. Although force was not measured in these eye tasks nor in the present study, SMUs in both motor systems are most likely to be increasing their firing rates to overcome the progressive increases in passive tensions that would be associated with progressive horizontal displacement of the jaw. Passive tensions have not been measured in the jaw motor system during horizontal tasks but have been assessed during jaw opening (*eg.*, Koolstra 1997; Peck et al. 2000).

7.4 Firing Rate and Speed of Jaw Displacement

Significant correlations between jaw displacement and mean firing frequency were observed in this study. The correlation coefficients were significantly higher at the fast rate than at the slow rate of movement. This difference in correlation 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, there would have been a longer early dynamic phase to correlate with the jaw displacement data at the fast rate. This would provide more data points for correlation over a longer period of ramp displacement in comparison with the data available at the slow rates of movement where thresholds were higher. The higher thresholds at the slower rates mean that there is a shorter period over which correlations between changing 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.

Nonetheless, it is likely 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 (*eg.*, Fig. 2C), does indeed point to a relationship between rate of movement and firing rate. This conclusion is valid despite the absence, in the present study, of a significant difference between firing rates at the fast and slow movements during the dynamic phases between step levels. An explanation for this absence of a significant difference 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.

7.5 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. III-16). This is consistent with previous findings in human limb and jaw muscles during isometric contractions (Tanji and Kato 1973a; Freund et al. 1975; Derfler and Goldberg 1978). 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, where many jaw movements are carried out, than for jaw positions further displaced from postural position. It should also 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 having 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 where 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.

8. MECHANISMS FOR MOVEMENT GENERATION

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 study does not specifically address this issue in the LP, the data demonstrated that IHLP SMUs could be recruited at jaw displacements up to 61-89% of the maximum contralateral or protrusive displacement. The data 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 non-human 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.

9. LEAST SUSTAINABLE FIRING FREQUENCIES (LSFFs)

The LSFFs in limb motor units (6 imp/s) is less than those for facial units (10 imp/s) (Petajan 1981). Previous studies have indicated that the masseter motor units could not be driven consistently below 8-10 imp/s (Nordstrom et al. 1989), although other studies (Eriksson et al. 1984; McMillan and Hannam 1992) indicated that the LSFFs fell within the range 5-8 imp/s. The temporalis units could not be fired continuously below 6 imp/s (McMillan 1993). The present study shows that the LSFFs of both SHLP and IHLP units appeared to be greater than those in the other jaw muscles. The study of McMillan and Hannam (1989), where subjects were instructed to maintain the firing rates of units at 10 or 15 imp/s by biofeedback techniques during incisal clenching and jaw opening against resistance, demonstrated that the lowest continuously maintainable firing rate was 8-10 imp/s and it was more easy to control at 15 imp/s. However, in the present study, trained subjects using visual feedback could not drive units below 11 imp/s without pauses.

The higher LSFF in the present study could be due to differences related to the tasks performed. In the masseter and temporalis muscles, the LSFF is task dependent (Eriksson et al. 1984; McMillan and Hannam 1992; McMillan 1993) and also varies according to anatomical site (McMillan and Hannam 1992). These observations suggest that voluntary drive to the masseter and tempolaris motoneurone pool is task dependent. In contrast, the present study showed that the LSFF of IHLP motor units did not vary with different horizontal jaw movement tasks. However, in the present study only two test tasks were performed. Further studies with more tasks need to be carried out to be able to draw a conclusion on the task dependence of LP SMUs. Our small sample size precluded an analysis of the LSFF at different anatomical sites. Such an analysis would require greater numbers of units to be sampled from different regions.

10. TECHNICAL DIFFICULTIES

It should be pointed out that the recordings from the LP, and especially the SHLP, were technically very difficult. There were a number of problems encountered during the experiments that limited the number of useful trials that could be recorded. The most common problem that occurred was the change of amplitude and/or shape of the SMU action potential during jaw movements. These changes were attributed to slight movement of the electrode in relation to motor unit current sources and sinks. It is considered that this movement was minimised by having the electrode wires bent back 2-3 mm over the tips of the inserting needle rather than <2 mm. Nonetheless, data was only used where it was confident that the same unit was being discriminated. Trials were discarded where it was not confident that the same unit was being discriminated. Another problem that was encountered was an absence of an electromyographic signal or the presence of a low amplitude signal, and this usually occurred at the beginning of an experimental session. Sometimes this spontaneously resolved after waiting a short time, or a slight pulling of the electrode wires frequently resulted in an improvement of the signal.

11. FUTURE STUDIES

The present study provides a methodology for standardising jaw movements and describes the basic functional properties of the LP SMUs in non-TMD subjects. This information can be used as a basis for comparison with TMD patients to clarify whether the functional properties of the LP SMUs are altered in these patients. The study in patients with TMD may ultimately provide a basis for improving treatment.

The data point towards the significance of the IHLP in the fine control of horizontal jaw movements. However, the IHLP is also active during jaw opening. The relative contribution of the IHLP SMUs to the horizontal and vertical tasks is a subject for future studies.

There is evidence that the SHLP and IHLP are functionally heterogeneous. More information regarding LP fibre architecture together with computer simulations of jaw biomechanics are necessary to provide a better understanding of the functions of the LP.

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