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Control of Jaw Orientation and Position in Mastication and Speech

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SUMMARY AND CONCLUSIONS

1. The kinematics of sagittal-plane jaw motion were assessed in mastication and speech. The movement paths were described in joint coordinates, in terms of the component rotations and translations. The analysis focused on the relationship between rotation and horizontal translation. Evidence was presented that these can be separately controlled.

2. In speech, jaw movements were studied during consonant-vowel utterances produced at different rates and volumes. In mastication, bolus placement, compliance, and size as well as chewing rate were manipulated. Jaw movements were recorded using the University of Wisconsin X-ray microbeam system. Jaw rotation and translation were calculated on the basis of the motion of X-ray tracking pellets on the jaw.

3. The average magnitudes of jaw rotation and translation were greater in mastication than in speech. In addition, in speech, it was shown that the average rotation magnitude may vary independent of the horizontal translation magnitude. In mastication, the average magnitude of vertical jaw translation was not dependent on the magnitudes of jaw rotation or horizontal jaw translation.

4. The magnitude of rotation and horizontal jaw translation tended to be correlated when examined on a trial by trial basis. Some subjects also showed a correlation between jaw rotation and vertical jaw translation. However, the proportion of variance accounted for was greater for all subjects in the case of rotation and horizontal translation.

5. Joint space paths in both mastication and speech were found to be straight. The pattern was observed at normal and fast rates of speech and mastication and for loud speech as well. Straight line paths were also observed when subjects produced utterances that had both the syllabic structure and the intonation pattern of speech. The findings suggest that control may be organized in terms of an equilibrium jaw orientation and an equilibrium jaw position.

6. Departures from linearity were also observed. These were typically associated with differences during jaw closing in the end time of rotation and translation. Start time differences were not observed in jaw closing and the movement paths were typically linear within this region.

INTRODUCTION

In this paper, we present two-dimensional (2D) X-ray microbeam recordings of human jaw movement in mastication and speech. We examine the kinematics of jaw motion in terms of its component rotations and translations. The aim is to assess the organization of central commands to the jaw and their coordination in orofacial behaviors.

The control underlying movement has been assessed typically in the context of arm movements. However, parallels to the problem of control in the jaw may be noted (see Flanagan et al. 1990). In both jaw and elbow movement, many muscles contribute to motion in more than one degree of freedom. Because there is no one-to-one mapping between individual muscle actions and kinematic degrees of freedom, the central control signals must be coordinated to produce movements such as elbow flexion alone, forearm supination alone, or muscle cocontraction without motion (Buchanan et al. 1986, 1990; Sergio and Ostry 1994; van Zuylen et al. 1988). This ability to produce, for example, flexion and supination movements separately, indicates that central control may be organized in terms of these component joint rotations.

In speech and in mastication, jaw movement in the sagittal plane involves a combination of rotation and translation (Baragar and Osborn 1984; Edwards and Harris 1990; Gibbs et al. 1971; Gibbs and Messerman 1972; Sarnat 1964). During opening, the jaw rotates downward and translates forward; during closing, the pattern is reversed. Jaw closers, such as temporalis, serve both to rotate and translate the jaw; jaw openers, such as the anterior digastric, act to lower and retract the jaw; protrusion and rotation are produced by the lateral pterygoid. Since, as in elbow movement, muscles have multiple mechanical actions, central control signals for individual muscles must be coordinated to produce movements such as rotation and translation, either alone or in combinations.

Elsewhere, we have proposed a model of jaw movement based on the equilibrium point (EP) hypothesis of motor control (λ model) (see Flanagan et al. 1990, for details). The model includes closer, opener, and protruder muscles, central neural commands, reflex mechanisms and muscle mechanical properties. According to the λ model, voluntary movements result from shifts in the equilibrium defined by the interaction of central commands, reflex mechanisms, muscle properties, and loads. Central commands control this process through the regulation of the motoneuron recruitment threshold lengths (λ) of multiple jaw muscles. The jaw model demonstrates that separate central commands can be defined for jaw rotation alone, jaw translation alone, and muscle coactivation without motion. Thus each of the commands affects the λs of all of the modeled muscles and the commands are coordinated to produce the basic modeled motions—jaw rotation and horizontal translation. In the present paper, we provide empirical evidence consistent with this view.

METHODS

The kinematics of 2D jaw and tongue movements were recorded with the University of Wisconsin X-ray microbeam system (Abbs et al. 1988; Westbury 1991). The microbeam is a low dosage X-ray scanner that under computer control tracks the motions of radio-dense markers (typically, 2–3 mm spherical gold pellets). Jaw rotation and translation in a sagittal plane were calculated from the motion of pellets on the jaw.

Two (or three) pellets were attached to the lower jaw and three to the tongue. The jaw pellets were placed between the mandibular

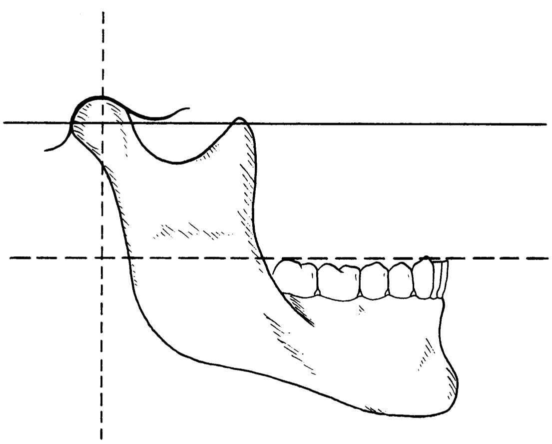

FIG. 1. Jaw position is represented in terms of the location of the condyle center along horizontal and vertical axes (parallel to and orthogonal to the occlusal axis). Jaw orientation is represented as the angle between the horizontal axis and an axis defined by corrected pellet positions on the mandibular teeth.

incisors and between the first and second or the second and third mandibular molars using a dental adhesive (Ketac). Tongue pellets were glued in positions corresponding to the tongue tip, blade, and dorsum. Single reference pellets were placed between the maxillary incisors, between the first and second maxillary molars, and on the nose bridge. The incisor and nose bridge pellets were used to correct for head movement in the sagittal plane. The maxillary molar and incisor pellets were used to locate the occlusal plane.

The microbeam system computes the positions of all pellets on a single image plane at a constant distance from the electron source. Thus pellets that are located off the image plane are registered at positions which are not at their true 2D coordinates but at points defined by the projective geometry of the microbeam's "pinhole camera" imaging system (see Westbury 1991 for a detailed description). Thus pellets located between the electron source and the image plane are registered in positions whose horizontal and vertical components are greater than their true 2D projections. Pellets located beyond the image plane have horizontal and vertical registrations that are less than their correct 2D positions.

The motions of the off-midline mandibular and maxillary molar pellets were corrected for their distance from the mid-sagittal plane (see Westbury 1991, for details). The off-midline corrections were based on distances between molar pellets and the midline, which were measured with calipers from dental impressions taken from the subjects. After completion of the experimental trials, mid-sagittal palate tracings were recorded.

Jaw movements were examined in both oral cavity and joint based coordinate systems (Munhall et al. 1991). Movements in the oral cavity were represented with the occlusal plane as the "horizontal" axis. The origin was set at the tip of the maxillary incisors. In the joint based representation (Fig. 1), movements were described in terms of the rotation of the jaw about the condyle center and the translation of the condyle center along axes parallel to and perpendicular to the occlusal plane (horizontal and vertical translation, respectively).

Jaw orientation angles (i.e., rotations) were computed as the scalar product of the vector defining the occlusal axis (obtained from the corrected positions of pellets on the maxillary molars and maxillary incisors) and the vector defining the mandible (obtained from the corrected to midline positions of a pellet on the mandibular molars and the pellet between the mandibular incisors). Jaw positions were expressed in terms of the motion of the condyle center. Condyle center positions were reconstructed from the recorded position of tracking pellets on the jaw. The distance and orientation of the condyle center relative to the pellets on the mandibular teeth were calculated using a scan X-ray and condyle center coordinates determined by palpation. (See Figs. 15 and 16 in the RESULTS section for an assessment of the effects of measurement error in determining the position of the condyle center on the computed patterns of jaw motion.) Note, that jaw positions were expressed in terms of the anatomic position of the condyle center, not in terms of the position of the instantaneous center of rotation.

Data were obtained from eleven subjects. Complete data sets for mastication and speech were obtained from eight; the remaining three subjects were tested only in speech conditions. For four subjects (S1–S4), speech movements were recorded during repetitions of consonant-vowel (CV) syllables and during a reiterant speech task (see below). Four different consonant-vowel (CV) types were tested. The CV combinations were produced continuously at a preferred or a fast speech rate. The utterances were composed of the vowels *a* and *e* and the consonants *t* and *k*. The selection of vowels enabled movement amplitude to be varied. The vowel *a* is associated with large amplitude jaw motion, whereas, the vowel *e* is associated with smaller amplitude motion. Ten to 15 tokens of each utterance type were collected.

In the reiterant speech task, subjects replaced target words with one, two or, three syllable sequences of the same stress pattern but composed entirely of repetitions of *ta* or *ka*. For example, subjects were shown on a video monitor the sequence "say bicycle nicely" and were told to repeat the phrase at a normal speech rate, replacing "bicycle" with "TA ta ta". The stress pattern of the original word was to be preserved in the syllabic sequence. In all cases, "say . . . nicely" was used as the utterance frame. One, two, and three syllable target items were tested enabling us to manipulate the position of the stressed vowel. "Deep" was used as the one syllable word; "Easy" and "Asleep" were used as the two syllable words; "Bicycle", "Relentless", and "Intervene" were used as the three syllable words. This condition was tested because it involves both the syllabic structure and the intonation pattern of continuous speech. Again, 10 to 15 tokens of each utterance type were collected.

Unilateral chewing with rubber tubing was tested. Subjects chewed continuously on hard or soft tubing at a preferred or a fast rate (see Bishop et al. 1987, 1988, for the effects of these variables on incisor trajectories). The hard tubing was 1 cm in diameter and was 3 mm thick. The soft tubing was also 1 cm in diameter but was only 2 mm thick. Rubber tubing was selected for this task for several reasons. The use of tubing ensured that load characteristics remained constant from cycle to cycle. Thus we were able to collect multiple chewing trials and to systematically vary load conditions. Although chewing with natural foods is more realistic, it may be difficult to identify regularities in motion or to infer control when the characteristics of the load change from cycle to cycle. Tubing was also used for practical reasons. Natural foods are unsuitable for X-ray microbeam studies because they might dislodge pellets and even lead to subjects swallowing them.

In the mastication trials, pieces of tubing, several centimeters in length, were placed in the mouth at about the position of the first molar. The free end of the tubing was held by the subject during the trial. The subject was instructed to maintain the position of the tubing throughout the trial. Ten to 15 cycles were collected in each condition.

The study was divided into trials of 5 s (syllable repetition and chewing) to 8 s duration (reiterant speech). During each trial, subjects repeated a given CV sequence or reiterant speech phrase continuously or chewed continuously on tubing. Several trials were recorded in sequence for each experimental condition until a sufficient sample of movements was obtained.

Five additional subjects (S5–S9) were tested with a second protocol. In the speech task, subjects produced six different consonant-vowel-consonant (CVC) utterances at either a preferred speech rate and normal volume or a preferred rate and loud volume. Loud speech was tested to obtain movement amplitudes which covered the full functional range for speech. The test utterances were composed of the vowels *a* and *o* and the consonants *k*, *t*, and *s*. Ten to 15 tokens of each utterance type were collected.

In the mastication trials, subjects chewed unilaterally on rubber tubing. The compliance and diameter of the tubing, and its position in the mouth were varied. Hard and soft tubing of three different diameters was tested. The hard tubing was in all cases 3.2 mm thick; the soft tubing was 2.4 mm thick. The overall tubing diameters were 9.6, 11.2, and 15.9 mm. The tubing was tested either at an anterior position between the second premolar and the first molar or a posterior position between the first and second molars. As in the other chewing task reported here, the subjects held the free end of the tubing and were instructed to maintain its position throughout the trial. Again, 10 to 15 cycles were collected for each condition.

The trial duration was 15 s for speech repetitions and 12 s for mastication. Subjects were instructed to continuously repeat the CVC token or to chew continuously on the tubing.

Two further subjects (S10, S11), were tested in a study involving loud and fast speech. The test items and procedure were similar to that of the study described immediately above.

The tracking pellets on the jaw and tongue were each recorded digitally at frequencies between 60 and 90 Hz. The reference pellets on the maxilla and nose bridge were similarly recorded at frequencies from 30 to 45 Hz. The trajectories of the individual pellets were low-pass filtered using a second-order zero phase lag Butterworth filter. The cut-off frequency was chosen on the basis of Fourier analysis and through direct comparison of raw and filtered records. In both mastication and speech, filtering frequencies between 8 and 10 Hz corresponded to points where the signal power had dropped between 30 and 40 dB from its maximum. Velocity and acceleration functions were derived using the least squares method (Dahlquist and Björck 1969).

Movements were scored using an interactive graphics program. Movement start and end were based on the tangential velocity of the mandibular incisor pellet. The filtered data point closest to but <10% of maximum tangential velocity was used to mark movement start and end. Jaw rotation and translation were calculated, as described above, from the motion of the tracking pellets on the jaw.

The sources of potential measurement error should be noted. Lateral head movements were minimized by providing the subject with a line up point, which was projected onto the forehead and could be monitored by the subject continuously. However, since the head was not fixed both head rotation and translation out of a midline measurement plane may have occurred. Head motions, which are out of the image plane, change the apparent position of all pellets and cannot be readily distinguished from motion within the plane. However, the magnitude of error due to head motion out of the image plane is relatively small. For example, with the subject positioned at a distance of 530 mm from the signal source, a lateral head motion of 10 mm would alter the apparent position of markers by 1.88%. That is, each x and y marker coordinate would be increased or decreased by this percentage depending on the direction of head translation.

Off-midline jaw motion such as in mastication may also introduce error. In speech, jaw motion is essentially planar (Bateson and Ostry 1992) and the error is minimal. However, in mastication, where the jaw typically opens medially and then deviates laterally at the beginning of the closing phase (Gibbs et al. 1972), the problem may be more serious. When pellets move at unknown distances from the image plane, error is introduced into measures of both jaw position and orientation.

The magnitude of lateral motion of the jaw in this task is unknown; however, typical magnitudes of lateral jaw motion in mastication range from ~5 to 15 mm (Gibbs et al. 1972). To estimate the error that would be introduced in measures of jaw position and orientation by lateral jaw motion in mastication, we numerically shifted the jaw laterally by 15 mm and recalculated the jaw position and orientation.

With subjects typically seated at a distance of 530 mm from the electron source, a 15-mm lateral shift in pellet position results in a 2.8% change in the pellet position coordinates. However, rather than estimate the effect of off-image plane jaw motion strictly on the basis of typical values such as these, we carried out the calculations using actual pellet positions. The data for the calculations were obtained from static X-ray scans that had been recorded to transform the "raw" microbeam data into data in an orofacial coordinate system. After correcting for static off-image plane distances of pellets, the orientation of the jaw relative to the occlusal plane was computed, as in experimental conditions, as the scalar product of the vectors defining the occlusal axis and the jaw. The position of the condyle center was also computed as in experimental conditions, on the basis of the distance and orientation of the condyle center from tracking pellets on the jaw. Calculations were repeated for all subjects tested in the study.

When jaw pellets were shifted 15 mm beyond the image plane, the jaw orientation angle was found to increase by a maximum of 0.002° (range −0.001°–0.002°). The horizontal coordinate of the condyle center (parallel to the occlusal plane) was found to decrease by a maximum of 0.118 mm (range −0.011– −0.118 mm); the vertical coordinate decreased by a maximum of 0.205 mm (range −0.205–0.053). (Both positive and negative changes in estimated orientation and position resulted from the specific pellet placements and jaw geometry.)

RESULTS

In this section, we present sagittal plane jaw motion paths in joint coordinates and we assess the contribution of jaw orientation and position to the motion in an oral cavity coordinate frame. We show that paths in joint coordinates form straight lines regardless of the initial orientation and position of the jaw. The slope of these paths and their initial orientation angle and position may vary suggesting that the nervous system can control jaw rotation (the sequence of jaw orientation angles) and translation (the sequence of jaw positions) separately.

In both mastication and speech, we have focused on the relationship between sagittal plane jaw rotation and horizontal jaw translation. Vertical jaw translation is considered in less detail because its contribution to motion paths in joint coordinates was variable. The patterns of jaw rotation and horizontal jaw translation were found to be unaffected by the vertical component of translation (see below). Moreover, by focusing on the kinematics of jaw rotation and horizontal jaw translation, we are able to assess the proposal outlined in the introduction that the nervous system organizes jaw movement in terms of an equilibrium jaw position and an equilibrium jaw orientation.

Basic patterns of jaw movement

Jaw movements in speech were recorded for various consonant-vowel combinations at different rates and speech volumes. In mastication, rate as well as bolus compliance, diameter, and position were studied. The goal was to assess the magnitudes of jaw motions in the two behaviors and the

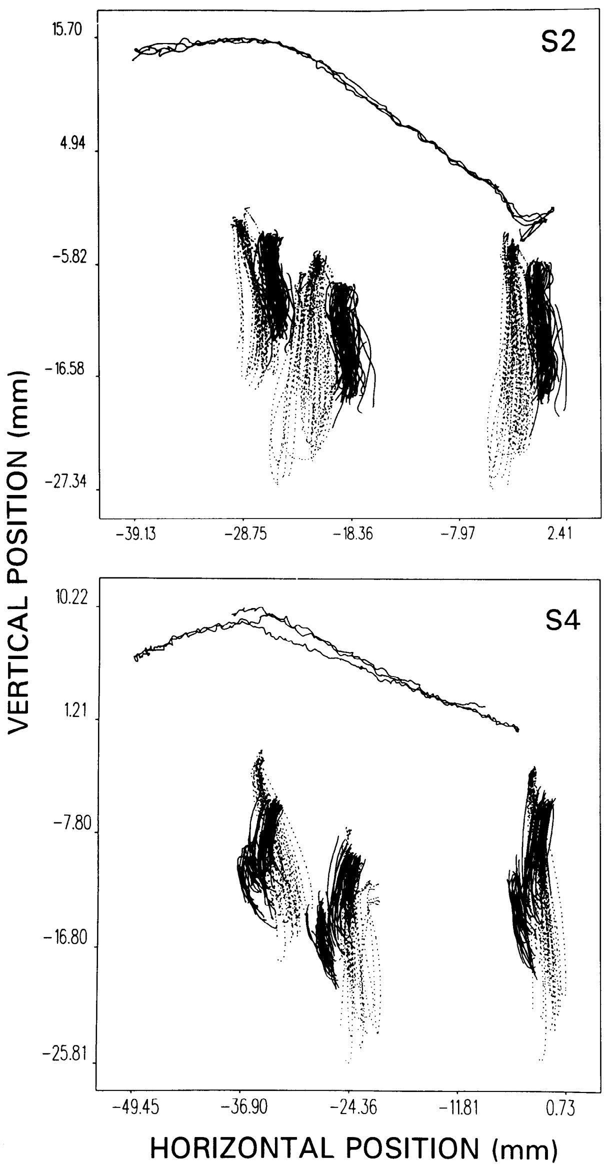

FIG. 2. Sagittal plane jaw motion in oral cavity coordinates. Paths for 3 pellets on the mandibular teeth are shown, with speech represented by solid lines and mastication by dots. Palate tracings are superimposed (continuous lines across the top of the Fig.). Incisor pellet paths are at the *right*.

dependence of motion in translation and rotation. We first examined jaw motions in an oral cavity coordinate system.

Figure 2 shows, for two different subjects, the typical paths of pellet motion in the oral cavity. The paths of three pellets attached to the mandibular incisor and molar teeth are shown for jaw movements in mastication (dots) and speech (solid). (The pellet positions have been corrected for off-midline placement.) A palate tracing is superimposed. For the subject shown in the *top panel,* the jaw is translated forward for speech and rotates over a different range than in mastication. In the *bottom panel,* two distinct sets of paths can be seen for speech movements. The range of movement is greater in mastication. For both subjects, paths are relatively straight. Note that the overall differences in the elevation of the three pellets are due to the positions of the pellets on the teeth. It should also be noted that considerable variation is observed between subjects in the specific patterns of pellet motion on the teeth. These differences reflect corresponding differences in subject's patterns of jaw rotation and translation (see below).

The basic patterns of jaw rotation and translation are shown in Fig. 3. The figure displays jaw movements in speech, however, the same basic patterns are observed in mastication. The figure displays jaw movements during several repetitions of a consonant-vowel-consonant utterance. Note that rotation and translation tend to begin and end simultaneously and that the trajectories are basically similar in form.

The magnitudes of rotation and translation in normal speed movements are shown in Fig. 4. It can be seen that the magnitudes of all variables tend to be greater in mastication. However, the increase in magnitudes is not strictly proportional. For example, for subject S1, the magnitudes of rotation and vertical translation increase in mastication, while the magnitude of horizontal translation decreases. For subject S3, there is a 25% increase in the magnitude of jaw rotation in mastication and a four-fold increase in the magnitudes of horizontal and vertical translation.

Jaw movements at fast and normal rates are presented in Figs. 5 and 6 for mastication and speech, respectively. Subjects S1, S2, and S3 in Fig. 5 all show that the average magnitude of vertical jaw translation in mastication is not dependent on the magnitudes of jaw rotation or horizontal jaw translation. For all three subjects, the magnitudes of rotation is greater at normal rates while the magnitude of vertical jaw translation is unaffected by chewing rate. For subject S4, the magnitudes of all variables are greater at fast chewing rates.

In speech, greater amplitude movements were observed at normal rates (Fig. 6). Note for subject S3, that the magnitude of horizontal translation is small and unaffected by speech rate. Thus rotation magnitude may vary while the magnitude of horizontal translation is fixed. Speech move-

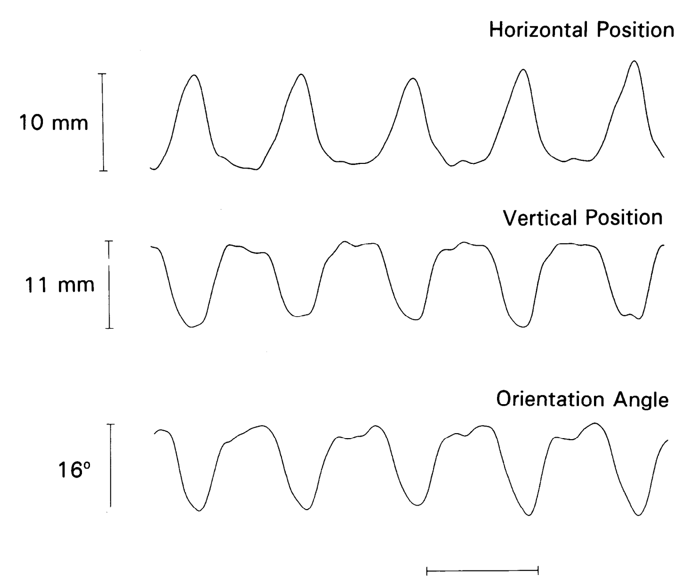

FIG. 3. Jaw position and orientation during repetitions of the syllable *kak*. Motion upward corresponds to protrusion, vertical elevation, and jaw closing for horizontal position, vertical position, and jaw orientation, respectively.

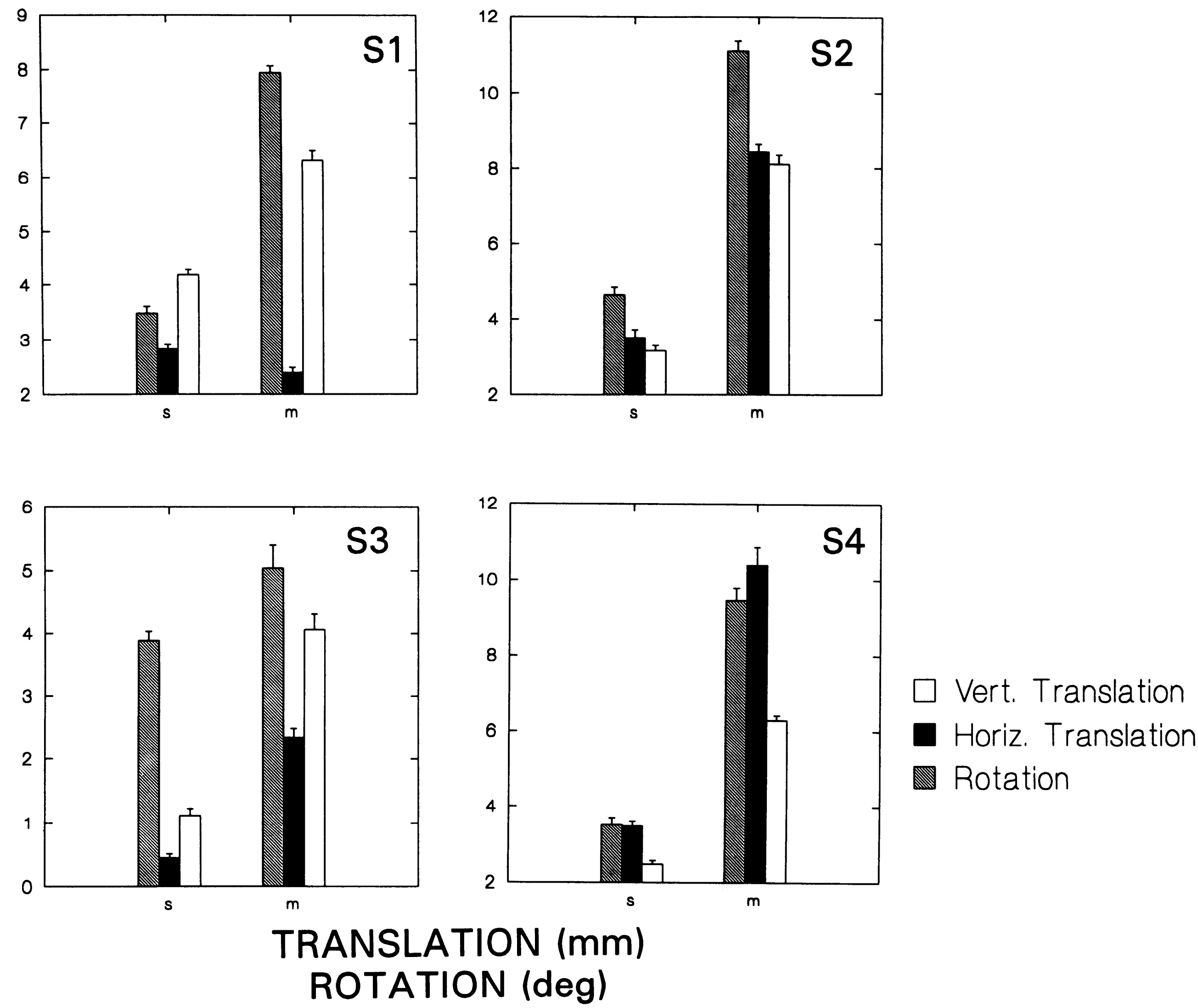

FIG. 4. Average amplitude of jaw rotation and translation during mastication (m) and speech (s) at normal rates. Standard errors are shown.

ments at normal and loud volumes are shown in Fig. 7. Note that speech movements with magnitudes comparable to those in mastication may be observed in loud speech.

The dependence of movement amplitude on rate, volume, phonetic context in speech and bolus characteristics and position in mastication was assessed statistically, on a subject by subject basis, using analysis of variance (ANOVA).

Individual subjects displayed systematic differences in rotation and translation amplitudes. However, the patterns varied from subject to subject. For example, of the eight subjects in which bolus compliance was manipulated, three had greater rotation magnitudes for soft tubing ($P < 0.01$), four for hard tubing ($P < 0.01$) and one showed no difference in rotation amplitude with differences in compliance. A similar picture emerged in speech. For three subjects, rotation amplitudes were greater for sequences involving the consonant *k* than for sequences involving *s* or *t* ($P < 0.01$). Two other subjects showed the opposite pattern ($P < 0.01$) and for two further subjects, no differences in rotation magnitude were observed for the different consonants.

The magnitudes of rotation and horizontal translation were generally related. This was demonstrated in two ways. For example, subjects that showed larger amplitude rotations for hard tubing than for soft tubing also tended to show greater amplitude horizontal translations for hard tubing. (The other subjects, who showed larger amplitude rotations for soft tubing than for hard tubing also tended to show greater amplitude horizontal translations for soft tubing.) When examined in this way, that is, on the basis of average values of rotation and horizontal translation across the levels of the individual test conditions, similar patterns of rotation and translation were observed for seven of eight subjects for different bolus compliances, all four subjects for different chewing rates, all four subjects for different bolus diameters, two of four subjects for different bolus placements, four of nine subjects for different consonants, six of nine subjects for different vowels, three of four subjects for different speech rates, and all five subjects for different speech volumes ($P < 0.01$ in all cases).

The relationship between rotation and translation magnitudes is shown in Fig. 8 on a trial to trial basis. Speech

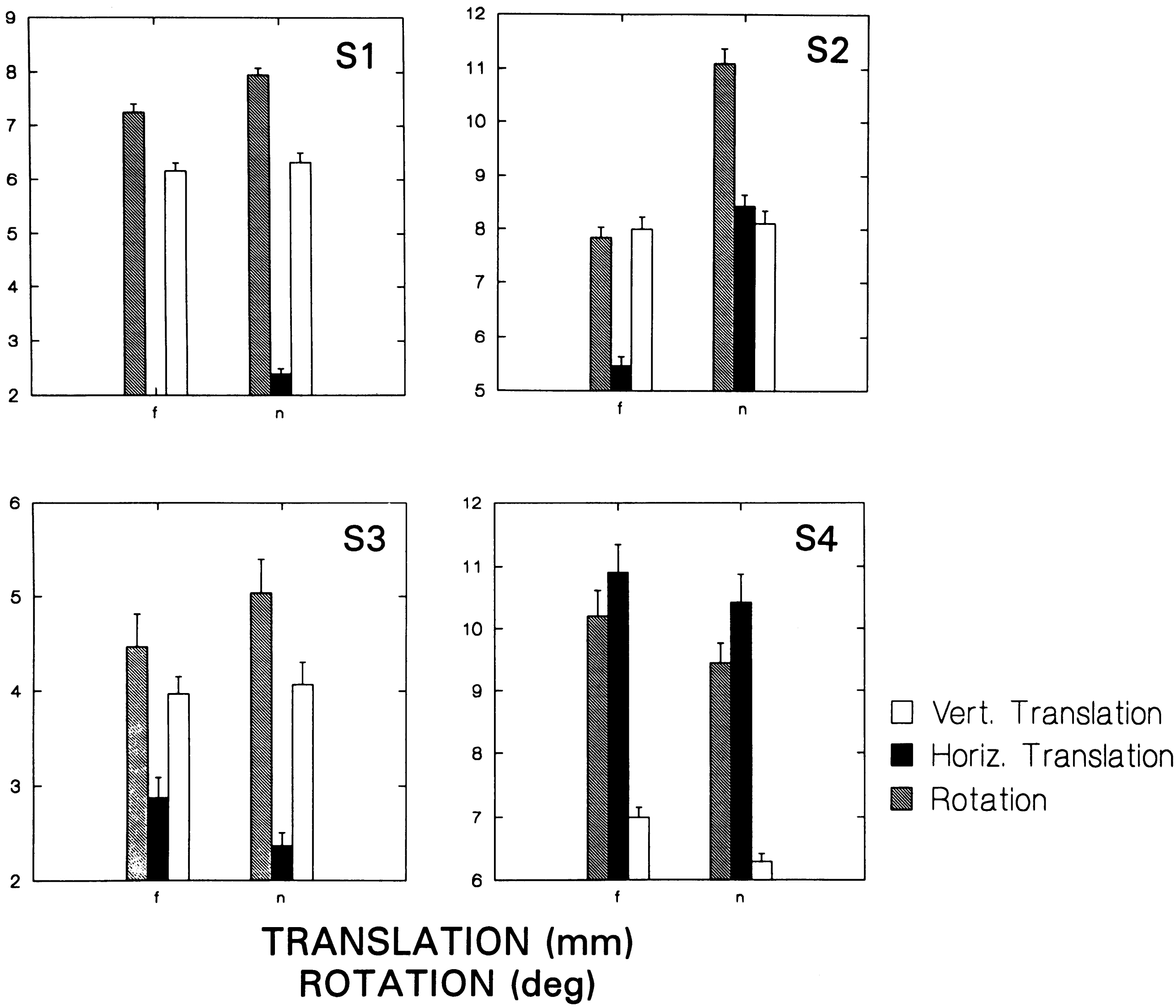

FIG. 5. Average amplitude of jaw rotation and translation in mastication at normal (n) and fast (f) rates. Standard errors are shown.

trials are shown as circles and mastication trials as squares. (The manipulation involved mastication as well as loud and normal speech volumes.) Two basic patterns are evident. All subjects show systematic increases in the magnitude of rotation with increases in horizontal translation ($P < 0.01$). For subjects S6 and S9, rotation also increases with vertical translation ($P < 0.01$). For subjects S7 and S8, increases in rotation are accompanied by decreases in vertical translation ($P < 0.01$). Although rotation is systematically related to both horizontal and vertical translation, the proportion of variance accounted for by these relationships was greater for all subjects in the case of rotation and horizontal translation: .47 (rotation and horizontal translation) as compared with .03 (rotation and vertical translation) for subject S6, .73 and .38 for subject S7, .91 and .42 for subject S8, and .47 and .17 for subject S9.

Motion paths in joint coordinates

Figure 9 presents jaw movement paths for different consonants in speech. The jaw orientation angle is given on the vertical axis, the horizontal jaw position is on the horizontal. The paths represent jaw position/orientation combinations over the course of individual movements. The solid lines are for speech movements involving the consonant *k*, the dotted lines are for *s* and the dashed lines are for *t*. The loud speech condition is shown. The paths are for the jaw closing movement and begin at the *bottom right* of each panel. The same patterns were observed for jaw opening. Thus, when jaw movements are plotted in joint coordinates it can be seen that, to a first approximation, straight line paths are observed. Moreover, the slope and the intercept vary suggesting that the nervous system can control the coordination of rotation and horizontal jaw translation. (Figure 10 shows the paths for the same subjects at normal speech volumes.) Note that straight line paths arise when rotation and translation start and end at the same time and have velocity profiles which are similar in shape.

The jaw motion paths for a subject tested in loud and fast speech conditions (S11) are shown in Fig. 11. The solid lines give paths for loud speech, the dashed lines are for the fast condition. It can be seen that the jaw can be translated forward, as in movements for the sound *sa* at a loud vol-

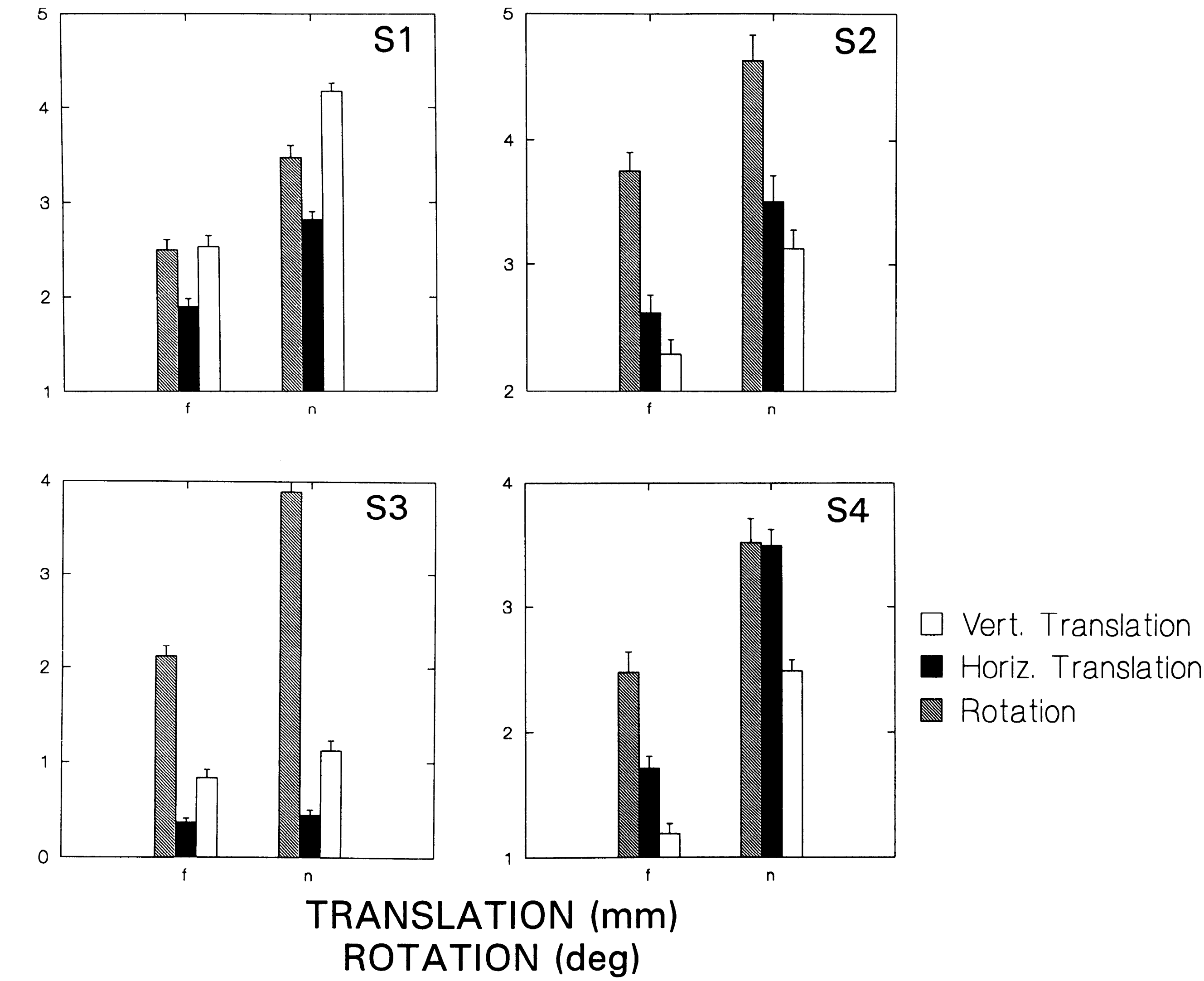

FIG. 6. Average amplitude of jaw rotation and translation in speech produced at normal (n) and fast (f) rates. Standard errors are given.

ume, independent of the rotation/translation slope. It can also rotate over a different range, as in movements for *ka* at a loud volume, again independent of the slope relating rotation and translation. The "main effects" of both rotation and horizontal translation, as well as their interaction, suggest that the system can control rotation alone, translation alone, and their combination.

Figure 12 shows paths for speech movements involving stressed (emphasized, shown as solid lines) and unstressed syllables (dashed lines). Although neither slope nor intercept differences arise as a function of syllabic stress in speech, simple straight line paths are again observed for all subjects. Moreover, it can be seen that for unstressed syllables, in some cases, paths involving pure rotation are observed. The figure suggests that jaw motion in joint coordinates is characterized by straight line paths in continuous speech conditions. Note, we have elsewhere reported motion paths in speech in which translation alone is observed (Bateson and Ostry 1992).

Figure 13 gives motion paths for both speech and mastication at normal and fast rates. Four subjects (S1–S4) are shown. The paths for speech movements are indicated by solid lines. Mastication is shown with dashed lines. Although nonlinearities are evident, jaw motion in joint coordinates is again approximated by straight line paths. For subject S1, the slopes differ for mastication and speech. For subject S2, the jaw is translated forward and rotated downward for speech. For subject S3, speech movements are small and predominantly rotational, whereas, for mastication relatively straight paths are observed. For subject S4, mastication and speech differ in terms of slope and intercept. In addition, two separate sets of paths corresponding to different consonants are observed for speech. The *top* set of solid lines are for the syllable *ta;* the *bottom* set are for *ka.*

In speech, the slope and intercept of the jaw path in joint coordinates varies both with phonetic variables such as the composition of the utterance and with nonlinguistic variables such as volume. In contrast, although differences in the compliance, diameter and position of the bolus have been tested in mastication, the slope and intercept of these functions did not vary.

A large proportion of the variance in the motion paths of the present study is accounted for by linear functions (typically >0.95). However, it is clear, that consistent nonlin-

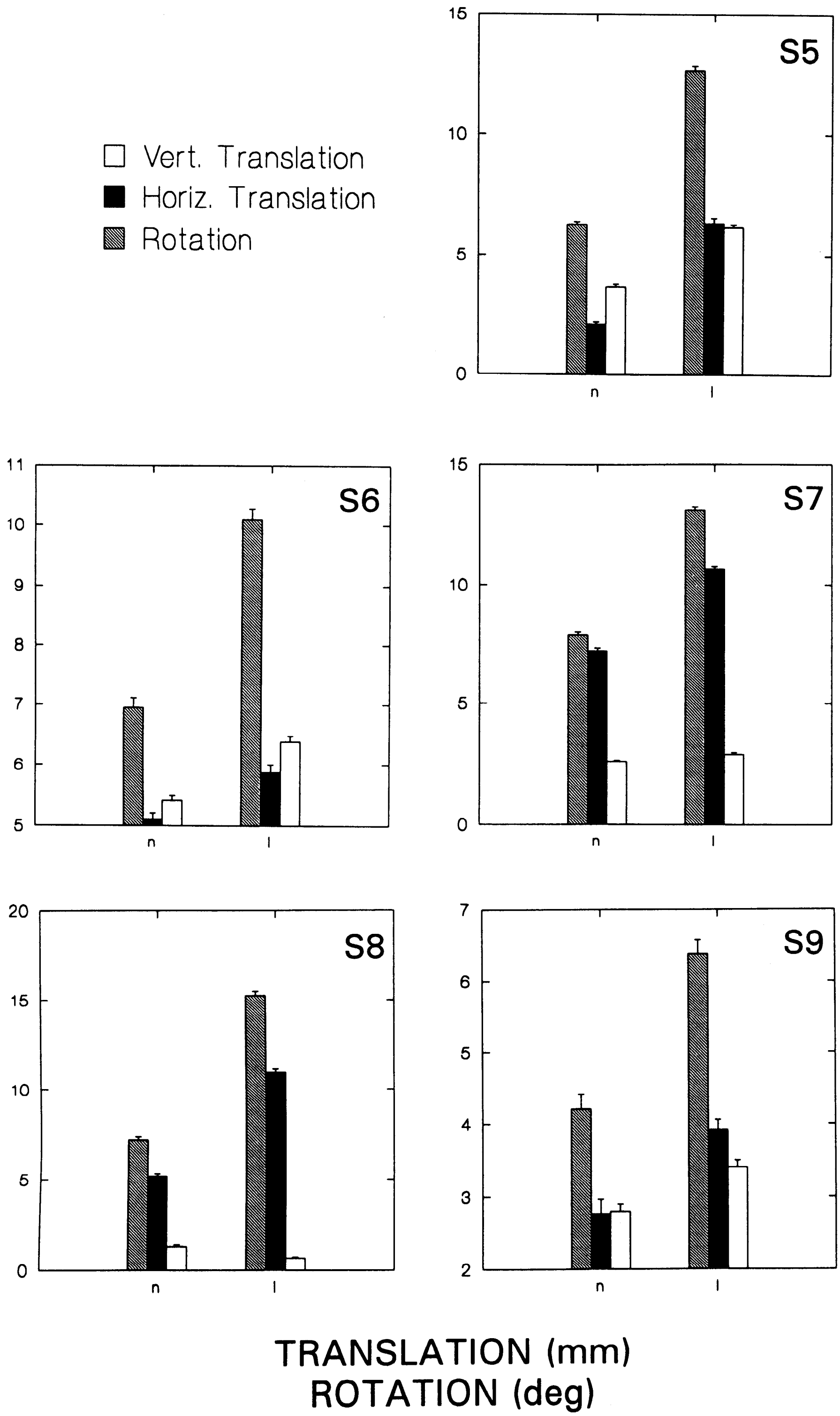

FIG. 7. Average amplitude of jaw rotation and translation at normal (n) and loud (l) speech volumes. Standard errors are indicated.

earities are present in the motion paths of almost all subjects. Nonlinearities due to differences in the start and end times of rotation and translation and differences in the shape of velocity profiles were assessed for the subjects shown in Figs. 9 and 10 (S5–S9).

The distribution of time differences in the start of rotation and translation and the time differences in their ending were calculated, as elsewhere, for jaw closing. Positive values indicate that horizontal translation starts or ends first; negative values indicate rotation is first to start or end.

Movement start time differences were small for all subjects. Average differences in the start time of rotation and translation ranged from an average of −4 to +8 ms for speech and from an average of −13 to −4 ms for mastication. There were larger time differences between the end of rotation and the end of horizontal translation, as evident in the curvature observed in the motion paths at movement end. These differences ranged from +5 to +58 ms in speech and from −60 to +37 ms in mastication. The effect of differences in the end time of rotation and translation can be

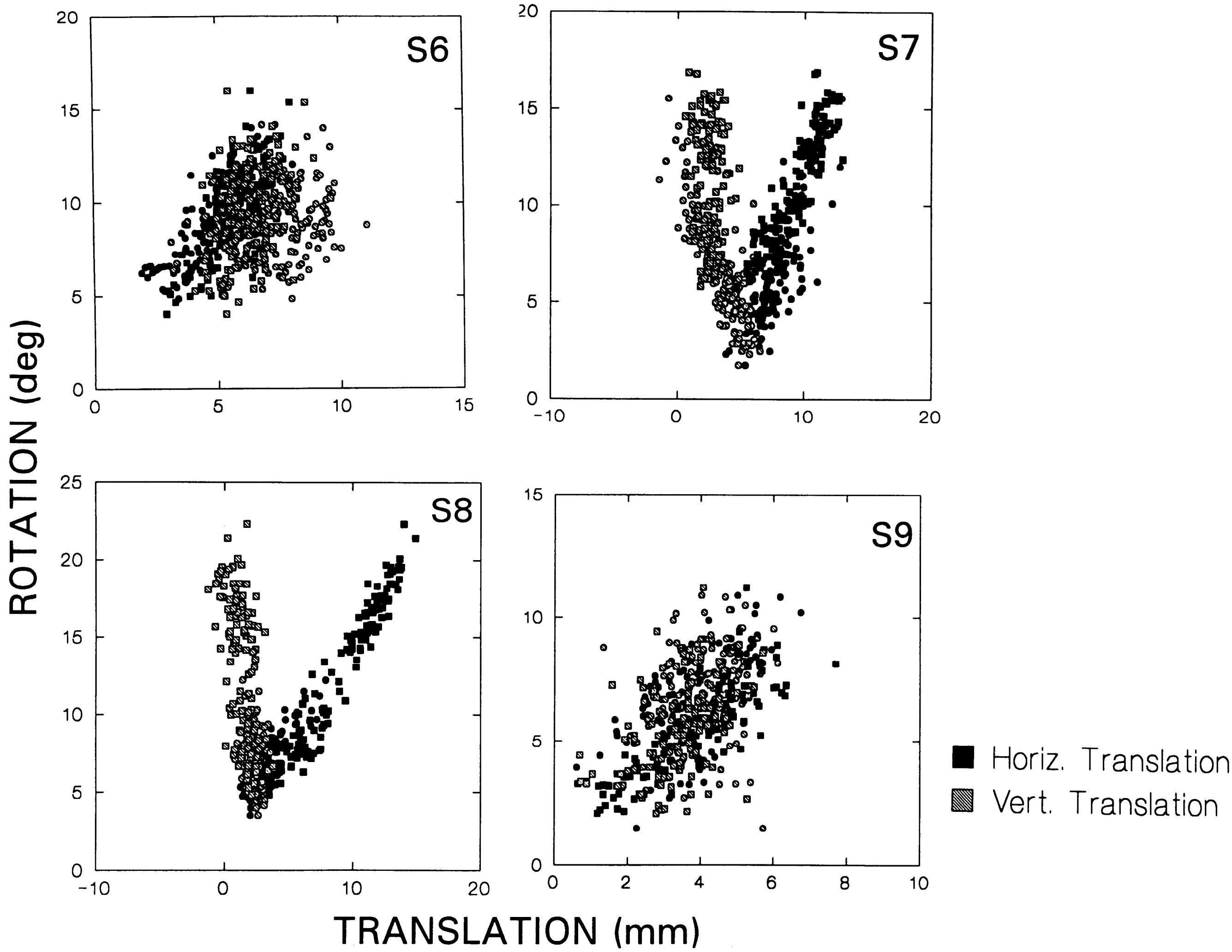

FIG. 8. Amplitude of jaw rotation as a function of horizontal and vertical jaw translation. Rotation/translation combinations are shown on a trial by trial basis. Mastication trials are shown with squares, speech trials are shown with circles. An orientation angle of 0° corresponds to occlusion; horizontal position indicates distance in millimeters from the maxillary incisors (incisors are to the *right*).

seen by examining Fig. 9. The greatest curvature at movement end is observed for Subject S6 and the least for Subject S7. The average time difference between the end of rotation and translation for these two subjects was 37 and 5 ms, respectively. The curvature at movement end is in some cases rather sudden and may reflect approach to workspace boundaries, that is, to joint motion limits.

Curvature in motion paths also arises from differences in the shapes of the velocity profiles of jaw rotation and translation. The magnitude of shape differences was assessed by calculating on a trial by trial basis, for both rotation and translation, the proportion of their movement time required to reach their maximum velocity. The ratio of the proportion of time to reach maximum rotation velocity divided by the proportion of time to reach maximum translation velocity served as an index of the similarity of the form of the rotation and translation velocity functions. A ratio of one is necessary if velocity profiles are similar in shape. In speech, median values of ratios varied from .90 (Subject S6) to 1.10 (Subject S5), averaging 1.01. In mastication, values ranged from 1.04 (S6) to 1.35 (S9), averaging 1.17.

The contribution of jaw rotation and translation to movement amplitude in the oral cavity is shown in Fig. 14. The vertical axis gives movement distance measured for pellets on the mandibular incisors. The horizontal axis gives the magnitude of jaw rotation and translation at the temporomandibular joint. Note that rotation and translation are shown on the same axis but represent movement in degrees and millimeters, respectively. The data for speech movements are shown with circles; mastication is shown with squares. For all subjects shown in the present figure, it can be seen that both rotation and horizontal jaw translation contribute significantly to jaw movement amplitude in the oral cavity ($P < 0.01$). In contrast, a contribution of vertical jaw translation to oral cavity movement amplitude is apparent only for Subjects S6 and S9 ($P < 0.01$). Nevertheless, further evaluations of both horizontal and vertical jaw motion components would seem appropriate.

A control study was carried out to assess the effects on jaw motion paths of measurement error in locating the condyle center relative to markers on the mandible. Consider, for example, a case involving pure jaw rotation. Any error in locating the condyle center will introduce both horizontal and vertical translation errors into the jaw motion re-

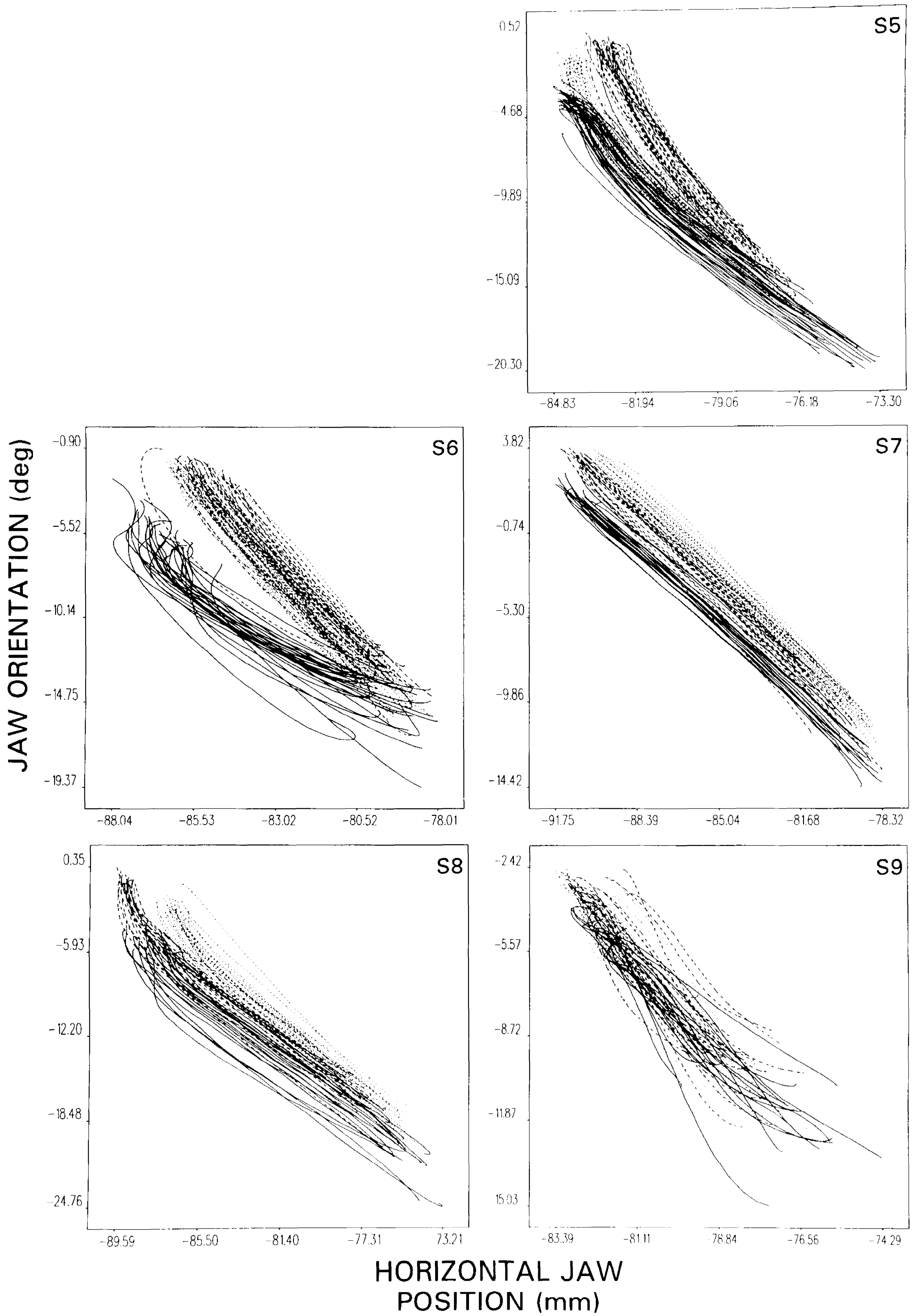

FIG. 9. Jaw motion paths in joint coordinates during speech production. Paths show jaw closing movements in loud speech. Jaw orientation angle is given relative to the occlusal plane. Horizontal jaw position is given relative to the maxillary incisors. Movements are for syllables involving *k* (solid), *s* (dots), and *t* (dashes).

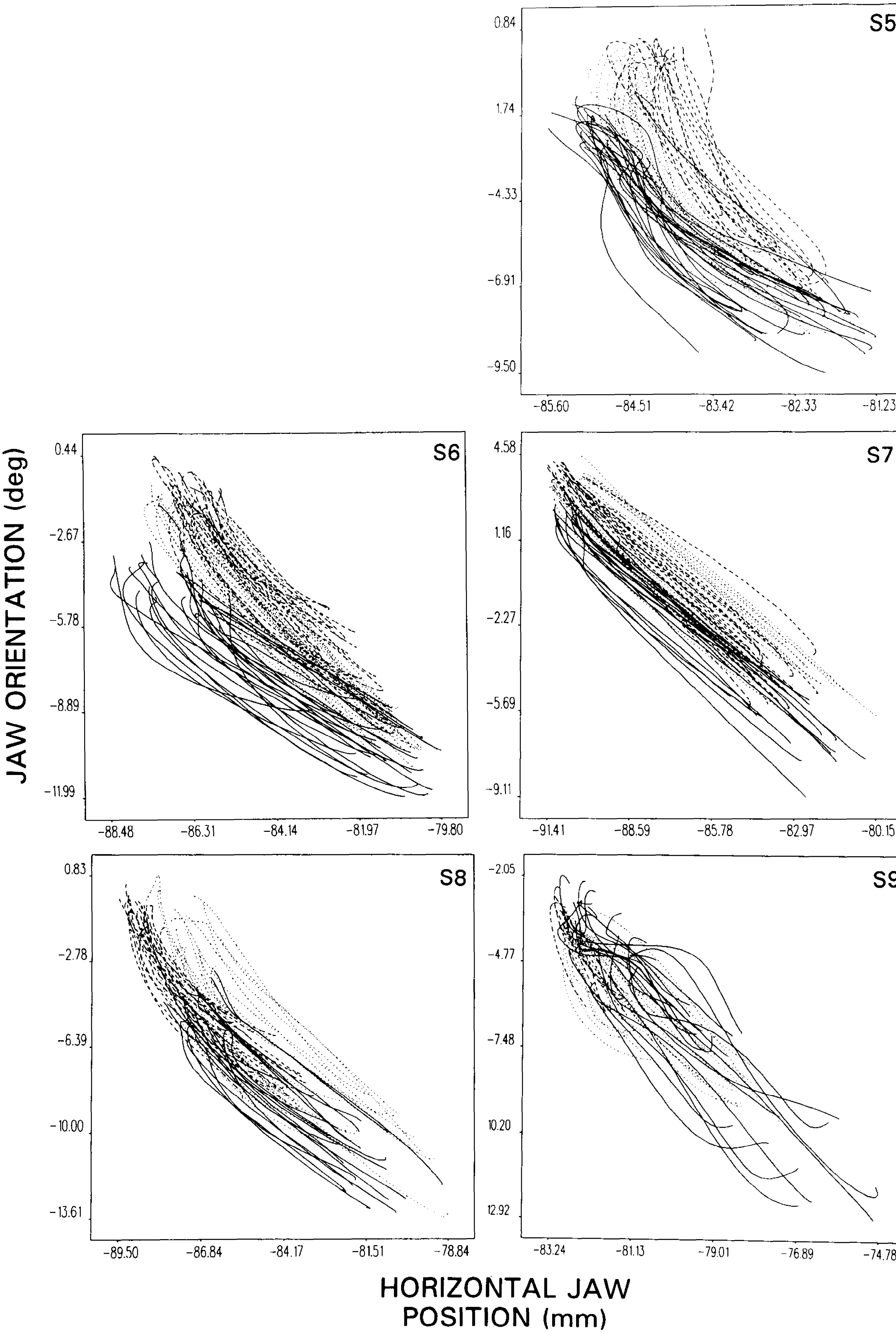

FIG. 10. Jaw motion paths during normal rate, normal volume speech movements; k (solid), s (dots), t (dashes). Jaw closing is shown.

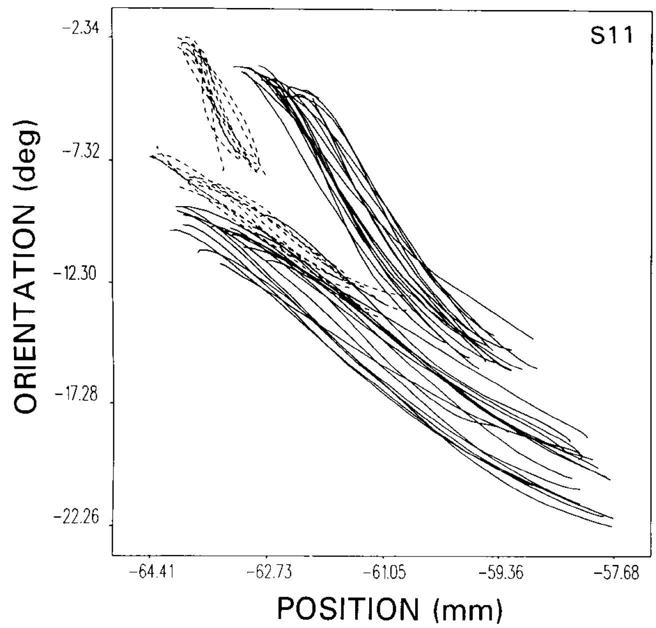

FIG. 11. Jaw closing paths during fast (dashes) and loud (solid) speech. The two sets of paths at the top of the Fig. are for the syllable *sa*. The paths at the bottom are for the syllable *ka*.

construction. The magnitude of the error depends both on jaw geometry and on magnitude and direction of error relative to the actual center of rotation. (Note, that only translation, not orientation angles are affected. Jaw orientation is calculated on the basis of vectors which define the occlusal plane and the mandible and is thus not affected by jaw position.) Two examples were chosen to examine the effects of incorrect location of the condyle center. In each case, jaw motion paths were recomputed after "shifting" the condyle center 7.5 mm in a vertical direction and 5 mm in a horizontal direction. Figure 15 shows a case involving straight line motion. The paths at the center of the figure are the original paths calculated for S7 in Fig. 9. The four corner panels are the recalculated paths based on shifting the presumed location of the condyle center to positions left or right by 5 mm and up or down by 7.5 mm. Figure 16 shows the effects for curved paths. In both figures, some differences can be seen as a result of changes to the measured position of the condyle center. However the basic form of the functions is preserved. (Note, that the changes in horizontal jaw position shown in Figs. 15 and 16 are not proportional to the magnitude of the "shift"; as noted above, the error in locating the condyle center depends on jaw geometry and upon the direction and magnitude of the error relative to the true center of rotation.)

DISCUSSION

Sagittal plane jaw motion was examined in mastication and speech. The goal was to determine how central commands to the jaw might be organized and to provide evidence for the view that jaw motions are specified in terms of

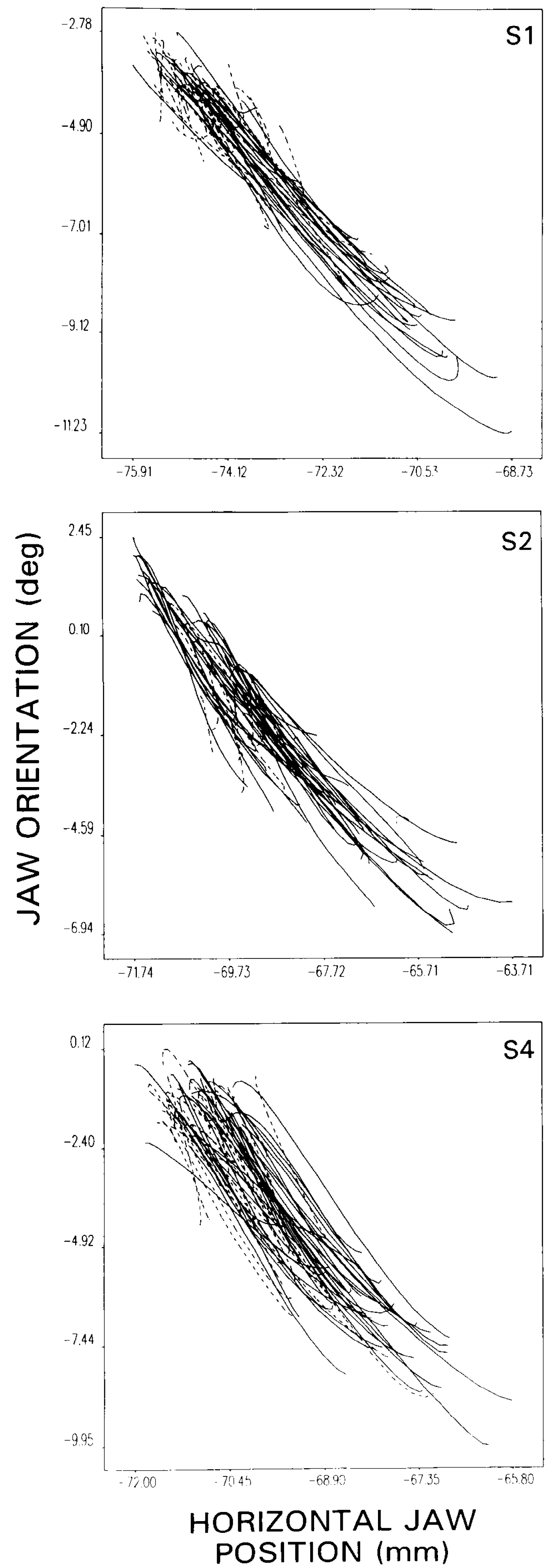

FIG. 12. Jaw closing paths during continuous speech-like sequences. Dashes are for syllables with unstressed vowels. Solid lines indicate syllables with stressed vowels.

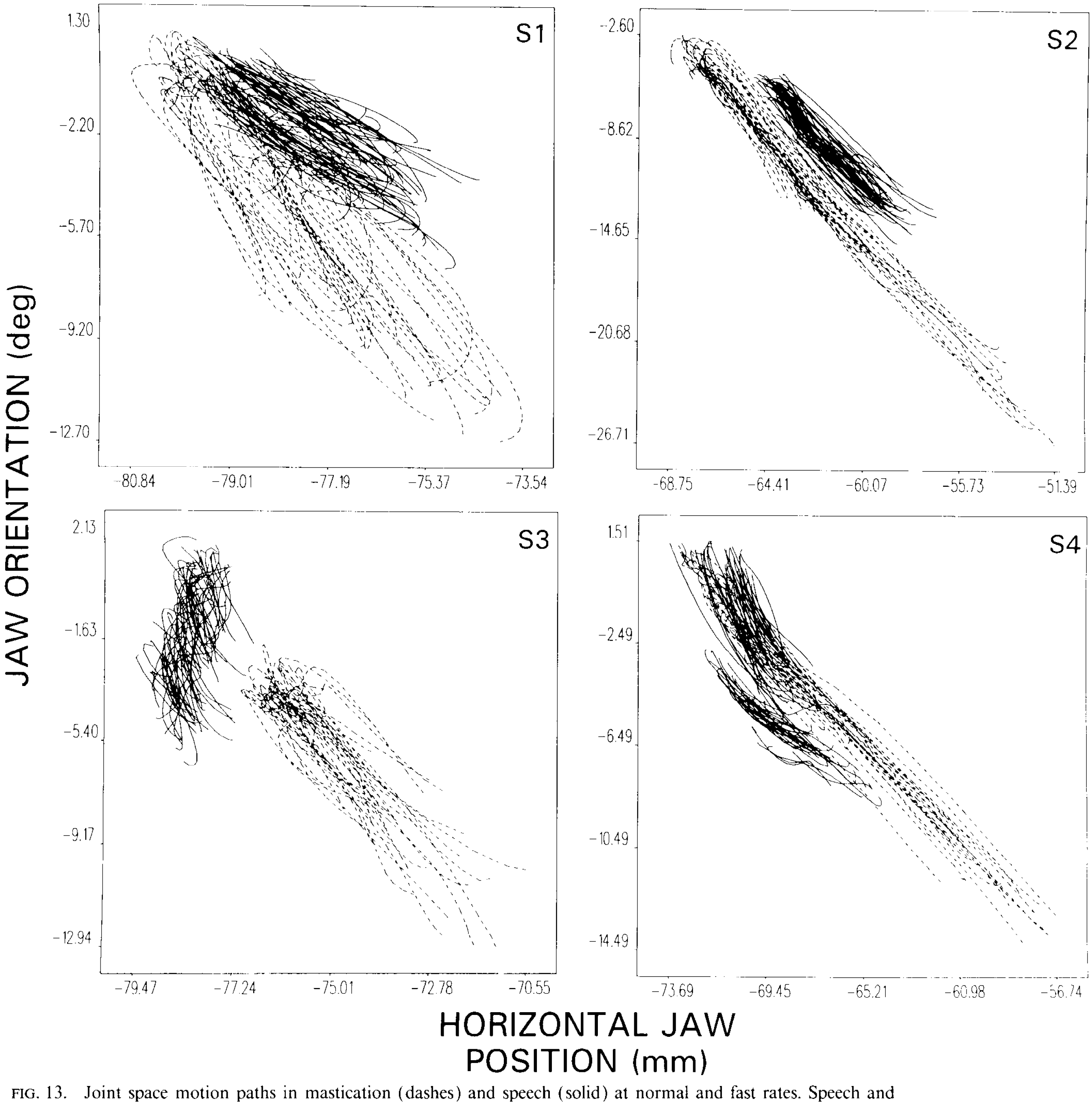

FIG. 13. Joint space motion paths in mastication (dashes) and speech (solid) at normal and fast rates. Speech and mastication paths differ both in slope and intercept. Normal and fast rate movements are completely superimposed. For subject S4, 2 sets of paths are shown for speech; the paths at the *top* are for the consonant *t*. The paths at the *bottom* are for *k*. Jaw closing is shown.

equilibrium jaw *orientations* and equilibrium jaw *positions*. In both speech and mastication, jaw movements were studied by examining jaw motion paths in a joint-based coordinate system. Speech movements were studied by varying rate, volume, syllabic stress, and the consonant-vowel composition of utterances. In mastication, rate was varied along with bolus compliance, position, and diameter.

Jaw motion paths in joint coordinates had three essential characteristics. *1*) Jaw paths formed straight lines. *2*) The slopes of the jaw paths in speech were different for different sounds. *3*) The intercepts of the jaw paths varied for different speaking volumes. Slope and intercept differences were not observed in mastication. Jaw motion paths in mastication were, nevertheless, straight in joint coordinates.

The findings are consistent with the organization of commands proposed in the λ model for jaw movement. According to the model outlined in the introduction (also see Flanagan et al. 1990), straight lines occur in joint equilibrium space when jaw equilibrium orientations and positions start to shift simultaneously and each shifts at the same relative velocity. Under these conditions, the actual joint space paths will be approximately straight, which was the case for both speech and mastication when jaw rotation was plotted as a function of horizontal jaw translation.

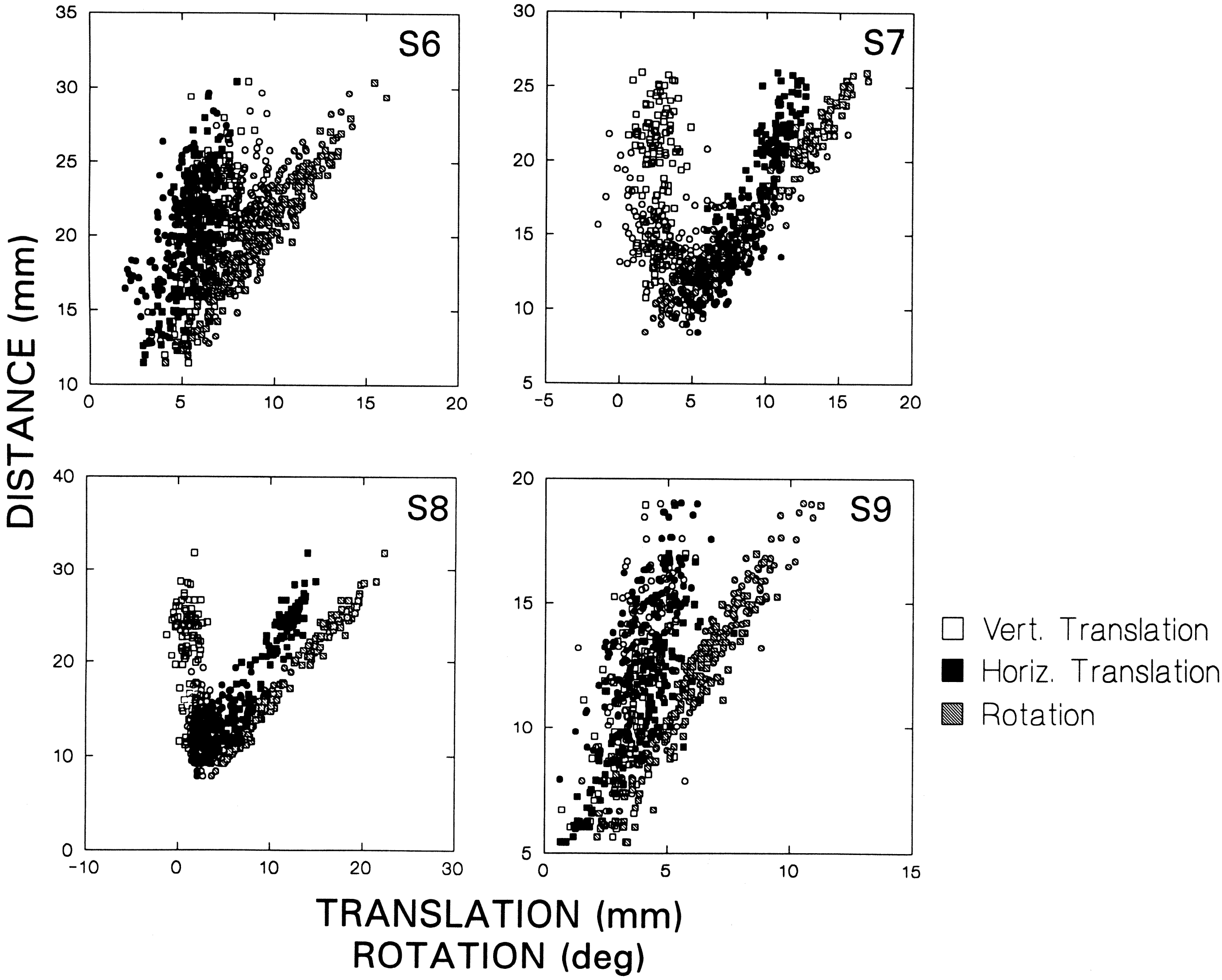

FIG. 14. Amplitude of movement at the incisors as a function of vertical and horizontal jaw translation and jaw rotation; speech (circles), mastication (squares).

The slopes of the joint space paths of jaw movement in speech varied for different consonant-vowel combinations. According to the model, this suggests that there are different rates of equilibrium shift in speech. In contrast, joint space paths in mastication were characterized by straight line motion paths of a constant slope. Thus, a single rate of shift of the jaw equilibrium angle and position may subserve mastication despite differences in bolus size, compliance, and position.

The intercepts of the paths differed with speech volume. Fig. 11 provides a good example of this pattern. The figure shows that the jaw can be translated forward or rotated downward while preserving the slope of the movement path. Variations in the intercept of the joint space path in speech, independent of its slope, suggest that the nervous system may organize commands to separately shift equilibrium jaw positions and equilibrium jaw orientations. That is, the system may specify translation and rotation separately.

It should also be noted that the same organization of commands was used in modeling speech and mastication (Flanagan et al. 1990). This is consistent with empirical findings in the present paper in which simple straight line paths in joint coordinates characterized jaw motion in both behaviors. Although the present data suggest that different combinations of rotation and translation commands are used by the system to produce the empirically observed differences in the slopes and intercepts of jaw motion, both can be accounted for in the model by simple linear shifts in the equilibrium orientation and position underlying rotation and translation of the jaw.

The findings have been discussed within the context of the λ model. However, we wish to emphasize that the main conclusion, that jaw rotation and translation may be controlled separately, is not tied to this or to alternate versions of the EP hypothesis (i.e., those proposing bell-shaped and nonmonotonic equilibrium shifts, see Flash 1987; Latash 1993) or to other accounts of control.

The suggestion that control may be organized in terms of the component rotations and translations is consistent with recent work on human arm movements. As in jaw motion, arm movements involving forearm flexion or extension

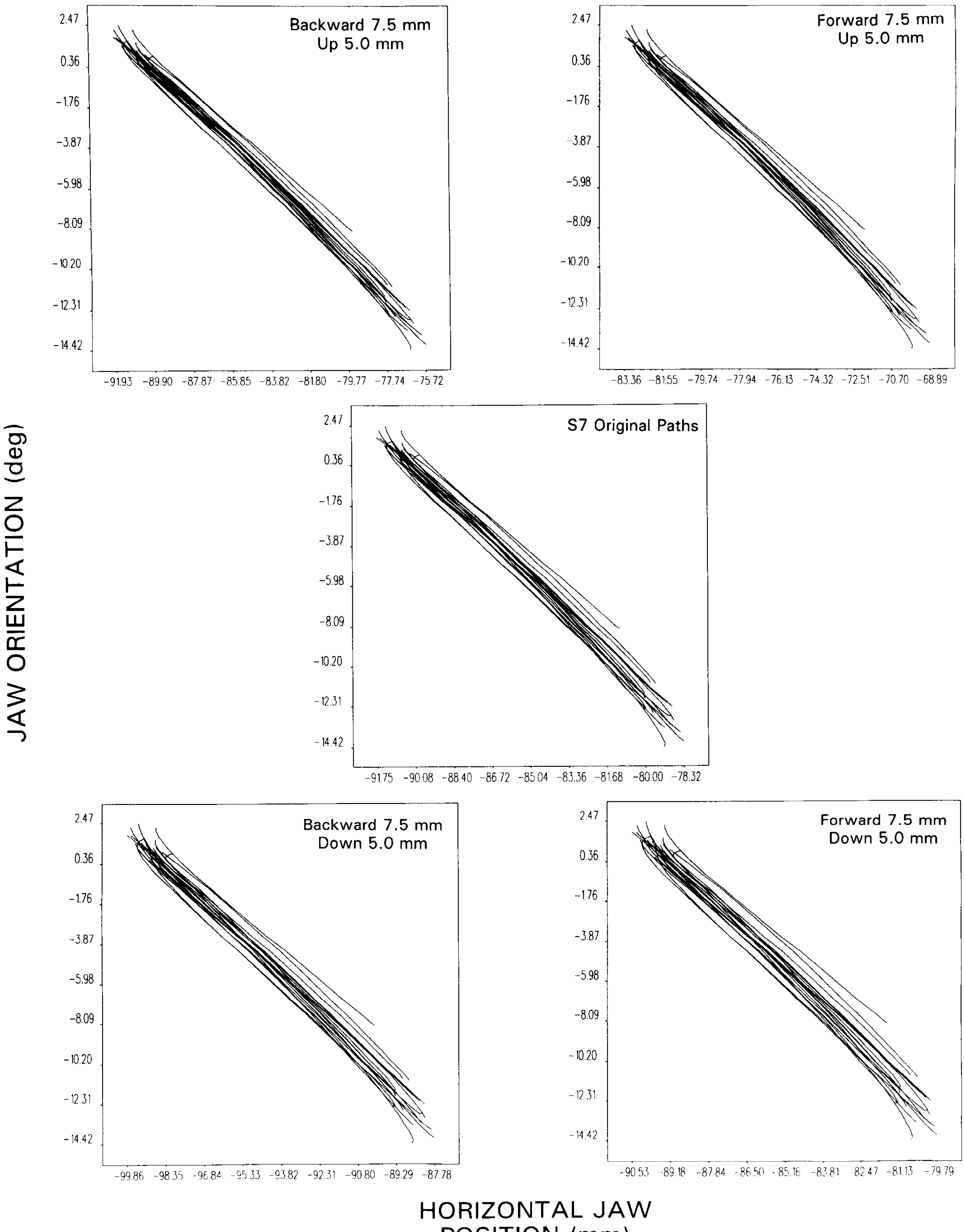

FIG. 15. The effects on jaw motion paths of error in locating the position of the condyle center. The "position" of the condyle center was shifted to cover a range of 1.5 cm in the vertical direction and 1 cm in the horizontal. The re-calculated paths are shown.

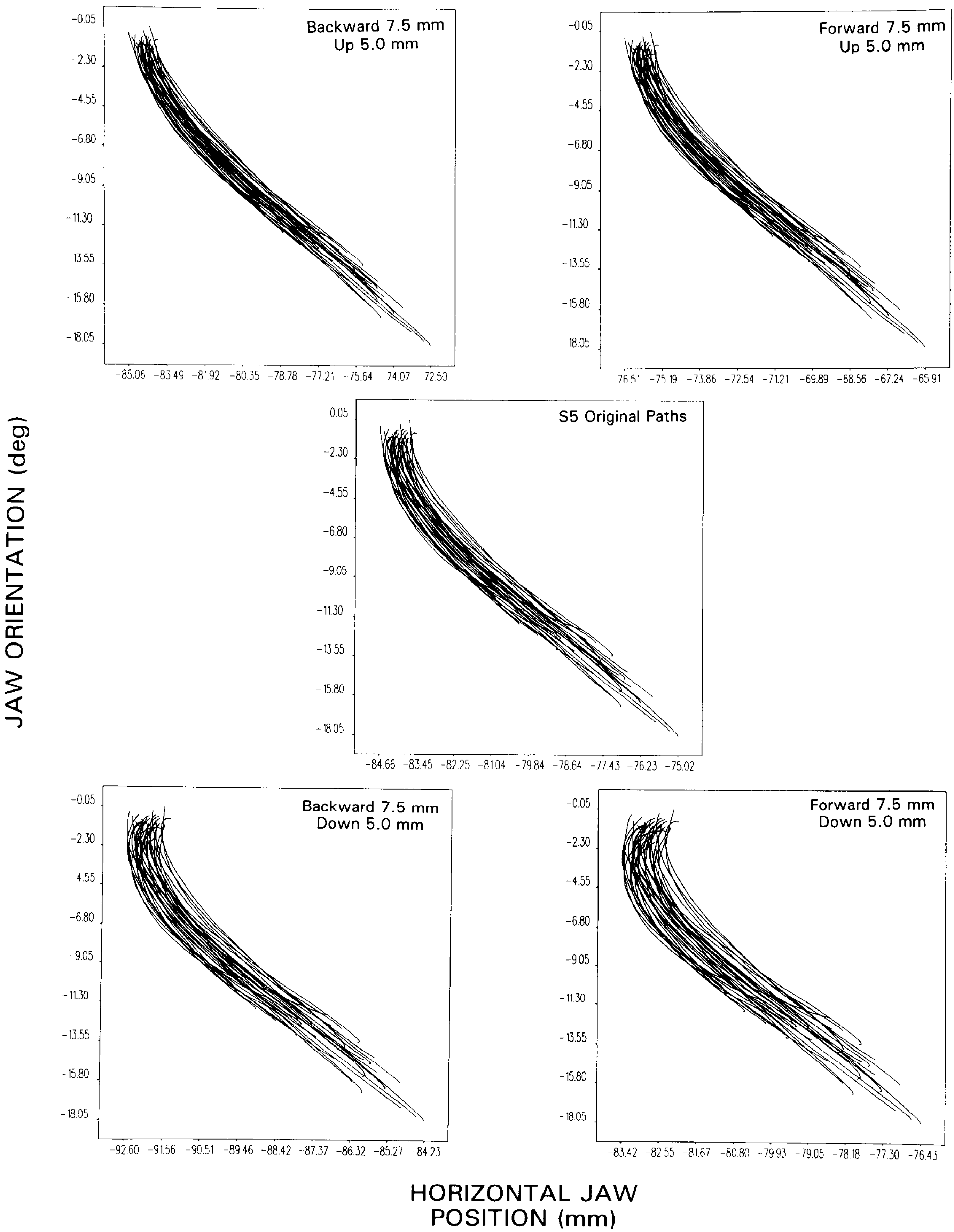

FIG. 16. The effects of shifting the position of the condyle center on jaw paths in joint coordinates. See Fig. 15 and text for details.

and pronation or supination can be produced alone or in combination. In addition, recruitment thresholds and EMG activity levels both suggest that neural commands may be organized to control motion in individual degrees of freedom (df) and may be superimposed to produce combined movements (Buchanan et al. 1986; Sergio and Ostry 1994; van Zuylen et al. 1988). For example, EMG activity in muscles such as medial triceps is greatest during combined isometric elbow torques in the valgus (external rotation about the humerus) and extension directions, less in extension or valgus alone, and less still in valgus and flexion directions (Buchanan et al. 1986). In biceps brachii and pronator teres, the amplitude of the agonist burst is greatest when the muscle acts as agonist in 2 df, less when the muscle acts as an agonist in a 1-df movement alone and still less when the muscle serves as agonist in 1 df and antagonist in the other (Sergio and Ostry 1994). Similarly, muscles, such as pronator teres, have motor units whose recruitment thresholds depend on motion in 2 df. For example, when subjects maintain a pronation torque while producing a flexion torque, motor unit recruitment thresholds in pronator teres are less than when subjects maintain a supination torque while producing a flexion torque. Thus, recruitment thresholds are less and EMG activity is greater when muscles act as agonists in 2 df than when they act as an agonist in 1 df and antagonist in the other. These findings suggest that both thresholds and EMG levels reflect a net contribution to motion in relevant degrees of freedom.

The data presented here bear on the issue of whether there is a pattern generator for chewing in humans (see Luschei and Goldberg 1981 for review). Although they do not rule out this possibility, they suggest that if one exists it would have to be of considerable complexity and of a highly individual nature. For example, when chewing rate is increased, the magnitudes of rotation and horizontal translation decrease for some subjects and increase for others (Fig. 5). When subjects chew at normal rates, the magnitude of horizontal translation varies widely with respect to the magnitude of rotation (Fig. 4). In addition, although rotation and horizontal translation are correlated on a trial by trial basis, vertical translation is correlated with rotation for some subjects but not for others (Fig. 8). Variability such as this does not seem compatible with the pattern generation concept.

The data presented here are consistent with a joint-based control strategy. However, it would seem essential, in both speech and mastication, that movements are also organized at the level of the oral cavity. Speech movements must in some way be specified in terms of vocal tract shapes since these are related directly to the acoustical output. Similarly, characteristics of bite force must be specified in mastication. The finding that variability in tongue position is less in acoustically relevant directions (Perkell and Nelson 1985) is consistent with the specification of speech movements in oral cavity coordinates, as is evidence in mastication that the direction of the bite force can be controlled (e.g., Osborn and Mao 1993; van Eijden et al. 1990).

To summarize, we have shown that jaw movements in joint coordinates are generally characterized by straight line paths. Both the slopes and the intercepts of these paths may vary indicating that the nervous system can control the equilibrium jaw orientation, the equilibrium jaw position, and their combination. However, several issues are unresolved. These include the control of vertical jaw position, the conditions that give rise to nonlinearities in jaw motion paths, the conditions that give rise to slope and intercept changes in both mastication and speech, and the relationship between the control of jaw position and orientation at the level of the temporomandibular joint and the control of jaw position in oral cavity coordinates.

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