Functional Properties of Neurons in the Primate Tongue Primary Motor Cortex During Swallowing

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Martin, Ruth E., Gregory M. Murray, Pentti Kemppainen, Yuji Masuda, and Barry J. Sessle. Functional properties of neurons in the primate tongue primary motor cortex during swallowing. J. Neurophysiol. 78: 1516–1530, 1997. Recent studies conducted in our laboratory have suggested that tongue-MI plays an important role in the generation and fine control of voluntary tongue movements in the primate. However, the possible involvement of tongue-MI in semiautomatic tongue movements, such as those in swallowing, remains unknown. Therefore the present study was undertaken in attempts to address whether tongue-MI plays a role in the semiautomatic tongue movements produced during swallowing. Extracellular single neuron recordings were obtained from tongue-MI, defined by intracortical microstimulation (ICMS), in two awake monkeys as they performed three types of swallowing (swallowing of a liquid bolus after successful tongue task performance, nontask-related swallowing of a solid bolus, and nontask-related swallowing of a liquid bolus) as well as a trained tongue-protrusion task. Electromyographic activity was recorded simultaneously from various orofacial and laryngeal muscles. In addition, the afferent input to each tongue-MI neuron and ICMS-evoked motor output characteristics at each neuronal recording site were determined. Neurons were considered to show swallowing and/or tongue-protrusion task-related activity if a statistically significant difference in firing rate was seen in association with these behaviors compared with that observed during a control pretrial period. Of a total of 80 neurons recorded along 40 microelectrode penetrations in the ICMS-defined tongue-MI, 69% showed significant alterations of activity in relation to swallowing of a liquid bolus, whereas 66% exhibited significant modulations of firing in association with performance of the trained tongue-protrusion task. Moreover, 48% showed significant alterations of firing in relation to both swallowing and the tongue-protrusion task. These findings suggest that the region of cortex involved in swallowing includes MI and that tongue-MI may play a role in the regulation of semiautomatic tongue movement, in addition to trained motor behavior. Swallow-related tongue-MI neurons exhibited a variety of swallowing-related activity patterns and were distributed throughout the ICMS-defined tongue-MI at sites where ICMS evoked a variety of types of tongue movements. These findings are consistent with the view that multiple efferron fields for the production of tongue movements are activated in swallowing. Many swallow-related tongue-MI neurons had an orofacial mechanoreceptive field, particularly on the tongue dorsum, supporting the view that afferent inputs may be involved in the regulation of the swallowing synergies.

INTRODUCTION

The region of the primate primary motor cortex from which tongue movements are evoked by intracortical microstimulation (ICMS) has been designated the ICMS-defined tongue primary motor cortex or “tongue-MI” (Murray and Sessle 1992a). Recent studies conducted in our laboratory have suggested that tongue-MI plays an important role in the generation and fine control of voluntary tongue movements (Murray and Sessle 1992b,c; Murray et al. 1991). Specifically, Murray et al. (1991) showed that reversible inactivation by cooling of the primate face motor cortex, including tongue-MI, significantly reduced the successful performance of a trained tongue-protrusion task by monkeys. Consistent with this finding, single neurons located at tongue-MI sites exhibited activity patterns that were related to a trained tongue-protrusion task but not to a trained biting task (Murray and Sessle 1992b,c).

Whereas tongue-MI has been implicated in the control of voluntary tongue movements, the extent to which tongue-MI also plays a role in the regulation of semiautomatic tongue movements, such as those produced during swallowing, remains unclear. Mounting evidence from cortical ablation, cortical stimulation, functional neuroimaging, and cortical recording studies points to the likelihood, however, that the lateral pericentral cerebral cortex may play a prominent role in swallowing (Aziz et al. 1996; Carpenter 1989; Doty 1968; Hamdy et al. 1996; Lang et al. 1994; Martin et al. 1995; Martin and Sessle 1993; Miller 1982; Sessle et al. 1995a). For example, reversible inactivation or unilateral or bilateral ablation of the anterolateral frontal cortex was reported to suppress swallowing and chewing elicited by electrical stimulation of the pons in the anesthetized rabbit (Sumi 1972). In awake monkeys, bilateral ablation of the lateral precentral gyrus disrupts the transport of ingested material posteriorly through the oral cavity (Larson et al. 1980). Similarly, bilateral ablation of the face area of the primate precentral cortex, including Brodmann’s areas 4 and 6 (Luschei and Goodwin 1975), and of the more laterally located cortical masticatory area (CMA) (Lund and Lamarre 1974) was reported to give rise to masticatory deficits. Recent studies from our laboratory have shown that reversible inactivation by cooling of the lateral pericentral cortex results in a reduction of the incidence of swallowing after chewing as well as alterations in swallow- and chewing-related electromyographic (EMG) patterns in awake monkeys (Narita et al. 1995; Sessle et al. 1995b).

Cortical stimulation studies also have pointed to a prominent role for the lateral pericentral cerebral cortex in swal-
owing. Repetitive electrical stimulation of regions of the anterolateral frontal and lateral pericentral cortex was shown to evoke swallowing in a number of species, including man (Car 1970; Martin et al. 1993, 1995; Miller and Bowman 1977; Penfield and Rasmussen 1950). This evoked swallowing frequently is accompanied by rhythmic chewing-like movements; the latter also can be elicited from more widespread cortical areas (Huang et al. 1989a; Lund and Lamarre 1974; Sumi 1969). Electrical stimulation of the anterolateral frontal and lateral precentral cortex also has been reported to facilitate swallowing elicited by other means, for example, by stimulation of the superior laryngeal nerve (Sumi 1969) or pons (Sumi 1972), and to give rise to evoked potentials in certain medullary "swallow-related" neurons (e.g., Amri et al. 1991; Car 1973).

Single neuron recording studies in monkeys have shown that some neurons within the lateral precentral cortex, including Brodmann’s areas 4 and 6, and the CMA, exhibit activity patterns related to the orofacial movements executed during ingestion, licking, food transport, mastication, and/or swallowing (Hoffman and Luschei 1980; Kubota and Niki 1971; Lund and Lamarre 1974; Luschei et al. 1971; Murray and Sessle 1992b). For example, Luschei et al. (1971) reported that many hundreds of neurons in Brodmann’s areas 4 and 6, which failed to show modulation of activity in relation to a trained biting task, exhibited phasic alterations of firing in association with rhythmic ingestive movements. Moreover, with regards to tongue-MI, Murray and Sessle (1992b) observed that some tongue-MI neurons that were active in relation to a trained tongue-protrusion task also exhibited rhythmic bursting activity that appeared to be related to the licking and swallowing of a juice reward after successful tongue-protrusion task trials performed by monkeys.

Taken together, these studies implicate overlapping regions of the cerebral cortex in swallowing and in a number of related ingestive and alimentary functions such as sucking and mastication. We chose to examine specifically the role of tongue-MI in swallowing for several reasons. First, our previous observations in awake monkeys that some tongue-MI neurons appear to show modulated activity during ingestive movements and that swallowing can be evoked by ICMS of MI (Martin et al. 1993, 1995; Sessle et al. 1995a) and may be disrupted by cold block of the ICMS-defined swallow cortex including the lateral portion of tongue-MI (Sessle et al. 1995b) implicated tongue-MI in the control of swallowing. Second, given the previous findings of Murray et al. (1991) and Murray and Sessle (1992b,c) suggesting a prominent role for tongue-MI in voluntary tongue movements, an investigation of tongue-MI in swallowing would afford the opportunity to clarify and compare the role of this cortical region in semiautomatic versus voluntary motor behaviors. Finally, tongue movements are critical to several components of the swallowing sequence including bolus formation, bolus transport through the oral cavity, and bolus propulsion through the pharynx (for reviews, see Cunningham et al. 1991; Miller 1982). As such, a fuller account of the neural mechanisms mediating swallow-related tongue movement is essential to a comprehensive understanding of swallowing.

Therefore the aims of the present study were: 1) to determine whether neurons within the ICMS-defined tongue-MI significantly alter their firing rates in relation to swallowing; 2) to determine whether tongue-MI neurons that exhibit swallow-related activity patterns also significantly alter their firing rates during a voluntary, trained tongue-protrusion task; 3) to compare the firing patterns and properties of single tongue-MI neurons in relation to the swallowing of a fruit juice reward after successful performance of a trained tongue-protrusion task and the swallowing of solid food or fruit juice that occurred outside of the trained tongue-protrusion task paradigm, and thereby determine whether the activity of tongue-MI neurons is differentially related to swallowing in different behavioral contexts; 4) to determine the ICMS effects at tongue-MI sites where neurons exhibiting swallow-related firing patterns are found and to relate these ICMS effects to the swallow-related neuronal firing patterns observed; and 5) to determine the mechanoreceptive field properties of tongue-MI neurons exhibiting firing patterns related to swallowing.

Some data from this study have been reported briefly (Martin et al. 1991, 1994, 1995; Murray and Sessle 1990; Sessle et al. 1995a).

Methods

This investigation employed two adult female monkeys (Macaca fascicularis: H5, H7; weight 2.5–3.5 kg) that were cared for according to the Guiding Principles of the American Physiological Society and the guidelines of the Canada Council for Animal Care (Guide to the Care and Use of Experimental Animals, vols. I and II). Many of the methods have been described in previous studies (Huang et al. 1988; Murray and Sessle 1992a–c; Murray et al. 1991). The animals were studied during an ongoing investigation of MI and CMA/swallow cortex that lasted 24 mo in monkey H5 and 11 mo in monkey H7. Periods of 8 wk (i.e., H5) and 6 wk (i.e., H7) were spent in microelectrode recordings (1 or 2 microelectrode penetrations per day) from MI. Single-neuron recordings were made from the tongue-MI in one hemisphere of monkey H5 and in both hemispheres of monkey H7 to examine the activity of neurons at ICMS-defined sites (Huang et al. 1988; Murray and Sessle 1992b) during swallowing of solid and liquid materials and during a trained tongue-protrusion task. EMG recordings were made simultaneously with single neuron recordings (see below). In addition, the afferent input of each neuron and ICMS-evoked motor output characteristics at each neuronal recording site were determined. Because the tongue-protrusion task and most aspects of the present methodology (e.g., animal preparation, surgery, and training, ICMS, single neuron and EMG recording, and mechanoreceptive field testing) were reported in our previous studies (see Huang et al. 1988, 1989a,b; Murray and Sessle 1992a–c; Murray et al. 1991; Sessle and Wiesendanger 1982), the following will focus primarily on methodological details not described in previous reports, namely, the experimental paradigms within which swallowing was examined and small variations in the details of surgery, training, and data analysis that apply only to monkey H7.

Training procedures and preliminary surgical procedures

TONGUE-PROTRUSION TASK AND TASK-RELATED SWALLOW. The tongue-protrusion task was the same as that previously described in detail by Murray et al. (1991) and Murray and Sessle (1992b,c). Briefly, the task required the monkey to protrude its tongue onto a force transducer that was affixed rigidly to a beam on the primate chair in front of the monkey. The transducer output controlled the vertical position of a cursor on a computer monitor located in front of the monkey. During each tongue-protrusion trial,
a computer-controlled baseline window appeared initially at the bottom of the computer screen and, after a pretrial period (PTP), was displaced instantaneously to a preset target-window level (equivalent to a force of 1.0 N for monkey H5 and 0.67 N for monkey H7) on the computer screen. This was the cue for the monkey to open its mouth and protrude its tongue symmetrically toward a conical force plate that was attached to the transducer. The force plate was located in the midline, 2 mm anterior to the most anterior portion of the upper lip, with its center level with the vermillion border of the upper lip. The monkey was required to move the cursor into the target window and then hold the cursor within the target window for a specified minimum holding phase.

The following periods were defined for the tongue protrusion task: a PTP (randomly varied between 1.0 and 1.5 s) during which the baseline window remained at the bottom of the screen; a dynamic phase: the period from the onset of significant rise in genioglossus (GG) EMG activity to the moment that the cursor entered the target window; a holding phase: the period from entry of the cursor into the target window to the end of the 1.0-s holding phase; a swallow, and a 50-ms period preceding the swallow (see Fig. 1A and description below). The task period was defined as the period composed of both the dynamic and holding phases.

A successful tongue-protrusion trial was defined as one that met the following criteria: the cursor remained within the baseline window during the 1- to 1.5-s PTP; the cursor exited the baseline window within 3 s of target window appearance; and the cursor remained within the target window for the specified minimum holding phase. A successful trial was rewarded at the termination of the holding phase with 0.4 ml of fruit juice that was delivered automatically to the monkey through a tube that opened at the apex of the force plate. The swallowing of the juice reward after a successful tongue-protrusion trial constituted a task-related swallowing trial. “Unsuccessful” trials were not rewarded. A minimum of seven successful tongue-protrusion trials was required for a neuron to be included in the data analyses.

NONTASK-RELATED SWALLOWING. Single-neuron and EMG recordings also were obtained from each monkey as it ingested and swallowed fruit juice or apple presented to it by one of the experimenters (i.e., nontask-related swallowing). The fruit juice was administered to the monkey through a graduated 10-ml syringe, the tip of which was placed on the labial surface of the maxillary incisors. The liquid bolus was administered at a standard rate of 1 ml/s. During each trial, a total volume of between 3 and 10 ml was administered. Therefore the monkey was required to swallow several times in succession to clear the entire volume of juice. A single swallow within this series constituted a nontask-related liquid-bolus swallowing trial; the number of these swallowing trials carried out during the study of a given neuron varied from 8 to 20. Standardized (1 cm³) pieces of apple also were presented to

![Graphs and diagrams showing electromyographic (EMG) activity associated with task-related swallow, nontask-related solid-bolus swallow, and nontask-related liquid-bolus swallow.](http://jn.physiology.org/)

**FIG. 1.** Electromyographic (EMG) activity associated with task-related swallow (A), nontask-related solid-bolus swallow (B), and nontask-related liquid-bolus swallow (C). A: cricothyroid (CT) and genioglossus (GG) EMG activity and force corresponding to one successful tongue-protrusion trial. ▲ “swallow onset” (see text for details). Traces show pretrial period and tongue protrusion followed by the licking and swallowing of a juice reward. Below, time-expanded diagram of task-related swallow shows 50-ms interval immediately preceding swallow onset, swallow-lick-related EMG burst, mean lick duration, and swallow duration (see text). B: CT and GG EMG activity associated with 1 nontask-related solid-bolus swallowing trial, ▲ swallow onset. Early increases in GG and CT activity are artifact associated with administration of the solid bolus to the monkey by the experimenter. C: CT and GG EMG activity associated with several nontask-related liquid-bolus swallowing trials, ▲ swallow onsets.
the monkey; one of the experimenters placed the apple between the monkey’s maxillary and mandibular teeth, typically contralateral to the recording microelectrode. The ingestion and swallowing of a single piece of apple constituted a nontask-related solid-bolus swallowing trial; the number of these trials obtained during the study of a given neuron ranged from 8 to 10.

For each nontask-related swallowing trial, a PTP was defined as an interval of between 1.0 and 1.5 s that occurred immediately before the swallowing of juice or chewing and swallowing of apple and during which the monkey was at rest and there were no EMG activity bursts in either GG or cricothyroid (CT).

To stabilize the head during both the tongue-protrusion task and task- and nontask-related swallowing trials, a headcap of dental acrylic was fixed to the skull while the animal was anesthetized deeply (Murray and Sessle 1990, 1992a; Murray et al. 1991) to allow the head to be centered mediolaterally with respect to the body, with the interaural line parallel to the floor and the Frankfort horizontal plane elevated 15° from the horizontal. When the tongue protrusion task could be performed by the awake monkey with at least a 50% success rate for 1 wk, the animal was anesthetized again and stainless steel cylinders were implanted over the lateral pericentral cortex. In monkey H5, chronic EMG electrodes were placed in GG, digastric, masseter, and the perilyrngeal musculature, usually contralateral to the recording microelectrode. In monkey H7, chronic EMG electrodes also were placed specifically in the CT muscle as a means of recording swallow-related laryngeal EMG activity.

Electrophysiological recording and intracortical microstimulation

Transdural microelectrode penetrations were made into the tongue motor cortex and extracellular single-neuron recordings and ICMS effects obtained as previously described (Murray and Sessle 1992a). Tongue-MI was defined as that contiguous precentral region within which short-train ICMS (T/S; 20 μA for monkey H5 and 30 μA for monkey H7, 35-ms duration train of 12 cathodal pulses, each pulse: 0.2 ms duration, and delivered at 333 Hz) could evoke twitch-like movements of the tongue. At each neuronal recording site, ICMS was delivered and the type and threshold of the evoked response was determined. ICMS was delivered after neuronal mechanoreceptive field testing and recording of movement-related neuronal activity had been completed (see below). Neuronal activity was monitored from a loudspeaker, an oscilloscope, and from an on-line computer display of the digitized force, EMG, and neuronal spike signals. Each neuron also was tested for a mechanoreceptive field by applying light tactile stimuli with hand-held probes and firm nonnoxious mechanical stimuli to the skin of the face and to the oral cavity (Murray and Sessle 1992a).

Data analysis

For monkey H5, force and EMG signals were digitized (EMG activity was full-wave rectified and smoothed; time constant 20 ms, sampling rate/channel: 200/s), and the intervals between neuronal spikes were stored with the use of a 68000 coprocessor in an IBM-compatible PC with an interface to CAMAC modules (Kinetic, Lockport, IL) for data analysis and display (Murray and Sessle 1992b). For monkey H7, force, EMG, and neuronal spike data were digitized (EMG activity full-wave rectified and smoothed; time constant 32 ms, sampling rate/channel: force 200/s, EMG 3125/s, neuronal spike event data 200/s) with the Cambridge Electronics 1401 data acquisition board and Spike2 analysis package.

DATA ANALYSIS FOR TONGUE-PROTRUSION TASK. As previously described (Murray and Sessle 1992b), digitized data were analyzed by aligning trials to the onset of the significant increase in GG activity after target window appearance. The onset of a significant increase in EMG activity was defined as the point in each trial at which the analog signal exceeded two standard deviations (SD) of the mean level of EMG activity during the PTP for the trial for ≥200 ms. Neurons were considered to be task related only if the neuronal firing frequency during the task period was statistically significantly different from that during the PTP of the same task (paired t-test; P < 0.05) and if the onset of neuronal activity occurred within 580 ms of the onset of GG EMG activity associated with the tongue-protrusion task (i.e., in effect, the onset of neuronal activity had to occur by the beginning of the holding phase of the task).

DATA ANALYSIS FOR SWALLOW. Identification of swallowing: Swallowing was identified on the basis of a characteristic EMG profile in GG (see RESULTS); in the case of monkey H7, a characteristic EMG profile in CT (see RESULTS and Fig. 1A); and for monkey H5, a slow wave potential change in the perilyrngeal EMG signal. In addition, swallowing was confirmed by direct visual observation of the monkey during the experimental session and by reviewing videotaped recordings of the monkey’s behavior, in particular the prominent and rapid elevation and subsequent descent of the larynx characteristic of swallowing (Miller 1982).

For both task- and nontask-related swallowing, swallow onset was defined as the point at which the level of GG EMG activity associated with swallowing exceeded, for ≥200 ms, 2 SD of the mean GG EMG activity that occurred during the PTP (see METHODS for definition of PTP). Swallow offset was defined differently for task- and nontask-related swallowing for the following reason. During the juice reward phase immediately after each successful tongue protrusion trial, swallowing was followed immediately by a lick; this swallow-lick sequence, which was consistent both within and between monkeys, was associated with a prolonged, double-peaked EMG burst in GG (mean duration 523 ± 76 ms; see Fig. 1A). The presence of a lick immediately after the task-related swallow also was confirmed by visual observation of the monkey’s extraoral tongue movements and by the observation that the force transducer was engaged as the monkey licked immediately after swallowing (see force recording in Fig. 1A). Therefore, for task-related swallowing, swallow offset was defined in the following manner. First, a mean lick duration was calculated as the mean of the first two licks that occurred immediately after delivery of the juice reward at the end of the tongue-protrusion task (see Fig. 1A). Swallow offset then was determined by subtracting this mean lick duration from the time at which the swallow-lick-related GG burst fell below 2 SD of the mean GG activity assessed during the PTP. In contrast, the nontask-related swallow was not followed by a lick. This was confirmed by direct observation of the monkey and by the observation that the GG burst associated with swallowing was single peaked (see Fig. 1) and was of significantly shorter duration (mean duration 245 ± 74 ms; t-test; P < 0.001) than the swallow-lick-related GG burst observed after trials of the tongue-protrusion task (see above). As such, the offset of the nontask-related swallow was defined as the time at which the swallow-related GG burst fell <2 SD of the mean EMG activity in GG during the PTP.

Criteria for swallow-related neuronal activity. For each tongue-MI neuron examined, mean firing rates were determined for the following intervals (see Fig. 1): the PTP (see definition above), a 50-ms interval immediately before the GG activity-defined swallow onset, and the interval between the GG activity-defined swallow onset and offset (as defined above). The 50-ms interval preceding swallow onset was examined as a means of determining whether tongue-MI neurons altered their firing rates in advance of swallowing. A 50-ms interval was employed because the average duration between the offset of the preceding lick and the onset of swallowing in the tongue protrusion task was ~100 ms and we
wanted to avoid the possibility of including neuronal activity that occurred during or immediately after this lick, possibly related to reaference, and because 50 ms was considered a sufficient duration to assess changes in neuronal firing rate related to driving muscles active in the earliest part of the swallow, such as GG (Lowe 1981; Lowe and Sessle 1973).

For each neuron, a repeated measures analysis of variance and post hoc comparisons (Duncan’s multiple range test; \( P < 0.05 \) considered statistically significant) were performed to determine whether the average rates of neuronal activity during these three intervals were significantly different. A swallow-related neuronal activity pattern was defined as a significant alteration of neuronal firing rate, relative to that during the PTP, during the 50-ms interval immediately preceding swallow onset, the swallow (i.e., the interval between swallow onset and offset), or both the 50-ms interval and the swallow.

RESULTS

**EMG activity patterns associated with swallowing**

Task- and nontask-related liquid- and solid-bolus swallowing was associated with characteristic EMG activity patterns (see Fig. 1) involving bursts in GG and CT, with the activity in GG preceding and overlapping in time that in CT. Table 1 provides a summary of the temporal features of these EMG patterns. For GG, the duration of EMG activity (i.e., measured from “swallow onset to swallow offset”): see METHODS) associated with the nontask-related solid-bolus swallow was significantly greater \( (P < 0.001) \) than that associated with the nontask-related liquid swallow and the task-related swallow. Further, the duration of GG activity during the nontask-related liquid bolus swallow also was significantly greater \( (P < 0.001) \) than that associated with the task-related swallow. Similarly, for CT, the duration of swallow-related activity (see METHODS) was significantly greater \( (P < 0.001) \) for the nontask-related solid-bolus swallow than the nontask-related liquid-bolus swallow. However, unlike GG, the duration of CT activity associated with the task-related swallow was greater \( (P < 0.001) \) than that associated with the nontask-related liquid swallow and was not significantly different from the nontask-related solid-bolus swallow.

We also compared the duration of swallow-related activity, from GG onset to CT offset, across swallowing conditions. The durations of swallow-related activity associated with the task-related swallow and the nontask-related solid swallow were both significantly greater \( (P < 0.001) \) than the duration of swallow-related activity during the nontask-related liquid-bolus swallow. The durations, from GG onset to CT offset, for the task- and nontask-related solid swallow were not significantly different.

Comparisons across muscles indicated that, for both the liquid and solid nontask-related swallowing conditions, the duration of GG activity was significantly greater \( (P < 0.001) \) than the duration of CT activity. However, for the task-related swallow, the duration of swallow-related activity in CT was greater than that in GG.

Regarding the relative timing of swallow-related GG and CT activities, the onset of GG activity preceded the onset of CT activity for 100% of the swallows examined. However, the latency between GG and CT onsets differed across the three swallowing conditions studied. Specifically, the latency between GG and CT onsets associated with the nontask-related liquid-bolus swallow was significantly greater \( (P < 0.001) \) than that for both the nontask-related solid swallow and the task-related swallow. The GG-to-CT onset latencies for the nontask-related solid swallow and the task-related swallow were not significantly different. In summary, both the durations of GG and CT swallow-related bursts and the relative timing of GG and CT swallow-related activity varied across the task- and nontask-related swallows.

**Tongue-MI neurons active in relation to swallowing and/or tongue protrusion**

The activity of a total of 80 single neurons recorded along 40 microelectrode penetrations in the ICMS-defined tongue-MI in three hemispheres of the two awake monkeys was studied during both the trained tongue-protrusion task and task-related swallowing. Of these 80 neurons, the activity of 17 also was studied during nontask-related swallowing of the solid and/or liquid bolus. A major finding of the present study was that, not only were many tongue-MI neurons related to the tongue-protrusion task, as previously reported (Murray and Sessle 1992b), but also many tongue-MI neurons showed activity related to swallowing. Further, some neurons showed both task- and swallow-related activity. Specifically, of the 80 neurons examined during the tongue-protrusion task and task-related swallowing, 53 (66%) exhibited significant alterations of firing rates in relation to the trained tongue-protrusion task. Further, of the 80 neurons, 55 (69%) showed altered firing in relation to task-related swallowing. Moreover, of the total of 80 neurons examined, 38 (48%) exhibited significant alterations of firing in relation to both the tongue-protrusion task and task-related swallowing. By comparison, 17 (21%) neurons showed altered activity in relation to task-related swallowing but not in relation to the tongue-protrusion task. Of the total of 80 neurons,

**TABLE 1. Temporal features of EMG activity associated with task- and nontask-related swallowing**

<table>
<thead>
<tr>
<th></th>
<th>Duration of GG Activity, ms</th>
<th>Duration of CT Activity, ms</th>
<th>Latency Between GG and CT Onsets, ms†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Task-related swallow</td>
<td>245* ± 74 (839)</td>
<td>352 ± 86 (131)</td>
<td>89 ± 47 (131)</td>
</tr>
<tr>
<td>Nontask-related liquid-bolus swallow</td>
<td>367 ± 116 (208)</td>
<td>229 ± 59 (98)</td>
<td>127 ± 59 (98)</td>
</tr>
<tr>
<td>Nontask-related solid-bolus swallow</td>
<td>430 ± 98 (141)</td>
<td>331 ± 85 (55)</td>
<td>91 ± 48 (55)</td>
</tr>
</tbody>
</table>

Values are means ± SD. Parentheses contain numbers of swallowing trials obtained that varied across task- and nontask-related conditions; CT data were unavailable for some swallowing trials. See text for statistical comparisons. EMG, electromyographic; GG, genioglossus; CT, cricothyroid. * Value refers to the duration of the swallow-lick-related EMG burst in GG minus the mean duration of the lick-related EMG burst in GG (see text for details). † Swallow-related EMG onset in GG preceded CT activity onset for 100% of the swallows examined.
10 were not related to either behavior. Figure 2 shows the activity of a single tongue-MI neuron that exhibited statistically significant alterations of firing rates in relation to both the tongue-protrusion task and the task-related swallow. This neuron was relatively silent during the pretrial period, showed a modest increase in firing during the tongue task (Fig. 2B) and a greater increase in firing during the 50-ms interval immediately preceding swallow onset (Fig. 2A and C). The neuron also exhibited increased activity immediately after the tongue protrusion and during the licking of the juice reward before swallowing but was silent during the lick immediately after the swallow. This neuron was recorded at a site where ICMS evoked tongue protrusion at a threshold of 12 μA.

Of the 17 neurons that were studied during the tongue-protrusion task and task- and nontask-related swallowing, most showed modulated activity related to the swallow. Overall, 14 showed activity related either to the solid- or liquid-bolus nontask-related swallow or both. Of 16 and 15 neurons that were examined during the solid- and liquid-bolus swallowing conditions, respectively, all those that did show altered firing in relation to the nontask-related swallow (i.e., 12 neurons for solid bolus, 10 for liquid bolus condition) also showed significantly altered activity associated with the task-related swallow. The activity of only three neurons (i.e., out of the total of 17 neurons) was not related to either the task- or nontask-related swallow. Further, of the 14 neurons that had activity related to the nontask- and

![Figure 2](https://example.com/f2.png)

**FIG. 2.** Activities of a single tongue motor cortex (tongue-MI) neuron recorded from monkey H7 during 7 task-related swallowing trials (A) and 7 successful tongue-protrusion task trials (B). A time-expanded display of A is shown in C. For each trial, force and EMG activity in GG also are shown. Traces have been aligned to the significant increase in GG activity associated with the task-related swallow (A) and tongue-protrusion task (B). Figureine to right of B indicates threshold tongue-protrusive movement (T = 12 μA) evoked by intracortical microstimulation (ICMS) at the neuronal recording site.
FIG. 3. Activity of a single tongue-MI neuron recorded from monkey H7 during 7 successful tongue-protrusion task trials with task-related swallowing of juice reward (A). Time-expanded display of A is shown in B. Force and CT and GG EMG activity also are shown. Traces have been aligned to significant swallow-related increase in GG corresponding to swallow onset. Figurine at top indicates threshold tongue movement (T = 15 μA) produced by ICMS at the neuronal recording site.

the task-related swallow, 6 also were related to the tongue-protrusion task, whereas 2 of the neurons were unrelated to all swallowing conditions as well as the tongue-protrusion task.

Swallow-related neuronal activity patterns

Single swallow-related tongue-MI neurons exhibited one of three swallow-related neuronal activity patterns, as summarized in Table 2. Of the 55 tongue-MI neurons that showed significant alterations of activity in relation to task-related swallowing, 30 (55%) showed a significant alteration of firing during either the 50-ms interval preceding swallow onset (20 neurons) or during the swallow (10 neurons) but not during both. For 22 of these 30 neurons, the altered activity was reflected in a significant increase in mean firing rate (e.g., Fig. 2). The remaining 25 (45%) of the 55 swallow-related neurons showed significant alterations of firing during both the 50-ms interval preceding swallow onset and during the swallow; 13 showed a significant decrease during both periods (e.g., Fig. 4), whereas 9 showed a significant increase that spanned both periods (e.g., Fig. 3). Three of the 25 neurons showed both decreased and increased activity in relation to swallowing, that is, decreased activity during the 50-ms interval and increased activity during the swallow (i.e., 2 neurons) or the reverse (1 neuron).

Within these three groups of neurons exhibiting different swallow-related activity patterns, the proportions of neurons that also exhibited tongue-protrusion task-related activity were determined, as summarized in Table 2. It can be seen that the great majority of neurons that showed modulated activity during the 50-ms interval preceding swallow onset and/or during the swallow also showed tongue-protrusion task-related activity. It also should be noted that, of the 38 tongue-MI neurons that showed altered firing in relation to both the task-related swallow and the tongue-protrusion task, 32 (84%) showed a significant increase in activity during the tongue protrusion, regardless of the particular temporal pattern or direction (i.e., increase or decrease) of activity exhibited in relation to swallowing. For the 14 tongue-protrusion task-related neurons that showed alterations of firing during the 50-ms interval preceding swallow onset only, 50% exhibited the same direction of modulation during both conditions. However, for the nine tongue-task-related neurons that showed alterations of firing during the swallow only, 78% showed the same direction of modulation during both.

Comparison of neuronal activity patterns in relation to task- and nontask-related swallow

It has been noted above that, of 16 tongue-MI neurons recorded during the nontask-related solid-bolus swallow and
task-related swallow, 12 showed altered activity in relation to both types of swallow. Of these, 50% exhibited similar patterns of neuronal activity during the task- and nontask-related swallow, that is, increased or decreased firing during the 50-ms interval, during the swallow, or during both. A similar proportion (50%) of the 10 tongue-MI neurons that showed altered activity during both the nontask-related liquid-bolus and the task-related swallow exhibited similar patterns of neuronal activity in association with swallowing. Furthermore, of tongue-MI neurons with activity related to both solid and liquid nontask-related swallows, 38% showed similar patterns of activity.

Figure 4 shows the activity of a neuron that showed similar patterns of neuronal activity in relation to the task-related (Fig. 4, A and D) and nontask-related solid-bolus (Fig. 4, B and E) and liquid-bolus (Fig. 4, C and F) swallows. This neuron was tonically active during the PTP and did not exhibit a significant alteration of firing during the tongue-protrusion task but showed a significant decrease in mean firing rate during the 50-ms interval preceding swallow onset.
TABLE 3. Associations between ICMS-evoked motor effects and swallow and tongue-protrusion task relations

<table>
<thead>
<tr>
<th>ICMS-evoked tongue movement</th>
<th>Task-Related Swallow</th>
<th>Tongue-Protrusion Task</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Related Unrelated</td>
<td>Related Unrelated</td>
</tr>
<tr>
<td>Anteroposterior*</td>
<td>16 10</td>
<td>16 10</td>
</tr>
<tr>
<td>Lateral</td>
<td>19 9</td>
<td>20 8</td>
</tr>
<tr>
<td>Complex†</td>
<td>20 6</td>
<td>17 9</td>
</tr>
</tbody>
</table>

ICMS, intracortical microstimulation. * Includes both tongue protrusion and tongue retraction. † Includes depression of tongue dorsum, transverse bilateral contraction, elevation of anterior one-third of tongue, combinations of these movements, and composite movements involving tongue protrusion and lip contraction.

(χ², P > 0.05) and also equally likely to show tongue-protrusion task-related activity (χ², P > 0.05; see Fig. 5). That is, the proportions of neurons related to the swallow were not significantly different when these proportions were compared across the different categories of ICMS-evoked tongue movement; the same applied for neurons related to the tongue-task.

Of the total of 55 tongue-MI neurons that showed swallow-related activity, 20 (36%) were recorded at sites where ICMS evoked tongue movements at low threshold, that is, thresholds of 5 μA. Further, all major types of tongue movement (i.e., protrusion/retraction, lateral, and complex) were evoked at these low thresholds. Of the 20 neurons recorded at low-threshold ICMS sites, 17 (85%) were neurons that altered their firing rates in advance of the GG-defined swallow onset.

FIG. 5. Spatial distribution within tongue-MI of the left hemisphere of monkey H5 of penetration tracks within which neurons were found that exhibited significant alterations of firing in relation to the task-related swallow, tongue-protrusion task, both the task-related swallow and tongue-protrusion task, or neither the swallow nor tongue-protrusion task. Swallow-related *, task-related swallow only; Cen., central sulcus. Inset: continuous line encloses stimulation/recording sites from which tongue movements could be evoked by ICMS; ●, sites of microelectrode penetrations in precentral and postcentral cortex. Camera lucida drawings of parasagittal histological sections corresponding to planes “a”, “b”, and “c” are shown (right). Electrode penetration tracks in each plane have been superimposed on the corresponding histological sections and the task and/or swallow relations of neuron recorded at each site are indicated. → in b indicates an electrolytic lesion. Rostral-most tracks in planes a and c are ICMS penetrations within tongue-MI along which neurons were not recorded. Rostral- and caudal-most tracks seen in drawing of plane b are ICMS tracks used to define the border of tongue-MI.
Mechanoreceptive field properties of swallow-related and tongue-protrusion task-related tongue-MI neurons

Of the 80 tongue-MI neurons examined during the task-related swallow and the tongue-protrusion task, 79 were tested for afferent inputs. Of these, 53 (67%) showed a mechanoreceptive field: 17% had ipsilateral, 28% contralateral, and 55% bilateral afferent inputs. In 44 (83%) of these 53 cases, the mechanoreceptive field was found on the superior tongue surface; the remaining neurons had a mechanoreceptive field on the lip, soft palate, hard palate, modiolus, tongue and soft palate, or tongue and upper lip (e.g., Fig. 6). One neuron that had a mechanoreceptive field on the soft palate also responded to passive jaw opening. Neurons that did or did not exhibit a mechanoreceptive field were equally likely to exhibit significant alterations in activity in association with task-related swallowing (Fisher’s exact test, $P > 0.05$) and equally likely to show tongue-protrusion-task-related activity (Fisher’s exact test, $P > 0.05$). Furthermore, neurons with a mechanoreceptive field on the tongue surface and those with mechanoreceptive fields localized to other structures were equally likely to show swallow-related activity (Fisher’s exact test, $P > 0.05$) and also equally likely to be related to the tongue-protrusion task (Fisher’s exact test, $P > 0.05$). Note from Fig. 6 that ICMS at the recording sites of several “swallow-related” neurons with a lingual mechanoreceptive field could evoke a variety of tongue movements.

DISCUSSION

The present study has shown that many tongue-MI neurons that altered their firing rates in relation to a voluntary orofacial movement, in the form of the trained tongue protrusion, also showed modulated activity in relation to swallowing. Some tongue-MI neurons that did not show activity related to the tongue-protrusion task also exhibited altered firing rates in relation to swallowing. The swallow-related tongue-MI neurons exhibited a variety of swallow-related activity patterns, many received orofacial afferent inputs especially from the superior tongue surface, and they were recorded at sites where ICMS evoked a variety of types of tongue movement such as protrusion, retraction, or depression of the tongue dorsum. We previously have reported that continuous-train ICMS at some sites within the primate lateral tongue-MI can evoke swallowing movements at short latency (Martin et al. 1993; Sessle et al. 1995a). These findings suggest the possibility that tongue-MI plays a role not only in the control of voluntary movements, such as trained tongue protrusion, but also in semiautomatic movements such as swallowing. Moreover, the variety of swallow-related firing patterns identified for swallow-related tongue-MI neurons and the variety of input-output properties found for sites within tongue-MI where swallow-related neurons were recorded suggest that, rather than simply playing a role in the activation of swallowing, tongue-MI may also be involved in the sensorimotor regulation of the swallow synergy.

Identification of swallowing

Our primary evidence for the occurrence of a swallow was a characteristic EMG activity profile that was generally similar across the three swallowing conditions examined in the present study. Both the task- and nontask-related swallow were associated with prominent bursts of activity in GG and CT or other perilaryngeal muscles; the onset of...
EMG activity in GG preceded that in CT by 89–127 ms. This profile, which is consistent with the characteristic swallow-related muscle activity patterns described in detail by previous investigators (e.g., Doty 1968; Dubner et al. 1978; Lowe 1981; Miller 1982), was not seen during the licking of juice after the tongue-protrusion task nor during chewing of the solid bolus during the nontask-related swallowing trials. The occurrence of a swallow also was indicated by the rapid elevation and subsequent descent of the thyroid cartilage (Miller 1982).

Although the patterns of swallow-related muscle activity were generally similar across the three swallow conditions, the nontask-related liquid swallow was characterized by a significantly shorter EMG burst duration in GG and CT and a significantly longer latency between GG and CT onsets compared with the nontask-related solid-bolus swallow. These findings are consistent with our previously reported findings of differences in the temporal features of swallows occurring in different behavioral contexts (Kemppainen et al. 1993). For example, nontask-related swallowing of liquid from a syringe was characterized by significantly shorter burst durations in GG and CT/thyrohyoid (TH), and a significantly longer latency from GG to CT/TH burst onset, compared with the swallowing of a raisin after mastication by the awake monkey. These findings of modulation in the duration and relative timing of EMG activity across swallowing conditions support the view (Dodds et al. 1988; Dubner et al. 1978; Kahrilas et al. 1993) that certain aspects of the timing of the swallow-related muscle synergy, both within and across muscles, can vary as a function of bolus characteristics and/or behavioral context.

Another difference in the temporal features across the three swallowing conditions in the present study was that the duration of GG swallow-related activity associated with the nontask-related swallow was significantly longer than that associated with the task-related swallow. This difference may reflect the different bolus volumes employed in the nontask-related (i.e., 10 ml at 1 ml/s) and task-related (i.e., 0.4 ml) swallow, based on evidence from previous human studies showing volume effects on oropharyngeal swallowing patterns (e.g., Kahrilas et al. 1993; Martin 1991; and see below). Alternatively, this difference may have reflected the method by which we defined swallow offset for the task- and nontask-related swallows. That is, because the task-related swallow was followed immediately by a lick, swallow duration was defined as the mean duration of the swallow-lick–related EMG burst minus the mean lick duration. Thus the duration of the EMG activity associated with the task-related swallow was somewhat shorter than that related to the nontask-related swallow duration where there was no lick immediately after the swallow and where the descending portion of the EMG envelope was included in the swallow duration.

**Involvement of motor cortex in swallowing**

Whereas voluntary movements of the body classically are considered to be controlled by supraspinal and suprabulbar structures including the primary motor cortex in particular, semiautomatic movements are thought to be generated and regulated primarily at the spinal and bulbar levels. In the case of swallowing, much of the circuitry for the control of swallow-related movements is thought to be located within and around the medullary swallowing center (for reviews, see Carpenter 1989; Jean 1990; Miller 1982; Sessle and Henry 1989). Although there is both electrophysiological and clinical evidence for an involvement of the lateral pericentral cortex particularly in the early oral stage of swallowing (for review, see Martin and Sessle 1993), there has been relatively little emphasis on the contribution of suprabulbar systems to the regulation of swallowing.

Previous cortical surface stimulation studies have indicated that swallowing can be evoked from a region of cerebral cortex lateral to MI (Miller and Bowman 1977); this area has been termed the swallowing cortex. However, our present finding that single neurons within tongue-MI showed swallow-related activity supports the view that a more extensive region of cortex, one that includes the primary motor cortex, is involved in the regulation of swallowing. Further, we have shown that continuous-train ICMS can evoke swallowing not only from a region immediately anterior and/or lateral to tongue-MI but also from some sites within the most lateral region of tongue-MI (Martin et al. 1993; Sessle et al. 1995a). These findings pointing toward an involvement of MI in swallowing are in keeping with our earlier data showing that continuous-train ICMS within face MI, as well as lateral to MI, can evoke other types of semiautomatic movements (e.g., chewing) in the awake monkey (Huang et al. 1989b).

**Role of tongue-MI in swallowing**

The sophistication required for the sensorimotor control of swallowing (e.g., Doty 1968; Miller 1982) is exemplified by the complexity, speed, and diversity of swallow-related tongue movements. Unlike the limb or jaw, the tongue lacks a rigid skeletal framework and behaves as a muscular hydraulic device that, is, a decrease in any one of its dimensions is associated with a corresponding increase in another dimension (Smith and Kier 1989). Although there is extensive literature on the role of the cortex in the movements produced by structures that have a skeletal framework, little is known about the higher central control of muscular hydrostats such as the tongue. Nevertheless, previous work from our laboratory (Murray and Sessle 1992a–c; Murray et al. 1991) has suggested an important role for tongue-MI in the control of tongue movements. For example, like limb-MI, tongue-MI is organized in discrete efferent zones for the production of subunits of tongue movement (Murray and Sessle 1992a). Further, certain of these efferent zones are activated during a trained tongue-protrusion movement (Murray and Sessle 1992b). In the present study, tongue-MI neurons that exhibited swallow-related activity also were distributed throughout the ICMS-defined tongue-MI. Furthermore, swallow-related neurons were recorded at sites where ICMS evoked, at low threshold (i.e., 5 μA), all major types of tongue movement, that is, protrusion/retrusion, lateral movements, or complex movements such as depression of the tongue dorsum or transverse bilateral contraction. In addition, swallow-related tongue-MI neurons showed a variety of swallow-related activity patterns. Taken together with our previous results, these findings are consistent with the
view that multiple, discrete efferent zones for the production of elemental tongue movements are activated during swallowing and that the combined activation of different efferent zones could provide a basis for the complexity of tongue movements in swallowing. This suggestion is in keeping with Smith and Kier (1989) that a muscular hydrostat could produce a virtually limitless range of movements.

Swallow-related MI neuronal activity patterns

The variety of swallow-related activity patterns found for tongue-MI neurons may reflect the fact that the neurons represented different types of cortical neurons, for example, corticobulbar projection neurons, cortical interneurons, and corticocortical association neurons involved in driving swallow-related movements or responding to movement-evoked afferent inputs or in some other form of sensorimotor integration related to swallowing. Future studies should be aimed at examining the linkages between neuronal activity and the activity of specific muscles with the use of techniques such as spike-triggered averaging (Fetz and Cheney 1980). It is nonetheless of interest that approximately one-third of the swallow-related tongue-MI neurons examined in the present study showed altered activity only during the interval immediately preceding the GG EMG-defined swallow onset, that is, in advance of the swallow. Thus it is likely that these neurons may be involved in driving tongue motor units in swallowing rather than their activity being, for example, simply a reflection of reafference. Furthermore, 85% of these swallow-related neurons, which modulated their firing in advance of swallow onset, were located at low-threshold (i.e., 5 μA) ICMS tongue-MI sites; these neurons may well have been cortical output neurons given that corticomotoneuronal and pyramidal tract neurons are more likely to be found at low-threshold ICMS sites (Buys et al. 1986; Lemon et al. 1986; see also Cheney and Fetz 1985). This interpretation also is in keeping with previous anatomic evidence for the existence of direct projections from the caudal part of the lateral precentral cortex to the hypoglossal nucleus (Kuypers 1958a,b). Our finding that some tongue-MI units fired in advance of the GG-defined swallow onset is of particular interest in so far as GG has been shown to be among the earliest muscles activated in the oral phase of swallowing (Lowe and Sessle 1973). As such, it is possible that these early firing tongue-MI neurons could be involved in the cortical initiation of swallowing, including the driving of specific muscles such as GG. This possibility is further supported by our previous finding that swallowing can be evoked by ICMS applied at tongue twitch output sites (Martin et al. 1993; Sessle et al. 1995a). Nonetheless, other swallow-related tongue-MI neurons were activated during the swallow itself, and so, these neurons may initiate or drive motor units later in the swallow synergy, such as those associated with posterior tongue, pharyngeal, or laryngeal muscle activity during the late oral or pharyngeal stage of the swallow.

The present study also showed that, for neurons recorded during task- and nontask-related swallowing, all neurons that showed activity associated with the nontask-related swallow also showed activity related to the task-related swallow. Further, those that did not exhibit task-related swallow activity also were not activated in relation to the nontask-related swallow. These findings suggest a consistency across the three swallowing conditions examined in terms of the possible involvement of tongue-MI. However, we also found that, for at least half the tongue-MI neurons examined, the different types of swallows were associated with different patterns of neuronal activity. These different neuronal firing patterns may have been related to differences in the durations and relative timing of swallow-related EMG bursts across swallowing conditions.

Tongue-MI neuronal activity in licking and/or chewing

Some tongue-MI neurons that showed activities related to swallowing, and the tongue-protrusion task also showed activity in relation to the semiautomatic movements of licking and/or chewing. One possible interpretation for this finding is that the tongue movements involved in swallowing and tongue protrusion are not specific to these behaviors but rather, also are incorporated into the movement sequence of licking and/or chewing. Thus a given tongue-MI neuron may be activated during both activities because the same movement subunit is recruited. The population of activated tongue-MI units presumably would be distinct, however, underlying the distinct tongue movement sequences seen in, for example, swallowing, licking, and chewing (Dubner et al. 1978; Hiiemae and Crompton 1985; Thexton and McGarrick 1988, 1989). Another interpretation is that the activity of these tongue-MI neurons in both swallowing and licking or chewing reflects the need for a close neuronal integration of control of these various motor activities. This is also consistent with our previous finding of an extensive overlap of the ICMS-defined swallow cortex and cortical masticatory area (Martin et al. 1993; Sessle et al. 1995a).

Contribution of somatosensory inputs

The data describing the mechanoreceptive afferent input to tongue-MI in the present study are consistent with our previous descriptions (Murray and Sessle 1992a) in terms of the proportion of recorded neurons with identified mechanoreceptive fields and the locations of these fields. The present study confirmed that tongue-MI receives a substantial sensory input from intraoral mechanoreceptive fields, in particular on the tongue dorsum. Our finding that the majority of swallow-related tongue-MI neurons were characterized by a mechanoreceptive field on the tongue dorsum is consistent with the view that oral mechanosensory inputs are important in the regulation of swallow-related orofacial movements in so far as such inputs provide information regarding the bolus as it passes through the uppermost parts of the alimentary and respiratory tracts. The likelihood that such afferent information plays an important role in swallowing is supported by the findings that certain aspects of the swallow, including the amplitude and velocity of tongue movements (Hamlet 1989; Kahrilas et al. 1993; Martin 1991), the magnitude of hyoid movement (Dodd et al. 1988), and opening of the upper esophageal sphincter (Kahrilas et al. 1988), can be modulated by bolus characteristics.

It is still unclear the extent to which movement-related
activity patterns of motor cortical neurons (whether in limb-MI or face-MI) reflect inputs from central sites or peripheral receptors (i.e., reafferentation). Nevertheless, there are several lines of evidence supporting the view that the movement-related activity patterns associated with swallowing were not simply a result of reafference or other peripheral input. First, not all swallow-related tongue-MI neurons had detectable orofacial mechanoreceptive fields. Second, as discussed above, a substantial proportion of swallow-related tongue-MI neurons fired in advance of the GG EMG-defined swallow onset, and so it is unlikely that these activity patterns were exclusively due to reafference. Finally, other studies in our laboratory have demonstrated a gating of somatosensory inputs to face-SI neurons immediately preceding and during the monkey’s performance of the tongue-protrusion or biting tasks (Lin and Sessle 1994). This suggests the possibility that some input to face-MI also is suppressed, given that face-SI is a major source of input to face-MI (Dubner et al. 1978; Huang et al. 1989a; Jones 1986; Murray and Sessle 1992a). It is possible that, as suggested for limb-MI, afferent inputs to face-MI are modulated during orofacial movements so that only selected inputs useful in guiding the movement or in adapting the movement to an altered orofacial environment gain access to MI. All these lines of evidence support the contention that movement-related activity patterns may not simply be a result of reafference arising because of the movement performed.

Implications for motor cortex in voluntary and involuntary movements

Motor cortex generally is considered to play a primary role in the generation of voluntary movement (Armstrong 1986; Evarts 1981; Humphrey 1986; Lemon 1988) and not a major role in the generation of semiautomatic movements. However, our finding of swallow-related tongue-MI neurons, many of which also were related to the tongue-protrusion task, is consistent with our previous finding that some face-MI neurons show modulated firing in relation to the tongue task and to GG activity during mastication (Sessle et al. 1995a). These findings indicate that tongue-MI may participate in semiautomatic movements as well as trained tongue motor tasks and are of particular interest in relation to information on the role of the limb-MI in locomotion. For example, studies in awake cats have shown that the activity of some limb-MI neurons is correlated only weakly with self-paced (treadmill) locomotion but is modulated substantially more when the animal adjusts its gait to negotiate obstacles during locomotion (Drew 1988; Marple-Horvat et al. 1993). These observations have been taken to support the view that limb-MI modifies the step cycle in light of incoming sensory inputs that reflect changing environmental conditions. This is done by superimposing a transcortical modulation of subcortical locomotor networks that modifies muscle activity patterns during the step cycle without disrupting the overall locomotor rhythm.

In a similar fashion, face-MI has been thought to superimpose a repertoire of specific motor synergies principally on subcortical circuits responsible for the basic timing and sequencing of muscle activity of semiautomatic movements (Dubner et al. 1978; Lund and Enomoto 1988; Martin and Sessle 1993). Indeed, in agreement with the findings of Drew (1988) above, Hoffman and Luschei (1980) found that most biting task-related MI neurons did not exhibit a strong relation with chewing. This led Evarts (1986) to the general conclusion that MI plays a major role in controlling operantly conditioned movements and a minor role in the control of semiautomatic movements involving the same muscles. This view, however, may need to be reassessed in light of our present data and previous findings (Sessle et al. 1995a) of a substantial number of tongue-MI neurons that exhibit significant alterations in their activity patterns in relation to both the tongue-protrusion task, an operantly conditioned movement, and the semiautomatic movement sequences of swallowing or chewing. However, any revision of Evarts’ general conclusion of the relative roles of MI in operantly conditioned and semiautomatic movements involving the same muscles would be premature at this stage and further experiments addressing the relative roles of different types of MI neurons are needed.

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