

Cortical Control Mechanisms in Volitional Swallowing: The Bereitschaftspotential

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Summary: Objective: This research sought to identify a well-defined pre-motor potential, the Bereitschaftspotential (BP), as a manifestation of cortical contribution to the pre-motor planning of volitional swallowing. Methods: EEG data were collected from 20 research participants during volitional execution of swallowing and finger movement tasks. A 5 second pre-movement epoch for each task was triggered on EMG identification of movement onset. A grand average for each task representing approximately 2400 trials across all research participants was derived to compare and contrast morphological features of the derived waveform. Results: Volitional pharyngeal swallowing and finger movement generated similar waveform characteristics of duration and slope; however, statistically significant differences were identified in polarity and in amplitude at four points both early and late in the epoch. Additionally, swallowing produced a pre-motor waveform with a rapid declination of EEG activity in the final 500 msec prior to movement onset. Conclusions: This study demonstrates activation of the supplementary motor cortex preceding the onset of volitional swallowing. However, unlike purely voluntary movements, the volitional pharyngeal swallowing task, as assessed with this methodology, does not appear to recruit the primary motor cortex. Thus engagement of the swallowing response appears to rely on indirect parallel pathways between extrapyramidal cortical motor planning regions and lower motor neurons.

Key words: Bereitschaftspotential; Deglutition; Volitional; Premotor; Supplementary Motor Area (SMA).

Introduction

The role of the brainstem in swallowing has been extensively evaluated by Jean, Doty, Car and others (Doty 1968; Doty et al. 1967; Car et al. 1975; Amri et al. 1984; Jean 1984, 1986, 1990), who have outlined the critical role of medullary circuitry in the regulation of pharyngeal and esophageal swallowing. The role of the cerebral cortex in swallowing is less well defined. Only recently have researchers begun to evaluate *in situ* cortical and subcortical activation during the condition of normal human swallowing using brain imaging techniques (Birn et

al. 1998; Mosier et al. 1999; Birn et al. 1999; Hamdy et al. 1999a,b; Zald and Pardo 1999).

This research has been fraught with difficulty. Execution of the pharyngeal phase of swallowing requires less than one second to complete. Thus, many of the functional neuroimaging models lack the temporal sensitivity to accurately record the event. Repetitive execution of swallowing for multiple samples averaging results in increased lingual movement, posing the substantial complication of extra-cranial artifact which compromises cortical imaging. A final limitation of the approaches taken toward functional neuroimaging of swallowing lies in the methods. In studies to date, researchers have attempted to identify cortical regions activated during the entire swallowing process. The results have revealed a broad range of cortical regions that contribute to this complex, functional activity. However, the complexity of the task is likely blurring the results. Are the cortically activated regions identified through these studies contributing to the motor planning for swallowing, to the oral volitional components of swallowing, to the pharyngeal reflexive components of swallowing or to the sensory feedback elicited through swallowing? Given the current methodologies, this question cannot be answered as there has been no attempt to factor out individual sensorimotor components. A more reasonable approach to the problem of delineating cortical contribution to the

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temporal sequence of swallowing would be to break down the task into its component parts and evaluate these parts section by section. This may yield a more precise cortical map.

One possible technique for evaluation of cortical brain activity during swallowing is electroencephalography (EEG). As with other neural imaging techniques, movement artifact is highly likely to limit application, particularly when evaluating regions of the head and neck. With the relatively close proximity of the tongue to cortical brain regions, evaluation of cortical activity during the execution of the swallow is problematic, if not prohibitive. However, if information is sought as to the preparation for swallowing, or the issue of pre-motor programming, EEG may provide a reliable means to evaluate cortical activation.

The *bereitschaftspotential* (BP), or "readiness potential", was first described in a German publication by Kornhuber and Deecke (1965). This phenomenon is a gradually rising negative potential that precedes voluntary motor action by approximately 1-2 seconds. It has been described as consisting of two distinct components. The early component (BP1) begins approximately 1 to 1.5 seconds prior to movement onset and is bilaterally symmetrical over the vertex of the skull, even when preceding unilateral movement. The second component (BP2) occurs approximately 0.5 seconds preceding movement onset and shifts toward the hemisphere contralateral to movement (Deecke and Kornhuber 1978; Shibasaki et al. 1980; Deecke et al. 1985; Boschert and Deecke 1986). The BP is not measurable before reflexive or passive movement and characteristically presents increased amplitude when motor demands are higher, some risk is associated with execution of the motor task and/or a judgment of accuracy of task execution is provided (Regan 1989). It is considered to have generator sites in the supplemental motor area (BP1) and primary motor cortex (BP2) (Regan 1989; Deecke and Kornhuber 1978).

The supplemental motor area (SMA) is considered to be involved in the planning and initiation of voluntary movement (Parent 1996). This association of structure to function is supported by studies that document regional blood flow during the performance of sequential finger movement (Orgogozo and Larsen 1979; Roland et al. 1980). The role of the SMA in the deglutitive process has not been fully evaluated. Although electrical stimulation of the primary motor cortex will not evoke a complex motor pattern characteristic of a swallowing response, electrical stimulation of other cortical regions, including the SMA, will evoke more complex patterns characteristic of oral, pharyngeal swallowing patterns (Luschei and Goldberg 1981; Lund and Enomoto 1988). In addition, PET and fMRI studies have identified that the SMA is ac-

tivated during the swallowing task (Hamdy et al. 1999b; Mosier et al. 1999). Thus it was hypothesized that pre-motor activation of the cortex would be a measurable phenomenon.

The purpose of this research was to evaluate the role of the cerebral cortex in the motor planning and initiation of deglutitive behavior. Specifically the study focused on the assessment of the BP as a manifestation of cortical contribution to the pre-motor planning of volitional swallowing. The fundamental question was whether or not the act of swallowing, which is traditionally considered to receive its motor program from the central pattern generator of the brainstem, utilized cortical motor planning under the condition of volitional swallowing.

Methods

Participants

Twenty right-handed individuals (10 males, 10 females) between the ages of 18 and 35 years participated in the study. The participants were assessed as strongly right handed (Edinburgh Handedness Scale; Oldfield 1971; Boschert and Deecke 1986) and reported no recent or remote history of neurologic disease, pulmonary disease, motor impairment or dysphagia. Swallowing competence was screened based on the protocol for the timed test of swallowing described by Hughes and Wiles (1996). Informed consent was obtained from all research participants.

Recording Parameters

EEG Electrodes

For each research participant, an array of 45 silver silver chloride (Ag/AgCl) surface electrodes, as illustrated in figure 1, were mounted on the scalp using collodion and a conductive electrolytic gel with electrode to skin surface impedance maintained below 5 k Ω . Nineteen of the electrodes conformed to the standard positions according to the International 10/20 System (Jasper 1958) with locations identified by direct measurement of the individual scalp. Additionally, a central and midline cluster of electrodes was positioned to concentrate heavily over the cortical regions that have been implicated in motor planning and the presence of the BP (Orgogozo et al. 1979; Roland et al. 1980; Ikeda et al. 1993; Rektor et al. 1994). Two lateral clusters of electrodes were placed over cortical brain regions that have been associated with swallowing based on naturally occurring lesions or upon direct electrical stimulation (Meadows 1973; Kubota 1976; Miller and Bowman 1977; Robbins and Levine 1980).



Figure 1. Electrode Configuration for Cortical Array. Shaded electrodes adhere to the International 10/20 system; white electrodes are represented in higher density in region of SMA; black electrodes are represented in higher density overlying the lateral motor cortices.

Artifact Management

In order to monitor for the potential contaminating respiratory potential associated with swallowing, a commercially available thermistor with standard bead probes of 1.0-mm diameter was inserted into both nostrils to record airflow temperature changes during respiration. The electro-oculogram (EOG) was used to evaluate eye movement using bipolar pairs of electrodes on the lateral orbital rim of the right and left eyes and the upper orbital rims of the right eye only.

Triggering Systems for EEG Epochs

The EEG epoch of interest for the finger movement task was triggered by pressing a small button embedded in the right armrest of the participant's chair. Depression of this button generated a digital pulse signal, which was input directly into the experiment-controlling computer.

During off-line analysis of the data, the trigger point for averaging was repositioned to the onset of SEMG activity associated with finger movement. As a marker for off-line averaging of the finger press task, surface electrodes were placed over the extensor digitorum communis muscle, to record muscle potentials associated with finger movement.

Epoch identification for the swallowing task was considerably more complex than for finger movement. Pilot testing for this project indicated that extraneous lingual movements not associated with swallowing had the potential to complicate the triggering of epochs from submental SEMG data by producing false triggers. Therefore, an external auditory meatus microphone (EAMM) was inserted into the right ear canal to record the acoustic waveform associated with onset of swallowing (Hiimae 1994). The microphone (E.K. Series Model 3024, Knowles Electronics, Inc.) was inserted into the

right ear canal with a foam eartip forming a relative seal. The acoustic signal was amplified $\times 10,000$ then fed through a simple comparator device which produced a digital signal pulse when the designated intensity threshold level was reached. Both the digital pulse and the analogue acoustic signal were input into signal channels of the experiment-controlling computer and displayed on the EEG monitor.

As a marker for off-line repositioning for the swallowing related tasks, surface electrodes were placed submentally to record muscle potentials from the collective suprahyoid musculature. Electrodes were placed no greater than 3 cm apart, equidistant and anterior to posterior between the spine of the mandible and the superior palpable notch of the thyroid cartilage.

During off-line data analysis, only epochs with evidence of swallowing on EAMM and EMG were utilized in data analysis. By using methodology that pairs an acoustic trigger for epoch identification and SEMG onset for averaging, the temporal precision of an SEMG trigger was maintained while identifying and avoiding the technical complications associated with myogenic and acoustic artifact.

EEG and EMG Settings

EEG and EMG data were amplified and digitized on a custom made PC-supported 64-channel DC-EEG amplifier with digital filtering (Lindinger, Svasek, Lang, and Deecke 1991). The EEG recordings were amplified $\times 7200$ and filtered with a bandpass range from DC to 70 Hz. Continuous recordings were collected at a rate of 250 samples/second/channel. EOG recordings were amplified $\times 3600$, with a bandpass range from DC to 70 Hz. Time constant of the EMG recordings was set at 0.1 sec with a high frequency cut-off at 300 Hz. EMG signals were rectified and amplified $\times 3600$. The thermistor signal was input into the system through an EMG channel and was amplified $\times 7200$, with a bandpass range from DC to 300.

Post-hoc analyses of continuous EEG recordings were based on a series of 6 sec epochs, time-locked to the designated trigger associated with a given task. The six sec of activity consisted of 5.0 sec preceding the trigger and 1.0 sec subsequent to the trigger.

Procedures

Participants were seated in a comfortable chair located in an electrically shielded and quiet room and were observed for a period of two to five minutes at rest to assure measurable swallowing associated EMG discharges from the submental muscle group and clear tracings derived from the EAMM and thermistor. Threshold levels for trigger activation for each individual were set during this preliminary period.

Experimental Tasks

EEG recordings were collected during two conditions, repetitive finger press movements and repetitive dry swallows. For the volitional finger movement task, participants were instructed to rest their index finger lightly on the digital trigger button, and then briefly and with effort, press the button to its maximum extent followed by a prompt release of pressure. For the volitional swallowing task, participants were instructed to swallow their secretions "with effort". The use of an effortful swallow was employed to assure that the task was fully within the conscious volitional realm. Participants were instructed to minimize mouth and tongue movement in anticipation of swallowing and were asked to comfortably fix their gaze to a target placed approximately four feet in front of them.

To address the potential complication of respiratory artifact influencing the swallowing-related potentials, both tasks were preceded by a "breath stop" as described by Deecke et al. (1986). Research participants were instructed to "stop breath" (as opposed to a deep inspiration and breath holding), wait approximately 4-6 seconds and then complete the motor task. Additionally, both tasks were completed at a participant-determined rate averaging two tasks per minute; a small glass of tap water was available to moisten the oral mucosa as needed. Tasks were completed separately in alternating and counter-balanced blocks of 12 movements per block. A total of 15 blocks were completed for each task by each research participant, providing 180 potential trials for analysis.

Data Analysis

Epoch Preparation

Post-hoc analyses of continuous EEG recordings were based on a series of 6-sec epochs, time locked to the designated trigger associated with a given task. The 6 sec of activity consisted of 5.0 sec preceding the trigger and 1.0 sec subsequent to the trigger for both conditions (swallowing and finger press). Epochs were identified and isolated during the on-line acquisition of EEG data. All raw data epochs were computer processed to identify and remove records with significant electrical artifact or electrode drift using an internal artifact rejection software program (Lindinger et al. 1991).

Trigger Re-positioning for Data Averaging

Once the final trials were selected, the trigger point for back averaging was repositioned to facilitate more temporally precise measurement. For the finger press task, the trigger was re-positioned to the onset of SEMG activity in the extensor digitorum communis muscle. For the swallowing task, the trigger point for back averaging

was placed at the initiation of the peak of the waveform component representing initiation of lingual propulsive movement that initiates the pharyngeal response. In order to minimize the contaminating effects of glossokinetic potentials, if EMG activity on individual trials preceded the repositioned trigger by more than 500 msec, that trial was excluded from the final analysis.

Referencing

For data acquisition, all EEG data were referenced to a single cortical electrode, CPz, which was chosen as the data reference as it is centrally located over the cortical vertex and thus would not pose a hemispheric bias during data acquisition. However, data files were mathematically re-referenced to the average of the amplitude at the two electrodes overlying the mastoids (TP9 & TP10) for analysis. As the BP is presumed to be generated within the supplemental motor area, an analysis reference of CPz would inhibit assessment of cortical activity at the vertex, thus minimizing measurable supplemental motor activation. For this reason, linked mastoid referencing is the standard reference site for assessment of BP reported in the existing literature.

Data Reduction and Analysis

Individual subject averages were derived from approximately 120 usable epochs of each condition and a grand average representing the average waveforms of all 20 participants on each condition was calculated. The grand average for each condition was derived from approximately 2,400 trials. Initial analysis of the data descriptively evaluated swallowing and finger movement for the consistency of occurrence of the potential and the polarity of the waveform on those potentials. For purposes of this analysis, BP was defined as cortically measured activation preceding the onset of motor activity by one to three seconds measured at electrodes Cz, FCz, FC1z, and FC2z using linked mastoid referencing. Three raters with experience in measurement of pre-motor potentials evaluated the averaged waveforms generated from these electrodes from each of the 20 participants and for both tasks. Raters were advised of the number of tracings contributing to the averages but were not given information as to which task generated each waveform. Raters were asked to categorize the waveforms using one of three possible ratings: 1 = BP, 2 = other significant premotor activation (PMA) that does not, in their experience, match the morphology of a typical BP, 3 = no identified significant premotor potential, and were asked to identify either a positive or negative-going polarity. If 2 of 3 raters agreed on a given assignment, that rating was chosen as the final category.

Next, the morphology of the BP for each task was evaluated using both descriptive and statistical methods.

For purposes of describing the waveform, this project adhered to the two component definition of the BP as described by Deecke and colleagues (Deecke et al. 1969, 1976, 1978, 1985; Boschert et al. 1986; Kristeva et al. 1990; Lang et al. 1988, 1991). The independent variables for analysis were electrodes and task within and across research participants. These variables were evaluated with respect to the dependent variables of waveform onset, amplitude and slope. Statistical analyses utilized permutation statistics as described by Karniski et al. (1994).

Comparisons were made between the grand averaged Laplacian values for the swallowing data set and the finger press data set of the grand averaged data (across all research participants). Morphological features were evaluated for consistency between conditions. Regression procedures were utilized to define the slope, in degrees, of derived potential from point of onset of the potential to point of onset of motor activity. These two measurements of slope were then statistically evaluated between tasks. Consistency between tasks for onset time and amplitude of the derived potentials at three points within the waveform also were evaluated using statistical techniques.

Results

Visual Inspection of the Data

Three raters judged the presence or absence of a typical BP in the averaged waveforms for each task from each participant. For the finger movement task, 19 of the 20 participants demonstrated what was judged to be substantial pre-motor activation, whereas 18 of the 20 participants demonstrated identifiable pre-motor activation for swallowing. Evaluating more specifically for the presence of a characteristic BP, 12 participants were judged to demonstrate a clear BP waveform for finger movement, whereas 10 of the participants were judged to demonstrate a BP waveform for the swallowing task. Using a non-parametric Friedman Test of Related Samples, no statistically significant differences between tasks were identified in frequency of occurrence for BP, other pre-motor activation or no premotor activation ($p=.739$). Spearman Rho correlation coefficients were found to be between .408 ($p=.074$) and .600 ($p=.005$) when evaluating the agreement between raters on the presence of BP in the individual subject data, with correlation coefficients ranging between -.187 ($p=.429$) and .688 ($p=.001$) when evaluating the agreement between raters on the presence of any pre-motor activation in the individual subject data.

The grand averaged waveforms for finger movement and swallowing are represented in figure 2. The most notable difference between tasks is the appearance of remarkably smaller amplitude for the swallowing condition than for the finger movement condition. The second most

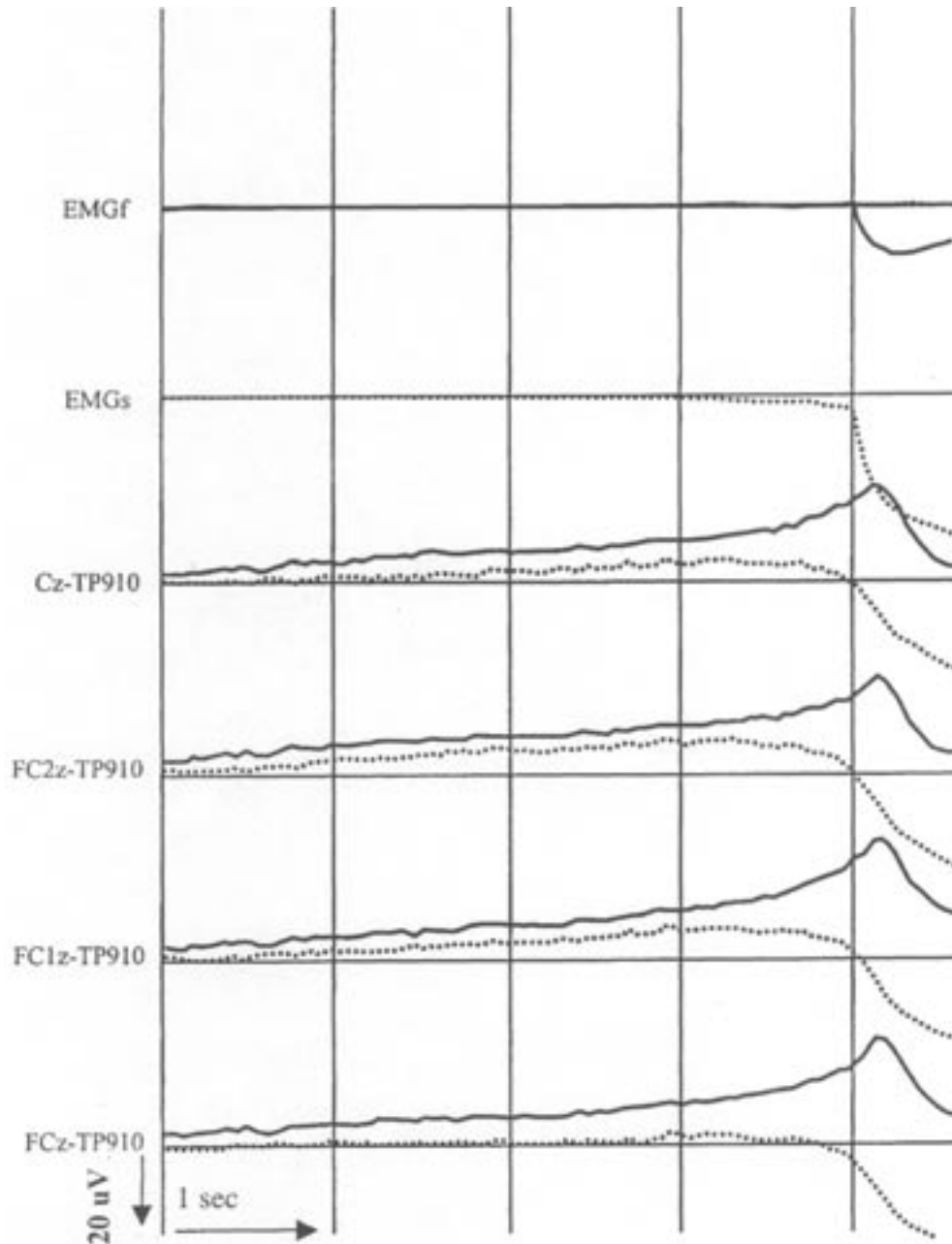


Figure 2. Tracing of original EEG averaged waveforms across all research participants for finger movement (solid) and swallowing (dashed). A negative potential is represented as upward-going.

notable difference relates to waveshape. Figure 3 depicts the potential generated from finger movement with fairly clear BP1 and BP2 components. However, the potential generated from the swallowing task is characterized by a long, slow rising slope BP1 component with no subsequent BP2 component, also seen in figure 3. A series of statistical analyses were utilized to further address the significance of perceived morphological differences.

Polarity

At all central electrodes (CZ, FCz, FC1z, FC2z) a negative polarity, consistent with typical BP, was observed for both tasks in the grand averaged data as represented in figure 2. However, Cochran's Q procedure identified a statistically significant difference between the finger movement and swallowing tasks in respect to polarity of the potential ($Q = 4.00, p = .046$) as classified by the three raters.

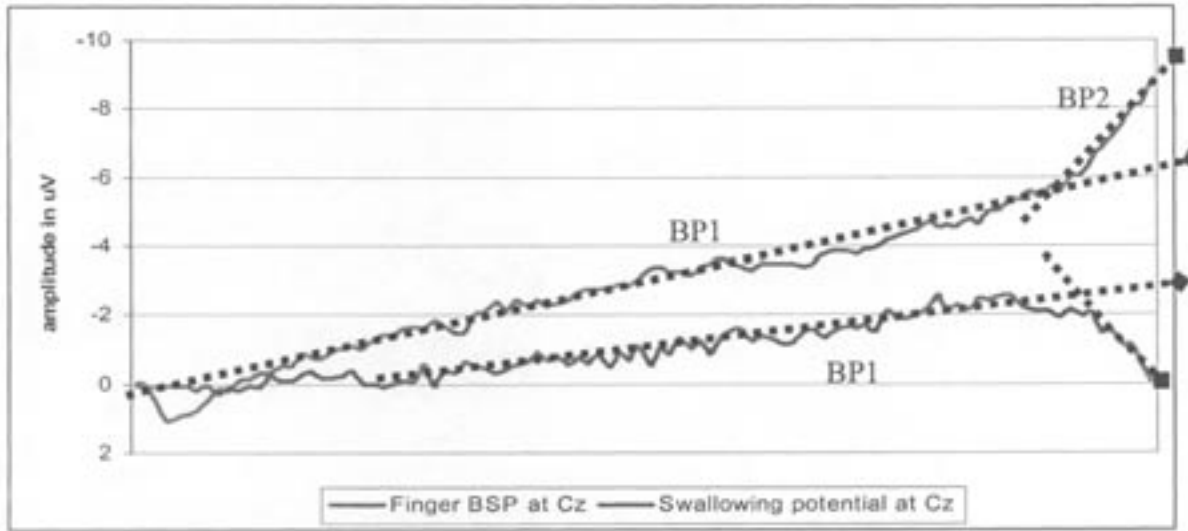


Figure 3. Identification of two components of the typical BP (BP1 & 2) for the finger movement task and only the first component (BP1) for the swallowing task for the grand average waveforms at electrode Cz. Note BP2 for the swallowing task with a decline of amplitude to baseline prior to movement onset. Negative polarity is represented in the waveform as upward-going.

Thus, although the averaged data across individuals produced a negative going potential for both conditions, variability within the individual data suggested that polarity of the potential may differentiate the two tasks.

Onset Time

Onset time for the averaged waveforms at the four central electrodes (Cz, FC1z, FC2z, FCz) for each participant and each condition (finger movement and swallowing) was identified by using a straight edge to follow the slope from its peak edge to its initiation. The point of initiation, or onset time, for each subject’s averaged data on the two tasks is summarized in table I. At all electrodes, the finger movement task resulted in a pre-motor cortical potential with an earlier onset than that for the swallowing task; however, paired samples t tests revealed no statistically significant differences between conditions ($p > .06$). Reliability of this measurement between three

raters was assessed on 25% of the waveforms, which identified very high agreement ($r = .989, p < .01$).

Amplitude

A visual analysis of the four primary waveforms (Cz, FC1z, FC2z, and FCz) suggested a fairly remarkable difference in amplitude at some regions of the waveform (figure 2). Statistical analyses based on permutation testing were utilized to evaluate for significance of these differences for the averaged group data (Blair and Karniski 1994; Karniski et al. 1994). Rather than evaluating every single time point within the four-second epoch, statistical comparisons were made at 250 msec. intervals beginning at 3.750 seconds pre-movement onset and terminating at the point of movement onset. Analyses identified significant differences in the overall brain map (irrespective of individual electrodes) at three time points at the beginning of the epoch (3.750 [$\text{maxt} = -3.674, p = 0.027$], 3.5

Table I. Mean and standard deviations of onset times averaged across all research participants for finger movement and swallowing at the four central electrodes. Value represents seconds of time pre-movement onset.

	Finger Movement				Swallowing			
	FCz	FC1z	FC2z	Cz	FCz	FC1z	FC2z	Cz
Mean Onset Time	3.29	2.79	2.99	2.03	2.78	2.55	2.54	2.82
Std. Deviation	1.83	1.09	1.03	1.12	1.07	1.19	1.25	1.18

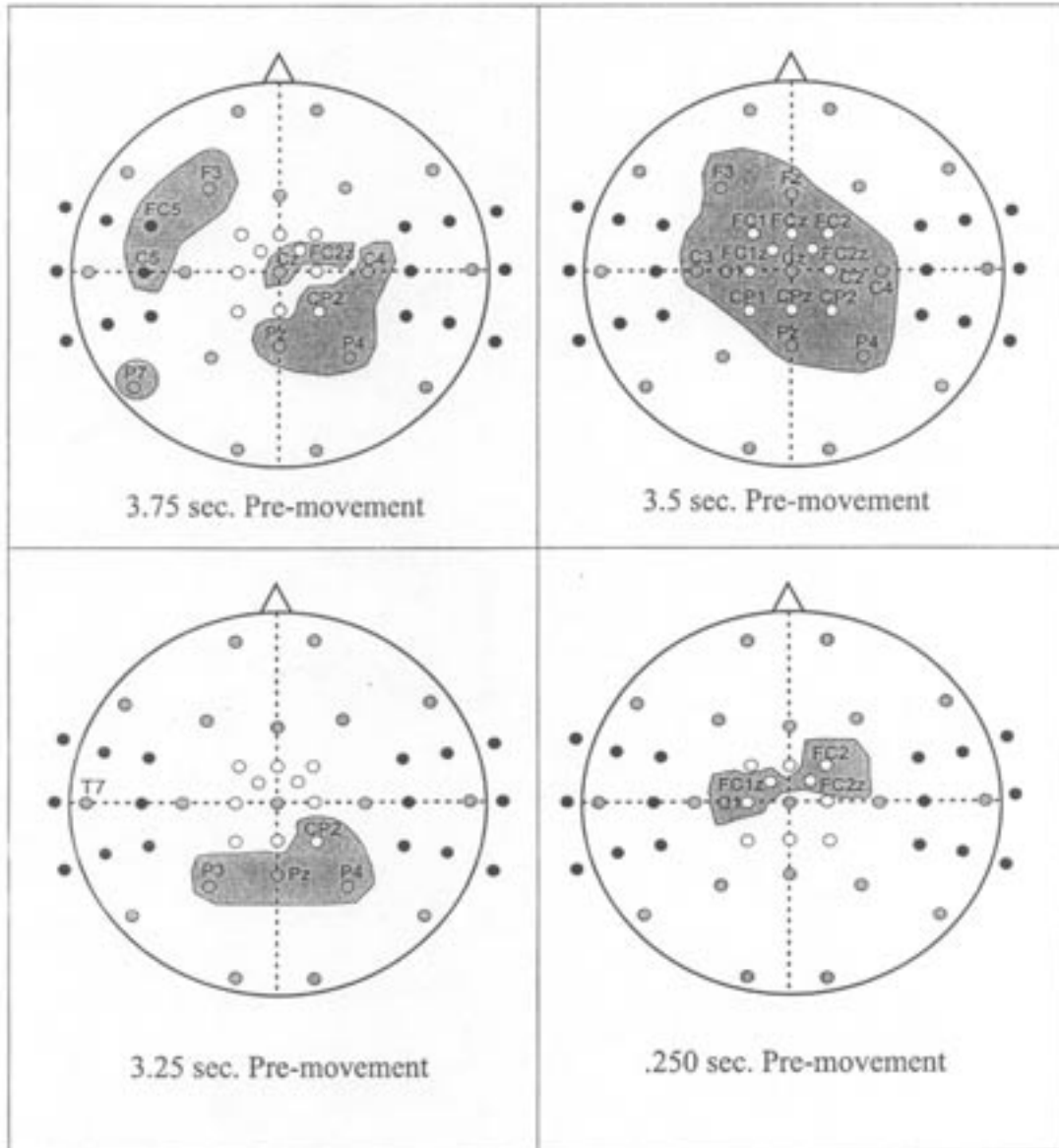


Figure 4. The four topographic maps represent time points in the pre-motor epoch with statistically significant amplitude differences in overall brain maps between the two conditions ($p < 0.10$). The shaded areas represent specific electrodes in which amplitude of measured cortical activity differentiated the tasks of swallowing and finger movement.

[$\text{maxt} = -3.993$, $p = 0.012$] and 3.25 [$\text{maxt} = -4.138$, $p = 0.008$] seconds prior to movement onset) and at one time point at the termination of the epoch (.250 [$\text{maxt} = -3.517$, $p = 0.042$]).

With the identification of time points in the epoch where statistically significant differences were detected in the overall brain maps, post-hoc testing of individual electrodes could be undertaken. According to Blair (personal communication 1999), the electrode subtest is extremely conservative, thus, the critical significance value for electrode differences was adjusted to a $p = .10$ level. At the four

pre-movement onset sites identified in the initial statistical analysis, a statistical comparison was conducted to compare amplitude values at each individual electrode in the cortical array between the conditions of finger movement and swallowing. Significantly different amplitudes between conditions were demonstrated within the cortical regions on the topographic maps seen in figure 4. Thus, surface measured cortical activity in these regions differentiated the tasks of finger movement and swallowing at time points early and late in the epoch of interest.

Slope

Analyses of slope of the waveform were conducted on the data from the four central electrodes using linked mastoid referencing. Using regression procedures, the calculation of slope for each waveform was based only on the slope of the identified potential rather than the slope of the entire recorded 5 second pre-movement epoch. At electrode Cz, the b value for finger movement is $-.73$, compared to that for swallowing at $-.70$. At electrode FCz, the b value for finger movement is $-.76$, whereas the b value for swallowing is calculated to be $-.73$. At electrodes FC1z and FC2z, the slopes were calculated for finger movement at $-.79$ and $-.76$ respectively; while the calculated slopes for swallowing at FC1z and FC2z were $-.74$ and $-.66$ respectively.

Paired t-tests analyses revealed no statistically significant differences in calculated slope at any of the four central electrodes ($p > .05$). Correlation coefficients comparing slope between conditions were significant at the Cz and FC1z electrodes ($r = .465$, $p = .039$ and $r = .569$, $p = .009$ respectively), suggesting moderate positive relationships between conditions at these electrodes.

Cortical Representation and Hemispheric Lateralization for Swallowing

Lateralization of the raw EEG data from the grand average data file for the swallowing task was evaluated by comparing the EEG measured amplitudes from corresponding electrodes on the two hemispheres. Figures 5a and 5b represent the amplitude data comparing corresponding electrodes at the time points 1.85 and 0.25 sec prior to movement onset. Permutation statistics identified no statistically significant differences between hemispheres at any point in time throughout the entire pre-movement epoch ($p > .05$). In summary, these data suggest that cortically generated motor preparation for swallowing is, at least statistically, a bilaterally represented task.

Discussion

Neuroimaging techniques have to date identified a broad range of cortical regions that contribute to the swallowing process; however, this research is hindered by a lack of specificity in the targeted hypotheses and difficulty managing extra-cranial artifact. This project sought to evaluate an isolated component of the entire swallowing process using electrophysiologic recording techniques, specifically, cortical activation during motor preparation for volitional swallowing. It was postulated that comparing and contrasting the cortical pre-motor potentials for swallowing with those associated with volitional activity such as finger movement (i.e., the BP), would provide information as to the role of the cortex in motor planning for swallowing.

As this was the first known experiment to investigate cortical pre-motor activation patterns in swallowing, it was necessary first to confirm the presence of pre-motor cortical activation preceding the deglutitive process. Although most individuals demonstrated substantial cortical participation in the preparatory process, evidence of this participation does not necessarily mimic that which has been previously described for volitional motor tasks, suggesting differing neurologic processes between conditions. Therefore, it is important to discuss the specific features of the morphology of the swallowing pre-motor potential, as it compares and contrasts with the BP for finger movement.

With regard to polarity, grand averaged data across research participants reveals a negative-going potential for both the swallowing and the finger movement tasks. However, statistical analysis revealed a statistically significant difference in the polarity of the individual data when grouped by condition. The polarity of a potential reflects the differential electric potential at each of the two input electrodes (Misulis 1994). Although the presentation of polarity within a single experiment is based on convention for a given task (negative-going is viewed as an upward deflection for BP research), a polarity change within a given experiment would suggest a differential input to the amplifier from the electrode in question and the reference electrode. Thus, there appears to be greater variability in the electrical activity of the cortical potential associated with swallowing than for finger movement. This variability may reflect inconsistent source generation between individuals for the swallowing task.

Another possible explanation for this unexpected finding may come from the instruction and methods used in this study. The target behavior for the swallowing task was a volitionally initiated pharyngeal swallow. This required that participants hold the oral-lingual structures very still and attempt to elicit only a pharyngeal swallow or swallow only from the throat, without extraneous lingual movement. Submental muscle activity was monitored with surface electromyography and trials in which significant extraneous motor activity occurred were deleted from the average. Similar careful instructions were not provided to research participants in reference to the finger movement task. They were asked only to keep their hand on the armrest and press the button with their index finger. It is plausible that the instructions and methods in this experiment produced an overlapping positivity for the swallowing task, similar to that described by Chisolm and Karrer (1986) who observed inhibition of associated movements produced a slow sustained positivity. This is likely to have been influenced both by the difficulty of the swallowing task and the instructional bias. In some cases, research participants reported execution of the task to be very difficult.

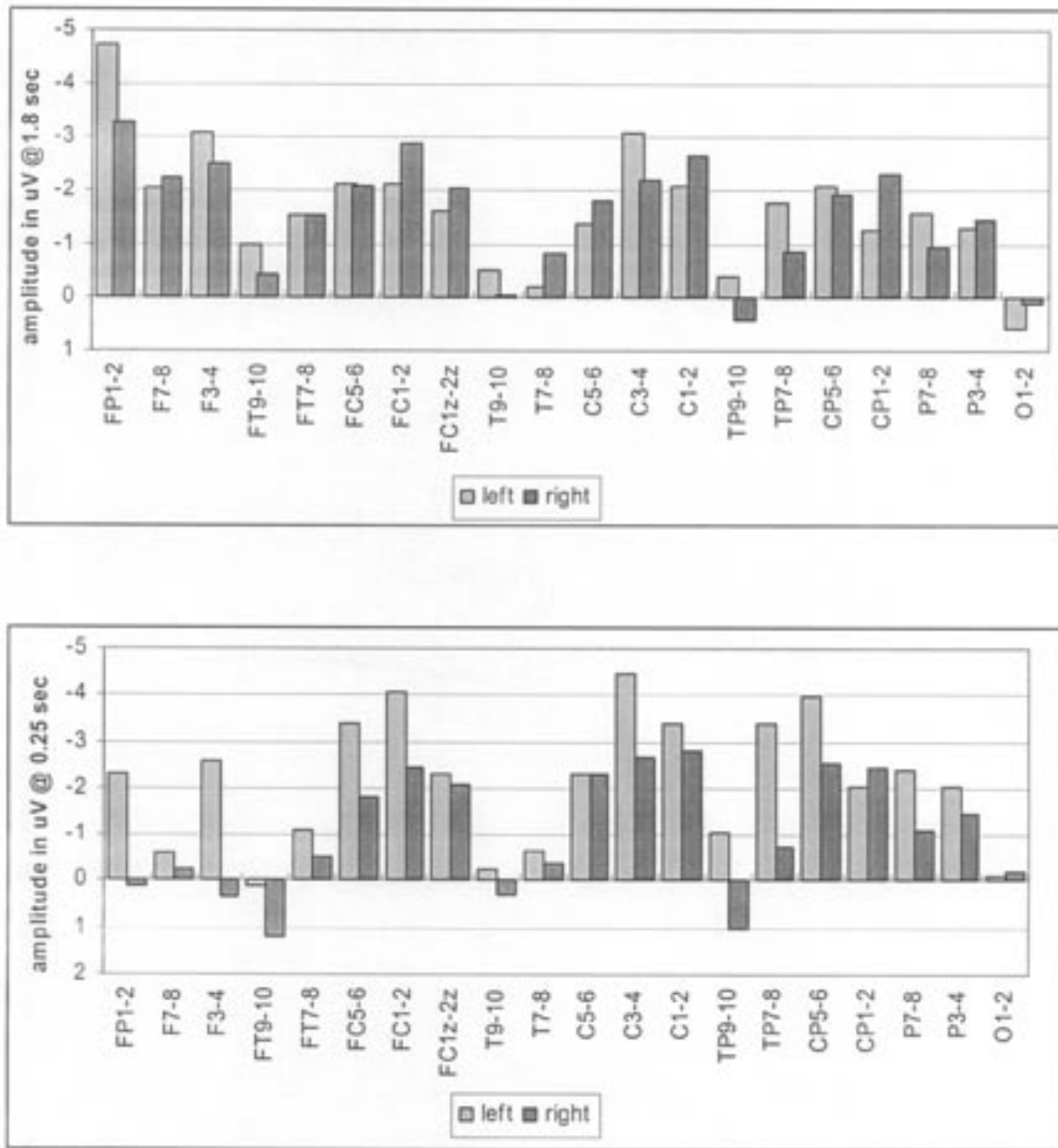


Figure 5. Top. Amplitude values for corresponding inter-hemispheric electrode pairs for the swallowing task at a time point 1.85 sec prior to movement onset. Bottom. Amplitude values for corresponding inter-hemispheric electrode pairs for the swallowing task at a time point 0.25 sec prior to movement onset.

Thus it is conceivable that for some participants, the positivity associated with effort required to inhibit oral lingual movement prevailed over the negativity created from the motor planning task, thus producing an overall positive-going waveform. A thorough evaluation of this phenomenon would be difficult in EEG research since the extra-cranial artifact offered by the tongue during oral preparation would inhibit measurement of cortical swallowing potentials that are free of artifact.

In relation to onset time, group averages across all participants showed that the task of volitional swallowing produces a negative-going potential at the four central electrodes that rises slowly over a period of approximately 2.54 to 2.82 sec preceding the onset of pharyngeal swallowing. Interestingly, the finger movement task produced a pre-motor waveform of longer duration than swallowing at 3 of the 4 central electrodes (FCz, FC1z, FC2z; finger movement onset ranges from

2.03 to 3.29 sec.), suggesting slightly earlier onset of pre-planning for this task. This long rise-time, however, is not significantly different than that of the swallowing task executed during the same experiment within the same research participants. It is possible that the shorter duration of the potential for the swallowing task reflects the preparation of the data for averaging. For both tasks, the acquisition trigger was repositioned post-hoc to identify a more precise onset of movement. For the swallowing task, there was characteristically greater SEMG measured movement prior to the onset of swallowing than for the finger movement task. Thus, for most swallowing trials, the post-hoc trigger was repositioned to a point more distant from the acquisition trigger than for the finger movement task, thereby shortening the duration of the averaged epoch. Trials in which anticipatory muscular artifact exceeded 500 msec, were excluded from analysis in order to minimize this effect. However, within a range of 500 msec, this variation in trigger repositioning may contribute to the observed difference in onset time between conditions.

The long durations of the pre-motor potentials elicited during this experiment are remarkable considering the pre-motor potential durations reported most frequently in the literature. Reports of BP associated with finger movement suggest pre-motor potential durations of 2.0 to 1.0 sec (Cui et al. 1993; Ikeda et al. 1993; Cui et al. 1999). It could be speculated that the longer swallowing BP is an artifact of the breath-holding methodology used to control for presence of a respiratory wave in the pre-swallow potential. This methodology was initially utilized by Deecke and colleagues (1986), who reported BP duration of 2 seconds. Respiratory apnea is an inherent component of the swallowing process. Thus by instituting the methodological control of breath-holding, the sequence of motor events is static with only the temporal features adapted. Respiratory inhibition is not a time-locked phenomenon associated with finger movement. Thus, by utilizing the breath-holding method with the finger press task, a sequentially executed "dual task" paradigm is induced, the two tasks being finger movement and respiratory suppression. This may explain the disparity in the durations of the BP associated with finger movement in this experiment and that reported elsewhere in the literature.

There appear also to be notable differences in the amplitude of the potentials for finger movement and swallowing based on visual inspection of the grand averaged data. Statistical analyses support this observation only at five points in time during the entire movement epoch: three time points at the beginning of the potential which can be explained by the earlier onset time of the BP for finger movement and at two points immediately preceding movement onset. These final two points are con-

sistent with the second component of the BP, and thus represent a substantial difference between tasks in waveform morphology.

There was a tendency for the finger movement task to present a higher EEG amplitude compared to the swallowing task. These results appear counter-intuitive to what might be expected for a typical BP. The BP is "influenced by intention, motivation, effort and the muscle strength exerted in the movement; the greater these factors are, the larger the amplitude of the BP". (p. 526, Shibasaki et al. 1980). The swallowing task in this experiment would appear to be more complex than the finger movement task. Subjects were specifically instructed to inhibit oral motor movements and produce, to the best of their ability, a pharyngeal swallow in isolation. Constrained volitional swallowing can be difficult to initiate, requiring significant concentration to the task. Thus, it would have been reasonable to expect the swallowing potential to be of greater amplitude. However, this was not the case.

A possible explanation for this unexpected finding may again come from methodology employed in this study, specifically from the influence of motor inhibition. It is possible that inhibition of oral lingual movement in the swallowing task induced a positivity in the waveform which, when averaged with the negativity associated with motor planning, reduced the overall negativity of the waveform. This also may provide partial explanation for the later onset observed for the swallowing potential than that observed for finger movement. However, it also is plausible that the dual task nature of the finger movement task (generated by the breath-hold methodology) may have contributed to the increased amplitude of the finger movement BP. Similar to the results of Cui and Deecke (1999), the amplitude of the bilateral finger movement task was significantly greater than that for the unilateral finger movement task. Finally, as previously discussed, the swallowing task produces pre-motor potentials that are of significantly different polarity than the BP. Although the grand average for swallowing is negative-going, there are individual variations with some research participants presenting a positive-going waveform. Thus, averaging of these positive-going potentials with the negative-going raw data will reduce the overall amplitude.

Information regarding lateralization of the EEG waveform was evaluated without specific inference to the source of signal generation. Using statistical procedures to evaluate differences in amplitude between corresponding electrodes from the scalp array, no statistically significant inter-hemispheric differences were identified at any point of interest in the pre-movement epoch. Thus, based strictly on statistical analysis of the raw EEG data, motor preparation for swallowing was observed to be a bilater-

ally represented task. Previous neuroimaging studies have reported cortical lateralization of swallowing that is irrespective of handedness (Hamdy et al. 1997a; Hamdy et al. 1999a,b; Zald and Pardo, 1999). However, these studies have identified cortical asymmetry occurring at some point in the entire swallowing process, with no distinction made between pre-movement motor planning, motor onset, motor execution or post onset sensory feedback mechanisms. Additionally, previous research investigating the neurological substrates reflected by the BP suggest that motor planning is a bilaterally represented task in the supplemental motor area with cortical asymmetries apparent only in the final 250 msec as the neural signal is transmitted to the lateral motor strip (McAdam 1974; Regan 1989). There is a non-significant trend for cortical asymmetry that favours the right hemisphere in the final 250 msec prior to the onset of movement; however a visual inspection of the electrodes in which cortical asymmetry appears to be present does not yield a logical pattern of final common pathway motor activation. As well, the final BP component is absent for the swallowing task. Thus, data from this experiment suggest that cortical motor preparation for volitional swallowing is a bilaterally represented task, with a proposed inference that the previously reported asymmetries of swallowing relate to motor execution and maintenance, or sensory feedback.

Perhaps the most interesting analysis from this study arises from the description of overall waveshape. The prototypical BP is usually described as consisting of an early component (BP1) and a late component (BP2) (Deecke and Kornhuber 1978; Shibasaki et al. 1980; Deecke et al. 1985; Boschert and Decke 1986). This two-component model is interpreted to suggest that the early signal reflects bilateral activation of the SMA for the organization of the motor activity, followed by activation of the contralateral motor cortex, associated with direction of the neural command to lower motor neuron pools for task execution (Deecke and Kornhuber 1978; Shibasaki et al. 1980; Deecke et al. 1985). Thus, in evaluating the pre-motor activation associated with swallowing in this experiment, an analysis of the two components of the BP was in order.

Visual inspection of the averaged waveform for the finger movement task revealed a waveform pattern that is characteristic of the previously described BP. Visual inspection of the grand averaged waveform for the swallowing task reveals a remarkable absence of the late (BP2) component. The early (BP1) component was clearly present and did not differ significantly from that seen in the finger movement task in terms of amplitude, slope or onset time. These similarities support the conclusion that this early potential represents contribution of the SMA to motor preparation for volitional swallowing.

In contrast to the finger press task, a characteristic BP2 component was not evident prior to onset of swal-

lowing. The waveform dramatically decreased in amplitude between 500 and 250 msec prior to the onset of the swallow-related motor activity. The potential reached the baseline at the point of movement onset for all 4 vertex electrodes. Upon further inspection, this same pattern was observed for all other cortical electrodes. If the motor act of volitional swallowing were to follow the same motor planning processes as volitional finger movement, increased amplitude would be expected in the cortical electrodes overlying the lateral motor cortex in the area representing the pharyngeal musculature. However, there is no region of the cortex in which amplitude of the waveform increases with a sharp slope within the last 500 ms prior to movement onset. Indeed, at all electrodes, there is an apparent diminution of cortical amplitudes in this time period.

An absence of scalp recorded potentials suggests that either cortical activity is extinguished, or that the dipole source of the signal is not perpendicular to the cortical surface, thereby canceling the measurable electrical current. Thus, several possible interpretations can be proposed for these data. One possibility is that the neural command in the final 500 msec is transferred either to a region of the cerebrum that lies deep in the cortex, or to an area for which the neuronal dipole is oriented transversely or parallel to the cortical surface. In either case, this would inhibit measurement of cortically generated electrophysiologic activity. The anterior insular cortex has been reported to show swallow-related activity, both in neuroimaging studies and in reports of lesion-induced dysphagia (Daniels and Foundas 1997; Hamdy et al. 1999b; Mosier et al. 1999; Zald and Pardo 1999). Electrophysiologic activity from the insula would be impossible to measure from the cortical surface because of the orientation of the neuronal dipole to the surface. Thus, for the current data, the role of the insula in swallowing motor planning cannot be explicitly evaluated.

Attributing the absence of a BP2 component in the present data to the insula would imply that the insula serves as a corticobulbar conduit between pre-motor planning and motor execution in swallowing. Previous research exploring the role of the insula in swallowing suggests a more substantial contribution in oral sensori-motor integration and taste. The anterior insula is known to project descending, efferent fibers to the nucleus tractus solitarius (Shibley 1982), affording a possible role in swallowing motor control. However, the anterior insula also projects efferent fibers to the supplemental motor area, (Mesulam and Mufson 1985). Daniels and Foundas (1997) present a review of the neurophysiologic role of the anterior insula in swallowing. They state that "lesions restricted to the anterior insula may produce dysphagia by disrupting the processing of gustatory input, which may in turn yield a de-

lay in triggering of a swallowing response" (p. 151). This information, paired with the knowledge that there are numerous connections between the insula and gustatory, olfactory and limbic regions of the brain (Miller 1999), suggests that the insula contributes sensory input to the preparation for swallowing, rather than serving as a primary relay between the supplemental motor area and the nucleus tractus solitarius. Thus, although the role of the insula in motor preparation for swallowing is not negated, it does not seem likely that insular activation in the final 500 msec prior to movement onset is responsible for declination of the BP2 component associated with swallowing.

A second possible interpretation is that the neurologic signal transfers to a location other than the primary motor cortex in activation of the final common pathway innervating the swallowing musculature. Recalling that the methods utilized in this study required an inhibition of volitional oral preparation for swallowing, it is speculated that the observed early pre-motor activation, or BP1, involved inhibition of volitional movement in addition to volitional motor planning. Barlow states that "the supplemental motor area also serves to regulate the amount and type of information flowing into the M1 and is capable of selectively inhibiting conflicting inputs from subcortical centers" (p. 115, Barlow 1999). This methodological constraint also provided a mechanism to evaluate what might be perceived as different motor sets for swallowing. The inhibition of volitional oral movement represents a "decoupling" of the oral preparatory, volitional components of swallowing from subsequent pharyngeal, or reflexive components of swallowing. It is not our intention to argue the well established fact that the motor cortex participates actively in the deglutitive process; rather, these data provide new insights regarding activity of the motor cortex in pre-swallow motor planning. By isolating individual components of the swallowing process, it is postulated that the motor strip can be bypassed for volitionally initiated pharyngeal swallowing; this implies that motor strip activity plays a more critical role in oral preparation and transfer of the bolus.

Support for the proposed revised interpretation of swallowing neurophysiology is threefold in the literature. First, stimulation mapping studies of monkeys by Macpherson, Wiesendanger, Marangoz and Miles (1982) document that 68% of corticofugal projections from the SMA terminate at the level of the brainstem. The conduction velocities of these corticobulbar pathways is likewise relatively slow, at approximately 10 msec, thus durations of the BP2 component in the range of 500-250 msec would be plausible. Secondly, Ghez summarizes that "the central nervous system can shift control of a given set of muscles from one neural system to another" (Ghez 1985, p. 493). This statement is based on research

by Fetz, Cheney, & German (1976) in which corticospinal neurons of a monkey that were activated during skilled lever movement were noted to deactivate when the monkey was agitated and banged the lever from side to side. This suggests that corticospinal neurons can be circumvented based on behavioral influences or the motor set in which the activity occurs.

Finally, Miller (1999) provides support for this interpretation in a detailed disquisition regarding the role of the SMA in swallowing. According to Miller, there are cortical supplementary motor regions that represent and coordinate the functional tasks of chewing and tongue movement, and then coordinate these tasks with the oral and pharyngeal phases of swallowing. This coordination is accomplished via parallel excitatory and inhibitory neural tracts that communicate between the SMA and the brainstem central pattern generators. These functionally opposing tracts have the responsibility of carrying neural signals from the SMA to the brainstem which trigger the switching mechanism within the central pattern generator. Thus, within the deglutitive process, the SMA sends an inhibitory signal to the brainstem in order to arrest motor output for chewing, and subsequently excites the central pattern generator for oral pharyngeal swallowing. Miller states, "the control of the final common pathway, the motoneuron innervating a motor unit in a muscle, depends on two hierarchical controls, the immediate central pattern generators of the brainstem that effectively compete to control its discharge, and the supplementary cortical regions that switch one central pattern generator off and turn another on and sequentially organize their triggering" (p. 155, Miller, 1999).

Given this model of SMA and brainstem coordination, one can infer that the swallowing potential recorded in this experiment represents activation of the SMA, followed by neural transmission to the medullary central pattern generator for excitation and inhibition of motor patterns required for execution of the volitional swallowing response. This may provide additional support for the previously discussed smaller amplitude of the swallowing potential in relation to the finger movement Bereitschaftspotential. If the role of the SMA within the swallowing context is to regulate excitatory and inhibitory influences on the brainstem, the conscious inhibition of the oral preparatory process leading up to swallowing in this experiment may significantly influence the measured cortical activation.

Is there a BP associated with volitional swallowing? Results of this experiment indicate that although there are similarities between the two cortically measured potentials, there are also substantial differences. Specifically, although supplementary motor activation is apparent for both tasks to a similar degree, the two tasks diverge immediately before movement onset. The volitional swallow-

ing task, as assessed with this methodology, did not recruit the primary motor cortex, thus reflecting different underlying neural mechanisms and neural pathways responsible for the engagement of the swallowing response. Definitions of the BP vary among researchers with classification schemes including up to five distinct components. However, even adhering to the most basic classification scheme adopted for this study (a two component model including BP1 and BP2), the electrophysiologic correlates of swallowing do not conform to the characteristics of a Bereitschaftspotential. It is thus proposed that there exists a distinct "schluckpotential", or swallowing potential, which may be observed and measured using neurophysiological techniques in the events preceding execution of volitional pharyngeal swallowing.

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