Responsiveness of Single Afferents in the Infraorbital Nerve to Oral Air Pressures Generated by Consonants

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The responsiveness of receptors supplying the oral mucosa to air pressures generated during consonant production was investigated to obtain information about hypothetical mechanisms underlying speech deficits. The delay between the onset of the neural discharge and the pop puff of phonation (mouth-exit pressure) for /pa/ production was significantly shorter and less variable than it was for /ta/ and /ka/ production, suggesting that the discharge is more closely coupled to the onset of /pa/ production. The data were interpreted to imply that single fibers of the infraorbital nerve respond to the build-up of oral air pressure during /pa/ production. This, and similar sensory information, may be used by the central neural mechanisms which monitor and control the air pressures required for phonation.

KEY WORDS: *consonant, infraorbital nerve, oral air pressure, phonation*

Language disorders can involve deficits in perceptual, cognitive, and linguistic processing. Intelligibility of speech is influenced by many factors involving both the speaker and the listener, such as, speaking ability and proficiency, articulatory skills, cognitive development, and hearing acuity. Speech production has also been shown to be impaired by anesthesia of the sensory nerves to the face and mouth (Ringel and Steer, 1963; Gammon et al., 1971; Scott and Ringel, 1971). As controlled oral air pressures are required for speech (Subtelny et al., 1966), it seems reasonable to assume that the discharge activity of afferents in these nerves encodes functionally important information that is used by the speech delivery system. However, little attention has been paid to the physiology of afferents supplying the human orofacial region with the exceptions of the studies of Johansson et al. (1988 a, b), Nordin and Hagbarth (1989), Nordin and Thomander (1989), and Furusawa et al. (1992). These studies make it clear that afferents within the infraorbital nerve are highly responsive to (1) the application of external stimuli to their respective fields, and (2) minute degrees of lateral stretch of the receptive field (Johansson et al., 1988 a, b; Nordin and Hagbarth, 1989; Nordin and Thomander, 1989; Furusawa et al., 1993). Normally, receptive fields are stretched by external stimuli applied within or outside their boundaries, and importantly, as a result of the orofacial movements that accompany speech and mastication (Johansson et al., 1988 b, Nordin and Hagbarth, 1989; Nordin and Thomander, 1989). Although receptive-field stretch/stimulation is clearly achieved by facial and masticatory muscle contraction, we have previously shown that it is also achieved, at least for the mucosal units, by the build-up of intraoral air pressure (Furusawa et al., 1992). Moreover, the magnitude of the pressure is reflected by the evoked mean firing rate. Our previous and current work differ from that of Johansson and colleagues and Nordin and colleagues in that air pressure is sampled during speech in addition to the sounds produced.

The purpose of this study was to evaluate the relationship among the discharge activity evoked during the production of three consonants in individual afferents supplying the mucosa of the upper lip, the onset of sound, the onset of mouth-exit air pressure, and the onset of oropharyngeal air pressure.

METHOD

Subjects

Data were obtained during a total of 125 trials from 20 women and 23 men (23–35 years of age), none of whom exhibited any evidence or past history of speech or hearing disorders. Informed consent was obtained before conducting the experiments.

Single Unit Recordings

Microneurography was used to directly record the electrical activity from single nerve fibers. A tungsten mi-

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croelectrode (10MΩ, FHC product, Type 25-15-1) was percutaneously inserted into the infraorbital nerve as described by Johansson et al. (1988 a, b), Nordin and Hagbarth (1989), Nordin and Thomander (1989), and Furusawa et al. (1992), under loudspeaker monitoring. Neural activity was displayed on an oscilloscope with a bandwidth of DC–10 kHz, processed through a pre-amplifier and a main amplifier, and stored with sound and mouth-exit air pressure signals using a pulse code modulation data recorder (RD–100T, TEAC Co.) (Fig. 1). After a single afferent had been isolated, tactile stimuli were applied to the skin at the upper lip (moving brush and static light touch) to identify units with cutaneous receptive fields. Data from such units were recorded for comparative purposes, but were excluded from the subsequent experiments. Multiple-unit records, when identification was facilitated by the application of the face mask, were also excluded. The receptive fields of units supplying the mucosa were not precisely determined. The phonemes /p/, /t/, and /k/ were selected for study because they have different articulation points, but equal air flow rates behind the point of vocal tract closure (Isshiki and Ringel, 1964). The neural activity evoked during phoneme production was sampled to evaluate each single fiber's response to the accompanying changes in oral air pressure exerted over the oral mucosa. Before the recording sessions, the subjects were instructed to phonate as uniformly as possible, and to minimize voluntary lip and buccal movements. The latter, when uncontrolled, not only displaces the microelectrode, but movement is known to modulate the transmission of afferent discharges from the oral mucosa and to induce afferent discharge (Johansson et al., 1988 b; Nordin and Hagbarth, 1989).

Measurement of Air Pressures

Phonations of the consonant-vowels /pa/, /ta/, and /ka/ were studied and recorded through a microphone placed in the face mask. Each mask was individually molded to fit the subject's face and allowed measurement of the mouth-exit air pressure without air leakage. In addition, air pressures in the oropharynx were obtained through a catheter inserted through the left nostril. The plastic catheter (2 mm inner diameter and 30 cm in length) transmitted pressure fluctuations to a differential pressure transducer (AK-601G, Nihon Koden) for recording. The delay between the onset of air pressure in the oropharyngeal area and the onset of oral airflow at the exit of the mouth was studied during phonation (Fig. 2).

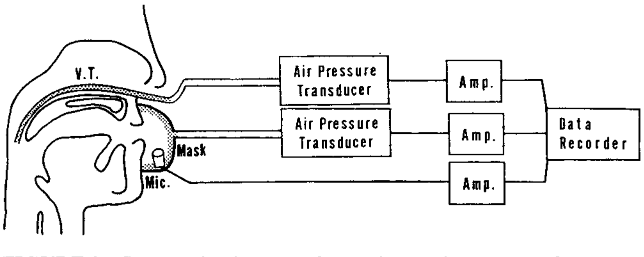

FIGURE 2 Schematic diagram of experimental apparatus for measuring air pressure in the oropharynx via a plastic catheter, and at the oral opening via a face mask.

Data Analysis

Each subject was instructed to articulate the consonant-vowel syllable /pa/,/ta/, and /ka/ five times each. An afferent was included in the data set if a response was evoked to at least one of the three consonants. Only discharge phases (i.e., the evoked spike trains) that were similar on three or more trials were included in the analysis. The number of spikes and the mean firing rate were calculated for the evoked response, and the delay (ds) between the onset of discharge and the onset of the mouth-exit air pressure was measured for comparison among the three consonant-vowels.

RESULTS

Discharge activity was recorded in 42 single afferents of the infraorbital nerve during /pa/, /ta/, and /ka/ production (Table 1). Because the phonemes were studied in the order /pa/, /ta/, and /ka/ and unit isolation was sometimes difficult to maintain, fewer units were studied with /ka/ than with /pa/. The discharge evoked by /pa/, /ta/, and /ka/ production was quantitatively investigated to characterize

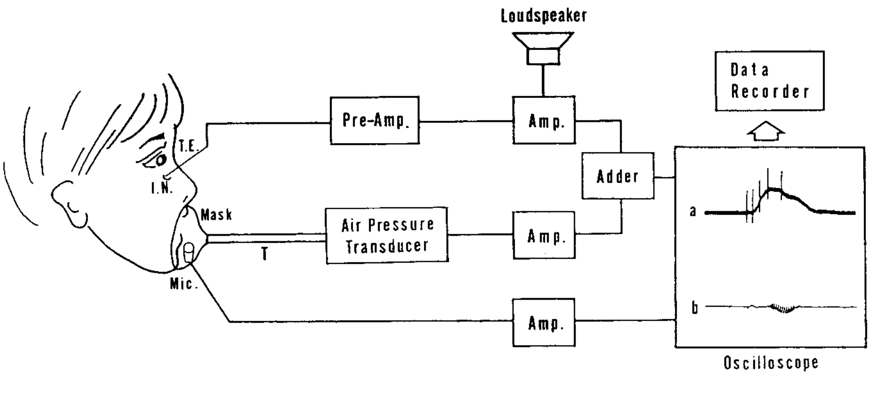

FIGURE 1 Experimental apparatus for recording single afferents in the infraorbital nerve, oral air pressure, and phonation using a face mask. I.N. = infraorbital nerve, T.E. = tungsten electrode, a = synthesized tracing of single afferent nerve discharge and air pressure, and b = sound signal tracing.

TABLE 1 Number of Single Units Studied During Production of Three Consonant-Vowels

Consonant-Vowel	*Total Number of Trials*	*Number of Single Units*
/pa/	125	42
/ta/	125	40
/ka/	125	39

TABLE 2 Number and Percentage of Single Units Exhibiting Each Type of Response During Production of the Three Consonant-Vowels

Consonant-Vowel	*BR*	*SR*	*Unidentified*	*Total*
/pa/	27 (64.3%)	12 (28.6%)	3 (7.1%)	42
/ta/	26 (65.0%)	10 (25.0%)	4 (10.0%)	40
/ka/	24 (61.5%)	11 (28.2%)	4 (10.3%)	39

BR = brief response; SR = sustained response.

the infraorbital nerve response to these phonemes (Fig. 3). Three distinct patterns of discharge were observed. The most common pattern consisted of discharge only preceding the onset of the consonants — 'brief response.' The second type of neural response consisted of discharge preceding the onset of consonant production and continuing during vowel phonation — 'sustained response.' A minority of afferents exhibited discharges unrelated to the rise of oral air pressure and phonation, and were classified as 'unidentified.' For the total sample, 27 units (64%) exhibited only brief responses; 12 units (29%) sustained responses; and 3 units (7%) were unresponsive to /pa/ production (Table 2). For the brief and sustained response patterns, the number of evoked spikes and the mean firing rates are shown in Table 3. The mean firing rate differed significantly between the brief responses evoked by /ka/ and /pa/. No other difference was noted.

The onset of neural discharge occurred 68 ± 23 ms, 247 ± 106 ms, and 281 ± 89 ms prior to the onset "pop puff" of phonation of /pa/, /ta/, and /ka/, respectively (Figs. 4 and 5). The pop puff coincided with the onset of mouth-exit air pressure. The delay (ds) between the onset of discharge and that of the sound showed marked variability for /ta/ and /ka/ production as compared to /pa/ production (see Fig. 5). This suggests that the discharge was closely coupled to the onset of /pa/ production, whereas it was not associated with the onset of either /ta/ or /ka/ production.

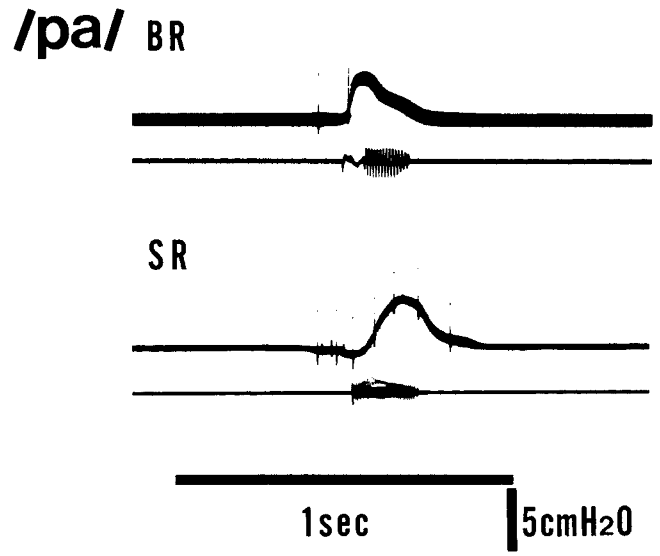

FIGURE 3 Air pressure in the face mask and microneurogram during /pa/ production. All units exhibited one of three types of discharge patterns during /pa/ production. The brief response (BR) consisted of discharge preceding the onset of phonation, whereas the sustained response (SR) consisted of discharge preceding and during phonation.

The time between the onset of air pressure in the oropharyngeal region and the onset of air pressure at the exit of the mouth was compared (Fig. 6). The onset time of air pressure in the oropharyngeal region preceded the onset of air pressure at the exit of the mouth by 147 ± 24 ms (n = 18). The delay between the onset of discharge and the onset of the mouth-exit pressure during /pa/ production was 66 ± 25 ms (for the 18 subjects who did not become nauseous from insertion of the nasal catheter.) Note that the former delay (147 ± 24 ms) exceeded the latter (66 ± 25 ms) during production of /pa/. This suggests that the discharge of the infraorbital nerve during the production of /pa/ resulted from the oral air pressures associated with phonation. Whereas, the discharge during /ta/ and /ka/ production resulted from the deformation of soft tissue and airflow after articulation.

DISCUSSION

Language-learning problems in young children commonly result from environmental events and deficits in the physiologic capacities of receptive, cognitive, and expressive processes, such as, impairment of a sensory function, of the central nervous system, of motor innervation, or of the structures of the respiratory, laryngeal, pharyngeal, and oral systems. Speech is produced in conjunction with auditory and oral sensory feedback (Fairbanks, 1954). MacNeilage et al. (1967) reported the almost totally unintelligible speech of a patient with a generalized congenital deficit of higher level transmission and/or processing of

TABLE 3 The Number of Spikes and the Mean Firing Rates for Single Units Exhibiting Two Types of Responses During the Three Consonant-Vowels

	Brief Response		*Sustained Response*	
Consonant-Vowel	*S.N.*	*F.R.*	*S.N.*	*F.R.*
/pa/	2.2 ± 0.4	37.5 ± 15.4	5.8 ± 1.6	28.8 ± 8.8
/ta/	3.2 ± 1.6	36.5 ± 9.1	4.5 ± 1.5	25.1 ± 8.3
/ka/	3.3 ± 1.5	20.2 ± 9.3*	6.3 ± 1.4	16.8 ± 7.2

S.N. = number of spikes. F.R. = mean firing rate (imp/s) * = $p < .05$, /pa/ vs /ka/ production.

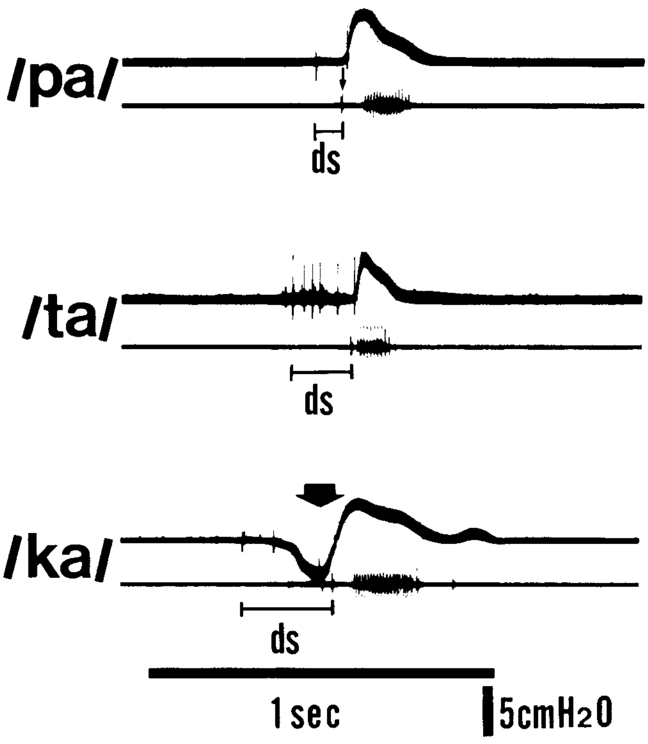

FIGURE 4 Representative recordings of air pressure in the face mask and microneurogram for one subject during phonation of /pa/, /ta/, and /ka/. Neural discharge was superimposed on air pressure tracings by an adder circuit. Note short delay (ds) between the onset of discharge and the pop puff of sound during /pa/ production as compared to /ta/ and /ka/ productions. ↓ = pop puff. Pop puff coincided with the onset of the mouth-exit air pressure. Negative air pressure ↓ was evident immediately before the rise of air pressure during /ka/ production.

somatic sensory information, who had no damage to the auditory or motor systems and no other apparent reason for the speech disorder. Considerable effort has been devoted to the description of speech production, such as the effect on speech intelligibility of local anesthesia of the oral mucosa and the trigeminal nerve (Ringel and Steer, 1963; Gammon et al., 1971; Scott and Ringel, 1971; Putnam and Ringel, 1972), although Smith (1992) stated that it cannot be determined whether changes in motor performance following a nerve block result from reduced afferent information or whether they were caused by some other factor. Scott and Ringel (1971) stated that the prolonged release phase of voiceless stops in the anesthetized condition suggests a possible connection between peripheral feedback and timing of the cerebral instructions to the articulators, although they did not implicate a delaying factor because of incomplete information. These data may indicate that cognitive abilities are important for proficiency in the monitoring of oral air pressure and vibration, and that the motor processing of speech is accomplished using sensory information. Gracco and Abbs (1985) suggested that afferent information from the perioral region is used in multiple ways in the control of lip movements for speech. McClean (1991) also suggested that mechanoreceptor responses to intraoral pressure changes are involved in sensorimotor integration.

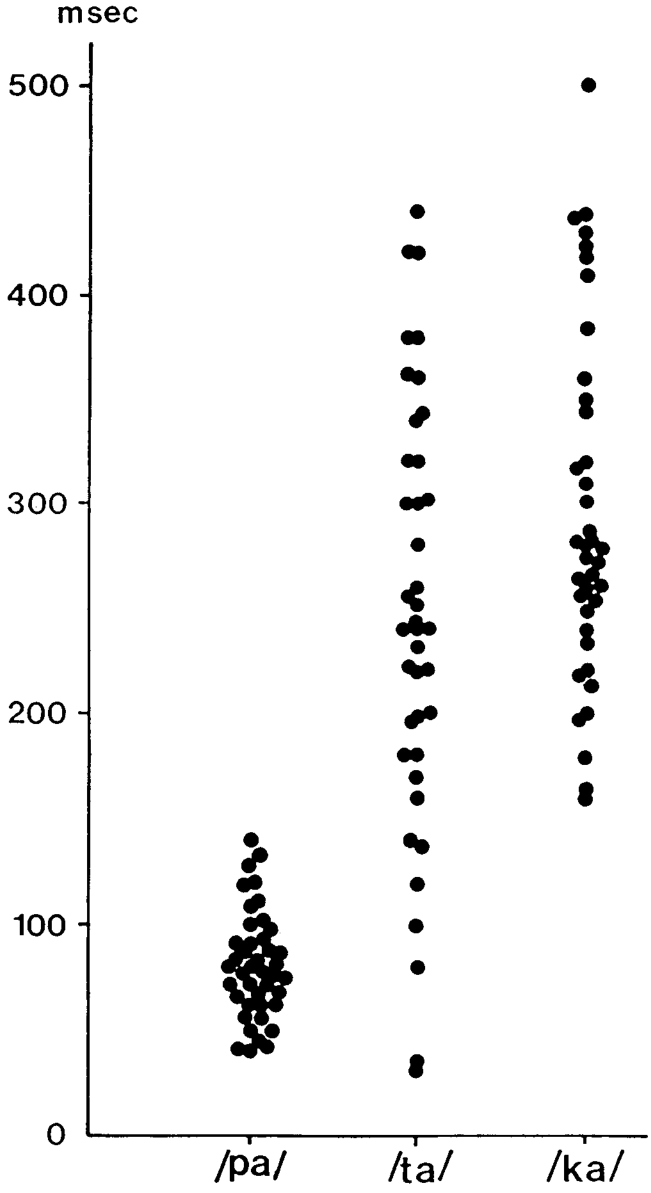

FIGURE 5 Delay (ds) between the onset of discharge and the onset of pop puff, that is, the onset of mouth-exit pressure during phonation of /pa/, /ta/, and /ka/. Estimates of ds were available for 42, 40, and 39 units for /pa/, /ta/, and /ka/, respectively. Means ± SD were 68 ± 23 ms for 42 units during /pa/ production, 247 ± 106 ms for 40 units during /ta/ production, and 281 ± 89 ms for 39 units during /ka/ production. Grand mean of ds was 196 ± 121 ms. Note that the variability in the delay during /pa/ production was significantly smaller than it was during /ta/ and /ka/ productions.

The shape of the pressure-sending tube might be changed to produce airflow resistance as a result of feedback provided by airflow receptors, which are naturally susceptible to respiratory airflow and are controlled by the anterior ethmoidal nerve (Tsubone, 1987), the pharyngeal branch of the IXth nerve (Grélot et al., 1989; Furusawa, 1991), and the internal branch of the superior laryngeal nerve (Sant'Ambrogio et al., 1983).

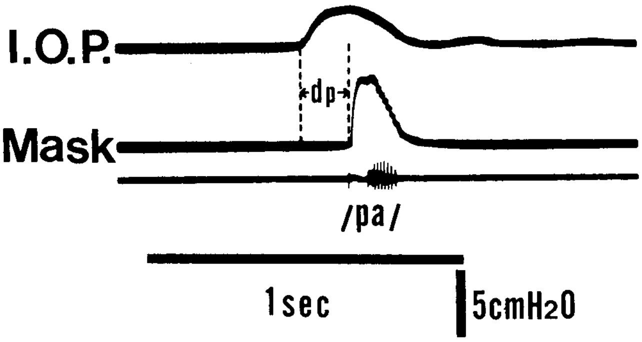

FIGURE 6 Pressure recordings from one subject during /pa/ production. Note delay (dp) between onsets of air pressure in the oropharyngeal area (I.O.P.) and in the face mask. For 18 subjects mean dp was 147 ± 24 ms. dp = delay in onset of air pressure in the face mask as compared to the oropharynx.

The neurologic mechanisms related to the role of sensory information in speech motor control are difficult to investigate in humans. Microneurography, used by Johansson et al. (1988 a, b), Nordin and Hagbarth (1989), and Nordin and Thomander (1989), is an excellent means of studying the distinctive features of single afferent's responses during speech behaviors. Using this technique, Furusawa et al. (1992) previously showed that discharge of the infraorbital nerve increases with oral air pressure during blowing. The present study extends this work by showing that the infraorbital nerve discharges in response to the oral air pressures generated during phonation.

To establish the nature of the receptive system in the oral region, the responses of the infraorbital nerve were preliminarily investigated through a series of experiments involving the production of consonants. We used pressure transducers connected to polyethylene tubing (which projected into the oropharyngeal area and to a face mask) to measure the air pressures produced during phonation. Analysis of the delay between the onset of neural discharge and the onset of sound (the onset of mouth-exit air pressure) is the key to understanding how, and to what mechanical event, the infraorbital nerve responds. Because discharge from mechanoreceptive afferents in the infraorbital nerve was not evoked by tactile stimulation of the face or by voluntary lip movements, the afferents likely supplied the oral mucosa of the upper lip. Although the single units may have responded to indentation on their receptive fields, they were not tested in this manner because the focus of the present study was on the somatosensory response evoked by air pressures.

The delay (ds) between the onset of neural discharge and the onset of the sound during /pa/ production was short and showed little variation compared to that for /ta/ and /ka/. Importantly, the delay (ds) was shorter and was included in the delay (dp) between onsets of air pressure in the oropharynx and in the mask. This indicates that the infraorbital nerve is sensitive to the build-up of oral air pressure during /pa/ production. Moreover, the majority (64%) of afferents exhibited brief responses during /pa/ production, while 12 units (29%) out of 42 units exhibited sustained responses. The two types of responses may be important to the control of the transition from consonant to vowel, or signal recovery from pressure-associated indentation of the mucosa, or vibration by the oral air stream.

Discharge in the infraorbital nerve was evoked not only for /pa/, but for other phonemes which had different points of articulation. There were individual timing differences in response to each consonant that suggests airflow associated with phonation may be monitored in the lip and buccal mucosa even for those consonants which have different articulation points. However, the response to /pa/ was distinctly different from that for /ta/ and /ka/. Given the tight coupling of the neural response and build-up in oral air pressure, it can be inferred that the infraorbital nerve plays a fundamental role in signaling attainment of this speech goal. We suspect that the oral mucosa has a role in oral sensory feedback for the allophones, but that oral air pressure and vibration are sensed at sites close to the point of articulation: e.g., /p/ in the lip and buccal mucosa, /ta/ in the palatal mucosa, and /ka/ in the palatal and pharyngeal mucosa. Unfortunately, it is impossible to perform microneurography in the palatine and glossopharyngeal nerves because of difficulty in inserting a tungsten electrode into these nerves.

Oral air pressure and hyper- or hyponasality might be important feedback parameters for the control of articulation. In our study, the sustained responses exhibited by some infraorbital nerve fibers indicated sensitivity, not only to the build-up, but also to the maintenance of oral air pressure during /pa/ production. During speech, control of oral airflow and pressure is attempted by stopping the air at the lips and by oropharyngeal opening and closing. The resulting vocal tract configurations and constrictions, with their considerable variations, have been shown to play a role in the attainment of plosives and fricatives. Indeed, the jaw position adopted during a given initial segment shows very little variation (1–2 mm) with repetition of the same utterance. Whereas, there are several millimeters of variation under nonspeech conditions (MacNeilage, 1970). The process by which sensory feedback is provided to motor mechanisms needs to be understood in order to comprehend how the articulators strike a relatively constant target and to understand speech development and disorders, as described by Scott and Ringel (1971) and Bernstein and Stark (1985).

Based on the hypothesis that interactions among receptive functions, and increases in oral air pressure, may be involved in the production of intelligible sounds, improvement in receptive functions might provide an effective mechanism for achieving velopharyngeal closure, and enhancement of pronunciation skills, through enhanced ability to sense oral air pressures. Indeed, children with unrepaired cleft palates or oropharyngeal inadequacies, or who suffer from pneumonia and frequent colds (especially in the first 2 years of life) are prone to develop delayed speech (van Riper, 1961), and may also have aberrations in the receptive functions. If this is true, perceptual development might be impacted negatively, since intraoral air pressure during blowing and phonation would be abnormal. Babbling, characterized by age-appropriate vocalization, utilizes the natural airflow through the mouth and comprises the first stage in the acquisition of speech. Although the dynamics of perceptive verbal development remain unknown, babbling develops during the stage before that of uttering the first words, and children may establish a link between babbling and their receptive functions through the sensory monitoring of their own oral air pressure and vibration. We can consider that children with delayed language development may suffer, in part, from a lack of normal sensory feedback during their development, because perceptual processes involving receptive organs may affect their fine speech production skills, such as, the weak production of the stop consonants.

Furthermore, it is conceivable that the tactile or pressure stimulation of mechanoreceptors supplying the oral mucosa, achieved by holding a nipple in the baby's mouth and manipulating appropriate toys in the young child's mouth, might contribute to the normal development of babbling. It seems reasonable to suggest that the vibration created by the oral air stream, and by early speech, may also contribute to a child's developing oral kinesthesia and motor control skills.

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