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Modulation, adaptation, and control of orofacial pathways in healthy adults

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Abstract

Although the healthy adult possesses a large repertoire of coordinative strategies for oromotor behaviors, a range of nonverbal, speech-like movements can be observed during speech. The extent of overlap among sensorimotor speech and nonspeech neural correlates and the role of neuromodulatory inputs generated during oromotor behaviors are unknown. The focus of this review is to consider the adaptive capacity of the orofacial substrate, and the neural correlates of kinematic parameter encoding at cortical and subcortical levels subserving oromotor behaviors. Special emphasis is directed toward distributed neural networks that are dynamically modulated by environment and task related demands.

Learning outcomes: Readers will (1) gain a better understanding of healthy adult orofacial pathways, (2) be able to identify orofacial pathway components that contribute to sensorimotor integration, and (3) better understand the flexible connectivity among distributed neural networks subserving oromotor behavior.

Keywords

Corticobulbar system; neural encoding; sensorimotor control; speech kinematics

1. Introduction

The kinematics of muscle synergists are often based on a desired outcome within a given behavioral context. Different muscle subgroups cooperate in variable fashions to produce more than one form of behavior, modify an ongoing behavior, or generate corrective motor responses (Islam, Zelenin, Orlovsky, Grillner, & Deliagina, 2006; Mentel, Krause, Pabst, El Manira, & Buschges, 2006; Mentel, Cangiano, Grillner, & Buschges, 2008; Zelenin, Grillner, Orlovsky, & Deliagina, 2003). Goal oriented behavior and adaptive movements are encoded by forebrain structures, particularly the basal ganglia and their thalamic connections, together with the brainstem/spinal cord (Lund & Kolta, 2006; Nakamura & Katakura, 1995). Extensive corticostriatal projections and direct corticopontine and corticospinal projections contribute to skilled hand and finger movements and possibly speech motor coordination (Grillner, Wallen, Saitoh, Kozlov, & Roberson, 2008; Lund & Kolta, 2006). Adaptability of ororhythmic motor

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pattern generation in humans has been demonstrated in the context of simple speech tasks (Estep & Barlow, 2007), the nonnutritive suck response to pacifiers of varying stiffness (Zimmerman & Barlow, 2008), and changes in food hardness during chewing (Takahashi, Miyamoto, Terao, & Yokoyama, 2007). It is yet to be determined how a network such as that encoding speech versus nonspeech oromotor behaviors is modulated by task demands and what functions the changing interregional interactions might subserve for the functionally specific ensembles of muscles and joints (Kelso & Tuller, 1983; Moore, Smith, & Ringel, 1988; Tuller & Kelso, 1984).

Functional neuroimaging investigations of human speech and nonspeech behaviors have highlighted a range of shared-to-unique neural activations among cortical areas, brainstem nuclei and their adjacent interneuronal sites (Alario, Chainay, Lehericy, & Cohen, 2006; Bohland & Guenther, 2006; Bonilha, Moser, Rorden, Baylis, & Fridriksson, 2006; Ozdemir, Norton, & Schlaug, 2006; Soros et al., 2006; Terumitsu, Fuji, Suzuki, Kwee, & Nakada, 2006; Wise, Greene, Buchel, & Scott, 1999). However, it remains unclear to what extent specific oromotor performances may share central neural circuitry while utilizing task-specific physiological mechanisms. Understanding the presence and degree of functional correlates associated with changes in the orosensory environment or goal oriented oromotor behavior is of major significance for fundamental communication neuroscience research as well as a potential aid in understanding mechanisms of peripheral damage/inflammation (e.g., orofacial surgery) or central nervous system injuries (e.g., stroke, traumatic brain injury) associated with difficulty in speaking and aerodigestive behaviors.

2. Adaptive mechanisms of the trigeminal somatosensory system

Healthy perception requires an integration of spatiotemporal patterns of sensory input at multiple levels of the mammalian trigeminal somatosensory system which adapts its responsiveness for appropriate detection and discrimination of peripheral stimuli (Fanselow & Nicolelis, 1999; Moore, 2004). It is hypothesized that the magnitude of response to a sustained stimulus is adapted to effectively reduce cortical gain and match neuronal sensitivity to the particular input conditions (Higley & Contreras, 2006). Repetitive stimulation has been demonstrated to evoke a balanced reduction in the magnitude and timing of thalamocortical and corticocortical excitatory and inhibitory synaptic relays (Chung, Li, & Nelson, 2002; Higley & Contreras, 2007a, 2007b). For example, local circuit operations within subcortical afferent pathways contribute to sensory integration mechanisms that can result in suppression or amplification of output from the thalamus and cortex (Castro-Alamancos, 2002; Higley & Contreras, 2007a, 2007b; Varga, Sik, Lavalée, & Deschenes, 2002). Frequency dependent adaptation is sensitive to changes in stimulus rate or velocity and results in cortical neuroplastic changes such as reduced response magnitude (Estep, Barlow, Auer, Kieweg, Lee, & Savage, 2007; Khatri, Hartings, & Simons, 2004) and decreased receptive field size (Katz, Heiss, & Lampl, 2006).

Appropriate gating of orofacial cutaneous stimuli is achieved by modulation of cortical, subcortical, and brainstem activities (Sessle, 2000; Sessle et al., 2005; Trulsson & Essick, 2004). The trigeminal brainstem complex contains relay neurons that serve as interneurons in reflex circuits (Estep & Barlow, 2007) or project to the thalamus directly or via polysynaptic pathways that may involve the reticular formation (Alipour, Chen, & Jurgens, 2002; Krout, Belzer, & Loewy, 2002). Brainstem neural circuits may be operational in varying degrees affecting perception at higher brain centers. Alteration in central activation threshold to peripheral stimuli contributes to tenderness, hyperalgesia and allodynia of superficial as well as deep tissues (Sessle, 2000; Svensson, Baad-Hansen, Thygesen, Juhl, & Jensen, 2004; Svensson & Sessle, 2004). For example, prolonged irritation, damage, or inflammation of peri- and intraoral tissues associated with medical interventions requiring trussing of the face with

surgical tape to secure feeding or ventilation tubes contribute to hypersensitization of the human infant orofacial sensorium (Barlow, Finan, Chu, & Lee, 2008; Barlow, Poore, Zimmerman, & Finan, 2008).

The range of adaptive potential of craniofacial tissues can be compromised by an overload of stimulation. Positive adaptive responses to mechanical loading, infection, or trauma include hand-to-face protective responses, tongue-protrusion reflexes, and reversible nociceptive changes in the CNS. When the threshold of the adaptive potential of the tissues is exceeded, negative outcomes such as persistent maladaptive behavior and neurologic disorders (e.g., chronic pain or dyskinesia) tend to occur (Sessle, 2000, 2005). Determining how well an individual adapts to acute or chronic environmental alterations may be an indicator of the integrity of orofacial pathways (Buonomano & Merzenich, 1998; Henry & Marasco, 2005; Sessle et al., 2005). Further investigation of 1) the biologic reactions to mechanical stress (e.g., displacement, force, stress, strain induced by medical intervention) endured by orofacial region, and 2) the extent to which structural or functional changes in orofacial pathways are correlated to sensitization are required to better understand the environmental factors that compromise the adaptive capacity of the orofacial system. This knowledge is anticipated to improve our ability to differentiate between adaptive processes such as protective reflexes compared to pathologic states such as maladaptive behaviors.

3. Neural encoding of oromotor kinematic parameters

Sensorimotor adjustments are presumed to provide anatomical stability and kinematic variability associated with speech (Nasir & Ostry, 2006; Shiller, Houle, & Ostry, 2005; Shiller, Ostry, & Laboissiere, 2002). Kinematic parameters such as force, rate, or velocity of articulators are often used as outcome measures for examining the relation between changes in motor function and brain function (Ludlow, 2008). Dysarthric motor speech profiles often present numerous kinematic parameter deficits (e.g., articulator timing patterns, range of movement, peak velocity) specific to neurologic diseases (Ackermann, Hertrich, & Scharf, 1995; Ackermann, Konczak, & Hertrich, 1997; Caligiuri, 1987; Connor, Abbs, Cole, & Gracco, 1989; Forrest & Weismer, 1995; Kent & Netsell, 1978; Yunusova, Weismer, Westbury, & Lindstrom, 2008). Disproportionate breakdowns in timing patterns of speech have been noted in speakers with the lowest intelligibility scores (Yunusova et al., 2008; Weismer, Yunusova, & Westbury, 2003), possibly due to the severity of impairment.

Functional neuroimaging investigations of the orofacial system have provided some insight on the nature of distributed neural networks activated by speech and nonspeech tasks such as speaking a single syllable (Riecker et al., 2000), syllable trains produced at different frequencies (Riecker et al., 2005), whistling (Dresel et al., 2005), and opening the mouth altered with protruding the lips (Soros et al., 2006). The interconnected cortical and subcortical regions are commonly and differentially recruited for rate and complexity of speech (Bohland & Guenther, 2006; Riecker, Brendel, Ziegler, Erb, & Ackermann, 2008; Riecker, Kassubek, Groschel, Grodd, & Ackermann, 2006) and nonspeech tasks (Corfield et al., 1999; Dresel et al., 2005; Tamura, Kanayama, Yoshida, & Kawasaki, 2003). Task dependent scaling of basal ganglia, frontomesial motor areas, and cerebellar correlates is hypothesized to reflect the internal encoding of movement kinematics (Ackermann & Hertrich, 2000; Dresel et al., 2005; Hertrich & Ackermann, 1997; Pope, Wing, Praamstra, & Miall, 2005; Riecker et al., 2006; Vaillancourt, Mayka, Thulborn, & Corcos, 2004). Increasing task complexity further engages the speech production system by recruiting areas beyond the primary sensorimotor cortices that are also known to be involved in nonspeech motor sequencing (Ackermann, 2008; Bohland & Guenther, 2006; Guenther, Ghosh, & Tourville, 2006; Riecker et al., 2000, 2005, 2006, 2008).

4. Direction for future studies

Functional neuroimaging is anticipated by many researchers to address questions of how the healthy brain encodes fundamental units of oromotor coordination, implements these units in a range of task- or environment- related contexts, and how the central representation of units interacts with feedback. Investigations of the cortical and subcortical correlates that encode articulatory kinematic parameters may provide insight to how task, neuronal context, and/or disease affect the neural bases of: 1) coordination of segment related movements, 2) speech intelligibility, and 3) compensatory mechanisms of the articulatory system (Ackermann et al., 1997; Estep, Barlow, Auer, Kieweg, Lee, & Savage, 2008; Max, Caruso, & Gracco, 2003; Hirose, 1986; Indefrey & Levelt, 2000; Nasir and Ostry, 2006; Weismer, Jeng, Laures, Kent, & Kent, 2001; Yunusova et al., 2008). Combining functional neuroimaging data with recordings of movement kinematics could ultimately be useful in understanding functional changes in plasticity after stroke or injury, and the disordered orofacial sensorimotor functions in clinical populations (e.g., Parkinson's disease, cerebellar disease, TBI, cerebral infarction), and optimize speech and nonspeech rehabilitative strategies.

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Appendix A. Continuing education (*correct answer)

1. Different muscle subgroups cooperate in variable fashions to perform all of the following EXCEPT:
 - a. Produce more than one form of behavior.
 - b. Modify an ongoing behavior.
 - c. Generate corrective motor responses.
 - d. Disrupt ongoing adaptive movements.*
2. Which of the following outcomes tend to occur when the adaptive threshold of orofacial tissues is exceeded?
 - a. Reversible changes in pain threshold.
 - b. Persistent maladaptive behavior.*
 - c. Temporary protective responses.
 - d. Increase in orofacial pathway development.
3. How well an individual adapts to environmental changes may be an indicator of what?
 - a. Integrity of the individual's orofacial pathways.*
 - b. Competing modes of somatosensory perception.
 - c. The minimal range of articulator movement.
 - d. Kinematic parameter encoding that is task specific.
4. Task dependent scaling of oromotor cortical and subcortical correlates is hypothesized to reflect which of the following:
 - a. Decreased motor control.
 - b. Impaired sensorimotor integration.

- c. The encoding of movement kinematics.*
 - d. Long-term memory capacity.
5. Distributed neural networks are activated by:
- a. Speaking a single syllable.
 - b. Speaking repetitive syllable trains.
 - c. Nonspeech movements.
 - d. All of the above.*

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