Muscle-fiber heterogeneity in craniofacial muscles: Implications for speech development and speech motor control

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INTRODUCTION:

The essential enzyme of muscle contraction is myosin, which hydrolyzes ATP to provide the energy that activates actin-myosin crossbridges to generate force or to do physical work. The various subunits of myosin are expressed as families of isoforms that have the same general function but allow for variations in quantitative aspects such as contraction rate and metabolism. The different muscle fiber types create a continuum of different contraction speeds ranging from low to high as follows.

I - IC - IIC - IIAC - IIA - IIAB - IIB - IIX

SLOW ⟷ FAST

The continuum is enhanced by the presence of developmental isoforms (e.g., Fetal), specialized isoforms (e.g., Mandibular, Cardiac), and hybrid fibers (e.g., IM/IIC). Hybrid fibers usually have a contraction speed that is intermediate to their constituent pure isoforms.

METHODS:

A review of the literature was conducted using High Wire Press, PubMed, and other literature retrieval systems. Search terms included: muscle fibers, craniofacial muscles, myosin heavy chain, and the names of individual muscles. The primary goal was to collate information on the relative proportion of muscle-fiber types, but information on other properties, such as metabolism and developmental transitions, was also noted. Muscle fiber data were obtained for the following muscle groups, with individual muscles identified in parentheses:

Facial (orbicularis oris, buccinator, zygomatic)
Lingual (genioglossus; superior, longitudinal, and transverse intrinsic muscles*)*
Jaw elevators (masseter, medial pyerygoid, temporalis *)*
Jaw depressors (digastric, geniohyoid, mylohyoid*)*
Palatal elevators (levator veli palatini, tensor veli palatini)
Palatal depressors (palato-pharyngeus, uvula)
Pharyngeal (cricopharyngeus, superior pharyngeal constrictor, cricothyro-pharyngeus)
Laryngeal (posterior cricoarytenoid, cricothyroid, lateral crycoarytenoid, thyroarytenoid, vocalis).

RESULTS:

Main results are summarized with arithmetic signs:
= (roughly equal), > (more than) and >> (much more than)
to show the relative number of different fiber types in a muscle. For example, a muscle with a predominance of type I fibers and only a few type IIA fibers would be expressed as I >> IIA.

Facial muscles

Orbicularis oris (OO): IIA >> I = IIC
Zygomatic (Zyg): I = IIA > IIC

Implications:
Abundance of type II fibers in OO is consistent with the rapid acceleration and high speed needed for intermittent orofacial movements, such as bilabial stops. NB: OO and Zyg share embryologic origin and innervation but differ in function; therefore muscle fiber composition seems to be determined largely by function.

Tongue muscles

Intrinsic muscles in anterior tongue: IIA >>>I = IM/IIC
Intrinsic muscles in posterior tongue: I = IM/IIC > IIA

Implications:
The predominance of small type IIA fibers in the anterior portion permits rapid movements of tongue tip and blade, whereas a proportionately larger population of larger type I and type IM/IIC fibers in the posterior region aids postural support of the tongue body and relatively slow vowel-to-vowel movements.

Jaw muscles

Jaw elevators: I = Hybrid >> IIA = IIX = Fetal = Cardiac
Suprahyoid depressors: I = IIA > IIX > Hybrid
Infrahyoid depressors: I = IIA >> IIX = Hybrid

Implications:
The jaw elevators are adapted for relatively slow, tonic movements such as postural support for speech and swallowing movements, whereas the depressors are suited to faster, phasic movements, such as jaw opening for syllables, and presumably consonant-to-vowel transitions in babbling. Fiber polymorphism enables the jaw muscles to achieve different specializations in chewing, swallowing, and speech.

Pharyngeal muscles

Pharyngeal constrictor: IIA > I > Hybrid
Cricopharyngeal: IIA > I > Hybrid
Cricothyopharyngeus: I > IIA = Tonic > IIX
Other histological features

Implications:
Studies document substantial inter-individual variability, presence of hybrid fibers, and a predominance of Type IIA fibers. Mu and Sanders (2008), in their description of a newly discovered muscle, the cricothyropharyngeus, noted unusual MyCH isoforms including slow-tonic, alpha-cardiac, neonatal, and embryonic. They concluded that this muscle "appears to be a newly described and uniquely human muscle with characteristics suggesting a specialized function that may be speech related" (p. 927).

Palatal muscles

Palate elevators: I >> IIA = IIAB
Palate depressors: IIA = IIAB > I

Implications:
Elevators are designed for tonic contraction to support prolonged velopharyngeal closure as needed for non-nasal sound sequences (e.g., canonical babbling), whereas depressors are more suited to rapid phasic movements of the palate. The agonist-antagonist muscles have a different fiber composition that appears to meet functional needs.

Laryngeal muscles

Posterior cricoarytenoid (PCA): I >> IIA = Hybrid
Lateral cricoarytenoid (LCA): I = IIA = IIX
Thyroarytenoid (TA): I = IIX > IIA > Hybrid
Vocalis: I = IIA = IIX
Cricothyroid: IIA > I = Tonic

Implications:
The PCA, the laryngeal abductor, has a slower fiber type profile than the principal adductor, the TA, a difference that may be related to the tonic activity of the PCA during respiration.

Development of the vocal fold can be summarized as:

1) monolayer of cells in the neonate
2) bilaminar structure by about two months
3) a more fully constituted bilaminar structure by five months
4) a trilayer by the age of seven years

Therefore, the lamina propria undergoes substantial change during early periods of vocal experience. A study of unphonated vocal folds in three young adults with severe cerebral palsy evinced abnormalities in vocal fold mucosa presumably due to the lack of mechanical stimulation normally provided by phonation (Sato, Nakashima, Nonaka, & Harabuchi, 2008).

SUMMARY:

a) Slower-type profiles are found in: zygomatic, jaw elevators, posterior tongue, palatal elevators, and the laryngeal abductor (posterior cricoarytenoid). These profiles are suited to tonic contractions and postural support.

b) Faster-type profiles are found in: lips (orbicularis oris), jaw depressors, anterior tongue, palatal depressors, pharyngeal muscles, and laryngeal adductors. These profiles are suited to rapid phasic movements.

GENERAL PROPERTIES OF MUSCLE FIBERS IN CRANIOFACIAL MUSCLES:

1. These muscles are unique in their genetic, developmental, functional, and phenotypical properties (Schuler & Dalrymple, 2001; Tzahor, 2009).
2. The muscle-fiber composition of these muscles differs (a) from muscles of the limbs or trunk, (b) from homologous muscles in nonhuman species, (c) across muscles and sometimes from one region or belly of a muscle to another, and (d) across agonist-antagonist muscle sets (e.g., laryngeal adductors/abductors, jaw depressors/elevators, velar depressors/elevators) (reviewed in Kent, 2004).
3. The degree of hybridism in muscle fibers may reflect the diversity or specialization of activity in a given muscle (Hoh, 2002, 2005; Wu, Crumley, & Caiozzo, 2000; Stephenson, 2006). Speech is a beneficiary of this feature.
4. Variation in muscle-fiber types within a muscle, together with localized motor unit territories, enables task-specific motor activity (Van Eijden & Turkawski, 2001).
5. Speech motor control is a beneficiary of these properties, which have general relevance in explaining certain aspects of speech development including motor patterns in babbling.

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A full set of references is available at http://www.waisman.wisc.edu/vocal/.

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