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Developmental and functional considerations of masseter muscle partitioning

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ABSTRACT

The masseter muscle participates in a wide variety of activities including mastication, swallowing and speech. The functional demands for accurate mandibular positioning and generation of forces during incising or a power stroke require a diverse set of forces that are determined by the innate muscle form. The complex internal tendon architecture subdivides the masseter into multiple partitions that can be further subdivided into neuromuscular compartments representing small motor unit territories. Individual masseter compartments have unique biomechanical properties that, when activated individually or in groups, can generate a wide range of sagittal and off-sagittal torques about the temporomandibular joint. The myosin heavy chain (MyHC) fibre-type distribution in the adult masseter is sexually dimorphic and is influenced by hormones such as testosterone. These testosterone-dependent changes cause a phenotype switch from slower to faster fibre-types in the male. The development of the complex organization of the masseter muscle, the MyHC fibre-type message and protein expression, and the formation of endplates appear to be pre-programmed and not under control of the muscle nerve. However, secondary myotube generation and endplate maturation are nerve dependent. The delayed development of the masseter muscle compared with the facial, tongue and jaw-opening muscles may be related to the delayed functional requirements for chewing. In summary, masseter muscle form is pre-programmed prior to birth while muscle fibre contractile characteristics are refined postnatally in response to functional requirements. The motor control mechanisms that are required to coordinate the activation of discrete functional elements of this muscle remain to be determined.

1. Introduction

The masseter muscle, one of the four muscles of mastication, participates in a wide variety of activities including mastication, swallowing and speech. This diversity of function requires coordination of motor output elements of masticatory muscles (i.e., compartments) along with appropriate activation of tongue, facial and oropharyngeal muscles. Mastication involves diverse and accurate mandibular movements to incise and grind food suitable for swallowing. Accurate mandibular positioning in the medial–lateral or anterior–posterior positions combined with the generation of high forces during a protruded jaw position for incision or a lateral to medial power stroke requires the ability to activate distinct combinations of muscle compartments to accomplish the required task. This overview will focus on one jaw-closing masticatory muscle, the masseter, and the behaviour of this muscle along with other masticatory muscles to produce a

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variety of torques about the temporomandibular joint. In addition, the temporospatial development of the form and function of the masseter muscle will be examined relative to other jaw and tongue muscles.

2. Masseter muscle architecture and function

The masseter muscle has been viewed for a long time as a complex muscle that is composed of three layers: superficial, intermediate and deep.[1] The functional elements of the masseter anatomy have been examined in an attempt to understand their fundamental properties. The complex internal tendon architecture subdivides the muscle into multiple partitions[2–4] that can be further subdivided into neuromuscular compartments representing small motor unit territories within each anatomical partition.[5,6] The individual masseter compartments have unique biomechanical properties that can generate a wide range of sagittal and off-sagittal torques about the temporomandibular joint.[7] In studies of regional masseter muscle activation during unrestricted mastication or during cortical stimulation to induce rhythmic jaw muscle activation, it has been shown that the individual compartments can be uniquely activated depending on the task but are more commonly activated in discrete groups with other jaw muscles.[2,8] The independent activation of masseter compartments is more apparent during production of off-sagittal torques about the TMJ compared with mid-sagittal, high-level torques. The motor control of these output elements has been examined at the level of the organization of the motoneurons, yet no distinct clustering of motoneurons representing each compartment has been observed.[9] Generation of complex behaviours requires coordination of discrete functional elements of multiple muscles on both sides of the jaw. This ability may be dependent on the functional organization of pre-motoneurons into movement control modules located in the brainstem that can be differentially sequenced and summed (see review by Mussa-Ivaldi and Bizzi).[10] However, this hypothesis remains to be tested for the masticatory muscle system.

3. Masseter muscle sexual dimorphism

The myosin heavy chain (MyHC) fibre-type distribution in the adult rabbit masseter generally does not vary among the different compartments (except for the faster contracting fibres in the deep compartment) but does differ between sexes.[11] A consistent finding of sex differences across species for the masseter muscle has been reported with a higher proportion of fibres with faster MyHC isoforms found in the adult male compared with the adult female.[11–13] In the rabbit, the male masseter has approximately 80% of the fibres containing MyHC type IIa phenotype. In contrast, the female masseter is composed of approximately 50% MyHC IIa and is similar to young adult rabbits (2-months old) where no sexual dimorphism of the MyHC protein can be observed.[14] In the adult mouse, an increased proportion of MyHC IIb isoform is found in the male mouse masseter while the female has a higher proportion of IIa[4,13] and these isoforms are regionally distributed. These masseter muscle sex differences can be observed early postnatally (days 1 and 8) in mice with females having higher levels of developmental and α-cardiac MyHC message expression compared with males.[15] In the early adult at postnatal day (pn) 28, the female mouse masseter is characterized by a slightly increased expression of α-cardiac and IIa isoform message, whereas the male masseter has an increased IIx and IIb expression. This differential expression of faster MyHC isoform message is consistent with hormonal changes observed during maturation. The male masseter MyHC fibre type is influenced by testosterone causing a proportional phenotype transition from slower to faster fibre-types.[13,16] The functional significance of faster contracting muscle fibres in males is unclear but may be based on the need for high force generation by jaw muscles for survival during food gathering and defence mechanisms.

4. Masseter muscle development

The development of the complex organization of the masseter muscle has been recently studied to further refine our understanding of this intricate and multifaceted process. Muscle–nerve interactions have a predominant role in post-natal muscle maturation and plasticity, but the role of these interactions in masticatory muscle development is unknown. The muscles of mastication are derived from the segmentation of a single muscle mass at gestational day (gd) 11. The partitioning of this mass into specific jaw muscles and compartments is concomitant with the branching of the trigeminal nerve in intact embryos.[17] In our studies of the role of the muscle nerve during development, we evaluate an embryo mouse model lacking sensory and motor innervation. Aneural embryos are generated by the injection of a 1 μl solution (0.5 μg/μl) of β-bungarotoxin into the amnionic sac at gd12 and compared with a littermate that receives a control injection of PBS. At gd18, patterning of different jaw muscles and their anatomical layers is not found to be dependent on muscle–nerve interactions but appears to be pre-programmed.[18] These findings support the concept that the complexity of the masseter muscle architecture is established prior to birth. However, the muscle volume of different jaw muscles in aneural embryos is smaller and may be related to the limited ability to generate secondary myotubes in the absence of innervation.

Message for all MyHC isoforms (embryonic, neonatal, slow, α-cardiac, IIa, IIx, IIb) is detected within the mouse masseter at gd13/14 with adult isoforms co-expressed with developmental isoforms.[19–21] Embryonic and neonatal isoforms increase in expression with developmental age and then decrease postnatally.[22,23] These developmental MyHC isoforms have a prolonged postnatal expression in the masseter compared with limb and tongue muscles and are gradually replaced by the adult isoforms in the mouse.[21] Interestingly, the neonatal MyHC isoform has been found to be co-expressed with slow or fast isoforms in a significant proportion of adult masseter fibres in rabbit and humans.[24–26] The expression of slow MyHC isoforms, observed throughout the masseter at gd14, is also gradually replaced postnatally by fast isoforms.[27] MyHC IIb has an early and transient appearance at gd14, but is a