Chapter

Proprioceptors in Cephalic Muscles

Juan L. Cobo, Sonsoles Junquera, José Martín-Cruces, Antonio Solé-Magdalena, Olivia García-Suárez and Teresa Cobo

Abstract

The proprioception from the head is mainly mediated via the trigeminal nerve and originates from special sensitive receptors located within muscles called proprioceptors. Only muscles innervated by the trigeminal nerve, and rarely some muscles supplied by the facial nerve, contain typical proprioceptors, i.e. muscle spindles. In the other cephalic muscles (at the exception of the extrinsic muscles of the eye) the muscle spindles are replaced by sensory nerve formations (of different morphologies and in different densities) and isolated nerve fibers expressing mechanproteins (especially PIEZO2) related to proprioception. This chapter examines the cephalic proprioceptors corresponding to the territories of the trigeminal, facial, glossopharyngeal and hypoglossal nerves.

Keywords: proprioception, muscle spindles, atypical proprioceptors, cephalic muscles, PIEZO2, mechanoproteins

1. Introduction

Proprioception is a quality of the somatosensory system that informs the central nervous system about the static and dynamics conditions of muscles and joints. This type of sensitivity has been studied in deep in the muscles depending on the spinal nerves and today the neurobiology of spinal proprioception is well known [1–4]. On the contrary, the neuroanatomy as well as the cellular and molecular bases of the proprioception in the cephalic muscles is not well known. Nevertheless, it is clear that cephalic muscles permanently develop fine adjustments of stretching and tone in facial movements, regulation of chewing force, oromotor reflex behaviors, verbal and nonverbal facial communication, swallowing, coughing, vomiting or breathing [5–7].

The skeletal muscles contain an intrinsic mechanosensory system, the proprioceptive system, which provides unconscious and conscious information to the central nervous system. The proprioceptive inputs originate in specialized sensory organs (proprioceptors) present in muscles (muscle spindles [8, 9]), tendons (Golgi's tendon organs [10]), joint capsules (Ruffini-like sensory corpuscles, Pacinian corpuscles and free nerve endings [11]), and presumably also the skin but their physiological properties suggest they are not the alternative to muscle spindles [2, 12–14]. The information encoded by the propioceptors gives rise to unconscious and conscious sensations, necessary for most basic motor functions [15]. For those interested in a recent review and in detail on both types of proprioceptors, we refer to the Banks [8] and Macefield and Knellwolf [16].

Some decades ago, Baumel [17] suggested that proprioceptive impulses from facial muscles are conveyed to the central nervous system via different branches of trigeminal nerve throughout multiple communications with the branches of the facial nerve. Actually, it is accepted that the proprioception of all cephalic muscles depends on the trigeminal nerve [6, 18].

Therefore, the first unresolved issue in cephalic proprioception is whether all cranial nerves that innervate striated muscles also collect their proprioceptive innervation. According to Lazarov [18] the proprioceptive innervation of all cephalic muscles depends exclusively on the trigeminal nerve. In other words: the sensory ganglia of cranial nerves lack of primary sensory neurons and the proprioceptors of the cephalic muscles are supplied by neurons from the trigeminal mesencephalic nucleus [19].

The second aspect pending clarification is: if the proprioception of the cephalic muscles depends exclusively, or mainly, on the trigeminal nerve, how do the fibers of this nerve reach the muscles of the territories of other nerves? This question can be answered because to extensive communications of the trigeminal nerve with other cranial nerves. The trigeminal nerve has numerous connections to the facial nerve [20–34] and the data collected from animal models indicate that the nerve fiber interchange is always from the trigeminal to the facial nerve and not on the contrary [35]. To serve facial proprioception additional connections between the facial and cervical spinal nerves exists [36, 37]. Apart from those communications no specific reference of communications between the trigeminal nerve with the glossopharyngeal, vagal and hypoglossal nerves were found. But presumably the trigeminal proprioceptive fibers pass from the trigeminal nerve to them directly on the target organs themselves (tongue, pharynx, palate) or through their connections with the facial nerve [28, 31, 32].

And the third main question of cephalic proprioception regards the identification and characterization of proprioceptors in the cephalic muscles. The skeletal muscles innervated by spinal nerves contain neuromuscular spindles and Golgi tendon organs, in addition to other types of corpuscles with less functional entity [8–11]. However, only the cephalic muscles supplied by the mandibular branch of the trigeminal nerve, and *the platysma colli* muscle contain neuromuscular spindles [38–40]. Therefore, cephalic proprioceptors, if any, have to be represented by other sensory nerve formations other than neuromuscular spindles. Recent studies, using immunohistochemistry techniques associated with specific markers related to mechanization, have shown that facial muscles [34, 41, 42] and some pharyngeal muscles [43] have differentiated sensory structures that presumably replace proprioceptors. However, it cannot be ruled out that sensitive nerve fibers reaching the muscles (especially nociceptive ones) can function as mechanoreceptors-proprioceptors (see [44]).

2. Distribution of typical proprioceptors in cephalic muscles

Typical proprioceptors of human cephalic muscles are represented by neuromuscular spindles as most of them lack Golgi tendon organs since they lack true tendons.

Muscle spindles have been found in muscles innervated by the trigeminal nerve while in the territory of the other cranial nerves, with very rare exceptions, are absent [6]. Recently, Junquera [45] determined the relative density of muscle

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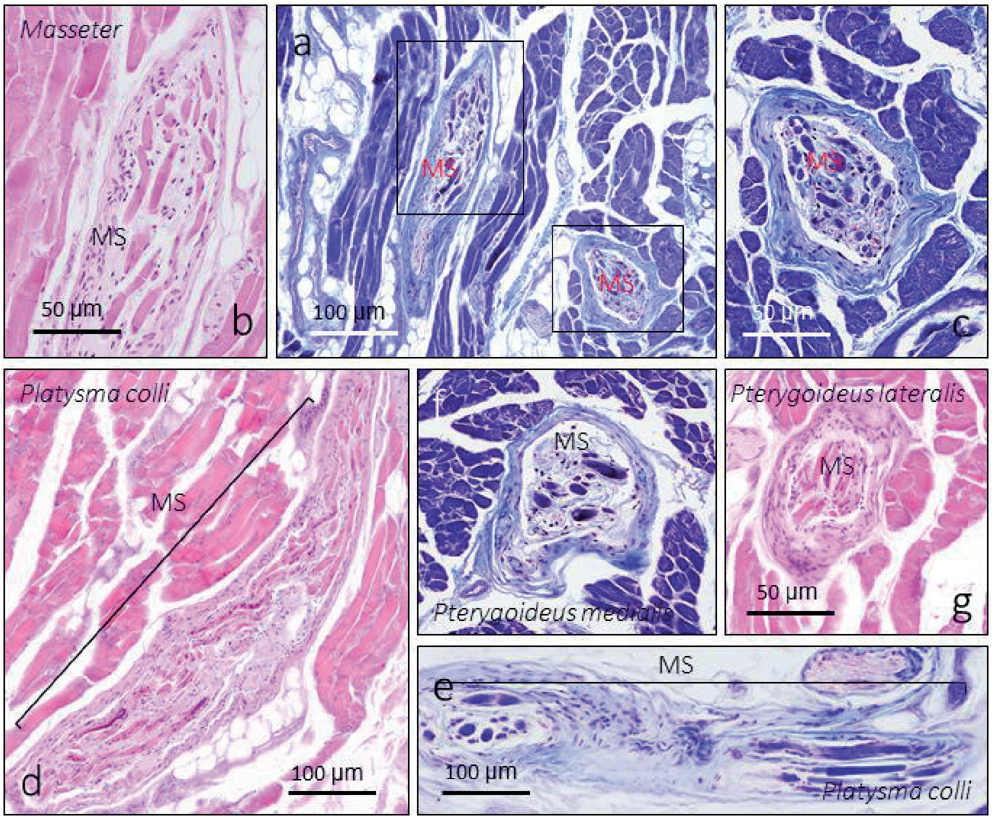

Figure 1.
Longitudinal and transversal sections of muscle spindles from different cephalic muscles. MS: muscle spinde.

spindles in human jaw muscles (**Figure 1**; **Table 1**). The *M. temporalis*, *m. masseter*, *m. perygoideus medialis* and m. *pterygoideus lateralis* contained numerous muscle spindles whereas they were less abundant in the *digastricus* and *mylohyoideus* muscles [45, 46]. The absence [45, 47] or presence [48] of muscle spindles in the *tensor veli palatini* muscle, also innervated by the trigeminal nerve, has been reported. It should be noted that atypical proprioceptors were also found in these muscles (**Table 1**; see below).

In muscles where the density of muscle spindles is higher, they consist of thick capsule, a shallow intracapsular space filled with variable number of intrafusal muscle fibers (ranging from 4 to 12). In muscles where the density of neuromuscular spindles was low, in general, the size of the spindles was smaller, had fewer intrafusal fibers and the capsule was less developed [45].

In the territory of the facial nerve one muscle spindle was found in the muscle *orbicularis oculi* in one pediatric specimen [49] whereas abundant muscle spindles have been found in the *platysma colli* [40]. Junquera [45] in her doctoral dissertation also observed typical muscle spindles in the *plastysma colly* more numerous in the cervical segment of the muscle than in the suprahyoid one.

3. Atypical putative proprioceptors cephalic muscles

3.1 Criteria to characterize atypical proprioceptors

The identification of putative sensory receptors in the cephalic muscles that may serve as proprioceptors was based on the following criteria: independence of the nerve trajectory, be placed in close relation to muscle fibers, show a morphologically differentiated aspect, and display immunoreactivity for any putative mechanoprotein [34].

Muscle	MS	Type I	Type II	Type III	INS*
M. temporalis	14	6	8	6	Yes
M. masseter	23	3	3	6	Yes
M. pterygoideus lateralis	18	3	14	7	Yes
M. pterygoideus medialis	21	5	10	3	Yes
Venter anterior m. digastricus	2	3	1	1	Yes
M. mylohyoideus	1	3	1	1	Yes
M. tensor veli palatini	0	2	2	1	Yes
M. corrugator supercilii + M. depresor supercilii		1	3	7	Yes
M. orbicularis oculii					
pars palpebralis	0	3	11	9	Yes
pars orbitalis	0	1	7	9	Yes
M. orbicularis oris					
pars marginalis	0	5	19	12	Yes
pars labialis	0	7	13	7	Yes
M. zygomaticus maior	0	1	4	4	Yes
M. zygomaticus minor	0	1	2	0	Yes
M. buccinator	0	19	28	10	Yes
M. depressor labii inferioris + mentalis	0	0	8	2	
M. levator labii superioris	0	1	1	3	Yes
Platysma colli**	12/8	11/7	4/7	6/8	Yes/ Yes
M. genioglossus	1	16	28	10	Yes
M. palatoglossus	0	0	5	3	Yes
M. uvulae	0	0	7	3	Yes
M. constrictor pharyngis superior	0	0	6	14	Yes
M. constrictor pharyngis inferior	0	0	5	9	Yes

**Isolated nerve fibers displaying immunoreactivity for any of the mechanoproteins investigated.*
***facial/cervical segments.*

Table 1.
Distribution and density of muscle spindles (MS), atypical proprioceptors (types I to III) and isolated nerve fibers (INF) in muscles supplied by the trigeminal nerve (green), facial nerve (blue), hypoglossal nerve (white) and glossopharyngeal nerve (brown).

In agreement with the above premises, capsulated and non-capsulated corpuscle-like structures of variable size and shape containing numerous axon profiles complexly arranged, have been identified. Given the morphologic heterogeneity of the corpuscle-like structures that fulfill the preestablished criteria we attempt to classify them into three types: type I, capsulated by a thin capsule, the glial cells variably arranged and showing different morphologies; type II, partially capsulated (the capsule being continuous with the perimysium), with variable morphology and in most of the cases the direction of the long axis was parallel to the one of muscular fibers; type III, non-capsulated and both the axon and Schwann-like cells are variably arranged (**Figure 2**).

On the other hand, it is now well established that at the basis of mechanosensitivity are mechanically-gated ion channels [50]. At present acid-sensing ion

Figure 2.
Types of putative proprioceptors in human cephalic muscles. INF: Isolated nerve fibers.

channel 2 (ASIC2) and Piezo2 have been detected in muscle spindles and are strong candidates to initiate the mechanotransduction in proprioceptors [50–56]. Also, the putative mechanoprotein transient-receptor potential vanilloid 4 (TRPV4) was detected in proprioceptors of the facial and pharyngeal muscles [42, 43].

3.2 Distribution in the territory of the facial nerve

No typical muscle spindles have been found in the human facial muscles [42, 57–61] with the exception of on the facial part of the muscle *platysma colli* [40, 45]. Conversely, they contain numerous atypical proprioceptors (**Table 1**) the type II of being the predominating and the greater density being observed in the *buccinator* and *orbicularis oris* muscles.

3.3 Distribution in the territory of the glossopharyngeal nerve

Most research have not found typical muscle spindles in the muscles innervated by the glossopharyngeal nerve although they are present in the human *palatoglossus* muscle [48].

Regarding the pharyngeal muscles, typical muscle spindles were never found with the exception of the *constrictor pharyngis inferior* of the crab-eating monkey (*Macaca irus*) [62]. Nevertheless, human pharyngeal muscles are richly innervated. In particular, the *constrictor pharyngis superior* and muscle *constrictor pharyngis inferior* (innervated by branches of the pharyngeal plexus, derived from the glossopharyngeal and vagal nerves, and a small contribution of facial nerve; [63]) contain type II and III putative proprioceptors and isolated nerve fibers that display immunoreactivity for mechanoproteins (**Table 1**) [43].

3.4 Distribution in the territory of the hypoglossal nerve

As far as we know no muscles spindles have been reported in togue muscles. Junquera [45] observed one muscle spindle in the genioglossus muscle as well as numerous putative proprioceptors (**Table 1**).

Therefore, as a whole, the cephalic muscles have proprioceptive inervation, although only the muscles innervated by the trigeminal nerve and the *platysma colli* muscle innervated by the facial nerve contain neuromuscular spindles. The cephalic proprioceptors may be is involved in the coordination of facial movements and non-verbal communication, in language, swallowing and some other reflexes [64–66].

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