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Predicting Muscle Anatomy from Vibrissa Kinematics and *Vice Versa* in Whisking Mammals

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Abstract

Exploratory behavior in whisking mammals involves whisking and sniffing that are driven and controlled by facial muscles. The first half of the 20th century marked a significant progress in the identification of individual facial muscles in mammals and their functional contribution to motion. Recently, the study of facial musculature attracted renewed attention aimed to discover the mechanics underlying complex vibrissa and snout movements during whisking and sniffing. The principle of functional morphology asserts that a structure predetermines a function as much as a function predetermines a structure. Guided by this notion, we analyzed the structure and positions of the origin and insertion sites of facial muscles to infer their contribution to the complex vibrissa and rhinarium movements. Considering the shape, size and architecture of the snout in whisking mammals, we developed new methods of tissue treatment and obtained slices that contain all the vibrissa follicles with the relevant muscles, separately or within the entire snout. When the known structures could not fully explain the kinematics of complex motion, we used the function to predict the structural features of the muscles. Based on these predictions we designed the anatomical search. This complementary approach facilitated the discovery of several unknown facial muscles and a comprehensive understanding of mechanisms that drive and control complex motion of vibrissa and rhinarium in whisking rodents.

Keywords: Muscle anatomy forecast; Whisking; Sniffing; Mammals

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Abbreviations

MP: Mystacial Pad; CCO: Cytochrome Oxidase; OIM: Oblique Intrinsic Muscle; SLIM: Sling-Like Intrinsic Muscle

Introduction

During the last century, the functional anatomy of facial musculature in rodents gained much research attention [1-4]. While outlining the contribution of individual muscles to whisking motion, these studies could not fully explain the variety of whisker movements described by studies of tactile perception in whisking rodents. For example, the available data about the structure and function of facial musculature controlling whisking could not explain whisker torsion, a rotary motion of the whisker shaft around its own axis that was described in rats [5]. In this case, it was the analysis of whisker kinematics that preceded and defined the search for the structure.

A comprehensive understanding of motion thus benefits from the research approach that: (i) anatomically identifies new muscles and reveals their function; and (ii) analyzes the kinematics of the moving parts of the mammalian body and searches for the relevant muscles that can perform the observed movements. Here, we review studies, which by combining the anatomy to function axis, where structure predicts function, and the motion to anatomy axis, where function predicts structure, led to the description of novel facial muscles.

Finding anatomically appropriate muscles by analyzing vibrissa kinematics

The rich repertoire of the mystacial vibrissae movements in whisking mammals is so complex that whisking was termed a "sophisticated" behavior [6]. Whisking is performed by a group of anatomically and functionally connected muscles of the Mystacial Pad (MP). Vibrissa kinematics was characterized in detail by Knutsen and colleagues [5]. Reconstructing whisker position in 3D, they were able to decompose whisker motion to all its degrees of freedom. They found that whisker motion is characterized by translational movements and three rotary components: azimuth, elevation, and torsion. Azimuthal motion of the whiskers can be fully explained by contraction of the Sling-Like Intrinsic Muscles (SLIMs) of the MP and the extrinsic whisker protracting and

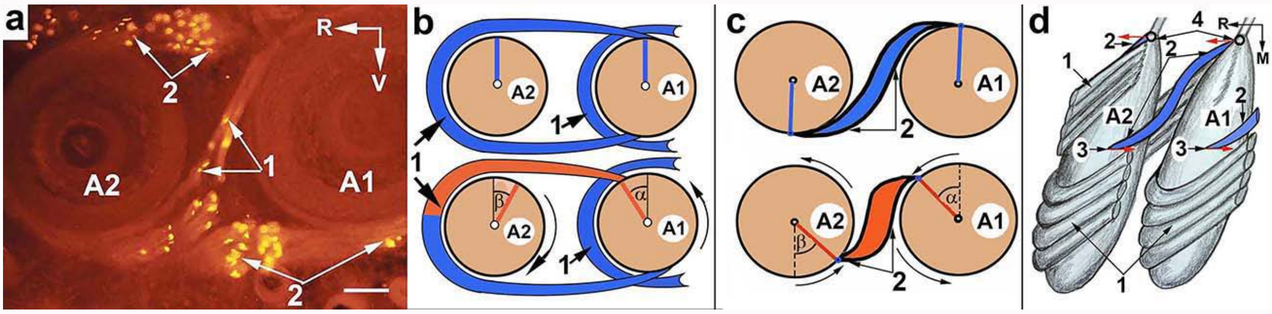

Figure 1: Intrinsic muscles of the mouse MP and their function. (**a**) Motor end plates in intrinsic muscles. Staining with rhodamin conjugated bungarotoxin. A1, A2, whisker follicles; (1) end plates in an OIM; (2) end plates in SLIMs. Scale bar = 0.1 mm. (**b-d**) Schematic drawings illustrating suggested mechanisms of whisker torsion and protraction. (1) SLIMs; (2) OIM (blue filling - relaxed muscles, red filling - contracted); (3) OIM origin; (4) whisker pivot points. (α,β) Angles of torsion of the whisker follicles A1 and A2, respectively. Curved arrows indicate the direction of torsion, red arrows show direction of pulling the follicles that causes whisker protraction. M: Medial; R: Rostral; V: Ventral. Modified from [7].

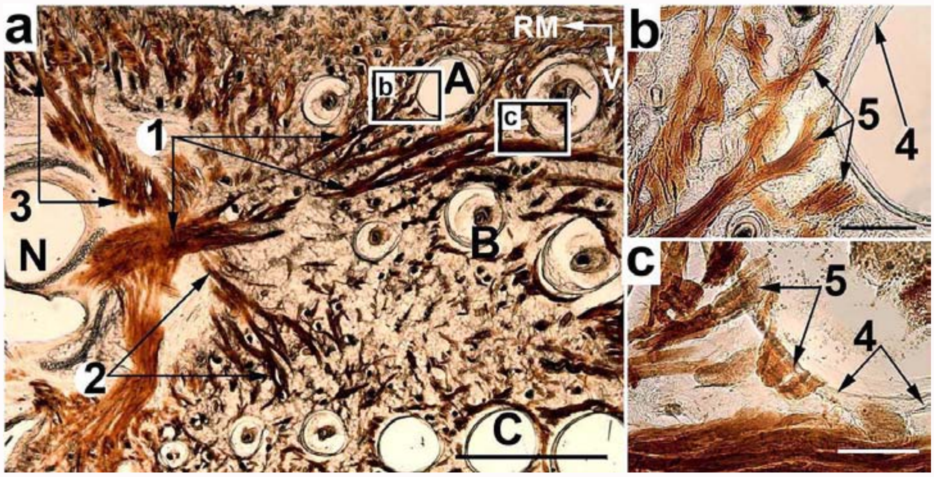

Figure 2: Pseudointrinsic slips. (a) Oblique tangential slice of the rostral part of the rat snout stained for CCO activity. (**b,c**) Enlarged boxed areas in (**a**). **A, B** and **C**, rows of vibrissae. (1) pseudointrinsic, (2) posterior, and (3) the most superficial slips of the pars interna of the *M. nasolabialis profundus;* (4) capsules of the vibrissa follicles; (5) insertion sites of the pseudointrinsic slips. N: Nostril; RM: Rostromedial; V: Ventral. Scale bars = 1 mm (**a**) and 0.1 mm (**b, c**). Modified from [11].

retracting muscles. The elevation component of whisker motion is driven by the *M. transversus nasi* that deflects the whiskers dorsally, and the *Pars orbicularis oris* of the *M. buccinatorius* that drives ventral deflections. Whisker torsion, a rotary motion of the whisker shaft around its own axis, was a newly described motion that could not be mechanistically explained by contraction of any of the known muscles. It was suggested that torsional rotation may result from asymmetric motor innervations of the SLIMs, leading to a stronger contraction of one of the two arms of the sling and thus to rotation of the whisker shaft. However, we excluded this mechanism demonstrating that the extremities of the SLIMs receive similar innervations (Figure 1a). Moreover, such asymmetric contraction would have caused the two neighboring whiskers in a row to rotate in opposite directions (Figure 1b), whereas the direction of rotational motion is similar for all whiskers in a row [5]. In contrast, based on the structure and anchoring points of the Oblique Intrinsic Muscle (OIM), we hypothesized that their contraction would rotate (Figure 1c) and protract (Figure 1d) neighboring vibrissae in the same direction. To confirm this anatomically based suggestion, we stimulated an OIM electrically and indeed observed resulting torsional rotation in the same direction and protraction of both neighboring vibrissae [7].

During whisking, all the vibrissae of the MP move synchronously and with similar amplitudes [8-10]. We observed that while most vibrissae have two SLIMs, vibrissae A4 and B4 have only one each. This structural difference in the face of functional homogeneity encouraged us to look for an additional muscle that can protract vibrissae A4 and B4 and compensate for the missing SLIMs. For this purpose, we prepared oblique tangential slices of the rostral part of the MP that included the nostrils. These slices revealed several muscle slips originating from the lateral wall of the nasal cartilaginous skeleton (Figure 2). Some of them were directed caudally and anchored into the corium of the MP that is occupied by rows A and B. Others anchored into the rostral surface of the vibrissa capsules of rows A and B.

Before this study was performed, it was known that whiskers of the MP in whisking mammals are driven by two groups of muscles: (i) extrinsic, that originate from the bones or cartilages outside the MP and insert into the corium of the MP, and (ii) intrinsic, that originate from and insert into different sites of the vibrissa capsules. Since the newly described muscle slips originate outside the MP, similar to extrinsic muscles, but insert into the capsules of the vibrissa follicles, similar to intrinsic muscles, we named them "pseudointrinsic". Anatomically, these slips belong to the Pars interna of the *M. nasolabialis profundus,* of which few parts are involved in active whisker retraction. Functionally however, pseudo intrinsic slips of the Pars interna should be considered an accessory whisker protractor.

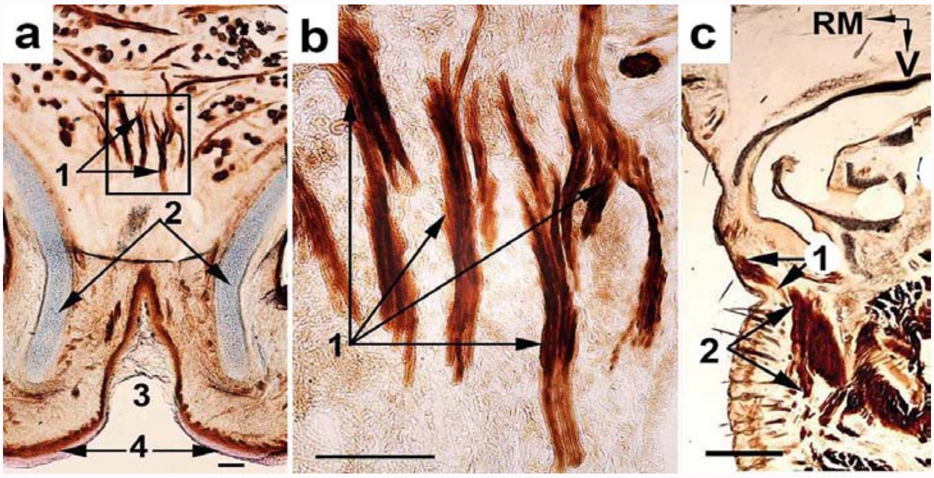

Figure 3: Rhinarial muscles. (**a**) Central part of a coronal slice of the mouse snout. (**b**) Enlarged boxed area in (**a**). Staining for CCO activity supplemented with alcian blue and thiazine red. (1) *M. levator rhinarii*; (2) ventrolateral processes of the nasal cartilaginous skeleton; (3) median sulcus; (4) narial pads (ventral edges). Scale bars = 0.1 mm. (**c**) A deep oblique slice of the rostral end of the snout of an adult mouse. (1) *M. depressor rhinarii*; (2) *M. depressor septi nasi*. RM: Rostromedial; V: Ventral. Scale bar = 1 mm. Modified from [11,16].

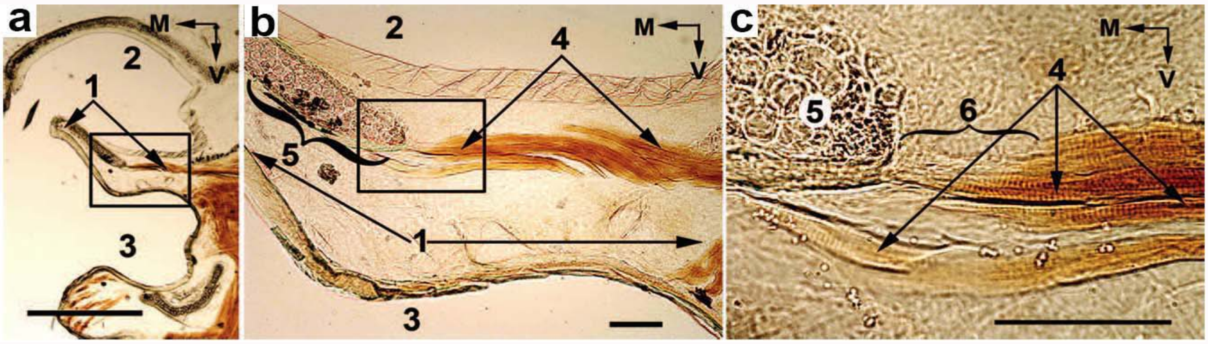

Figure 4: Intraturbinate muscle. (**a**) A coronal slice of the rostral part of the rat snout stained for CCO. (**b** and **c**) Enlarged boxed areas in (**a**) and (**b**), respectively. (1) Atrioturbinate; (2) dorsal meatus; (3) ventral meatus; (4) intraturbinate muscle; (5) intraturbinate cartilage; (6) muscle attachment to cartilage. M: Medial; V: Ventral. Scale bars are 1 mm (**a**), and 0.1 mm (**b,c**). Adapted from [20].

Rhinarium motility inspired successful search for rhinarial muscles

In whisking mammals, the rostral part of the snout and rhinarium move during active tactile sensing by the micro vibrissae and rhinarium. The rhinarium is densely innervated by tactile receptors [11-13] and participates not only in active tactile [14,15] but also in olfactory sensing [16,17]. Rats move the nose in different directions during exploratory behavior and even initiate contact with the objects using the rhinarium [18,19]. Yet, there was no knowledge about the muscles that move the rhinarium. We suggested that rhinarium movements are evoked by the facial muscles that are attached to the rhinarium itself or to the movable part of the nasal cartilaginous skeleton, whose rostral end anchors the rhinarial pads. Using different plane cuts of the rostral part of the snout and CCO staining, we revealed three, not yet known, striated facial muscles: *Mm. levator* and *depressor rhinarii* and *M. intraturbinalis* (Figure 3 and Figure 4).

The function of the *Mm. levator* and *depressor rhinarii* in control of the snout and rhinarium movements is clearly suggested from their origin and insertion sites. The function of Intraturbinate muscle, on the other hand, is less clear. Based on its morphology, we hypothesize that its contraction changes the shape of the atrioturbinate, and thus the direction of air flow during inhalation and exhalation. This morphologically inspired functional hypothesis requires experimental confirmation.

Predicting torsional whisker motion on the basis of snout muscle anatomy

Oblique Intrinsic Muscles (OIMs) were anatomically discovered in the MP of the marsupial *Monodelphis domestica* [21]. They were found between the neighboring whisker follicles in rows A and B (Figure 5). While the authors did not directly study the function of the OIMs, they suggested, based on the origin and insertion sites, that OIMs are involved in torsional rotation of the whiskers in rows A and B, and in the deflection of whisker shaft during object palpation by the vibrissae. Later, after OIMs were revealed also in the MP of mice and rats, their role in torsional rotation of the vibrissae was examined and indeed confirmed using electrical microstimulations and recordings of the resulting vibrissal motion [7].

Conclusion

The idea that structure reflects function and *vice versa*, led us to assume a complementary approach, whereby anatomical discoveries of muscles suggest their functional involvement in motion, and the detailed functional analysis of kinematics is used to predict the existence of muscles. Working in both axes, this approach proved to facilitate the discovery of few facial muscles, and their involvement in whisker and snout motion during exploratory behavior. Moreover,

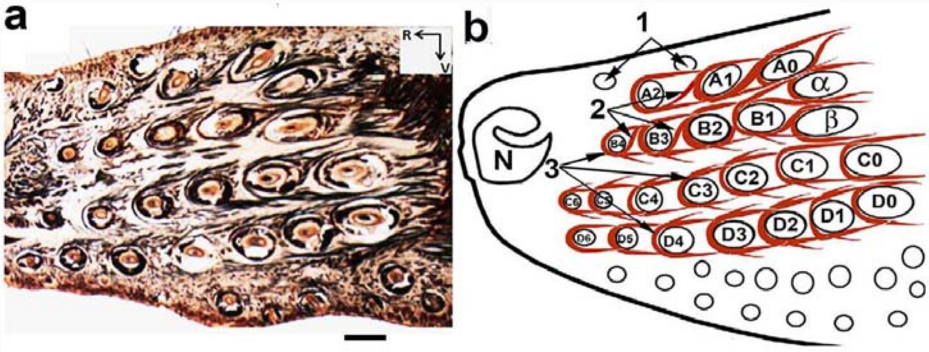

Figure 5: Intrinsic muscles in the MP of the opossum *Monodelphis domestica*. (**a**) A tangential slice of the MP stained for CCO. (**b**) Schematic representation of mystacial vibrissae (black ovals) and intrinsic muscles (red). (1) Nasal vibrissae, (2) OIMs, (3) SLIMs. R: Rostral; V: Ventral. Scale bar = 1 mm. Modified from [21].

the predictive power of this approach allowed elaborating insights across species, e.g., the functional prediction of newly revealed muscles in the MP of marsupials was confirmed using electrical microstimulation of homologous muscles that were later discovered in the MP of rats and mice. We assert that this approach is essential for gaining a comprehensive understanding of complex motions, such as those in the vibrissal system, and for further revelations of new and surprising features of muscle anatomy in the snout of whisking rodents.

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