

Muscles Involved in Naris Dilation and Nose Motion in Rat

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ABSTRACT

In a number of mammals muscle *dilator nasi (naris)* has been described as a muscle that reduces nasal airflow resistance by dilating the nostrils. Here we show that in rats the tendon of this muscle inserts into the aponeurosis above the nasal cartilage. Electrical stimulation of this muscle raises the nose and deflects it laterally towards the side of stimulation, but does not change the size of the nares. In alert head-restrained rats, electromyographic recordings of muscle *dilator nasi* reveal that it is active during nose motion rather than nares dilation. Together these results suggest an alternative role for the muscle *dilator nasi* in directing the nares for active odor sampling rather than dilating the nares. We suggest that dilation of the nares results from contraction of muscles of the maxillary division of muscle *nasolabialis profundus*. This muscle group attaches to the outer wall of the nasal cartilage and to the plate of the mystacial pad. Contraction of these muscles exerts a dual action: it pulls the lateral nasal cartilage outward, thus dilating the naris, and drags the plate of the mystacial pad rostrally to produce a slight retraction of the vibrissae. On the basis of these results, we propose that muscle *dilator nasi* of the rat should be re-named muscle *deflector nasi*, and that the maxillary parts of muscle *nasolabialis profundus* should be referred to as muscle *dilator nasi*. *Anat Rec*, 298:546–553, 2015. © 2014 Wiley Periodicals, Inc.

Key words: facial muscles; *dilator nasi*; respiration; upper airway; nose movement

The transport of odorants to the olfactory epithelium critically depends on nasal airflow, which is driven by the negative pressure generated in the lungs by the respiratory pump muscles, which include the diaphragm, intercostals, and abdominal muscles. Nasal airflow is also controlled by the size of the nares, which accounts for over 50% of upper airway flow resistance (Haight and Cole, 1983). Most anatomical studies propose that muscle (*M.*) *dilator nasi* dilates the nostrils (Klingener, 1964; Meinerz, 1942; Priddy and Broie, 1948; Rinker, 1954; Ryan, 1989; Whidden, 2002). This muscle has also been referred to as *M. dilatator naris* (Greene, 1935; Diogo, 2009).

M. dilatator nasi takes origin at the orbital edge of the maxilla, and the insertion site of its long tendon varies

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TABLE 1. Origin and insertion sites of *M. dilator nasi* (naris)

Author	Species	Origin	Insertion
Meinertz, 1942	Sciuris vul.	Os maxillare, rostral edge of the Foramen infraorbitale	The skin at the tip of the nose
Priddy and Brodie, 1948 Rinker, 1954	Hamster Cricetinae	Dorsal to infraorbital foramen Medial half of the dorsal margin of the zygomatic notch	Dorsal to the nostril Lateral part at the dorsal border of rhinarium
Klingener, 1964	Rodents	Aponeurosis from the outer surface of outer rim of the infraorbital foramen	Dorsal part of the nasal cartilage
Herring, 1972	Suoidea	Facial crest of the maxilla	Subcutaneous tissue on the side of the rhinarium
Ryan, 1989	Rodentia	Dorsal surface of the zygomatic plate anterior to the eye	The dorsolateral portion of nasal cartilage
Whidden, 2002	Insectivora	Anterior surface of the antorbital ridge and fossa that lies anterior to the orbit	Aponeurosis over the cartilaginous rings of the snout tip

in different species (Table 1). In hamsters, it is the nostril (Priddy and Brodie, 1948); in cricetinae and suidea, the rhinarium (Rinker, 1954; Herring, 1972); in sciurus vulgaris, the skin at the tip of the nose (Meinertz, 1942); in rodents, the cartilages of the nose (Klingener, 1964; Ryan, 1989); and in insectivora, the aponeurosis over the nasal cartilages (Whidden, 2002). Based on these anatomical data, it is unclear whether *M. dilator nasi* actually controls nose motion or the shape and size of the nostrils, or both. In the present study we re-examined the anatomical features of *M. dilator nasi* in rats, and assessed its function by electrical stimulation, electromyography (EMG) and high-speed videography.

MATERIALS AND METHODS

Anatomy

Twelve 2-week-old, and six adult male albino Wistar rats were used for anatomical studies. All procedures for animal maintenance and experimentation were approved by the Institutional Animal Care and Use Committee at the Weizmann Institute of Science. Rats were anesthetized intraperitoneally with urethane (25%; (w/v); 0.65 mL/100 g body weight), and perfused transcardially with (4% (w/v) paraformaldehyde, and 5% (w/v) sucrose in 0.1 M phosphate buffer, pH 7.4). The musculature of the snout was visualized from serial sections stained for cytochrome oxidase (CO) activity.

To reveal the sites of muscle attachment to the bones, we used 2-week-old rats because bones are soft enough to be cut with a regular microtome. Postfixation was carried out for the entire rostral part of the snout. In adult rats, CO activity was visualized in sections that were prepared from hemi-snouts because bone decalcification affects CO reactivity. After perfusion, hemi-snouts of adult rats were excised, and placed between two pieces of stainless steel mesh within RCH-44 perforated plastic histology cassettes (Proscitech.com) to prevent tissue curling. The cassettes were placed into 4% paraformaldehyde solution with 30% (w/v) sucrose for postfixation. After 48 h of postfixation, tissue samples were sectioned at 30 μ m in the tangential, horizontal or coronal planes on a sliding microtome (SM 2000R, Leica Instruments, Germany).

Cytochrome oxidase activity was revealed according to a modification (Haidarliu and Ahissar, 2001) of the procedure described by Wong–Riley (1979). Briefly, free-floating slices were incubated in an oxygenated solution of 0.02% (v/v) cytochrome c (Sigma–Aldrich, St. Louis, MO), catalase (200 g mL⁻¹), and 0.05 % (w/v) diaminobenzidine in 100 mM phosphate buffer at room temperature under constant agitation. When a clear differentiation between highly reactive and non-reactive tissue structures was observed, the incubation was arrested by adding 0.5 mL of 100 mM phosphate buffer into the incubation wells. Stained slices were washed, mounted on slides, cover-slipped with Entellan (Merck KGaA 64271 Darmstadt, Germany) or Kristalon (Harleco; Lawrence, KS), and examined and photographed using light microscopy (Nikon Eclipse 50i microscope). The brightness and contrast of the images were digitally adjusted for clarity (Adobe Photoshop).

Physiological Experiments

Physiological experiments were carried out in an additional nine adult Long Evans rats (250–350 g) according to the National Institutes of Health Guidelines, and were approved by the Institutional Animal Care and Use Committee at Laval University and University of California, San Diego. Rats were anesthetized with ketamine (75 mg kg⁻¹)–xylazine (5 mg kg⁻¹), and placed in a stereotaxic apparatus. Body temperature was maintained at 37.5°C with a thermostatically controlled heating pad.

It was previously reported that electrical stimulation of *M. dilator nasi* produces nose and vibrissa movement (Haidarliu et al., 2012). We thus reinvestigated this issue in four rats. For these experiments, a head-restraint post was affixed to the surface of the skull with screws and acrylic cement. Two burr holes of 0.7 mm diameter were made in the thick lateral crest of os parietale on each side of the skull. Holes were located 1mm rostral and 5 mm caudal to the bregma. Self-tapping stainless steel screws (3.2 mm length; Small Parts SCT0152-0003-P-PH-S2; Logansport, IN) were disinfected in ethanol, and screwed into the pre-drilled holes. Maximally two turns were applied to the screw, to

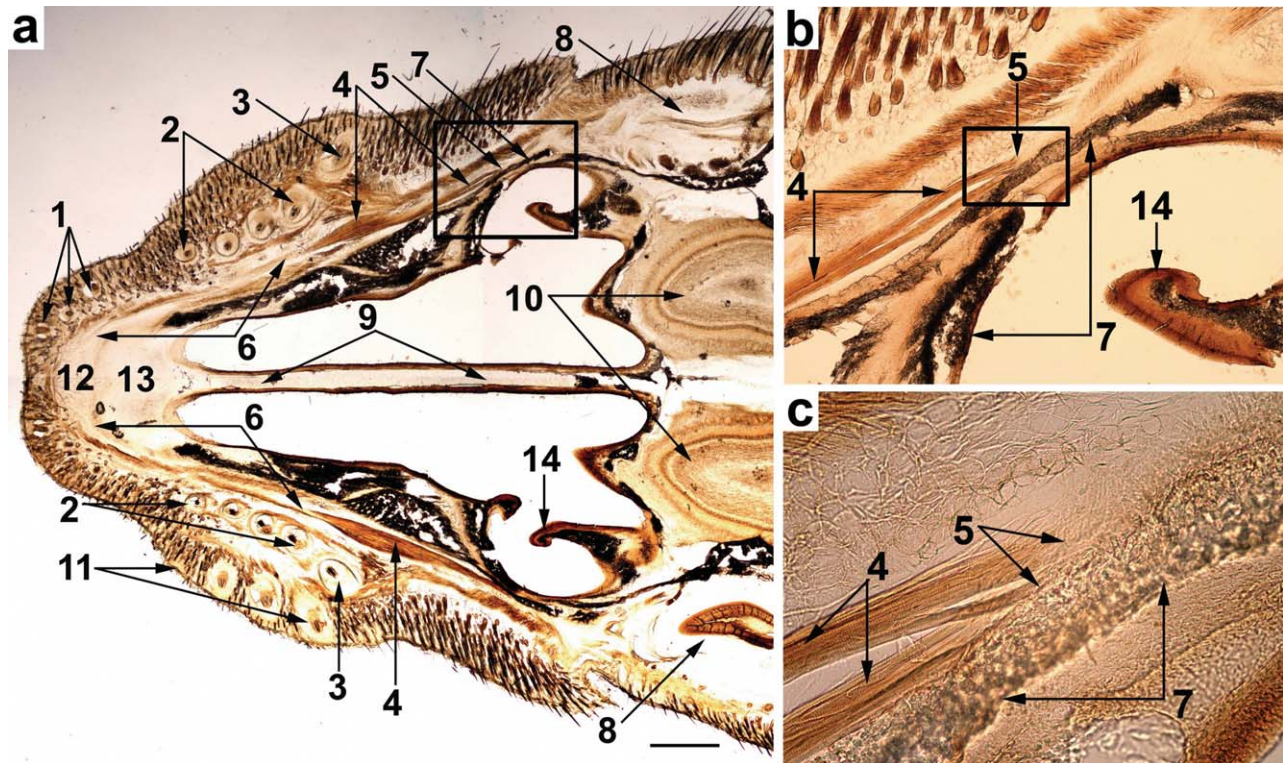


Fig. 1. Light microscopy (CO staining) of a horizontal section of the head of a 2-week-old rat at the level of vibrissa row A (a). (b) Enlarged boxed area in (a); (c) enlarged boxed area in (b). (1) Nasal vibrissae; (2) follicles of the vibrissal row A; (3) follicle of the straddler α ; (4) belly

of *M. dilator nasi*, (5) origin, and (6) tendon of *M. dilator nasi*; (7) maxilla; (8) eyes; (9) septum; (10) olfactory bulbs; (11) follicles of vibrissal row B; (12) aponeurosis above the nasal cartilaginous skeleton (13). Scale bar in (a) = 1 mm.

prevent the tip of the screw to protrude into the head cavity and potentially damage the surface of the brain. Visual inspection of the brains after fixation did not reveal any cortical injury.

An incision was made along the midline of the nose, and a cotton-tipped applicator was used to separate the medial slip of the *nasolabialis* muscle from the maxillary bone. Deflecting the medial slip of the overlying *M. nasolabialis* reveals the belly of *M. dilator nasi* at the level of the first arc of vibrissae. A platinum-iridium microelectrode (0.4–0.8 mOhm) was inserted into the muscle and a reference electrode was placed on the dorsal part of the maxillary bone. Respiration was monitored with a piezoelectric film (cantilever type; LDT1 028K; Measurement Specialities) resting on the rat's abdomen just caudal to the torso. The effect of stimulation was assessed by videographic recording with a high-speed video camera (100 frames per second; HiSpec 2G Mono camera; Fastec Imaging, CA) equipped with a zoom lens to record nose motion, or with a 2.5 \times tube lens to capture the opening of the nares. Respiratory signals were sampled at 1 kHz, and synchronized with video frames through a NI USB-6221 acquisition board (National Instruments). Nose motion and naris dilation were extracted from video recordings off line using custom scripts written in Matlab (Mathworks).

To further assess the role of *M. dilator nasi* in orofacial behavior, two additional rats were acclimated to body restraint over a 5-day period. They were then

implanted with a head-restrain plate affixed to the surface of the skull with screws and acrylic cement. A small hole was drilled through the left nasal bone at the level of the frontal-nasal fissure (1 mm lateral from midline) for the placement of a stainless steel cannula (16G) that was then lowered over the hole and fixed in place with dental cement. The cannula was sealed with silicone elastomer (Kwik-Cast Sealant; WPI). Two teflon-coated tungsten wires (diameter: 50 μ m) were inserted chronically in *M. dilator nasi* for differential recording of EMG activity (Hill et al., 2008). Rats were allowed to recover for 3 days before the onset of behavioral experiments.

During the subsequent recording sessions, rats were placed inside a body-restraining cloth sack and rigid tube, and the animals were head-restrained. The elastomer was removed from the cannula and respiration was monitored with a thermocouple (5TC-TT-K-36-36, Omega Engineering) that was lowered into the cannula. The thermocouple was used to measure the cooling and warming of air as it passes through the nasal cavity. A Basler A602f camera equipped with a macro video zoom lens (Edmund Optics) was used to record lateral deflection of the nose from above the head (spatial resolution: 120 μ m per pixel; 100 frames per second). A mirror was placed at 45 degree angle in front of the snout, within the field of view of the camera, to capture lateral and vertical deflections of the nose. Respiratory signals from the thermocouple were synchronized with video frames through a PCI-6024E acquisition board (National

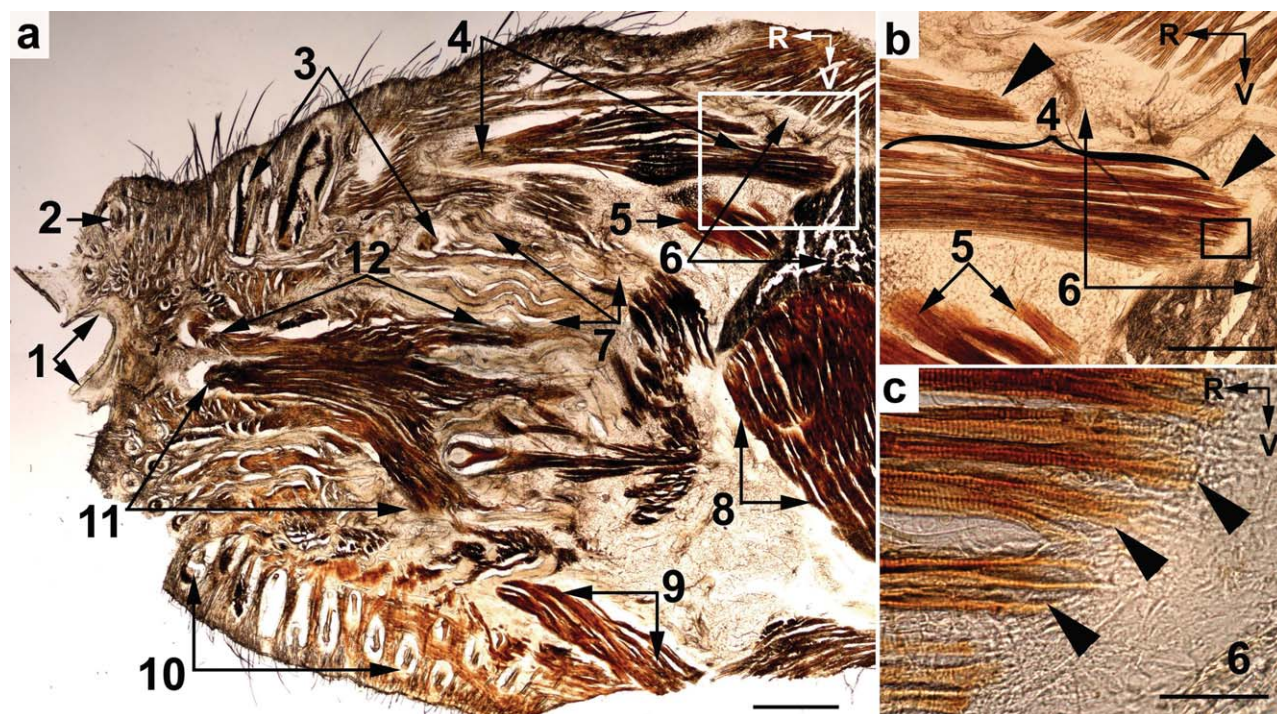


Fig. 2. Light microscopy of a tangential section of the snout of a 2-week-old rat (a). (b) and (c), higher magnification of the boxed areas in (a) and (b), respectively. The section was stained for CO activity. Arrow heads point at the tapered muscle fibers at the origin of the *M. dilator nasi*. (1) Nostril; (2) follicle of a nasal vibrissa; (3) follicles of vibrissae in row A; (4) belly of *M. dilator nasi*; (5) anterior unit of the medial layer of the masseter muscle; (6) zygomatic notch and transversal profile at

the base of the processus zygomaticus of the maxilla; (7) subcapsular fibrous mat; (8) anterior part of the masseter muscle; (9) Pars orbicularis oris of the *M. buccinatorius*; (10) furry buccal pad; (11) and (12) Partes maxillares profunda and superficialis, respectively, of the *M. nasolabialis profundus*. R, rostral; V, ventral. Scale bars = 1 mm in (a), 0.5 mm in (b), and 0.1 mm (c).

Instruments). Nose motion was extracted from video recordings off line using custom scripts written in Matlab.

Finally, in three additional rats, a head post was fixed to the surface of the skull for concurrent recording of naris dilation, whisker motion and breathing. Recordings were carried out as described above while rats recovered from anesthesia. In these acute experiments, vibrissae were clipped, except vibrissa C2, whose motion was monitored in real time with a CCD linear sensor (S3904-2048Q; Hamamatsu).

RESULTS

Anatomical Features of *M. dilator Nasi*

Horizontal plane. Horizontal sections of the snout of 2-week-old rats reveal the anatomy of the entire *M. dilator nasi*: origin, belly, tendon, and insertion sites, that lie underneath the most medial row of vibrissae (row A; Fig. 1a). Collagenous fibers of the endomysium, perimysium, and epimysium of the muscle are attached to the collagenous fibers of the periosteum of the maxilla (Fig. 1b,c). The long tendon of the *M. dilator nasi* inserts in the aponeurosis of the dorsum nasi that separates the skin from the dorsal nasal cartilage. Similar features are observed in horizontal sections of hemi-snouts in adult rats.

Tangential plane. In tangential slices of the snout of 2-week-old rats, the belly of *M. dilator nasi* is about

1.5 mm in diameter. The caudalmost segment of the muscle is divided into two parts. The dorsal part originates from the anterior orbital bridge of the maxillary bone, and the ventral part originates from the rostral edge of the zygomatic plate (Fig. 2a). At high magnification, the dual origin of the muscle can be clearly observed (Fig. 2b). In particular the endomysial and perimysial collagenous envelopes of the tapered ends of the muscle fibers of the ventral part of the *M. dilator nasi* are associated with the collagenous structures of the periosteum of the zygomatic process (Fig. 2c). Both muscle parts run in the rostral direction, but fuse near the rostral end of the muscle, to form a single belly with a multipennate appearance. The tendon forms a single strand. In tangential sections of hemi-snouts of adult rats, the belly and tendon of the *M. dilator nasi* shows similar features, but are relatively larger, with the belly reaching more than 2 mm in thickness.

Coronal plane. The belly of the *M. dilator nasi* is easily distinguishable by its strong CO reactivity when observed in coronal slices. The tendon does not stain for CO activity, but appears as a compact oval formation among other collagenous structures. At the level of the straddlers vibrissae, *M. dilator nasi* appears as an elongated structure in dorso-ventral direction. The muscle consists of short fragments of fibers that are cut obliquely. Most of the muscle fibers have a concentric orientation. In more rostral sections, the muscle contains

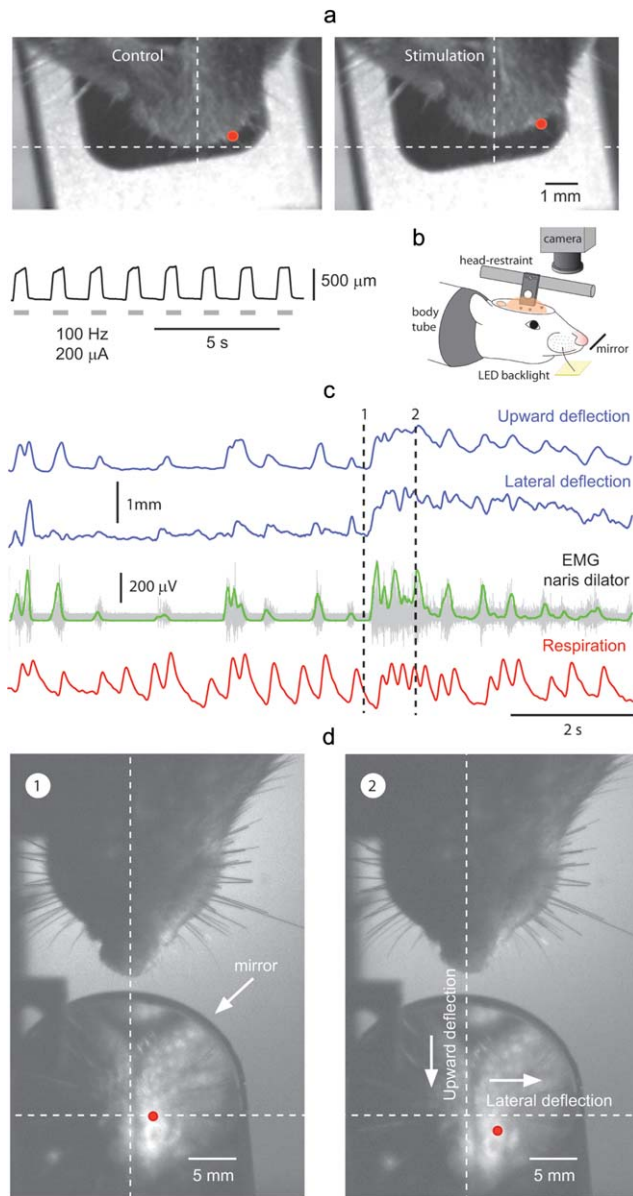


Fig. 3. Muscle dilator nasi in rats deflects the nose. **a**, electrical stimulation of the left dilator nasi induces retraction of the nose and lateral deflection towards the side of stimulation. Gray bars indicate stimulus trains. **b**, experimental setup for recording vibrissa and nose motion in head-restrained rats. **c**, recording of nose movements, muscle dilator nasi EMG (raw recording in grey and smoothed rectified EMG in green), and respiration (inspiration up) in an alert head-restrained rat. Video frames in **d** correspond to time points labeled 1 and 2 in **c**. Nose movement was tracked from images of the rhinarium reflected in a mirror placed at an angle of 45° in front of the rat. Red dots in **a** and **d** show the displacement of the reference point used to track nose motion.

an increasing number of tendinous fibers that eventually fuse into a single tendon.

Function of Muscle Dilator Nasi

The function of *M. dilator nasi* was assessed by monitoring the motion of the nose, vibrissae and nares

following electrical stimulation of the muscle in lightly anesthetized rats. Low-intensity (100–200 μA) stimulation of *M. dilator nasi* exclusively produces upward and lateral deflection of the tip of the nose towards the side of stimulation (Fig. 3a). As viewed from above, the upward deflection appears as a retraction. Vibrissa motion was only elicited at stimulus intensity two to three times above threshold intensity for nose motion (ca., 800 μA), which suggests the recruitment of additional muscles or nerves by current spread.

To further assess the exclusive role of *M. dilator nasi* in nose motion, we carried out EMG and videographic recordings in head-restrained alert rats. We observe that, irrespective of the respiratory frequency, *M. dilator nasi* EMG activity is tightly coupled to nose motion (Fig. 3b,c). Yet, time-locked bursts of EMG activity and nose deflections do not occur in a one-to-one manner with each breath. In addition, sustained deviation of the nose is associated with sustained EMG activity. Together, these observations indicate that contraction of *M. dilator nasi* does not open the nares, but rather that it deflects the nose.

Muscles Involved in Opening the Nares

A prior anatomical study of facial musculature in rats (Haidarliu et al., 2010) identified two parts of the *M. nasolabialis profundus* termed *Partes maxillares superficialis et profunda* that attach rostrally to the outer wall of the nasal cartilage (Fig. 4), and caudally to the plate of the mystacial pad (Fig. 5). It was previously suggested that these muscle parts exert a dual action: (1) dilation of the nares by pulling outwardly the lateral wall of the nasal cartilage, and (2) retraction of the vibrissae by pulling rostrally the plate to which the proximal end of vibrissa follicles is attached. Accordingly, one would expect naris dilation to be associated in a one-to-one manner with whisker retraction. We therefore tracked the opening of the nares and whisker motion as rats recovered from anesthesia. Naris dilation was not observed under deep anesthesia, which was assessed by the absence of a withdrawal reflex to pinch of the hindlimbs. As the plane of anesthesia diminishes, the lateral wall of the atrium turbinate begins to move outwardly in association with retraction of the large caudal vibrissae (up to arc 3; Fig. 6a). Retractions are small in amplitude (i.e., 2–3°), synchronous on both sides of the face, and tightly coupled with naris dilation (cross correlogram, Fig. 6b). This co-ordinated activity occurs at the onset of inhalation, and remains clearly observable until the animal begins moving its vibrissae and nose actively.

Both naris dilation and vibrissa retraction are abolished during apnea, induced here by application of a puff of ammonia to the snout (Fig. 6c). Critically, both naris dilation and whisker retraction recover synchronously when the rat begins to breathe again after apnea. In summary, the above physiological results fully agree with the suggestion that the maxillary parts of *M. nasolabialis profundus* in rat are involved in opening the nares and retracting the mystacial vibrissae.

DISCUSSION

Origin and Insertion Site of *M. dilator Nasi*

In several species *M. dilator nasi* was reported to originate at the orbit or the zygomatic plate of the maxilla

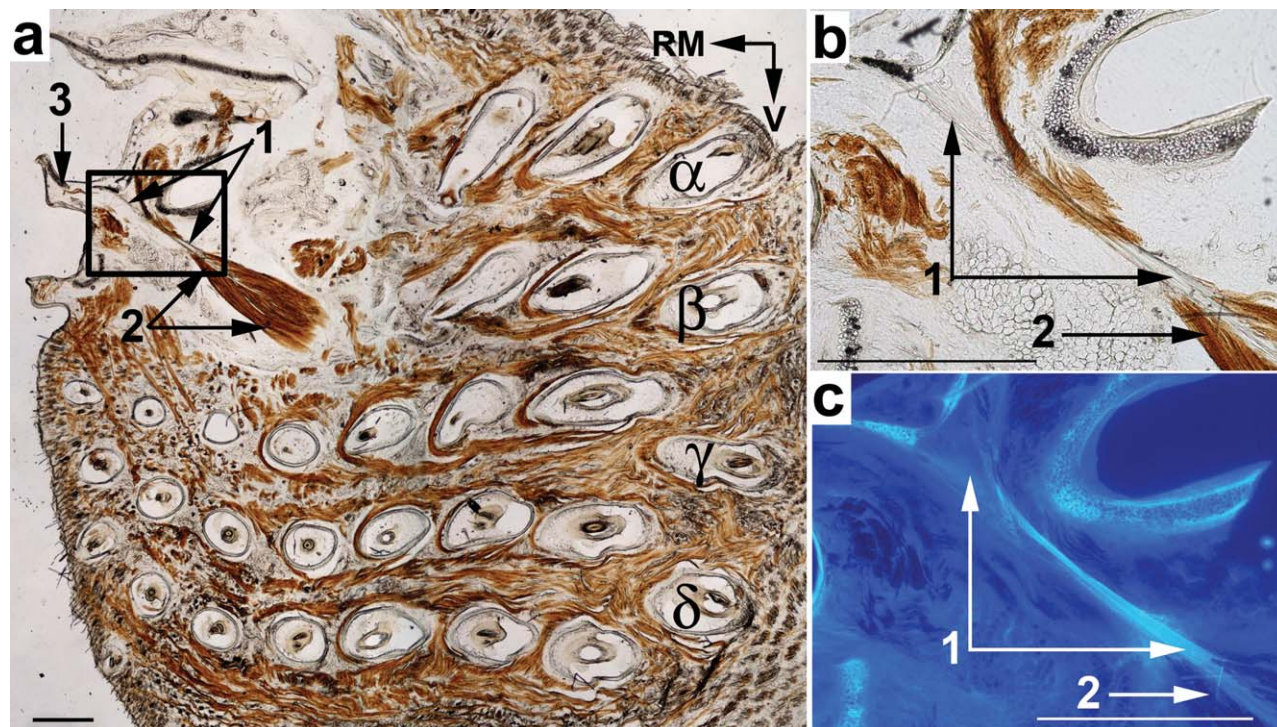


Fig. 4. Light microscopy of an oblique section through the snout of an adult rat (a). Light microscopy (b), and autofluorescence (c) of the boxed area in (a). (1) tendon, and (2) belly of the Pars maxillaris superficialis of the *M. nasolabialis profundus*; (3) atrioturbinates; $\alpha - \delta$, straddler follicles; RM, rostromedial; V, ventral. Scale bars = 1 mm.

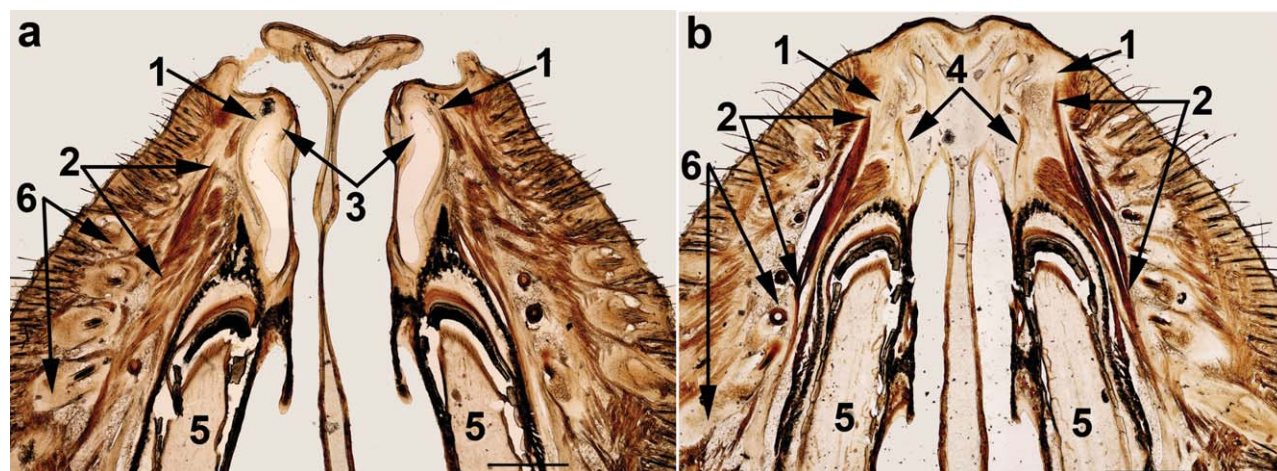


Fig. 5. Light microscopy of horizontal slices of the snout of a 2-week-old rat. Sections were stained for CO activity. Section in (a) is more superficial than section in (b). Note that the belly of Pars maxillaris superficialis (a) and pars maxillary profunda (b) of *M. nasolabialis profundus* run deep in the mystacial pad under the vibrissa follicles.

(1), Tendon; (2), bellies of the maxillary parts of the *M. nasolabialis profundus* (3), atrioturbinates; (4), anterior transverse lamina (5), incisives; (6) vibrissa follicles. Note that the bellies of the maxillary parts run deep in the mystacial pad under the vibrissa follicles. Scale bars = 1 mm.

(Table 1). None of these studies, however, identified the precise sites of contact of this muscle with the skull. In some species, *M. dilator nasi* may have two separate bellies and multiple tendons, as described in Suidea by Herring (1972). In rats, we found that the caudal end of *M. dilator nasi* is divided into two parts: (i) a dorsal part

that attaches to the anterior orbital ridge of the maxilla, and (ii) a ventral part that attaches to the rostral edge of the zygomatic process. Near the rostral end of the muscle, these two parts appear to fuse, and the muscle looks like a multipennate muscle that possesses a long single-stranded tendon. It is likely that the ventral and

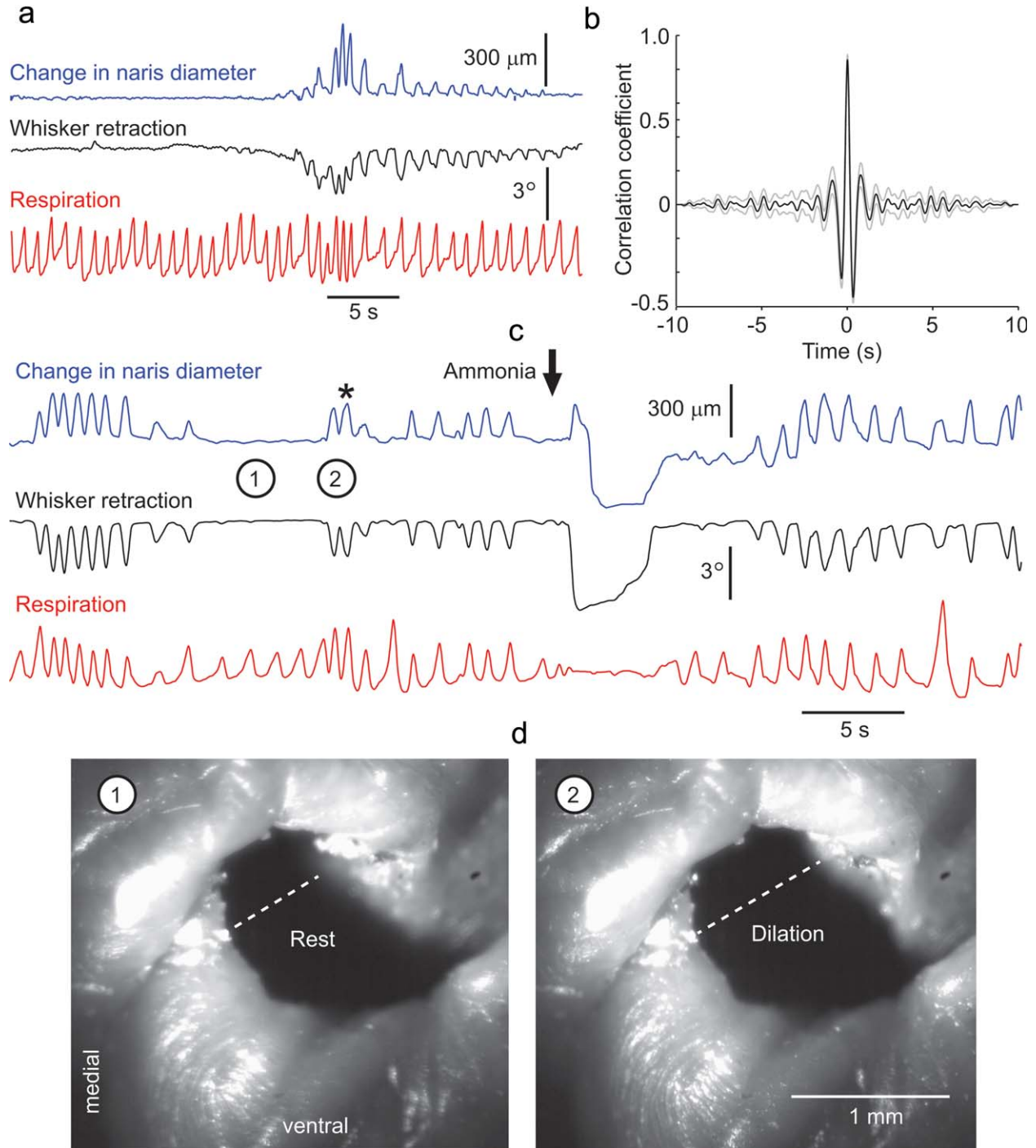


Fig. 6. Opening of the naris is coupled with whisker retraction in the lightly anesthetized rat. **a**, As rats recover from anesthesia, the onset of naris dilation occurs in synchrony with the onset of whisker retraction. Both actions are time locked to the inspiratory phase of the respiratory cycle (inspiration up). **b**, Cross correlation between change in naris diameter and whisker retraction. Averaged cross correlograms were computed from 30 sequences of 10 s each in three rats. Gray

lines indicate 95% confidence intervals. The one-to one relationship between naris dilation and whisker retraction is further revealed after an apneic reaction induced by applying a puff of ammonia to the snout. Note the synchronous recovery of both naris dilation and whisker retraction when respiration resumes. Video frames in **d** show naris size corresponding to time points 1 and 2 (asterisk) in **c**. The dotted line indicates where naris diameter was measured.

dorsal slips of muscle dilator nasi exert different actions: the dorsal slip may raise the nose, while the ventral slip may deflect the nose laterally. Yet, the small size of

these muscles makes this hypothesis difficult to test by selective stimulation or EMG recording of the individual slips.

The insertion site of *M. dilator nasi* seems to vary in different species (Table 1). In Suidea, the insertion site is located within the rhinarium, laterally to the nostrils, which suggests that contraction of this muscle can indeed dilate the nares (Figs. 4 and 5 in Herring, 1972). In the other studies mentioned in Table 1, it is not clear whether contraction of *M. dilator nasi* can produce naris dilation, because the insertion sites are located mostly in the dorsal part of the tip of the nose (i.e., the aponeurosis, or the dorsal part of the nasal cartilage). These structures are not directly connected to the nostrils or to the cartilaginous processes that maintain the shape of the nasal openings.

Effect of *M. dilator Nasi* Contraction

It has been proposed that *M. dilator nasi* is a multifunctional muscle that takes part in three different motor plants: vibrissa motion, nose movement, and olfactomotor activity (i.e., sniffing; Haidarliu et al., 2012). Based on the electrical stimulation with transcutaneous electrodes, it was shown that this muscle deflects the nose, and protracts the rostral arcs of vibrissae. The role of this muscle as a component of olfactomotor plant (i.e., naris dilation) was not directly assessed, but rather inferred from previous anatomical studies. However, it appears likely that motion of the rostral vibrissae as reported in that study, is attributable to current spread to neighboring muscles or nerves. In the present study, we dissected facial tissue to ensure that *M. dilator nasi* was selectively stimulated, and in accord with the anatomical data (origin and insertion sites), *M. dilator nasi* stimulation solely produced nose motion. This result was confirmed by EMG recordings, which reveal *M. dilator nasi* activity associated with nose motion, but not with nares dilation. Yet, it is worth noting that nose motion is an integral part of the sniffing behavior. Therefore, whisking and sniffing are likely to be coordinated with nose motion, as initially reported by Welker (1964).

Our results show that naris dilation is tightly coupled to small amplitude whisker retractions, which are only discernable when the rat is sessile, or when it recovers from anesthesia. Such a coupling was previously proposed on the basis of the attachment points of the maxillary parts of *M. nasolabialis profundus* (Haidarliu et al., 2010). These muscle slips attach to the outer wall of the nasal cartilage and to the plate of the mystacial pad. Therefore, contraction of these muscles pulls the lateral nasal cartilage outward, thus dilating the nostrils, and also pulls the plate rostralward, provoking a slight retraction of the vibrissae. Because of the small amplitude of the retraction it is unlikely that the latter action plays a significant role in whisking; rather these slight retractions appear as a side effect of the action of these muscles on opening the naris. It should be noted that other small muscles in the rhinarium may also take part in naris dilation or nose movement. Interested readers should refer to the papers by Haidarliu et al. (2010, 2012) for a detailed account of the layout of these muscles.

Note on Terminology

The present study reveals an inconsistency between the name "*M. dilator nasi (naris)*," and the actual role of

this muscle as assessed by electrical stimulation and EMG recordings. Our results provide direct evidence that this muscle has no effect on the size or shape of the nostrils, but that its function is to raise the nose and deflect it laterally. A similar inconsistency between the name "*M. dilator naris*" and the function of this muscle was reported in other animals. In moose, Clifford and Witmer (2004) found that *M. dilator naris medialis*, according to its origin and insertion sites, constricts rather than dilates the nostril as its name suggests. Just like in rats, in the other species in which *M. dilator nasi* inserts into the dorsal part of the nasal cartilage (Table 1), one would expect this muscle to be mainly involved in nose motion. We therefore propose that this muscle be termed *M. deflector nasi* in rats. The name *dilator nasi* should refer to the maxillary parts of *M. nasolabialis profundus*. It appears doubtful that the results obtained in this study may have any relevance or direct applicability to human pathology or surgery.

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