

Innervation Patterns of the Canine Masticatory Muscles in Comparison to Human

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ABSTRACT

The aim of this study was to clarify the nerve distribution of the masseter, temporalis, and zygomaticomandibularis (ZM) muscles to elucidate the phylogenetic traits of canine mastication. A detailed dissection was made of 15 hemisectioned heads of adult beagle dogs. The innervations of the masticatory nerve twigs exhibited a characteristic pattern and were classified into seven groups. Twig innervating the anterior portion of the temporalis (aTM) was defined as the anterior temporal nerve (ATN). Anterior twig of ATN branched from the buccal nerve and innervated only the aTM, whereas posterior twig of ATN innervated both of the aTM and deep layer of the temporalis (dTM). From this and morphological observations, it was proposed that the action of the canine aTM is more independent than that of the human. The middle temporal nerve ran superoposteriorly within the dTM and superficial layer of the temporalis (sTM) innervating both of them, whereas the posterior temporal nerve innervated only the posterior region of the sTM. The masseteric nerve (MSN) innervated the ZM and the three layers of the masseter. Deep twig of MSN was also observed innervating sTM after entering the ZM in all cases. The major role played by the canine ZM might thus underlie the differential arrangement of the distribution of the masticatory nerve bundles in dogs and humans. Although the patterns of innervation to the canine and human masticatory muscles were somewhat similar, there were some differences that might be due to evolutionary adaptation to their respective feeding styles. *Anat Rec*, 293:117–125, 2010. © 2009 Wiley-Liss, Inc.

Key words: dog; masseter; temporalis; zygomaticomandibularis; masseteric nerve; deep temporal nerve; comparative anatomy

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The masticatory musculature of the tetrapods (adductor mandibulae) comprises the pterygoid, temporalis, zygomaticomandibularis (ZM), and masseter, which originate from the first pharyngeal arch and are supplied by the mandibular nerve (Kent and Carr, 2001; Budras et al., 2002; Sadler, 2006).

The masticatory muscles of various mammals have been compared according to their nerve supply by researchers at the German comparative anatomy school, such as Luter (1909, 1914) and Lubosch (1918, 1929, 1933). They researched the evolutionary pathways of fish, amphibians, and reptiles, but did not examine mammals (Tomo et al., 1993). Yoshikawa et al. (1961) and Schumacher (1961) classified the masseter of dogs by identification of the spatial relationship between the muscle bundles and tendons, but their method, which was based on morphology, was not particularly reliable. Tomo et al. (1993) studied the classification of the canine masticatory muscles based on their innervation pattern; however, they used only three dogs as specimens and compared their classification of the canine masticatory muscles with other studies of canine masticatory muscles, not with those of humans or other mammals.

Regarding other head and neck structures, there were many studies for elucidating the comparative traits of specific species with the human. Diogo et al. (2008) performed the comparative anatomical study from the modern fish to the human, in which they mainly focused on the transition from the nonmammalian tetrapods such as sarcopterygians to therian mammals, comprising modern humans. Tomo et al. (2002) used the buccinator muscles of the 12 adult cat specimens, and reported their buccinator muscle to be similar to human homologues in the aspects of anatomical traits such as facial nerve distribution, the presence of the modiolous, and the courses of the buccal nerve (BN) on the muscle. Dvorak (1976) performed the comparative study on the weight of the masticatory muscles, using apes, carnivores, herbivores, rodents, and human, and he concluded that the distinct strengthening was found in the digastric and lateral pterygoid muscles of the human. However, the masticatory muscle of the dog remains to be observed for the comparative study with humans.

Because dogs have a narrow skull and perform limited lateral movements, there might be some morphological differences between the masticatory muscles of these animals and humans, despite both belonging to the subclass Theria (Hilderbrand and Goslow, 2001), and both masticatory systems bearing common anatomical traits. For instance, the canine ZM is highly developed, whereas that of the human is only weakly developed (Hwang et al., 2005).

Various researchers such as Toldt (1905), Yoshikawa et al. (1961) and Schumacher (1961) classified the masseter and temporalis. Toldt (1905) reported that the masseter is divided into deep (*M. masseter profundus*) and superficial (*M. masseter superficialis*), and that the temporalis and ZM could each be regarded as having only a single part. Schumacher (1961) classified the masseter into six portions, each of which has an independent tendon and distinguished the suprazygomatic part (*M. temporalis, pars suprazygomatica*) of the temporalis from its main part. Tomo et al. (1993) classified the dog masticatory muscles into six layers and their innervating nerves

into eight categories. The ZM was regarded as being part of the masseter (*M. temporalis, pars zygomaticomandibularis*) in their study. Like Tomo et al. (1993), Schumacher (1961) thought that the ZM was part of the masseter. Despite this lack of distinction of the canine ZM between studies, this muscle is found in many species of mammals.

About the ZM, Shimokawa et al. (2002) observed that the small muscle bundle that adjoins the lateral surface of the temporalis corresponds to the human ZM based on the dissections of eight hemifaces of *Suncus murinus*, having no zygomatic arch. The ZM of the great-gray kangaroo (*Macropus giganteus*) is innervated by the masseteric nerve (MSN) (Tomo et al., 2007).

Akita et al. (2000) studied the developmental formation of the masticatory muscles by observing the positional relationship between them and their innervating nerves. In their study, the muscle bundles of the temporalis were categorized into six groups, which were innervated by the anterior (ADTN), middle (MDTN), and posterior deep temporal nerves (PDTN). They reported that the ZM and masseter have the same origin and are innervated by the MSN, as is the case in the aforementioned mammals. Similar to the detailed classification of the temporalis muscle by Akita et al. (2000), Brunel et al. (2003) and Gaudy et al. (2000, 2001) mentioned the functional organization of each masticatory muscle. Brunel et al. (2003) reported the presence of the intramasseteric aponeuroses in the human adult by means of the magnetic resonance imaging and gave us suggestions to the subdivision topography of the masseter. Gaudy et al. (2000) confirmed three subdivision of the masseter by their cadaveric study. Gaudy et al. (2001) described the distinct anatomical portion in the middle of the temporalis muscle by the functional classification by electromyographic study.

Animals of the order carnivores have a high coronoid process and a horizontally oriented temporalis (Ström et al., 1988; Hilderbrand and Goslow, 2001), whereas the human temporalis is oriented almost vertically from the temporal fossa and the temporal fascia to the coronoid process. Ström et al. (1988) described that the canine temporal fossa was horizontally oriented, and that the dog had a backwardly curved retroarticular process, which was based on their 15 dissections of the dog. These differences are attributable to the mechanical behavior of the feeding style, for example, the hinge-like movement shown by dogs (Ström et al., 1988). It was proposed that for elevation of the jaw, the action of the posterior portion of the canine horizontally oriented temporalis is more important than that of the anterior portion of the temporalis (aTM). The anteromedial bundle of the human temporalis originates from the infratemporal crest of the sphenoid bone and inserts into the anterior margin of the condylar process, with an extension to the retromolar region (Akita et al., 2000). The anteromedial bundle of the human temporalis is innervated by the ADTN, which is a branch of the BN. Because homologous twigs from the BN innervate the anterior deep region of the canine temporalis, which is attached to the anterior surface of the canine high-positioned coronoid process, the corresponding canine bundle is located in a more unfavorable position with regard to taking leverage of mastication than the human homolog (Tomo et al., 1993).

Therefore, it is important that the topographic and functional relationships between the respective innervations of the canine temporalis, masseter, and ZM are established, so that the phylogenetic traits of canine mastication when compared with human mastication can be established.

The aims of this study were to collect reliable data regarding the nerve distribution of the canine jaw elevator masticatory muscles (i.e., the temporalis, masseter, and ZM), and to compare them with the equivalent human masticatory muscles.

MATERIALS AND METHODS

Preparation for Gross Observations

Fifteen hemisectioned heads of adult beagle dogs (average age ~20 months) were used for this study. To examine the nerve distribution of the temporalis, masseter, and ZM, the specimens were decalcified and the bony elements except for the mandible were removed *en bloc*. Before dissection, the dog hemifaces were decalcified by means of 40 L of decalcification solution for 4–7 days. The decalcification solution was composed of 7 g of aluminum chloride hexahydrate (Al₂Cl₃6H₂O), 8.5 mL of 30% hydrochloric acid, and 5 mL of 100% formic acid, which was diluted to 100 mL with distilled water. For neutralization, the specimens were treated in a neutralization solution (5 g of sodium sulfate in 100 mL of distilled water) for 2–3 days.

For the first dissection, we removed the medial pterygoid muscles and detected the trigeminal ganglion. The twigs innervating each masticatory muscles were preserved. After the detection of the BN and its ramified twigs for the aTM muscle, the remaining bony structure, which was located anterior to the temporalis muscle, was removed. And then, the innervation patterns to the temporalis muscle were observed from the medial side, and the loop of the MSN was examined (Figs. 1, 2). The bony element that bones the mandibular condyle was removed. To observe the musculatures and their innervations on the lateral side, we removed the zygomatic arch. The branches of mandibular nerve were conserved following the detection of a trigeminal ganglion and mandibular nerve trunk before removal of the bony tissue. After removal of the bony elements, the courses and innervating patterns of the branches of the mandibular nerve to the three muscles were examined.

Classification of the Muscles and Nerve Branch Groups

Classification of the temporalis, masseter, and ZM was performed by their morphological appearance. The aTM was defined as the temporalis portion for which the insertion was attached to the superoanterior part of the medial side of the coronoid process. The belly of the aTM was distinct from the deep layer of the temporalis muscle (dTM) at its posterior border of the insertion. Anteriorly, the tendon of the aTM was separated from the superficial layer of the temporalis (sTM) (Fig. 1). The sTM and dTM were separated by the thick fascia (Fig. 2). The ZM was laid between the sTM and the dMS. The distributing pattern into the ZM was different from the temporalis muscle; the ZM was innervated by the twigs

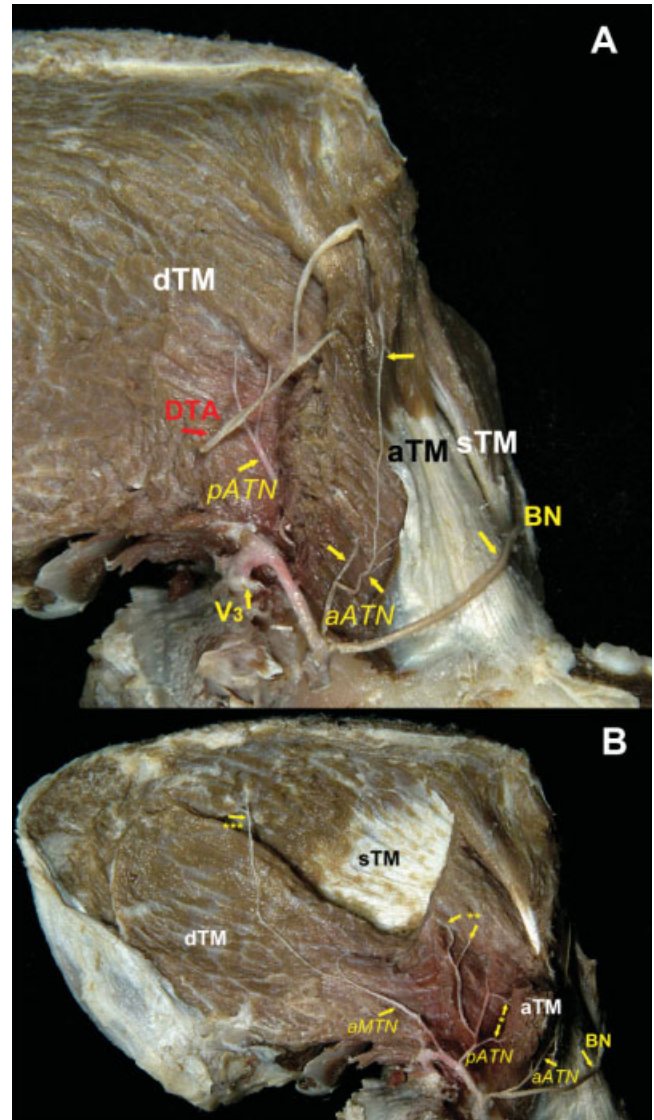


Fig. 1. Nerve twigs innervating the temporalis muscle (aATN, pATN, and aMTN). All branches supplying the temporalis muscle arose from mandibular nerve (V₃). **A:** aATN supplies twigs to the anterior portion of temporalis muscle (aTM). All aATN twigs arose from the buccal nerve (BN). There was an aATN twig that ascended vertically within the AT. pATN supplied the deep layer of temporalis muscles (dTM). The tendon of the superior layer of the temporalis muscle (sTM) was clearly separate from the tendon of the aTM. **B:** pATN twigs innervated both the aTM (*) and the dTM (**). aMTN gave off twigs to the dTM as it proceeded superoposteriorly. It penetrated the dTM and terminated in the sTM (***) Part of the dTM was removed to reveal the distributions of pATN and aMTN. The sTM was revealed by removing the superior part of the dTM. Both specimens shown were hemifaces of the left side. DTA, branch of deep temporal artery.

from the masseteric branches (Fig. 3). Additionally, the inserting tendon of TM was distinct from the masseter muscle (Fig. 4). The masseter was also divided into the sMS, intermediate (iMS), and deep (dMS) layers, which were distinguished by distinct fascias and independent tendons (Fig. 4). The seven partitions of the three

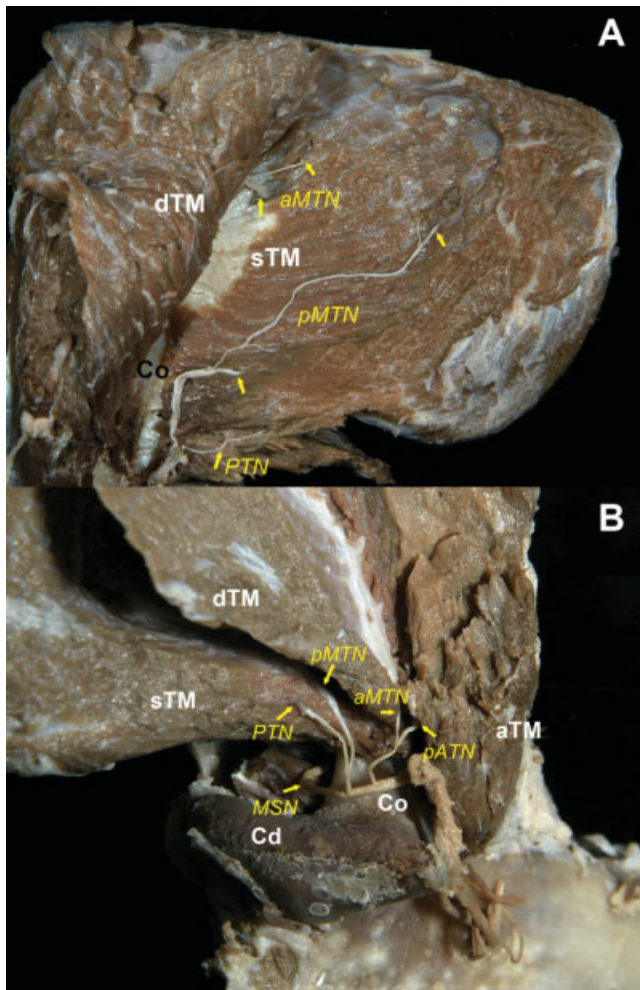


Fig. 2. Nerve twigs innervating the temporalis muscle (pATN, aMTN, pMTN, and PTN). **A:** aMTN, pMTN, and PTN twigs supplying the superficial layer of the temporalis muscle (sTM). aMTN twigs penetrated the deep layer of the temporalis muscle (dTM) and terminated at the sTM. The sTM had a separate tendon that was distinct from the insertion of the dTM. pMTN ran superoposteriorly between the dTM and the sTM. The main trunk turned around the coronoid process of the mandible (Co) after giving off a PTN twig to the posterior area of the sTM. **B:** Posterior view of the masticatory nerve. aMTN entered the dTM and pMTN passed between the sTM and dTM before looping around the coronoid process, PTN arose from the main trunk and inserted into the sTM, near to its inferior margin. The remaining main trunk of the masticatory nerve after giving off PTN was defined as the masseteric nerve (MSN), which comprised dMSN and sMSN. The specimen in A was a right hemiface and the specimen in B was a left hemiface. Cd, condylar process; aTM, anterior portion of the temporalis muscle.

muscles were thus established for subsequent observation of the innervation of the masticatory muscles.

Groups of the mandibular nerve branches innervating the seven partitions were classified into seven groups, and named serially according to their distributions as follows:

1. aATN (anterior twigs of anterior temporal nerve): Nerve twigs branched from BN and innervating the aTM (Fig. 1A).

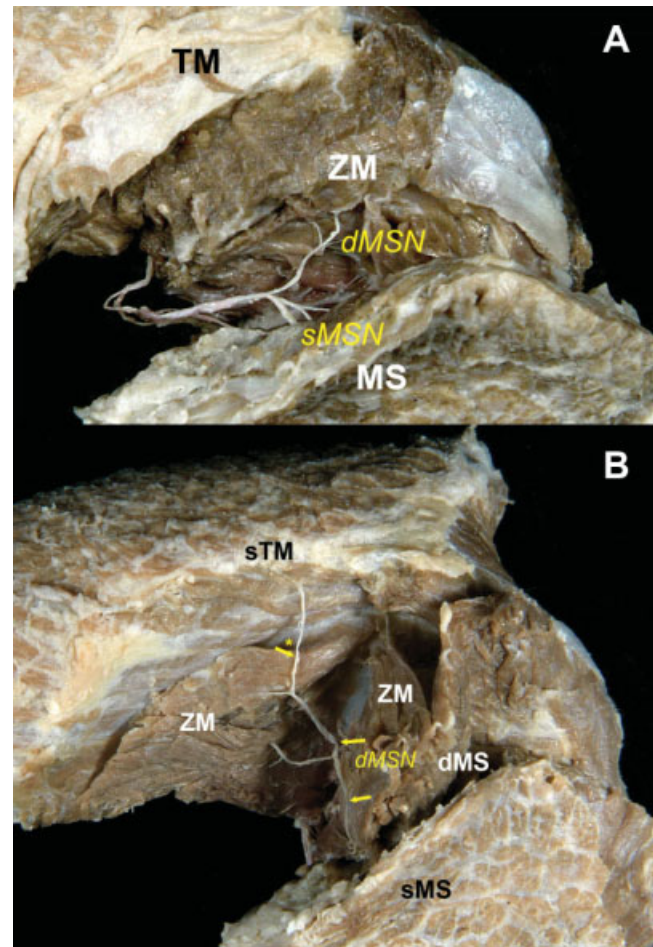


Fig. 3. The zygomaticomandibularis muscle (ZM) and its nerve supply. **A:** The ZM was located between the temporalis muscle (TM) and the masseter muscle (MS). After looping around the coronoid process, the masticatory nerve trunk was divided into dMSN and sMSN. dMSN twigs innervated the ZM and sMSN inserted into the MS. **B:** dMSN twigs innervating the ZM. Some of these (*) proceeded superiorly and terminated in the superficial layer of the TM (sTM). Both specimens shown were right hemifaces.

2. pATN (posterior twigs of anterior temporal nerve): Nerve twigs branched from main trunk of masticatory nerve and innervating the aTM and sTM (Fig. 1A).
3. aMTN (anterior twigs of middle temporal nerve): Nerve twigs innervating the dTM and sTM, after approaching from the medial side and directly inserting into the dTM (Fig. 1B).
4. pMTN (posterior twigs of middle temporal nerve): Nerve twigs traveling within the fascia between the dTM and sTM (Fig. 2A), after directly inserting the gap between them (Fig. 2B).
5. PTN (posterior temporal nerve): Nerve twigs inserting into the temporalis from its posterior side and then innervating the sTM (Fig. 2B).
6. dMSN (deep twigs of masseteric nerve): Nerve twigs innervating the ZM (Fig. 3).

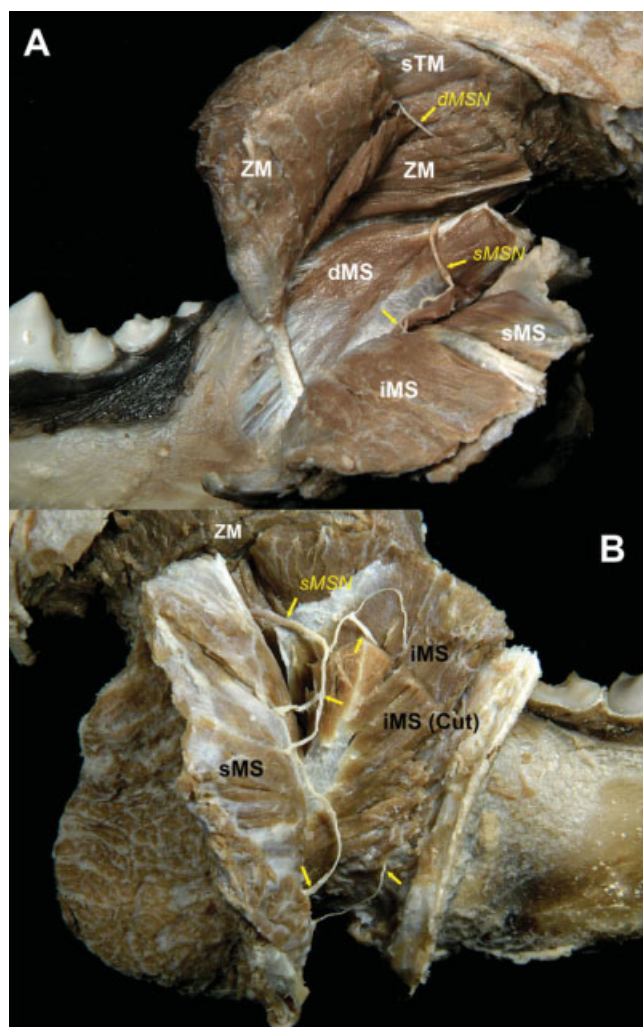


Fig. 4. Three layers of the masseter muscle and its nerve distribution. The three layers of the masseter and zygomaticomandibularis muscle (ZM) were clearly distinct from each other. **A:** sMSN passed between the ZM and the deep layer of the masseter (dMS). The posterior area of the intermediate layer of the masseter (IMS) was removed to reveal the superficial layer of the masseter (sMS). **B:** After entering the masseter, sMSN traveled inferoanteriorly, supplying the three layers of the masseter. Part of the IMS was removed to show the nerve distribution. A dMSN twig innervated the sMS after penetrating the ZM. The specimen in A was a left hemiface and the specimen in B was a right hemiface.

7. sMSN (superficial twigs of masseteric nerve): Nerve twigs innervating the masseter (Figs. 3A, 4).

RESULTS

The nerve trunk, which gave off twigs innervating the temporalis, masseter, and ZM, was collectively termed the masticatory nerve in this study. The main trunk of the masticatory nerve was arising from the mandibular nerve (V₃) and proceeded anterolaterally, passing the posterior margin of the lateral pterygoid muscle (LPt). However, some of the twigs that innervated the aTM in

particular were branches from either the masticatory nerve or the BN (Fig. 1B). The nerve trunk of the masticatory nerve traveled posteriorly, innervating the aTM, dTM, and sTM. The nerve trunk turned around the coronoid process and proceeded between the ZM and the dTM (Fig. 2B), and finally penetrated the three layers of the masseter (Fig. 4). The twigs of the masticatory nerve were categorized into seven groups according to their course and distribution. The innervation patterns of the masticatory nerve twigs of all 15 specimens were almost the same.

Nerve Twigs to the Anterior Portion of the Temporalis

ATN originated from both the BN and the main trunk of the masticatory nerve. The set of twigs arising from the BN was named aATN (Fig. 1) and were found in all 15 specimens. aATN twigs entered the aTM inferiorly and then ascended vertically. aATN did not supply the sTM or the dTM. pATN twigs arose from the main trunk of the masticatory nerve and innervated the aTM (Fig. 1B). These nerves were found in 11 of the 14 specimens (78.6%). Unlike aATN, the pATN twigs supplied both the dTM and the aTM. Some of the pATN twigs supplied the lower region of the aTM as they traveled anteriorly (Fig. 1B). The remaining pATN twigs innervated the dTM as they proceeded superiorly (Fig. 1B).

Nerve Twigs Supplying the Superficial and Deep Layer of the Temporalis

The aMTN bundle, which comprised those twigs that inserted directly into the dTM after approaching from the medial side, was found in 9 of the 11 specimens (81.2%, Fig. 1B). aMTN twigs ran superoposteriorly within the dTM. All aMTN twigs entered at the postero-superior area of the dTM and terminated in the sTM (Fig. 1B). After approaching the inferior side of the temporalis, pMTN twigs (Fig. 2) traveled between the dTM and sTM. These twigs were observed in all cases of the observed 14 specimens. Like aMTN, the pMTN twigs ran superoposteriorly and supplied both the dTM and the sTM.

After the main trunk of the masticatory nerve had given off aATN, pATN, aMTN, and pMTN, it entered the mandibular notch. Before entering the mandibular notch, the main trunk supplied branches to the posterior portion of the sTM near to its inferior margin (Fig. 2). These branches formed the PTN bundle, which was found in all cases of the observed 13 specimens. PTN did not supply the dTM (Fig. 2B).

The Masseteric Nerve and Its Innervation of the Zygomaticomandibularis and Masseter

After passing the mandibular notch and turning around the coronoid process, the main trunk of the masticatory nerve reached the lateral side of the mandible. The remaining trunk of the masticatory nerve was known as the MSN, which was divided into the dMSN and sMSN bundles; these innervated the ZM and masseter (Fig. 3A). dMSN supplying the ZM was observed in all cases of the observed 13 specimens. In all cases, there were twigs that ran upward within the ZM ultimately

TABLE 1. Classification and terminology of the nerves innervating to temporalis, zygomaticomandibularis, and masseter in humans and dogs

Human	Dog	
Akita et al. (2000)	Tomo et al. (1993)	Yang et al. (2009, this study)
Anterior deep temporal n. (ADTN)	Anterior temporal n. (ATN)	Anterior br. of anterior temporal n. (aATN)
Middle deep temporal n. (MDTN)	Posterior temporal n. (PTN)	Posterior br. of anterior temporal n. (pATN)
		Anterior br. of middle temporal n. (aMTN)
		Posterior br. of middle temporal n. (pMTN)
Posterior deep temporal n. (PDTN)	Superficial temporal n. (STN)	Posterior temporal n. (PTN)
Masseteric n. (MS)	Masseteric n. (MS)	Deep br. of masseteric n. (dMSN)
		Superficial br. of masseteric n. (sMSN)

n., nerve; br., branch.

reaching the sTM (Fig. 3B). The remaining twigs from dMSN innervated the ZM (Fig. 3B). sMSN, the terminal branch of the masticatory nerve, was terminated by innervating the masseter in all cases. sMSN traveled between the ZM and the dMS (Fig. 4A) and supplied branches to the three layers of the masseter, running inferoanteriorly (Fig. 4B).

DISCUSSION

The finding of a characteristic distribution of nerves to the ZM, temporalis, and masseter provided evidence for phylogenetic traits that were specific to canine mastication.

Comparison of the Present Results with the Previous Studies of the Dog

The existence of species-specific innervation traits might be elucidated by making a comparison between the respective innervation patterns of, for example, human and canine masticatory muscles (Table 1). However, few studies have classified the canine masticatory muscles according to their innervation patterns. To the author's knowledge, the only such classification has been performed by Tomo et al. (1993), and hence the results of this study were compared with that classification. They reported that the ATN divides into an anterior branch, which supplies both the aTM and the dTM, and a posterior branch, which travels near the LPt. They also reported that the ATN is a branch of the BN and does not communicate with the posterior temporal nerve (PTN). They regarded the portion innervated by the ATN as the anterior deep temporalis. Because in this study, aATN was identical to the ATN, as evidenced by the finding that it arises from the BN, the anterior deep temporalis of Tomo et al. (1993) corresponded to part of the aTM in our study. From the morphological point of view, the areas of muscle innervated by aATN were not clearly demarcated from those supplied by pATN, and hence the muscular bundles innervated by aATN and pATN appear to act as a singular vectorial force (Fig. 1).

Additionally, Tomo et al. (1993) classified the masseter into two layers, whereas we classified it into three; however, there was no significant difference in the nerve distributions between their study and ours.

Comparison Between Dog and Human Masticatory Muscles

With regard to the case in humans, the correspondence between dog and human in the masticatory nerve and masseteric muscles area was found (Fig. 5). The canine aATN, which was defined as the twigs ramified from the BN, corresponded to the human ADTN innervating the AM, anterior portion of the main part of temporalis (TM), and anterolateral temporal bundle (AL). The canine PTN was branched from the MSN and distributed to the posterior region of the sTM, and the human PDTN gave off the twigs into the posterior part of the TM and distotemporal bundle (DT). And hence the canine PTN might innervate to the canine DT homologue. The bundles, which were distributed by canine pATN, aMTN, and pMTN, were not exactly examined in this study. Thus, we do not know a detailed area of the canine homologues that corresponded to human mid-medial temporalis bundle (MM) and mid-lateral temporal bundle (ML). Although the detailed examination of the distributing patterns to the tiny bundles is absent, we assumed that the canine aMTN or dMSN was innervating to the ML homologue because the superficial part of the sTM was innervated by the twig of the dMSN, and the aMTN was reaching the most superficial layer. Regarding the topographic arrangement of the canine aMTN, in which aMTN approached the dTM from the medial side, the canine MM homologue might be innervated by the aMTN. A more accurate observation of the detail muscle bundle of the masseteric muscles would be needed to elucidate the homologue between the dog and human.

The canine pATN-innervated area is located more anteriorly than the human MDTN-innervated area, and the area of aTM supplied by pATN in the dog is distinct from that supplying the sTM, whereas the ADTN- and MDTN-innervated areas in the human are not distinct (Fig. 1B). The vectorial directions of the human and dog temporalis were reflected by these findings. The more horizontally positioned canine temporalis was attached to the posterior portion of the coronoid process; therefore, the ability to distinguish between the horizontal and vertical parts might be more appropriate with regard to their mechanics. However, it seems that their embryonic origin does not concur with the functional and morphological findings.

A nerve connection between the zygomaticomandibular part of the masseter and temporalis was found in the study of Tomo et al. (1993), and dMSN twigs penetrating the ZM and reaching the sTM were observed in this

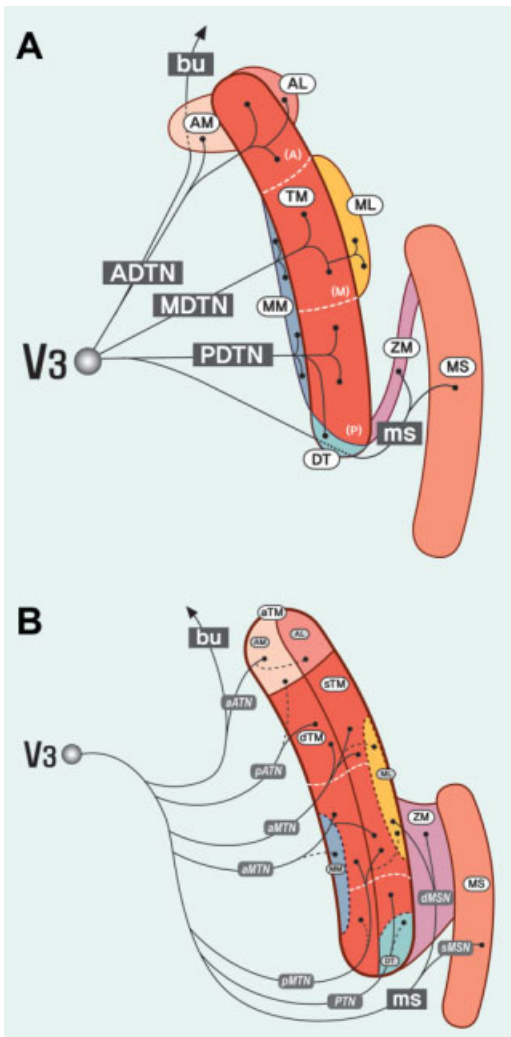


Fig. 5. Comparison of the innervation patterns of canine masticatory muscles with the human deep temporal nerves classified by Akita et al. (2000). **A:** Innervation patterns of human masticatory muscle. **B:** Innervation patterns of canine masticatory muscles in this study. V3, mandibular nerve; bu, buccal nerve; ms, masseteric nerve; ADTN, MDTN, and PDTN, anterior, middle, and posterior deep temporal nerve; aATN and pATN, anterior and posterior twigs of anterior temporal nerve; aMTN and pMTN, anterior and posterior twigs of middle temporal nerve; PTN, posterior temporal nerve; sMSN and dMSN, superficial and deep masseteric nerve; AL, anterolateral temporalis bundle; AM, anteromedial temporalis bundle; DT, distotemporalis bundle; ML, midlateral temporalis bundle; MM, midmedial temporalis bundle; TM, main part of temporalis; MS, masseter; ZM, zygomaticomandibularis; aTM, anterior portion of the temporal muscle; sTM, superior layer of the temporal muscle; dTM, deep layer of the temporal muscle.

study. Akita et al. (2000) did not report such a connection between the ZM and temporalis.

Nomenclature of the Dog and Human Masticatory Muscles

The distribution of the canine PTN in the study of Tomo et al. (1993) is similar to that of pATN, aMTN, pMTN, and PTN in our study, and the innervation pat-

tern of the human MDTN in the study of Akita et al. (2000) is homologous to that of pATN, aMTN, and pMTN in our study (Table 1, Fig. 5). Like aMTN, pMTN, and PTN in this study, the PTN in the study of Tome et al. (1993) proceeds superoposteriorly (Figs. 1B, 2A). The canine PTN seems to be homologous to the human PDTN, and hence the distotemporal temporalis bundle of the human temporalis (Akita et al., 2000) is homologous to the posterior portion of the canine sTM (Fig. 5). In the study of Tomo et al. (1993), the layer of the temporalis that was shown to be attached to the lateral side of coronoid process was innervated by the superficial temporal nerve (STN); PTN of this study is thus identical to the STN.

Pattern of Distribution of the Masseteric Nerve to the Well-Developed Zygomaticomandibularis

The ZM of mammals is a powerful masticatory muscle that functions as a coordinator of the temporalis and masseter. However, in humans it has become less powerful or even rudimentary (Hwang et al., 2005). Tomo et al. (1993) thought that the canine ZM was not an independent muscle, that it was in fact part of the masseter. However, we found that the ZM was independent and existed as a massive and fan-shaped muscle located between the sTM and the dMS (Fig. 3B). A tendon of the ZM was attached to the lateral side of the mandible near the mandibular angle (Fig. 4A). The direction of force exerted by the action of the ZM was anterosuperior, and so one would expect the ZM to perform the significant action of rotating the mandible about an axis that might be located at the temporomandibular joint.

In all cases, the twigs that innervate the ZM were branches from the nerve trunk that enters the masseter after turning around the coronoid process. It has been reported that in humans both the masseter and the ZM were innervated by the MSN (Shimokawa et al., 1999), and both were derived from the posterior area of the common anlage of the masticatory muscles (Edgeworth, 1914). It was reported that the MSN innervated both the masseter and ZM of *S. murinus* (Shimokawa et al., 2002). Tomo et al. (1993) pointed out that the zygomaticomandibular part of the masseter was supplied by the MSN in the dog. In studies of the great-gray kangaroos (*M. giganteus*), it was proposed that these two muscles are also supplied by the same MSN (Tomo et al., 2007). Similarly, Liu et al. (2004) observed 25 miniature pigs and reported that their ZM and masseter were innervated by same MSN.

Most researchers agree that the mammalian ZM and masseter have a common developmental origin. However, the nervous connection between the temporalis and ZM has not been clear in the human (Akita et al., 2000). On the other hand, in dogs, there are twigs that pass through the ZM and terminate by innervating the sTM. Hence, there is a more intimate relationship between the temporalis and the ZM in dogs. Considering the significant action of the canine ZM, this close relationship with the temporalis suggests that a portion of the anlage of the ZM formed a small area of the sTM. The fact that the canine ZM plays a more important role—especially, passive contralateral excursion for the repositioning mandible after lateral movement—in mastication than does its human counterpart implies the occurrence of

evolutionary adaptation of the masticatory muscle bundle in these animals, leading to the observed differences.

Independent Innervations of Twigs Arising From the Buccal Nerve to the Anterior Portion of the Temporalis: Mechanics of Jaw Movement

There have been several studies regarding the relationship between the human LPt and the temporalis from the view of development. The human LPt is dominantly engaged in the lateral movement of the jaw, but the canine LPt is poorly developed despite the lateral movement of the jaw dogs are able achieve (Ström et al., 1988; Akita et al., 2000; Kim et al., 2003; Kwak et al., 2003). Ström et al. (1988) described the temporalis as the largest masticatory muscle, and in one textbook the temporalis of the carnivores was reported to be a dominant elevator (Hilderbrand and Goslow, 2001).

In this study, the muscle fibers of the aTM were oriented vertically. Tomo et al. (1993) reported that the anterior deep part of the temporalis was supplied by the ATN in dog. Similar innervation patterns of the aTM were observed in our study. Shimokawa et al. (1998) reported the presence of partitioned muscle bundles in the human temporalis, and Akita et al. (2000) observed six muscle bundle groups within the temporalis in their human cadaveric studies. The canine aTM in this study appears to be homologue of the human AM and the anterior part of the midmedial temporalis bundle, as described in the study of Akita et al. (2000). The ADTN, which innervated the aTM and the AM in humans, arose from the BN (Akita et al., 2000), and aATN, which we found supplied the canine AT in this study, also arose from the BN. pATN also innervates the aTM, and both aATN and pATN seem to be homologous to the human ADTN. However, the observation in this study that aATN does not supply the sTM and dTM demonstrates that the aTM has an independent nerve distribution. Together with the observation of separate insertion and a distinct horizontal orientation of the muscle bundles, this finding is considered as evidence supporting the hypothesis that the aTM could perform a more independent action in dogs.

Mechanically, the canine temporalis provides a horizontally oriented force to the coronoid process (Hilderbrand and Goslow, 2001). Therefore, our findings regarding the independent innervation and the mechanics of the canine temporalis suggest that rather than being majorly involved in jaw elevation, the vertically oriented aTM serves as an assistant for the jaw-elevating action or as a coordinator of jaw stability.

In his EMG study of the canine masticatory muscles, Iinuma et al. (1991) suggested that the masseter is a more dominant adductor than the temporalis in the adult dog. However, they inserted an electrode into the aTM and not the posterior portion, where the muscle bundles are oriented horizontally (Iinuma et al., 1991). The movement of the canine mandible, mainly hinge-like, and the massive temporalis, which is bulkier than the masseter, was interpreted as a predominance of the canine temporalis during mastication (Ström et al., 1988; Hilderbrand and Goslow, 2001). However, our findings suggest that Iinuma et al. (1991) measured only the EMG muscle activities of the aTM, because the canine aTM plays only a minor role during mastication. This

hypothesis requires clarification by examining the EMG activity of every part of the canine temporalis.

There is need to perform more detailed and experimental study such as horseradish peroxidase method by which the researcher can find the relationship between the central neural system (e.g., brainstem nuclei, brain) and its controlled muscle bundles, and then the comparative study as to the higher regulation of the masticatory muscles, because the knowledge of the motor command was necessary for more reliable study (Matsuda, 1979). Additionally, the broader species of the mammals comprising the herbivores should be used for more general traits of the phylogeny of the mammal masticatory muscles.

A close similarity was observed between the innervation of the canine and human masticatory muscles; however, there exist some differences, which might be attributable to evolutionary adaptation to their respective feeding styles. Although independence of a muscle bundle does not depend only on the presence of a separate nerve supply, this study provided the topographic evidence to consider the canine masticatory muscles in the comparative point of view. To the authors' knowledge, this report is the first to describe the comparative anatomy of the innervation of the masticatory muscles of humans and dogs.

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