Brain Research Bulletin xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Brain Research Bulletin

journal homepage: www.elsevier.com/locate/brainresbull

Research report

Termination of trigeminal afferent fibers on facial motoneurons: Possible neural network mediating jaw opening during prey-catching behavior of the frog☆

Gabriella Kovalecz[a], Szilvia Kecskes[b], András Birinyi[b], Clara Matesz[b,c,d,*]

[a] Department of Pediatric Dentistry and Orthodontics, Faculty of Dentistry, University of Debrecen, Nagyerdei krt. 98, Debrecen H-4032, Hungary
[b] Department of Anatomy, Histology and Embryology, Faculty of Medicine, University of Debrecen, Nagyerdei krt. 98, Debrecen H-4032, Hungary
[c] MTA-DE Neuroscience Research Group, University of Debrecen, Nagyerdei krt. 98, Debrecen H-4032, Hungary
[d] Division of Oral Anatomy, Faculty of Dentistry, University of Debrecen, Nagyerdei krt. 98, Debrecen H-4032, Hungary

ARTICLE INFO

Article history:
Received 15 July 2015
Received in revised form
10 September 2015
Accepted 29 September 2015
Available online xxx
Section Editor: K.P. Giese, Mechanisms of Behavior & Cognition

Keywords:
Brainstem
Nucleus nervi facialis
Neuronal labeling
Neurolucida reconstruction

ABSTRACT

The prey-catching behavior of the frog is a complex, well-timed sequence of stimulus response chain of movements. After visual analysis of the prey, a size dependent program is selected in the motor pattern generator of the brainstem. Besides this predetermined feeding program, various direct and indirect sensory inputs provide flexible adjustment for the optimal contraction of the executive muscles. The aim of the present study was to investigate whether trigeminal primary afferents establish direct contacts with the jaw opening motoneurons innervated by the facial nerve.

The experiments were carried out on Rana esculenta (*Pelophylax esculentus*), where the trigeminal and facial nerves were labeled simultaneously with different fluorescent dyes. Using a confocal laser scanning microscope, close appositions were detected between trigeminal afferent fibers and somatodendritic components of the facial motoneurons.

Quantitative analysis revealed that the majority of close contacts were encountered on the dendrites of facial motoneurons and approximately 10% of them were located on the perikarya. We suggest that the identified contacts between the trigeminal afferents and facial motoneurons presented here may be one of the morphological substrate in the feedback and feedforward modulation of the rapidly changing activity of the jaw opening muscle during the prey-catching behavior.

1. Introduction

Prey-catching behavior (PCB) of the frog consists of a series of movements in which each action triggers the subsequent motor activity. After visual analysis of the potential prey, the feeding program is selected in the motor pattern generators (MPGs) of the brainstem which determines the appropriate spatial and temporal patterns of the desired motor activity (Corbacho et al., 2005; Ewert et al., 1990; Matsushima et al., 1989; Schwippert and Framing, 1989; Weerasuriya, 1983, 1989). In ranid frogs and toads the characteristic pattern for feeding is called tongue prehension behavior (TPB) (Monroy and Nishikawa, 2011; Nishikawa, 2000). Although feeding movements are essentially organized by this genetically predetermined program, various sensory signals may provide flexible fine tuning for the ongoing motor action (Anderson and Nishikawa, 1993; Anderson, 2001; Harwood and Anderson, 2000; Nishikawa and Gans, 1992; Weerasuriya, 1989). Several studies (Anderson, 2001; Corbacho et al., 2005; Mandal and Anderson, 2010; Matsushima et al., 1986; Nishikawa, 2000) suggested polysynaptic pathways between sensory fibers and motoneurons involved in the prey catching behavior. Although the possible influence of the primary afferents on the activity of jaw opening muscle is not yet determined, direct contacts have been verified between sensory fibers and various motoneurons supplying jaw closing and tongue muscles as well as those involved in swallowing (Deak et al., 2009; Kecskes et al., 2013, 2015; Matesz et al., 2008).

Abbreviations: MPGs, motor pattern generators; PCB, prey-catching behavior; TPB, tongue prehension behavior; tspV, spinal tract of the trigeminal nerve; Vmes, mesencephalic tract of the trigeminal nerve.

☆ *Grant Support*: This work was supported by grants from the Hungarian Academy of Sciences (MTA TKI 11008), DE OEC Bridging Fund.

* Corresponding author at: Department of Anatomy, Histology and Embryology, Faculty of Medicine, University of Debrecen, Nagyerdei krt. 98, Debrecen H-4032 Hungary. Fax: +36 52 255 115.
E-mail address: matesz@anat.med.unideb.hu (C. Matesz).

http://dx.doi.org/10.1016/j.brainresbull.2015.09.012
0361-9230/

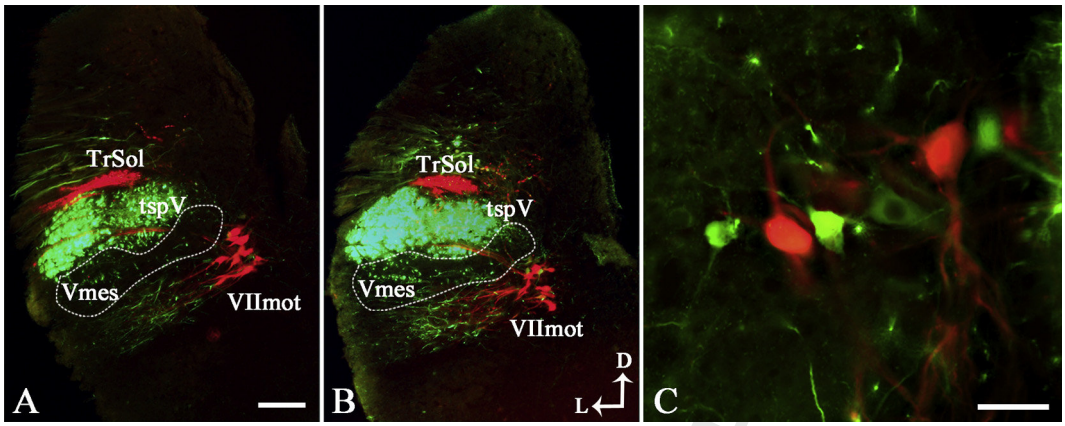

Fig. 1. Photomicrographs showing distribution of labeled trigeminal afferents (green) as well as somata and dendrites of facial motoneurons and the solitary tract (red) at the rostral (A) and caudal (B) parts of facial motor nucleus. The overlap between the position of facial (red) and trigeminal (green) motoneurons is shown on C. TrSol: solitary tract; tspV: spinal tract of trigeminal nerve; Vmes: mesencephalic tract of trigeminal nerve (encircled area); VIImot facial motoneurons; D: dorsal; L: lateral. Scale bar 100 μm on A, B, and 50 μm on C. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The jaw opening is executed by the contraction of depressor mandibulae muscle (DMm) under the control of the facial nerve (Gans and Gorniak, 1982; Gaupp, 1904). The possible candidates for sensory inputs to facial motoneurons innervating depressor mandibulae muscle are conveyed by hypoglossal and trigeminal nerves. The sensory fibers of the hypoglossal nerve innervate the tongue. Earlier experiments showed that after transection of hypoglossal nerves jaw opening disappeared even though the facial nerve remained intact and concluded that sensory feedback from the tongue is necessary to trigger mouth opening (Anderson and Nishikawa, 1993; Corbacho et al., 2005; Nishikawa and Gans, 1992; Weerasuriya, 1991, 1989). Based on neuronal labeling studies, the hypoglossal afferents and collaterals appeared very rarely in the territory of facial motoneurons, therefore polysynaptic pathways were hypothesized (Matesz and Szekely, 1978; Stuesse et al., 1983). The sensory fibers of trigeminal nerve carry information from the proprioceptors of jaw muscles, the Golgi tendon organs and the mechanosensory receptors of the oral cavity and tongue (Mandal and Anderson, 2010). Our earlier cobalt labeling studies showed that trigeminal afferents were distributed around the perikarya and dendritic trees of the facial motoneurons suggesting the possibility of monosynaptic connections.

Therefore, the goal of our present study was to investigate whether the afferent fibers of trigeminal nerve can establish direct contacts with the facial motoneurons and to provide quantitative description concerning the location and spatial distribution of these connections on the somato-dendritic compartments of facial motoneurons in the frog.

2. Materials and methods

The experiments were carried out on ten adult common water frogs, Rana esculenta (*Pelophylax esculentus*). The study protocol was reviewed and approved by the Animal Care Committee of the University of Debrecen, Debrecen, Hungary, according to national and EU laws (European Communities Council Directive of 24 November 1986 (86/609/EEC)), and it was properly carried out under the control of the University's Guidelines for Animal Experimentation (license number: 11/2011/DEMAB).

The animals were anaesthetized with 0.01% of MS 222 (tricaine methane-sulfonate, Sigma, St. Louis, MO) applied to the wet skin. The facial and trigeminal cranial nerves were approached from an oropharyngeal view. First the mucosa on the roof of oral cavity was incised then a portion of the parasphenoidal bone was clipped away to open the cranial cavity. After cutting the dura mater, the facial and trigeminal nerves were prepared and sharply transected proximal to the ganglion prooticum commune. Crystals of neurobiotin (Vector Laboratories, Burlingame, CA) was put on the proximal stump of trigeminal nerve and dextran conjugated Alexa Fluor 555 (10,000 MW, Molecular Probes Inc., Eugene, OR, USA) was applied to the proximal cut end of facial nerve on ipsilateral side of the brainstem. To avoid nonspecific labeling and to prevent leakage of the tracer, the stumps of nerves were covered with a mixture of silicone oil and grease.

The frogs were kept in a wet chamber for 7 days at a temperature of 10 °C. Then the animals were reanaesthetized and transcardially perfused with isotonic saline for 20 min, followed by 4% paraformaldehyde in 0.1 M phosphate buffer (pH 7.4) for fixation. The brainstems were removed and postfixed overnight in 4% paraformaldehyde, then immersed in 20% sucrose dissolved in the same buffer solution. Transverse serial sections of the brainstems were cut with a freezing microtome at a thickness of 50 μm. For visualization of neurobiotin, the sections were treated with streptavidin Alexa Fluor 488 (1:1000, Molecular Probes, Invitrogen) for 2 h at room temperature. Finally the sections were coverslipped with Vectashield Mounting Media for Fluorescence (Vector Laboratories).

Confocal images were recorded using Olympus FV1000 confocal laser scanning microscope (40× oil immersion lens, NA: 1.3). Series of 1 μm thick optical slices were captured from four animals along the rostrocaudal extent of the facial motor nucleus. Close appositions between primary afferents of trigeminal nerve and dendrites or cell bodies of the motoneurons in the facial nucleus were counted manually on the *Z*-stack images. The contacts were considered as close apposition if the surfaces were at the same focal plane and there was no discernible gap between the two profiles (Wouterlood et al., 2002, 2003). The distance of a connection was measured as radial distance from the nearest cell body with the help of Olympus FluoView Software.

In order to illustrate the location of motoneurons and afferent collaterals in the brainstem, low magnification images were photographed by using Olympus DP 72 camera. The spatial distribution of trigeminal afferents in the brainstem along with the perikarya and the dendritic arborization field of the facial motoneurons were revealed by using our earlier specimens where the trigeminal and the facial nerves were separately labeled with cobalt chloride (Matesz and Szekely, 1978). The three-dimensional reconstruction was performed from the serial sections with Neurolucida 8.0 program (MBF Bioscience, Inc., Williston, VT, USA).

Please cite this article in press as: Kovalecz, G., et al., Termination of trigeminal afferent fibers on facial motoneurons: Possible neural network mediating jaw opening during prey-catching behavior of the frog. Brain Res. Bull. (2015), http://dx.doi.org/10.1016/j.brainresbull.2015.09.012

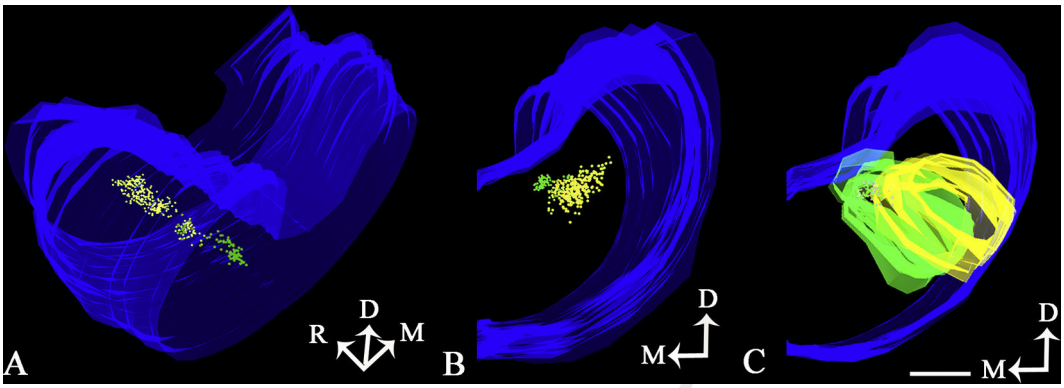

Fig. 2. Three-dimensional reconstruction of the brainstem (blue) showing the somata of the trigeminal (yellow) and facial (green) motoneurons (A and B) and the overlapping areas between trigeminal afferents (yellow) and dendritic field of facial motoneurons (green) (C). Scale bar 500 μm. D: dorsal, M: medial, R: rostral. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

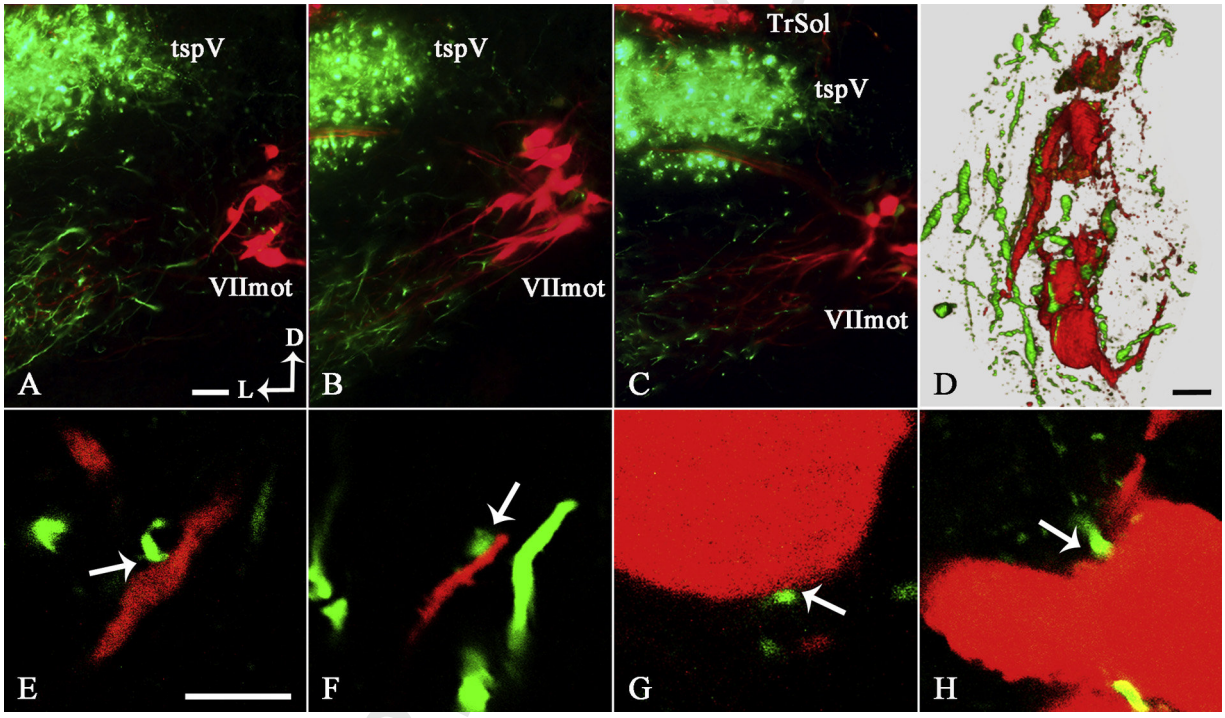

Fig. 3. Photomicrographs showing the overlap between trigeminal axons (green) and dendritic arborization of the facial motoneurons (red) (A–C). D: three-dimensional reconstruction of confocal imiges showing the position of somata and dendrites of facial motoneurons (red) and trigeminal afferents (green). Confocal micrographs illustrating direct contacts (arrows) between the trigeminal primary afferent terminals (green) and the dendritic segments (E and F) (arrows) or cell bodies (G and H) of the facial motoneurons (red). TrSol: solitary tract; tspV: spinal tract of trigeminal nerve; VIImot facial motoneurons; Scale bar 50 μm on A, B, C, 25 μm on D and 10 μm on E–H. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

Application of Alexa Fluor 555 to the cut end of the facial nerve resulted in retrograde labeling of perikarya and dendritic tree of the facial motoneurons and anterogradely labeled axons of the solitary tract (Fig. 1A and B). The majority of the facial dendrites directed ventrolaterally from the cell bodies and a weaker array of dendritic branches in the dorsomedial direction. Neurobiotin labeling of the trigeminal nerve revealed the cell bodies of motoneurons located rostrally to the column of facial motoneurons, some of the trigeminal somata were intermingled with the perikarya of the facial motoneurons (Fig. 1C). The labeled trigeminal nerve constituted well defined bundles of axons running in the spinal and mesencephalic tracts on the medial side of the solitary tract and sent off several collaterals towards the facial motoneurons (Fig. 1A and B). The distribution and the appearance of the labeled neurons were similar to the results of previous experiments where the same cranial nerves were revealed by using cobalt chloride (Matesz and Szekely, 1978, 1996).

In order to reveal the potential overlapping fields between the territory of trigeminal afferents and the area occupied by the somatodendritic compartments of facial motoneurons, we reconstructed the brainstem containing the labeled neurons. We have found that trigeminal afferents and collaterals were distributed among the facial perikarya and showed significant overlap with the territory of ventrolateral dendritic tree (Fig. 2). These overlapping areas were also detected on the photomicrographs of neurons labeled with different fluorochromes (Fig. 3A–C). Accordingly, the axon collaterals of the trigeminal nerve extended into the territory of perikarya and as the confocal images revealed they formed a dense meshwork in

Please cite this article in press as: Kovalecz, G., et al., Termination of trigeminal afferent fibers on facial motoneurons: Possible neural network mediating jaw opening during prey-catching behavior of the frog. Brain Res. Bull. (2015), http://dx.doi.org/10.1016/j.brainresbull.2015.09.012

Table 1
Number of connections between trigeminal afferent terminals and facial motoneurons.

	Axo-somatic	Axo-dendritic	Average distance from the soma (μm)
Frog 1	28 (17%)	132 (83%)	218 ± 11
Frog 2	25 (13%)	162 (87%)	269 ± 14
Frog 3	27 (10%)	237 (90%)	308 ± 14
Frog 4	27 (12%)	193 (88%)	277 ± 12
Mean ± SEM	27 ± 1	181 ± 23	275 ± 7
Total	107 (13%)	724 (87%)	

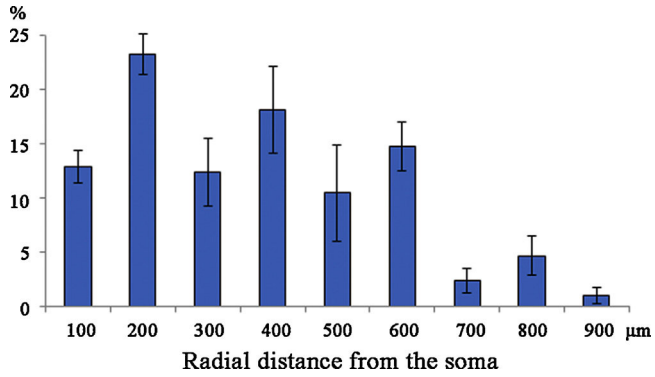

Fig. 4. Distribution of the distance of the close appositions between trigeminal afferent terminals and facial motoneuron.

close vicinity of the cell bodies and proximal dendrites of the facial motoneurons (Fig. 3D).

With confocal laser scanning microscopy we could confirm direct connections between anterogradely labeled trigeminal axon terminals and dendritic trees (Fig. 3E and F) and cell bodies (Fig. 3G and H) of retrogradely labeled facial motoneurons. We investigated 5050 optical slices from the brainstem of four animals and detected altogether 831 contacts between trigeminal axon terminals and facial motoneurons. The majority of identified appositions were located on the dendrites (87%), whereas 13% were encountered on the somata (Table 1). The largest number of axodendritic contacts was observed within 600 μm distance from the cell body of the facial motoneurons (Fig. 4).

4. Discussion

Using confocal laser scanning microscopy we have demonstrated for the first time that large number of direct contacts exist between the sensory trigeminal fibers and the facial motoneurons innervating jaw opening muscle in the frog. We assume that the majority of the close appositions should be synaptic contacts as it was confirmed at the electron microscope level in various parts of the central nervous system (Wouterlood et al., 2002, 2003; Corson and Erisir, 2013). The identified direct connections may function as one of the morphological substrates for very quick feedback and feedforward modulation of motor responses during the prey-catching behavior.

In the frog, the depressor mandibulae muscle lowers the jaw and consequently the mouth opens. However, its contribution to the prey-catching behavior is more complex as the activity level of muscle contraction is changing continuously during the execution of tongue prehension behavior (Gans and Gorniak, 1982). High-speed cinematography synchronized with computer-analyzed electromyograms (EMGs) revealed that the first peak of the contraction in depressor mandibulae muscle appeared in the preparatory phase of prey-catching behavior prior to mouth opening when the activity level of muscle fluctuated between 10 and 100% (Gans and Gorniak, 1982). The subsequent initial rapid opening took only 16 ms and it was continued in the protrusive phase when the activity of depressor mandibulae was close to maximum level. At the end of the protrusive phase, when the tongue is projected toward the prey, the activity of the depressor mandibulae decreased between 10 and 50%. At the beginning of the retraction phase, the activity of depressor mandibulae muscle increases to open the mouth wider for pushing the prey into the oral cavity. In later phase of retraction the activity of depressor mandibulae drops and then becomes silent before the tongue reaches the back of the oral cavity. Taking into consideration the very quick time course of prey-catching behavior (Gans and Gorniak, 1982), we supposed that feedback and feedforward modulations of rapidly changing activity of the depressor mandibulae muscle could be provided via the monosynaptic sensory input transported by the trigeminal nerve to the facial motoneurons.

Sensory fibers of the trigeminal nerve related to the prey catching behavior carry information from different receptors associated with different axonal morphology and physiological properties. One type of the receptors are the proprioceptors in the muscle spin-

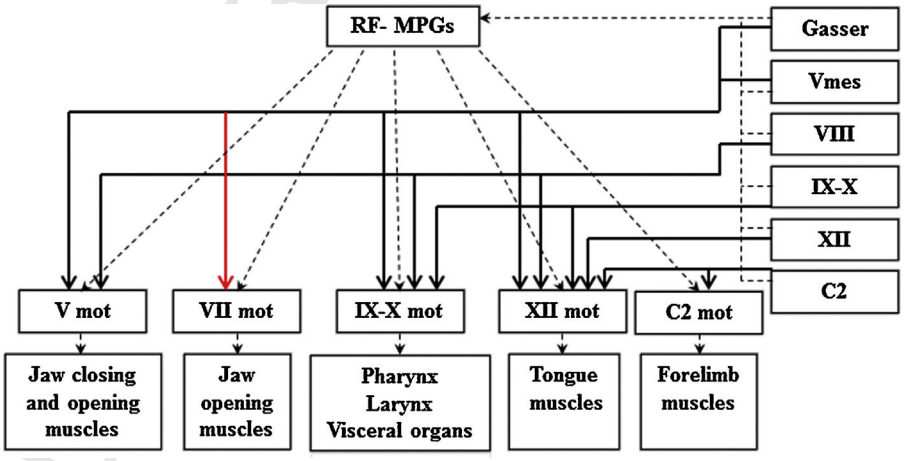

Fig. 5. Schematic illustration of the organization of the neuronal networks underlying the prey-catching behavior in the frog. Dashed lines indicate the indirect, solid lines show direct pathways. Red line illustrates the identified direct contacts between trigeminal sensory fibers and facial motoneurons. RF-MPGs: reticular formation-motor pattern generators; Vmot: trigeminal motor nucleus; VIImot: facial motor nucleus; IX-Xmot: glossopharyngeal-vagal nerve motor nuclei; XIImot: hypoglossal motor nucleus; C2mot: motoneurons of the second cervical spinal segment; Vmes: mesencephalic tract of the trigeminal nerve; Gasser: the sensory ganglion of the trigeminal nerve; Roman numerals correspond to the cranial afferents. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Please cite this article in press as: Kovalecz, G., et al., Termination of trigeminal afferent fibers on facial motoneurons: Possible neural network mediating jaw opening during prey-catching behavior of the frog. Brain Res. Bull. (2015), http://dx.doi.org/10.1016/j.brainresbull.2015.09.012

dles and the Golgi tendon organs of the jaw muscles having mostly large diameter axons (Granit, 1975; Proske, 1969a,b). The other group of receptors are the mechanoreceptors of the oral mucosa and tongue with small and medium sized fibers. The wide range of sensory modalities from different receptors which are propagated along the primary afferent axons with different velocity of impulses may be responsible for the fine tuning of the very rapid switch from one phase of tongue prehension to the other. The further adjustment of muscular activity during various phases of prey-catching behavior is very likely as two types of muscle spindles were identified in jaw muscles of marine toads (Mandal and Anderson, 2010) and the presence of distinct phasic and tonic responses from the two types was also confirmed in reptiles (Proske, 1969a,b).

Quantitative analysis on close contacts established by the trigeminal axon terminals revealed that the majority of them were encountered on the dendrites of facial motoneurons and approximately 10% of them located on the perikarya. The axodendritic contacts were within the proximal two thirds of the ventrolateral dendritic trees. According to the termination areas of the mesencephalic (Vmes) and spinal tract of the trigeminal nerve (tspV) fibers obtained from our earlier cobalt labeling studies it seems very likely that the Vmes exerts stronger influence on the depressor mandibulae activity as its fibers terminates in the territory of perikarya and proximal dendrites (Matesz and Szekely, 1978; Matesz, 1994). It is in agreement with the results of previous physiological findings that the proprioceptors of jaw muscles are continuously active during tongue protraction and retraction whereas the oral mechanoreceptors are stimulated by the captured prey during the initial phase of tongue retraction (Corbacho et al., 2005; Nishikawa and Gans, 1992). In line with this, morphological studies in marine toads suggested that the major sources of trigeminal input are the muscle spindles in the jaw-tongue coordination (Mandal and Anderson, 2010). As the facial motoneurons are involved in other behaviors like vomiting, respiration, vocalization (Schmidt, 1966; Broch et al., 2002; Torgerson et al., 2001; Liao et al., 1996; Martin and Gans, 1972) the direct trigeminal input described here may contribute to the rapid modification of these motor programs.

5. Conclusion

Fig. 5 summarizes the present and previous data concerning the direct and indirect sensory input to the brainstem networks of prey-catching behavior in the frog (Anderson, 2001; Antal et al., 1980; Corbacho et al., 2005; Deak et al., 2009; Harwood and Anderson, 2000; Kecskes et al., 2013, 2015; Mandal and Anderson, 2010; Matesz, 1994; Matesz et al., 2008, 2014; Nishikawa, 2000). We can hypothesize that direct contacts of the trigeminal fibers with the trigeminal and facial motoneurons can be the morphological background of the synchronization and timing of the jaw closing and opening during the feeding movements. Combination of direct and polysynaptic pathways may provide high degree of plasticity in the motor activity during the tongue prehension behavior.

Conflict of interest

The authors declare that no other supports for this study have been paid for their work except for the grants listed above from funding agencies. The authors also declare no conflict of interest in the content of this study.

Acknowledgement

The authors thank Ms. Tímea Horváth for skillful technical assistance.

References

Anderson, C.W., Nishikawa, K.C., 1993. A prey-type dependent hypoglossal feedback system in the frog *Rana pipiens*. Brain Behav. Evol. 42, 189–196.
Anderson, C.W., 2001. Anatomical evidence for brainstem circuits mediating feeding motor programs in the leopard frog, *Rana pipiens*. Exp. Brain Res. 140, 12–19.
Antal, M., Tornai, I., Szekely, G., 1980. Longitudinal extent of dorsal root fibres in the spinal cord and brain stem of the frog. Neuroscience 5, 1311–1322.
Broch, L., Morales, R.D., Sandoval, A.V., Hedrick, M.S., 2002. Regulation of the respiratory central pattern generator by chloride-dependent inhibition during development in the bullfrog (*Rana catesbeiana*). J. Exp. Biol. 205, 1161–1169.
Corbacho, F., et al., 2005. Schema-based learning of adaptable and flexible prey-catching in anurans I. The basic architecture. Biol. Cybern. 93, 391–409.
Corson, J.A., Erisir, A., 2013. Monosynaptic convergence of chorda tympani and glossopharyngeal afferents onto ascending relay neurons in the nucleus of the solitary tract: a high-resolution confocal and correlative electron microscopy approach. J. Comp. Neurol. 521, 2907–2926.
Deak, A., et al., 2009. Vestibular afferents to the motoneurons of glossopharyngeal and vagus nerves in the frog, *Rana esculenta*. Brain Res. 1286, 60–65.
Ewert, J.P., et al., 1990. Responses of medullary neurons to moving visual stimuli in the common toad. I. Characterization of medial reticular neurons by extracellular recording. J. Comp. Physiol. A 167, 495–508.
Gans, C., Gorniak, G.C., 1982. Functional morphology of lingual protrusion in marine toads (*Bufo marinus*). Am. J. Anat. 163, 195–222.
Gaupp, E., 1904. A. Ecker's und R. Wiedersheim's Anatomie des Frosches, vol. 3. Vieweg und Sohn, Braunschweig.
Granit, R., 1975. The functional role of the muscle spindles—facts and hypotheses. Brain 98, 531–556.
Harwood, D.V., Anderson, C.W., 2000. Evidence for the anatomical origins of hypoglossal afferents in the tongue of the leopard frog, *Rana pipiens*. Brain Res. 862, 288–291.
Kecskes, S., Matesz, C., Birinyi, A., 2013. Termination of trigeminal primary afferents on glossopharyngeal-vagal motoneurons: possible neural networks underlying the swallowing phase and visceromotor responses of prey-catching behavior. Brain Res. Bull. 99, 109–116.
Kecskes, S., et al., 2015. Neural circuits underlying tongue movements for the prey-catching behavior in frog: distribution of primary afferent terminals on motoneurons supplying the tongue. Brain Struct. Funct., http://dx.doi.org/10.1007/s00429-014-0988-1.
Liao, G.-S., Kubin, L., Galante, R.J., Fishman, A.P., Pack, A.I., 1996. Respiratory activity in the facial nucleus in an in vitro brainstem of tadpole, *Rana catesbeiana*. J. Physiol. 15 (Pt 2), 529–544.
Mandal, R., Anderson, C.W., 2010. Identification of muscle spindles in the submentalis muscle of the marine toad:Bufo marinus and its potential proprioceptive capacity in jaw-tongue coordination. Anat. Rec. (Hoboken) 293, 1568–1573.
Martin, W.F., Gans, C., 1972. Muscular control of the vocal tract during release signaling in the toad *Bufo valliceps*. J. Morphol. 137, 1–27.
Matesz, C., 1994. Synaptic relations of the trigeminal motoneurons in a frog (*Rana esculenta*). Eur. J. Morphol. 32, 117–121.
Matesz, C., Szekely, G., 1978. The motor column and sensory projections of the branchial cranial nerves in the frog. J. Comp. Neurol. 178, 157–176.
Matesz, C., Szekely, G., 1996. Organization of the ambiguus nucleus in the frog (*Rana esculenta*). J. Comp. Neurol. 371, 258–269.
Matesz, C., et al., 2008. Vestibulotrigeminal pathways in the frog, *Rana esculenta*. Brain Res. Bull. 75, 371–374.
Matesz, K., et al., 2014. Brainstem circuits underlying the prey-catching behavior of the frog. Brain Behav. Evol. 83, 104–111.
Matsushima, T.A., Satou, M., Ueda, K., 1986. Glossopharyngeal and tectal influences on tongue-muscle motoneurons in the Japanese toad. Brain Res. 365, 198–203.
Matsushima, T., Satou, M., Ueda, K., 1989. Medullary reticular neurons in the Japanese toad: morphologies and excitatory inputs from the optic tectum. J. Comp. Physiol. A 166, 7–22.
Monroy, J.A., Nishikawa, K., 2011. Prey capture in frogs: alternative strategies, biomechanical trade-offs, and hierarchical decision making. J. Exp. Zool. A: Ecol. Genet. Physiol. 315A, 61–71.
Nishikawa, K.C., Gans, C., 1992. The role of hypoglossal sensory feedback during feeding in the marine toad, *Bufo marinus*. J. Exp. Zool. 264, 245–252.
Nishikawa, K.C., 2000. Feeding in frogs. In: Schwenk, K. (Ed.), Feeding in Tetrapod Vertebrates: Form, Function and Evolution in Tetrapod Vertebrates. Academic Press, New York, pp. 117–144.
Proske, U., 1969a. An electrophysiological analysis of responses from lizard muscle spindles. J. Physiol. 205, 289–304.
Proske, U., 1969b. The innervation of muscle spindles in the lizard *Tiliqua nigrolutea*. J. Anat. 105, 217–230.
Schmidt, R.S., 1966. Central mechanisms of frog calling. Behaviour 26, 251–285.
Schwippert, W.B.T., Framing, E., 1989. Visual integration in bulbal structures of toads: intra/extra-cellular recording and labeling studies. In: Ewert, J.-P., Arbib, M.A. (Eds.), Visuomotor Coordination, Amphibians, Comparisons, Models, and Robots. Plenum, New York, pp. 481–536.
Stuesse, S.L., Cruce, W.L., Powell, K.S., 1983. Afferent and efferent components of the hypoglossal nerve in the grass frog, *Rana pipiens*. J. Comp. Neurol. 217, 432–439.

Please cite this article in press as: Kovalecz, G., et al., Termination of trigeminal afferent fibers on facial motoneurons: Possible neural network mediating jaw opening during prey-catching behavior of the frog. Brain Res. Bull. (2015), http://dx.doi.org/10.1016/j.brainresbull.2015.09.012

Torgerson, C.S., Gdovin, M.J., Remmers, J.E., 2001. Sites of respiratory rhythmogenesis during development in the tadpole. Am. J. Physiol. Regul. Integr. Comp. Physiol. 280, R913–20.
Weerasuriya, A., 1983. Snapping in toads: some aspects of sensorimotor interfacing and motor pattern generation. In: Ewert, J.-P., Capranicca, R.R., Ingle, D.J. (Eds.), Advances in Vertebrate Neuroethology. Plenum, NewYork, pp. 613–627.
Weerasuriya, A., 1989. In search of the motor pattern generator for snapping in toads. In: Ewert, J.-P., Arbib, M.A. (Eds.), Visuomotor Coordination: Amphibians, Comparisons, Models, and Robots. Plenum, New York, pp. 589–614.
Weerasuriya, A., 1991. Motor pattern generators in anuran prey capture. In: Ewert, J.-P., Arbib, M.A. (Eds.), Visual Structure and Integrated fFunctions. Research Notes in Neural Computing. Springer, NewYork, Berlin Heidelberg, pp. 255–270.
Wouterlood, F.G., et al., 2002. Double-label confocal laser-scanning microscopy, image restoration, and real-time three-dimensional reconstruction to study axons in the central nervous system and their contacts with target neurons. Appl. Immunohistochem. Mol. Morphol. 10, 85–95.
Wouterlood, F.G., Bockers, T., Witter, M.P., 2003. Synaptic contacts between identified neurons visualized in the confocal laser scanning microscope. Neuroanatomical tracing combined with immunofluorescence detection of post-synaptic density proteins and target neuron-markers. J. Neurosci. Methods 128, 129–142.

Please cite this article in press as: Kovalecz, G., et al., Termination of trigeminal afferent fibers on facial motoneurons: Possible neural network mediating jaw opening during prey-catching behavior of the frog. Brain Res. Bull. (2015), http://dx.doi.org/10.1016/j.brainresbull.2015.09.012