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**Research Report**

# Anatomical organization of brainstem circuits mediating feeding motor programs in the marine toad, *Bufo marinus*

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**ABSTRACT**

The goal of our research has been to investigate the neuronal integration that coordinates feeding movements in the marine toad (genus *Bufo*). Using injections of fluorescein dextran amines, combined with activity-dependent uptake of sulforhodamine 101, peripheral hypoglossal and trigeminal nerves involved with tongue and jaw movements were labeled. We identified the rostrocaudal distribution of hypoglossal and trigeminal motor nuclei, and their sensory projections. We also identified the extent of neuronal networks for the medial reticular formation, the raphe nucleus, the glossopharyngeal nuclei, and the Purkinje cell layer of the cerebellum. The sensory fibers of the hypoglossal and trigeminal nerves were found projecting to the Purkinje cell layer of the cerebellum and the trigeminal motor nuclei. The activity-dependent sulforhodamine 101 uptake after the trigeminal and hypoglossal nerves stimulation labeled the bilateral hypoglossal motor nuclei, the trigeminal motor nuclei, the medial reticular formation nuclei, the raphe nuclei, the glossopharyngeal nuclei, and the Purkinje cell layer of the cerebellum, suggesting that all these neurons have the potential to be the components of feeding pathways. Taken together, these data are important for understanding the neuronal integration of extremely rapid jaw–tongue coordination during feeding in the marine toad.

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**1. Introduction**

Among the various nerves involved in the initiation of feeding movements in anurans, the primary cranial nerves involved are the hypoglossal, trigeminal and glossopharyngeal, as these nerves directly innervate the tongue and jaw muscles. The hypoglossal nerve innervates the tongue protractor muscle, the m. genioglossus and the tongue retractor muscle, the m. hyoglossus. The trigeminal nerve innervates the jaw levator muscles and the m. submentalialis which is a transversely orientated muscle at the mandibular tip. The basic neural circuits in the brainstem that mediate rapid tongue protrusion are reasonably well characterized in the leopard

frog, *Rana pipiens* (Anderson, 2001; Clark et al., submitted). Although the basic mechanism for jaw–tongue coordination appears similar in *Rana* and *Bufo*, long protrusible tongues have independently evolved multiple times in these anurans (Nishikawa, 2000). Evolutionary shifts in morphology can modify structural and functional aspects of an organism (Lauder, 1981; Lauder and Liem, 1989; Roth and Wake, 1989). In fact some biomechanical differences have already been demonstrated between *Rana* and *Bufo*. Thus it is important to investigate the neuroanatomical differences in these different anurans' genera in order to understand apparently simple but highly complex neuronal pathways for extremely rapid jaw–tongue coordination during feeding motor programs.

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Previous work has focused on identifying the descending pathways involved in the generation of amphibian feeding motor patterns (Matesz, 1979; Marin et al., 1997; Dicke et al., 1998; Ewert et al., 1999; Roth et al., 1999; Sanchez-Camacho et al., 2001). Our focus has been on the ascending neuronal pathways. While the existence of muscle spindles in the tongue has been shown to help regulate tongue movements in mammals, studies have additionally demonstrated the presence of a sensory afferent component of the peripheral hypoglossal nerve that is used in regulating tongue and jaw movements; for example in mammals (Tarkhan and Abou-El-Naga, 1947; Tarkhan and El-Malek, 1950; Zimny et al., 1970), in birds (Wild, 1981, 1990), and in amphibians (Downman, 1939; Stuesse et al., 1983; Nishikawa and Gans, 1992; Anderson and Nishikawa, 1993, 1996, 1997). Recently published data has shown the presence of a sensory pathway in the leopard frog, *Rana pipiens*, that originates from the tongue epithelium (Harwood and Anderson, 2000) and is carried in the hypoglossal nerve (Anderson and Nishikawa, 1996, 1997). This feedback pathway coordinates the timing of the tongue with the jaw so that the muscular system can properly time these movements during feeding (Anderson and Nishikawa, 1993).

The hypoglossal nerve does not innervate the mandibular depressors and levators, thus theoretically denervation of this nerve should not affect the jaw closing or opening. But the electrophysiological and biomechanical studies show that this is not the case. Following bilateral peripheral hypoglossal nerve transection in toads, the jaw fails to open due to simultaneous activation of both the mandibular depressors and levators (Nishikawa and Gans, 1992). This suggests further the physiological role of sensory feedback in jaw–tongue coordination that is carried by the hypoglossal nerve. Recent studies in our lab in *Bufo* have shown that following bilateral mandibular nerve transection just prior to innervation of the submentalis muscle, the jaw opens but the tongue fails to protract initially to its full length (Anderson, personal communication). The submentalis muscle is hypothesized to be involved with jaw–tongue coordination through sensory feedback as it has no mechanical role in jaw opening (Nishikawa, 2000; Wolff et al., 2004). Thus, there is a reciprocal organization for a sensory control mechanism in that hypoglossal afferents affect jaw movements and trigeminal (mandibular branch) afferents affect tongue movements. The integration of feedback information from both of these nerves is likely important for coordinating jaw–tongue motor output in toads. Electrophysiological studies have shown that the trigeminal sensory afferents integrate within the brainstem for coordinated tongue movement in several animals (Morimoto et al., 1978, 1989; Tolu et al., 1994; Ishiwata et al., 2000; Luo et al., 2001, 2006; Rácz et al., 2008), however, there is minimal data to verify these physiological findings anatomically and the pattern of sensory integration within the brainstem of toads.

We began with single labeling the distal branches of the hypoglossal nerve and the mandibular branch of the trigeminal nerve to identify the exact distribution of motor nuclei of these nerves. There are minimal studies on toads regarding the distribution of the hypoglossal and trigeminal nuclei. Oka et al. (1987) described dorsomedial and ventrolateral subnuclei

of the hypoglossal nerve, and other cranial nerves in the Japanese toad but did not describe any other subnuclei of the hypoglossal. Once we identified the distribution of the hypoglossal and trigeminal nerve nuclei, we used several labeling techniques to investigate the convergence of these nerve afferents in the brainstem.

Using bath-applied SR 101 to a semi-intact brainstem, we stimulated the peripheral hypoglossal nerve to identify the location and distribution of pre-motor and motor nuclei. This resulted in the labeling of the ventrolateral, intermediate, dorsomedial and the previously undescribed medial group of subnuclei of the hypoglossal nerve. Additionally, the raphe nuclei, the trigeminal motor nuclei, the medial reticular formation and the Purkinje cell layer of the cerebellar cortex were labeled. The activity-dependent SR 101 uptake after the peripheral trigeminal stimulation resulted in the labeling of the same groups of nuclei as mentioned above for the hypoglossal stimulation. These data suggest that all these nuclei are components of the neural pathway of interest and that there is a reciprocal loop among the trigeminal motor nuclei, the medial reticular formation and the hypoglossal nuclei.

Anatomical data in *Rana* has shown that sensory neurons from the hypoglossal nerve and other nerves project to a specific portion of the medulla, the medial reticular formation, and here it is hypothesized that the integration of sensory and motor commands occurs before the muscle commands are sent out to the various skeletal muscles (Weerasuriya, 1989; Anderson and Nishikawa, 1997; Anderson, 2001; Rácz et al., 2008). In addition, hypoglossal afferents have been shown to project to the cerebellum (Anderson and Nishikawa, 1997; Anderson, 2001), a pathway likely involved in coordinating the proper timing of various postural and locomotor movements during feeding. We investigated in more detail the anatomical connections between motor neurons innervating the tongue and jaw musculatures and their sensory afferents projecting to the brainstem and cerebellum. We analyzed further if the data in *Bufo* support the hypothesis for the medial reticular formation as the location of sensory-motor integration.

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## 2. Results

Because different techniques of labeling were utilized in this study, the results are presented by the type and tracer experiment performed.

### 2.1. Injection of tracer into the hypoglossal nerve

For the injections into the peripheral hypoglossal nerve, numerous labeled nuclei were identified in the spinal cord and the brainstem. Two groups of subnuclei were identified in the ventral horn of the spinal cord (Figs. 1A, B). The lateral subnucleus appeared homologous to the ventrolateral subnucleus in *Rana*, but the medial group has not been previously described. We termed this medial subnucleus as the ventromedial subnucleus. This additional ventromedial group of neurons in the ventral horn of the spinal cord was fewer in

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