Brain Research 1687 (2018) 11–19

Contents lists available at ScienceDirect

Brain Research

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

Research report

Transcortical descending pathways through granular insular cortex conveying orofacial proprioception

Etsuko Ikenoue [a], Fatema Akhter [a,1], Yumi Tsutsumi [a], Fumihiko Sato [a], Haruka Ohara [a], Katsuro Uchino [a,b], Takahiro Furuta [a], Yoshihisa Tachibana [c], Atsushi Yoshida [a,*]

[a] Department of Oral Anatomy and Neurobiology, Graduate School of Dentistry, Osaka University, Suita, Osaka 565-0871, Japan
[b] Department of Acupuncture, Takarazuka University of Medical and Health Care, Takarazuka, Hyogo 666-0162, Japan
[c] Division of System Neuroscience, Kobe University Graduate School of Medicine, Kobe, Hyogo 650-0017, Japan

ARTICLE INFO

Article history:
Received 13 December 2017
Received in revised form 28 January 2018
Accepted 21 February 2018
Available online 23 February 2018

Keywords:
Proprioception
Insula
Corticofugal
Supratrigeminal nucleus
Ventral posteromedial thalamic nucleus
Feedback

ABSTRACT

Our motor behavior can be affected by proprioceptive information. However, little is known about which brain circuits contribute to this process. We have recently revealed that the proprioceptive information arising from jaw-closing muscle spindles (JCMSs) is conveyed to the supratrigeminal nucleus (Su5) by neurons in the trigeminal mesencephalic nucleus (Me5), then to the caudo-ventromedial edge of ventral posteromedial thalamic nucleus (VPMcvm), and finally to the dorsal part of granular insular cortex rostroventrally adjacent to the rostralmost part of secondary somatosensory cortex (dGIrvs2). Our next question is which brain areas receive the information from the dGIrvs2 for the jaw-movements. To test this issue, we injected an anterograde tracer, biotinylated dextranamine, into the dGIrvs2, and analyzed the resultant distribution profiles of the labeled axon terminals. Anterogradely labeled axons were distributed in the pontomedullary areas (including the Su5) which are known to receive JCMS proprioceptive inputs conveyed directly by the Me5 neurons and to contain premotoneurons projecting to the jaw-closing motoneurons in the trigeminal motor nucleus (Mo5). They were also found in and around the VPMcvm. In contrast, no labeled axonal terminals were detected on the cell bodies of Me5 neurons and motoneurons in the Mo5. These data suggest that jaw-movements, which are evoked by the classically defined jaw-reflex arc originating from the peripheral JCMS proprioceptive information, could also be modulated by the transcortical feedback connections from the dGIrvs2 to the VPMcvm and Su5.

© 2018 Elsevier B.V. All rights reserved.

Abbreviations: 3, oculomotor nucleus; 5C, trigeminal caudal subnucleus; 5Idm, dorsomedial part of trigeminal interpolar subnucleus; 5Ivl, ventrolateral part of trigeminal interpolar subnucleus; 5Odm, dorsomedial part of trigeminal oral subnucleus; 5Ovl, ventrolateral part of trigeminal oral subnucleus; 7, facial nucleus; 12, hypoglossal nucleus; AI, agranular insular cortex; BDA, biotinylated dextranamine; Cl, claustrum; CL, centrolateral thalamic nucleus; cp, cerebral peduncle; Cu, cuneate nucleus; dGIrvs2, dorsal part of GI rostroventrally adjacent to the rostralmost part of S2; DI, dysgranular insular cortex; ECu, external cuneate nucleus; fr, fasciculus retroflexus; GI, granular insular cortex; GiA, alpha part of gigantocellular reticular nucleus; Gr, gracile nucleus; Ins, insular cortex; IO, inferior olive; IP, interpeduncular nucleus; KF, Kölliker-Fuse nucleus; lfp, longitudinal fasciculus of the pons; LHb, lateral habenular nucleus; MD, mediodorsal thalamic nucleus; Me5, trigeminal mesencephalic nucleus; MG, medial geniculate nucleus; ml, medial lemniscus; Mo5, trigeminal motor nucleus; OPC, oval paracentral thalamic nucleus; PAG, periaqueductal gray; PB, parabrachial nucleus; PhB, phosphate buffer; PhBS, phosphate-buffered saline; PC, paracentral thalamic nucleus; PF, parafascicular thalamic nucleus; Pn, pontine nuclei; Po, posterior thalamic nucleus; Pr5, trigeminal principal nucleus; py, pyramidal tract; R, red nucleus; RF, rhinal fissure; RMg, raphe magnus nucleus; ROb, raphe obscurus nucleus; RPa, raphe pallidus nucleus; Rt, reticular thalamic nucleus; S1, primary somatosensory cortex; S2, secondary somatosensory cortex; SC, superior colliculus; scp, superior cerebellar peduncle; SN, substantia nigra; Sol, nucleus of the solitary tract; sp5, spinal trigeminal tract; Su5, supratrigeminal nucleus; Ve, vestibular nucleus; VM, ventromedial thalamic nucleus; VPL, ventral posterolateral thalamic nucleus; VPM, ventral posteromedial thalamic nucleus; VPMcvm, caudo-ventromedial edge of the VPM; VPPC, parvicellular part of ventral posterior thalamic nucleus.

* Corresponding author at: Department of Oral Anatomy and Neurobiology, Osaka University Graduate School of Dentistry, 1-8 Yamadaoka, Suita, Osaka 565-0871, Japan.
E-mail address: yoshida@dent.osaka-u.ac.jp (A. Yoshida).
[1] Present address: College of Dentistry, Dar Al Uloom University, Riyadh 11512, Saudi Arabia.

https://doi.org/10.1016/j.brainres.2018.02.033
0006-8993/© 2018 Elsevier B.V. All rights reserved.

1. Introduction

Proprioceptive signals arising from muscles are known to play a crucial role in sensorimotor reflexes at the levels of lower brainstem and spinal cord. The proprioception arising from jaw-closing muscle spindles (JCMSs) (JCMS proprioception) is conveyed by primary afferents (spindle Me5 afferents) whose neuronal cell bodies are located in the trigeminal mescencephalic nucleus (Me5) (Fujio et al., 2016; for review, see Dubner et al., 1978; Taylor, 1990). Intraaxonal labeling studies have revealed that the rat spindle Me5 afferents ipsilaterally project not only to jaw-closing motoneurons in the trigeminal motor nucleus (Mo5) but also to pontomedullary regions such as the supratrigeminal nucleus (Su5), dorsomedial part of the trigeminal principal nucleus (Pr5) and dorsomedial part of trigeminal oral subnucleus (5Odm); these regions contain premotoneurons projecting to the Mo5 bilaterally with an ipsilateral predominance (Luo et al., 1995, 2001). These earlier findings indicate that the JCMS proprioceptive information can directly or indirectly exert reflexive jaw-movements (Goldberg and Nakamura, 1968; Kidokoro et al., 1968; Ohta and Moriyama, 1986; Shigenaga et al., 1988, 1990).

We have recently demonstrated that the rat JCMS proprioceptive signals through the spindle Me5 afferents are conveyed to the Su5, then to the caudo-ventromedial edge (VPMcvm) of the ventral posteromedial thalamic nucleus (VPM) on the contralateral side, and finally to the dorsal part (dGIrvs2) of granular insular cortex (GI) rostroventrally adjacent to the rostralmost part of secondary somatosensory cortex (S2) (Fujio et al., 2016; Sato et al., 2017; Yoshida et al., 2017). Repetitive electrical stimulation of rat insular cortex induces rhythmical jaw movements (Zhang and Sasamoto, 1990; Satoh et al., 2007; Maeda et al., 2014), suggesting that, besides the shortcut sensorimotor reflex arc in the lower brainstem which links the JCMS proprioception to motoneurons/premotoneurons, there are pathways arising from the dGIrvs2 to the motoneurons/premotoneurons in order to control the sensorimotor coordination. On the other hand, it is known that the auditory, visual and somatosensory cortices send transcortical feedback pathways to the ascending relay sites conveying the sensation to the respective cortices themselves (Diamond et al., 1969; Cole and Gordon, 1992; Malmierca and Nuñez, 1998, 2004; Haque et al., 2012; Tomita et al., 2012; for review, see Deschênes et al., 1998; Nuñez and Malmierca, 2007), suggesting that there are transcortical feedback pathways arising from the dGIrvs2 to the VPMcvm and Su5. If there exist such pathways, jaw-movements exerted by the jaw-reflex arc originating from orofacial primary afferents to the motoneurons/premotoneurons could be modulated through the transcortical feedback connections from the dGIrvs2 to the VPMcvm and Su5. Thus, the goal of this study is to examine which parts of the brain (including the lower brainstem and the thalamus) receive the transcortical proprioceptive information through the dGIrvs2. To this end, we injected an anterograde neural tracer into the dGIrvs2 and analyzed the distribution profiles of labeled axon terminals.

2. Results

2.1. BDA injection sites

For injections of an anterograde tracer, biotinylated dextranamine (BDA) into the dGIrvs2, this structure was identified by recording large field potentials in response to electrical stimulation of the contralateral masseter nerve (Fig. 1A) and by recording large unit responses during a passive, sustained jaw-opening (Fig. 1B) as in our previous study (Sato et al., 2017). Then, a small injection of BDA was made in the recording site in eleven rats, and the location of the injection sites was finally confirmed histologically. In all of the eleven cases the BDA injection sites covered at least a part of the dGIrvs2, they were mostly confined to the dGIrvs2 in three cases (R407, R608, R622) (e.g., Fig. 1C–F, H–J). In a representative case (R407), the injection site was well confined in the dGIrvs2, but slightly extended into the ventral GI (Fig. 1C–F, H); it mainly covered layers IV and V, and outer part of layer VI of the GI (Fig. 1C–F). However, the injection site did not extend ventrally into the dysgranular insular cortex, caudodorsally into the S2, and dorsally into the S1 (Fig. 1C–F, H).

2.2. Anterogradely labeled axons in lower brainstem

In the three cases (R407, R608, R622), the anterogradely BDA-labeled axon fibers and terminals were distributed in a very similar pattern in the lower brainstem. In a representative case (R407), rostrally in the mesencephalon (Fig. 2A), a large number of labeled axon fibers were found in the cerebral peduncle and a moderate number of labeled axons in the lateral tegmental field ventrolateral to the superior colliculus on the side ipsilateral to the BDA injection site. In addition, a small number of labeled axon terminals were ipsilaterally seen in the substantia nigra and the periaqueductal gray. However, no axons were labeled in the rostral and middle levels of Me5.

At the level of pons (Fig. 2B–E), labeled axon fibers further descended ipsilaterally in the longitudinal fasciculus of pons, and then in the pyramidal tract. At the rostral level of pons, a large number of labeled axon terminals and a moderate number of them were ipsilaterally found in the pontine nuclei and the dorsal part of parabrachial nucleus, respectively (Fig. 2B). A considerable number of labeled axon terminals were found contralaterally in the Su5, especially in its lateral part (Figs. 2C, D, 3). They were also seen almost contralaterally in the rostro-dorsomedial part of Pr5 (Fig. 2C, D). However, no axons were labeled in the Mo5 and the caudal level of Me5 (Fig. 2B–D). At the caudal level of pons, a considerable number of labeled axon terminals were almost contralaterally seen in the 5Odm (Fig. 2E) and the dorsolateral part of lateral reticular formation adjacent to the 5Odm. A large number of labeled axon terminals were densely seen in the rostralmost level of solitary tract nucleus (Sol), especially in its lateral part, bilaterally but with a contralateral predominance (Fig. 2E). Interestingly, a large number of labeled axon fibers extended from the ipsilateral pyramidal tract, passed in the rostral ventromedial nucleus which contains the raphe magnus nucleus, and traveled laterally towards the contralateral Su5, Pr5 or 5Odm (Fig. 2D, E). However, no labeled axon terminals were seen in the rostral ventromedial nucleus.

At the level of medulla oblongata (Fig. 2F–I), a large number of labeled axon fibers further descended in the ipsilateral pyramidal tract. A moderate number of labeled axon terminals were seen almost contralaterally in the rostral part of Sol, especially in its lateral part (Fig. 2F), but no labeled axon terminals in the middle and caudal levels of Sol (Fig. 2G–I). A small number of axon terminals were also labeled contralaterally in the medial region of the dorsomedial part of trigeminal interpolar subnucleus (5Idm) and in the dorsolateral part of lateral reticular formation adjacent to the 5Idm (Fig. 2F). In the trigeminal caudal subnucleus (5C), a number of labeled axon terminals were contralaterally seen mainly in the dorsomedial part of superficial layer in the rostral level of 5C (Fig. 2G, H), but only a few labeled axons in the caudal level of 5C (Fig. 2I). At the caudalmost level of 5C, a large number of labeled axon fibers extending from the ipsilateral pyramidal tract were seen in the pyramidal decussation (Fig. 2I); They slightly traveled laterally towards the dorsomedial part of contralateral 5C, and mainly traveled caudodorsally to enter the contralateral pyramidal tract dorsal to the central canal at the upper cervical level (not

Download English Version:

https://daneshyari.com/en/article/8839823

Download Persian Version:

https://daneshyari.com/article/8839823

Daneshyari.com