Neuroscience Letters 482 (2010) 198–202

Contents lists available at ScienceDirect

Neuroscience Letters

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

Novel approach for understanding the neural mechanisms of auditory-motor control: Pitch regulation by finger force

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ARTICLE INFO

Article history:
Received 10 March 2010
Received in revised form 23 June 2010
Accepted 13 July 2010

Keywords:
Audiomotor integration
Auditory feedback
Bidigital pinching
fMRI
Pitch perception
Precision grip

ABSTRACT

Music performance and speech production require neural circuits to integrate auditory information and motor commands to achieve rapid and accurate control of sound properties. This article proposes a novel approach for investigating neural substrates related to audiomotor integration. An experiment examined the brain activities involved in sensorimotor integration in a simplified audiomotor task: pitch regulation using finger-pinching force. The brain activities of the participants were measured using functional magnetic resonance imaging (fMRI) while they were performing the task. Two additional tasks were performed: an auditory-only task in which subjects listened to sound stimuli without any motor action and a motor-only task where they applied their finger force to the sensor in the absence of auditory feedback. The fMRI results showed the brain activities related to the online pitch regulation in the dorsal premotor cortex (dPMC), planum temporale (PT), primary auditory cortex, and part of the midbrain. The involvement of dPMC and PT was consistent with findings in previous studies on other audiomotor systems, implying that these regions appeared to be important for connecting the auditory feedback to motor actions.

Music performance and speech production require rapid and accurate online control of sound properties. Successful achievement of this goal requires that motor responses reflect the information received via auditory feedback. Artificial delays in auditory feedback can produce stuttering in normal talkers [13] and interrupt successful performances of musicians [18,19]. Electrophysiological study focusing on a pianist's keystroke has suggested that the event-related potential elicited by errors in auditory feedback was increased when the pianist actually played piano [14]. These examples demonstrate the existence of neural circuits tightly connecting auditory perception with motor actions.

Neural substrates related to sensorimotor integration have been studied primarily with respect to the visual modality, using various experimental paradigms, such as reaching, grasping, ocular movements, and manipulation of a joystick or computer mouse. These studies have demonstrated that the posterior parietal cortex (PPC) and the premotor cortex (PMC) play roles in the transformation of visual cues into appropriate motor commands [1,8,9].

On the other hand, the neural substrates related to audiomotor integration have yet to be clearly identified. Neuroimaging studies using PET and fMRI technologies to examine audiomotor integration have focused on the online adjustment of vocalization. A simple singing task, in which a prolonged vowel was vocalized at a constant pitch, activated the supplementary motor area, the anterior cingulate cortex, the precentral gyrus, the anterior insula, Heschl's gyrus, a posterior part of the superior temporal gyrus (STG), and parts of the cerebellum to a greater extent than did a simple listening task [17]. The delay and pitch shift in the auditory feedback during speech production increased activities in the STG, suggesting enhanced monitoring of one's own voice [5,7,15]. However, the shift in pitch reflected in the auditory feedback provided during simple singing activated a greater number of regions, including the PMC, the anterior insula, the intraparietal sulcus, and the supramarginal gyrus [22,25]. Additionally, many studies have reported the activation of the anterior insula during vocalization tasks [17,22,25]. Various regions have been proposed as candidates for the neural substrate of audiomotor integration, but no general agreement has emerged with respect to this issue.

The enigmatic character of neural substrates involved in audiomotor integration may be attributable to several limitations in vocalization experiments. First, it has been difficult to identify the function served by activated regions, because vocal control rests on a complex system including multiple neural pathways from brainstem nuclei to cerebral cortices. Second, vocalization frequently produces head movements that cause artifact noises to appear in MRI data. We also do not know whether the brain regions previously identified as candidates are vocal-specific or are more generally involved in audiomotor integration because

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doi:10.1016/j.neulet.2010.07.032

similar activities have not been confirmed with respect to non-vocal effectors.

In this study, we used fMRI to record brain activities in a simplified audiomotor situation in which the subjects were asked to manipulate tone pitch with their fingers. The fundamental frequency (F_0) of the generated tone changed in proportion to the force with which the subject gripped a designated object in real-time. The finger-grip task is a valuable tool for investigating sensorimotor integration [21,23], and the control system for the finger force is appear to be simpler than that for vocalization, having advantage on minimization of the head movements during fMRI scanning. This novel approach would also provide us insights for discrimination between effector-independent and effector-specific regions.

The purpose of this study was to demonstrate the usefulness of our novel approach in investigations of audiomotor integration such as those examining the brain activities involved in pitch regulation by finger force. Moreover, we assumed that the brain region involved in pitch regulation might be more activated if the amount of error correction was increased by pitch perturbation. Thus, we applied the pitch perturbation to the auditory feedback without evoking subjects' notice by slowly changing the relationships between force and pitch during the pitch regulation task.

Twelve subjects (7 males and 5 females, age between 21 and 27 years) participated in this experiment. They had musical experience as amateurs (e.g., playing the piano, violin, trumpet, for an average of 9.1 ± 5.4 years). No participant had absolute pitch. All subjects were right-handed and had normal hearing level (125–8000 Hz in octave steps, <15 dB HL). The study was approved by the safety committee of the ATR Institute International and the ethics board of Doshisha University. Written informed consent was obtained from each subject before participation.

The force of each finger grip was measured isometrically with a strain-gauge-type force sensor (KEITEC System; Fig. 1A). The subject used the tips of the thumb and index finger of the right hand (i.e., precision grip) to grasp a sensor with flat parallel contact surfaces spaced 18 mm apart. The feedback tone of F_0 presented to each participant varied according to the force measured. In this article, the F_0 of all sounds is described in cents, logarithmically converted from Hertz using the equation: cents = $1200 \times \log_2 (f/f_n)$, where f is the F_0 of the feedback tone in Hz and f_n is the frequency of the arbitrarily chosen note C5 (525.25 Hz). The F_0 of the feedback tone varied proportionately as a function of the finger force according to: $f_c = P - 500 + S$, where f_c denotes the F_0 of the feedback tone [cents], P denotes the finger force [gf], and S denotes the F_0 shift in cents for varying force targets and perturbation conditions (Fig. 1B). Thus, force at 500 gf produced F_0 at 0 cents (525.25 Hz) when $S = 0$. The force change spanning +1 gf corresponds to the F_0 change spanning +1 cents, regardless of S. The body of the sensor consisted of plastic, aluminum, and titanium, and the contact surfaces were made of thin felt and hard rubber. The waveform of the feedback tone was a saw-tooth signal consisting of the lowest four harmonics (−6 dB/oct, 20 ms rise/decay). The real-time generation of the feedback tone was achieved by a digital signal processor (s-BOX, MTT).

Subjects were asked to perform three types of experimental tasks: audiomotor (AM), motor-only (M), and auditory-only (A).

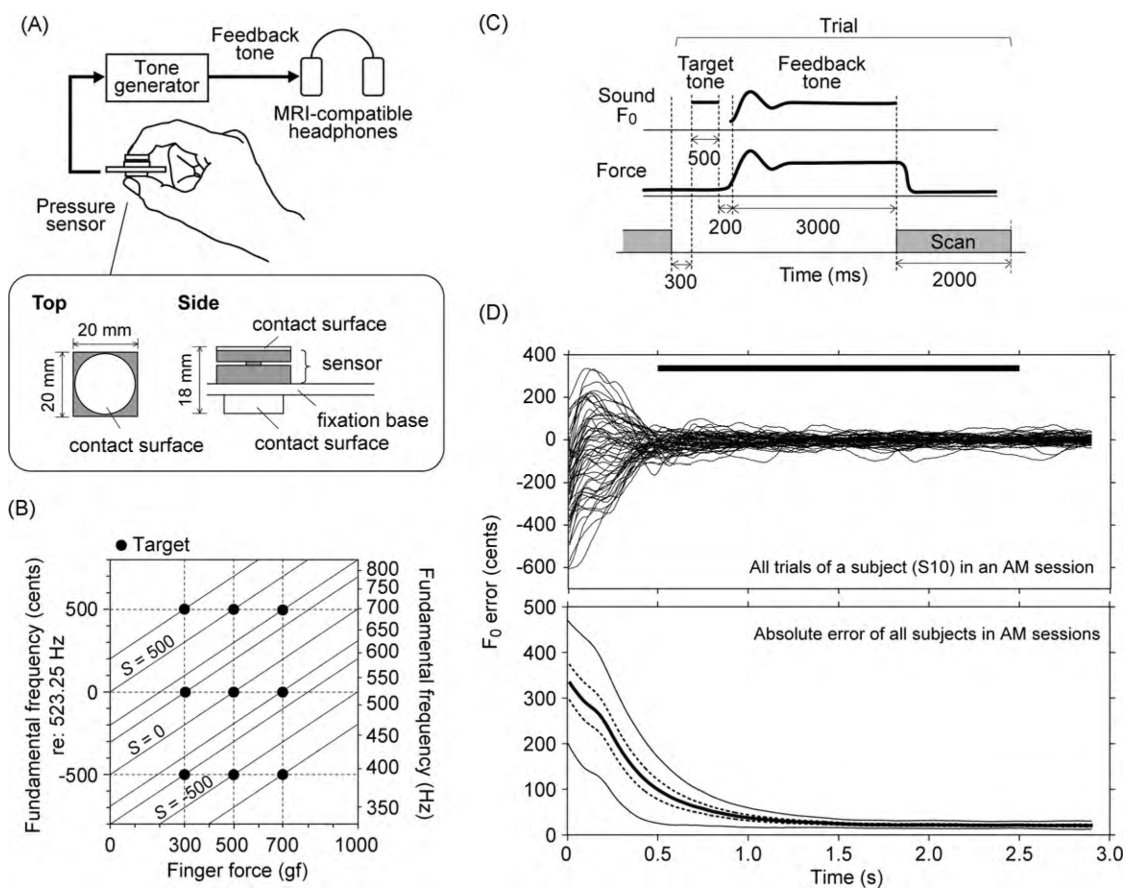

Fig. 1. (A) Experimental arrangement and details of the force sensor. (B) Relationship between the finger force and the F_0 of the feedback tone. Black dots indicate the target conditions. The parallel oblique line represents the relationship under each target condition. S indicates the F_0 shifts in cents. (C) Illustration of trial procedure. Top, middle, and bottom parts indicate the F_0 of sound stimuli, the applied finger force, and the scanning sequence, respectively. (D) Examples of F_0 data. The time courses of F_0 errors committed by one subject (S10) in all trials during an AM session are shown in the upper panel. The bold black bar indicates the duration of the pitch-shift perturbation. The mean (bold line), the standard deviation (thin), and the standard error of the mean (dashed) of the absolute F_0 error obtained from all subjects are shown in the lower panel.