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Quick compensatory mechanisms for tongue posture stabilization during speech production

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[1]*GIPSA-lab, Grenoble Institute of Engineering, CNRS–University of Grenoble Alpes, Grenoble, France; and* [2]*Haskins Laboratories, New Haven, Connecticut*

Ito T, Szabados A, Caillet JL, Perrier P. Quick compensatory mechanisms for tongue posture stabilization during speech production. *J Neurophysiol* 123: 2491–2503, 2020. First published May 20, 2020; doi:10.1152/jn.00756.2019.—The human tongue is atypical as a motor system since its movement is determined by deforming its soft tissues via muscles that are in large part embedded in it (muscular hydrostats). However, the neurophysiological mechanisms enabling fine tongue motor control are not well understood. We investigated sensorimotor control mechanisms of the tongue through a perturbation experiment. A mechanical perturbation was applied to the tongue during the articulation of three vowels (/i/, /e/, /ɛ/) under conditions of voicing, whispering, and posturing. Tongue movements were measured at three surface locations in the sagittal plane using electromagnetic articulography. We found that the displacement induced by the external force was quickly compensated for. Individual sensors did not return to their original positions but went toward a position on the original tongue contour for that vowel. The amplitude of compensatory response at each tongue site varied systematically according to the articulatory condition. A mathematical simulation that included reflex mechanisms suggested that the observed compensatory response can be attributed to a reflex mechanism, rather than passive tissue properties. The results provide evidence for the existence of quick compensatory mechanisms in the tongue that may be dependent on tunable reflexes. The tongue posture for vowels could be regulated in relation to the shape of the tongue contour, rather than to specific positions for individual tissue points.

NEW & NOTEWORTHY This study presents evidence of quick compensatory mechanisms in tongue motor control for speech production. The tongue posture is controlled not in relation to a specific tongue position, but to the shape of the tongue contour to achieve specific speech sounds. Modulation of compensatory responses due to task demands and mathematical simulations support the idea that the quick compensatory response is driven by a reflex mechanism.

compensatory response; mechanical perturbation; orosensory feedback; reflex; speech motor control

INTRODUCTION

The tongue is a fundamental organ in a variety of basic biological functions for humans, such as breathing, swallowing, and speaking. Loss or damage of tongue function and its control severely affects daily life. While understanding the mechanisms of tongue control is crucial, the investigation of its sensorimotor foundations has been impeded for a long time, mostly due to the technical difficulty of having access to the tongue during its movement. Although a variety of measurement techniques (X-ray, electromagnetometer, ultrasound devices, or magnetic resonance imaging) have been proposed for the study of tongue motor control (Hoole and Zierdt 2010; Perkell et al. 1992; Westbury 1994; Whalen et al. 2005; Xing et al. 2013), investigations were limited to descriptive studies of the kinematic characteristics of tongue movements, and hence little is known about the cortical or subcortical control of these movements.

Most of the volume of the tongue is made of muscles, which are quasi-incompressible deformable bodies. As a consequence, tongue movements correspond to soft tissue deformations that are deeply constrained by this quasi-incompressibility. Thus the tongue behaves dynamically like a muscular hydrostat (Kier and Smith 1985), which is clearly different from the behavior of a skeletal system, such as the limb or the arm, in which solid bony structures move around joints.

In case of speech production, the mechanisms of tongue motor control have been investigated especially through the adaptation paradigm using static perturbation, such as holding jaw positions with a bite block (Fowler and Turvey 1981; Gay et al. 1981), altering lip geometry with a lip tube (Savariaux et al. 1995), or modifying the palate shape by inserting an artificial palate (Brunner et al. 2011; Honda et al. 2002; McFarland et al. 1996). The produced sounds become quite similar to the original sounds after a short time of adaptation following the perturbation, suggesting that the tongue control system quickly adapts to new environments as we experience in daily life situations (e.g., speaking while chewing gum). While those adaptive changes provide evidence for efficient and robust control of the tongue, little is known about the neurophysiological and physical phenomena enabling the control of tongue posture stabilization during the production of speech sounds, in particular to compensate for time-varying perturbations as experienced in our daily life.

In regard to speech production, a well-known hypothesis suggests that tongue motor control consists in moving the tongue toward target postures associated with phonemes (Keating 1990; MacNeilage 1970; Patri et al. 2015). In the production of consonants, such as /t/ or /s/, the tongue must not only target postures precisely but also maintain them for a sufficient amount of time, which requires the capacity to efficiently stabilize the tongue in the target postures. This task could be

accomplished by moving the tongue, or a part of the tongue, toward a specific location in the oral cavity, such as toward the upper teeth, just as it is done in pointing or reaching tasks with the arm by moving the different arm segments around their joints. It is however unclear whether the postural stabilization of the deformable tongue relies on control principles that are similar to those of the stabilization of arm segments around a joint.

The control mechanisms involved in limb and body posture stabilization have often been investigated using time-varying perturbations (Burdet et al. 2001; Gomi and Osu 1998; Gottlieb and Agarwal 1988; Marsden et al. 1972; Pruszynski and Scott 2012; Soechting 1988; Soechting and Lacquaniti 1988). Immediate compensation for time-varying perturbations can be driven by impedance control and neural feedback control. Responses associated with impedance control are intrinsic physical responses of the motor plant associated with passive elastic properties (Gomi and Osu 1998; Gottlieb and Agarwal 1988). As a consequence, they are very fast. The response induced by neural feedback control, such as stretch reflex, arrives later due to the delay in neural transmission, which ranges from 20 to 50 ms for short-latency stretch reflex and from 50 to 100 ms for the long-latency stretch reflex (Pruszynski and Scott 2012). This time sequence of responses was examined in the speech articulatory system using a mechanical perturbation of the jaw (Gomi et al. 2002; Ito et al. 2005). The compensatory response due to stiffness in the linkage between lip and jaw occurred less than 20 ms after the onset of the movement induced by the perturbation; in contrast, the muscle activation due to reflex was induced longer than 50 ms after this movement onset (Gomi et al. 2002). This compensatory reflex was mediated by the motor cortex (Ito et al. 2005). As in limb studies, applying a time-varying mechanical perturbation to the tongue and observing the behavioral response is an efficient approach to examine whether the tongue shows compensatory responses with latencies comparable to those of responses induced by impedance control and by neural feedback control in the limb system.

Task-dependent modulation can be seen in both impedance control and reflex mechanisms. In impedance control, mechanical properties of the motor system (such as stiffness or damping) can be adjusted for external constraints (Burdet et al. 2001; Gomi and Osu 1998). It has been found in the speech articulatory system that the stiffness in the linkage between the jaw and upper lip increased for the production of the bilabial fricative consonant /Φ/ as compared with the neighboring vowels in vowel-consonant-vowel sequences (Gomi et al. 2002). In reflex control, long-latency reflexes in the limb system have been shown to vary depending on the task demands in a variety of situations (see review in Pruszynski and Scott 2012). In the orofacial system, the magnitude of compensatory reflexes in the upper lip has been shown to vary depending on the speech task: the magnitude of the muscle activation due to reflex was significantly larger during the production of bilabial fricatives than during vowel production (Gomi et al. 2002), and little or no response was induced in a resting condition (Ito and Gomi 2007). Similarly, Kelso et al. (1984) observed an increase of muscle activation in the tongue in response to a force perturbation applied to the jaw during the production of alveolar consonants /z/, but not during the production of bilabial consonants /b/. Thus compensatory responses induced in the tongue by a force perturbation applied to the jaw seem also to be modulated across different speech tasks and/or across speech and nonspeech (resting) tasks.

In speech production, a number of converging experimental and modeling results suggest that tongue stiffness varies across the front vowels, such as /i/, /e/, and /ɛ/, in conjunction with the amount of tongue positioning variability: the stronger the stiffness, the smaller the variability. Previous studies (Beckman et al. 1995; Perkell and Nelson 1985) showed that front-high vowels /i/ and /e/ have less articulatory variability than lower vowels like /ɛ/ and /a/. In addition, using electropalatography (Stone and Lundberg 1996) and MR imaging (Badin et al. 2002), a strong relationship was found between the intensity of the linguo-palatal contact and the activation of the posterior genioglossus, which pulls forward the back part of the tongue, as evidenced by magnitude of grooving the back part of the tongue. The idea is also supported by the simulations with a three-dimensional (3-D) biomechanical model of the tongue showing that for a given height of the tongue, an increase in the amount of lateral contacts between the tongue and the palate is achieved through an increase in tongue muscle activation, specifically activation of the posterior genioglossus (Buchaillard et al. 2009; Gick et al. 2017). An increase in muscle activation induces an increase in muscle tissue stiffness called the stress-stiffening effect (Nazari et al. 2011). Applying a mechanical force perturbation to the motor system, as used in previous studies (Burdet et al. 2001; Gomi and Osu 1998; Gottlieb and Agarwal 1988), allows stiffness to be measured by observing the displacement induced by the perturbation, since for a given magnitude of the force, the magnitude of the displacement is proportional to the stiffness, assuming linear dynamical properties. Hence, force perturbation can be an efficient tool to reveal task-dependent changes in stiffness of the tongue or of the linguo-palatal system.

For the reflex mechanism, it is still unclear whether or not a stretch reflex or similar types of reflex are involved in the postural control of the tongue. In the tongue, it is still under debate which sensory receptors play a role in proprioception and in stretch reflex. In general, muscle spindles are considered as the main source of proprioception and stretch reflex (Schmidt and Lee 2005). Cooper (1953) had found muscle spindles in the muscles of the human tongue. However, Neilson et al. (1979) did not find any evidence that tonic stretch reflex was induced in the tongue in response to stretching of the tip of the tongue. In this context, we can assume that muscle spindles in the tongue may not work like those in the skeletal muscles of the limbs. Showing a compensatory response with an appropriate latency can provide a clue for the involvement of reflex mechanism in the control of posture stabilization and can suggest how muscle spindles or proprioceptive organs are involved in the compensatory responses.

In our study, we focus on quick compensatory responses for the stabilization of the tongue. We examined whether perturbations of tongue postures were compensated by online feedback control mechanisms by observing the time course of the tongue response due to time-varying perturbations. For this purpose, a novel mechanical perturbation system was specifically developed using a robotic device. We applied the mechanical perturbation in an unanticipated manner while subjects were holding specified tongue postures. Electromagnetic

articulography was used to measure the displacement of the articulatory organs (jaw, lips, and tongue).

We expected to observe different phases over time in the compensatory responses to the perturbation, with different latencies, due to the successive involvement of different feedback mechanisms: impedance control associated with mechanical stiffness of the tongue muscles, short-delay stretch-like reflexes, and long-delay auditory and/or somatosensory feedback. We also expected to observe a variation in the magnitude of the displacement induced by the perturbation according to *1)* the vowel posture, because of differences across vowels in the stiffness of tongue muscles, and *2)* articulatory manners (speaking vs. nonspeaking), because of differences in the requirements in terms of postural control accuracy between these two tasks.

To analyze the time course of the responses to perturbation, especially in terms of the shape of the kinematic responses respectively induced by impedance control and by stretch-like reflex, we simulated the tongue force perturbations using a mathematical biomechanical model of the tongue (Perrier et al. 2003). Since this mathematical simulation includes an account of short-delay somatosensory feedback for reflex response, it can be used to dissociate a reflex contribution from the response by impedance control through manipulation of the amplitude of the reflex gain in the model. By comparing the simulated movements of the tongue in the model with those observed experimentally, we could assess whether the reflex mechanism as implemented in the model could explain the experimentally observed compensatory responses.

METHODS

Participants. Nine native French speakers (18–35 yr old, 3 women) participated in the experiment. The participants were all healthy young adults who reported normal hearing. The protocol for this experiment was approved by the local ethical committee of the University of Grenoble Alpes [Comité d'Ethique pour les Recherches non Interventionnelles (CERNI)-AvisConsultatif-2017-01-17-04]. All participants signed the corresponding consent form.

Articulatory measurement and tongue perturbation. Electromagnetic articulography (Wave, Northern Digital Inc.) was used to measure articulation. For vowel production, the articulation is primarily characterized by the geometry of the vocal tract shape in the midsagittal plane. Hence, the measurement sensors were glued in the midsagittal plane: tongue tip (TT), tongue blade (TB), and tongue dorsum (TD) on the tongue surface, upper and lower lips (UL and LL), and jaw (J). Four reference sensors, located on the nasion, the left and right mastoids, and the upper incisors (see Fig. 1*A*), were also used for the measurement of head movements and their subtraction from the other sensors' movements in an off-line analysis. The sensor data were recorded with a 400-Hz sampling rate, and the produced speech sound was recorded synchronously with a 22.05-kHz sampling frequency.

A small robotic device (Phantom Premium 1.0, Geomagic) was used to apply a force to the tongue (see Fig. 1*A*). The robot was set in front of the subject and connected to the tongue surface through a thin thread. At both extremities of the thread, two small anchors (see TP in Fig. 1*B*) were glued on the tongue surface on both sides of the tongue blade sensor (TB) of the articulograph. The tongue perturbation was produced by pulling the tongue forward with a 1-N force for 1 s. The force was applied with 5-ms rising and falling phases to avoid mechanical noise of the robot. The subject's head was held in place by a head holder to maintain a constant stable position.

Experimental tasks: vowels and articulatory manners. The first focus of this study is to compare perturbed responses in different vowel postures. We focused on three French vowels, /i/, /e/, and /ɛ/, that are expected to be produced with different amounts of tongue muscle activation. Vowels /i/, /e/, and /ɛ/ are close neighbors in terms of both acoustical and articulatory characteristics. In the acoustical domain, vowels are efficiently described by the first two formants, F1 and F2, which are the lowest two resonance frequencies of the vocal tract and correspond to the first two maxima of the frequency spectrum of the sound. The first formant gradually decreases from /ɛ/ to /e/ and /i/, while the second formant increases. There is no other vowel between them in French phonetics. In the articulatory domain, these vowels are usually discriminated along the tongue height (or jaw height) dimension, which corresponds to the vocal tract aperture. The production of /i/ requires a high and anterior tongue position, corresponding to the narrowest aperture of the vocal tract in the palatal region. As compared with the production of /i/, tongue height grad-
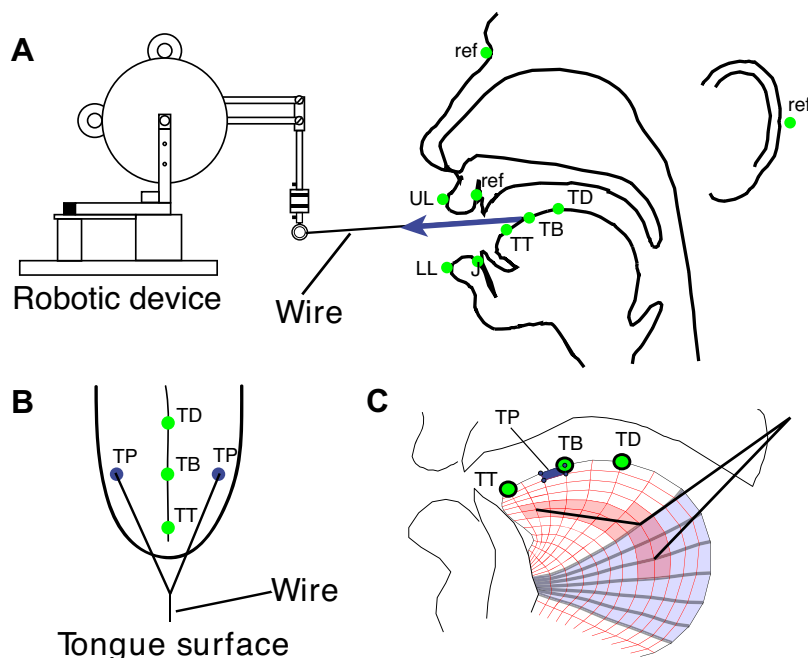

Fig. 1. *A*: experimental setup of tongue perturbation. Green points represent the location of sensors of electromagnetic articulograph [TT, tongue tip; TB, tongue blade; TD, tongue dorsum; UL, upper lip; LL, lower lip; J, jaw; and ref, reference makers (nasion, right and left mastoid, and upper incisor)]. *B*: view of the tongue surface representing the locations of sensors of electromagnetic articulograph (TT, TB, and TD) and anchor points for the tongue perturbation (TP). *C*: schematic view of the 2-dimensional (2-D) tongue model. Nodes on the tongue surface are numbered from *1* (tongue root) to *16* (tongue tip). *Nodes 11*, *13*, and *16* were chosen as the corresponding locations of measured sensors TD, TB, and TT, respectively. The 4 nodes (*nodes 13* and *14* and two nodes below those) represented by blue-filled points were chosen as the area for the tongue perturbation (TP). Muscle representations of styloglossus and posterior genioglossus were shown as representative examples. Styloglossus is shaded in red and posterior genioglossus in light blue. The bold thick lines (styloglossus in black and posterior genioglossus in gray) represent macrofibers, and the shaded area represents the elements whose mechanical stiffness was changed by muscle activation.

ually decreases and moves backward for the production of /e/ and /ɛ/. This variation is associated especially with a decrease in the activation of the posterior genioglossus.

The second focus is to examine the effect of speaking vs. nonspeaking conditions. We compared compensatory responses in voicing, whispering, and posturing conditions. In the three conditions, the subjects were asked to sustain the tongue position for a few seconds. In voicing and whispering conditions, they were asked to do so while voicing or whispering. In the nonspeech posturing condition, they were asked to do so silently. To have the same set of reference vowel tongue positions as for the speaking conditions, subjects were instructed to produce the vowel briefly at the beginning of each trial of the posturing condition, and then to maintain the posture silently (without voicing or whispering).

Experimental procedure. Nine experimental tasks (3 vowels under 3 articulatory manners) were tested in random order. At the beginning of each trial, visual instruction on a monitor was used to inform the subjects about the task for the coming trial. The trial was launched by the experimenter after examining whether the participant was ready for the task. The subjects were instructed to start their task via visual and auditory cues. The perturbation was applied 1 s after the trial onset on a randomly selected third of the trials to avoid any anticipation by the subject. There were 270 trials in total. As a result, 10 perturbed responses were recorded in each condition. The total experimental time was ~2 h including the preparation time for placing the sensors of the articulograph and gluing the wires of the robotic arm on the participant's tongue, and the experimental session itself. The long duration of the experiment and the complexity of the tasks made it difficult to record a larger number of subjects.

Data analysis. For preprocessing of articulatory movement data, three-dimensional head movement correction was done off-line based on the head position data provided by reference sensors. We also subtracted the movement information of the jaw from the tongue and lower lip values since those are carried by the jaw. Velocity and

acceleration were calculated to detect changes in movement. As shown in Fig. 2 and beyond, the forward direction of movement corresponds to a decrease of the measured values in the presented figures. The failed trials were excluded from the analysis (no exclusion for 1 subject, one exclusion for 3 subjects, two exclusions for 5 subjects).

For the data analysis, movement data were averaged across subjects. In this averaging, we did not consider raw position data due to large interindividual differences in size and shape of the tongue and the vocal tract. Instead, we took the average of the displacement relative to the position of the tongue at the time of the perturbation onset, which was calculated by aligning the data at this time to 0. We also estimated the tongue contour for each produced tongue posture by calculating direction vectors between two neighbor sensors (TB and TT; TB and TD), although this is a rough estimation since we have only three sensors. The angles of those vectors were also averaged across subjects.

In the temporal patterns of the perturbation response, we expected to observe multiple phases due to the combination of reactions associated with purely passive and reflex components of the tongue. To assess this multiple-phase organization of the responses, we divided the perturbation response into four intervals based on evident local peaks on the horizontal displacement of the TB sensor. Those intervals are shown in Fig. 2, numbered from R1 to R4 (see RESULTS for detailed explanation of the extraction of the intervals). The locations of these local peaks were extracted at the point when the absolute value of horizontal velocity became sufficiently small (less than 10 mm/s). In our analysis we mostly focused on intervals R1, R2, and R4 since those intervals reflect response mechanisms that were at the core of this study: response due to passive components and task-related compensatory response. The possibility of the existence of overlapping responses with different latencies was further examined by looking for any inflection point in the compensatory response. We then looked for peaks in the absolute value of the horizontal

Fig. 2. *A*: horizontal displacement change in the jaw (J), upper and lower lips (UL and LL), and tongue tip, blade, and dorsum (TT, TB, and TD). Shaded area represents SE across subject. Vertical dashed and dotted lines represent remarkable inflection points in the trajectory that was detected in TB. *B*: magnified view of the horizontal displacement, horizontal velocity, and horizontal acceleration in TB. Time range corresponds to the range shown by the thick horizontal bar in *A*. Vertical lines also correspond to the ones in *A*. R1–R4, response intervals.
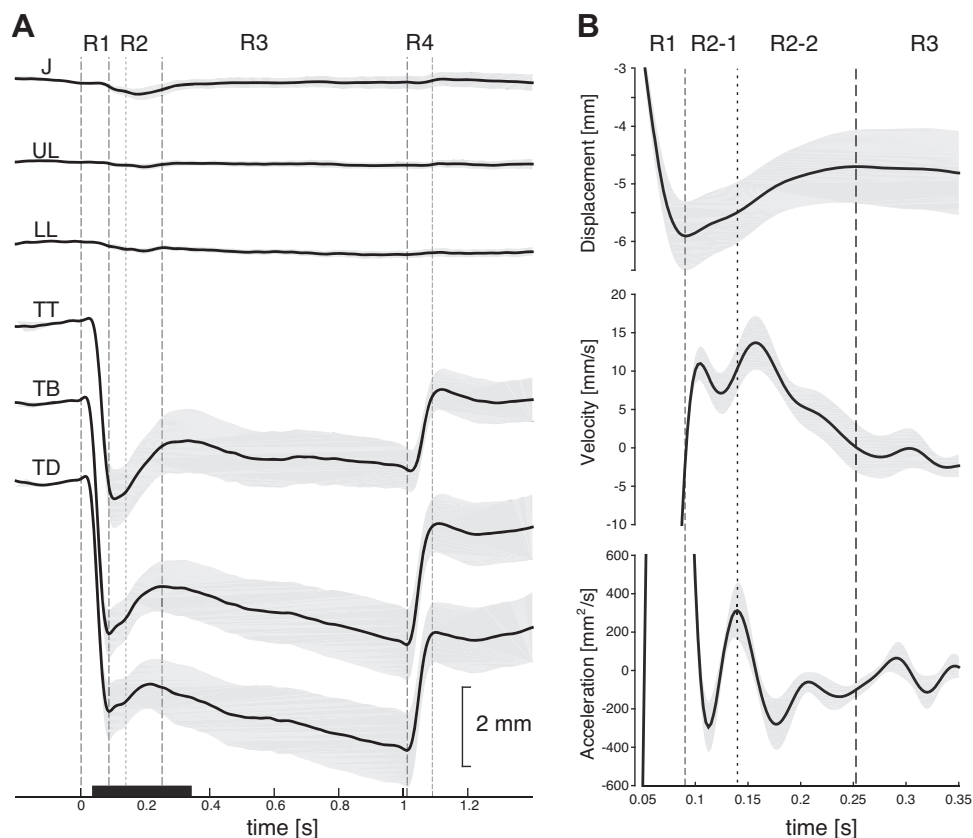
acceleration to detect subtle changes in movement characteristics. For statistical analysis, the amplitudes of tongue displacement in the sagittal plane within each of the intervals were quantified using both vertical and horizontal displacements, based on the detected peak points in each response phase. A mixed-effects model was applied with three fixed effects: vowel (/i/, /e/, and /ɛ/), articulatory manner (voicing, whispering, and posturing), and sensor location (TT, TB, and TD). Individual variability across subjects was taken into consideration as a random effect. Post hoc tests were carried out with Bonferroni correction ($P < 0.05$).

For the acoustical analysis, we extracted the first three formants (F1, F2, and F3) using linear predictive coding analysis (Rabiner and Schafer 1978). Although vowels /i/, /e/, and /ɛ/ can be efficiently separated in the (F1, F2) plane, we included F3 because it provides informative cues about local articulatory changes around these vowels. This analysis was only used for the data recorded under the voicing condition. For statistical analysis, the amplitudes of F1, F2, and F3 were calculated at the representative time points that were defined on the basis of the tongue displacement peaks mentioned above. We examined whether the sound produced at these key time points of the response to the perturbation was significantly different from the sound just before the perturbation onset ("original sound" henceforth). We carried out a paired t test between the sound characteristics at the key time points and those of the original sound.

Simulations with the 2-D biomechanical model. We carried out mathematical simulations using a 2-D biomechanical model of the tongue. The model was originally developed in previous studies (Payan and Perrier 1997; Perrier et al. 2003) and implements both passive stiffness and a stretch-like reflex to produce accounts of tongue kinematics in speech production. Details are described in those previous studies. Briefly, the tongue in the midsagittal plane is modeled as a biomechanical finite element model with 221 nodes (see Fig. 1*C*). Seven primary intrinsic and extrinsic muscles of the human tongue (posterior and anterior genioglossus, hyoglossus, styloglossus, inferior longitudinalis, superior longitudinalis, and verticalis) were embedded in the model as force actuators acting via macrofibers on selected elements, whose stiffness increases with muscle activation. Details on the insertion points and muscle description can be found in Perrier et al. (2003). As representative examples, we show the implementation of the styloglossus and posterior genioglossus (Fig. 1*C*) since these two muscles are considered to have a major role in the response to the mechanical perturbation used in this study. The styloglossus is the primary muscle for tongue retraction and also for the reaction against our study's perturbation, which was applied in the direction of tongue protrusion. The posterior genioglossus is the main muscle responsible for the tongue elevation and protrusion associated with the production of the front /i/, /e/, and /ɛ/ vowels.

The upper contour of the tongue mesh model has 16 nodes, which are numbered in increasing order from the tongue root to the tongue tip. *Nodes 11, 13,* and *16* were chosen as the corresponding locations of the sensors used in the test, TD, TB, and TT, respectively (see Fig. 1*C*). The perturbation force was applied to four nodes consisting of *nodes 13* and *14* and two nodes below those (TP in Fig. 1*C*) in the horizontal direction. Due to numerical instability issues in the numerical simulation and to differences between the experimental tongue configurations and the modeled ones, we applied a perturbation force of 0.25 N in each perturbed node for a shorter duration (200 ms) for the production of vowel /e/.

In the model, muscle force is generated based on the λ-model (Feldman 1986) as follows:

$$F(t) = \rho(e^{cA} - 1)$$

where A is the muscle activation level, c is the reflex gain parameter, and $\rho(\cdot)$ is the factor accounting for the force generation capacity of each muscle, which is a function of its cross-sectional area and its fiber density in each muscle. The muscle activation level A is itself determined as a function of the current muscle length L and a value λ',

which depends on the threshold muscle length λ' for activation and on the rate of change in muscle length ($\lambda' = \lambda$ then in static configurations), as follows:

$$A = \begin{cases} L - \lambda', L > \lambda' \\ 0, L \le \lambda' \end{cases}$$

To evaluate the potential role of the embedded short-latency somatosensory reflex in the tongue response to the perturbation, we carried out a series of simulations in which we modified the amplitude of this reflex. The simulation always started from the posture at rest (zero muscle forces), which corresponds to the posture for the production of a schwa. In the formula shown above, the muscle activation level includes both descending activations adapted to the achievement of the posture for a specific vowel and reflex activation. To control the gain for reflex activation separately, we reformulated muscle activation A in two parts as follows:

$$F(t) = \rho(e^{c(L_e - \lambda) + kc(L - L_e)} - 1)$$

where L_e and λ are the actual length and the centrally specified motor command of the muscle in the tongue posture selected for vowel /e/, respectively. These L_e and λ values were determined in previous studies (e.g., Perrier et al. 2003). The activation $A_e = L_e - \lambda$ corresponds to the baseline activation level, reached in vowel /e/ before the perturbation started. The reflex activation induced by the perturbation was represented as the difference between the muscle length L measured during the response to the perturbation and the baseline muscle length L_e. In this formula, k enables controlling the gain of the reflex activation induced by the perturbation. We tested in the simulations several amplifications of this gain, from 0 to 10. Condition $k = 0$ simulates the situation in which reactions to the perturbation are strictly limited to the consequences of passive mechanical components.

RESULTS

Overview of the time course of the response in the direction of the perturbation. We first considered the time course of the response to the perturbation in the direction of the perturbation, i.e., along the horizontal axis. Figure 2*A* shows the averaged horizontal displacement for vowel /ɛ/ under voicing condition for all the sensors (UL, LL, J, TT, TB, and TD). Increasing values correspond to a backward horizontal movement. The vertical dashed lines indicate the displacement peaks delimiting intervals R1 to R4 on the TB sensor, and the dotted line marks for the same sensor an inflection point that is interpreted as evidence for an overlap of responses with different latencies. As shown here, the perturbation induced a large tongue displacement in the forward direction (R1), and a certain amount of this change was then recovered by a compensatory movement (R2). After reaching the peak compensatory response on TB (end of R2), the tongue could not precisely hold the same posture; rather, the tongue gradually drifted forward (R3). This indicates that the tongue posture was more efficiently controlled to resist against the transient change, than against the constant bias force. This may be due to the fact that a constant force constraint is quite rare in daily life, whereas transient changes are often experienced when biting and drinking. As soon as the perturbation force was removed, the tongue moved in the backward direction, but it did not completely return to its original position (R4). This aspect of the response amplitude will be discussed later in *Geometrical path of the response in the midsagittal plane.* The upper and lower lips and the jaw also showed significant displacements in the R2 interval, al-

though the amplitude was considerably smaller than the ones in the tongue. Considering that there is some delay between the perturbation onset and the displacement onsets of these articulators, these displacements may be interpreted as a consequence of a heterogenic reflex loop arising from muscles that are not in the tongue.

Figure 2*B* represents a magnified view of the compensatory response in TB as representative data. This plotted part of the signal began 50 ms after the perturbation onset and lasted 300 ms, as marked by the black thick horizontal bar on the *x*-axis in Fig. 2*A*. During this time interval, there was an inflection point associated with a peak in the second derivative at around 140 ms after the perturbation onset (vertical thin-dotted line in Fig. 2*B*, *top*), indicating a significant change in the response at this time. We also observed an interesting velocity profile (Fig. 2*B*, *middle*) with two peaks of velocity, one before and one after the inflection point, indicating that the compensatory response was not a single phase response, but rather a sequence of at least two responses: the first component may be a passive reaction due to the passive stiffness of the tongue, and the second component may result from an active reflex-based compensatory response with some delays due to neural transmission. Based on this observation, we divided the compensatory response in two parts, before (interval R2-1) and after (interval R2-2) the inflection points on the displacement curve. We analyzed these two compensatory responses separately.

Geometrical path of the response in the midsagittal plane. Next, we considered the displacement of the tongue in the midsagittal plane. Figure 3*A* represents the averaged trajectory of sensor TB. The three graphs represent the three vowel conditions. In each graph, the different lines represent the different articulatory manners (voicing, whispering, and pos-

turing). We aligned the data at zero at the onset-time of the tongue perturbation. The displacement peaks, which are represented by the vertical dashed lines in Fig. 2*A*, are presented by asterisks in Fig. 3*A*.

In general, the detailed responses from the onset to the offset of the perturbation are quite similar across articulatory manners and vowels. We can also confirm the temporal structure of the response observed in the previous section as follows. Once the perturbation was applied in the forward direction, the tongue moved first in the same direction (initial response, interval R1). The precise direction of this initial response varied slightly depending on the articulatory configuration at the time of the perturbation onset, because of slight differences in the orientation of the wire connected to the robotic arm due to differences in jaw opening. After reaching the peak displacement of the initial response, the tongue moved back in a compensatory response (R2-1 and R2-2). The position then gradually drifted mostly in the direction of the perturbation force (R3). When the perturbation force was removed, the tongue moved back in the posterior direction (R4).

The trajectories in the midsagittal plane revealed that the compensatory response in the interval R2 did not tend to bring the sensor back to its original position, because of a significant and continuous lowering of the tongue. To analyze this diagonal direction of the compensatory movement, we superimposed our rough estimation of the original tongue contour at the perturbation onset on the sensor trajectories in Fig. 3*A* (dashed lines in each graph). Based on this original contour, we found that the tongue tended to return to its original contour, instead of its original position. The direction of this compensatory movement was nearly perpendicular to the original tongue contour ($81.7° \pm 2.02°$). This tendency was consistent

Fig. 3. *A*: trajectory of tongue blade (TB) displacement due to the perturbation from the onset of the perturbation to the offset in voicing condition. Each line represents 3 vowel conditions. Asterisks represent a detected local peak of the movement. Plus signs represent acceleration peaks during compensatory response. Onset of the perturbation corresponds to (0, 0). Estimated tongue surfaces in each vowel condition are superimposed as dashed lines. *B*: averaged displacements in each phase. *Top*, grouping according to the vowels; *middle*, grouping according to articulatory manners; *bottom*, grouping according to the sensor locations. Error bars represent SE. R1–R4, response intervals; TD, tongue dorsum; TT, tongue tip.
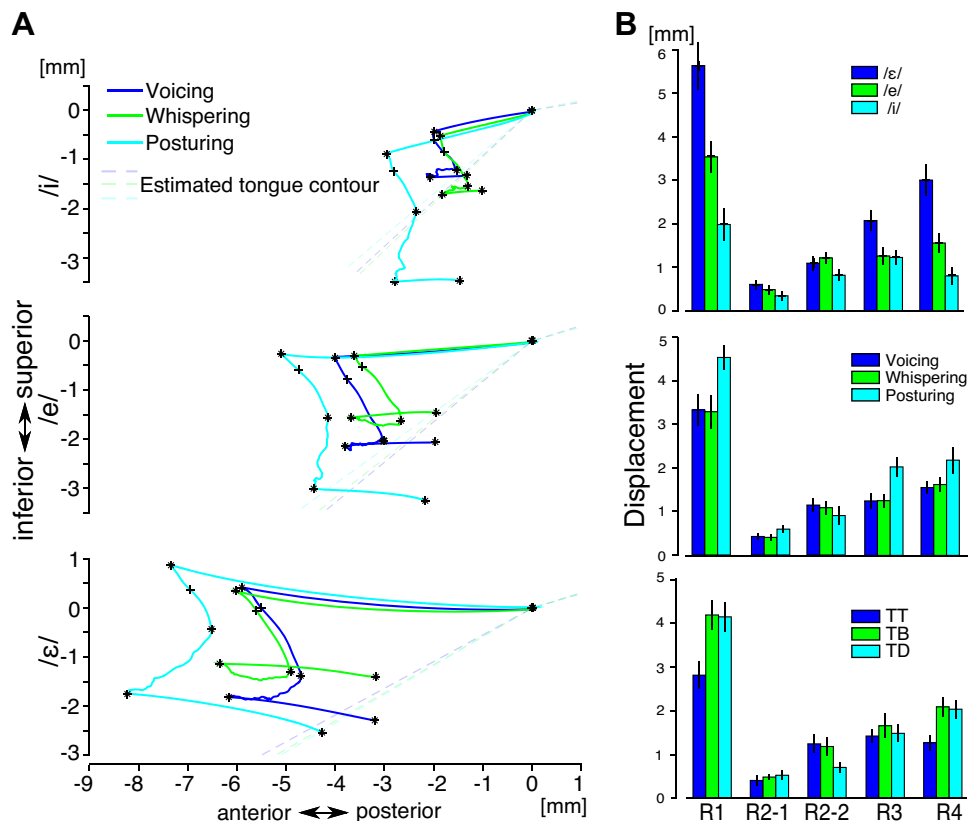
across all articulatory manners and all vowels. This suggests that the compensatory mechanism underlying tongue posture control is not to maintain or recover the exact whole same position of the tongue, but rather to maintain the same local shape of the tongue contour in the region described by the sensors. This statement is also supported by the observation of the tongue position after the perturbation removal, since the final positions of the sensors did not match the original positions, but were close to the original tongue contour, specifically in the speaking conditions (voicing and whispering).

Quantitative analysis of the response amplitudes. Displacement amplitudes in each response phase were statistically compared across tasks using linear mixed-effects models with three fixed effects [vowel (/i/, /e/, and /ɛ/), articulatory manner (voicing, whispering, and posturing), and sensor location (TT, TB. and TD)]. We found an interaction between sensor location and articulatory manner in the later part of the compensatory response [R2-2: $F(4,182) = 7.32$, $P < 0.001$]. All other contrasts (R1, R2-1, R3, and R4) did not show any reliable interaction effect. Accordingly, we present first the compensatory response in the interval R2-2, and then the fixed effects in other contrasts, particularly in R1, R2-1, and R4.

For a better understanding of the interaction effect in R2-2, we took an average across the vowels as shown in Fig. 4. The pattern of the amplitude variation across the sensor locations was different in each articulatory manner. In the voicing condition, the amplitudes of tongue tip (TT) and blade (TB) movements were larger than that of the tongue dorsum (TD; $P < 0.001$ in both), and TT and TB were not different from each other ($P > 0.2$). A similar tendency was found in whispering condition ($P < 0.001$ between TT and TD and between TB and TD), but TT and TB were modestly different ($P = 0.08$). On the other hand, in the posturing condition, there was no significant difference between TT and TD and between TB and TD ($P > 0.9$), but there was a significant difference between TT and TB ($P < 0.05$). When we compared the differences across articulatory manners in each tongue location, TT showed larger amplitude of movements for compensation when subjects were producing speech sounds ($P < 0.001$). Contrarily, TD moved less when subjects were speaking ($P < 0.05$). TB was not significantly different across the articulatory manners ($P > 0.5$). The tendency of reduced compensatory response in TD was more remarkable along the
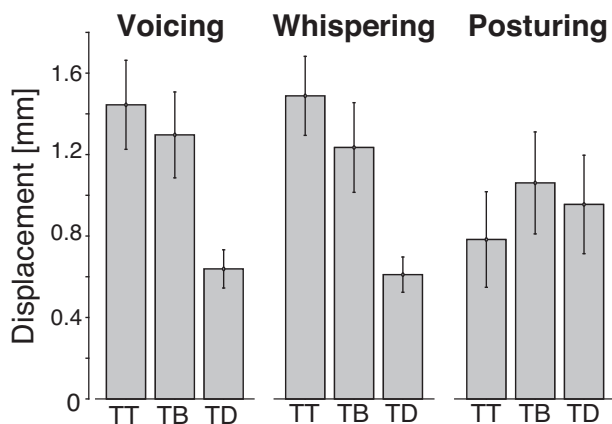

Fig. 4. Displacements of compensatory response (interval R2-2 in Fig. 2). Error bars represent SE. TB, tongue blade; TD, tongue dorsum; TT, tongue tip.

vertical direction ($P < 0.001$ both for voicing vs. posturing and for whispering vs. posturing), but not along the horizontal one ($P > 0.4$ in all 3 comparisons). This suggests that the posterior section of the tongue may be controlled to maintain an appropriate amount of constriction opening between tongue and palate for speaking, which would induce a small tolerance to changes in response to the perturbation, unlike what is observed for TT. In summary, our results suggest that the gain of the compensatory response was specifically increased in the front part of the tongue (TT) and decreased in the back part of the tongue (TD) in both speaking conditions. This is consistent with the idea that the tongue shape is controlled in a systematic way to preserve tongue characteristics that are crucial for targeted speech sounds.

For the fixed-effect components in all contrasts, we took an average in each fixed effect as shown in Fig. 3B. We found a reliable difference across the different levels of the fixed effects (vowel, articulatory manner, and sensor location). As an overall tendency, the influence of each fixed effect on the amplitude of tongue displacement was similar in the intervals R1, R2-1, and R4, and the R2-2 intervals were different from the others. This also supports the idea that the compensatory response in R2-2 may be driven differently from the ones in R1, R2-1, and R4.

In regard to the vowel influence (Fig. 3B, *top*), the displacement amplitude was reliably different [$F(2,182) = 175.5$, $P < 0.001$ in R1, $F(2,182) = 13.45$, $P < 0.001$ in R2-1, and $F(2,182) = 142.2$, $P < 0.001$ in R4]. The largest displacement was seen in the production of /ɛ/ and the amplitude of displacement was gradually reduced for /e/ and /i/. The post hoc test showed there was a significant difference in all of the pairwise comparisons ($P < 0.02$) consistently in the three response intervals R1, R2-1, and R4. In the comparison of the three articulatory manners (Fig. 3B, *middle*) we observe that the displacements in whispering and voicing conditions were consistently smaller than those in the posturing condition in the initial part of the perturbation response [interval R1: $F(2,182) = 24.01$, $P < 0.001$]. There was no reliable difference between voicing and whispering ($P > 0.9$). A similar tendency in the difference between the voicing and whispering manners and the posturing manner was also found in the earlier phase of compensatory movement [$F(2,182) = 4.823$, $P < 0.01$]. In R4, the averaged values showed a similar tendency, although no difference was found across the three articulatory manners [R4: $F(2,182) = 1.774$, $P > 0.15$].

Finally, we found a significant difference according to the sensor location on the tongue [$F(2,182) = 26.22$, $P < 0.001$] in R1 (Fig. 3B, *bottom*). The displacement in the tongue blade (TB) was not different from the one in the tongue dorsum (TD; $P > 0.9$), whereas the displacement in tongue tip (TT) was smaller than the other two ($P < 0.001$ in both). This was also seen when the perturbation was removed [R4: $F(2,182) = 22.74$, $P < 0.001$], and a modest difference was found in R2-1 [$F(2,182) = 2.384$, $P = 0.09$]. The small movement amplitude of the TT sensor does not seem to be due to contact with the teeth, since it was observed both in the forward and backward direction after the onset and the offset of the perturbation.

Formant patterns in speech sounds. The changes in tongue shape due to the tongue perturbation also resulted in changes in the produced sounds. Particularly, a compensation for the perturbation in the space of the first three formants was

observed in relation with the amount of compensatory movement. Figure 5 represents the temporal pattern of the three formants averaged across the participants. Triangles represent the times at the key points in the horizontal movement as mentioned above (dashed and dotted lines on Fig. 2*A*), with the first triangle corresponding to the end of interval R1 and the beginning of interval R2. The acoustic impact of the perturbation varied across vowels. The peak changes occurred at the onset of the reflex-like compensatory movement (second triangle corresponding to the beginning of interval R2-2). The largest changes were induced during the production of the vowel /ɛ/.

For vowel /ɛ/, the changes at the first negative peak were significant for F1 and F3 ($P < 0.005$ for both), but not for F2 ($P > 0.3$). Those were significantly reduced at the peak displacement of the compensatory response (third triangle corresponding to the end of interval R2-2; $P < 0.03$ for F1 and $P < 0.002$ for F3), although their frequencies were still significantly different from their values at the perturbation onset ($P < 0.003$ for F1 and $P < 0.05$ for F3). When the perturbation was removed, the changes between the fourth and fifth triangles were induced again in F1 and F3 ($P < 0.03$ for F1 and $P < 0.002$ for F3). For vowel /e/, the initial change due to the perturbation was induced in all three formants (F1: $P < 0.05$, F2: $P < 0.002$, F3: $P < 0.005$). At the end of the compensatory response R2 (third triangle), the changes in F1

and F3 were significantly reduced (F1: $P < 0.01$, F3: $P < 0.0001$) with no reliable difference from their original frequencies ($P > 0.1$ for F1 and $P > 0.4$ for F3). On the contrary, the compensatory movement did not reduce the alteration of the second formant induced by the perturbation ($P > 0.6$), which remained even after the removal of the perturbation. The removal of the perturbation changed F1 ($P < 0.01$) and F3 ($P < 0.001$), but not F2 ($P > 0.2$). For vowel /i/, the initial change was induced in F1 and F2, but not in F3. Those formants returned to their original values at the perturbation onset by the compensatory response.

Interestingly, the early component R2-1 of the compensatory response (between the first and second triangles) was not effective in compensating the acoustic effects of the perturbation. Rather acoustic compensation occurred mostly in the second component R2-2 of the compensatory response (between the second and third triangles). This suggests the second component of the compensatory response (R2-2) may be specifically controlled to maintain and recover the intended speech sound.

Taken together with the displacement results, these results suggest that the tongue position is controlled not to maintain a specific tongue position, but to maintain the shape of the tongue surface in the region that is crucial for the perceptual characteristics of the sound.

Simulation with the biomechanical model: effect of the reflex gain. We carried out simulations of the force perturbation of the tongue using the 2-D biomechanical model and examined the model's perturbation response. The general pattern of movement along the horizontal direction was very similar to the experimental one (see Fig. 6*A*, $k = 1$). The trajectory showed a first immediate forward movement (interval R1) followed by a backward movement (interval R2) and a strong final backward movement once the perturbation was removed (interval R4). However, the gradual drift experimentally observed during the holding phase in interval R3 did not exist in the simulation: the tongue model remained stable.

We then tested how the compensatory response changed depending on changes in reflex gain. Figure 6*A* shows the temporal pattern of horizontal displacement in simulation with several reflex gains ranging from 0 to 10 times the gain in the original tongue model. Change in reflex gain affected the responses to the perturbation. The strongest consequence was observed in the amplitude of the compensatory response corresponding to interval R2 in the experimental data. The largest response was obtained with the largest reflex gain ($k = 10$). On the other hand, when the gain was set to 0, which corresponds to the situation where the tongue responded with its passive stiffness only, the compensatory response was not observed. This finding supports the idea that the compensatory response is not driven by a passive component alone, but by an additional neural feedback mechanism, possibly by a reflex arc. Figure 6*D* displays the compensatory amplitudes in each observed location on the tongue contour. The amplitude of TT was smaller than the other two, TB and TD, and the amplitudes of TB and TD were almost the same. This simulated variation across the locations on the tongue was similar to our behavioral observations under posturing condition (Fig. 4, *right*). In the current simulations, the reflex gain was set to the same value in all the tongue muscles. The differences between the results of our simulations and the experimental observations in speaking
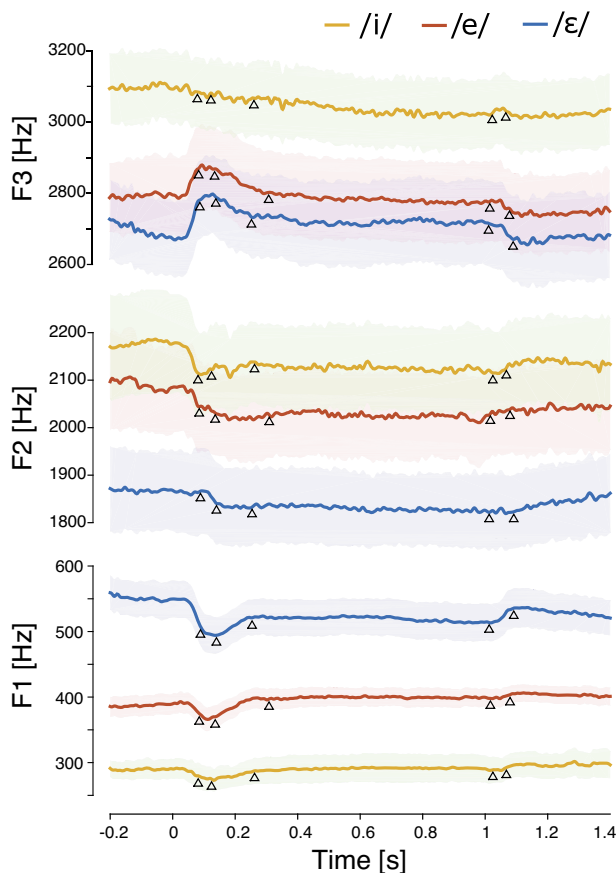

Fig. 5. Temporal patterns of the first, second and third formants (F1–F3) in speech sounds. Triangles represent the temporal points corresponding to the inflection points in displacement, which are represented as vertical lines in Fig. 2. Shaded area represents the SE across participants.
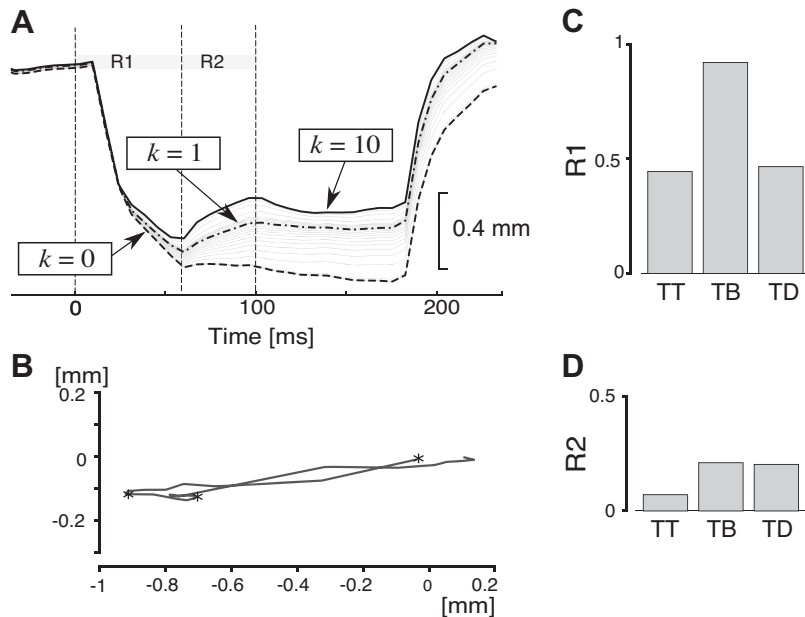
Fig. 6. Simulated results. *A*: time response in horizontal displacement of tongue blade (TB) with each reflex gain (*k*). Vertical lines represent the peak points of the first initial response (R1) and of the compensatory responses (R2). *B*: TB displacement in the sagittal plane. *C*: peak displacement of R1 in 3 tongue sites: tongue tip (TT), TB, and tongue dorsum (TD). *D*: peak amplitude of compensatory response (R2) in 3 tongue sites.

condition suggest that our subjects could have regulated the reflex gain specifically in each muscle to achieve the stability requirement of the speech production tasks.

The simulated muscle activation patterns are shown in Fig. 7. The model has seven tongue muscles (posterior genioglossus, GGp; anterior genioglossus, GGa; hyoglossus, Hyo; styloglossus, Sty; superior longitudinalis, SupLongi; inferior longitudinalis, IntLongi; and verticalis, Vert). Figure 7*A* represents the temporal patterns of the changes in muscle activations after the perturbation. The values represent relative changes from the baseline activations in the tongue posture at the perturbation onset with various amplitudes of the reflex gain. Figure 7*A*, *top*, is a magnified view of the corresponding tongue blade (TB) displacements that is already shown in Fig. 6*A*. Figure 7*B* shows the baseline activation levels in tongue posture of vowel /e/ reached at the perturbation onset.

In these four muscles, we found that the activation of the styloglossus and the posterior genioglossus was most affected by the perturbation, while the activation of the anterior genioglossus and the inferior longitudinalis changes relatively little. The styloglossus muscle showed excitatory patterns of activation, while the posterior genioglossus showed inhibitory pattern of activation in contrast. These observations are consistent with the fact that the forward displacement of the tongue due to the perturbation caused an elongation of the fibers of the styloglossus, which increases the difference between the actual fiber length and the corresponding threshold muscle command λ, and a decrease in the length of the fibers of the posterior genioglossus, which reduces the difference between the actual fiber length and the corresponding λ command. As a result, styloglossus activation increases and pulls the tongue backward to change the fiber length back to a value closer to the λ command, and the activation of the posterior genioglossus is reduced. Although there were reflex activations in the hyoglossus and verticalis, this effect is small because, due to their orientation in the tongue, their fibers were less impacted by the forward displacement of the tongue.

We also found differences between recorded and simulated responses in the midsagittal plane. Figure 6*B* shows the sim-

ulated trajectory in the sagittal plane. As in the recorded data, the tongue was moved horizontally by the perturbation force. The compensatory response was then induced in the direction of the original position. After the release of the perturbation force, the tongue almost returned to the original location. Contrary to our experimental observations, the simulated compensatory response did not induce the tongue to recover its original contour, but rather to return directly to its original shape at the perturbation onset.

We examined the amplitude of the initial displacement immediately after the perturbation (interval R1 in the experimental data) at three tongue sites (TT, TB, and TD; Fig. 6*C*). The largest amplitude was seen in TB, where the perturbation was applied. The displacements in TT and TD were almost the same, and they were smaller than in TB. These differences could originate in the fact that the tongue model includes an isotropic account of tongue biomechanics (see Nazari et al. 2013 for a more realistic account).

DISCUSSION

The current study enabled the first observation of a rapid compensatory response in the tongue induced by an external mechanical perturbation. The mathematical stimulations using a 2-D biomechanical model of the tongue strongly support the hypothesis of the existence of a reflex mechanism by showing that a sequence of compensatory responses similar to the one observed experimentally can be reproduced with a reflex arc. In addition, the reflex-like part of the simulated compensatory response was systematically modified in vowel posturing depending on the task. More specifically, the anterior part of the tongue showed greater amplitudes of the compensatory response in the speaking tasks than in the posturing task. In contrast, the posterior part of the tongue showed a smaller response in the speaking tasks. Speaking requires more precise control to maintain the target tongue contour. Our experimental observations also suggest that the control of the tongue for vowel production does not aim at producing a specific tongue position, but rather at preserving the shape of tongue contour in
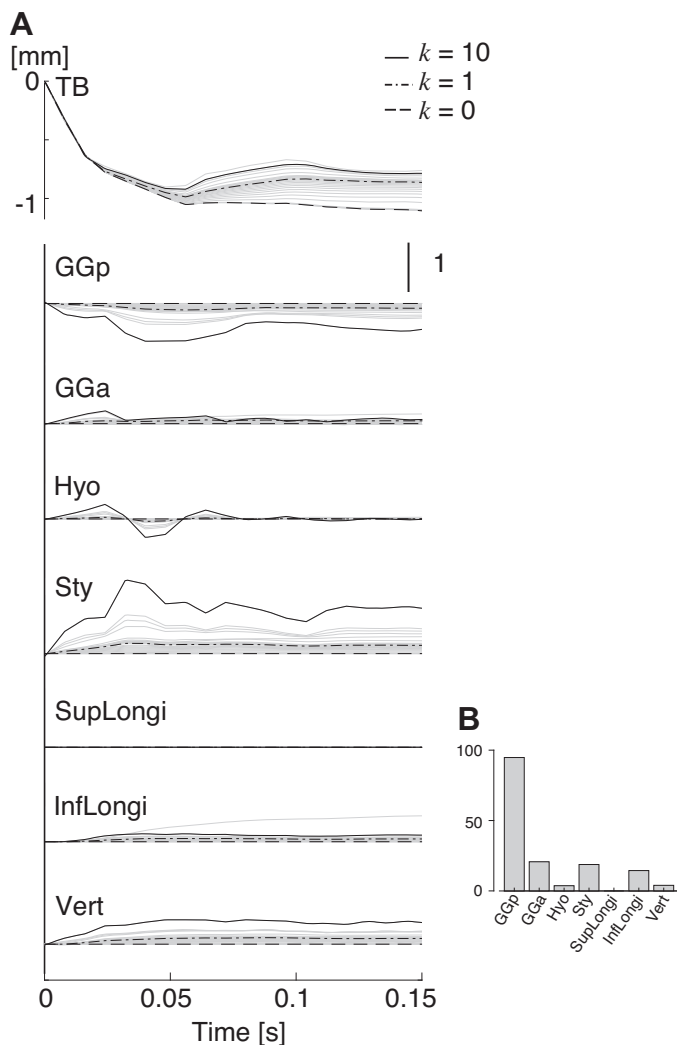
A

B

Fig. 7. Simulated results. *A*: time response of muscle activation level. The amplitude of muscle activation was represented in local unit of the simulation. *B*: baseline muscle activity for the production of /e/ in simulation. GGa, anterior genioglossus; GGP, posterior genioglossus; Hyo, hyoglossus; IntLongi, inferior longitudinalis; Sty, styloglossus; SupLongi, superior longitudinalis; TB, tongue base. Vert, verticalis.

error correction for movement and posture stabilization by feedback loops, and update of feedforward commands by adaptation and learning. In the current study, this approach enabled us to show, for the first time, a rapid compensatory response with a strong evidence for the role of a neural feedback loop. Interestingly in our experiment, this feedback control does not seem to preserve the exact tongue posture, but to preserve the shape of the tongue contour, which is crucial for vowel production. Such a feedback mechanism is difficult to predict from the generalization of control mechanisms observed in skeletal systems, in which restoring the original position is the basis of postural control. This flexibility (or redundancy) may be a special feature of tongue posture control due to the muscular hydrostat system. As a possible mechanism, a basic muscle tonus of the genioglossus, which is the largest muscle in the tongue musculature (Takemoto 2001), may be involved in the stabilization of the original tongue contour. Due to the fanlike orientation of the fibers of the genioglossus, this basic tonus applies a main stress that acts in the direction to the tongue root for maintaining the tongue posture in usual situations, and this may largely contribute in the studied compensatory movement to maintain the same tongue contour as before the perturbation. The compensatory nature can also fit to the task demand to maintain a specific shape of the tongue contour for the production of a variety of vowel sounds.

The observed compensatory responses worked to recover the auditory characteristics (formant patterns) of the original sound. This is consistent with previous experimental observations such as those of Gay et al. (1981) in which a bite block was used to perturb subjects during the articulation of English vowels, resulting in compensation strategies that preserved the shape of the vocal tract constriction. This recovering of the original contour could be guided by a voluntary compensation mechanism. Since voluntary reactions involve a cortical processing and a decision process, the resultant latency for voluntary compensation is typically long. Previous studies demonstrated that the reaction time of muscle activation in response to external stimulations was 150 ± 13 ms in the jaw (Ottenhoff et al. 1992), 315.7 ± 98.4 ms in lips (Ito et al. 2005), and 154 ms in fingers (Cole and Abbs 1987). The compensatory response observed in our study was induced less than 100 ms after the perturbation onset, for the first phase of the response (R2-1) and 140 ms after the perturbation for the second phase (R2-2). Considering muscle contraction delays from muscle activation onset to force generation (Ito et al. 2004; Mannard and Stein 1973) and the duration of the mechanical response from force generation to the onset of movement, we established that the latencies measured in the current compensatory responses were shorter than the latencies of voluntary reaction observed in former studies. Accordingly, we conclude that the current compensatory response does not result from a voluntary action, but from other faster mechanisms.

Given the findings in Gomi et al. (2002), these faster mechanisms can be driven by passive mechanical properties and by reflexes. These two mechanisms are distinguished based on response latency. Mechanical response is the fastest response, which can be induced just after the movement change by the perturbation. We have assumed that the articulatory manner (voicing, whispering, posturing) can be con-

the region close to the palate. These compensatory movements changed the formant patterns of the perturbed speech signal and enabled recovering formant patterns that were closer to the original ones. As an additional finding, the current study quantitatively demonstrated the empirically known fact that tongue stiffness can be changed according to the vowel and the articulatory manner, and that it influences the stability of the tongue posture. The limited number of subjects (9) included in this experiment obviously calls for some caution in relation to these general conclusions. However, the consistency of the response across all the participants and the systematic nature of the observations across repetitions argue strongly for the generalization of our results.

Tongue motor control mechanisms have been investigated mostly based on empirical observations of tongue kinematics and inspired by findings from other organs such as the limb. Applying a newly developed mechanical perturbation to the tongue during postural control aims at allowing the discovery of detailed clues about tongue control mechanisms, such as

trolled depending on the adjustment of mechanical properties, such as stiffness and viscosity (Burdet et al. 2001; Gomi et al. 2002; Gomi and Osu 1998). A reflex response occurs after the passive response due to neural transmission delays (Gomi et al. 2002). Depending on the pathway of neural feedback, such as via the brain stem or up to the cortex, there are several possible response latencies (Ito et al. 2005; McClean 1991). In our experimental data, we found an inflection point during compensatory response that corresponds to the acceleration peak around 140 ms after the perturbation onset. We interpreted this inflection point in displacement as the point of initiation of a reflex response, which means that the remaining part of the compensatory response (R2-2 interval in Fig. 2B) was driven by reflex mechanisms. Our mathematical simulation supports this idea because the change in reflex gain in the model induced significant changes of the amplitude of the compensatory response. In the orofacial system, cortical reflexes have been shown to be involved in compensatory responses in the lips, with lip muscle responses occurring 47.5 ms (±27.5 ms) after perturbation of the jaw, with the corresponding change in movement observed 100 ms after the perturbation onset (Gomi et al. 2002). Since the latency of the kinematic compensatory response in our experiment was longer than the one observed in lip adjustments due to cortical reflex in jaw perturbation studies, a cortical reflex could also be involved in the response of our subjects.

Neilson et al. (1979) had failed to find clues for tonic stretch reflex of the tongue with electromyographical recording from five tongue muscles (genioglossus, geniohyoid, mylohyoid, styloglossus, and tongue intrinsic muscle). They used a sponge forceps to grip and stretch the tongue. It can be difficult to apply a force to the tongue in a consistent manner with such a manual perturbation. Moreover, the force to grip the tongue with the sponge forceps could have had an undesired effect and suppressed any reflexes, including a stretch reflex. Contrary to this finding, we found concordant elements in the latency of the experimentally observed responses and in the similarities between simulated responses with the biomechanical model and observed responses. These results support the hypothesis of the existence of a reflex in the control of the tongue posture. Given the nature of the current tongue perturbation, the observed compensatory response may correspond directly to the stretch reflex as it would be in skeletal muscles. This can be supported by the observation of the activation pattern of the styloglossus in our biomechanical model. Since the neural connection and the sensory origin could not be determined in the behavioral study alone, further investigation including the recording of muscle activation is required to confirm the existence of stretch-like reflex in the tongue.

The current study can provide a direct clue about stiffness variations of the tongue during speech production. By using a robotic device, we consistently applied the same amount of force to the tongue in the three vowel articulations (/i/, /e/, and /ɛ/) and in the three articulatory manners (voicing, whispering, and posturing). Comparing the vowel articulation, the smallest displacement due to the perturbation was induced in the articulation of /i/ and the displacement was increased from /e/ to /ɛ/. This is consistent with the previous findings described in the Introduction. The current study experimentally examined the variation of tongue stiffness depending on the requirements of speech utterances. Changes in tongue stiffness also explain the

differences observed across articulatory manners. We found that the displacement induced by the force perturbation was smaller in the voicing and whispering conditions than in the posturing condition. This indicates that intrinsic tongue mechanical stiffness was larger when the subjects were actually producing speech sounds and suggests that speech production requires a larger amount of muscle activation. Since we do not find any difference between voicing and whispering condition, the activation level of tongue muscles seems not to be reliably affected by the simultaneous involvement of vocal fold vibrations. Taken altogether, these findings support the idea that the stiffness of the tongue can be modified depending on the vowel and on the articulatory manner. Interestingly, response patterns in the R2-2 interval were different from the response patterns in all the others (R1, R2-1, and R4 intervals); this result also supports the idea that the compensatory response in R2-2 was not driven by a passive component, but rather by neural feedback loop, such as a reflex.

Stiffness can also be different between anterior and posterior parts of the tongue. We found that displacement due to the passive component of the perturbation response was different across sensor locations on the tongue (TT, TB, and TD). While TB and TD responded with a similar amplitude of displacement, that of TT was smaller than the others. The results indicate that the passive stiffness of the tissue connecting TB and TD is high enough to synchronize their movements, while the stiffness of the connection between TB and TT is relatively low. Accordingly, the passive mechanical characteristics of the tongue may not be homogeneous in the tongue body. Investigating mechanical properties of the tongue body is difficult because those properties may be different in tests carried out on cadavers and in living subjects due to basic muscle tonus. Applying a mechanical stretch to the several different sites during the same task is one way to further investigate the mechanical properties of the tongue body in detail.

We found that the amplitude of the compensatory response in speaking tasks was greater in the anterior region of the tongue than in the posterior region. This may be related to the composition of the muscle fibers. Stål et al. (2003) found that fiber composition in intrinsic tongue muscles varied depending on the part of the tongue. The anterior region of the tongue contained predominantly fast-twitch fibers (type II), in contrast to the posterior region which contains more slow-twitch fibers (type I) than type II fibers. This difference in muscle composition may be due to the functional role of the different muscles in making quick and flexible movements. Accordingly, compensatory responses to external disturbances may be included in those functional demands.

In speech motor control, auditory feedback can also be a possible loop to induce compensatory movements together with somatosensory feedback (Houde and Jordan 1998; Lametti et al. 2012). In previous studies (Larson et al. 2000; Purcell and Munhall 2006), the onset of auditory compensation was found to be more than 200 ms after the perturbation onset when a sustained vowel was perturbed at a certain time in pitch or formant due to altered auditory feedback, which is a situation similar to the one in the current study. In Purcell and Munhall (2006), when the first formant was suddenly shifted by 136 Hz on average at a certain time during the sustained vowel production, the auditory perturbation was gradually compensated from around 300 ms after the perturbation onset,

and the amplitude of compensation reached more than 20 Hz at 800 ms after the perturbation onset (~15% of compensation). This manner of compensation is different from the findings of our study, in which the acoustic changes induced by the tongue perturbation were immediately compensated at the latest 300 ms after the perturbation onset, without any gradual compensation afterward. In addition, the maximum change of the first formant induced by the tongue perturbation during the production of /ɛ/ was ~55 Hz on average across subjects, which is about half of Purcell and Munhall's acoustical perturbation. In contrast, the magnitude of the compensation in the tongue perturbation was 27 Hz on average, which corresponds to ~50% of the magnitude of the initial formant change. Thus larger amounts of acoustical compensation were achieved in our study than in the case of auditory perturbation. Considering that the acoustical change was synchronized with the compensatory movement in the tongue, we believe that the current compensation is induced predominantly by somatosensory error rather than auditory error. In addition, the auditory error that remained after the first compensatory response (i.e., after 250 ms) in the production of /ɛ/ was not further compensated. Since the sound in perturbed condition was still in the perceptual range of vowel /ɛ/, this acoustical error may be ignored to be corrected, as opposed to the somatosensory error. The auditory error accompanying the articulatory perturbation, as in the current study, may be easily compensated by simply compensating for the articulatory changes. On the contrary, the auditory error that occurs with unperturbed articulation, such as in altered auditory feedback, may be difficult to compensate for probably due to a conflict between auditory and somatosensory requirements (Katseff et al. 2012; Lametti et al. 2012; Patri et al. 2019).

Although the previous studies (Larson et al. 2000; Purcell and Munhall 2006) showed that the compensatory response via auditory feedback is longer than 200 ms, Cai et al. (2011) also reported a relatively faster auditory compensation (~120 ms). Since this latency is comparable to the one in the current compensatory response, auditory feedback may be involved in the production of the current compensatory movement. Different from the current situation where the perturbation was applied during the static articulation of the vowels, as it was in Larson et al. (2000) and Purcell and Munhall (2006), Cai et al. (2011) applied auditory perturbation in a dynamical manner since the first formant was altered during the production of a vowel-to-vowel gesture. The arm motor control studies suggested that the latency of compensation to sensory errors can be different between dynamical and static motor situations. The changes of muscle activation by reflexes in response to a force perturbation occur with a longer latency during a static posturing (80 ms; Soechting and Lacquaniti 1988) than during a movement (40 ms; Soechting 1988). This suggests that the response via auditory feedback in static situation can take longer than the 120-ms latency found in Cai et al. (2011) and that the response to the current compensatory response occurred sufficiently early to reject the possibility that it would be due to auditory feedback. We conclude that the possible involvement of auditory feedback is unlikely in the compensation observed in our study.

These converging indications concerning a major role for somatosensory feedback in the current compensatory response also suggest that correcting the somatosensory error is enough to recover the perceptually relevant characteristics of the original speech sound. Since similar speech sounds can be produced with different articulatory configurations, multiple choices for articulatory compensation can be possible for compensation of the speech sound. However, the compensatory movement observed in our study was achieved in a consistent manner across the vowels and subjects, which tends to preserve the tongue shape in the constriction region. This suggests that the speech motor control system could make use of a one-to-one auditory-somatosensory mapping to achieve a specific auditory goal using somatosensory feedback alone.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

T.I. and P.P. conceived and designed research; T.I., J.-L.C., and P.P. performed experiments; T.I., A.S., and P.P. performed simulations; T.I., A.S., and P.P. interpreted results of experiments and simulations; T.I. prepared figures; T.I. drafted manuscript; T.I. and P.P. edited and revised manuscript; T.I., A.S., J.-L.C., and P.P. approved final version of manuscript.

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