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1 **Title:** Quick compensatory mechanisms for tongue posture stabilization during speech
2 production

3

4 **Abbreviated title:** Tongue posture control for speech production

5

6 **Authors:** Takayuki Ito ^{1,2*}, Andrew Szabados ¹, Jean-Loup Caillet ¹, Pascal Perrier ¹

7

8 **Author's affiliations:**

9 1: Univ. Grenoble Alpes, CNRS, Grenoble INP*, GIPSA-lab, 38000 Grenoble, France

10 * Institute of Engineering Univ. Grenoble Alpes.

11 2: Haskins Laboratories, 300 George Street, New Haven, CT, 06511, USA

12

13

14 *: **Corresponding author:** Takayuki Ito

15 Takayuki Ito

16 Address: GIPSA-lab, CNRS, 11 rue des Mathématiques, Grenoble Campus BP46, F-

17 38402, Saint Martin d'Hères Cedex, France

18 Email: takayuki.ito@gipsa-lab.grenoble-inp.fr

19 Tel: +33 (0)4 76 82 70 46

20 Fax: +33 (0)4 76 57 47 10

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23 **Abstract (250 words)**

24 The human tongue is atypical as a motor system since its movement is determined by
25 deforming its soft tissues via muscles that are in large part embedded in it (muscular
26 hydrostats). However, the neurophysiological mechanisms enabling fine tongue motor
27 control are not well understood. We investigated sensorimotor control mechanisms of the
28 tongue through a perturbation experiment. A mechanical perturbation was applied to the
29 tongue during the articulation of three vowels (/i/,/e/, /ɛ/) under conditions of voicing,
30 whispering and posturing. Tongue movements were measured at three surface locations
31 in the sagittal plane using electromagnetic articulography. We found that the
32 displacement induced by the external force was quickly compensated for. Individual
33 sensors did not return to their original positions but went towards a position on the
34 original tongue contour for that vowel. The amplitude of compensatory response at each
35 tongue site varied systematically according to the articulatory condition. A mathematical
36 simulation that included reflex mechanisms suggested that the observed compensatory
37 response can be attributed to a reflex mechanism, rather than passive tissue properties.
38 The results provide evidence for the existence of quick compensatory mechanisms in the
39 tongue that may be dependent on tunable reflexes. The tongue posture for vowels could
40 be regulated in relation to the shape of the tongue contour, rather than to specific
41 positions for individual tissue points.

42

43

44 **New & Noteworthy**

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

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54 **Keywords**

55 Speech motor control, Mechanical perturbation, Reflex, Compensatory response,
56 Orosensory feedback.

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59

60 **Introduction**

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

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

78 In case of speech production, the mechanisms of tongue motor control have been
79 investigated especially through the adaptation paradigm using static perturbation, such as
80 holding jaw positions with a bite block (Fowler and Turvey 1981; Gay et al. 1981),
81 altering lip geometry with a lip tube (Savariaux et al. 1995) or modifying the palate shape
82 by inserting an artificial palate (Brunner et al. 2011; Honda et al. 2002; McFarland et al.

83 1996). The produced sounds become quite similar to the original sounds after a short time
84 of adaptation following the perturbation, suggesting that the tongue control system
85 quickly adapts to new environments as we experience in daily life situations (e.g.
86 speaking while chewing gum). While those adaptive changes provide evidence for
87 efficient and robust control of the tongue, little is known about the neurophysiological
88 and physical phenomena enabling the control of tongue posture stabilization during the
89 production of speech sounds, in particular to compensate for time-varying perturbations
90 as experienced in our daily life.

91 In regard to speech production, a well-known hypothesis suggests that tongue
92 motor control consists in moving the tongue toward target postures associated with
93 phonemes (Keating 1990; MacNeilage 1970; Patri et al. 2015). In the production of
94 consonants, such as /t/ or /s/, the tongue must not only target postures precisely, but also
95 maintain them for a sufficient amount of time, which requires the capacity to efficiently
96 stabilize the tongue in the target postures. This task could be accomplished by moving the
97 tongue, or a part of the tongue, toward a specific location in the oral cavity, such as
98 toward the upper teeth, just as it is done in pointing or reaching tasks with the arm by
99 moving the different arm segments around their joints. It is however unclear whether the
100 postural stabilization of the deformable tongue relies on control principles that are similar
101 to those of the stabilization of arm segments around a joint.

102 The control mechanisms involved in limb and body posture stabilization have
103 often been investigated using time-varying perturbations (Burdet et al. 2001; Gomi and
104 Osu 1998; Gottlieb and Agarwal 1988; Marsden et al. 1972; Pruszynski and Scott 2012;
105 Soechting 1988; Soechting and Lacquaniti 1988). Immediate compensation for time-

106 varying perturbations can be driven by impedance control and neural feedback control.
107 Responses associated with impedance control are intrinsic physical responses of the
108 motor plant associated with passive elastic properties (Gomi and Osu 1998; Gottlieb and
109 Agarwal 1988). As a consequence, they are very fast. The response induced by neural
110 feedback control, such as stretch reflex, arrives later due to the delay in neural
111 transmission, which ranges from 20 to 50 ms for short-latency stretch reflex and from 50
112 to 100 ms for the long-latency stretch reflex (Pruszynski and Scott 2012). This time
113 sequence of responses was examined in the speech articulatory system using a
114 mechanical perturbation of the jaw (Gomi et al. 2002; Ito et al. 2005). The compensatory
115 response due to stiffness in the linkage between lip and jaw occurred less than 20 ms after
116 the onset of the movement induced by the perturbation; in contrast, the muscle activation
117 due to reflex was induced longer than 50 ms after this movement onset (Gomi et al.
118 2002). This compensatory reflex was mediated by the motor cortex (Ito et al. 2005). As in
119 limb studies, applying a time-varying mechanical perturbation to the tongue and
120 observing the behavioral response is an efficient approach to examine whether the tongue
121 shows compensatory responses with latencies comparable to those of responses induced
122 by impedance control and by neural feedback control in the limb system.

123 Task-dependent modulation can be seen in both impedance control and reflex
124 mechanisms. In impedance control, mechanical properties of the motor system (such as
125 stiffness or damping) can be adjusted for external constraints (Burdet et al. 2001; Gomi
126 and Osu 1998). It has been found in the speech articulatory system that the stiffness in the
127 linkage between the jaw and upper lip increased for the production of the bilabial
128 fricative consonant / ϕ / as compared to the neighboring vowels in vowel-consonant-vowel

129 sequences (Gomi et al. 2002). In reflex control, long latency reflexes in the limb system
130 have been shown to vary depending on the task demands in a variety of situations (See
131 review in Pruszynski and Scott (2012)). In the orofacial system, the magnitude of
132 compensatory reflexes in the upper lip has been shown to vary depending on the speech
133 task: the magnitude of the muscle activation due to reflex was significantly larger during
134 the production of bilabial fricatives than during vowel production (Gomi et al. 2002), and
135 little or no response was induced in a resting condition (Ito and Gomi 2007). Similarly,
136 Kelso et al. (1984) observed an increase of muscle activation in the tongue in response to
137 a force perturbation applied to the jaw during the production of alveolar consonants /z/,
138 but not during the production of bilabial consonants /b/. Thus, compensatory responses
139 induced in the tongue by a force perturbation applied to the jaw seem also to be
140 modulated across different speech tasks and/or across speech and non-speech (resting)
141 tasks.

142 In speech production, a number of converging experimental and modeling results
143 suggest that tongue stiffness varies across the front vowels, such as /i/, /e/ and /ε/, in
144 conjunction with the amount of tongue positioning variability: the stronger the stiffness,
145 the smaller the variability. Previous studies (Beckman et al. 1995; Perkell and Nelson
146 1985) showed that front-high vowels /i/ and /e/ have less articulatory variability than
147 lower vowels like /ε/ and /a/. In addition, using electropalatography (Stone and Lundberg
148 1996) and MR imaging (Badin et al. 2002), a strong relationship was found between the
149 intensity of the linguo-palatal contact and the activation of the posterior genioglossus,
150 which pulls forward the back part of the tongue, as evidenced by magnitude of grooving
151 the back part of the tongue. The idea is also supported by the simulations with a 3D

152 biomechanical model of the tongue showing that, for a given height of the tongue, an
153 increase in the amount of lateral contacts between the tongue and the palate is achieved
154 through an increase in tongue muscle activation, specifically activation of the posterior
155 genioglossus (Buchaillard et al. 2009; Gick et al. 2017). An increase in muscle activation
156 induces an increase in muscle tissue stiffness called the stress-stiffening effect (Nazari et
157 al. 2011). Applying a mechanical force perturbation to the motor system, as used in
158 previous studies (Burdet et al. 2001; Gomi and Osu 1998; Gottlieb and Agarwal 1988),
159 allows stiffness to be measured by observing the displacement induced by the
160 perturbation, since for a given magnitude of the force the magnitude of the displacement
161 is proportional to the stiffness, assuming linear dynamical properties. Hence, force
162 perturbation can be an efficient tool to reveal task-dependent changes in stiffness of the
163 tongue or of the linguo-palatal system.

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

174 mechanism in the control of posture stabilization and can suggest how muscle spindles or
175 proprioceptive organs are involved in the compensatory responses.

176 In our study, we focus on quick compensatory responses for the stabilization of
177 the tongue. We examined whether perturbations of tongue postures were compensated by
178 on-line feedback control mechanisms by observing the time course of the tongue
179 response due to time-varying perturbations. For this purpose, a novel mechanical
180 perturbation system was specifically developed using a robotic device. We applied the
181 mechanical perturbation in an unanticipated manner while subjects were holding
182 specified tongue postures. Electromagnetic articulography was used to measure the
183 displacement of the articulatory organs (jaw, lips and tongue).

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

193 In order to analyze the time-course of the responses to perturbation, especially in
194 terms of the shape of the kinematic responses respectively induced by impedance control
195 and by stretch-like reflex, we simulated the tongue force perturbations using a
196 mathematical biomechanical model of the tongue (Perrier et al. 2003). Since this

197 mathematical simulation includes an account of short-delay somatosensory feedback for
198 reflex response, it can be used to dissociate a reflex contribution from the response by
199 impedance control through manipulation of the amplitude of the reflex gain in the model.
200 By comparing the simulated movements of the tongue in the model with those observed
201 experimentally, we could assess whether the reflex mechanism as implemented in the
202 model could explain the experimentally observed compensatory responses.

203

204 **Methods**

205 **Participants**

206 Nine native French speakers (18-35 years old, 3 females) participated in the
207 experiment. The participants were all healthy young adults who reported normal hearing.
208 All participants signed informed consent forms approved by the local ethical committee
209 of the University Grenoble Alpes (CERNI: Comité d'Ethique pour les Recherches non
210 Interventionnelles: CERNI-AvisConsultatif-2017-01-17-04).

211

212 **Articulatory measurement and tongue perturbation**

213 Electromagnetic articulography (Wave, Northern Digital Inc.) was used to
214 measure articulation. For vowel production, the articulation is primarily characterized by
215 the geometry of the vocal tract shape in the mid-sagittal plane. Hence, the measurement
216 sensors were glued in the mid-sagittal plane: tongue tip (TT), tongue blade (TB), and
217 tongue dorsum (TD) on the tongue surface, upper and lower lips (UL and LL), and jaw
218 (J). Four reference sensors, located on the nasion, the left and right mastoids and the
219 upper incisors (see Fig. 1), were also used for the measurement of head movements and

220 their subtraction from the other sensors' movements in an off-line analysis. The sensor
221 data were recorded with a 400 Hz sampling rate, and the produced speech sound was
222 recorded synchronously with a 22.05 kHz sampling frequency.

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

232

233 **Experimental tasks: vowels and articulatory manners**

234 The first focus of this study is to compare perturbed responses in different vowel
235 postures. We focused on three French vowels, /i/, /e/ and /ɛ/ that are expected to be
236 produced with different amounts of tongue muscle activation. Vowels /i/, /e/ and /ɛ/ are
237 close neighbors in terms of both acoustical and articulatory characteristics. In the
238 acoustical domain, vowels are efficiently described by the first two formants, F1 and F2,
239 which are the lowest two resonance frequencies of the vocal tract and correspond to the
240 first two maxima of the frequency spectrum of the sound. The first formant gradually
241 decreases from /ɛ/, to /e/ and /i/, while the second formant increases. There is no other
242 vowel between them in French phonetics. In the articulatory domain, these vowels are

243 usually discriminated along the tongue height (or jaw height) dimension, which
244 corresponds to the vocal tract aperture. The production of /i/ requires a high and anterior
245 tongue position, corresponding to the narrowest aperture of the vocal tract in the palatal
246 region. As compared to the production of /i/, tongue height gradually decreases and
247 moves backwards for the production of /e/ and /ɛ/. This variation is associated especially
248 with a decrease in the activation of the posterior genioglossus.

249 The second focus is to examine the effect of speaking versus non-speaking
250 conditions. We compared compensatory responses in voicing, whispering and posturing
251 conditions. In the three conditions, the subjects were asked to sustain the tongue position
252 for a few seconds. In voicing and whispering conditions, they were asked to do so while
253 voicing or whispering. In non-speech posturing condition, they were asked to do so
254 silently. In order to have the same set of reference vowel tongue positions as for the
255 speaking conditions, subjects were instructed to produce the vowel briefly at the
256 beginning of each trial of the posturing condition, and then to maintain the posture
257 silently (without voicing or whispering).

258

259 **Experimental procedure**

260 Nine experimental tasks (three vowels under three articulatory manners) were
261 tested in random order. At the beginning of each trial, visual instruction on a monitor was
262 used to inform the subjects about the task for the coming trial. The trial was launched by
263 the experimenter after examining whether the participant was ready for the task. The
264 subjects were instructed to start their task via visual and auditory cues. The perturbation
265 was applied 1s after the trial onset on a randomly-selected third of the trials in order to

266 avoid any anticipation by the subject. There were 270 trials in total. As a result, 10
267 perturbed responses were recorded in each condition. The total experimental time was
268 approx. 2 hours including the preparation time for placing the EMA sensors and gluing
269 the wires of the robotic arm on the participant's tongue, and the experimental session
270 itself. The long duration of the experiment and the complexity of the tasks made it
271 difficult to record a larger number of subjects.

272

273 **Data analysis**

274 For pre-processing of articulatory movement data, three-dimensional head
275 movement correction was done off-line based on the head position data provided by
276 reference sensors. We also subtracted the movement information of the jaw from the
277 tongue and lower lip values since those are carried by the jaw. Velocity and acceleration
278 were calculated to detect changes in movement. As seen in Figure 2 and beyond, the
279 forward direction of movement corresponds to a decrease of the measured values in the
280 presented figures. The failed trials were excluded from the analysis (no exclusion for 1
281 subject, one exclusion for 3 subjects, two exclusions for 5 subjects).

282 For the data analysis, movement data were averaged across subjects. In this
283 averaging, we did not consider raw position data due to large inter-individual differences
284 in size and shape of the tongue and the vocal tract. Instead we took the average of the
285 displacement relative to the position of the tongue at the time of the perturbation onset,
286 which was calculated by aligning the data at this time to zero. We also estimated the
287 tongue contour for each produced tongue posture by calculating direction vectors
288 between two neighbor sensors (TB and TT; TB and TD), although this is a rough

289 estimation since we have only three sensors. The angles of those vectors were also
290 averaged across subjects.

291 In the temporal patterns of the perturbation response, we expected to observe
292 multiple phases due to the combination of reactions associated with purely passive and
293 reflex components of the tongue. To assess this multiple-phase organization of the
294 responses, we divided the perturbation response into four intervals based on evident local
295 peaks on the horizontal displacement of the TB sensor. Those intervals are shown in
296 Figure 2, numbered from R1 to R4 (See Results for detailed explanation of the extraction
297 of the intervals). The locations of these local peaks were extracted at the point when the
298 absolute value of horizontal velocity became sufficiently small (less than 10 mm/s). In
299 our analysis we mostly focused on intervals R1, R2 and R4 since those intervals reflect
300 response mechanisms that were at the core of this study: response due to passive
301 components and task-related compensatory response. The possibility of the existence of
302 overlapping responses with different latencies was further examined by looking for any
303 inflection point in the compensatory response. We then looked for peaks in the absolute
304 value of the horizontal acceleration to detect subtle changes in movement characteristics.
305 For statistical analysis, the amplitudes of tongue displacement in the sagittal plane within
306 each of the intervals were quantified using both vertical and horizontal displacements,
307 based on the detected peak points in each response phase. A mixed-effect model was
308 applied with three fixed effects: vowel (/i/, /e/ and /ɛ/), articulatory manner (voicing,
309 whispering, and posturing) and sensor-location (TT, TB, and TD). Individual variability
310 across subjects was taken into consideration as a random effect. Post-hoc tests were
311 carried out with Bonferroni correction ($p < 0.05$).

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

323

324 **Simulations with the 2D biomechanical model**

325 We carried out mathematical simulations using a 2D biomechanical model of the
326 tongue. The model was originally developed in previous studies (Payan and Perrier 1997;
327 Perrier et al. 2003), and implements both passive stiffness and a stretch-like reflex to
328 produce accounts of tongue kinematics in speech production. Details are described in
329 those previous studies. Briefly, the tongue in the mid-sagittal plane is modeled as a
330 biomechanical finite element model with 221 nodes (See Fig. 1C). Seven primary
331 intrinsic and extrinsic muscles of the human tongue (posterior and anterior genioglossus,
332 hyoglossus, styloglossus, inferior longitudinalis, superior longitudinalis, and verticalis)
333 were embedded in the model as force actuators acting via macrofibers on selected
334 elements, whose stiffness increases with muscle activation. Details on the insertion points

358 activation level A is itself determined as a function of the current muscle length L and a
359 value λ' , which depends on the threshold muscle length λ for activation and on the rate of
360 change in muscle length ($\lambda' = \lambda$ then in static configurations), as follows:

$$361 \quad A = \begin{cases} L - \lambda', & L > \lambda' \\ 0, & L \leq \lambda' \end{cases}$$

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

$$370 \quad F(t) = \rho(e^{c(L_e - \lambda) + kc(L - L_e)} - 1)$$

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

380 which reactions to the perturbation are strictly limited to the consequences of passive
381 mechanical components.

382

383 **Results**

384 *Overview of the time course of the response in the direction of the perturbation*

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

403 lower lips, and the jaw also showed significant displacements in the R2 interval, although
404 the amplitude was considerably smaller than the ones in the tongue. Considering that
405 there is some delay between the perturbation onset and the displacement onsets of these
406 articulators, these displacements may be interpreted as a consequence of a heterogenic
407 reflex loop arising from muscles that are not in the tongue.

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

423

424 *Geometrical path of the response in the mid-sagittal plane*

425 Next, we considered the displacement of the tongue in the mid-sagittal plane.
426 Figure 3A represents the averaged trajectory of sensor TB. The three panels represent the
427 three vowel conditions. In each panel, the different lines represent the different
428 articulatory manners (voicing, whispering and posturing). We aligned the data at zero at
429 the onset-time of the tongue perturbation. The displacement peaks, which are represented
430 by the vertical dashed lines in Figure 2, are presented by asterisks in Figure 3A.

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

442 The trajectories in the mid-sagittal plane revealed that the compensatory response
443 in the interval R2 did not tend to bring the sensor back to its original position, because of
444 a significant and continuous lowering of the tongue. To analyze this diagonal direction of
445 the compensatory movement, we superimposed our rough estimation of the original
446 tongue contour at the perturbation onset on the sensor trajectories in Figure 3A (light-
447 dashed lines in each panel). Based on this original contour, we found that the tongue

448 tended to return to its original contour, instead of its original position. The direction of
449 this compensatory movement was nearly perpendicular to the original tongue contour
450 (81.7 degrees \pm 2.02). This tendency was consistent across all articulatory manners and
451 all vowels. This suggests that the compensatory mechanism underlying tongue posture
452 control is not to maintain or recover the exact whole same position of the tongue, but
453 rather to maintain the same local shape of the tongue contour in the region described by
454 the sensors. This statement is also supported by the observation of the tongue position
455 after the perturbation removal, since the final positions of the sensors did not match the
456 original positions, but were close to the original tongue contour, specifically in the
457 speaking conditions (voicing and whispering).

458

459 *Quantitative analysis of the response amplitudes*

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

468 For a better understanding of the interaction effect in R2-2, we took an average
469 across the vowels as shown in Figure 4. The pattern of the amplitude variation across the
470 sensor locations was different in each articulatory manner. In the voicing condition, the

471 amplitudes of tongue tip (TT) and blade (TB) movements were larger than that of the
472 tongue dorsum (TD) ($p < 0.001$ in both), and TT and TB were not different from each
473 other ($p > 0.2$). A similar tendency was found in whispering condition ($p < 0.001$ between
474 TT and TD and between TB and TD), but TT and TB were modestly different ($p = 0.08$).
475 On the other hand, in the posturing condition, there was no significant difference between
476 TT and TD and between TB and TD ($p > 0.9$), but there was a significant difference
477 between TT and TB ($p < 0.05$). When we compared the differences across articulatory
478 manners in each tongue location, TT showed larger amplitude of movements for
479 compensation when subjects were producing speech sounds ($p < 0.001$). Contrarily, TD
480 moved less when subjects were speaking ($p < 0.05$). TB was not significantly different
481 across the articulatory manners ($p > 0.5$). The tendency of reduced compensatory
482 response in TD was more remarkable along the vertical direction ($p < 0.001$ both for
483 voicing *versus* posturing and for whispering *versus* posturing), but not along the
484 horizontal one ($p > 0.4$ in all three comparisons). This suggests that the posterior section
485 of the tongue may be controlled to maintain an appropriate amount of constriction
486 opening between tongue and palate for speaking, which would induce a small tolerance to
487 changes in response to the perturbation, unlike what is observed for TT. In summary, our
488 results suggest that the gain of the compensatory response was specifically increased in
489 the front part of the tongue (TT) and decreased in the back part of the tongue (TD) in
490 both speaking conditions. This is consistent with the idea that the tongue shape is
491 controlled in a systematic way to preserve tongue characteristics that are crucial for
492 targeted speech sounds.

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

500 In regard to the vowel influence (top panel in Figure 3B), the displacement
501 amplitude was reliably different ($[F(2,182) = 175.5, p < 0.001]$ in R1, $[F(2,182) = 13.45,$
502 $p < 0.001]$ in R2-1 and $[F(2,182) = 142.2, p < 0.001]$ in R4). The largest displacement was
503 seen in the production of /ε/ and the amplitude of displacement was gradually reduced for
504 /e/ and /i/. The post-hoc test showed there was a significant difference in all of the
505 pairwise comparisons ($p < 0.02$) consistently in the three response intervals R1, R2-1 and
506 R4. In the comparison of the three articulatory manners we observe that the
507 displacements in whispering and voicing conditions were consistently smaller than those
508 in the posturing condition in the initial part of the perturbation response (interval R1) [F
509 $(2,182) = 24.01, p < 0.001]$. There was no reliable difference between voicing and
510 whispering ($p > 0.9$). A similar tendency in the difference between the voicing and
511 whispering manners and the posturing manner was also found in the earlier phase of
512 compensatory movement [$F(2,182) = 4.823, p < 0.01]$. In R4, the averaged values
513 showed a similar tendency although no difference was found across the three articulatory
514 manners [R4: $F(2,182) = 1.774, p > 0.15]$.

515 Finally, we found a significant difference according to the sensor location on the
516 tongue [$F(2,182) = 26.22, p < 0.001$] in R1 (bottom panel in Fig. 3B). The displacement
517 in the tongue blade (TB) was not different from the one in the tongue dorsum (TD) ($p >$
518 0.9), whereas the displacement in tongue tip (TT) was smaller than the other two ($p <$
519 0.001 in both). This was also seen when the perturbation was removed [R4: $F(2,182) =$
520 $22.74, p < 0.001$], and a modest difference was found in R2-1, [$F(2,182) = 2.384, p =$
521 0.09]. The small movement amplitude of the TT sensor does not seem to be due to
522 contact with the teeth, since it was observed both in the forward and backward direction
523 after the onset and the offset of the perturbation.

524

525 *Formant patterns in speech sounds*

526 The changes in tongue shape due to the tongue perturbation also resulted in
527 changes in the produced sounds. Particularly, a compensation for the perturbation in the
528 space of the first three formants was observed in relation with the amount of
529 compensatory movement. Figure 5 represents the temporal pattern of the three formants
530 averaged across the participants. Triangles represent the times at the key points in the
531 horizontal movement as mentioned above (dashed and dotted lines on Figure 2), with the
532 first triangle corresponding to the end of interval R1 and the beginning of interval R2.
533 The acoustic impact of the perturbation varied across vowels. The peak changes occurred
534 at the onset of the reflex-like compensatory movement (second triangle corresponding to
535 the beginning of interval R2-2). The largest changes were induced during the production
536 of the vowel / ϵ /.

537 For vowel /ε/, the changes at the first negative peak were significant for F1 and F3
538 ($p < 0.005$ for both), but not in F2 ($p > 0.3$). Those were significantly reduced at the peak
539 displacement of the compensatory response (third triangle corresponding to the end of
540 interval R2-2; $p < 0.03$ for F1 and $p < 0.002$ for F3), although their frequencies were still
541 significantly different from their values at the perturbation onset ($p < 0.003$ for F1 and p
542 < 0.05 for F3). When the perturbation was removed, the changes between the fourth and
543 fifth triangles were induced again in F1 and F3 ($p < 0.03$ for F1 and $p < 0.002$ for F3). For
544 vowel /e/, the initial change due to the perturbation was induced in all three formants (F1:
545 $p < 0.05$, F2: $p < 0.002$, F3: $p < 0.005$). At the end of the compensatory response R2 (third
546 triangle), the changes in F1 and F3 were significantly reduced (F1: $p < 0.01$, F3:
547 $p < 0.0001$) with no reliable difference from their original frequencies ($p > 0.1$ for F1 and
548 $p > 0.4$ for F3). On the contrary, the compensatory movement did not reduce the
549 alteration of the second formant induced by the perturbation ($p > 0.6$), which remained
550 even after the removal of the perturbation. The removal of the perturbation changed F1 (p
551 < 0.01) and F3 ($p < 0.001$), but not F2 ($p > 0.2$). For vowel /i/, the initial change was
552 induced in F1 and F2, but not in F3. Those formants returned to their original values at
553 the perturbation onset by the compensatory response.

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

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

564

565 ***Simulation with the biomechanical model: effect of the reflex gain***

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

574 We then tested how the compensatory response changed depending on changes in
575 reflex gain. Figure 6A shows the temporal pattern of horizontal displacement in
576 simulation with several reflex gains ranging from 0 to 10 times the gain in the original
577 tongue model. Change in reflex gain affected the responses to the perturbation. The
578 strongest consequence was observed in the amplitude of the compensatory response
579 corresponding to interval R2 in the experimental data. The largest response was obtained
580 with the largest reflex gain ($k = 10$). On the other hand, when the gain was set to zero,
581 which corresponds to the situation where the tongue responded with its passive stiffness
582 only, the compensatory response was not observed. This finding supports the idea that the

583 compensatory response is not driven by a passive component alone, but by an additional
584 neural feedback mechanism, possibly by a reflex arc. Figure 6D displays the
585 compensatory amplitudes in each observed location on the tongue contour. The amplitude
586 of TT was smaller than the other two, TB and TD and the amplitudes of TB and TD were
587 almost the same. This simulated variation across the locations on the tongue was similar
588 to our behavioral observations under posturing condition (right panel in Fig. 4). In the
589 current simulations, the reflex gain was set to the same value in all the tongue muscles.
590 The differences between the results of our simulations and the experimental observations
591 in speaking condition suggest that our subjects could have regulated the reflex gain
592 specifically in each muscle to achieve the stability requirement of the speech production
593 tasks.

594 The simulated muscle activation patterns are shown in Figure 7. The model has
595 seven tongue muscles (GGp: Posterior genioglossus, GGa: Anterior genioglossus, Hyo:
596 Hyoglossus, Sty: Styloglossus, SupLongi: Superior longitudinalis, IntLongi: Inferior
597 longitudinalis, and Vert: Verticalis). Figure 7A represents the temporal patterns of the
598 changes in muscle activations after the perturbation. The values represent relative
599 changes from the baseline activations in the tongue posture at the perturbation onset with
600 various amplitudes of the reflex gain. The top panel is a magnified view of the
601 corresponding tongue blade (TB) displacements that is already shown in Figure 6A.
602 Figure 7B showed the baseline activation levels in tongue posture of vowel /e/ reached at
603 the perturbation onset.

604 In these four muscles, we found that the activation of the styloglossus and the
605 posterior genioglossus was most affected by the perturbation, while the activation of the

606 anterior genioglossus and the inferior longitudinalis changes relatively little. The
607 styloglossus muscle showed excitatory patterns of activation, while the posterior
608 genioglossus showed inhibitory pattern of activation in contrast. These observations are
609 consistent with the fact that the forward displacement of the tongue due to the
610 perturbation caused an elongation of the fibers of the styloglossus, which increases the
611 difference between the actual fiber length and the corresponding threshold muscle
612 command λ , and a decrease in the length of the fibers of the posterior genioglossus,
613 which reduces the difference between the actual fiber length and the corresponding λ
614 command. As a result, styloglossus activation increases and pulls the tongue backward in
615 order to change the fiber length back to a value closer to the λ command, and the
616 activation of the posterior genioglossus is reduced. Although there were reflex activations
617 in the hyoglossus and verticalis, this effect is small because, due to their orientation in the
618 tongue, their fibers were less impacted by the forward displacement of the tongue.

619 We also found differences between recorded and simulated responses in the mid-
620 sagittal plane. Figure 6B shows the simulated trajectory in the sagittal plane. As in the
621 recorded data, the tongue was moved horizontally by the perturbation force. Then the
622 compensatory response was induced in the direction of the original position. After the
623 release of the perturbation force, the tongue almost returned to the original location.
624 Contrary to our experimental observations, the simulated compensatory response did not
625 induce the tongue to recover its original contour, but rather to return directly to its
626 original shape at the perturbation onset.

627 We examined the amplitude of the initial displacement immediately after the
628 perturbation (interval R1 in the experimental data) at three tongue sites (TT, TB and TD)

629 (Figure 6C). The largest amplitude was seen in TB, where the perturbation was applied.
630 The displacements in TT and TD were almost the same and they were smaller than in TB.
631 These differences could originate in the fact that the tongue model includes an isotropic
632 account of tongue biomechanics (see Nazari et al. 2013, for a more realistic account).

633

634 **Discussion**

635 The current study enabled the first observation of a rapid compensatory response
636 in the tongue induced by an external mechanical perturbation. The mathematical
637 stimulations using a 2D biomechanical model of the tongue strongly support the
638 hypothesis of the existence of a reflex mechanism by showing that a sequence of
639 compensatory responses similar to the one observed experimentally can be reproduced
640 with a reflex arc. In addition, the reflex-like part of the simulated compensatory response
641 was systematically modified in vowel posturing depending on the task. More specifically,
642 the anterior part of the tongue showed greater amplitudes of the compensatory response
643 in the speaking tasks than in the posturing task. In contrast, the posterior part of the
644 tongue showed a smaller response in the speaking tasks. Speaking requires more precise
645 control to maintain the target tongue contour. Our experimental observations also suggest
646 that the control of the tongue for vowel production does not aim at producing a specific
647 tongue position, but rather at preserving the shape of tongue contour in the region close to
648 the palate. These compensatory movements changed the formant patterns of the perturbed
649 speech signal and enable recovering formant patterns that were closer to the original
650 ones. As an additional finding, the current study quantitatively demonstrated the
651 empirically known fact that tongue stiffness can be changed according to the vowel and

652 the articulatory manner, and that it influences the stability of the tongue posture. The
653 limited number of subjects (nine) included in this experiment obviously calls for some
654 caution in relation to these general conclusions. However, the consistency of the response
655 across all the participants and the systematic nature of the observations across repetitions
656 argue strongly for the generalization of our results.

657 Tongue motor control mechanisms have been investigated mostly based on
658 empirical observations of tongue kinematics and inspired by findings from other organs
659 such as the limb. Applying a newly developed mechanical perturbation to the tongue
660 during postural control aims at allowing the discovery of detailed clues about tongue
661 control mechanisms, such as error correction for movement and posture stabilization by
662 feedback loops, and update of feedforward commands by adaptation and learning. In the
663 current study, this approach enabled us to show, for the first time, a rapid compensatory
664 response with a strong evidence for the role of a neural feedback loop. Interestingly in
665 our experiment, this feedback control does not seem to preserve the exact tongue posture,
666 but to preserve the shape of the tongue contour, which is crucial for vowel production.
667 Such a feedback mechanism is difficult to predict from the generalization of control
668 mechanisms observed in skeletal systems, in which restoring the original position is the
669 basis of postural control. This flexibility (or redundancy) may be a special feature of
670 tongue posture control due to the muscular hydrostat system. As a possible mechanism, a
671 basic muscle tonus of the genioglossus, which is the largest muscle in the tongue
672 musculature (Takemoto 2001), may be involved in the stabilization of the original tongue
673 contour. Due to the fan-like orientation of the fibers of the genioglossus, this basic tonus
674 applies a main stress that acts in the direction to the tongue root for maintaining the

675 tongue posture in usual situations and this may largely contribute in the studied
676 compensatory movement to maintain the same tongue contour as before the perturbation.
677 The compensatory nature can also fit to the task demand to maintain a specific shape of
678 the tongue contour for the production of a variety of vowel sounds.

679 The observed compensatory responses worked to recover the auditory
680 characteristics (formant patterns) of the original sound. This is consistent with previous
681 experimental observations such as those of Gay et al. (1981) in which a bite-block was
682 used to perturb subjects during the articulation of English vowels resulting in
683 compensation strategies that preserved the shape of the vocal tract constriction. This
684 recovering of the original contour could be guided by a voluntary compensation
685 mechanism. Since voluntary reactions involve a cortical processing and a decision
686 process, the resultant latency for voluntary compensation is typically long. Previous
687 studies demonstrated that the reaction time of muscle activation in response to external
688 stimulations was 150 ± 13 ms in the jaw (Ottenhoff et al. 1992), 315.7 ± 98.4 ms in lips (Ito
689 et al. 2005) and 154 ms in fingers (Cole and Abbs 1987). The compensatory response
690 observed in our study was induced less than 100 ms after the perturbation onset, for the
691 first phase of the response (R2-1) and 140 ms after the perturbation for the second phase
692 (R2-2). Considering muscle contraction delays from muscle activation onset to force
693 generation (Ito et al. 2004; Mannard and Stein 1973) and the duration of the mechanical
694 response from force generation to the onset of movement, we established that the
695 latencies measured in the current compensatory responses were shorter than the latencies
696 of voluntary reaction observed in former studies. Accordingly, we conclude that the

697 current compensatory response does not result from a voluntary action, but from other
698 faster mechanisms.

699 Given the findings in Gomi et al (2002), these faster mechanisms can be driven by
700 passive mechanical properties and by reflexes. These two mechanisms are distinguished
701 based on response latency. Mechanical response is the fastest response, which can be
702 induced just after the movement change by the perturbation. We have assumed that the
703 articulatory manner (voicing, whispering, posturing) can be controlled depending on the
704 adjustment of mechanical properties, such as stiffness and viscosity (Burdet et al. 2001;
705 Gomi et al. 2002; Gomi and Osu 1998). A reflex response occurs after the passive
706 response due to neural transmission delays (Gomi et al. 2002). Depending on the pathway
707 of neural feedback, such as via the brainstem or up to the cortex, there are several
708 possible response latencies (Ito et al. 2005; McClean 1991). In our experimental data, we
709 found an inflection point during compensatory response that corresponds to the
710 acceleration peak around 140 ms after the perturbation onset. We interpreted this
711 inflection point in displacement as the point of initiation of a reflex response, which
712 means that the remaining part of the compensatory response (R2-2 interval in the right
713 panel of Figure 2) was driven by reflex mechanisms. Our mathematical simulation
714 supports this idea because the change in reflex gain in the model induced significant
715 changes of the amplitude of the compensatory response. In the orofacial system, cortical
716 reflexes have been shown to be involved in compensatory responses in the lips, with lip
717 muscle responses occurring 47.5ms (\pm 27.5ms) after perturbation of the jaw, with the
718 corresponding change in movement observed 100 ms after the perturbation onset (Gomi
719 et al. 2002). Since the latency of the kinematic compensatory response in our experiment

720 was longer than the one observed in lip adjustments due to cortical reflex in jaw
721 perturbation studies, a cortical reflex could also be involved in the response of our
722 subjects.

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

739 The current study can provide a direct clue about stiffness variations of the tongue
740 during speech production. By using a robotic device, we consistently applied the same
741 amount of force to the tongue in the three vowel articulations (/i/, /e/, and /ε/) and in the
742 three articulatory manners (voicing, whispering and posturing). Comparing the vowel

743 articulation, the smallest displacement due to the perturbation was induced in the
744 articulation of /i/ and the displacement was increased from /e/ to /ɛ/. This is consistent
745 with the previous findings described in the Introduction. The current study
746 experimentally examined the variation of tongue stiffness depending on the requirements
747 of speech utterances. Changes in tongue stiffness also explain the differences observed
748 across articulatory manners. We found that the displacement induced by the force
749 perturbation was smaller in the voicing and whispering conditions than in the posturing
750 condition. This indicates that intrinsic tongue mechanical stiffness was larger when the
751 subjects were actually producing speech sounds, and suggests that speech production
752 requires a larger amount of muscle activation. Since we do not find any difference
753 between voicing and whispering condition, the activation level of tongue muscles seems
754 not to be reliably affected by the simultaneous involvement of vocal fold vibrations.
755 Taken altogether these findings support the idea that the stiffness of the tongue can be
756 modified depending on the vowel and on the articulatory manner. Interestingly, response
757 patterns in the R2-2 interval were different from the response patterns in all the others
758 R1, R2-1 and R4 intervals; this result also supports the idea that the compensatory
759 response in R2-2 was not driven by a passive component, but rather by neural feedback
760 loop, such as a reflex.

761 Stiffness can also be different between anterior and posterior parts of the tongue.
762 We found that displacement due to the passive component of the perturbation response
763 was different across sensor locations on the tongue (TT, TB and TD). While TB and TD
764 responded with a similar amplitude of displacement, TT was smaller than the others. The
765 results indicate that the passive stiffness of the tissue connecting TB and TD is high

766 enough to synchronize their movements, while the stiffness of the connection between
767 TB and TT is relatively low. Accordingly, the passive mechanical characteristics of the
768 tongue may not be homogeneous in the tongue body. Investigating mechanical properties
769 of the tongue body is difficult because those properties may be different in tests carried
770 out on cadavers and in living subjects due to basic muscle tonus. Applying a mechanical
771 stretch to the several different sites during the same task is one way to further investigate
772 the mechanical properties of the tongue body in detail.

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

783 In speech motor control, auditory feedback can also be a possible loop to induce
784 compensatory movements together with somatosensory feedback (Houde and Jordan
785 1998; Lametti et al. 2012). In previous studies (Larson et al. 2000; Purcell and Munhall
786 2006), the onset of auditory compensation was found to be more than 200 ms after the
787 perturbation onset when a sustained vowel was perturbed at a certain time in pitch or
788 formant due to altered auditory feedback, which is a situation similar to the one in the

789 current study. In Purcell and Munhall (2006), when the first formant was suddenly shifted
790 by 136 Hz on average at a certain time during the sustained vowel production, the
791 auditory perturbation was gradually compensated from around 300 ms after the
792 perturbation onset, and the amplitude of compensation reached more than 20 Hz at 800
793 ms after the perturbation onset (approx. 15% of compensation). This manner of
794 compensation is different from the findings of our study, in which the acoustic changes
795 induced by the tongue perturbation were immediately compensated at the latest 300 ms
796 after the perturbation onset, without any gradual compensation afterwards. In addition,
797 the maximum change of the first formant induced by the tongue perturbation during the
798 production of /ε/ was approximately 55 Hz on average across subjects, which is about
799 half of Purcell and Munhall's acoustical perturbation. In contrast, the magnitude of the
800 compensation in the tongue perturbation was 27 Hz on average, which corresponds to
801 approximately 50% of the magnitude of the initial formant change. Thus, larger amounts
802 of acoustical compensation were achieved in our study than in the case of auditory
803 perturbation. Considering that the acoustical change was synchronized with the
804 compensatory movement in the tongue, we believe that the current compensation is
805 induced predominantly by somatosensory error rather than auditory error. In addition, the
806 auditory error that remained after the first compensatory response (i.e. after 250 ms) in
807 the production of /ε/ was not further compensated. Since the sound in perturbed condition
808 was still in the perceptual range of vowel /ε/, this acoustical error may be ignored to be
809 corrected, as opposed to the somatosensory error. The auditory error accompanying the
810 articulatory perturbation, as in the current study, may be easily compensated by simply
811 compensating for the articulatory changes. On the contrary the auditory error that occurs

812 with unperturbed articulation, such as in altered auditory feedback, may be difficult to
813 compensate for probably due to a conflict between auditory and somatosensory
814 requirements (Katseff et al. 2012; Lametti et al. 2012; Patri et al. 2019).

815 Although the previous studies (Larson et al. 2000; Purcell and Munhall 2006)
816 showed that the compensatory response via auditory feedback is longer than 200 ms, Cai
817 et al. (2011) also reported a relatively faster auditory compensation (approx. 120 ms).
818 Since this latency is comparable to the one in the current compensatory response,
819 auditory feedback may be involved in the production of the current compensatory
820 movement. Different from the current situation where the perturbation was applied during
821 the static articulation of the vowels, as it was in Larson et al. (2000) and Purcell and
822 Munhall (2006), Cai et al. (2011) applied auditory perturbation in a dynamical manner
823 since the first formant was altered during the production of a vowel-to-vowel gesture.
824 The arm motor control studies suggested that the latency of compensation to sensory
825 errors can be different between dynamical and static motor situations. The changes of
826 muscle activation by reflexes in response to a force perturbation occur with a longer
827 latency during a static posturing (80 ms, Soechting and Lacquaniti 1988)), than during a
828 movement (40 ms, Soechting (1988)). This suggests that the response via auditory
829 feedback in static situation can take longer than the 120 ms latency found in Cai et al.
830 (2011), and that the response to the current compensatory response occurred sufficiently
831 early to reject the possibility that it would be due to auditory feedback. We conclude that
832 the possible involvement of auditory feedback is unlikely in the compensation observed
833 in our study.

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

844

845

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References

Badin P, Bailly G, Reveret L, Baciú M, Segebarth C, Savariaux C. Three-dimensional linear articulatory modeling of tongue, lips and face, based on MRI and video images. *J Phon* 30: 533–553, 2002.

Beckman ME, Jung T, Lee S, de Jong K, Krishnamurthy AK, Ahalt SC, Cohen KB, Collins MJ. Variability in the production of quantal vowels revisited. *J Acoust Soc Am* 97: 471–490, 1995.

Brunner J, Hoole P, Perrier P. Adaptation strategies in perturbed /s/. *Clin Linguist Phon* 25: 705–24, 2011.

Buchillard S, Perrier P, Payan Y. A biomechanical model of cardinal vowel production: muscle activations and the impact of gravity on tongue positioning. *J Acoust Soc Am* 126: 2033–51, 2009.

Burdet E, Osu R, Franklin DW, Milner TE, Kawato M. The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature* 414: 446–449, 2001.

Cai S, Ghosh SS, Guenther FH, Perkell JS. Focal manipulations of formant trajectories reveal a role of auditory feedback in the online control of both within-syllable and between-syllable speech timing. *J Neurosci* 31: 16483–90, 2011.

Cole KJ, Abbs JH. Kinematic and electromyographic responses to perturbation of a rapid grasp. *J Neurophysiol* 57: 1498–510, 1987.

Cooper S. Muscle spindles in the intrinsic muscles of the human tongue. *J Physiol* 122: 193–202, 1953.

Feldman AG. Once more on the equilibrium-point hypothesis (lambda model) for motor control. *J Mot Behav* 18: 17–54, 1986.

Fowler CA, Turvey MT. Immediate compensation in bite-block speech. *Phonetica* 37: 306–26, 1981.

Gay T, Lindblom B, Lubker J. Production of bite-block vowels: acoustic equivalence by selective compensation. *J Acoust Soc Am* 69: 802–10, 1981.

Gick B, Allen B, Roewer-Després F, Stavness I. Speaking Tongues Are Actively Braced. *J Speech Lang Hear Res* 60: 494–506, 2017.

Gomi H, Ito T, Murano EZ, Honda M. Compensatory articulation during bilabial fricative production by regulating muscle stiffness. *J Phon* 30: 261–279, 2002.

Gomi H, Osu R. Task-dependent viscoelasticity of human multijoint arm and its spatial characteristics for interaction with environments. *J Neurosci* 18: 8965–8978, 1998.

- Gottlieb GL, Agarwal GC.** Compliance of single joints: elastic and plastic characteristics. *J Neurophysiol* 59: 937–951, 1988.
- Honda M, Kaburagi T, Fujino A.** Compensatory responses of articulators to unexpected perturbation of the palate shape. *J Phon* 30: 281–302, 2002.
- Hoole P, Zierdt A.** Five-dimensional articulography. *Speech Motor Control: New Developments in Basic and Applied Research*, 2010.
doi:10.1093/acprof:oso/9780199235797.003.0020.
- Houde JF, Jordan MI.** Sensorimotor adaptation in speech production. *Science* 279: 1213–6., 1998.
- Ito T, Gomi H.** Cutaneous mechanoreceptors contribute to the generation of a cortical reflex in speech. *Neuroreport* 18: 907–10, 2007.
- Ito T, Kimura T, Gomi H.** The motor cortex is involved in reflexive compensatory adjustment of speech articulation. *Neuroreport* 16: 1791–4, 2005.
- Ito T, Murano EZ, Gomi H.** Fast force-generation dynamics of human articulatory muscles. *J Appl Physiol* 96: 2318–24; discussion 2317, 2004.
- Katseff S, Houde J, Johnson K.** Partial compensation for altered auditory feedback: a tradeoff with somatosensory feedback? *Language and speech* 55: 295–308, 2012.
- Keating PA.** The window model of coarticulation: articulatory evidence. In: *Papers in Laboratory Phonology*. Cambridge University Press, 1990, p. 451–470.
- Kelso JAS, Tuller B, Vatikiotis-Bateson E, Fowler CA.** Functionally specific articulatory cooperation following jaw perturbations during speech: evidence for coordinative structures. *J Exp Psychol Hum Percept Perform* 10: 812–832, 1984.
- Kier WM, Smith KK.** Tongues, tentacles, and trunks: The biomechanics of movement in mucular-hydrostats. *Zool J Linn Soc* 83: 307–324, 1985.
- Lametti DR, Nasir SM, Ostry DJ.** Sensory preference in speech production revealed by simultaneous alteration of auditory and somatosensory feedback. *J Neurosci* 32: 9351–8, 2012.
- Larson CR, Burnett TA, Kiran S, Hain TC.** Effects of pitch-shift velocity on voice F0 responses. *J Acoust Soc Am* 107: 559–64, 2000.
- MacNeilage PF.** Motor control of serial ordering of speech. *Psychol Rev* 77: 182–196, 1970.
- Mannard A, Stein RB.** Determination of the frequency response of isometric soleus muscle in the cat using random nerve stimulation. *J Physiol* 229: 275–296, 1973.

- Marsden CD, Merton PA, Morton HB.** Servo action in human voluntary movement. *Nature* 238: 140–3, 1972.
- McClellan MD.** Lip muscle reflex and intentional response levels in a simple speech task. *Exp Brain Res* 87: 662–70, 1991.
- McFarland DH, Baum SR, Chabot C.** Speech compensation to structural modifications of the oral cavity. *J Acoust Soc Am* 100: 1093–104, 1996.
- Nazari MA, Perrier P, Chabanas M, Payan Y.** Shaping by stiffening: a modeling study for lips. *Motor Control* 15: 141–168, 2011.
- Nazari MA, Perrier P, Payan Y.** The distributed lambda (λ) model (DLM): a 3-D, finite-element muscle model based on Feldman's λ model; assessment of orofacial gestures. *J Speech Lang Hear Res* 56: S1909-1923, 2013.
- Neilson PD, Andrews G, Guitar BE, Quinn PT.** Tonic stretch reflexes in lip, tongue and jaw muscles. *Brain Res* 178: 311–27, 1979.
- Ottenhoff FA, van der Bilt A, van der Glas HW, Bosman F.** Peripherally induced and anticipating elevator muscle activity during simulated chewing in humans. *J Neurophysiol* 67: 75–83, 1992.
- Patri J-F, Diard J, Perrier P.** Optimal speech motor control and token-to-token variability: a Bayesian modeling approach. *Biol Cybern* 109: 611–626, 2015.
- Patri J-F, Diard J, Perrier P.** Modeling Sensory Preference in Speech Motor Planning: A Bayesian Modeling Framework. *Front Psychol* 10, 2019.
- Payan Y, Perrier P.** Synthesis of V-V sequences with a 2D biomechanical tongue model controlled by the Equilibrium Point Hypothesis. *Speech Commun* 22: 185–205, 1997.
- Perkell JS, Cohen MH, Svirsky MA, Matthies ML, Garabieta I, Jackson MT.** Electromagnetic midsagittal articulometer systems for transducing speech articulatory movements. *J Acoust Soc Am* 92: 3078–3096, 1992.
- Perkell JS, Nelson WL.** Variability in production of the vowels /i/ and /a/. *J Acoust Soc Am* 77: 1889–1895, 1985.
- Perrier P, Payan Y, Zandipour M, Perkell J.** Influences of tongue biomechanics on speech movements during the production of velar stop consonants: a modeling study. *J Acoust Soc Am* 114: 1582–99, 2003.
- Pruszynski JA, Scott SH.** Optimal feedback control and the long-latency stretch response. *Exp Brain Res* 218: 341–359, 2012.
- Purcell DW, Munhall KG.** Compensation following real-time manipulation of formants in isolated vowels. *J Acoust Soc Am* 119: 2288–97, 2006.

- Rabiner LR, Schafer RW.** *Digital processing of speech signals.* Prentice-Hall, 1978.
- Savariaux C, Perrier P, Orliaguet JP.** Compensation Strategies for the Perturbation of the Rounded Vowel [U] Using a Lip Tube - a Study of the Control Space in Speech Production. *J Acoust Soc Am* 98: 2428–2442, 1995.
- Schmidt RA, Lee TD.** *Motor Control And Learning: A Behavioral Emphasis.* Human Kinetics, 2005.
- Soechting JF.** Effect of load perturbations on EMG activity and trajectories of pointing movements. *Brain Res* 451: 390–396, 1988.
- Soechting JF, Lacquaniti F.** Quantitative evaluation of the electromyographic responses to multidirectional load perturbations of the human arm. *J Neurophysiol* 59: 1296–1313, 1988.
- Stål P, Marklund S, Thornell LE, De Paul R, Eriksson PO.** Fibre composition of human intrinsic tongue muscles. *Cells Tissues Organs* 173: 147–61, 2003.
- Stone M, Lundberg A.** Three-dimensional tongue surface shapes of English consonants and vowels. *J Acoust Soc Am* 99: 3728–3737, 1996.
- Takemoto H.** Morphological analyses of the human tongue musculature for three-dimensional modeling. *J Speech Lang Hear Res* 44: 95–107, 2001.
- Westbury JR.** *X-Ray Microbeam Speech Production Database User's Handbook.* Waisman Center on Mental Retardation & Human Development, 1994.
- Whalen DH, Iskarous K, Tiede MK, Ostry DJ, Lehnert-Lehouillier H, Vatikiotis-Bateson E, Hailey DS.** The Haskins optically corrected ultrasound system (HOCUS). *J Speech Lang Hear Res* 48: 543–53, 2005.
- Xing F, Woo J, Murano EZ, Lee J, Stone M, Prince JL.** 3D tongue motion from tagged and cine MR images. *Med Image Comput Comput Assist Interv* 16: 41–48, 2013.

Figure Legends

Figure 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 reference makers (nasion, right and left mastoid and upper incisor)]. B: the view of tongue surface representing the locations of EMA sensors (TT, TB and TD) and anchor points for the tongue perturbation (TP). C: Schematic view of the 2D tongue model. The nodes on the tongue surface are numbered from 1 (tongue root) to 16 (tongue tip). The nodes, 11, 13 and 16 were chosen as the corresponding location of measured sensors (TD, TB, and TT, respectively). The four 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 is in light blue. The bold thick line (styloglossus in black and posterior genioglossus in gray) represents macrofibers and the shaded area represents the elements whose mechanical stiffness was changed by muscle activation.

Figure 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). The shaded area represents the standard error across the subject. The vertical dashed and dotted lines represent remarkable inflection points in the trajectory that was detected in TB. B: The magnified view of the horizontal displacement, horizontal velocity and horizontal acceleration in

TB. The time range corresponds to the range shown with the thick horizontal bar in A. The vertical lines also correspond to the ones in A.

Figure 3: A: Trajectory of tongue blade (TB) displacement due to the perturbation from the onset of the perturbation (circle mark) to the offset (x mark) in voicing condition. Each line represents three vowel conditions. * marks represent a detected local peak of the movement. + marks represent acceleration peaks during compensatory response. The estimated tongue surfaces in each vowel condition are superimposed as gray lines. B: Averaged displacements in each phase. Top panel: grouping according to the vowels; Middle panel: grouping according to articulatory manners; Bottom panel: grouping according to the sensor locations. Error bars represent standard error.

Figure 4: Displacements of compensatory response (R2-2 in Figure 2). Error bars represent standard error.

Figure 5: Temporal patterns of the first, second and third formants in speech sounds. Triangles represent the temporal points corresponding to the inflection points in displacement, which is represented as the vertical line in Figure 2. The shaded area represents the standard error across participants.

Figure 6: Simulated results. A: time response in horizontal displacement of TB with each reflex gain. The 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: The

peak displacement of R1 in three tongue sites (TT, TB and TT). D: The peak amplitude of compensatory response (R2) in three tongue sites.

Figure 7: Simulated results. A: time response of muscle activation level. The amplitude of muscle activation was represented in local unit of the simulation. B: base line muscle activity for the production of /e/ in simulation.













