Motor compensation, not sensory error, regulates sensorimotor adaptation in human vocal pitch production in continuous speech

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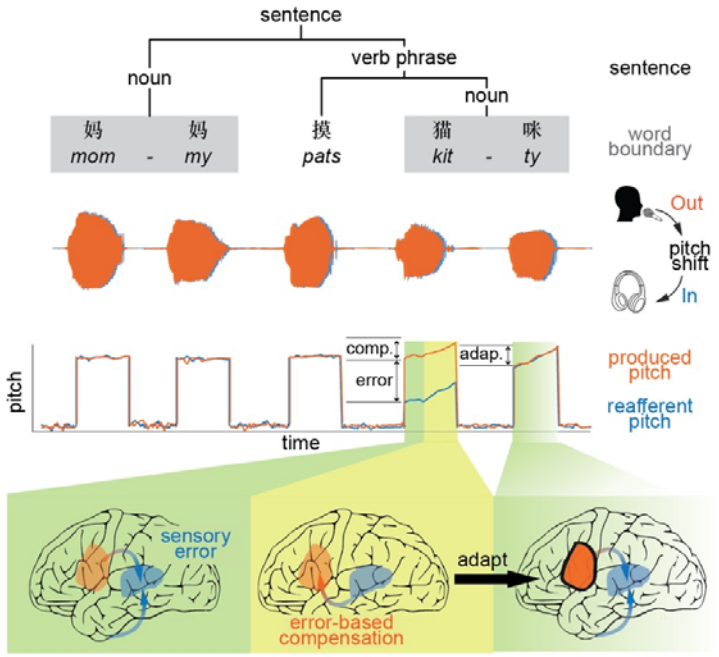
Abstract

Motor control is essential for organisms to efficiently interact with the external world by maintaining accuracy and precision of actions and adapting to changes in the future. For example, speaking, one of the most complicated scenarios of motor control, utilizes sensory errors and resultant motor compensation to precisely control articulation. However, how sensory errors and compensations regulate subsequent production remains in debate. Here, we implemented a serial-dependence paradigm by randomly perturbing the pitch of auditory feedback in a sequence of trials to dissociate the effects of sensory errors and motor compensation in controlling continuous speech. We found that motor compensation in preceding trials, rather than sensory errors, affected the compensatory responses in the current trial. Critically, this compensation-driven adaptation remained across speaking of different vowels but only when adjacent vowels were embedded within the word boundary. The study provides ecologically valid evidence supporting that error-based motor compensation, incorporating cognitive constraints, regulates adaptive changes in successive actions.

Graph abstract



Motor compensation, not sensory error, influences behavioral changes in next utterance only within word boundary.

Introduction

The accuracy and precision of motor output, as results of efficient interplay among motor, sensory and cognitive systems, are crucial for human survival and social interactions [1-3]. In the domain of speaking, for example, the control of articulators relies on real-time integration among the language system, speech motor system and sensory feedback from the external environment [4-7]. Specifically, the brain anticipates the sensory consequences of articulatory movements via the mechanisms of internal forward models [8-13], continuously compares the sensory predictions to actual somatosensory and auditory feedback, and adjusts articulation by correcting any sensory errors in either domain [14, 15]. Extended from the instant computation of the speech motor control, within-trial perturbation and its resultant motor compensation can adapt to the next-trial production [16-18], suggesting a fast, trial-to-trial recalibration for successive production.

It remains heavily debated how the preceding speech motor control regulates the subsequent speech production. One hypothesis suggests that error-based motor compensation is incorporated into the feedforward motor program for future speech productions, driving learning and adaptation to reduce future errors [17, 19, 20]. Supporting this compensation-driven adaptation hypothesis, studies on reaching suggest that motor response to error serves as a template that updates motor commands for improved performance [21] ; in speech production, a weak correlation was observed between compensation to formant perturbations and adaptation in the next trial [18]. Alternatively, another hypothesis posits that sensory errors are integrated into the internal model, which predicts future sensory consequences of motor actions and guides subsequent movements [5, 22-24]. Saccadic and reaching studies have shown that adaptation can still occur even when sensory errors are presented with minimal motor compensation [25] or when errors are too rapid to allow compensation [26]. Studies on speech production emphasized the essential role of sensory error in sensorimotor adaptation [27, 28].

It is challenging, however, to dissociate the effects of sensory error and its resultant motor compensation in speech production control since they are strongly coupled. For example, speech motor adaptation studies use consistent perturbation to observe opposing compensations over trials [29]. The trends of both sensory error and motor compensation remain constant, causing their effects on the subsequent trial to overlap. To overcome this obstacle, we introduce a novel serial dependence paradigm that can dissociate the influence of previous sensory and motor responses by independently manipulating the similarity between preceding and current stimuli [c.f., 30, 31]. Furthermore, previous studies focus on speech motor control in isolated vowels or words [32, 33] whereas little is known about how linguistic contexts, such as vowel categories and syntactic structures, modulate the sensorimotor adaptation effects in more ecologically valid scenarios [34].

The study investigates how sensory error and compensation in the preceding trial regulate the adaptive changes in current vocal production, both in terms of reaction to feedback perturbation and behavioral changes in regular speaking, and how these adaptative changes were modulated across different linguistic contexts. By randomly perturbing auditory pitch

feedback during vocal production, this study dissociate the influence of sensory errors and motor compensation on the subsequent trial. Using a series of experiments involving vowel sequences and sentences, we show that preceding-trial motor compensation drives trial-to-trial adaptation across consecutive productions, but this adaptation is constrained by syntactic boundary. These results strongly suggest a direct compensation-driven learning in speech motor control.

Results

Experiment 1: Trial-to-trial adaptation in repeated production of identical vowel

In the first experiment, we used the simplest setting where participants repeatedly produced a single vowel continuously for 2.5 sec, while their auditory feedback was unexpectedly downward or upward perturbed (*N* = 14; **Fig. 1A**). Through a long sequence of trials in which six levels of perturbation amount were randomly applied to each trial (**Fig. 1B**), we can separately explore how the adaptation of the current trial depends on the sensory error and motor compensation of the immediately preceding trial. Throughout the study, we defined each within-trial perturbation and compensation as C_t and P_t, and its preceding-1-trial perturbation and compensation as C_{t-1} and P_{t-1}.

We first measured motor responses to perturbation in the current trial (i.e., the relationship between C_t and P_t). We averaged across trials with the same amount of perturbation. It demonstrated that motor compensations were opposed to the direction of pitch perturbation, started around 150 ms after the onset of the perturbation in the conditions of -300 cents, -180 cents, -60 cents, and 60 cents pitch shift (**Fig. 1C**, from left to right, respectively, *ts*(13) = 36.13, 56.36, 109.85, and -92.86, *ps* = 0.043, 0.021, 0.008, and 0.024, cluster-based permutation test), yet this effect was not significant in the condition of 180-cent and 300-cent perturbations (*ps* > 0.203). To compare conditions, we selected 150~250 ms window that was commonly used to quantify the amount of motor compensation [18, 35]. Compensation amounts were not significantly differed across upward and downward perturbations (*p* > 0.067, Friedman's chi-square test, FDR corrected).

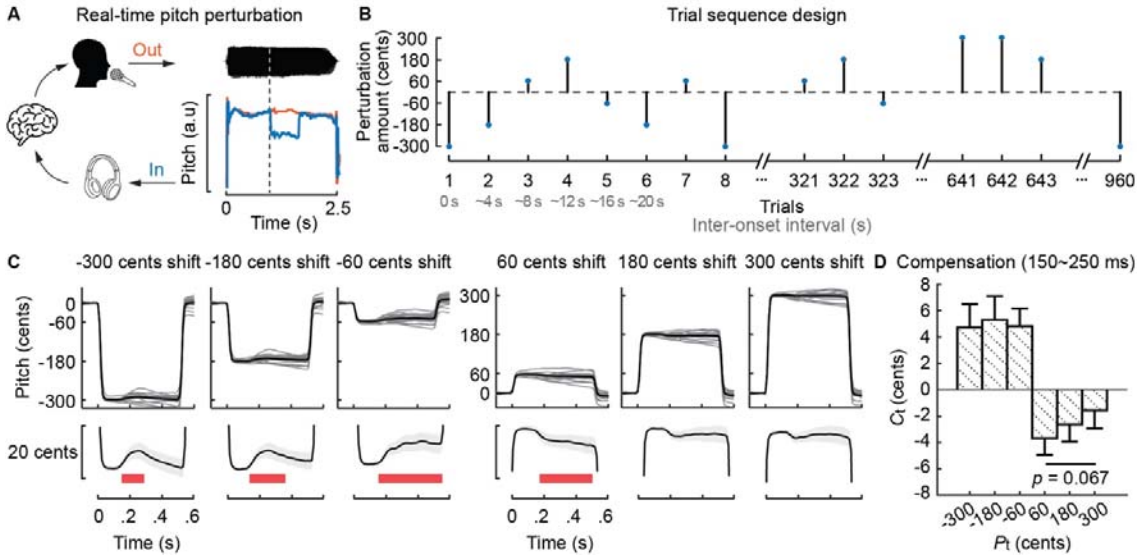


Figure 1. Motor compensation to pitch perturbation in the current trial. A, The trial procedure of pitch perturbation design. Real-time pitch perturbation during production of vowel /a/. The onset of perturbation is denoted by a dashed line. The pitch of auditory feedback sent to earphones (blue) is shifted from the original utterance recorded in the microphone (orange). **B**, The trial sequence of the experiment. Participants undergo 320 trials each day for three consecutive days. The perturbation amounts and directions are

randomly applied to each trial. **C**, Pitch traces with upward and downward perturbations and resultant compensation. The bold black lines denote the averaged pitch trace across trials for each participant (thin grey curves). Lower panels show magnified pitch traces from the above plots. The red horizontal bars denote the times of the significant effects of compensation ($p < 0.05$). **D**, Temporal averaged compensation in the periods of interest (150-250 ms after the perturbation onset). In **C** and **D**, shaded areas and error bars denote the standard error of mean (SEM) across participants. *$p < 0.05$, **$p < 0.005$.

Next, we tested the motor-compensation and sensory-error hypotheses by separately measuring the dependency of preceding-1-trial sensory error or motor compensation on its subsequent trial. Specifically, we characterized if C_t (in each trial) would follow or oppose C_{t-1} or P_{t-1} (in its preceding trial) (**Fig. 2A**). Therefore, we plotted C_t as a function of C_{t-1} and P_{t-1} - P_t, respectively, in both trial level and participant level (**Fig. 2BC**, left). The averaged data across trials and participants demonstrated that both functions yielded a derivative-of-Gaussian-shaped (DoG) curve (ps = 0.0001 for both, two-sided bootstrap, FDR corrected) (**Fig. 2BC,** right). That is, C_t in the current trial followed either C_{t-1} or P_{t-1} - P_t in the preceding trial, especially around 0; if C_{t-1} or P_{t-1} - P_t were approaching the extreme condition (far from 0), the following effect became weak. It suggested that within-trial compensation was likely to be adapted to both preceding sensory error and motor compensation. The adaptation was quantified as the height of the DoG curve (shown as grey double arrows).

Caution should be taken, however, that the adaptation effect of P_{t-1} - P_t could be merely driven by the opposing effect of P_t on C_t, as shown in **Fig. 1CD.** Therefore, we further combined trials with the same P_t to isolate the dependency of P_{t-1} on C_t. The main effect of P_{t-1} was not significant ($\chi^2(5) < 6.65$, $p > 0.247$; Friedman's chi-square test, FDR corrected), suggesting that the preceding sensory error only contributed to the instant computation for compensation, but not directly to the future production. We further built a linear mixed-effect model to assess the contribution of P_t, P_{t-1}, and C_{t-1} to the C_t. The results revealed a significantly negative coefficient of P_t and a significantly positive coefficient of C_{t-1} ($t(11,680) = -21.8$ and 3.03, p = 0.0001 and 0.004, respectively, one-sample *t*-test, FDR corrected; **Fig. 2E**). No effect was found for P_{t-1} ($t(11,680) = 1.55$, $p = 0.160$). We confirmed that C_{t-1}, but not P_{t-1}, had an adaptative change in C_t.

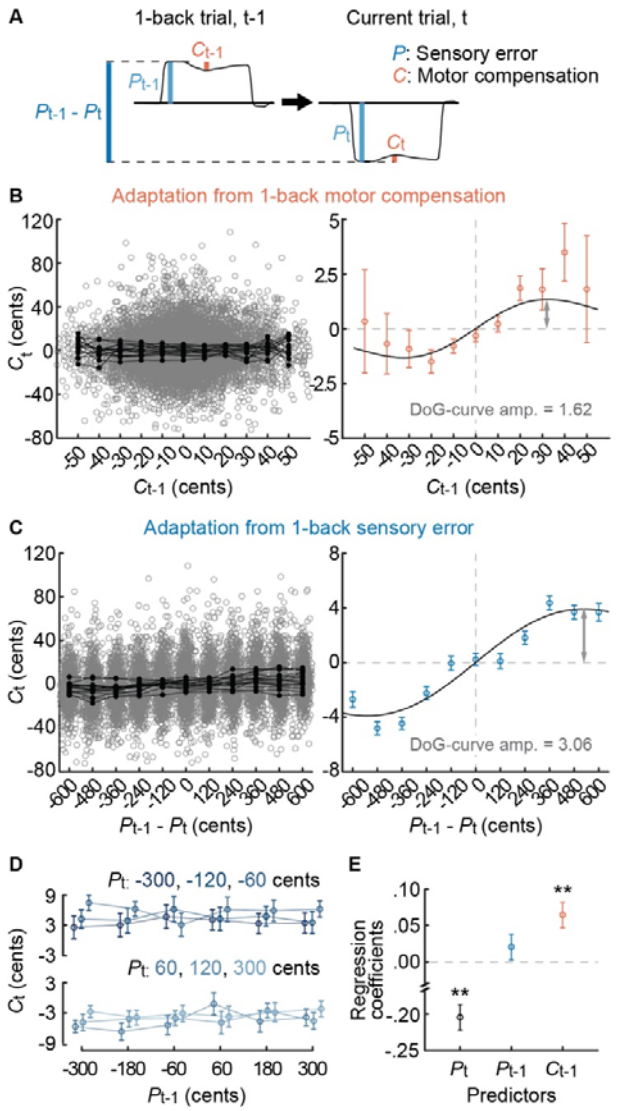


Figure 2. Adaptation of the immediately preceding trial on the compensatory responses of the current trial. A, Pitch trace of two adjacent trials. We measure the dependency of preceding sensory error and compensation on current speech production. In **B** and **C**, We plot compensation of the current trial, C_t, as a function of compensation in the immediately preceding trial, C_{t-1}, and as a function of the perturbation differences between the current and immediately preceding trial, P_{t-1} - P_t. In the left plots, each dot represents one trial and each black curve represents one participant. The right plots show the relationship between preceding and current trials after averaging across trials and participants. Color dots projecting to the same sign on the x and y axes indicate that C_t is in the same direction as C_{t-1} and P_{t-1} - P_t. **D**, C_t as a function of P_{t-1} does not show significant effects, suggesting the current compensation is not influenced by the perturbation amount of the immediately preceding trial. Error bars denote SEM across participants. **E**, The effects of current perturbation (P_t), preceding perturbation (P_{t-1}) and preceding compensation (C_{t-1}) on current compensation (C_t) revealed by a generalized linear mixed-effect model. Regression coefficients for each predictor are extracted from the model. Current perturbation and

preceding compensation exert opposite influences on the current compensation. Error bars denote SEM across trials. $^{**}p < 0.005$.

Experiment 2: Trial-to-trial adaptation across the production of different words

Speech production involved variable vowel categories and thus in Experiment 2, we explored whether the adaptation effect of C_{t-1} remained across different vowels. In a new experiment 2a, participants (N = 17) were asked to produce four different vowels that were randomly presented in each trial, i.e., 啊 (/a1/), 咿 (/i1/), 呃 (/e1/), and 哦 (/o1/). We observed a similar adaptation effect of C_{t-1} on C_t (p = 0.0001, two-sided bootstrap, FDR corrected; **Fig. 3A**), but not for the effect of P_{t-1} (**Fig. S1**). When comparing experiments 2a and 1, the amplitude of the DoG curve was significantly lower when participants produced different vowels than when they produced the same vowel (p = 0.036, two-sided bootstrap, FDR corrected; **Fig. 3C**). The reduction of adaptation can be caused by different vowels or by the uncertainty of next vowel. To exclude the latter possibility, we conducted an extra experiment 2b where the four vowels were presented in a fixed order; that is, participants would anticipate the identity of the next vowel. We found a consistent adaptation effect caused by C_{t-1} (N = 12; p = 0.0001, two-sided bootstrap, FDR corrected; **Fig. 3B**). Importantly, the amplitude of the DoG curve during fixed-order vowel production was similar to that during random-order (p = 0.307, two-sided bootstrap, FDR corrected; **Fig. 3C**), suggesting that adaptation of motor compensation was reduced due to different vowels, instead of uncertainty of next production.

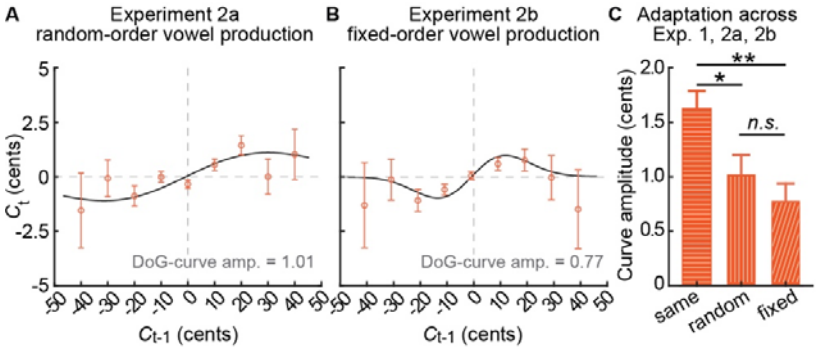


Figure 3. Adaptation effects across different vowel categories. A and **B**, C_t as a function of C_{t-1} when participants produce randomly-presented vowels (**A**) and when participants produce expectedly-presented vowels (**B**). In both experiments, significant adaptation changes to the current motor compensation are observed. **C**, The amount of compensation, characterized by the amplitude of the DoG curve shows differences between experiments 1, 2a, and 2b, where participants produce the same vowel, different vowels with uncertainty, and different vowels with certainty, respectively. The adaptation effects are weaker when producing different vowels, compared with that of the same vowels. Error bars denote one SD of the bootstrap distribution. $^{*}p < 0.05$, $^{**}p < 0.005$.

Experiment 3: inter-syllabic adaptation in the sentence production within and across word boundary

In speech production, not only did vowels change continuously, but also the syntactic

structures of sentences. In Experiment 3a and 3b (N = 15 and 13, respectively), we designed a controlled naturalistic-like sentence production paradigm to investigate whether the compensation-driven adaptation persisted within or across syntactic structures. We manipulated the auditory feedback during the continuous production of sentences at different positions of syntactic structures. During sentence production, auditory pitch perturbation was randomly applied to either the second, third, or fourth syllable in each trial (**Fig. 4AC**). We quantified compensation in the perturbed syllable and its adaptation in the next syllable, which could be within or across the word boundaries (shown as grey rectangles in insets; **Fig. 4BD**). We showed that upward pitch perturbation drove a significant compensatory response around 200 ms after perturbation onset, compared with the pitch trace without perturbation ($t(14) < -40.30$, $p < 0.009$, cluster-based permutation test; **Fig. S2**). We extracted 200-300 ms mean pitch as compensation amount in the perturbed syllable and as adaptation amount in its next syllable. Only when the two syllables formed a word, the compensation in the preceding syllable influenced the production of the current syllable (right plot in **Fig. 4B:** $r = 0.09$, $p = 0.003$; left plot in **Fig. 4D**: $r = 0.22$, $p = 1 \times 10^{-11}$; Spearman correlation). The correlation coefficients were larger in the within-word-boundary condition than in the across-word-boundary condition (**Fig. 4B**: $p = 0.180$ and 0.026 for position 2 vs 4 and for position 3 vs 4, respectively; **Fig. 4D**: $p = 0.010$ and 0.0005 for position 2 vs 3 and for position 2 vs 4, respectively; one-sided bootstrap, FDR corrected). These results strongly suggested that inter-syllabic adaptation of motor compensation was constrained by word boundary.

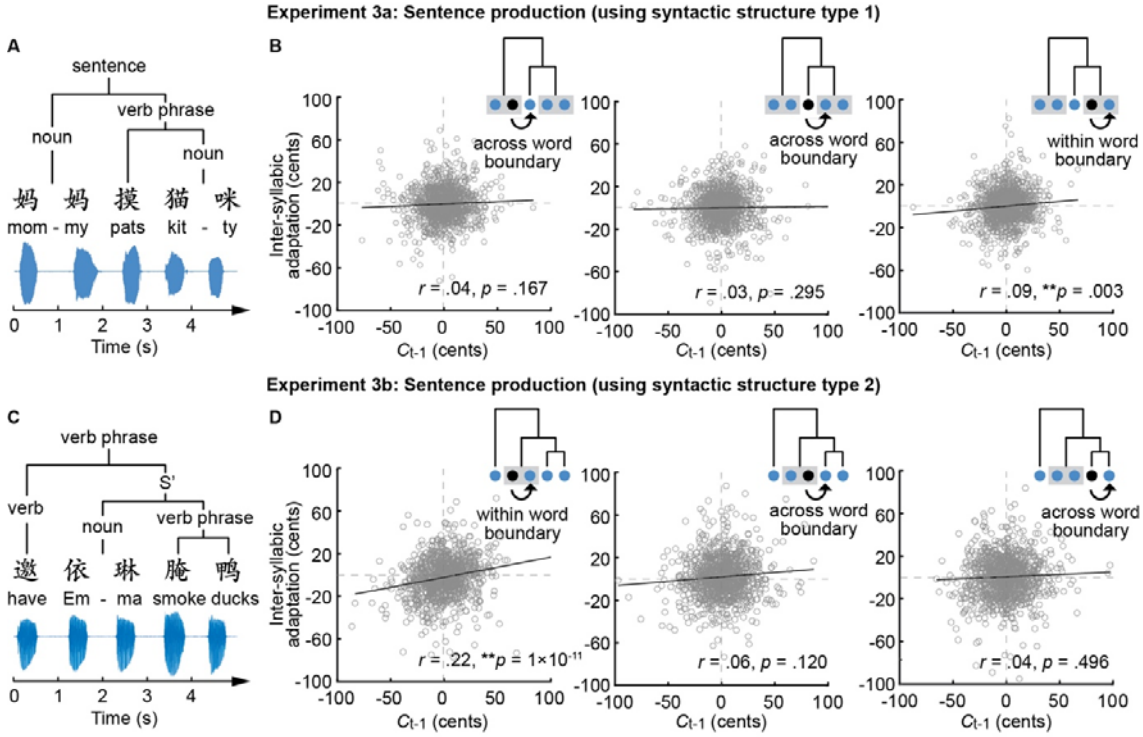


Figure 4. Inter-syllabic adaptation persists only within the word boundary. A and **C**, Experiment 3a and 3b. Participants are asked to produce three 5-syllabic sentences that have the same syntactic structure in each experiment. The position of the two-syllable noun

is either at the end (Exp. 3a) or in the middle of the sentence (Exp. 3b). Each character is presented on the screen for 500 ms, followed by a blank for 500 ms. **B** and **D**, Relations between the compensation amount of the preceding syllable (x-axis) and adaptation amount of the current syllable (y-axis) in Exp. 3a and 3b. Mean pitch averaged across 200-300 ms are separately extracted from the perturbed syllable (black dots in the insert plots) and the subsequent syllable (the dot pointed by a black arrow). The grey-shaped rectangle denotes the two-syllabic word. Only when the two syllables are within a word boundary, significant inter-syllabic adaptation is observed. **$p < 0.005$.

Discussion

We investigated how previous sensory error and motor compensation regulated trial-to-trial adaptation. We showed that motor compensation in the preceding trial can adapt to the next trial, whereas sensory errors did not have any effects. Crucially, this compensation-driven adaptation was modulated by linguistic contexts -- persisting across different vowels but only when adjacent vowels were embedded within the word boundary. These results suggested that sensorimotor adaptation was driven by motor compensation and was constrained by the linguistic system in continuous speech.

The study introduces a serial dependence paradigm in the domain of speech production that successfully dissociates the influence of previous sensory error and motor compensation on the current vocal production. Our main finding shows a direct compensation-driven adaptation across trials (**Fig. 2BC**), whereas sensory prediction error that induces compensation did not significantly contribute to changes in production across trials. This finding is consistent with DIVA model's prediction, where corrective action generates feedback that updates the internal forward model, enabling a more accurate prediction to reduce future sensory error and a more accurate motor command in the next trial [19]. The across-trial effects suggest that the time constant in the feedforward motor process is longer than that in the sensory process and regulates speech production in a temporal continuous manner.

The relationship between within-trial compensation and next-trial adaptation is not linear; it is more likely a DoG-shaped curve. Specifically, if the previous compensation is large, the adaptive changes in the current trial become smaller, suggesting a dynamic adjustment process during speech planning [5, 6, 36]. Furthermore, this process is also constrained by the similarity of production targets between trials. If the target in the next trial changes to a different vowel, the trial-to-trial adaptation becomes weaker (**Fig. 3C**). Rochet-Capellan, et al. [37] tested whether sensorimotor adaptation during training transfers to new utterances with different sounds and demonstrates that it is highly dependent on the specific utterances. That is, the experience in the motor domain becomes less useful when the next utterance is different.

Lastly, the extension of compensation-driven adaptation into sentence production reveals that the adaptation only exists within word boundary (**Fig. 4**). In Experiment 3, participants may simply read out aloud each visually presented word without syntactic processing. If this were true, inter-syllabic adaptation, as observed in Experiments 1 and 2, would occur between every two syllables. However, the observed significant effects of syntactic structures are inconsistent with the alternative 'reading-only' hypothesis. Moreover, the extensive training on the three 5-syllabic sentences ensured that participants were extremely familiar with the materials and retrieved the simple sentential structure at the visual presentation of the first word. All the experimental settings and positive results support the hypothesis regarding the role of syntactic constraints in compensation-driven adaptation.

The results of within-word-boundary inter-syllabic adaptation suggest that words serve as a central unit in speech planning. Motor compensation in the preceding syllable can be adapted to the next within-word syllable. However, any compensation-based experience is not available for the syllables across words. Psycholinguistic studies, such as those by Levelt [38], propose that during speech production, words are retrieved from the mental lexicon as a whole unit, followed by phonological encoding into syllabic and phonetic representations. The entire course of speech production at the linguistic level would interact with sensorimotor processes via internal forward models and regulate feedforward processes at both featural and temporal domains [11, 13, 39-43], to achieve efficient online control. The observed adaptative effects within word structure suggest that the programming and regulation of speech production are presumably in the size of the encoding unit within the word structure, which is consistent with the hypothesis of interaction between linguistic and sensorimotor systems in speech production control [4].

The study showed that previous motor compensation can modulate the subsequent vocal pitch production; whether this compensation-driven adaptation can be generalized to other speech domains, such as formants [16] and intensity [11] that are controlled by distinct vocal apparatus and may be mediated by potentially different mechanisms, requires further investigation. Considering a broader linguistic context in speech motor control is challenging and relevant studies are rare [44, 45]. In this study, we used pitch as a representative dimension and carefully selected different combinations of consonants and vowels in continuous speech to pioneer the investigation. Future studies should be carried out with caution and careful controls. For example, pitch contours in continuous speech can be potentially interfered from consonantal perturbations [46] or sentence intonation [47]. During the production of non-sonorant consonants, the vibration of vocal folds will be affected, leading to a break and a carry-over rising or falling in the pitch contours [48].

In summary, by implementing a novel serial-dependence paradigm in the domain of speaking, we found distinct functions of sensory error and motor compensation in sensorimotor adaptation in continuous speech. The compensation regulates trial-to-trial adaptation that was constrained by linguistic contexts, while sensory error only contributes to the instant computation of compensation. These results suggest that the history of motor processes significantly contributes to speech adaptation and control. Systematic interplay among cognitive, motor, and sensory systems regulates behaviors.

Methods

Participants

In five experiments, i.e., Experiments 1, 2a, 2b, 3a, and 3b, we recruited 14 participants (9 females, 18-27 years old, mean 21 years old), 17 participants (11 females, 19-32 years old, mean 23 years old), 12 participants (8 females, 20-27 years old, mean 22 years old), 15 participants (9 females, 19-25 years old, mean 22 years old), and 13 participants (7 females, 18-26 years old, mean 21 years old), respectively. They were college students with self-reported normal hearing and speech. All participants were right-handed and were native Chinese speakers. Each volunteer only participated in one experiment. Written informed consent was obtained from each participant before the experiment. The experimental procedures were approved by the Research Ethics Committee at the East China Normal University and New York University Shanghai.

Procedure

Experiment 1

Participants were asked to produce the vowel /a/ in a total of 960 trials over three days. Each trial began with a white fixation cross, displayed at the center of the screen for a randomized duration of 0.8–1.2 s (uniform distribution), signaling participants to be prepared for vocalization. When the cross turned green, participants were instructed to vocalize no more than 500 ms and sustain the /a/ sound with a steady and natural tone for 2.5 s until the cross disappeared. A pitch perturbation for a duration of 500 ms was randomly introduced 0.8–1.2 s after vocal onset. The direction (i.e., upward or downward) and magnitude (i.e., 60, 180, or 300 cents) of the pitch shift were randomly assigned across the 960 trials for each participant. At the end of each trial, participants received visual feedback: "Good," "Too slow," or "Too short." Participants completed 95.86% ± 0.02% (s.d.) of trials that met criteria. Each trial was followed by a silent interval with a random duration of 1–2 s (uniform distribution) before the next trial began.

Participants completed 320 trials in 10 blocks each day, with self-paced rest periods of at least 1 minute between blocks. At the beginning of each session, participants underwent a training block of 10 trials. The mean pitch from these trials was used to define the pitch range in the Audapter toolbox (see *Auditory feedback perturbation* below).

Experiment 2a

The procedure for Experiment 2a was identical to Experiment 1, except participants were required to produce four different vowels without semantic meaning—啊 (/a1/), 咿 (/i1/), 呃 (/e1/), and 哦(/o1/)—randomly assigned in each trial. A white letter corresponding to the syllable was presented at the center of the screen, and upon turning green, participants were instructed to vocalize a vowel. Participants completed 94.82% ± 0.11% of trials that met the criteria.

Experiment 2b

The procedure for Experiment 2b was identical to Experiment 2a, except the order of four vowels were presented in a fixed order, i.e., /i1/-/a1/-/e1/-/o1/ in every four trials so that

participants would not anticipate the next vowel production. Participants completed 97.55% ± 0.03 of trials that met the criteria.

Experiment 3a

The procedure for Experiment 3a followed that of Experiment 1, with two differences. First, participants completed 300 trials in a single day. Second, they were required to produce sentences with the same syntactic structure rather than isolated vowels. In each trial, one of three five-syllable sentences (i.e., ▪▪▪猫咪 [ma1 ma1 lu1 mao1 mi1], ㄚㄚ邀巫医 [ya1 ya1 yao1 wu1 yi1], 依依摸▪▪ [yi1 yi1 mo1 wu1 ya1]) was randomly selected (uniform distribution), with each syllable appearing sequentially at the center of the screen for 500 ms, followed by a 500 ms blank screen. The whole duration for a sentence production was 5 s. During vocalization, a whole-utterance pitch perturbation (upward or downward perturbation at 60, 180, 300 cents, randomly assigned) was applied to the second, third, or fourth word during vocalization (uniformed distribution). In 20% of the sentences, no perturbation was applied. The speech materials and task were carefully chosen to avoid the effect of consonantal obstruction [49] and the effect of articulators' dynamics on pitch contour, respectively. Participants completed 94.44% ± 0.07% of trials that met the criteria.

Before the main experiment, participants completed a training session in which they produced each of the three sentences four times. They were explicitly instructed on the content and syntactic structure of the sentences. Additionally, they were instructed to vocalize each syllable within 500 ms of its appearance and to avoid coarticulation between words. Participants could repeat the training session upon request.

Experiment 3b

The procedure for Experiment 3b was the same as Experiment 3a, except that the three sentences were replaced with another three with a different syntactic structure, i.e., 邀依琳摸▪ [yao1 yi1 yi1 mo1 ying1], 拉▪▪腌▪ [la1 ma1 ma1 yan1 ya1], and ▪ㄚㄚ溜猫 [yue1 ya1 ya1 liu1 mao1], where the two-syllable noun was in the position of second and third character in the sentences. Participants completed 97.36% ± 0.03% of trials that met the criteria.

Auditory feedback perturbation

Participants' speech was recorded by a Shure beta 58A microphone that was placed 5 centimeters away from their mouths. The acoustic signals from the microphone were pre-amplified and then provided to an audio interface (MOTU Microbook IIc), collected at a 48k Hz sampling rate. The recorded speech was real-time manipulated (i.e., perturbation) in the audio interface, and the processed signal was split and sent both to the computer and to the headphones. The speech processing in the audio interface was performed using the Audapter toolbox [50]. The pitch of speech in each trial was shifted using the time-domain method. A 10-ms linear ramp was added at boundaries to attenuate possible abrupt jumps in the speech. A priori pitch range was set as +/-50 Hz relative to the mean pitch of a vocal /a/ for each participant. The rest of the parameters were set as default including algorithm, frame length, and cepstral liftering.

Acoustic analysis

In experiments 1 and 2, we first removed silence from the recordings of produced vowels in each trial using the *vad* function. Visual inspection was performed to make sure noise did not affect the voice activity detection. Pitch tracks (at a 100-Hz sampling rate) were measured using the Praat-based script ProsodyPro [51]. Default parameters were used. Perturbation onset in the pitch trace was obtained by a customized automatic algorithm combined with manual inspection. To convert hertz to cent scale, we defined baseline pitch by taking the mean of pitch trace in the -400 to -200 ms before perturbation onset. The pitch trace was transformed according to the formula: $cents = 1200 * \log_2(\frac{pitch}{pitch_{baseline}})$. A trial rejection was performed if the pitch trace was varied beyond its perturbation amount minus 100 cents (for downward-perturbation trials) or plus 100 cents (for upward-perturbation trials). To extract perturbation and compensation amounts for DoG-curve fitting and linear mixed effect model, the pitch trace in the 50-80 ms and the 150-250 ms windows were averaged, respectively, for each trial [18]. Compensation amounts for all trials and all participants were corrected by subtracting the grand average. This correction ensures that the DoG-curve fitting starts from zero, allowing its amplitude to be accurately measured and compared across experiments.

In Experiment 3, we applied the same pipeline except that only the perturbed syllable and its subsequent syllable were extracted to measure their pitch trace. Based on the visual inspection of pitch contours (**Fig. S2**), Mandarin tone 1 produced in isolation was characterized by a high-level tone and showed a pitch contour that typically involved a slight rising intonation at the onset, lasting around 0-150 ms, before stabilizing into a steady high pitch [52]. Therefore, we calculated the compensation amount in the perturbed syllable and adaptation amount in the following syllable using mean pitch in the 200-250 ms time window, with baseline pitch in the 150-200 ms time window.

In all experiments, we analyzed signalOut, the speech output routed through the sound card to earphones, which incorporated the pitch perturbation. This approach is standard in perturbation studies [e.g., 33]. A comparison of compensation amounts derived from signalIn and signalOut in Experiment 1 showed consistency between the two signals across participants (**Fig. S3**).

Statistical analysis and significance tests

Compensatory responses

For participant-level analysis, trials with the same perturbation condition were averaged, regardless of vowel categories in Experiment 2 and 3. To assess whether there was a compensatory response to perturbation, a two-sided cluster-based permutation test [53] was used to test averaged pitch traces against perturbation amount or between perturbed and normal conditions (**Fig. 1C** and **4B**). A one-sided one-sample t-test was used to test motor compensation extracted from time of interests against 0 (**Fig. 1D)**. Furthermore, to the main effect of P_{t-1} on C_t, a Friedman's chi-square test was used for multiple condition comparison

(**Fig. 2D** and **3C**)**.** Spearman correlation was used to find the relation between C_{t-1} and inter-syllabic adaptation within and across syntactic boundaries (**Fig. 4C-E**). To compare the correlation coefficient in within- and across-boundary conditions, a bias-corrected and accelerated bootstrap was used [54].

trial-to-trial adaptation effect

The serial dependence paradigm quantified the similarity between auditory perturbations in two consecutive trials, i.e., P_{t-1}-P_t, and motor responses in the preceding one trial, i.e., C_{t-1}, to access their adaptation effect on the current motor compensation, i.e., C_t. To explore the adaptation effect of sensory error on C_t, C_t was expressed as a function of the difference between P_{t-1} and P_t. For positive values of this difference, the preceding perturbation P_{t-1} was higher than the perturbation of the current trial P_t; similarly, a positive compensation amount denoted a trial in which participants compensated upward in response to perturbation. Consequently, data points in the scatter plot (**Fig. 2BC**) that had x- and y- values in the same sign indicated that C_t was in the direction of P_{t-1}. In addition, to explore the adaptation effect of motor compensation on C_t, C_t was expressed as a function of the compensation amount in the preceding trial C_{t-1}. Following the same principle, the positive value of previous and current compensation, which had x- and y-values in the same sign, denoted a trial in which C_t was in the direction of C_{t-1}.

We assess the trial-to-trial adaptation effect by polling the compensation amount of all trials and fitting the DoG-shape curve, a well-found psychophysical function in previous serial-dependence studies [30, 55]. The DoG was given as $y = x * a * w * c * e^{-(wx)^2}$, where *a* was the curve amplitude, *w* was the curve width, and *c* was the constant $\sqrt{2}/e^{-0.5}$. To assess adaptation effects of preceding sensory error, *x* was P_{t-1}-P_t, and width parameter *w* of the curve was constrained to a range of plausible values (*w* = 0.001-0.005, corresponding to the curve peak between 130 and 530 cents perturbation difference). To assess the adaptation effect of preceding motor compensation, *x* was C_{t-1}, and width parameter *w* of the curve was constrained to a range of plausible values (*w* = 0.019-0.071, corresponding to the curve peak between 10 and 36 perturbation pitch difference). The model fitting used the function *fmincon* with default parameters. We employed a bias-corrected and accelerated bootstrap to evaluate the significance of the DoG models and to compare DoG models between conditions. We applied a fitted DoG model to the pooled group data and generated a permutation distribution for the DoG-curve amplitude parameter [56, 57]. This permutation process was repeated 2,000 times. For a one-sided comparison of curve amplitude, if the data population in one condition was greater than A% of the data population in the other condition, the significance level was (100A + 1)/2,001. For a two-sided comparison, the significance level was (200A + 1)/2,001. A false discovery rate (FDR) correction was applied.

Generalized linear mixed-effect model

To quantitatively test the relations of C_t to P_t, P_{t-1} and C_{t-1}, we built a generalized linear mixed-effect models (**Fig. 2E** and **3D**). The model assumed that P_t, P_{t-1} and C_{t-1} together influenced C_t. The function 'fitglme' was performed and accounted for group-level fixed effects and random effects because of vocal pitch variation across participants. The model

was specified as $C_{t\ ij} = f(\beta_{0j} + \beta_{1j}P_{t\ ij} + \beta_{2j}P_{t-1\ ij} + \beta_{3j}C_{t-1\ ij} + 1|subjects)$, where *i* indicated participant index and *j* indicated j^{th} trial. The regression coefficient of each predictor, i.e., β, was accessed by the *t*-statistics against the null hypothesis test that the coefficient was equal to 0. FDR correction was applied.

Resource availability: All data and code that support the findings of this study will be available after acceptance.

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Supplemental information: Document S1. Figures S1-S3.

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Xing Tian (xing.tian@nyu.edu).

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