

Robust Sensorimotor Learning During Variable Sentence Level Speech

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Summary

Sensorimotor learning has been studied by altering the sound of the voice in real-time as speech is produced. In response to voice alterations, learned changes in production reduce the perceived auditory error and persist for some time after the alteration is removed [1–5]. The results of such experiments have led to the development of prominent models of speech production. This work proposes that the control of speech relies on forward models to predict sensory outcomes of movements, and errors in these predictions drive sensorimotor learning [5–7]. However, sensorimotor learning in speech has only been observed following intensive training on a handful of discrete words or perceptually similar sentences. Stereotyped production does not capture the complex sensorimotor demands of fluid, real-world speech [8–11]. It remains unknown whether talkers predict the sensory consequences of variable sentence production to allow rapid and precise updating of speech motor plans when sensory prediction errors are encountered. Here, we used real-time alterations of speech feedback to test for sensorimotor learning during the production of 50 sentences that varied markedly in length, vocabulary, and grammar. Following baseline production, all vowels were simultaneously altered and played back through headphones in near real-time. Robust feed-forward changes in sentence production were observed that, on average, precisely countered the direction of the alteration. These changes occurred in every participant and transferred to the production of single words with varying vowel sounds. The results show that to maintain accurate sentence production the brain actively predicts the auditory consequences of variable sentence-level speech.

Results

The examination of motor learning (adaptation) following real-time sensory perturbations is a dominant paradigm for studying sensorimotor planning and control in limb movements [12–14]. This approach, which traces its origins to Helmholtz’s 1860s [15] study of motor adaptation following prism-induced perturbations of vision, has been recently used to test the sensory basis of speech production [16–20]. Typically, participants repeat words into a microphone and the resonant frequencies (or formants; see Figure 1C) that define the vowel sounds they produce are altered and played back through headphones in near-real-time. For example, a real-time alteration in the first and second formant of the word “bed” can make it sound more like “bad” (see Figure 1D). Participants thus perceive themselves producing a different speech sound from what they intended to produce. Following repetitive word production with such altered feedback, learned changes in articulation that offset the perceived auditory error are typically observed [1–4].

While this paradigm has been highly influential for models of speech motor control [5–7], a fundamental limitation of this work lies in its reliance on the alteration of a single speech property (e.g., one vowel or transition) within the repeated production of a handful of isolated words or acoustically similar sentences [21–23]. During real-world speech, a single speech property is not

privileged over others; dozens of phonemes that span a talker's articulatory workspace are combined into complex, interacting, and overlapping motor and sensory patterns. Two factors suggest that the rapid adaptation to auditory perturbations observed during repetitive word production might not occur during variable sentence-level speech. One is the increased processing demands associated with the simultaneous planning, monitoring, and correcting of dozens of speech sounds. The second is the increase in the variability of oral motor patterns and associated acoustic signals owing to the scaling of neuromotor noise with movement rate [24,25], and coarticulation effects that reduce the acoustical distinctiveness of phonemes [8–11]. The heightened sensorimotor complexity of sentence production relative to word production is highlighted by neuromotor speech disorders. Apraxia of speech, for example, is characterized by substitution and distortion errors that increase in frequency with utterance length and complexity [26]. The occurrence of disfluencies in developmental stuttering is also strongly linked with the complexity and length of productions [27–29].

Given the clear differences between real-world speech and the speech used to study sensorimotor adaptation, it is questionable whether talkers are capable of maintaining predictions of all speech sounds during more natural production to enable rapid and precise updating of speech motor plans when sensory prediction errors are encountered. Successful adaptation across multiple vowels and contexts requires accounting for numerous differences in acoustic patterns and articulatory configurations. Failure to do so may lead to a lack of systematic adaptation across vowels, or speech changes that are appropriate for only a part of the vowel space. One animal model of human speech, the bird song of the Bengalese finch, suggests that compensation for real-time alterations of fluid vocal production can be observed, but it requires several days of continuous altered feedback [30]. In humans, the failure to observe sensorimotor adaptation in response to altered feedback during variable sentence production would challenge the notion that auditory-based adaptation plays a central role in everyday speech. Conversely, a successful demonstration of rapid simultaneous adaptation across varying sounds and contexts would validate the idea that sentence-level speech is actively maintained through auditory-sensory predictions.

Experiment 1

Experiment 1 examined the capacity for sensorimotor adaptation of speech to a perturbation of auditory feedback during the fluid production of 50 different sentences that varied markedly in syllable, word, and phrase structure. Each of the 50 sentences was presented once per production block, in a random order (Figure 1A). Following two *Baseline* production blocks, ten participants (Group 1) experienced a 49.5 mel decrease in their first formant (F1) and a 49.5 mel increase in their second formant (F2). Ten different participants (Group 2) experienced the opposite manipulation (Figure 1B, black vectors). Four blocks of the 50 sentences were produced with altered-feedback, followed by one block of trials with normal feedback (*Unlearning phase*).

Figure 1

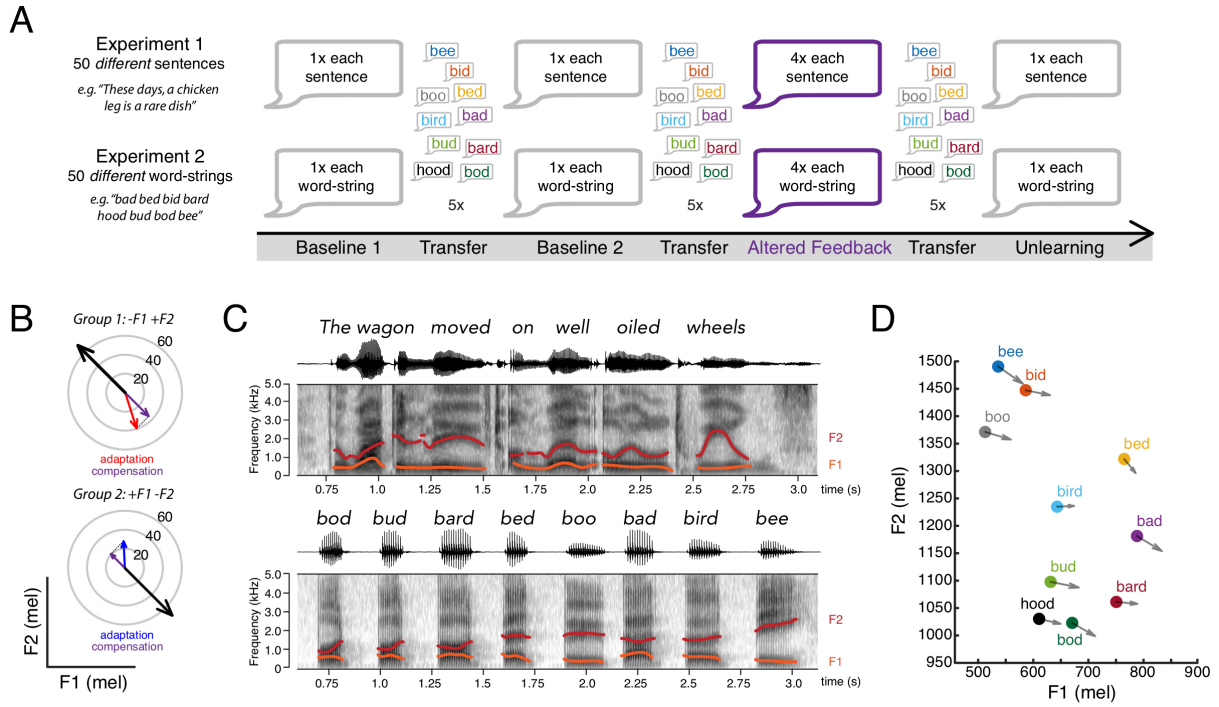
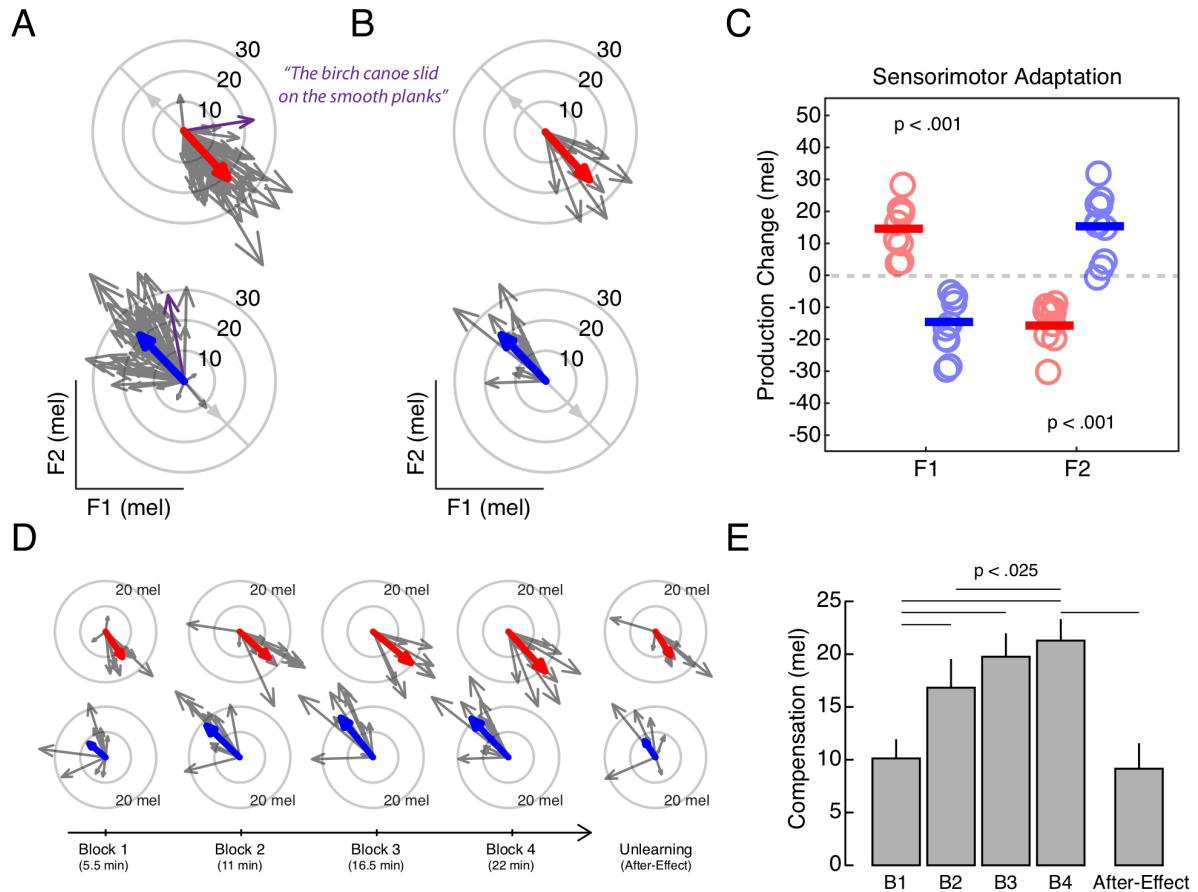


Figure 2A shows how F1 and F2 frequency, averaged across the vowels in each of the 50 sentences, changed relative to the second baseline block with altered auditory feedback. The grey vectors represent the magnitude and direction of compensation in F1-F2 space for each sentence, with the average compensation vector shown in red for Group 1 ($F1$ decrease, $F2$ increase) or blue for Group 2 ($F1$ increase, $F2$ decrease). Changes in sentence production opposed the applied change in the sound of the voice, on average. The changes in F1 and F2 are shown for each participant (averaged across all sentences) in Figure 2B and 2C. The direction of the feedback alteration drove significant between-group differences in the direction of F1 and F2 change. These changes differed between the groups ($F1$: $t(18) = 9.08$, $p < .001$; $F2$: $t(18) = 7.16$, $p < .001$) and from zero ($p < .002$ in all four cases). In all cases, the observed formant changes were compensatory: altered-feedback that decreased F1 and increased F2 (Group 1) led to an increase in F1 production and decrease in F2 production (Figure 2C, red circles), while altered feedback that increased F1 and an decreased F2 (Group 2) led to the opposite production change (Figure 2C, blue circles). On average, sensorimotor adaptation countered 30% of the applied acoustical error in F1 and 31% of the applied acoustical error in F2. The pattern of F1 and F2 change did not depend on the ratio of front versus back vowels contained within the sentences (see Figure S1A and Table S1). Finally, in contrast to the learned changes in F1 and F2 that followed sentence production with altered feedback, the fundamental

frequency (F0) did not change during the same period (Group 1: $t(9) = .22$, $p = .83$; Group 2: $t(9) = 1.20$, $p = .26$).

Figure 2



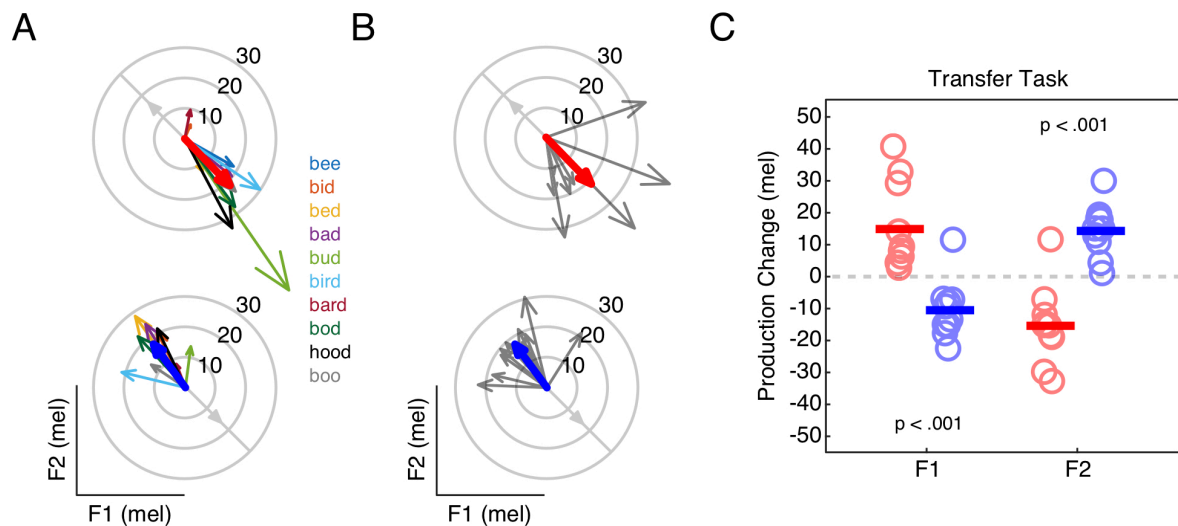
Production change in Group 1 was, on average, directed along a vector at 178.39 degrees (6.31 SE) relative to the axis of perturbation in F1-F2 space. Production change in Group 2 was directed along a vector at 176.73 degrees (7.24 SE) relative to the axis of perturbation in F1-F2 space. Thus, while variation existed among subjects and vowels, sensorimotor learning associated with sentence production nearly perfectly opposed (on average) the direction of the induced acoustical change in the vowel space.

To examine the time-course of adaptive changes in F1 and F2 frequency relative to baseline, a measure of *compensation* was calculated as the component of the production change that directly opposed the formant shift (see Figure 1B; 18). Compensation was pooled across the two directions of altered feedback and averaged within each production block. Figure 2E shows that significant compensation was observed following the first block of altered feedback ($t(19) = 5.55$, $p < .001$). Compensation grew over the course of altered feedback (blocks 1 to 4) and declined when the

feedback alteration was removed. Taken together, the group-level results in Figure 2 demonstrate that rapid and precise sensorimotor adaptation is observed during the fluid production of a large set of varied sentences.

To examine whether adaptation was primarily driven by reactive (i.e. online) adjustments in production or learned changes in the feedforward motor commands that guide speech, following both baseline production and altered feedback, participants performed a transfer task (see Figure 1A and 1D). The transfer task involved isolated productions of the words ‘bee’, ‘bid’, ‘bed’, ‘bad’, ‘bud’, ‘bird’, ‘bard’, ‘bod’, ‘hood’, and ‘boo’, produced five times in a random order, during which speech feedback was noise masked. The transfer task had two aims: 1) to test whether changes in sentence-level production associated with altered feedback would persist in the absence of altered feedback (i.e. whether compensation reflected a change in motor planning), and 2) to examine how changes in production, if present, might be applied at the word level.

Figure 3



The coloured vectors in Figure 3A show the magnitude and direction of production change in F1-F2 space for each word in the transfer task. The bottom and top panels show changes in transfer task production following sensorimotor adaptation for Group 1 ($-F1$, $+F2$) and Group 2 ($+F1$, $-F2$), respectively. The bold red and blue arrows show the average change in production for each condition. These changes in production are examined globally (averaged across all 10 words) for individual participants in F1-F2 space (Figure 3B) and separately for each formant (Figure 3C). The direction of altered feedback experienced during sentence production drove significant between-group differences in production change assessed by the transfer task. The direction of formant changes matched those observed during altered-feedback. Formant changes differed between the two groups (F1: $t(18) = 4.81$, $p < .001$; F2: $t(18) = 6.41$, $p < .001$) and from zero ($p < .01$ in all four cases). Changes in F1 and

F2 production observed during the transfer task opposed the altered feedback experienced during sentence production by 26% in F1 and 30% in F2. There was no reliable difference between the magnitude of adaptation during fluid sentence production and the transfer of adaptation to isolated word production (F1: $t(19) = -.65$, $p = .52$; F2: $t(19) = -.21$, $p = .84$). Furthermore, transfer did not differ between front, mid, and back vowels produced in the transfer task (see Figure S1B). Thus, sensorimotor adaptation associated with fluid sentence production persisted after the feedback alteration was removed, reflecting a change in speech motor planning, and these changes were readily applied to the isolated production of vowels spanning the production workspace.

Experiment 2

Experiment 1 showed that average patterns of adaptation during variable sentence production precisely countered 30% of the auditory feedback alteration and were observed to transfer broadly to word production (i.e., there was no decrease in compensation between sentence production and the transfer task). This result was observed despite a number of key differences between the current paradigm and past studies of speech adaptation. In particular, Experiment 1 involved adaptation to multiple phonetic targets (as opposed to a single target), and the embedding of adapted vowels within highly variable, fluid speech (as opposed to discrete, monosyllabic words).

To understand how the sensorimotor complexity of fluid speech may interact with adaptation of multiple vowel targets, we conducted a second experiment to examine adaptation of ten different vowels produced in the context of discrete, monosyllabic words. By simplifying the production context (thereby removing a key source of motor and sensory variability), we were able to more directly examine the capacity of talkers to simultaneously adapt to multiple vowel targets. The experiment was identical to Experiment 1, with the exception that the 50 sentences were replaced with 50 unique word-strings. The word-strings consisted of eight-word permutations of the ten transfer words (e.g. ‘bad bed bid bard hood bud bod bee’), such that each word was produced 160 times with altered feedback before being produced in the transfer test. Thus, the word-strings contained multiple speech targets, but the utterances were more like the stereotyped production used in prior studies.

Altered auditory feedback drove changes in word-string production that opposed the direction of the feedback alteration in F1-F2 space (see Figure S2A-C). These changes countered 47% of the induced acoustical error in F1 and 47% of the induced acoustical error in F2. As in Experiment 1, similar patterns of compensation in F1 and F2 were observed for vowels across the vowel space (see Figure S3) and there was no change in a speech property unrelated to the experimental manipulation, F0 (Group 1: $t(9) = -0.27$, $p = .79$; Group 2: $t(9) = .53$, $p = .61$). Sensorimotor adaptation associated with the production of word-strings transferred to the isolated production of the words that made up the word strings (see Figure S4A-C). Changes in production observed in the transfer task opposed the

voice alteration experienced during word-string production by 18% in F1 and 32% in F2. There was a significant decrease in adaptation between word-string production and word production in the transfer task (F1: $t(19) = -5.34$, $p < .001$; F2: $t(19) = -2.59$, $p = .018$). Thus, sensorimotor adaptation associated with word-strings persisted after the alteration was removed, but generalized incompletely.

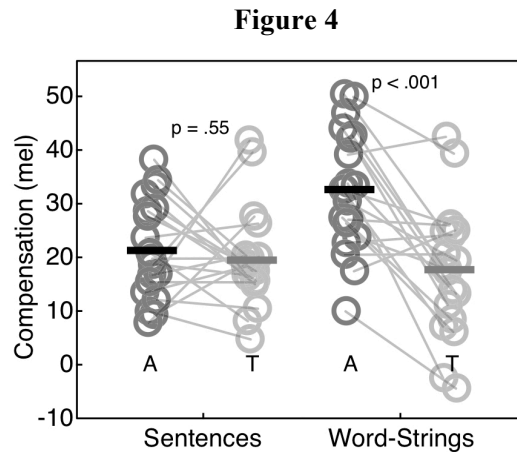


Figure 4 uses the *compensation* measure described previously to compare the magnitude of adaptation (A) and transfer (T) between Experiment 1 (fluid sentence production) and Experiment 2 (word-string production). An interaction was observed between condition (sentence vs. word-string production) and task (altered feedback vs. transfer task; rANOVA: $F(1,38) = 9.93$, $p = .003$). Participants who produced word-strings made up of the ten transfer words compensated more during altered feedback than participants who produced a varied set of sentences (47% versus 30%, respectively: $t(38) = 3.53$, $p < .002$). Compensation decreased between word-string production and the transfer task ($t(19) = 5.09$, $p < .001$). However, there was no decrease in compensation between sentence production and the transfer task ($t(19) = .61$, $p = .55$). There was also no difference in the amount of transfer between the two experiments ($t(38) = .54$, $p = .59$). The results indicate that compensation was stronger when participants practiced a series of simple, discrete words rather than fluid sentences. However, this increased compensation did not result in a greater persistence of learned changes in the transfer task.

At the level of individual participants, we computed the amount of compensation separately for each of the fifty sentences/word-strings produced in the final block of altered auditory feedback and each utterance produced in the transfer task. Then, for each participant, we tested whether measures of compensation were greater than zero using one-sample t-tests. All participants in Experiment 1 and Experiment 2 showed significant compensation for altered auditory feedback during sentence or word-string production ($p < .025$ in each case). Seventeen of the participants in Experiment 1 and fifteen of the participants in Experiment 2 showed significant compensation during the transfer test ($p < .05$ in each case).

Finally, for each vowel in the transfer test we pooled measures of compensation across the two perturbation directions and examined whether compensation was greater than zero using two-tailed t-tests. In Experiment 1, compensation was greater than zero for 8 of the 10 vowels ($p < .05$ for all except “bid” and “bard”). In Experiment 2, compensation was greater than zero for 7 of the 10 vowels ($p < .05$ for all except “bee”, “bad” and “boo”). Taken together, these group-level, subject-level and vowel-level analyses provide evidence that sensorimotor adaptation associated with sentence production transferred broadly to the production of vowels that span the acoustical workspace.

Discussion

Two groups of participants experienced systematic alterations of speech feedback during fluid sentence production. In response, learned changes in the first and second formant of speech were observed that rapidly grew with training and, on average, countered 30% of the induced acoustical error with directional precision. Critically, adaptation persisted during a transfer task involving masked production of single words. This demonstrates that the production changes observed during altered feedback reflected a true change in feedforward motor planning and were not a simple compensatory response to the altered auditory feedback. The results provide evidence that, despite the perceptual and motor complexity of fluid speech, the brain predicts acoustical outcomes during fluid sentence production and quickly updates sentence-level motor plans when sensory prediction errors are encountered.

Our study also examined the relationship between sentence-level and word-level speech motor adaptation. Specifically, if participants adapt the production of vowels during complex sentences, will learning transfer to the production of units represented at the phoneme-level? Few studies have examined the transfer of sensorimotor learning across phonetic contexts. The clearest indication of such transfer comes from Houde and Jordan [3], in which speech adaptation to a single vowel produced in four monosyllables showed limited transfer to untrained productions of the same vowel in different syllable contexts and different vowels produced in the trained syllable context. The magnitude of transfer averaged less than 50% of the learning effect in the trained vowel. The lack of complete transfer in that case suggests that sensorimotor learning was not global (i.e. applicable in any speech context). This is consistent with a more recent demonstration of local speech motor learning, in which speakers were able to simultaneously adapt their production of the same vowel to two different directions of auditory perturbation when the perturbations were associated with a different phonetic context [31]. In Experiment 1 of the present study, we observed robust transfer of sensorimotor learning between two substantially different speech contexts: fluid sentence production and isolated word production. Surprisingly, transfer that followed sensorimotor learning associated with sentence-level speech was equivalent to transfer that followed sensorimotor learning associated

with word-strings built from the transfer test words. This provides initial evidence that sentence-level changes in phoneme planning are readily applied at the word level.

More generally, this study shows how sensorimotor learning may be investigated in a more ecologically valid behaviour. A large number of studies have examined motor adaptation following perturbations of visual feedback of limb movements. In this work, participants interact with a joystick or robotic arm to control a cursor on a computer screen that is then systematically perturbed. This experimental model of visuomotor learning has been influential in shaping our current understanding of how we learn and maintain movements [12–14,32,33]. However, this method has limitations: participants must interact with an external device, adaptation is tied to an abstract representation of limb position, and the adapted movements are highly stereotyped. In contrast, adaptation to real-time alterations of speech feedback allows for the examination of sensorimotor learning in an unconstrained, complex movement where learning is driven by alterations in participants' own voice. Here we extend this experimental model to study sensorimotor learning in a more naturalistic behaviour: fluid, sentence-level speech.

Importantly, our results have limitations that could be addressed in future work. Participants in our study produced fluid, connected speech by reading sentences aloud. Although reading aloud is a behaviour that occurs in the real world, it is less common than unscripted speech and there are noted differences in both the perception and production of read speech as compared to unscripted speech [34]. For instance, conversational speech is often articulated less clearly than read speech [35]. Nevertheless, we believe that our study provides a template for how sensorimotor adaptation could be studied in unscripted speech. During unscripted speech, variation in sentence production makes it difficult to directly measure whether changes in speech reflect adaptation. Here, however, the observation of broad transfer of adaptation from sentence production to isolated word production suggests that a transfer test involving discrete vowels could be used to gauge sensorimotor learning during unscripted speech.

A second limitation of the study is that it does not directly address the specificity of the observed adaptation. In speech, sensorimotor adaptation can be accomplished in at least two ways. To reduce sensory prediction errors, the brain may learn multiple sensorimotor transformations, to adapt the movements of specific phonemes [31]. It may also reduce sensory prediction errors by altering a global property of articulation for all produced phonemes (e.g. jaw position). In Figures S1 and S3, we provide evidence that the sensorimotor learning observed here cannot be explained by a simple global change in articulation such as jaw raising or lowering. Specifically, if the observed production changes were primarily driven by changes in jaw position, one would expect that for front vowels (e.g. bee) increases in F1 would be accompanied by *decreases* in F2, whereas for back vowels (e.g.,

bod), increases in F1 would be accompanied by *increases* in F2 (see 36, 37, for articulatory modeling studies showing this effect). This pattern of results was not observed in the present study during the production of sentences or word-strings (see Figures S1 and S3). In both experiments, learned changes in production across the vowel space reflect opposition to the feedback alteration (-F1/+F2 or +F1/-F2), and not a pattern predicted by a simple jaw raising/lowering strategy. This suggests that compensation was achieved via phoneme-specific changes in speech motor planning, although the exact number of new sensorimotor transformations acquired remains unknown.

In summary, the idea that speech movements are planned to achieve sensory targets plays a central role in current models of speech production [5–7]. When sensory feedback of speech differs from predicted targets, the resulting error signal triggers corrective changes that are integrated into the feedforward motor commands that guide speech. Such models account for adaptive changes in speech movements during word repetition that offset sensory errors [21,38–40]. The extent to which precise auditory predictions maintain fluid, sentence-level speech remained unknown. Here we provide evidence that sensorimotor adaptation occurs during highly variable sentence-level speech. Critically, the speed and precision of the observed sensorimotor adaptation was comparable to that observed during stereotyped word repetition. The result bolsters current models of speech motor control by demonstrating that sensory prediction, and precise motor adaptation driven by sensory prediction errors, plays a central role during phoneme production at multiple levels of speech, from single words to full-length sentences.

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Author Contributions

DRL and DMS designed the experiments, helped collect the data, analyzed the data, created the figures and drafted the manuscript. HJS helped recruit and test participants. DRL, HJS, KW, and DMS edited the manuscript for publication.

Declaration of Interest

The authors declare no competing interests.

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Figure Legends

Figure 1. Procedure and methods. A) The experiments contained multiple blocks of sentence or word-string production. Transfer tests involving word production with noise masked speech occurred after each Baseline block and Altered Feedback block. B) In both experiments, 10 participants had the first formant (F1) of their vowel productions decreased by 49.5 mel and the second formant (F2) of their vowel productions increased by 49.5 mel (top panel, Group 1); 10 additional participants experienced an equal and opposite manipulation (bottom panel, Group 2). Compensation (purple vectors) was measured as the component of sensorimotor adaptation (red and blue vectors) that directly opposed the direction of altered auditory feedback (large black vectors). C) Spectrograms for an example sentence and word-string. The x-axis shows time from trial start. Changes in production were assessed by averaging F1 and F2 values across the voiced segments, shown by the highlighted formants. D) The location of Transfer task productions in F1-F2 space for a single participant. The arrows show compensatory production change following an F1 decrease and F2 increase for this participant.

Figure 2. Sensorimotor adaptation during fluid sentence production (Experiment 1). A) Grey vectors represent mean F1-F2 production change in mel for each sentence ('The birch canoe slid on the smooth planks' is shown in purple). Top panel: changes associated with a -F1, +F2 alteration (Group 1). Bottom panel: changes associated with a +F1, -F2 alteration (Group 2). The bold red and blue vectors represent the grand average change for each group. The light grey vectors show the feedback alteration direction. B) Grey vectors represent F1-F2 production change in mel for each participant. Top panel: changes associated with a -F1, +F2 alteration (Group 1, N=10). Bottom panel: changes associated with a +F1, -F2 alteration (Group 2, N=10). The bold red and blue vectors represent the grand average change for each group. The light grey vectors show the feedback alteration direction. C) F1 and F2 change for each participant during word-string production for a -F1, +F2 alteration (red circles) and a +F1, -F2 alteration (blue circles). The p-values indicate a group difference. D) Grey vectors represent F1-F2 production change in mel for each participant over the course of altered auditory feedback (blocks 1-4) and unlearning. The bold red and blue vectors represent the grand average change for each group. E) Compensation for altered auditory feedback for blocks 1 to 4 (B1 - B4) and the unlearning (after-effect) trials. There error bars are +/- 1 standard error. The lines indicate significant differences in compensation between blocks corrected for multiple comparisons. See also Figures S1A.

Figure 3. Transfer of sensorimotor adaptation from sentence production to word production with noise-masked speech (Experiment 1). A) Vectors represents F1-F2 production change in mel for the transfer task word of the same colour. Top panel: changes following a -F1, +F2 alteration

(Group 1) during sensorimotor adaptation. Bottom panel: changes following a +F1, -F2 alteration (Group 2) during sensorimotor adaptation. The red and blue vectors represent the grand average change for each group. The light grey vectors show the feedback alteration direction. B) Dark grey vectors represent F1-F2 production change in mel for each participant during the transfer task. Top panel: changes following a -F1, +F2 alteration (Group 1). Bottom panel: changes following a +F1, -F2 alteration (Group 2). The bold red and blue vectors represent the average change for each group. The light grey vectors show the feedback alteration direction. C) F1 and F2 production change for each participant during the transfer task following a -F1, +F2 alteration (red circles) and a +F1, -F2 alteration (blue circles). The p-values indicate a group difference. See also Figures S1B.

Figure 4. Compensation and transfer of altered feedback associated with sentence production (Experiment 1, left side) and word-string production (Experiment 2, right side). The black circles show the magnitude of compensation for each participant during altered feedback; the grey circles represent the magnitude of compensation transfer to isolated word production. The lines join adaptation (A) and transfer (T) for individual participants. The p-values indicate compensation change between adaptation (A) and transfer (T). See also Figures S2-S4.

Methods

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Daniel R. Lametti (danielrlametti@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Forty participants between the ages of 18 and 40 were recruited and divided into four groups of ten. In each group, half of the participants were male. Participation was restricted to native English speakers with no reported history of hearing or speech deficits. The Central University Research Ethics Committee (University of Oxford) approved the experimental protocol and participants gave informed consent. Participants wore circumaural headphones (Sennheiser, HD 280 Pro) and produced words and sentences into a head-mounted microphone (Shure, WH20). Speech-shaped masking noise (presented at 60 dB) was mixed with the speech signal (70-75 dB) and presented back to participants in near-real-time via the headphones using the Matlab-based program Audapter [41,42].

METHOD DETAILS

Procedure: Experiment 1

In Experiment 1, twenty participants read aloud sentences presented on a computer display. Fifty unique sentences were drawn from the Harvard sentences ([43], see Table S1 and S2). The sentences averaged eight words in length and were designed to be phonetically balanced. Pilot testing with male and female speakers confirmed that the sentences yielded formant patterns that spanned the entirety of the vowel space. Participants had 4.5 seconds to read each sentence. The inter-trial-interval was 2.0 seconds. During the experiment, participants produced the same set of 50 sentences seven times (*Production blocks*) for a total of 350 trials. The seven production blocks were carried out under three conditions: 1) two under normal auditory-feedback (*Baseline-phase*), 2) four under altered auditory-feedback (*AAF-phase*; see *Real-Time Feedback Alteration*, for details), and 3) one under normal feedback (*Unlearning Phase*). Each production block took 5.5 minutes.

In addition, participants produced three *Transfer blocks* consisting of the ten monosyllabic words, ‘bed’, ‘bid’, ‘bad’, ‘bod’, ‘bee’, ‘boo’, ‘hood’, ‘bard’, ‘bird’ and ‘bud’, presented on the screen one at a time. The words were chosen because they contained vowels that collectively span the English workspace [44]. These words were not included in any of the 50 sentences used during the Production blocks. Each word was displayed five times, totaling 50 trials, in a fully randomized order. Participants had 2.0 seconds to say each word and the inter-trial-interval was 1.5 seconds. During

these Transfer blocks, rather than the participant's speech feedback signal, only speech-shaped masking noise was presented over the headphones [3,45]. The noise was scaled in amplitude to match the amplitude envelope of the speech signal (70-75 dB). Thus, auditory feedback was significantly masked during the fifty trials (i.e. the signal to noise ratio was zero dB). By blocking sensory feedback during the *Transfer blocks* we aimed to limit feedback-driven unlearning [46]. The three Transfer blocks were carried out at the following time-points: 1) preceding the second Baseline Production block (*Pre-Baseline*), 2) preceding the first AAF Production block (*Pre-AAF*), and 3) following the last AAF Production block (*Post-AAF*). Figure 1A shows a schematic of the test sequence.

Procedure: Experiment 2

In Experiment 2, twenty different participants underwent the same sequence of *Production* and *Transfer* blocks as in Experiment 1. However, the seven Production blocks consisted of word-strings constructed from permutations of the ten words produced in the Transfer Blocks. The word-strings each contained eight words, matching the average length of the sentences in Experiment 1. A set of 50 unique word-strings was generated pseudo-randomly, such that each of the ten words would be produced 40 times in the set. The same 50 word-strings were produced in each Production block, with the order randomized between blocks.

Real-time Feedback Alteration

To induce sensorimotor adaptation, a key acoustic property of vowels—the first (F1) and second (F2) formant frequency—was altered and played back to participants in near-real-time (15 ms delay) during production. In order to account for the potentially large differences in F1 and F2 in Hz between vowels, the formant alteration was applied in *mels*—a commonly used, perceptually normalized scale characterizing the changes in frequency that are judged by listeners to correspond to equal changes in pitch [47]. The transformation from Hz to mel was:

$$\text{mel} = 1127.01048 \times \log(1 + \text{hz}/700)$$

Within the two experiments, half of the participants (five males and five females) experienced a 49.5 mel decrease in first formant (F1) production and a 49.5 increase in second formant (F2) production, for a combined perturbation of 70 mels in F1/F2 space (Figure 1B, top). The remaining ten participants experienced a perturbation in the opposite direction: a 49.5 mel increase in F1 and a 49.5 decrease in F2 (Figure 1B, bottom). These opposing alterations were built up linearly over the first 25 trials of the third Production block and held constant until the end of the sixth Production block.

Acoustic Analysis

Speech was recorded at 16000 Hz in Matlab and analyzed using Praat [48]. All vocalized/periodic portions of the acoustic signal were isolated (i.e. pauses and unvoiced consonants were eliminated) using Praat's autocorrelation method [49]. F1 and F2 values were then computed from these segments using Linear Predictive Coding (LPC) analysis. Within each Production block, F1 and F2 values were averaged across each sentence (Experiment 1) or word string (Experiment 2). In an additional analysis, for each of the individual words that made up the word strings produced in Experiment 2, F1 and F2 were averaged over a 40 ms window at the centre of each vowel.

For the Transfer blocks, the voiced segment of each word was isolated, and F1 and F2 values were computed using LPC analysis. Within each Transfer block, F1 or F2 values that differed from the mean by more than three standard deviations (computed separately for each word) were excluded (2.3% of the data in Experiment 1 and 1.8% of the data in Experiment 2). F1 and F2 values were then averaged for each of the ten transfer words. The average fundamental frequency (F0) was also computed for each sentence/word-string in the Production blocks and for each word in the Transfer blocks.

To assess compensation related to altered auditory feedback, changes in F1 and F2 frequency associated with sensorimotor adaptation and transfer of adaptation were projected onto a vector in F1-F2 space that perfectly opposed the direction of the applied change in the sound of the voice (Figure 1B). That is, compensation was defined as the scalar projection of the production change vector onto the inverse of the vector representing the feedback shift [18]. To do this, the angular difference between the inverse shift vector and the vector representing production change in F1-F2 space was found. The cosine of this difference was then multiplied by the magnitude of production change. In this way, the degree to which the observed change in formants precisely countered the perturbation was quantified.

Prior to altered feedback, formant production was similar across the groups in each experiment and stable during baseline production. In Experiment 1, F1/F2 frequency averaged 600/1621 Hz during the *Pre-Baseline* transfer blocks and 604/1615 Hz during the *Pre-AAF* transfer blocks. In Experiment 2, F1/F2 frequency averaged 611/1616 Hz during the *Pre-Baseline* transfer blocks and 611/1622 Hz during the *Pre-AAF* transfer blocks. In no case did changes in formant frequency production between the *Pre-Baseline* transfer test and the *Pre-AAF* transfer test approach statistical significance.

QUANTIFICATION AND STATISTICAL ANALYSIS

In both experiments, the change in produced F1 and F2 frequencies was computed between the sentences/word-strings in the second Production block (i.e. the baseline block immediately prior to

the onset of altered feedback) and the sixth Production block (i.e. the last block under conditions of altered feedback). Similarly, the change in produced F1 and F2 frequencies was measured between the words in the second Transfer block (i.e. immediately preceding altered feedback) and the third Transfer block (i.e. immediately following altered feedback). Altered-feedback related changes in F1 and F2 frequency and the index of compensation were assessed using repeated-measures ANOVA and two-tailed t-tests. Within individual participants, feedback related changes in compensation were assessed using one-sample t-tests. The significance level was 0.05 and corrected for multiple comparisons using the Holm-Bonferroni method. The sample size (N = 10 per group) was chosen based on prior work in which 8-12 participants showed significant sensorimotor learning (at the group level) in response to real-time formant manipulations [3,16,50,51].

DATA AND SOFTWARE AVAILABILITY

All data in the experiment and analysis code are available from the lead contact upon request.

Supplemental Data

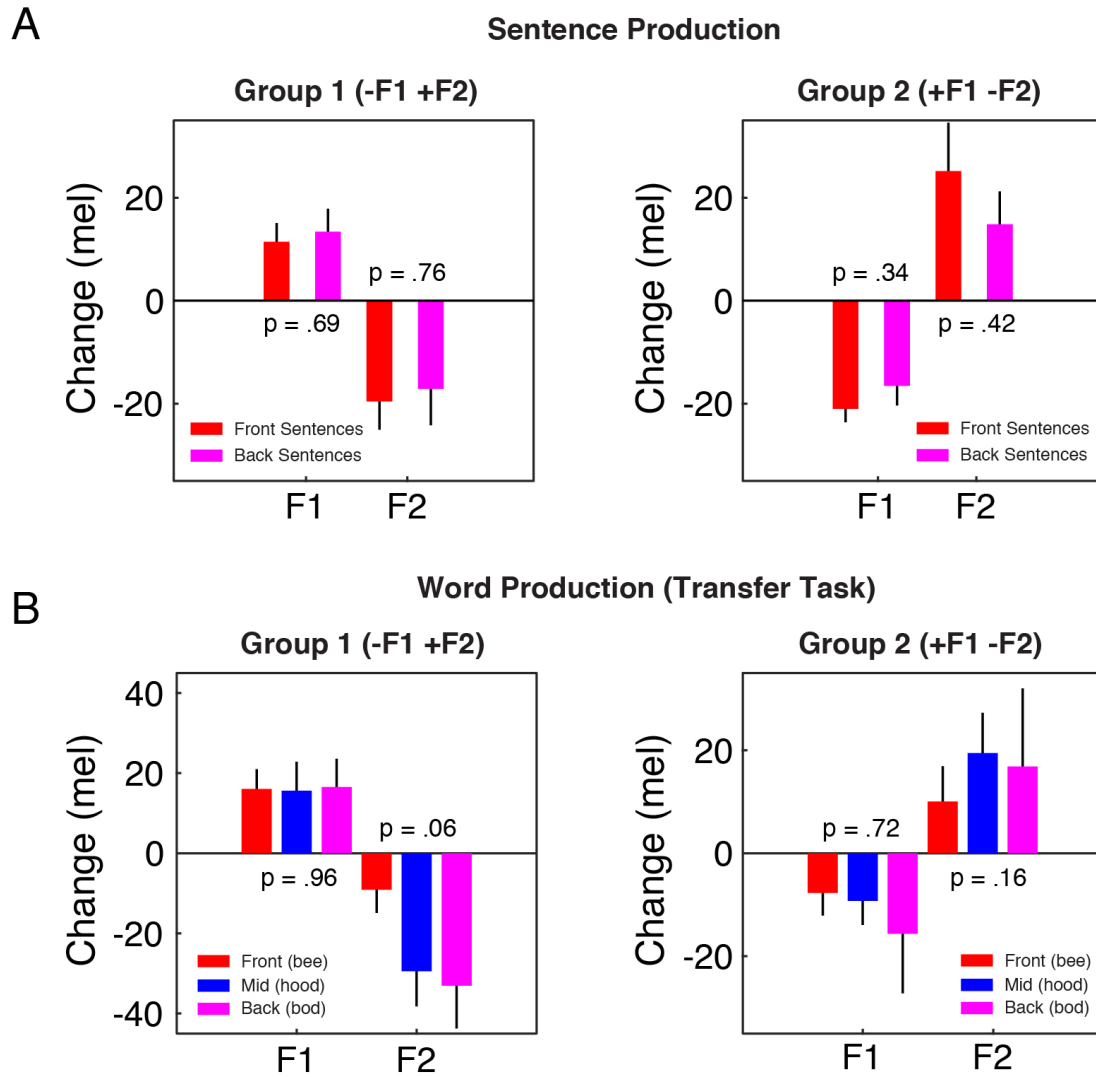


Figure S1. Compensation and transfer did not depend on the location of vowels in the vowel space, related to Figure 2 and Figure 3. A) The figure shows changes in F1 and F2 associated with sensorimotor adaptation for sentences with more front vowels (red/blue) and sentences with more back vowels (magenta/green) (see Table S1 for the sentences used). Group 1 (-49.5 mel F1, +49.5 F2 feedback alteration) is shown on the left and Group 2 (+49.5 mel F1, -49.5 mel F2 feedback alteration) is shown on the right. P-values reflect the outcome of paired sample t-tests comparing changes in formant production between sentences with more front vowels and sentences with more back vowels. B) The figure shows changes in F1 and F2 associated with the transfer of sensorimotor adaptation from sentences to a word with a front vowel (“bee”), a mid vowel (“hood”), and a back vowel (“bod”). Group 1 is shown on the left and Group 2 is shown on the right. P-values reflect the outcome of one-way ANOVA comparing changes in formant production between front, mid, and back vowel words. Error bars reflect +/- 1 standard error.

Supplemental Data

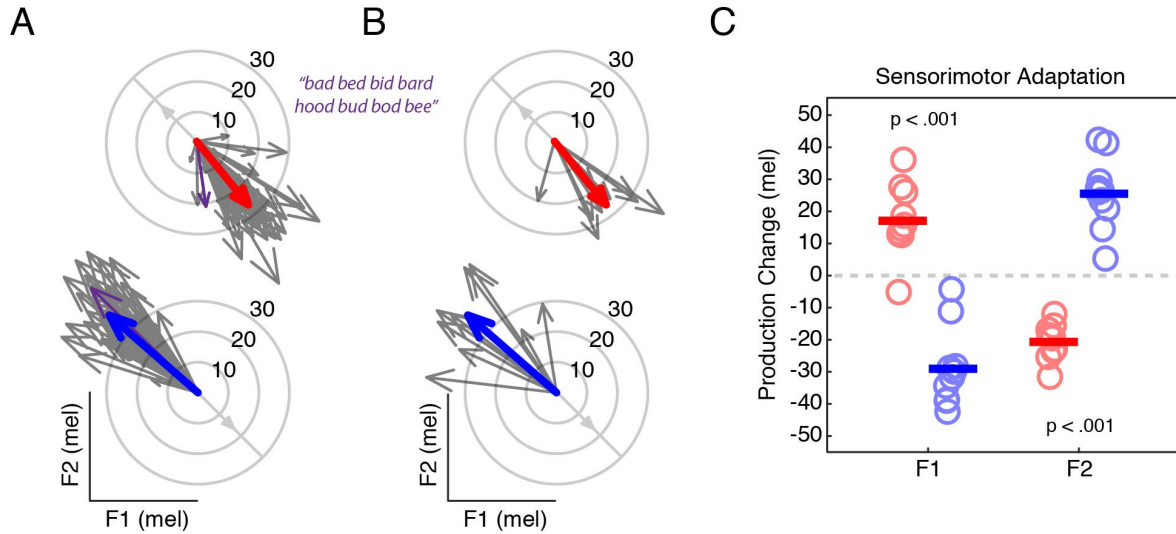


Figure S2. Sensorimotor adaptation was observed during the production of word-strings with varying vowel sounds (Experiment 2), related to Figure 4. A) The dark grey vectors represent F1-F2 production change in mel for each word-string (e.g., ‘bad bed bid bard hood bud bod bee’ is shown in purple). Top panel: changes associated with a -49.5 mel F1 alteration and a +49.5 mel F2 alteration (Group 1). Bottom panel: changes associated with a +49.5 mel F1 alteration and a -49.5 mel F2 alteration (Group 2). The red/blue vectors represent the average change. The light grey vectors show the direction of the feedback alteration. B) Dark grey vectors represent F1-F2 production change in mel for each participant. Top panel: changes associated with a -49.5 mel F1 alteration and a +49.5 mel F2 alteration (Group 1, N=10). Bottom panel: changes associated with a +49.5 mel F1 alteration and a -49.5 mel F2 alteration (Group 2, N = 10). The red/blue vectors represent the average change. The light grey vectors show the direction of the feedback alteration. C) F1 and F2 change for each participant during word-string production for Group 1 (red circles) and Group 2 (blue circles). The manipulation applied to Group 1 led to an increase in F1 production and a decrease in F2 production; and the manipulation applied to Group 2 led to a decrease in F1 production and a increase in F2 production. Compensatory changes in F1 and F2 each differed between the two groups (F1: $t(18) = 8.84$, $p < .001$; F2: $t(18) = 8.76$, $p < .001$). In each group, changes in F1 and F2 each differed from zero ($p < .001$ for all four cases).

Word-String Production

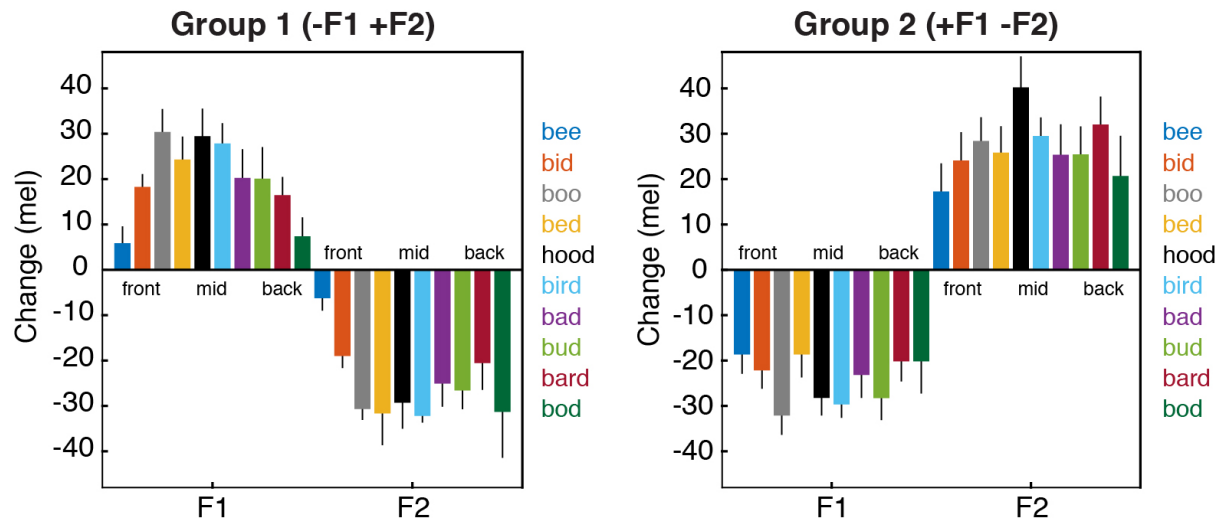


Figure S3. Compensation during word-string production did not depend on the location of vowels in the vowel space (Experiment 2), related to Figure 4. The figure shows changes in F1 and F2 associated with sensorimotor adaptation over a 40 ms at the centre of each of the vowels that made up the word-strings produced in Experiment 2. Group 1 (-49.5 mel F1, +49.5 mel F2 feedback alteration) is shown on the left and Group 2 (+49.5 mel F1, -49.5 mel F2 feedback alteration) is shown on the right. Front, mid, and back refers to the approximate location of the vowel in the vowel space. Error bars reflect ± 1 standard error. With one exception (“bee” in Group 1), compensation for altered feedback was similar between the vowels regardless of where they were located in the vowel space. In Group 1, one-way ANOVA compared changes in F1 and changes in F2 between the vowels (F1: $F(9,90) = 2.89$, $p < .005$, F2: $F(9,90) = 2.31$, $p = 0.021$). Bonferroni-corrected post hoc comparisons found differences in F1 change between “bee” and “boo” ($p = .037$) and differences in F2 change between “bee” and “bird” ($p < .041$). There were no differences in F1 and F2 change between the vowels in Group 2.

Supplemental Data

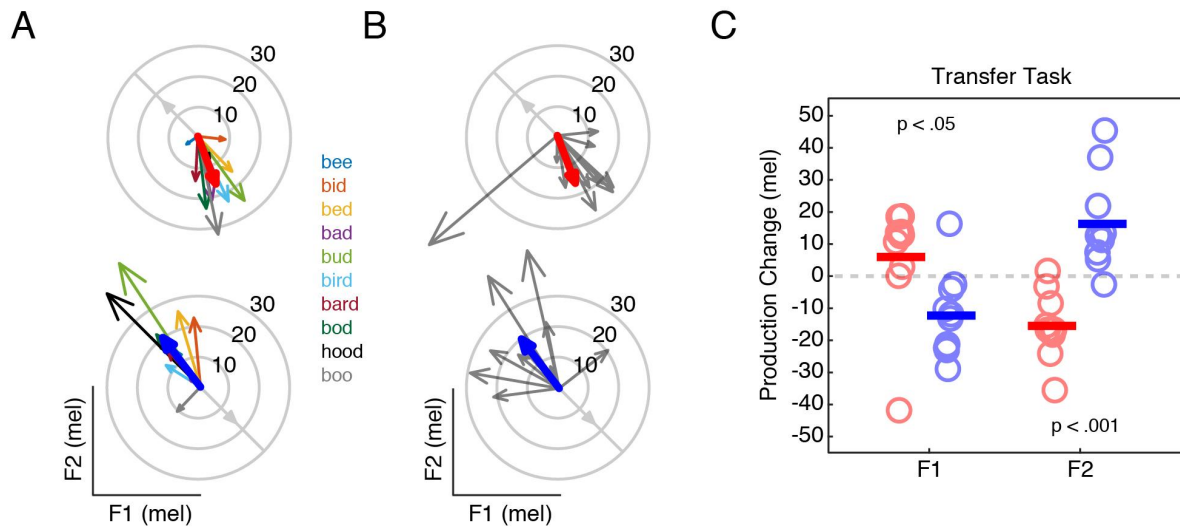


Figure S4. Sensorimotor adaptation transferred from word-string production to word production (Experiment 2), related to Figure 4. A) Vectors represent F1-F2 production change in mel for the transfer task word of the same colour. Top panel: changes associated with a -49.5 mel F1 alteration and a +49.5 mel F2 alteration (Group 1). Bottom panel: changes associated with a +49.5 mel F1 alteration and a -49.5 mel F2 alteration (Group 2). The red/blue vectors represent the average change. The light grey vectors show the direction of altered feedback. B) Dark grey vectors represent F1-F2 production change in mel for each participant during the transfer task. Top panel: changes following a -49.5 mel F1 alteration and a +49.5 mel F2 alteration (Group 1, N=10). Bottom panel: changes following a +49.5 mel F1 alteration and a -49.5 mel F2 alteration (Group 2, N=10). The red/blue vectors represent the average change. The light grey vectors show the direction of altered feedback. C) F1 and F2 production change for each participant during the transfer task for Group 1 (red circles) and Group 2 (blue circles). The direction of altered feedback experienced during sensorimotor adaptation drove significant between-group differences in production change in the transfer task that matched in direction those observed under altered feedback. Changes in F1 and F2 production during the transfer task differed between the groups (F1: $t(18) = 2.65$, $p = .018$; F2: $t(18) = 5.59$, $p < .001$) and, with the single exception of the F1 change in Group 1, all differed from zero ($p = .32$ for the F1 change in Group 1 and $p < .02$ for the remaining three cases).

Supplemental Data

Table S1. Sentences produced in Experiment 1 with more front than back vowels and vice versa, related to Methods.

Experiment 1	Number of Vowels		
Sentences with Primarily Front Vowels	Front	Mid	Back
“It's easy to tell the depth of a well.”	6	1	3
“These days a chicken leg is a rare dish.”	7	1	2
“Ten pins were set in order.”	4	2	1
“The bill was paid every third week.”	6	2	1

Experiment 1	Number of Vowels		
Sentences with Primarily Back Vowels	Front	Mid	Back
“The hogs were fed chopped corn and garbage”	2	1	6
“The boy was there when the sun rose”	3	2	4
“The soft cushion broke the man's fall”	1	3	4
“A saw is a tool used for making boards”	3	0	7

Supplemental Data

Table S2. Sentences Produced in Experiment 1, related to Methods.

<i>The birch canoe slid on the smooth planks.</i>	<i>Read verse out loud for pleasure.</i>
<i>Glue the sheet to the dark blue background.</i>	<i>The frosty air passed through the coat.</i>
<i>It's easy to tell the depth of a well.</i>	<i>The crooked maze failed to fool the mouse.</i>
<i>These days a chicken leg is a rare dish.</i>	<i>Adding fast leads to wrong sums.</i>
<i>Rice is often served in round bowls.</i>	<i>The show was a flop from the very start.</i>
<i>The juice of lemons makes fine punch.</i>	<i>A saw is a tool used for making boards.</i>
<i>The box was thrown beside the parked truck.</i>	<i>The wagon moved on well oiled wheels.</i>
<i>The hogs were fed chopped corn and garbage.</i>	<i>March the soldiers past the next hill.</i>
<i>Four hours of steady work faced us.</i>	<i>A cup of sugar makes sweet fudge.</i>
<i>A large size in stockings is hard to sell.</i>	<i>Place a rosebush near the porch steps.</i>
<i>The boy was there when the sun rose.</i>	<i>Both lost their lives in the raging storm.</i>
<i>A rod is used to catch pink salmon.</i>	<i>The slush lay deep along the street.</i>
<i>The source of the huge river is the clear spring.</i>	<i>A wisp of cloud hung in the blue air.</i>
<i>Kick the ball straight and follow through.</i>	<i>A pound of sugar costs more than eggs.</i>
<i>Help the woman get back to her feet.</i>	<i>The fin was sharp and cut the clear water.</i>
<i>A pot of tea helps to pass the evening.</i>	<i>The play seems dull and quite stupid.</i>
<i>Smoky fires lack flame and heat.</i>	<i>Bail the boat to stop it from sinking.</i>
<i>The soft cushion broke the man's fall.</i>	<i>The term ended in late June that year.</i>
<i>The salt breeze came across from the sea.</i>	<i>A tusk is used to make costly gifts.</i>
<i>The girl at the booth sold fifty bonds.</i>	<i>Ten pins were set in order.</i>
<i>The small pup gnawed a hole in the sock.</i>	<i>The bill was paid every third week.</i>
<i>The fish twisted and turned on the bent hook.</i>	<i>The beauty of the view stunned the young boy.</i>
<i>Press the pants and sew a button on the vest.</i>	<i>Two blue fish swam in the tank.</i>
<i>The swan dive was far short of perfect.</i>	<i>Her purse was full of useless trash.</i>
<i>It snowed, rained, and hailed the same morning.</i>	<i>The colt reared and threw the tall rider.</i>