

Sensorimotor Adaptation of Vocal Pitch Is Impaired in Cerebellar Ataxia

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Abstract

■ Sensory errors, mismatches between predicted sensory outcomes of movement and reafferent sensory feedback, drive changes in the feedforward control of future motor behavior that correct for those errors. Across a wide variety of motor behaviors, individuals with cerebellar damage show impairments in these corrections, strongly suggesting a key role of the cerebellum in sensorimotor adaptation. However, the extent to which the cerebellum is involved in controlling vocal pitch is currently unknown. Crucially, vocal pitch differs in several ways from other systems that suggest it relies more on feedback than feedforward control. Adaptation itself also differs in vocal pitch: Rather than the gradual buildup/decay of learning seen in other systems, pitch adaptation and deadadaptation are almost immediate. Together, this questions whether adaptation

in vocal pitch relies on the same mechanism as other motor domains. Here, we test the hypothesis that the cerebellum underlies sensorimotor adaptation in vocal pitch, testing the domain generality of this neurocomputational process. In both sustained vocalization and a more natural word production task, individuals with cerebellar ataxia fail to adapt to external auditory perturbation of vocal pitch. The lack of adaptation observed, compared to the impaired but present adaptation seen in other systems, suggests that the cerebellum plays an especially critical role in maintaining accurate control of vocal pitch. Conversely, we failed to detect a previously observed increase in online compensation to vocal pitch errors in ataxia, potentially suggesting this may be an idiosyncratic change in control rather than a common trait in this population. ■

INTRODUCTION

Vocal pitch is an important component of spoken communication, conveying pragmatic and, in some languages, lexical information. Auditory feedback plays a critical role in accurately producing pitch, shown experimentally when speakers adjust their vocalizations to counter external auditory perturbations of their perceived pitch (e.g., Jones & Munhall, 2000, 2002, 2005). When speakers' perceived pitch shifts up or down while speaking, they adjust their fundamental frequency (the rate at which the vocal folds vibrate, which is the physical correlate of pitch) in the opposite direction. These adjustments occur over multiple timescales and involve different underlying mechanisms—speakers reactively fine-tune their pitch in a feedback-driven response to unexpected perturbations during ongoing vocalizations (Hain et al., 2000; Burnett, Freedland, Larson, & Hain, 1998), characterized by fast reflexive responses that begin ~150–200 msec after the onset of the perturbation. Conversely, when the perturbation is consistently applied across repeated productions, speakers prospectively adjust their feedforward control of pitch to oppose the expected shift on future trials (Alemi, Lehmann, & Deroche, 2020; Behroozmand & Sangtian, 2018; Jones & Munhall, 2000, 2002, 2005). This latter process, sensorimotor adaptation, is thought to be

driven by comparing sensory predictions with incoming reafferent feedback; any discrepancies lead to updates to the internal models used in feedforward control (Parrell & Houde, 2019; Shadmehr & Krakauer, 2008).

Sensorimotor adaptation is thought to be driven largely by the cerebellum, reflected by impaired adaptation across multiple motor domains in individuals with cerebellar ataxia (CA), including oculomotor control, reaching, locomotion, and oral articulation (Parrell, Kim, Breska, Saxena, & Ivry, 2021; Parrell, Agnew, Nagarajan, Houde, & Ivry, 2017; Manto et al., 2012; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007; Morton & Bastian, 2006; Smith & Shadmehr, 2005; Flament, Ellermann, Kim, Ugurbil, & Ebner, 1996; Martin, Keating, Goodkin, Bastian, & Thach, 1996). Conversely, individuals with CA exhibit intact reflexive feedback-based responses in these domains, differing little from neurobiologically healthy (NH) individuals in the magnitude of online compensatory responses (Parrell et al., 2021; Zimmet, Cao, Bastian, & Cowan, 2020; Morton & Bastian, 2006). When exposed to unexpected, brief pitch perturbations, however, individuals with CA show larger feedback-driven reflexive responses than NH speakers (Houde et al., 2019; Li et al., 2019), suggesting that pitch control may differ in fundamental ways from oral articulation and other, nonspeech, motor domains.

Additionally, relative to controlling oral articulation, managing pitch is hypothesized to rely more directly on sensory feedback control than predictive, feedforward

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control. For example, the accurate control of vocal pitch and loudness rapidly declines in postlingually deaf individuals compared with the much slower changes in oral articulation in this population (Perkell et al., 1997; Cowie & Douglas-Cowie, 1992; Lane & Webster, 1991). Relatedly, producing a pitch contour—that is, realizing a sequence of high and low pitches to indicate prosodic events—relies on achieving pitch values relative to previous pitch targets, rather than on realizing absolute spatial targets (Wagner & Watson, 2010), as in oral articulation. Most strikingly, sensorimotor adaptation to pitch perturbations differs in several other important ways from patterns observed in oral articulation (and other motor domains). Adaptation across reaching, walking, eye movements, and oral articulation shows a gradual buildup over multiple trials, as well as a gradual return to baseline behavior once the perturbation is removed, and is consistently observed across studies. Conversely, pitch adaptation is sudden, stabilizes after only a few trials, disappears rapidly at perturbation removal (Alemi et al., 2020; Behroozmand & Sangtian, 2018; Keough, Hawco, & Jones, 2013; Jones & Keough, 2008), and varies substantially in magnitude across and within studies (Kapsner-Smith, Abur, Eadie, & Stepp, 2024).

These differences in controlling pitch relative to oral articulation raise questions about whether sensorimotor adaptation to pitch perturbations relies on a similar cerebellar learning circuit as oral articulation (and other motor domains). To answer this question, we test whether adaptation to perturbations of vocal pitch is impaired in individuals with CA. In addition, we measure online compensatory responses to pitch perturbations in the same cohort to (1) replicate previous findings of enhanced compensatory responses in CA compared with NH and (2) examine the potential relationship between impairments in sensorimotor adaptation and increases in feedback-based compensatory responses in CA, based on the hypothesis that enhanced compensatory responses indicate reorganization in the balance between feedforward and feedback control subsequent to impairments in the feedforward control system (Houde et al., 2019).

METHODS

Participants

Forty-three individuals with CA (17 men, 26 women; mean age = 51 years, $SD = 14$, age range: 21–74 years) and 48 age- and sex-matched NH individuals (18 men, 30 women; mean age = 53 years, $SD = 16$, age range: 22–80 years) participated in the study. A subset of these participants also completed Experiment 3 (CA: 30 total, 14 men and 16 women; mean age = 50 years, $SD = 15$, age range: 21–75 years; NH: 27 total, 11 men and 14 women; mean age = 50 years, $SD = 16$, age range: 22–77 years) and Experiment 4 (CA: 17 total, five men and 12 women; mean age = 51 years, $SD = 14$, age range: 21–73 years; NH: 17 total, nine men and eight women; mean age = 42 years, $SD = 15$, age range: 22–77 years). All participants

completed Experiments 1 and 2. The sample size was determined with reference to previous studies on adaptation and compensation in individuals with CA. Differences in behavior between CA and NH in feedback-based responses to vocal pitch perturbations have been observed in the studies by Houde and colleagues (2019), which included 16 participants with CA and 11 NH participants, and Li and colleagues (2019), which included 12 participants with CA and 12 NH participants. Our final experiment (see Table 1), added post hoc after the first series of experiments, matched these sample sizes; all other studies had substantially larger samples. All participants were native American English speakers and reported no hearing, speech, language, or neurological impairments other than CA. The etiology of individuals with CA was heterogeneous, but most received a diagnosis of some type of spinocerebellar ataxia (SCA) from their neurologist (Table 1). A subset of these individuals had also received a confirmation of spinocerebellar ataxia type by genetic testing. Detailed information about the exact lesion location or affected cerebellar regions is not currently available but would be expected to be fairly diffuse given the preponderance of degenerative SCA in our sample. All participants were assessed on their performance in executive functioning, spatial cognition, language, and affect, using the Cerebellar Cognitive Affective Syndrome scale. In addition, cognitive functioning was evaluated using the Montreal Cognitive Assessment. Individuals with CA received additional assessments to score the severity of their ataxia with the Scale for Assessment and Rating of Ataxia and to evaluate whether neurologic issues unrelated to ataxia were present with the Inventory of Non-Ataxia Signs. Participant hearing was tested with a Hughson–Westlake hearing screening, but given the prevalence of high-frequency hearing loss in older adults, participants were not excluded based on their hearing thresholds. No participant used assisted hearing devices. Participants were monetarily compensated for their participation. All procedures were approved by an institutional review board at the University of California, San Francisco (IRB protocol no. 2017-1128). Participants provided written informed consent before participation.

Software/Hardware

Participants' speech was recorded at 48 kHz using a Sennheiser MKE 600 shotgun microphone and a Focusrite Scarlett 2i2 sound card and downsampled to 16 kHz and processed (and, on some trials, perturbed), using Audapter (Cai, Beal, Ghosh, Guenther, & Perkell, 2014; Cai, Boucek, Ghosh, Guenther, & Perkell, 2008; Tourville, Reilly, & Guenther, 2008). The resulting output was played back to participants at ~80 dB SPL in near real time over closed-back, circumaural Beyerdynamic DT 770 PRO 250 Ω headphones. The output signal was calibrated each time before the start of the experiment with a CM-140 Checkmate SPL sound pressure meter, confirming that masking

Table 1. Participant Details for Individuals with CA

<i>Participant</i>	<i>Age</i>	<i>Sex</i>	<i>Subtype</i>	<i>MoCA</i>	<i>SARA</i>	<i>CCAS Raw</i>	<i>CCAS # Pass/Fail</i>	<i>INAS</i>
<i>Experiments 1 and 2</i>								
CA001	46	F	AOA2	26	24	95	2	6
CA031	65	F	SCA6	28	16	109	0	6
CA073	74	M	SCA6	23	9	91	2	3
CA086	70	F	CANVAS	23	20.5	88	4	8
CA085	52	F	Tumor	25	9	92	0	5
CA091	54	F	SCA14	29	8.5	103	0	2
CA092	39	F	SCA3	29	17.5	97	0	9
CA094	52	F	SCA5	28	13	90	2	5
CA062	32	M	SCA2	23	23.5	77	5	9
CA060	69	M	SCA2	23	10	83	3	2
CA095	44	F	SCA2	28	7.5	90	2	7
CA024	55	F	SCA3	25	18.5	81	3	8
CA089	60	F	SCA8	28	13.5	98	0	3
<i>Experiments 1, 2, and 3</i>								
CA088	25	F	SCA	25	11	77	3	2
CA103	63	M	SCA8	26	15.5	92	1	5
CA093	39	M	SCA8	26	2.5	99	1	3
CA098	59	M	SCA6	25	10	106	1	3
CA106	24	M	SCA16	27	20.5	81	4	1
CA096	62	M	SCA3	21	13	75	5	10
CA115	34	M	SCA2	30	11.5	111	0	7
CA109	52	M	Idiopathic	24	27	74	3	6
CA107	64	M	SCA2	27	11	91	1	5
CA111	41	F	SCA3	27	9	90	1	2
CA122	73	F	SCA8	26	19	79	4	7
CA065	44	M	SCA2	28	6.5	102	1	1
CA116	75	F	SCA3	26	1	102	2	3
CA069	39	F	SCA1	29	1	109	0	4
<i>Experiments 1, 2, 3, and 4</i>								
CA105	65	F	SCA27	27	1	107	0	1
CA110	60	M	SCA2	25	12	95	2	5
CA112	32	F	SCA5	29	2	111	0	2
CA114	52	F	SCA4	27	1	100	2	0
CA121	35	M	SCA4	23	10.5	89	1	3
CA119	35	F	SCA3	30	1	114	0	1

Table 1. (continued)

Participant	Age	Sex	Subtype	MoCA	SARA	CCAS Raw	CCAS # Pass/Fail	INAS
CA124	68	F	SCA2	24	17.5	84	1	5
CA043	52	F	SCA2	27	10	105	1	13
CA008	71	F	SCA3	27	30	93	1	21
CA126	43	M	SCA8	22	15	65	6	13
CA125	53	M	SCA8	25	9.5	90	1	11
CA030	63	F	SCA3	28	6	108	0	2
CA108	47	F	SCA2	30	14	115	0	5
CA118	43	M	SCA3	21	22	62	7	10
CA123	56	F	SCA5	28	12.5	92	2	2
CA127	21	F	SCA13	25	12	94	2	6

SARA: Higher scores indicate more severe ataxia (maximum score: 40). CCAS raw: Lower scores indicate more severe effects of ataxia (maximum score: 120). CCAS Pass/Fail: number of failed tests: 0 = normal, 1 = possible CCAS, 2 = probable CCAS, 3 or more = definite CCAS (maximum: 10). INAS: nonataxia signs; higher scores, more severe (maximum: 16). Two participants were excluded (indicated in gray): CA024 was not able to sustain pitch for the required time, and CA118 did not complete the full set of experiments. CCAS = cerebellar cognitive affective syndrome; INAS = Inventory of Non-Ataxia Signs; MoCA = Montreal Cognitive Assessment; SARA = Scale for Assessment and Rating of Ataxia.

noise, played back via the headphones, had an intensity of ~60 dBA. Although the speech signal was calibrated before the start of the experiment to play at ~80 dB, this calibration set a constant feedback gain applied to the input signal, such that if the speaker changed their intensity during the experiment, the intensity of the feedback signal changed accordingly. The output intensity level was monitored during the study, and in cases where a participant consistently spoke too loudly, which could result in clipping of the audio signal and artifacts in auditory playback, the microphone level was adjusted downward, maintaining the ~80-dB output in the signal that was fed back to the headphones.

All pitch shifts were implemented using the time-domain shifting algorithm in Audapter with a buffer length of 64 samples, which left the remainder of the spectral envelope, including vowel formants, unaffected. The pitch shift algorithm resulted in a measured delay of ~38 msec in the auditory feedback signal delivered to participants, which has been shown not to affect the magnitude of vocal responses (Weerathunge, Abur, Enos, Brown, & Stepp, 2020). To determine an estimate of the a priori frequency range to accurately track pitch in real time, the average fundamental frequency of vocal fold vibration (f_0 , the physical signal underlying the auditory percept of pitch) was estimated in a brief calibration period before each experiment for each participant. The stimuli for these calibration periods matched the stimuli for the relevant experiment. Participants produced one production of this stimulus, and their pitch was tracked using the *pitch* function in MATLAB (The MathWorks, Inc., 2022). Boundaries were generally set 20% above and 20% below the average f_0 ; some speakers required a larger range (two NH/11 CA: 25%, five NH/four CA: 30%, and one CA: 40%) because of

high variability in their produced pitch. Subsequently, during each study, these upper and lower f_0 values were updated after each trial using the same percentage window around the average f_0 of that specific trial. This was done to account for any drift in f_0 over time, which has been observed previously in studies of adaptation and which is also sometimes observed when producing a series of repeated vocalizations (Alemi et al., 2020; Jones & Munhall, 2000).

Experimental Design

Data were collected as part of a larger battery of experiments lasting approximately 9 hr in total, conducted over either 2 days (for individuals with CA) or 1–3 days (for NH individuals). All participants first completed Experiment 1 (examining pitch adaptation), followed by Experiment 2 (examining online, reflexive compensation to sustained mid-utterance perturbations of vocal pitch). On the basis of the adaptation and compensation responses from the first 13 participants with CA and 21 NH participants, a subset of participants (30 CA and 27 NH) additionally completed Experiment 3, examining reflexive compensation to transient perturbations of vocal pitch applied at vocalization onset. Finally, a smaller subset (17 CA and 17 NH) participated in Experiment 4, examining reflexive compensation to transient mid-utterance pitch perturbations. Data from one NH participant (Experiments 1–4) were disregarded because of technical difficulties with the software during collection of the unperturbed production of the sustained vowel, leaving a total of 47 NH participants. Data from two individuals with CA (one participating in Experiments 1–2; the other in Experiments 1–4) were disregarded because these speakers were unable to produce

extended phonation of sufficient duration, resulting in a final data set containing 41 individuals with CA.

The order of the experiments was identical for all participants. Experiment 1, examining adaptation, preceded the three compensation experiments (Experiments 2, 3, and 4). Experiment 1 was administered on a separate day than Experiment 2, 3, and 4 for most participants, except those NH individuals who chose to complete all experiments in a single day (14 NH individuals) and a few individuals with CA who, because of time constraints, did not complete the adaptation study on the first day of their visit (13 individuals with CA). Experiments 3 and 4 always followed Experiment 2 (in that order). Although Experiments 2, 3, and 4 were completed on the same day, they were always separated by other experiments in the larger battery unrelated to vocal pitch control.

During data analysis, we noticed post hoc that 19 of the NH participants performed Experiment 1 and Experiment 2 in reversed order (i.e., Experiment 2 followed by Experiment 1). To test whether the order of performing Experiment 1 and Experiment 2 affected participant responses, we conducted two-sided *t* tests to compare the effects of experiment order on (1) early adaptation in Experiment 1, (2) late adaptation in Experiment 1, (3) the early window of compensation in Experiment 2, and (4) the late window of compensation in Experiment 2. We found no effects of experiment order on any measure (all *ps* > .27). As such, we included data from all participants in our analysis without additionally accounting for this difference in experiment order.

During each experiment, the participants were comfortably seated in front of a computer screen. They were cued to produce speech by a written stimulus appearing on the screen. For all except two experiments (as noted below for part of Experiment 1), participants produced a sustained vowel (/a/ as in “hot”), indicated with the written stimulus “ah.” Participants were instructed to produce this vowel as soon as they saw the stimulus appear on the screen and to vocalize until the stimulus disappeared (after 1.4 sec), keeping their pitch as stable as possible. Pilot testing showed that this duration resulted in vocal productions of ~1 sec. The amplitude, onset time, and duration of vocal productions were monitored on every trial. On trials with vocalization durations <1 sec, participants were reminded to produce the vowel until it disappeared from the screen. When participants began vocalizing > 400 msec after stimulus onset, they were reminded to start sooner. On trials where the speech amplitude was below a preset threshold, they were prompted to speak a little bit louder. The intertrial duration was 1.25 sec with 0–0.25 sec of additional random jitter.

Experiment 1

Experiment 1 (Figure 1B) tested adaptive responses to consistent auditory pitch perturbations in both a word production task and, in a separate session, sustained vocalization. To account for the fact that pitch has been shown, in some cases, to drift over time, especially during sustained

vocalization (Alemi, Lehmann, & Deroche, 2023; Alemi et al., 2020; Jones & Munhall, 2000), we included an additional unperturbed control session for both sustained vocalization and spoken word stimuli. This resulted in four total sessions in this study. During the first two sessions, participants produced the word “bod” (/bad/), cued by the stimulus “bod” on the screen. During the second two sessions, participants produced a sustained vowel /a/, cued by the stimulus “ah.” Each session consisted of 80 trials.

Sessions 1 and 3 (“perturbed” sessions) consisted of a 20-trial baseline phase with no perturbation, a 40-trial exposure phase where pitch was shifted down by 100 cents, and a 20-trial washout phase with veridical feedback. A shift of 100 cents was chosen because larger shifts have been shown to evoke more following responses, potentially because the shift is treated as an external target rather than as a sensory prediction error (Burnett et al., 1998). Sessions 2 and 4 (“unperturbed” sessions) contained the same number of trials as the perturbed sessions (80), with no pitch perturbation applied at any point. Before the first and third sessions, participants produced five practice trials to make sure they understood and produced the target stimuli correctly. These practice trials were always unperturbed. A brief self-timed break occurred every 14 trials. The total duration of Experiment 1, including all four sessions, was ~20 min.

Experiment 2

Experiment 2 (Figure 1C) consisted of 105 trials, during which the participants produced a sustained vowel /a/. The first five trials received no perturbation. During 80 of the remaining 100 trials, pitch was shifted by ± 100 cents (40 trials in each direction) starting 200–500 msec after vocalization onset (randomly applied across trials) and continuing throughout the trial (see Figure 1B). On the remaining 20 trials, the participant received veridical auditory feedback. The 100 trials containing the three conditions (40 shift up, 40 shift down, 20 unperturbed) were randomized across trials. This randomization served to prevent any long-term adaptation of vocal pitch. A short self-timed break occurred every 21 trials. The total study took ~10 min to complete.

Experiments 3 and 4

The formats of Experiment 3 (Figure 1D) and Experiment 4 (Figure 1E) were essentially identical to that of Experiment 2, except for the timing of the pitch perturbation. Whereas the perturbation in Experiment 2 randomly started 200–500 msec after the onset of vocalization and was applied through the remainder of the trial, the perturbation in Experiment 3 always began at the onset of vocalization and was randomly removed 400–550 msec after vocalization (and perturbation) onset (drawn from a normal distribution across trials). In Experiment 4, the perturbation began 200–500 msec after vocalization onset (drawn from a normal distribution across trials), as in

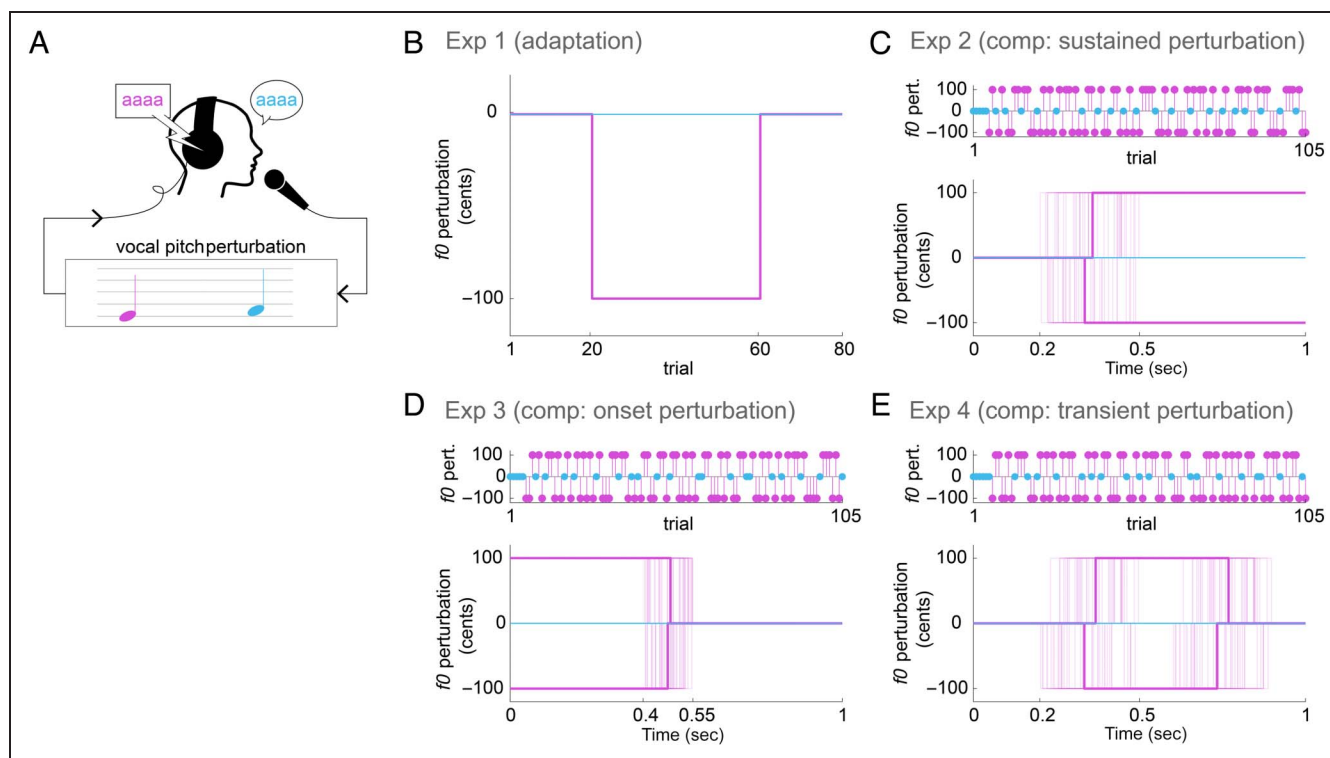


Figure 1. Schematic of experimental design. In all cases, unperturbed productions are shown in cyan, and productions with a vocal pitch perturbation are shown in magenta. (A) Illustration of pitch perturbation. The pitch of participants' produced vocalizations was shifted down by 100 cents and played back to them over headphones in essentially real time (~38-msec delay). (B) Perturbation schedule in Experiment 1, examining across-trial sensorimotor adaptation. The perturbation session (magenta) consisted of a 20-trial baseline phase with no pitch perturbation, a 40-trial exposure phase with a -100-cent perturbation, and a 20-trial washout phase with no perturbation. The control session (cyan) had veridical feedback throughout. (C) Design of Experiment 2, examining within-trial compensatory responses to sustained mid-vocalization perturbations. The perturbation direction was randomized across trials (top). Within each trial, perturbations started between 200 and 500 msec after vocalization onset and remained on until the end of the trial. Thick magenta lines show the mean time course of the perturbation; thin lines show individual trials. Example shown from an individual participant. (D) Design of Experiment 3, examining compensatory responses to transient perturbations beginning at the onset of vocalization, and removed between 400 and 550 msec after vocalization onset. Example perturbation data as in C. (E) Design of Experiment 4, examining compensatory responses to transient perturbations that began 200–500 msec after vowel onset and were removed after 400 msec. Sample perturbation data as in C. Exp = Experiment; comp = compensation; pert. = perturbation.

Experiment 2, but was removed 400 msec after perturbation onset.

Data Analysis

We extracted f_0 using pitch tracking algorithms from Praat (Boersma & Weenink, 2020) embedded within *wave_viewer* (Niziolek & Houde, 2015), a custom-built speech analysis package in MATLAB. The pitch floor in Praat was set at a default value of 75 Hz, and the upper threshold was set at 200 Hz for lower-pitched voices and 300 Hz for higher-pitched voices. The default voicing threshold was 0.45. When these values resulted in errors in pitch tracking (e.g., resulting in large jumps from sample to sample or pitch halving), the Praat pitch tracking parameters were changed on a trial-by-trial basis to remove these errors. Pitch floors were adjusted when pitch halving was observed. As different pitch floors result in different sampling rates in Praat, all trials were resampled to a uniform sampling rate of 100 samples per second. Trials with irresolvable tracking errors in the target window used for

analysis were excluded. Trials on which participants began phonation before the onset of the recording (equivalent to beginning before the stimulus presentation) were also excluded. For Experiments 2–4, trials with a duration less than 1000 msec were excluded, as this was the minimum duration necessary to capture the full dynamics of compensation (pitch perturbation began as late as 500 msec after vowel onset, with 500 msec needed to measure a response plateau). The total numbers of excluded trials were as follows: Experiment 1: 2.54%, $SD = 4.54\%$, range = 0–26% across participants; Experiment 2: 1.83%, $SD = 5.04\%$, range = 0–32%; Experiment 3: 0.80%, $SD = 1.44\%$, range = 0–7.76%; and Experiment 4: 0.63%, $SD = 1.22\%$, range = 0–4.74%.

Experiment 1

To isolate adaptive changes to pitch perturbations, the f_0 for each trial was extracted from a window 50–120 msec after vowel onset to avoid (1) irregularities in pitch production and pitch tracking that frequently occur during

the first few cycles of vocal fold vibration (Kapsner-Smith et al., 2024; Heller Murray & Stepp, 2020) and (2) potential online compensatory mechanisms, which typically start ~150 msec after the onset of a pitch perturbation (Burnett et al., 1998). Pitch values for all trials were transformed to a cent scale to be able to compare responses across participants with different f_0 values (cents are a logarithmic scale used to measure pitch intervals). First, the median f_0 of each of the 10 final trials during the baseline phase for each session was calculated over the 50- to 120-msec window, giving one f_0 value for each trial. Next, for each session, a baseline value was calculated as the median of these trials. This baseline value was then used to convert the pitch trajectories of all the 80 trials in that session to a cent scale using the formula $1200 * \log_2(f_0/f_{0\text{baseline}})$. Next, a single pitch value for each trial was calculated as the median pitch, expressed in cents, in the target time window of 50–120 msec. To account for the observable drift in pitch observed in the unperturbed sessions, especially during sustained vowel production (Figure 2A), f_0 values of all trials in the perturbation sessions were corrected by subtracting the moving average across 15 trials produced during the corresponding unperturbed session (Figure 2A and C, later in this article), consistent with approaches in the recent literature (Gaines, Dale, Houde, & Nagarajan, 2026; Dahl, Cádiz, Zuk, Guenther, & Stepp, 2024; Alemi et al., 2020).

For word production, pitch trajectories in English show a large decline in pitch over the course of the vowel during a trial. It may be that only a part of this pitch contour is adapted (e.g., the first high pitch target) rather than the full trajectory. To assess this possibility, we conducted an additional analysis using generalized additive mixed models (GAMMs) to examine the full time course of pitch values (10–250 msec after vowel onset), comparing the final 10 trials in the baseline phase with early exposure (first 10 trials), late exposure (final 10 trials), and washout phases (first three trials) across the CA and NH groups. Given that minimal changes in pitch were observed over the course of the unperturbed session (Figure 2C), pitch trajectories for this analysis were not normalized to the unperturbed session. Individual models were constructed to test for adaptation within each experimental group separately and, for each phase other than baseline, to test for differences between the CA and NH groups. For the between-group models, trajectories in each phase were first normalized by subtracting the mean baseline trajectory, on a participant-specific basis, to conservatively account for any potential differences in baseline trajectories between groups (although visual inspection of the group means shows broadly similar baseline behavior). The input to these models thus reflects the change in pitch trajectories from behavior in the baseline phase.

In addition to adaptation, we measured any potential compensatory behavior produced in response to the pitch perturbation, over and above changes driven by sensorimotor adaptation. For this analysis, we included only the sustained vowel sessions, as the short duration of the

spoken words prevented measuring this compensatory behavior. Reflexive compensatory responses were measured in a window 200–300 msec after vocalization onset (chosen a priori) and 400–500 msec after onset (chosen after examining the data). For this analysis of compensatory behavior, pitch trajectories (in cents) for each trial were normalized to the average value in that same trial during the 50- to 120-msec window after vocalization onset to isolate within-trial compensatory changes from any across-trial adaptive changes (Raharjo, Kothare, Nagarajan, & Houde, 2021; Franken, Acheson, McQueen, Hagoort, & Eisner, 2019).

Experiments 2–4

Trajectories for each trial were transformed to a cent scale using the median f_0 value in a baseline window spanning the 50-msec window immediately after the onset of the perturbation. For Experiment 3, where the perturbation began immediately at the onset of vocalization, the f_0 value in a baseline window spanning from 50 to 120 msec after vocalization onset was calculated to transform the trajectories to cents. Omitting the first 50 msec avoids the frequent initial transient errors in pitch tracking in this period; note that this window still avoids any potential compensatory behavior driven by the perturbed auditory feedback, which has a latency of ~150 msec (Burnett et al., 1998). Although the normalization procedure during Experiments 2 and 4 differs from that typically used in compensation studies (e.g., Houde et al., 2019), we chose this window to be more consistent across all compensation experiments. Crucially, this normalization window ends before any online compensation can occur, so the average pitch in this window does not differ substantially from the window 100 msec before the perturbation onset, and our choice of normalization did not substantially affect the results. The median trajectory, in cents, was calculated across all unperturbed trials as a measure of participants' typical baseline behavior in the absence of a perturbation (see Supplemental Figure S1). This baseline trajectory was then subtracted from each perturbed trial to derive a normalized trajectory of compensatory behavior. Finally, these normalized compensatory trajectories in trials with an upward pitch perturbation, expected to result in a downward response, were sign-flipped, such that compensation opposing the perturbation was reflected as a positive value in all trials.

Statistical Analysis

For all studies, statistical testing was conducted in R (R Core Team, 2024) using linear mixed effects (LMM) models with the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015). Model selection was conducted using the *buildmer* package to select the best-fitting model (Voeten, 2023). Both forward and backward model selection procedures were applied to ensure robustness and

consistency in model specification. Forward selection was based on likelihood ratio tests, starting with a simple model and sequentially adding predictors and random effects to identify the best-fitting model. Backward elimination started with the full linear mixed-effects model, with fixed-effect terms removed stepwise based on Wald-test p values until only statistically significant predictors remained. Both procedures used the default optimizer (*lmerControl*) to ensure stable model convergence. Using both approaches allowed cross-validation of the final model structure, minimizing the risk of overfitting or model misspecification that could arise from relying on a single selection path. Both forward and backward selection procedures yielded identical results in all cases; therefore, outcomes are reported based on the model obtained through forward selection. The final model was refitted using *lmer*, and statistical significance was assessed by maximum likelihood t tests using the Satterthwaite's method from the *lmerTest* package (Kuznetsova, Brockhoff, & Christensen, 2017). The final fits were evaluated using Type III ANOVAs and the *r.squaredGLMM* function from the *MuMIn* package (Bartoń, 2024).

For each fixed effect in the LMM, we report the F value and corresponding p value, as obtained from the linear mixed-effects analysis. Pairwise post hoc comparisons report marginal means and standard errors. Effect sizes, where applicable, were reported as conditional R^2 values for linear mixed-effects models (using *r.squaredGLMM*) and Cohen's d for post hoc comparisons and t tests (using the *eff_size* from the package *emmeans*; Lenth, 2024). For all experiments, statistical significance was determined using $\alpha = .05$.

The time course analysis of pitch trajectories during adaptation in words was conducted using GAMMs, built with the function *bam* from the *mgcv* package (Wood, 2003, 2004, 2011, 2017; Wood, Pya, & Säfken, 2016) and the *itsadug* package (van Rij, Wieling, Baayen, & van Rijn, 2022) for the figures. We included smooth terms for time by specifying a factor-smooth interaction for each experimental fixed effect (either group or condition), implemented as a thin plate regression with 10 basis splines. To account for interspeaker variability in trajectories, we included a random smooth for each speaker over time, using a factor-smooth interaction spline with 10 basis functions and a first-order difference penalty. Results from the GAMM analysis were corrected for multiple comparisons with false discovery rate with the *p.adjust* function in R (two separate comparisons for the NH and CA groups comparing changes across phases and three comparisons testing for differences between the NH and CA groups in the early exposure, late exposure, and washout phases). Residual autocorrelation was modeled using an AR(1) process. For the within-group analyses, "Condition" was coded using treatment contrasts, with the baseline condition specified as the reference level.

For the figures, we used custom-made scripts in MATLAB, the package *boundedline_plots* (Kearney, 2026) and the code *raincloud_plot* (Allen et al., 2021).

Experiment 1

Experiment 1 included analyses from both adaptation and online compensation during the adaptation task. The initial models for the LMM analysis of sensorimotor adaptation included the fixed effects Phase (baseline, early exposure, late exposure, and washout) and Group (CA vs. NH) and their interactions, as well as random intercepts for individual speakers. Simple contrast coding was used such that the baseline phase served as the reference against which the comparisons were made. The baseline phase consisted of the 10 final baseline trials, the early exposure phase consisted of the first 10 trials of the exposure phase, the late exposure phase included the final 10 trials of the exposure phase, and the washout phase consisted of the first three trials after the perturbation was removed. The early exposure phase was included given results from previous studies indicating that (1) maximum adaptation in pitch studies is typically reached quickly (Alemi et al., 2020) and (2) adaptation may, in some cases, diminish over extended exposure to a perturbation (Alemi et al., 2020). Using 10 trials in each half of the exposure phase allowed us to account for the high variability in f_0 from trial to trial. Conversely, adaptation in pitch has been shown to disappear rapidly (Alemi et al., 2020); using only the first three trials of the washout phase, while introducing some noise because of the small number of trials, is nonetheless necessary to measure this transient behavior.

For all five GAMM analyses (one for each group comparing across phases and three separate analyses comparing between groups in the early exposure, late exposure, and washout phases), the model components were the dependent variable Pitch, the fixed effect (Group or Condition), a smooth over time, and a random smooth over time by speaker. In the between-group comparison, pitch trajectories were normalized by subtracting the mean trajectory in the baseline phase on a per-participant basis, yielding trajectories that represented changes from the baseline behavior.

Compensatory behavior over and above adaptation during sustained vowel production was assessed by comparing pitch trajectories from the final 10 trials of the baseline phase to normalized trajectories (accounting for any adaptation effects) from the 40 trials produced in the exposure phase. Separate analyses were run for values extracted during an early window (200–300 msec after onset of the vocalization) and late window (400–500-msec windows after vocalization onset). The model included the fixed effects Phase (baseline and exposure phase) and Group (CA, NH) and the interaction between the two, as well as random intercepts for individual speakers.

Experiments 2–4

The same initial model structure was used for all three experiments, which included Group (CA, NH), Direction of Perturbation ("up" and "down"), and their interactions as well as random intercepts for individual speakers for

an initial analysis. This analysis tested whether the two groups of participants differed from each other in their compensatory behavior during pitch perturbation. Separate tests were conducted for early (200–300 msec after perturbation onset) and late (400–500 msec after perturbation onset) windows, similar to Experiment 1. An additional window was tested for Experiment 3, 400–500 msec after removing the perturbation, assessing whether participants fully returned to their unperturbed pitch trajectories. The length of the produced vowel was always longer than 1 sec, allowing us to capture this window. To test whether individuals with CA and NH individuals showed compensation, we ran four additional one-sample *t* tests against a normal distribution with 0 mean, one for each group and direction, using the *t* test function in the *stats* package, included in R.

RESULTS

Experiment 1

The goal of Experiment 1 was to examine whether participants with CA, as a group, show reduced adaptation to perturbations of vocal pitch similar to the impaired adaptation observed in CA across all other motor domains that have been examined. Sustained vocalization is the standard behavior examined in studies of vocal motor control using perturbation paradigms with NH speakers and speakers diagnosed with neurodegenerative disorders (Houde et al., 2019; Li et al., 2019; Abur et al., 2018). We thus included one assay of sustained vocalization of the vowel “ah” (/a/) to compare our results with the existing literature on adaptation in NH individuals and individuals with neurological disorders other than ataxia. However, it is not clear what pitch target, if any, participants are using in these tasks. Vocal pitch tends to drift substantially over the course of multiple sustained vocalizations even in the absence of any perturbation (Alemi et al., 2020; Jones & Munhall, 2000), suggesting that speakers may try to match the pitch they were producing at the end of one trial with the pitch at the start of the next trial. Moreover, the adaptive responses to pitch perturbations are larger when participants are instructed to reproduce a particular cued pitch compared to the more common instruction to “maintain” a steady pitch (Keough et al., 2013; Jones & Keough, 2008), suggesting that speakers do not have a particular pitch target during sustained vocalization. Finally, sustained vocalization is a highly unnatural task, with limited ecological validity, and the underlying control mechanisms might differ from pitch control during more typical speech production (Dahl et al., 2024). Thus, it is possible that changes in pitch behavior observed during repeated sustained vocalization reflect changes driven by other processes apart from sensorimotor adaptation, *per se*. To address these concerns, we additionally tested pitch adaptation during the production of a simple spoken word (“bod,” /bad/). Although we present the sustained vowel task first to be consistent with the general approach in the

literature, the word production task always occurred before the vowel production task during data collection.

Adaptation

In the sustained vowel production task (Figure 2A and B), both speakers with CA and NH speakers showed higher pitch values during the pitch perturbation, shown by a main effect of Phase, $F(3, 2748) = 10.69, p < .001, R^2 = .24$. Although there was no overall difference between NH participants and participants with CA, a significant interaction between Group and Phase was observed, consistent with our initial hypothesis of reduced adaptation in the CA group, $F(3, 2748) = 2.80, p = .038$.

NH speakers increased their pitch from baseline immediately after exposure to the perturbation (26 ± 5 cents), $t(2753) = 4.69, p < .001, d = 0.31$, and maintained roughly the same level through the final 10 trials of the exposure phase (21 ± 5 cents), $t(2753) = 3.88, p < .001, d = 0.26$, and into the first three repetitions of the washout phase (25 ± 8 cents), $t(2754) = 3.07, p = .012, d = 0.30$.

The speakers with CA showed a different pattern. Whereas the final 10 trials of the exposure phase were produced at a higher pitch compared to the baseline (22 ± 6 cents), $t(2754) = 3.75, p = .001, d = 0.27$, similar to the NH group (NH-CA: 5 ± 11 cents), $t(133) = 0.43, p = .67$, no significant adaptation was observed during the first 10 trials of the exposure phase in the CA group (8 ± 6 cents), $t(2754) = 1.28, p = .58$, unlike the immediate adaptation observed in the NH group (NH-CA: 24 ± 11 cents), $t(133) = 2.102, p = .037, d = 0.29$. Similarly, the changes observed at the end of the exposure phase in the CA group did not carry over into the washout phase, where participants with CA showed no observable adaptation (7 ± 9 cents), $t(2754) = 0.77, p = .87$, again differing from the clear retention of adaptation seen in the NH group, although the direct comparison between groups failed to reach statistical significance (NH-CA: 24 ± 14 cents), $t(330) = 1.68, p = .094$.

In the word production task (Figure 2C and D), we again found a main effect of Phase, suggesting an overall presence of adaptation, $F(3, 2726) = 8.73, p < .001, R^2 = .29$. As for the vowel production task, no main effect of Group was found, $F(1, 93) = 1.10, p = .30$, but we did observe an interaction between Group and Phase, $F(3, 2726) = 2.94, p = .032$.

Whereas the NH group showed an increase in pitch during the early part of the exposure phase compared with the baseline phase (17 ± 6 cents), $t(2729) = 2.72, p = .033, d = 0.18$, no such adaptive response was observed in the CA group (-9 ± 7 cents), $t(2738) = -1.30, p = .57$. There was a steady decline in pitch throughout the rest of the experiment observable in both groups. For the NH group, this resulted in a return of pitch to roughly the baseline level during the late exposure and washout phases (NH: late exposure: -0.5 ± 7 cents, $t(2730) =$

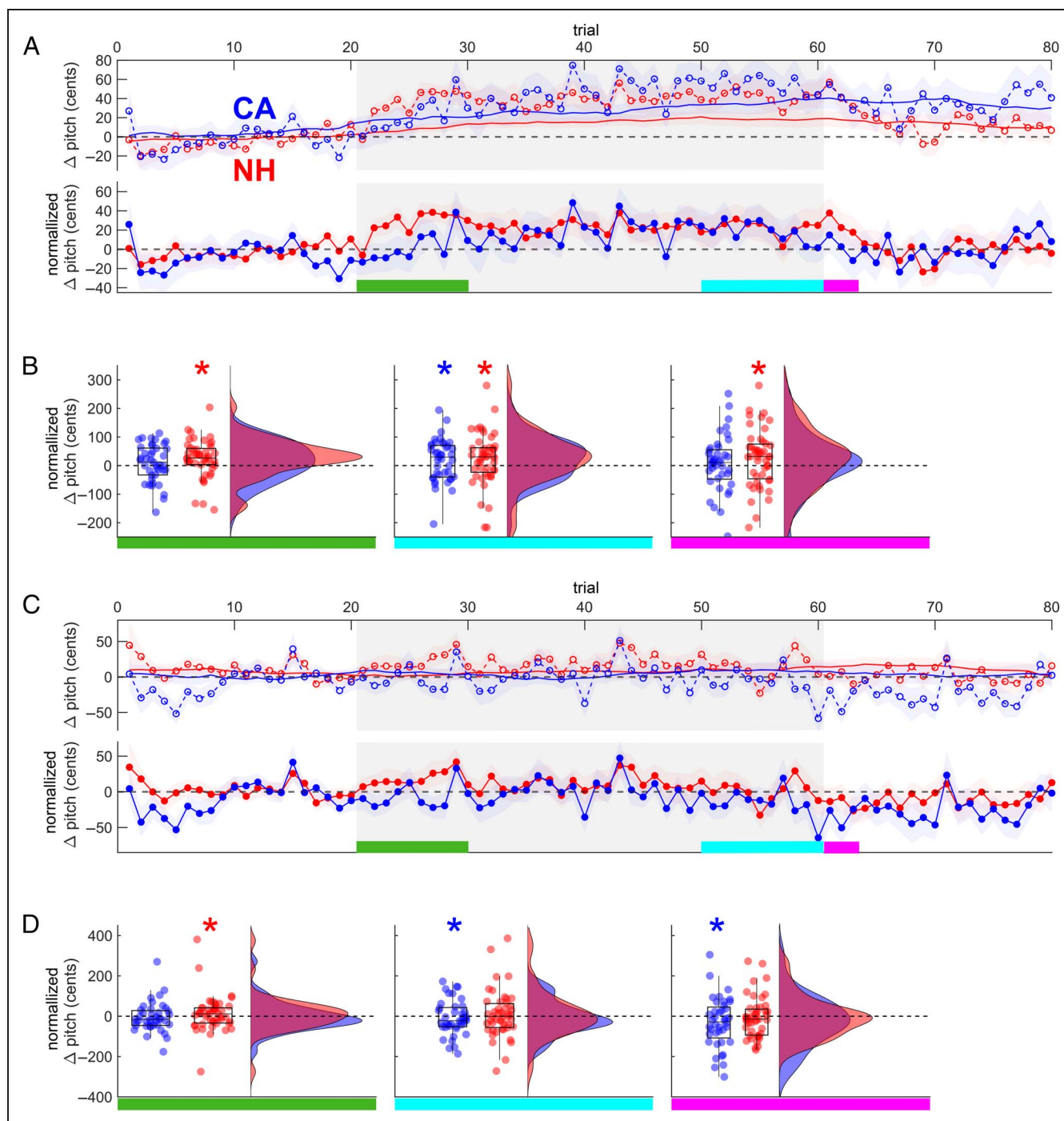


Figure 2. Adaptation results from Experiment 1. In all panels, blue indicates values for speakers with CA, and red indicates values for NH speakers. Red stars indicate a difference from the baseline for NH; blue stars indicate a significant difference from the baseline for the speakers with CA. (A, top) Pitch values during vowel production in the unperturbed (solid lines) and perturbed (dashed lines) sessions. (Bottom) Pitch values in the perturbed session, normalized by a moving average of the unperturbed session, during vowel production. Shaded areas represent standard error. Gray shading indicates exposure phase. Dark green, cyan, and magenta shading represent trials used to analyze the early exposure, late exposure, and washout phases, respectively. (B) Normalized pitch values produced in the perturbed session of the vowel production study in the early exposure phase (left), late exposure phase (middle), and washout phase (right). Dots and density plots represent participant means. (C–D) As for A and B, showing data for word production.

-0.08 , $p = 1.00$; washout: -17 ± 9 cents, $t(2729) = -1.80$, $p = .27$). For the CA group on the other hand, this same downward trend resulted in a lower pitch during the late exposure and washout phases than during the

baseline phase (CA: late exposure: -21 ± 7 cents, $t(2738) = -3.05$, $p = .012$, $d = -0.22$; washout: -37 ± 10 cents, $t(2733) = -3.67$, $p = .001$, $d = -0.40$). Although the pitch was higher for the NH than the CA

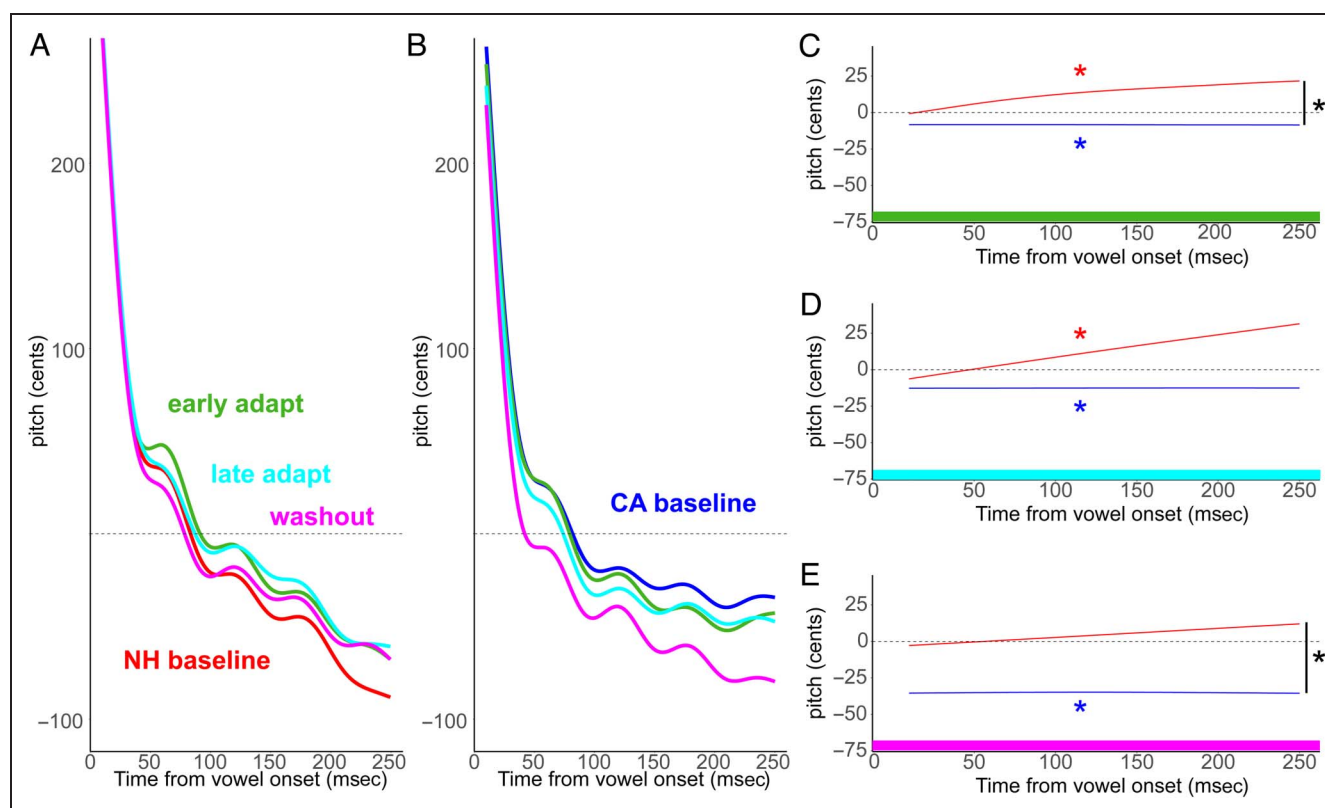


Figure 3. Results of GAMM analyses of the word production task from Experiment 1. In all panels, red indicates values for NH speakers, and blue indicates values for speakers with CA. Shading shows standard error. Red stars indicate a difference from the baseline for NH; blue stars indicate a significant difference from the baseline for the speakers with CA; black stars indicate significant differences between the two groups ($p < .05$). (A) Pitch trajectory smooths during word production for NH speakers in the baseline (red), early exposure (green), late exposure (cyan), and washout (magenta) phases. (B) Pitch trajectory smooths during word production for speakers with CA in the baseline (blue), early exposure (green), late exposure (cyan), and washout (magenta) phases. (C) Pitch trajectory smooths in the early exposure phase, normalized by subtracting the average trajectory on a per-participant basis in the baseline phase. (D–E) As for C, showing the late exposure and washout phases, respectively.

group across all phases after the baseline, likely driving the significant interaction between group and phase, direct comparisons between the NH and CA groups in each phase did not reach statistical significance (all p s $> .11$).

Unlike the steady-state pitch produced in sustained vocalization, however, pitch production in isolated English words consists of a large decline in pitch over the course of the vowel (Figure 3A and B). As a follow-up test, we used GAMMs to compare the full pitch trajectories produced in the early exposure, late exposure, and washout phases with the baseline phase to ensure that the lack of adaptation we observed in the CA group was not because of our chosen time window failing to capture changes in some part of this trajectory. For this post hoc analysis of the word production task, we used nonnormalized f_0 trajectories, as (1) visual inspection of the data showed no consistent trends in the control session (Figure 2C) and (2) additional post hoc analyses (Supplemental Tables S7–S8) showed largely comparable results between with and without normalization with the control session.

The results of these models largely replicated the window-based approach. NH speakers (Figure 3A; 56.8% variance explained by the model) showed increased pitch consistent with adaptive responses in both the early exposure phase ($\beta = 13.73$, $SE = 2.75$, $t = 4.98$, $p < .001$,

adjusted $p < .001$) and the late exposure phase ($\beta = 14.24$, $SE = 2.77$, $t = 4.14$, $p < .001$, adjusted $p = .001$), with pitch returning close to the baseline trajectory in the washout phase ($\beta = 4.88$, $SE = 4.06$, $t = 1.20$, $p = .23$, adjusted $p = .23$). Conversely, the speakers with CA (Figure 3B; 48.8% variance explained) did not show any increase in pitch. Rather, they showed a slightly reduced pitch during the early exposure phase ($\beta = -7.39$, $SE = 3.35$, $t = -2.21$, $p = .027$, adjusted $p = .040$), after which pitch continued to decline through the late exposure phase ($\beta = -11.95$, $SE = 3.34$, $t = -3.58$, $p < .001$, adjusted $p = .001$) and the washout phase ($\beta = -33.95$, $SE = 4.94$, $t = -6.87$, $p < .001$, adjusted $p < .001$). As expected, given the overall decline in pitch throughout the vowel, significant nonlinear effects of time were observed across all conditions for both speaker groups; random smooths for speakers improved the fits for both NH and CA models (Supplemental Table S1).

Directly comparing the CA and NH groups (Figure 3C–E) showed that the NH speakers produced significantly higher pitch trajectories than the speakers with CA during the early exposure phase (28.8% deviance explained, $\beta = 21.88$, $SE = 9.88$, $t = 2.21$, $p = .027$, adjusted $p = .040$) and the washout phase (69.5% deviance explained, $\beta = 39.82$, $SE = 18.82$, $t = 2.12$, $p = .034$, adjusted $p = .044$). Although the same

trend for higher pitch in the NH group was observed in the late exposure phase, the direct comparison in this phase did not reach statistical significance (49.2% deviance explained, $\beta = 25.87$, $SE = 15.51$, $t = 1.67$, $p = .087$, adjusted $p = .11$). Analysis of the smooth terms indicated significant fluctuations over time in both groups, although with different degrees of complexity. During the early and late exposure phases, only the NH group exhibited significant changes over time, with higher pitches (relative to baseline) later in the trajectory. During the washout phase, both the CA and NH groups exhibited significant time-dependent changes, although only in the NH group did this change show an increased pitch (relative to baseline) over the course of the trajectory. These nonlinear effects suggest that adaptation in pitch production affects the later, lower components of the trajectory rather than the initial high pitch, at least for this type of pitch contour in English. For all three phases, the random smooth for participants captured substantial interindividual variability.

Taken together, these results suggest that NH speakers adapted their pitch in word production in response to the auditory perturbation, observable most visibly in the early phase of the exposure period. Conversely, the CA group showed no adaptive increase in pitch, showing instead a steady decrease in pitch that continued to grow over the

course of the experiment. Although the pitch for both groups declined from the early adaptation phase through the washout phase, the pitch in the NH group remained consistently above that in the CA group. This suggests that, in the NH group, adaptation here served to counteract a natural downward trend in pitch over the course of the experiment (see Discussion section).

Compensation Over and Above Adaptation

Investigating compensatory responses later in the trial that may occur over and above any trial-to-trial changes (Raharjo et al., 2021; Franken et al., 2019), we assessed whether the previous findings of enhanced compensation in individuals with CA, as a response to inconsistent, transiently induced perturbations, can be generalized to compensatory responses when consistently exposed to perturbations beginning at vocalization onset.

To explore the existence of this potential behavior, we first examined compensatory responses that occur over and above adaptive changes to consistent perturbations during the window from 200 to 300 msec after vocalization onset (Figure 4). Responses in this early window were significantly larger in the direction opposing the perturbation than in the baseline phase across both groups ($18 \pm$

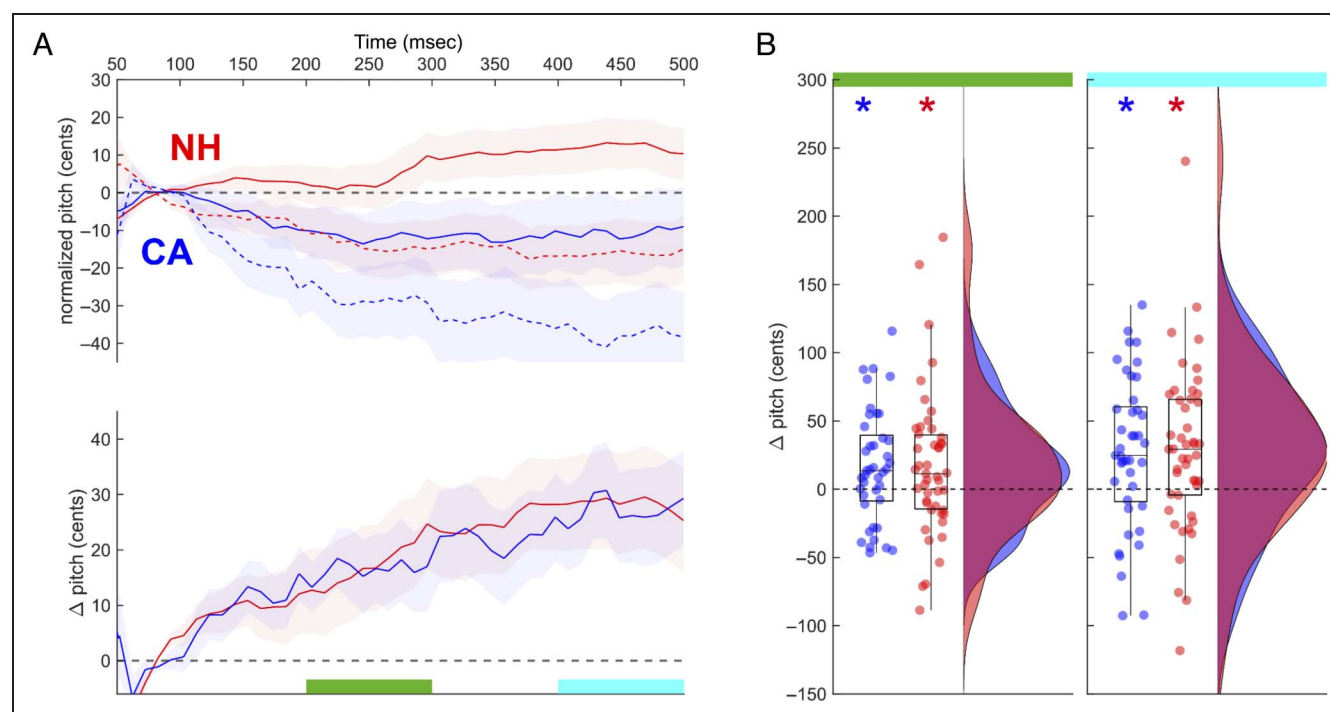


Figure 4. Compensation during exposure to consistent auditory perturbations during vowel production, over and above any adaptive changes in behavior. In all panels, blue indicates values for speakers with CA, and red indicates values for NH speakers. Red stars indicate a difference from the baseline for NH; blue stars indicate a significant difference from the baseline for the speakers with CA. (A, top) Mean pitch trajectories from the perturbed session during the exposure phase (solid lines) and the final 10 trials of the baseline phase (dashed lines). All trajectories were normalized to the unperturbed session. Shading shows standard error across participants. (Bottom) Online compensation, shown by the difference between pitch trajectories during the exposure phase and the mean pitch trajectory during the final 10 trials of the baseline phase. Shading shows standard error across participants. Green and cyan highlights show the early (200–300 msec post onset) and late (400–500 msec post onset) analysis windows, respectively. (B) Individual participant behavior in the early (left) and late (right) analysis windows. Dots and density plots show individual participant mean responses to the (downward) perturbation.

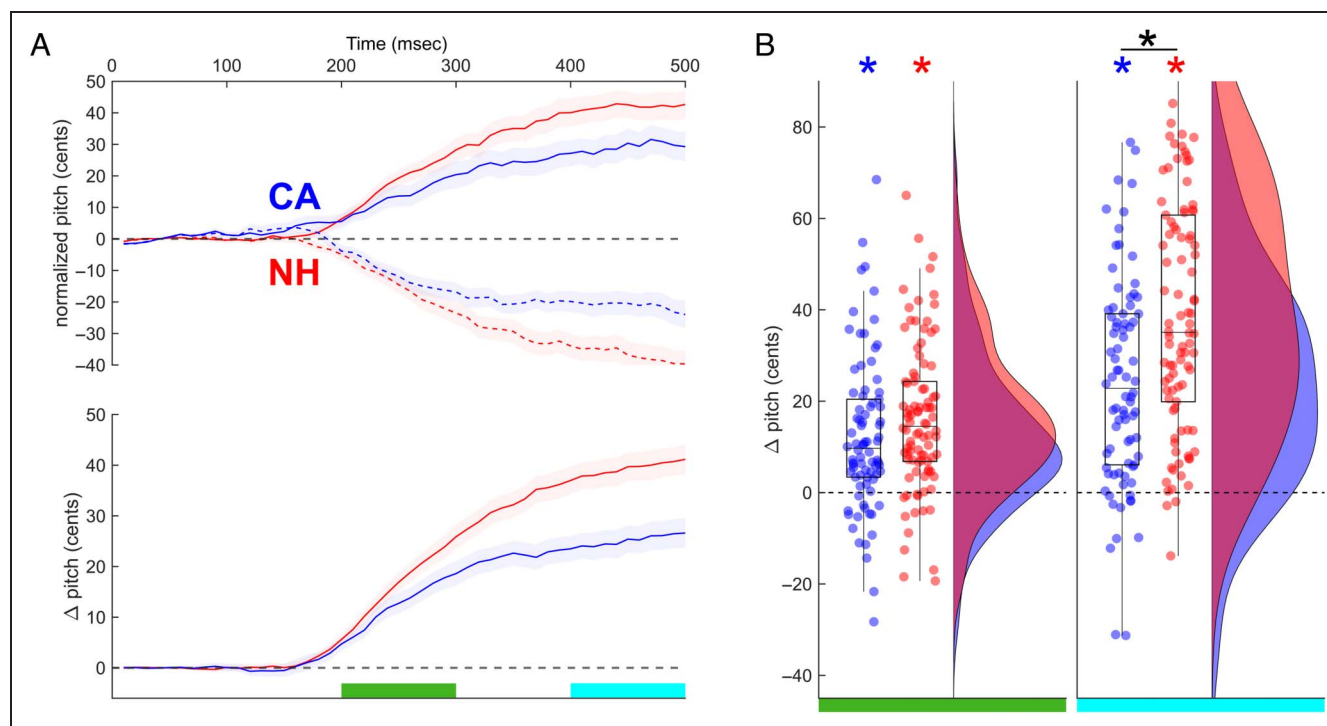


Figure 5. Compensation during sustained auditory perturbations delivered mid-vowel. In all panels, blue indicates values for speakers with CA, and red indicates values for NH speakers. Red stars indicate a difference from the baseline for NH; blue stars indicate a significant difference from the baseline for the speakers with CA; black stars indicate significant differences between the two groups. (A, top) Online compensation to upward (solid lines) and downward (dashed lines) perturbations, normalized by unperturbed trials. Shading shows standard error across participants. (Bottom) Compensation across both perturbation directions, measured by the mean pitch trajectory combining responses to upward (sign-flipped) and downward perturbations. Shading shows standard error across participants. Green and cyan highlights show the early (200–300 msec after perturbation onset) and late (400–500 msec after perturbation onset) analysis windows, respectively. (B) Individual participant behavior in the early (left) and late (right) analysis windows. Dots and density plots show individual participant mean responses to each perturbation direction (up/down, 2 points per participant).

3 cents), $F(1, 4114) = 26.93, p < .001, R^2 = .20$, confirming the presence of online compensatory behavior in addition to any trial-to-trial changes in production. No difference was found between the CA (16.06 ± 7.16 cents) and NH (19.95 ± 7.71 cents) groups, $F(1, 96) = 2.22, p = .14$, suggesting the magnitude of this compensatory response was intact, but not enhanced, in the CA group. No interactions were observed, $F(1, 4114) = 0.45, p = .50$.

After examining the data, we observed that compensatory pitch responses had not reached their plateau in our planned analysis window, but for both groups, it did plateau roughly 400 msec after vocalization onset (Figure 4A), suggesting our planned window likely failed to capture the true extent of compensation. Subsequently, we conducted a post hoc analysis using a later window capturing the maximal plateau of compensation, 400–500 msec after vocalization onset. Again, both groups produced a significantly higher pitch during the exposure phase than the baseline phase (difference between the phases across groups: 30 ± 4 cents), $F(1, 4108) = 54.53, p < .001, R^2 = .24$, but again, the CA and NH groups did not differ in their responses, $F(1, 95) = 3.13, p = .080$, and no interactions were observed, $F(1, 4108) = 0.39, p = .53$.

Experiment 2

Previous studies have shown that, compared with NH speakers, individuals with CA produced larger compensatory responses to unexpectedly introduced pitch perturbations during ongoing vocalizations, potentially reflecting increased reliance on feedback control strategies in the presence of impaired feedforward control (Houde et al., 2019; Li et al., 2019). To explore whether compensatory behavior to pitch perturbations in the current group of individuals with CA showed similar patterns, we examined compensatory changes in f_0 to unexpected vocal pitch perturbations, which began 200–500 msec after vowel onset and which varied in direction across trials. As for the compensation results in Experiment 1, we report results from both a planned “early” window 200–300 msec after perturbation onset and a “late” window 400–500 msec after vocalization onset that better captures the maximum compensatory responses.

In the early window (Figure 5), both CA and NH groups showed opposing compensatory responses to both perturbation directions (all p s $< .001, d \geq 0.54$; see Supplemental Table S2). Upward perturbations resulted in slightly smaller responses than downward perturbations

across both groups (up–down: -4 ± 1 cents), $F(1, 6931) = 11.20$, $p < .001$, $R^2 = .07$. NH speakers and speakers with CA did not show differences in the magnitude of compensation, $F(1, 88) = 2.53$, $p = .12$, nor was there any interaction observed between group and perturbation direction, $F(1, 6931) = 0.97$, $p = .32$.

Post hoc examination during a later time window from 400 to 500 msec after vowel onset, however, revealed a different pattern of results. Although both CA and NH groups showed a significant compensatory response to both perturbation directions (all $ps < .001$, all $ds \geq 0.83$; see Supplemental Table S3), individuals with CA showed smaller compensatory responses in this later time window than NH speakers (NH–CA: 14 ± 5 cents), $F(1, 88) = 8.98$, $p = .004$, $R^2 = .10$. Responses to the upward perturbation in this late window were again smaller than for the downward perturbation for both groups (-8 ± 1 cents), $F(1, 6902) = 27.78$, $p < .001$. No interactions between group and direction of perturbation were observed, $F(1, 6902) = 1.21$, $p = .28$.

Experiment 3

Results assessing compensation from Experiments 1 and 2 showed diverging results. Although no group difference between the CA and NH groups was found in compensation to pitch perturbations when they were applied continuously and consistently (Experiment 1), we found slightly reduced compensation in the CA group to inconsistent and unpredictable pitch perturbations delivered mid-vocalization (Experiment 2), especially when examining the maximal response 400–500 msec after vocalization onset. It is possible that this difference may have arisen either from differences in the consistency of perturbation across trials (predictable vs. unpredictable) or from the timing of the perturbation (vocalization at onset vs. mid-vocalization). In support of the latter, previous work has suggested that compensatory responses to perturbations beginning at the onset of vocalization may rely on a different mechanism than compensating to mid-vowel perturbations: Compensatory responses to onset perturbations must necessarily compare the auditory feedback signal with a desired target or predicted state, whereas responses to perturbations later in the vocalizations may be controlled by comparing reafferent auditory feedback information to the previous (ongoing) *f0* production to maintain a steady pitch (Scheerer & Jones, 2018; Hawco & Jones, 2009; Larson, Burnett, Bauer, Kiran, & Hain, 2001). After a preliminary (numerical) examination of data from 12 initial participants in both the CA and NH groups, which hinted at the pattern eventually observed in the full data set, we added an additional study to the larger battery of experiments to examine compensatory responses to unpredictable perturbations (which varied in direction across trials) delivered at vocalization onset, allowing us to test whether the timing of the perturbation was a source of the difference in compensatory behavior of the CA group between Experiments 1 and 2.

During the early window, 200–300 msec after onset, the CA group showed statistically significant evidence of a compensatory response to the upward perturbation ($p = .049$, $d = 0.38$), and NH speakers showed a significant response to the downward perturbation ($p = .029$, $d = 0.44$). The remainder of the responses were not significant ($p \geq .57$; Figure 6 and Supplemental Table S3). The CA and NH groups did not differ in their responses to onset perturbations, $F(1, 56) = 0.23$, $p = .63$, $R^2 = .005$, and responses to upward perturbations did not differ from responses to downward perturbations, $F(1, 4422) = 0.57$, $p = .45$. Group and Condition, however, did interact, $F(1, 4422) = 11.27$, $p < .001$. This interaction was caused by the fact that speakers with CA differed in their responses to downward and upward perturbations, with downward perturbations showing less compensatory response than upward perturbations (up–down: 9 ± 3 cents), $z(\text{inf}) = 2.96$, $p = .003$. This pattern also caused a difference between NH speakers and speakers with CA in the sense that speakers with CA compensated less than NH speakers for downward perturbations (CA–NH: -9 ± 3 cents), $z(\text{inf}) = -2.60$, $p = .009$. The two groups did not differ in response to upward perturbations (CA–NH: 6 ± 3 cents), $z(\text{inf}) = 1.88$, $p = .24$, and NH speakers did not show a difference between downward and upward perturbations (down–up: 6 ± 3 cents), $z(\text{inf}) = 1.81$, $p = .28$.

As for Experiment 2, we also inspected the compensatory behavior during a 400- to 500-msec window after perturbation (and vocalization) onset to estimate the maximum magnitude of this response. Although the window includes, in some cases, up to 100 msec after the perturbation was removed (which occurred randomly between 400 and 550 msec after vocalization onset), it is nonetheless possible to measure compensation in this window as the behavioral latency to auditory feedback is ~ 150 msec (Burnett et al., 1998). In this later window, compensation was clearly visible and significant for both the CA and NH groups for both perturbation directions (all $ps \leq .030$, all $ds \geq 0.44$; Supplemental Table S3). The magnitude of the response did not differ between the CA and NH groups, $F(1, 56) = 0.51$, $p = .48$, $R^2 = .03$, nor between the upward and downward perturbations, $F(1, 4418) = 3.26$, $p = .071$, nor was there any interaction between these factors, $F(1, 4418) = 0.90$, $p = .34$.

As an additional analysis of feedback-driven compensation, we analyzed the period after the removal of the pitch perturbation (starting 400–550 msec after vocalization, across trials; Figure 6C and D). Our reasoning here is that the removal of the pitch alteration can itself act as a type of perturbation, because speakers have begun to alter their behavior to correct for the initial alteration. Pitch tracks were aligned to the perturbation offset, and we examined a window 400–500 msec after this time point, expecting that the produced pitch would return to baseline values. This was indeed the case: For both groups, the produced pitch in this window, although numerically slightly above

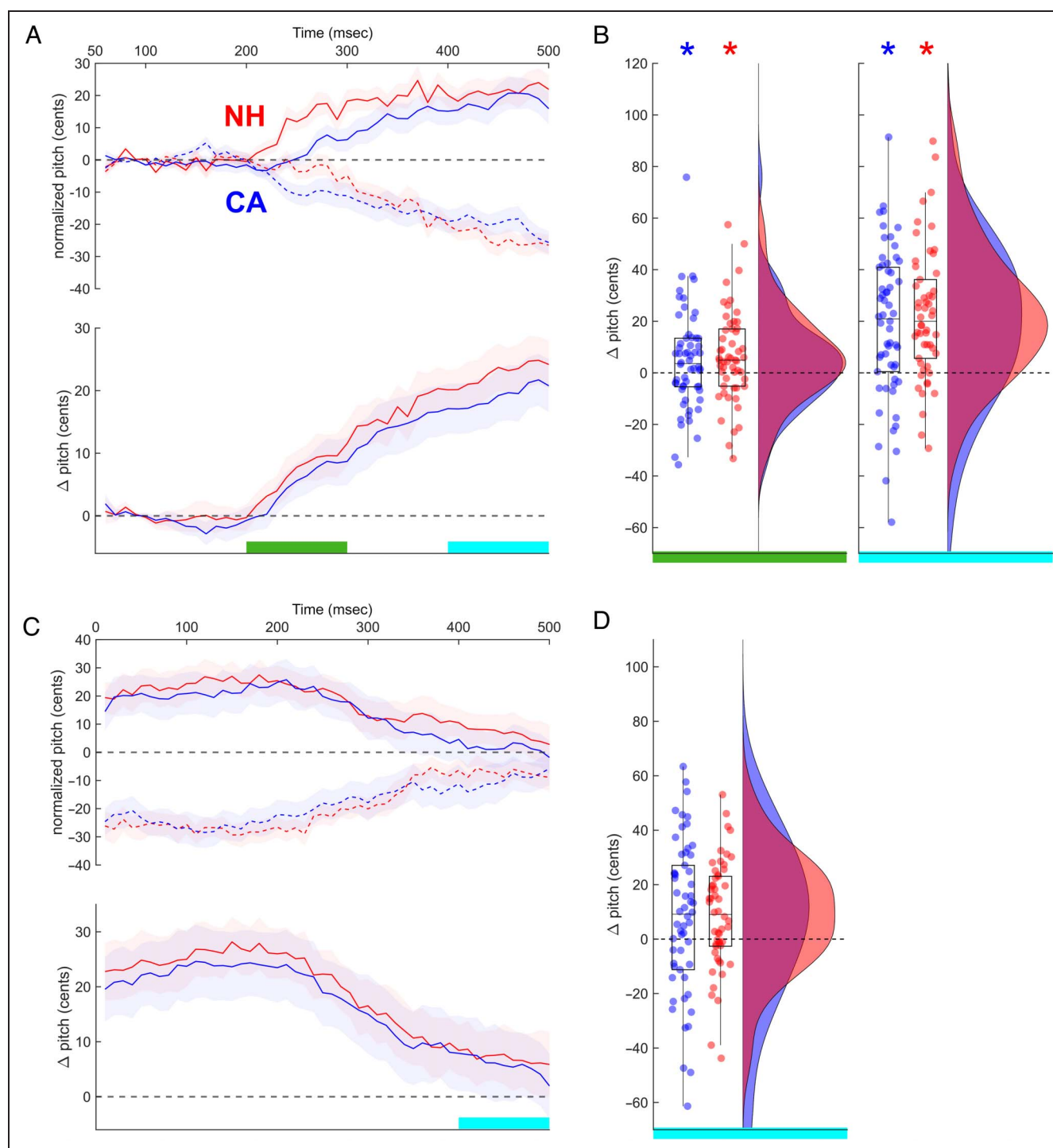


Figure 6. Compensation to transient auditory perturbations delivered at vowel onset. In all panels, blue indicates values for speakers with CA, and red indicates values for NH speakers. Red stars indicate a difference from the baseline for the speakers with CA. (A, top) Online compensation to upward (solid lines) and downward (dashed lines) perturbations, normalized by unperturbed trials. Shading shows standard error across participants. (Bottom) Compensation across both perturbation directions, measured by the mean pitch trajectory combining responses to sign-flipped upward and downward perturbations. Shading shows standard error across participants. Green and cyan highlights show the early (200–300 msec after vowel/perturbation onset) and late (400–500 msec after vowel/perturbation onset) analysis windows, respectively. (B) Individual participant behavior in the early (left) and late (right) analysis windows. Dots and density plots show individual participant mean responses to each perturbation direction (up/down, 2 points per participant). (C) As for A, showing the pitch response after the removal of the perturbation (Time 0 = perturbation offset). (D) As for B, showing pitch response 400–500 msec after perturbation removal.

baseline, did not differ from 0 for either perturbation direction ($p \geq .13$, $d \leq 0.30$; Supplemental Table S3). No differences in behavior were found between the CA and NH groups, $F(1, 55) = 1.16$, $p = .29$, $R^2 = .01$, or upward or downward perturbations, $F(1, 4371) = 0.85$, $p = .36$, nor was there an interaction between these factors, $F(1, 4372) = 2.17$, $p = .14$.

Experiment 4

Experiment 3 was designed to mediate between alternative explanations for the different results in compensation between Experiments 1 and 2: perturbation consistency or perturbation timing. The results, which largely mirror Experiment 1, suggest that the reduced compensatory response in the CA group in the late window in Experiment 2 may stem from the timing of the perturbation starting mid-vocalization versus at vocalization onset. This result emphasizes that changes in pitch perturbation timing may have unanticipated effects on the resulting compensatory behavior. Experiment 4 was designed to address a separate aspect of perturbation timing that may have affected the results in Experiment 2. Our initial (numerical) inspection of preliminary results from a subset of participants in Experiment 2, which was consistent with the final result, suggested equal or reduced compensation in the CA group compared to the NH group, a striking difference from previous studies showing increased pitch compensation in individuals with CA (Houde et al., 2019; Li et al., 2019). However, previous studies used transient perturbations that began after vocalization onset and, perhaps crucially, were removed before vocalization offset, differing from the perturbations in Experiment 2 that remained in place until the end of the trial. Experiment 4 was designed to test whether the seemingly minor difference in perturbation offset timing may have driven this difference in compensatory behavior. Here, the perturbation was randomly introduced but removed after 400 msec. Note that, as for Experiment 3, the late analysis window 400–500 msec after perturbation onset, while occurring after the removal of the perturbation in real time, nonetheless captures compensatory behavior to the perturbation given the >100-msec latency of auditory feedback responses.

In the early window 200–300 msec after perturbation onset, both groups of speakers compensated for both perturbation directions (all $ps \leq .040$, $d \geq 0.76$; Figure 7 and Supplemental Table S4). There were no difference in the magnitude of compensation between the NH and CA groups, $F(1, 32) = 0.05$, $p = .82$, $R^2 = .05$, no difference between upward and downward perturbations, ($F(1, 2525) = 0.16$, $p = .69$, and no interaction between these factors, $F(1, 2525) = 1.23$, $p = .27$.

In the late window 400–500 msec after perturbation onset, apart from the speakers with CA, who showed only a trend as a response to downward perturbation ($p = .056$, $d = 0.54$), both speakers with CA and NH speakers

showed large compensatory responses to both upward and downward perturbations ($p \leq .050$, $d \geq 0.54$; Supplemental Table S4). Although the results numerically resembled Experiment 2, with the CA group showing a slightly reduced compensation magnitude compared with the NH group, this between-group difference was much smaller and, crucially, was not statistically significant, $F(1, 32) = 2.62$, $p = .12$. Although upward perturbations resulted in larger compensatory responses than downward perturbations (up–down: 5 ± 2 cents), $F(1, 2520) = 5.16$, $p = .023$, $R^2 = .07$, this effect was similar for both groups as shown by the lack of any interaction effect, $F(1, 2520) = 0.43$, $p = .51$.

Summary

We conducted separate assays of feedforward adaptation in vowel and word production. During sustained vowel production, NH speakers adapted their vocalizations by increasing their pitch from baseline immediately after exposure to the perturbation, through the final 10 trials of the exposure phase and into the first three repetitions of the washout phase. This pattern of almost immediate adaptation and limited but present aftereffects reflects the pattern typically observed in the literature (Alemi et al., 2020; Behroozmand & Sangtian, 2018; Jones & Munhall, 2005). Conversely, although speakers with CA also produced the final 10 trials of the exposure phase at a higher pitch relative to the baseline phase, this change showed a gradual buildup rather than an immediate change after the onset of the perturbation. Crucially, the increase in pitch did not carry over into the washout phase, with pitch immediately returning to baseline values. During word production, NH speakers showed increased pitch in the early exposure phase, with a gradual trend downward in the rest of the experiment, such that pitch remained elevated during the late exposure phase and returned close to the baseline in the washout phase. Speakers with CA, conversely, showed a consistent decline in pitch throughout the experiment.

Results of the studies on feedback-based reflexive responses generally showed little difference between the CA and NH groups, although the precise results varied somewhat depending on the precise timing of the perturbation. In no case did we observe a larger reflexive response in the CA group than in the NH group. In response to online, sustained perturbations (Experiment 2), both the CA and NH groups showed compensatory responses in the 200- to 300-msec window and the 400- to 500-msec window. These responses were equivalent in the early window but were slightly smaller in speakers with CA than NH speakers in the late window. During transient perturbations occurring at the onset of vocalization (Experiment 3), the CA group showed compensatory responses to the upward perturbation and NH speakers showed significant responses to the downward perturbation during the 200- to 300-msec window. During the late

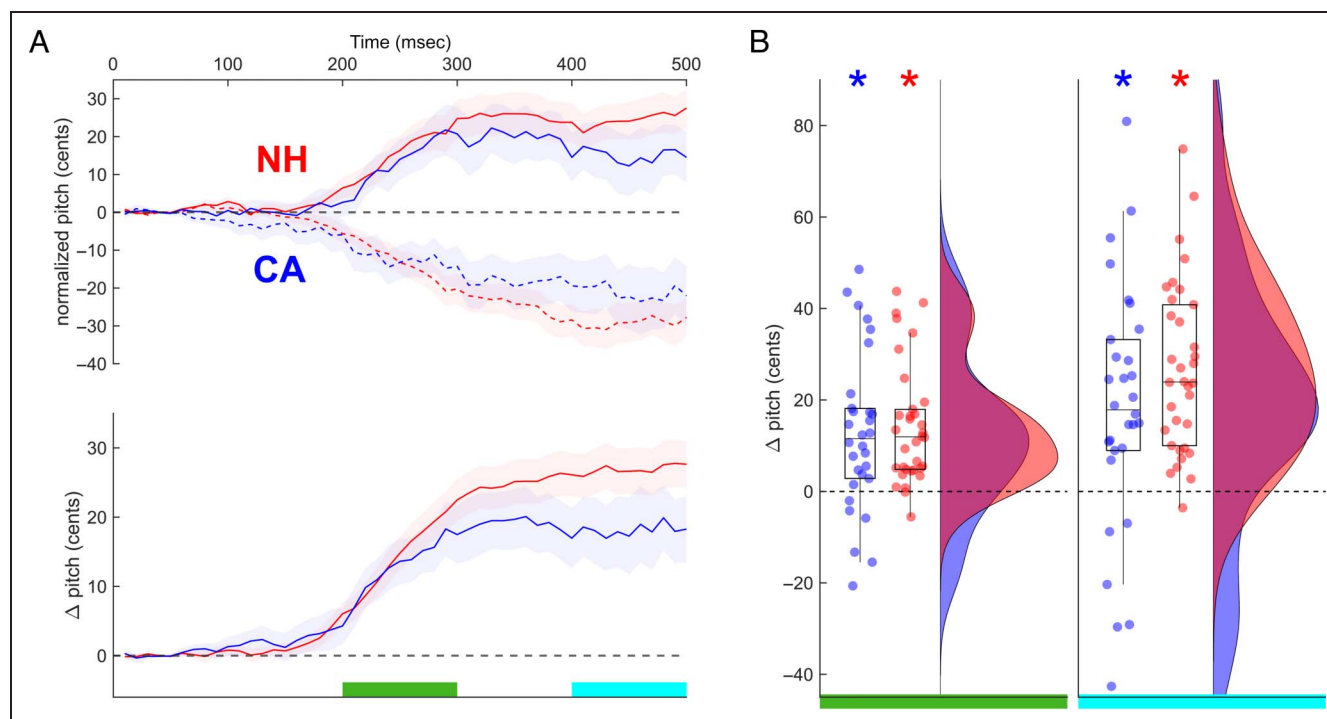


Figure 7. Compensation to transient auditory perturbations delivered mid-vowel. In all panels, blue indicates values for speakers with CA, and red indicates values for NH speakers. Red stars indicate a difference from the baseline for NH; blue stars indicate a significant difference from the baseline for the speakers with CA. (A, top) Online compensation to upward (solid lines) and downward (dashed lines) perturbations, normalized by unperturbed trials. Shading shows standard error across participants. (Bottom) Compensation across both perturbation directions, measured by the mean pitch trajectory combining responses to sign-flipped upward and downward perturbations. Shading shows standard error across participants. Green and cyan highlights show the early (200–300 msec after perturbation onset) and late (400–500 msec after perturbation onset) analysis windows, respectively. (B) Individual participant behavior in the early (left) and late (right) analysis windows. Dots and density plots show individual participant mean responses to each perturbation direction (up/down, 2 points per participant).

400- to 500-msec window after perturbation (and vocalization) onset, compensation was equivalent for the CA and NH groups. Both groups returned close to their baseline pitch in the window 400–500 msec after removing the perturbation. In response to online, transient perturbations (Experiment 4), the CA and NH groups showed equivalent responses in both the early 200- to 300-msec window and the late 400- to 500-msec window.

DISCUSSION

Sensorimotor adaptation has been shown to be impaired in individuals with CA across limb movements, saccades, walking, and oral articulation, indicating a critical, domain-general role of the cerebellum in this type of motor learning. We investigated whether the control of pitch, which differs substantially from other motor control activities in its higher reliance on feedback control than predictive/feedforward control, shows similar impairments in sensorimotor adaptation in individuals with CA. When we examined sensorimotor adaptation of pitch during both word production (a natural speech task) and sustained phonation (the standard task in measuring pitch adaptation), we found that NH speakers produced an immediate adaptive response at the onset of the applied pitch perturbation while the CA group showed no change

in behavior, actually showing a slight decrease in pitch over the course of the experiment in the word production task. Thus, despite the differences in reliance on predictive control in pitch compared with reaching and oral articulation, our results suggest that the cerebellum likely plays a similar role in sensorimotor adaptation of vocal pitch as in other motor domains. Notably, the absence of any consistent observable pitch adaptation in the CA group in our study, compared with the present but reduced adaptation typically observed in this group in oral articulation (Parrell et al., 2021) and other motor domains (Parrell et al., 2021; Schlerf, Xu, Klemfuss, Griffiths, & Ivry, 2013), may suggest that the cerebellum is particularly critical for the regulation of vocal pitch.

Although the initial patterns of adaptation (and lack of adaptation in the CA group) in the early exposure phase were similar in both word production and sustained phonation, behavior in the two tasks diverged in the later phases of the experiment. In the sustained phonation task, the NH group showed an immediate adaptive response at the very start of the exposure phase and maintained this elevated pitch through the late exposure phase and into the first few trials of the washout phase, as in previous studies (Alemi et al., 2020; Behroozmand & Sangtian, 2018). Such aftereffects are a hallmark of sensorimotor adaptation across motor domains. In addition, although

adaptation is typically gradual in other motor domains, adaptation in pitch has been shown to be very rapid (Alemi et al., 2020; Behroozmand & Sangtian, 2018; Keough et al., 2013; Jones & Keough, 2008), consistent with the observed behavior in the NH group. Conversely, although the CA group produced an elevated pitch during the late exposure phase, they showed no evidence of adaptation in the early exposure phase, nor in the washout phase, returning immediately to baseline behavior with no visible aftereffects. The lack of initial adaptation and any aftereffects, given the presence of learning in these phases both in the NH data and in the broader literature on pitch adaptation, strongly suggest that (cerebellar-driven) sensorimotor adaptation did not occur in the CA group. However, the mechanism driving elevated pitch production in the late exposure phase in this group remains unclear. Importantly, the task participants perform in this paradigm is vaguely defined; although we followed typical instructions that participants “try to maintain a steady pitch,” it is unlikely that participants are attempting to maintain some target, absolute pitch. This is shown by the gradual increase of pitch over time in the control session, when no perturbation is given. One possibility is that speakers try to reproduce the pitch they were producing on the previous trial; because the speakers with CA continue to produce compensatory responses that oppose the perturbation, this self-imitation may drive increases in pitch over time, resulting in behavior at the end of the exposure phase that is superficially similar to adaptation-driven changes.

Critically, the CA group showed no evidence of adaptation-like behavior in the word production task, in stark contrast to the NH group. Here, the NH participants immediately adapted to the perturbation (again, consistent with expectations from the pitch adaptation literature) but showed a subsequent downward trend in pitch, such that no aftereffects were observed in the washout phase. Notably, the CA group produced a similar downward trend, with pitch immediately lower than baseline in the early exposure phase that continued to drift downward over the course of the experiment. This consistent downward trend in both groups suggests that all participants showed a trend to lower their pitch over the course of the experiment—the adaptation visible in the NH group occurred on top of this trend; crucially, in all phases, the NH group produced higher pitch values than the CA group. In this task, unlike the vowel production task, there are no confounds of instruction or behavior: Participants merely speak the target word out loud. The lack of adaptation in the CA group in this word production task reinforces the idea that the observed increase in pitch in the vowel production task in this group likely arises from a separate learning mechanism outside of sensorimotor adaptation proper.

One potential caveat about these results is that the perturbed sessions were normalized to an unperturbed control session, which always followed the perturbed control

session, to account for a potential upward drift in f_0 over repeated vocalizations, which has been observed in the literature (Alemi et al., 2020; Jones & Munhall, 2000). It is thus possible that completing the perturbation task affected this f_0 drift for the vowel production task, although the precise reason why this should be the case and why it should differentially affect the two participant groups is not clear. Visual inspection of the nonnormalized data (Figure 2A), as well as the statistical analysis of nonnormalized data in Supplemental Tables S5–S6, still suggests that the CA and NH groups produced very different behavior. Consistent with previous reports of adaptation in the literature, the NH group produces almost immediate adaptation on introduction of the perturbation, reaching the level of the final plateau in ~ 5 trials, and on removal of the perturbation shows a gradual decline to the baseline values. The CA group, conversely, gradually increased f_0 , reaching a plateau much later. Most importantly, they did not show any decrease in f_0 after the perturbation was removed, maintaining an elevated pitch at the same level as in the exposure phase. This return to baseline in the absence of a perturbation not only occurs in f_0 adaptation (Alemi et al., 2020; Behroozmand & Sangtian, 2018) but also is a hallmark of sensorimotor adaptation across motor domains, although generally at a slower rate than f_0 (Parrell et al., 2021; Morton & Bastian, 2006). For the word production task, there is less of a concern about normalization: The results are broadly similar with or without the normalization to the control session (Figure 2C, Supplemental Tables S7–S8), and the trajectory-based GAMM analysis, which showed the same pattern of results as the time-window analysis, was not normalized to the control session.

One additional potential confound is that we used a fixed order for all experiments, including the four sessions in Experiment 1 (word/vowel production tasks each with perturbed/control sessions). This may have affected the magnitude of adaptation in the vowel production task, as a recent study showed that adaptation to a pitch perturbation during a word production task (similar to the word production task in Experiment 1) decreased when participants were reexposed to the perturbation multiple times during a single experimental session (Gaines et al., 2026). However, several studies have reported no such carryover effects of pitch adaptation when adaptation is assessed in separate sessions, whether these sessions were separated by breaks or other tasks (Tomassi et al., 2026; Kapsner-Smith et al., 2024; Alemi et al., 2020; Hawco & Jones, 2010). Although there is some evidence that adaptation to vowel formant perturbations may be reduced during a second exposure to the perturbation (Tomassi et al., 2026), this result may be because of the cognitively demanding task used in that study, as other work using a simpler (and more typical) word production task has not shown these order effects (Kim et al., 2025; Parrell et al., 2017). Thus, although it is possible that the fixed session order used in Experiment 1 may have caused reduced

adaptation in the vowel task, this is unlikely given findings from previous studies of pitch adaptation using methods comparable with those used here. Most critically, however, any order effect would not have affected the result of the word production task, where we see the strongest evidence for impaired adaptation in CA—the perturbed session for the word production task occurred first, before the control session for this task and both sessions of the sustained vowel task.

A second potential concern relates to the onset of the auditory perturbation in Experiment 1, which was introduced abruptly rather than gradually, as is sometimes done in the literature to minimize participant awareness. We used an abruptly introduced perturbation as this type of perturbation consistently causes measurable deficits in adaptation in individuals with CA in oral articulation (Parrell et al., 2017, 2021) and other motor domains (e.g., Parrell et al., 2021; Gibo, Criscimagna-Hemminger, Okamura, & Bastian, 2013; Schlerf et al., 2013). Moreover, comparing results from different studies, there is little difference in the adaptive pitch response in healthy controls between gradual and abrupt introductions of the pitch perturbation. For example, the adaptive responses to an abruptly introduced perturbation in Jones and Keough (2008) are around 80–100 cents, with a similar final level of adaptation seen using a gradually introduced perturbation in both Abur and colleagues (2018) and Behroozman and colleagues (2018). Although the level of adaptation observed in the current study was less than in these, it was similar to the ~18-cent adaptation seen in other previous work with a gradually introduced perturbation study (Alemi et al., 2020). Although the use of an abrupt perturbation is thus consistent with the literature on both adaptation impairments in CA and some studies of pitch adaptation, this leaves open the question of whether the result we found here (impaired adaptation in the CA group) may be specific to this (relatively large) initial perturbation. Although there have been some reports in upper limb control that participants with CA show impairments in adaptation only when adapting to sudden, but not gradually introduced, mechanical perturbations (Criscimagna-Hemminger, Bastian, & Shadmehr, 2010), the differences found in this study were likely an artifact of the specific mechanical perturbations used in the two conditions, as individuals with CA show equivalently impaired adaptation when adapting upper limb reaches to abruptly and gradually introduced identical mechanical perturbations (Gibo et al., 2013). Similarly, individuals with CA generally show impaired adaptation to both gradual and abrupt visual–motor rotations (Schlerf et al., 2013), although when tested using repeated reaches to a single target (rather than spatially varying targets as is typical), they may be able to learn to change their behavior through noncerebellar mechanisms (Izawa, Criscimagna-Hemminger, & Shadmehr, 2012), perhaps relying on reinforcement learning from targeting error, which is intact in CA (Therrien, Wolpert, & Bastian, 2016). In the speech domain,

individuals with CA show equivalently impaired adaptation when adapting their oral articulation to abruptly and gradually introduced auditory perturbations of vowel formants (Parrell et al., 2017). Given this, we do not expect that the results of our study would have been substantially different if we had used a gradual introduction of the vocal pitch perturbation, although future studies directly comparing gradual and abruptly introduced perturbations would be necessary to confirm this. Regardless, the impairment in adaptation in individuals with CA seen here in response to suddenly-introduced perturbations is consistent with similar effects seen in other motor domains and reinforces the critical role of the cerebellum in adapting to perturbations of vocal pitch.

Although the main aim of the current study was to assess cerebellar contributions to adaptation of vocal pitch, we also measured feedback-driven, real-time compensation to pitch perturbations. Unexpectedly, we found that compensatory responses of speakers with CA resembled the responses by NH speakers, and as such, we did not find evidence for the expected overcompensation previously reported in this population (Houde et al., 2019; Li et al., 2019) in our cohort of speakers. By including several additional studies with slightly different perturbation paradigms, we excluded the possibility that the timing of the perturbation within a trial contributed to our divergent results. Notably, we found a similar lack of group difference in compensatory responses to unpredictable vocal pitch perturbations in Experiments 2–4 and in compensatory responses above and beyond adaptive responses in Experiment 1 where, by normalizing each trial to the first 100 msec of vocalization, we can account for any adaptive changes in feedforward control to isolate a later, additional, compensatory component driven by online feedback (Franken et al., 2019; Raharjo et al., 2021). This result provides additional support, in a different paradigm, for the lack of a difference in online compensation between the speakers with CA and NH speakers. Several additional factors might have contributed to the lack of overcompensation in our study.

First, our cohort of speakers differs from these previous studies. Our CA cohort includes individuals with varying levels of ataxia severity and varying causes of ataxia, including a range of types of SCA. Li and colleagues (2019) tested a more homogenous population, including one speaker with SCA1 and 11 speakers with SCA3. Thus, it is possible that the overcompensation seen in Li and colleagues (2019) might be a unique characteristic of SCA3, as it is yet unknown whether differences in type of CA affect compensatory behavior. However, Houde and colleagues (2019) showed a similar overcompensation in a more diverse group of SCA types, including two SCA2, two SCA3, one SCA5, two SCA6, one SCA7, two SCA8, and six idiopathic cerebellar atrophy, broadly similar to the heterogeneity seen in our sample, making this explanation unlikely.

Second, the current study had a much larger sample size (45 individuals with CA) compared with 12 in Li and colleagues (2019) and 16 in Houde and colleagues

(2019). If indeed increased feedback-based responses are an idiopathic response to inaccurate feedforward control (Houde et al., 2019), the presence of some individuals with such an increased response may bias group results more in small samples. To examine this possibility, we performed a bootstrapping analysis using Monte Carlo resampling on the results of Experiments 2 and 4. On each of the 10,000 iterations, 12 speakers with CA and 12 NH speakers were randomly selected without replacement. For each participant, a mean compensatory response was calculated across trials and perturbation directions, and a one-tailed *t* test was conducted testing for differences between the groups (Supplemental Figure S2). For Experiment 2, although 16.62% of the cases resulted in higher compensation values in CA than NH in the early window 200–300 msec after vowel onset, this difference between CA and NH was significant in only 0.21% of the cases. During the late window (400–500 msec after perturbation), even fewer samples showed a group difference: Only 3.21% of simulations showed higher compensation in CA than NH, significantly so only in 0.02%. We found similar results for Experiment 4, where the perturbation was removed after 400 msec in the same manner as in Houde and colleagues (2019). In this case, the early analysis window did show numerically higher compensation in CA than NH in 35.46% of the samples, but this difference was significant in only 0.05% of cases. During the late window, compensation in CA was higher than in NH in only 0.30% of the samples, with no significant differences. In short, the results of these random subsampling analyses strongly suggest that the differences between our results and those of the two prior studies are unlikely to be because of differences in sample sizes.

Third, we employed a different approach in normalizing the data from previous studies, and it could be possible that these analysis choices influenced our results. Specifically, we normalized the perturbed trials by subtracting the mean trajectory from unperturbed trials, whereas Houde and colleagues (2019) used an average value of all upward and downward realizations and normalized their trials based on this average (necessary as this study did not include any unperturbed trials). To check for the possibility that this “average of perturbed trial” trajectory may diverge from the unperturbed pitch trajectories, which we used to normalize the data, we averaged the upward and downward responses from our data collected during Experiments 2 and 4 (Supplemental Figure S1). These average trajectories did not differ substantially from the trajectories of the unperturbed trials. It is thus unlikely that the differences in analyses approaches caused the divergent results.

Finally, although we controlled for the timing of the perturbation within the trial, there were still several methodological differences between these studies. Li and colleagues (2019) had participants produce long, sustained vocalizations, with several perturbations (± 200 or ± 500 cents) applied briefly in each vocalization. Houde

and colleagues (2019) used a design more similar to that in our Experiment 4, with a single transient ± 100 -cent perturbation, although (perhaps crucially) with no unperturbed trials. In both previous studies, the constant presence of unpredictable pitch perturbations on every trial may have induced the CA group to switch to a more feedback-driven control mode in response to the unstable environment, whereas the presence of unperturbed trials (20%) in our experiments (or, in the case of Experiment 1, the consistently applied perturbation) may have prevented such a switch in feedback control strategy. We believe this to be the most likely explanation for the discrepancy in our results. Future studies should test this by directly comparing compensation paradigms with and without unperturbed trials.

Our results largely suggest the CA and NH groups exhibit equivalent reflexive, online compensatory responses to pitch perturbations (regardless of the precise timing of the perturbation) in both an early window 200–300 msec after the onset of the perturbation and a late window 400–500 msec after perturbation onset. Our use of this later window was motivated, post hoc, by visual inspection showing compensatory behavior had not yet plateaued in the 200- to 300-msec window. In Experiment 2, this late window showed that the CA group actually showed a decrease, rather than the hypothesized increase, in reflexive compensation. As this later component of the reflexive response has been shown to be modifiable with volitional control (e.g., participants behavior can be changed when they are informed of the perturbation and instructed to alter their pitch in a certain way; Hain et al., 2000), this may be taken to indicate that speakers with CA are less able to consciously alter their pitch. Although this is possible, we believe this is likely not to be the case here. First, although the responses in this late window have been shown to be modifiable by instructions, this does not necessarily imply that the late window always directly reflects volitional control. In visual inspection of the data across all experiments, we see smooth trajectories across the entire postperturbation window (including a steady plateau after ~ 300 msec in Experiment 4), with no evidence of an additional, separate response. Second, the results of the other experiments showed no group difference in this late window, suggesting this is not a consistent effect such that, even if the late window does reflect volitional control, our results would suggest no consistent difference in this aspect of vocal pitch control between the CA and NH groups.

In summary, our results show that sensorimotor adaptation to externally applied perturbations of vocal pitch is impaired in individuals with CA, strongly supporting a critical role of the cerebellum in this process. This is consistent with a domain-general role for the cerebellum in adapting motor behavior in response to sensory errors. The near-complete absence of adaptation observed in the CA group, seen most clearly in the word production task where there are no potential confounds from task instructions, differs from the impaired, but present,

adaptation in this group typically observed in other motor domains, suggesting that the cerebellum may be particularly critical for the adaptive control of vocal pitch. Conversely, we found that online, feedback-driven compensation to pitch perturbations was intact in the CA group. Although this is similar to the observed behavior in other motor domains, this differs substantially from the enhanced compensatory response previously demonstrated in this population. This result suggests that any enhanced reliance on feedback for pitch control is not an automatic result of cerebellar damage but may rather be an individual-specific learned response, perhaps because of instability in the predictive control of pitch.

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Data Availability Statement

Data and analysis code is available at <https://osf.io/z42ek/>. Note that this includes only processed data—as speech inherently provides identifiable information, original audio files are not publicly available but can be requested from the authors. Supplemental Material can be accessed on this article’s homepage: <https://doi.org/10.1162/JOCN.a.2630>.

Author Contributions

Anneke Slis: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Software; Validation; Visualization; Writing—Original draft; Writing—Review & editing. Ben Parrell: Conceptualization; Data curation; Formal analysis; Funding acquisition; Methodology; Project administration; Resources; Software; Supervision; Validation; Visualization; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were $M(\text{an})/M = .407$, $W(\text{oman})/M = .32$, $M/W = .115$, and $W/W = .159$, the comparable proportions for the articles that these authorship teams cited were $M/M = .549$, $W/M = .257$, $M/W = .109$, and $W/W = .085$ (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article’s gender citation balance.

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