1 Variability is actively regulated in speech

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9 Abstract

- 10 Although movement variability is often attributed to unwanted noise in the motor system, recent
- 11 work has demonstrated that variability may be actively controlled. To date, research on
- 12 regulation of motor variability has relied on relatively simple, laboratory-specific reaching tasks.
- 13 It is not clear how these results translate to complex, well-practiced and real-world tasks. Here,
- 14 we test how variability is regulated during speech production, a complex, highly over-practiced
- 15 and natural motor behavior that relies on auditory and somatosensory feedback. Specifically, in a
- 16 series of four experiments, we assessed the effects of auditory feedback manipulations that
- 17 modulate perceived speech variability, shifting every production either towards (*inward-pushing*)
- 18 or away from (*outward-pushing*) the center of the distribution for each vowel. Participants
- 19 exposed to the *inward-pushing* perturbation (Experiment 1) increased produced variability while
- 20 the perturbation was applied as well as after it was removed. Unexpectedly, the *outward-pushing*
- 21 perturbation (Experiment 2) also increased produced variability during exposure, but variability
- returned to near baseline levels when the perturbation was removed. Outward-pushing
- 23 perturbations failed to reduce participants' produced variability both with larger perturbation
- 24 magnitude (Experiment 3) or after their variability had increased above baseline levels as a result
- 25 of the inward-pushing perturbation (Experiment 4). Simulations of the applied perturbations
- 26 using a state space model of motor behavior suggest that the increases in produced variability in
- 27 response to the two types of perturbations may arise through distinct mechanisms: an increase in
- 28 controlled variability in response to the inward-pushing perturbation, and an increase in
- 29 sensitivity to auditory errors in response to the outward-pushing perturbation. Together, these
- 30 results suggest that motor variability is actively regulated even in complex and well-practiced
- 31 behaviors, such as speech.
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- 34 35
- 36 Keywords: motor variability, speech motor control, sensorimotor adaptation, auditory
- 37 perturbation, error sensitivity.
- 38

39 Introduction

40 No matter how hard we practice, it is virtually impossible to generate exactly the same

41 movement twice. Such variation in performance across repetitions of the same movements, or

42 *motor variability*, is widely believed to be an inevitable consequence of noise in the nervous

43 system, arising from stochastic events presented across all scales of brain activity, from the

44 single-cell level to complex network dynamics (Churchland et al., 2006; Faisal et al., 2008;

45 Renart & Machens, 2014). Indeed, many current theories of motor behavior rely on this

46 assumption and posit that the motor system aims to minimize the detrimental effects of 'motor

47 noise' on motor task performance (Harris & Wolpert, 1998; Scholz & Schöner, 1999; Todorov,

48 2004).

49

50 However, recent work in reaching has demonstrated that variability is not always treated as

51 unwanted "noise" to be reduced by the motor system but may be more actively controlled.

52 Repeated exposure to position- or velocity-dependent force fields during reaching has been

53 shown to selectively increase task-relevant variability, potentially to facilitate more efficient

54 future learning (Wu et al., 2014). Conversely, task-relevant variability can also be reduced when

needed in some behaviors: participants exposed to a visual perturbation that magnified the

56 horizontal displacement of the hand away from the midline during point-to-point reaching

57 movements reduced their variability in this dimension (Wong et al., 2009). These results suggest

that variability is not simply noise but can also be an important part of the signal itself that

59 controls the motor movement (Stein et al., 2005).

60

61 Although variability poses a fundamental problem for motor control, studies on regulation of

62 motor variability are comparatively sparse and, to date, have relied principally on relatively

63 simple, laboratory-specific planar arm reaching tasks. While such tasks play an important role in

64 probing motor control systems, they tackle a relatively restricted range of motor tasks that do not

65 fully capture the complex demands of real-world behavior and, thus, may overlook some aspects

66 of motor control in real-world tasks which are naturally less constrained. Speech production is

67 one such task: as opposed to laboratory-specific arm reaching tasks, which involve an interaction

68 with an uncommon external device (e.g. a joystick) and typically constrain movements to two

69 joints, speaking is a highly over-practiced behavior that involves the coordination of roughly 100

muscles to precisely control the respiratory and phonatory systems as well as the movements of

71 lips, jaw, velum and tongue (a muscular hydrostat with highly complex control).

72

73 Here, we aimed to test how variability is regulated in speech production, a complex, well-

74 practiced task controlled via non-visual sensory feedback. Previous work has shown that

75 speakers are sensitive to real-time alterations to their auditory feedback (Houde & Jordan, 1998;

76 Purcell & Munhall, 2006). For example, speakers learn to alter their speech to oppose auditory

perturbations that shift the frequencies of vowel formants (resonances of the vocal tract which

78 serve to distinguish between different vowels). However, these studies have typically examined

79 formant shifts that are applied in a consistent direction, regardless of the produced vowel

- 80 formants, with the consequence that the mean formant values participants hear are altered, while
- 81 their formant variability remains unchanged. Here, we implement a novel auditory perturbation
- 82 that shifts vowel formants in a non-uniform manner, such that the mean formant values remain
- 83 unchanged while trial-to-trial variability is either increased or decreased (Fig. 1).
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85 By altering participants' perceived trial-to-trial variability without affecting their overall mean

86 behavior, we can test whether variability in speech production is actively monitored and

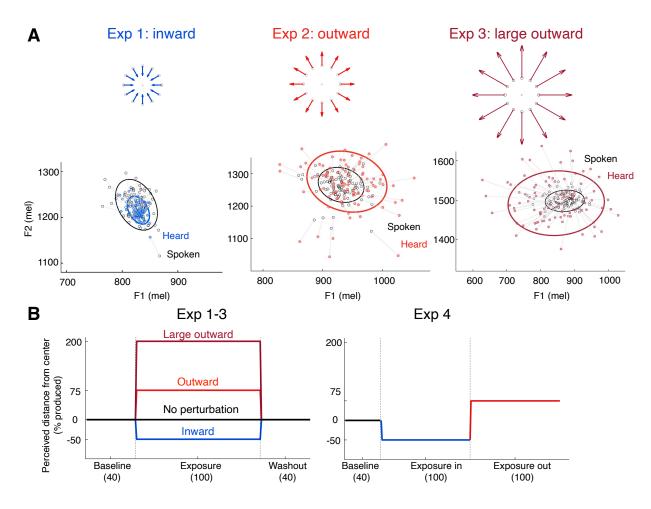
87 regulated. In a series of four experiments, we assess the effects of manipulations that both

- 88 increase and decrease the perceived variability of participant's speech behavior. We predicted
- that a perturbation that reduces perceived variability would lead to increases in produced
 variability, as participants would be free to be less precise in their production without negatively
- 91 affecting their perceived accuracy. Conversely, we expected that a perturbation that increases
- 92 perceived variability would have the opposite effect (i.e. lead to decreases in produced
- 93 variability). Surprisingly, we found that both types of perturbation caused participants to increase
- 94 their produced variability, while only the perturbation which increases perceived variability
- 95 affected a behavioral measure of error sensitivity. Simulations of the applied perturbations using
- 96 a well-established state space model of sensorimotor learning suggest that the increases in
- 97 produced variability in response to the two types of perturbations may arise through distinct
- 98 mechanisms: an increase in controlled variability in response to the perturbation that reduces
- 99 perceived variability, and an increase in sensitivity to auditory errors in response to the
- 100 perturbation that increases perceived variability. All together, these results suggest that motor
- 101 variability is actively monitored and regulated even in complex and well-practiced behaviors,
- 102 such as speech.
- 103

104 Methods

105 Participants

- 106 87 native speakers of American English between the ages of 18 and 66 years, with no reported
- history of hearing loss or neurological disorders, took part in the study (Experiment 1: N = 24,
- 108 28.8 ± 12.3 years, 18/6 females/males; Experiment 2: N = 22, 25.9 \pm 9.7 years, 14/8
- 109 females/males; Experiment 3: N = 21, 33.3 ± 13.6 years, 12/9 females/males; Experiment 4: N =
- 110 20, 28 ± 12.9 years, 15/5 females/males). Participants provided informed consent and were
- 111 compensated either monetarily or with course credit for their participation. The Institutional
- 112 Review Board of the University of Wisconsin–Madison approved the experimental protocol.
- 113
- 114
- 115



116 117

118 *Figure 1. Experiment design.* (A) Schematic (top) and examples from representative

119 participants (bottom) of perturbations applied to speech vowel formants: inward-pushing (Exp 1,

120 *left), outward-pushing (Exp 2, middle), and large outward-pushing (Exp 3, right). Note different*

121 axis scales in the example data across experiments. Black circles represent the formant values

122 participants produced and colored circles indicate what was played back to them over

123 headphones. The ellipses represent a 95% confidence interval around the data points of the same

124 color. (B) Experimental procedure and magnitudes of the perturbation applied in Experiments 1-

125 3 (left panel) and Experiment 4 (right panel).

126

127 Apparatus

128 Participants were exposed to a real-time perturbation of the first and second vowel formants

129 (F1/F2) designed to affect the perceived variability of their speech production. A modified

130 version of Audapter (Cai et al., 2008; Tourville et al., 2013) was used to record participants'

speech, alter the speech signal when necessary, and play the (potentially altered) signal back to

- 132 participants. The experiment was conducted in a quiet room with participants seated in front of a
- 133 computer screen. In each trial, one of the three stimulus words ("bead", "bad", and "bod" in

- Experiment 1, 2, 4 or "bead", "bad", and "bed" in Experiment 3) was pseudorandomly selected
- and displayed on the screen, and participants read it aloud. Speech was recorded at 16 kHz via
- 136 either a head-mounted microphone (AKG C520, Exp 1-2) or a desktop microphone (Sennheiser
- 137 MKE 600, Exp 3-4). The output of Audapter was played back to participants via closed-back
- 138 circumaural headphones (Beyerdynamic DT 770) with an unnoticeable delay of ~18 ms, as
- 139 measured on our system following Kim & Max (2020). All trials were processed through
- 140 Audapter in the same manner, regardless of whether a perturbation was applied. Speech was
- 141 played back at a volume of approximately 80 dB SPL and mixed with speech-shaped noise at
- 142 approximately 60 dB SPL, which served to mask potential perception of the participants' own
- 143 unaltered speech through air and bone conduction. The volume of speech playback varied
- 144 dynamically with the amplitude of participants' produced speech.
- 145

146 Experiment-specific auditory perturbation

147 We designed a modified version of Audapter (Parrell & Niziolek, 2021) that is able to affect the

- 148 perceived variability of speech production by specifying formant perturbations as a function of
- 149 the current values of F1 and F2 (Figure 1A). A participant-specific perturbation field was
- 150 calculated for each vowel such that every production during the exposure phase was shifted
- 151 toward (inward-pushing perturbation) or away from (outward-pushing perturbation) the mean
- 152 F1/F2 values of that participant's distribution for that vowel (the vowel "targets"). The
- 153 magnitude of the perturbation was defined as a percentage of the distance between the currently
- 154 produced vowel formants and the vowel targets. By scaling the error between the vowel formants
- and their targets, the inward- and outward-pushing perturbations respectively reduce and
- 156 magnify the perceived variability of speech production.
- 157
- 158 In Experiment 1 (inward-pushing perturbation), participants received a perturbation that
- 159 shifted every production *towards* the vowel target. The perturbation was 50% of the distance, in
- 160 F1/F2 space, between the current formant values and the vowel targets (see Figure S1).
- 161
- 162 In Experiment 2 (outward-pushing perturbation), participants received the opposite
- 163 perturbation, a shift of every production *away* from these targets, with a slightly larger
- 164 perturbation magnitude (i.e., 75% of the distance to the vowel target, Figure S1).
- 165
- 166 In Experiment 3 (large outward-pushing perturbation), we aimed to test the possibility that
- 167 the failure to find the hypothesized reduction in variability in response to the outward-pushing
- 168 perturbation applied in Experiment 2 was due to inadequate perturbation magnitude. We
- 169 suspected that a larger perturbation magnitude might be needed to drive participants to produce
- 170 compensatory reductions in variability. The perturbation magnitude was therefore increased to
- 171 200% of the distance to the vowel target in Experiment 3 (Figure S1) and one stimulus word was

changed from a corner vowel word ("bad") to a non-corner vowel word ("bed") to test the effectof the perturbation on non-corner vowels.

174

175 In Experiment 4 (inward-outward pushing perturbation), we further examined whether limits

176 on articulatory precision prevented participants from reducing their produced variability in

177 response to outward-pushing perturbations in Experiment 2 and 3: that is, if individuals already

178 produce vowels at the lower limit of variability, they may not be able to produce further

variability decreases. In Experiment 4, participants experienced two exposure phases: first, to an

180 inward-pushing perturbation, which served to increase participants' produced variability above

181 baseline levels, and then to an outward-pushing perturbation. The perturbation magnitudes were

- 182 50% of the distance to the vowel target for both inward-pushing and outward-pushing phases.
- 183

184 In order to control for potential changes in variability over the course of ~500 trials of single

185 word production, we additionally analyzed an existing dataset (Parrell & Niziolek, 2021) with a

186 similar experimental structure, though with no auditory perturbation applied (auditory feedback

187 was processed through Audapter in the same manner as the baseline phases in Experiments 1-4).

188 This control experiment included 460 trials of single word productions (115 repetitions of each

189 stimulus word in Experiments 1, 2 and 4 — "bead", "bad", and "bod"—as well as the word

190 "booed", which did not occur in Experiments 1-4 and was not analyzed). To match the

191 experimental design of the current study, the 460 trials were divided into four phases: baseline

192 (30 trials per stimulus), early exposure (30 trials per stimulus), late exposure (30 trials per

193 stimulus) and washout (25 trials per stimulus). The experimental setup for the control dataset,

194 including recording, processing, and headphone presentation of speech, was identical to the

195 Experiments 1-4.

196

197 Procedure

198 In all experiments, stimulus words were presented on the computer screen for 1.5 s, one at a

time. The interstimulus interval was randomly jittered between 0.25-1 s. Participants were

200 instructed to read each word out loud as it appeared.

201

202 Each experiment had three phases (Figure 1B). Experiments 1-3 were divided into baseline,

203 exposure and washout phases. In the baseline phase (40 trials per stimulus), participants received

unaltered auditory feedback and we measured participants' mean F1/F2 values for each vowel.

205 These values were subsequently used to calculate the participant-specific perturbation field (see

above). The exposure phase followed the baseline phase. In the exposure phase, participants

- 207 produced each stimulus 100 times while receiving either the inward-pushing, outward-pushing,
- 208 or large outward-pushing perturbation (see experiment-specific auditory perturbation above).
- 209 Experiments 1-3 ended with a washout phase where participants produced each word 40 times
- 210 with unaltered auditory feedback. In Experiment 4, following the baseline phase, participants

- 211 experienced two sequential 300-trial (each stimulus 100 times) exposure phases, first with an
- 212 inward-pushing perturbation and then with an outward-pushing perturbation. A short self-timed
- 213 break was given every 30 trials in all experiments.
- 214
- 215 After they completed the experiment, participants in all four experiments were given a brief
- 216 questionnaire to assess their awareness of the perturbation as well as whether they adopted any
- 217 strategy and, if so, what that strategy was.
- 218

219 Quantification and statistical analysis

F1 and F2 were tracked offline using wave_viewer (Niziolek & Houde, 2015), which provides a MATLAB GUI interface to formant tracking using Praat (Boersma & Weenink, 2019). Linear

predictive coding (LPC) order and pre-emphasis values were adjusted individually for each

- participant. All trials were first checked manually for errors in production (e.g., if the participant
- said the wrong word). Vowel onset and offset were detected automatically using a participant-
- sind the wrong word). Vower onset and oriset were detected automatically using a participant² specific amplitude threshold and errors in the location of these automatically-defined landmarks
- were manually corrected using the audio waveform and spectrogram. Vowel onset was marked at
- the point where periodicity was visible in the waveform and formants were visible in the
- 228 spectrogram. Vowel offset was marked at the point where formants, particularly F2 and higher,
- were no longer visible. Errors in formant tracking were manually corrected by adjusting the LPC
- order or pre-emphasis value on a trial-specific basis. In total, 1.9% of the data were excluded due
- to production errors or unresolvable errors in formant tracking. For each trial, F1 and F2 values
- 232 were calculated by averaging formants from a 50-ms segment at both the beginning (vowel
- 233 onset) and the middle (vowel midpoint) of each vowel.
- 234

The primary goal of the analysis was to test how variability changed across the different phases

236 of each experiment. For offline analysis, the exposure phase was equally divided into early

- 237 exposure and late exposure phases to make sure each phase contained a similar number of trials.
- 238 Variability within each experimental phase was calculated as the average of the 2D distances in
- 239 F1/F2 space between each production of a vowel and the center of the distribution for that vowel
- 240 in that phase, measured from the first 50 ms of vowel. In order to test how variability may
- change in specific dimensions, we additionally calculated formant variability separately along
- the F1 and F2 axes, as well as along the major and minor axes of produced variability in the
- baseline phase. The variability along the F1 and F2 axes was defined as the standard deviation
- 244 (SD) of F1 and F2 values of all productions of a stimulus word during each phase. For the major
- and minor axes of variability, an ellipse which represents a 95% confidence interval of trials in
- 246 F1-F2 spaces was fitted for each stimulus word and each experimental phase using the Principal
- 247 Components method. The vector representing the F1 and F2 values for each trial was projected
- into a component along the major axis of the fitted ellipse and a component along the minor axis
- 249 perpendicular to the major axis. The variability along the major and minor axes was defined as

the standard deviation (SD) of projected values along that axis of all productions of a stimulusword during each phase.

252

253 We additionally measured vowel centering, a measure of within-trial correction for variability,

calculated by the change in variability from vowel onset (first 50 ms) to vowel midpoint (middle

255 50 ms). Vowel centering allows us to determine whether participants altered their within-trial

control of variability in response to the perturbation (Niziolek & Guenther, 2013; Niziolek &

257 Kiran, 2018; Niziolek & Parrell, 2021). Centering was measured separately for each vowel in

- each experimental phase.
- 259

260 Repeated measure analyses of variance (ANOVAs) were conducted separately for the variability

and centering results and for each experiment, with phase and vowel identity as within-subject

factors. For the control data and Experiments 1-3, data from baseline, late exposure and washout

263 phases were included in the repeated ANOVAs, while data from baseline, inward-pushing

264 exposure, and outward-pushing exposure phases were included in Experiment 4. Post-hoc

265 comparisons (paired t-tests) were only conducted in the event of a significant main effect of

phase or interaction. As an exploratory analysis, multiple regression was conducted in each
 experiment to determine whether produced variability changes could be predicted by baseline

268 variability and vowel identity. Finally, variability changes along F1/F2 or major/minor axes were

269 examined separately by three-way repeated measures ANOVAs which included phase, vowel

identity and axis (i.e. F1/F2 or major/minor) as within-subject factors. The significance level for

all statistical tests was p < .05, with a Bonferroni correction for multiple comparisons for post-

hoc tests.

273 All statistical analyses were conducted in R (R Core Team, 2019). Repeated measures ANOVAs

and pairwise paired t-tests were conducted with the rstatix package (Kassambara, 2021), in

275 which partial eta squared (η_p^2) and Cohen's *d* were calculated for repeated ANOVAs and paired

t-tests, respectively, to determine effect size for statistically significant effects. Greenhouse-

277 Geisser Correction was applied automatically to correct the degrees of freedom when sphericity

was violated. Multiple regression models were constructed using the package stats. Data and

associated code is available at <u>https://osf.io/stjc9/</u>. Some functions rely on additional code

available at <u>https://github.com/carrien/free-speech</u>.

281

282 *Model simulations*

283 In order to assess the potential mechanisms underlying the patterns of variability changes

observed in Experiments 1-4, we conducted a simulation of speech behavior using a version of

the well-established state space models that have been used in studies of sensorimotor adaptation

to sensory perturbations in both limb (Baddeley et al., 2003; Donchin et al., 2003; Thoroughman

287 & Shadmehr, 2000) and speech (Daliri, 2021; Daliri & Dittman, 2019) motor control.

288 Importantly, analogous models have also been used successfully in studies of sensorimotor

corrections for self-produced variability in reaching (Ahn et al., 2016; Blustein et al., 2021;

290 Scheidt et al., 2001), similar to the current experiments. The model is:

291

292 $m_t = Am_{t-1} + Be_{t-1}$ 293 $x_t = m_t + N(0,K)$

$$e_t = -G_X$$

295

296 This model assumes that the intended production (m) on a given trial (t) aims to achieve a 297 particular target (by convention, set to 0) based on a weighted contribution of the production on 298 the previous trial (t - 1) and the error (e) experienced on the previous trial. A is the forgetting 299 factor that determines the contribution of the previous trial, and B represents the sensitivity of the system to errors. The error e is the difference between the actual production outcome (x) and the 300 301 target, where the production x is the result of the intended production m plus noise (N) drawn 302 from a gaussian distribution with a mean of 0 and a standard deviation of K. In order to account 303 for the gains applied to the auditory feedback in this experiment, the observed outcome x is 304 multiplied by a gain factor G to derive the error. Aside from the addition of the gain factor G, this 305 is identical to the formulation in Ahn et al., (2016), if A = 1.

306

307 While the state space model is often used to model sensorimotor adaptation to external 308 perturbations, the addition of the noise term on the final motor output also permits modelling of 309 correction for self-produced variability (Ahn et al., 2016; Blustein et al., 2021; Scheidt et al., 310 2001). For simplicity, we initially set A to 1 (Ahn et al., 2016) and B to 0.1 given previous results 311 fitting state space models to adaptation in speech (Daliri, 2021; Daliri & Dittman, 2019). We 312 then estimated an initial value of K that would generate an observed distribution similar to the 313 experimentally observed variability in the baseline phase across experiments (roughly 30 mels). 314 Because the errors in this model are generated stochastically, we need a large number of 315 simulations to achieve an accurate estimate of the underlying distribution of variability that 316 would be generated through this model. To that end, we ran batches of 1000 simulations while 317 varying K. Each simulation consisted of 40 trials, equivalent to the number of trials used to 318 estimate variability in our experimental data. Our initial simulations indicated that setting K to 30 319 resulted in a mean observed variability close to the observed values in the baseline phase across 320 experiments. Varying A within the range reported in (Daliri, 2021) had very minor effects on the 321 results; the effects of varying *B* are explored below.

322

323 Our goal in modeling was to assess the potential causes of the increase in variability observed in

324 the behavioral data in Experiments 1-4. To do this, we systematically varied the underlying

325 variability K as well as the sensitivity to errors B. K varied from 30 to 40 in steps of 0.5. B varied

from 0 to 1 in steps of 0.05, where 0 would represent no correction for observed errors and 1

327 would represent full correction. For each step of *K* and *B*, 1000 simulations (40 trials each) were

328 conducted. The standard deviation of *x* was calculated for each simulation, and the mean of these

329 standard deviations was calculated to generate an estimate of the expected variability with that

particular parameter set. We ran separate simulations for the inward-pushing perturbation in

- 331 Experiment 1 (setting G to 0.5) and the outward-pushing perturbation in Experiment 2 (setting G
- 332 to 1.75).
- 333

334 **Results**

335 Overall variability changes

336 Over four experiments, we implemented an auditory perturbation designed to increase or

337 decrease participants' perceived trial-to-trial variability without affecting their overall mean. To

confirm that this was achieved, the perturbations applied to F1 or F2 frequencies during the

exposure phase in each experiment were averaged for each participant and compared against

340 zero (no mean formant value change) using one-sample t-tests. The mean F1 perturbations

ranged between 2.5 and 13.4 mels in Experiments 1-4 and significantly differed from zero only

in Experiment 3 (large outward-pushing, mean F1 perturbation: 13.4 mels, t(20) = 2.47, p = 2.47,

0.023). Similarly, the mean F2 perturbations ranged between -1.23 and 12.39 mels in

Experiments 1-4, with no significant difference from zero in any case (uncorrected p > 0.05). It

is worth mentioning that the just noticeable difference (JND) in F1 and F2 for isolated English

vowels is around 14 mels and 20 mels, respectively (Kewley-Port & Watson, 1994).

347

348 We then measured how participants changed their produced variability after the perceived

349 variability had been increased or decreased. As a control, we analyzed an existing dataset (Parrell

- 350 & Niziolek, 2021) with no auditory perturbation. As expected, the control group showed no
- 351 change in variability over the course of the experiment (Figure 2A, F(2,48) = 0.434, p = 0.650).
- 352

353 Participants exposed to the **inward-pushing perturbation (Experiment 1)** increased produced

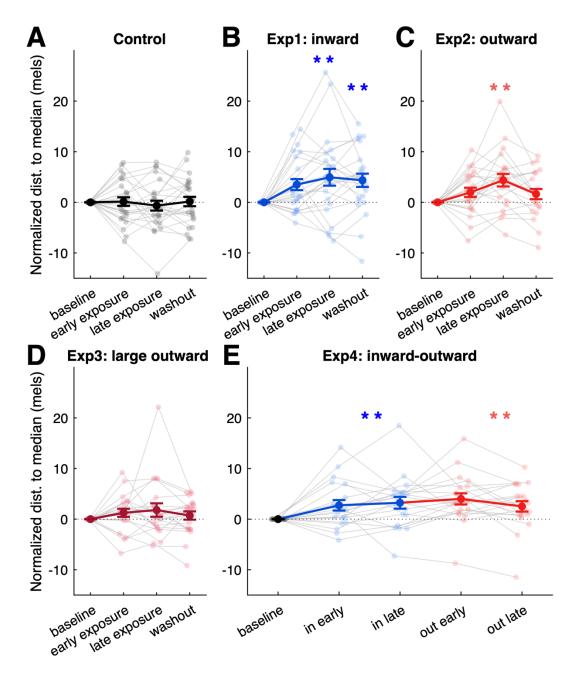
variability (Figure 2B, main effect of phase: F(2,46) = 7.55, p < 0.001, $\eta_p^2 = 0.25$) while the

perturbation was applied (+5.0 mels, t(71) = 4.59, p < 0.001, d = 0.54) as well as after it was

removed (+4.4 mels, t(71) = 4.89, p < 0.001, d = 0.58). Unexpectedly, participants exposed to

the **outward-pushing perturbation (Experiment 2)** also increased produced variability (Figure 2C, main effect of phase: F(2,40) = 7.93, p < 0.001, $n_p^2 = 0.28$). However, unlike the maintained

- variability change seen in the inward-pushing perturbation, the increased variability during
- exposure (+4.3 mels, t(65) = 4.10, p < 0.001, d = 0.50) returned to near-baseline levels when the
- outward-pushing perturbation was removed (+1.6 mels, t(62) = 1.93, p = 0.175).



362 363

364 *Figure 2. Baseline-normalized variability changes.* Individual (small transparent dots, thin

365 lines) and group means (large solid dots, thick lines) of baseline-normalized variability

(normalized by subtracting the average value in the baseline from the remaining trials) in the
 baseline, exposure and washout phases. Error bars show standard error. ** indicates significant

- 368 *change* (p < 0.001) *from baseline.*
- 369
- 370

We reasoned that the failure to find the hypothesized reduction in variability in response to the outward-pushing field could potentially be attributed to the size of the perturbation used.

373 Although this perturbation was slightly larger than in Experiment 1 (75% vs 50% of the distance

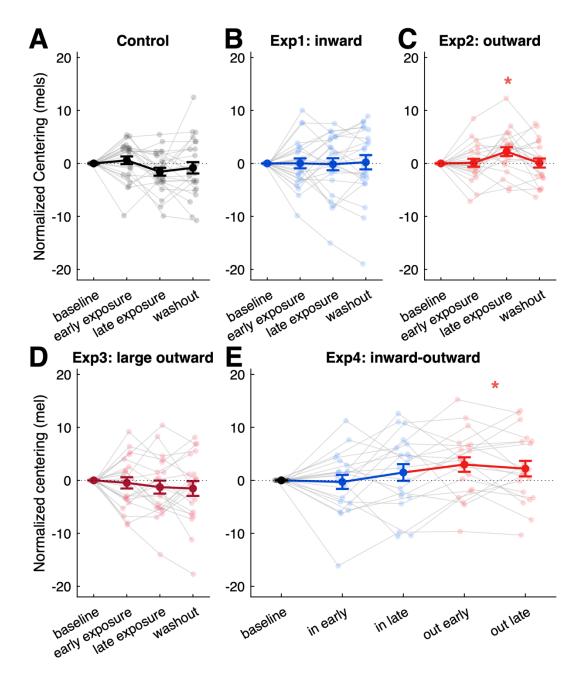
- to vowel target), it may still have been too small to induce participants to reduce their variability.
- 375 Experiment 3 (large outward-pushing perturbation) aimed to delineate this by testing another
- 376 group of participants who received outward-pushing perturbations with a 200% increase in
- 377 distance to the center of vowel distribution (vs 75% in Experiment 2). However, participants
- 378 exposed to this large outward-pushing perturbation did not change their produced variability
- 379 (Figure 2D, main effect of phase: F(1.55,30.95) = 1.39, p = 0.26).
- 380
- 381 Together, the results of both experiments employing outward-pushing perturbation fields
- 382 (Experiment 2 and 3) suggest these perturbations do not drive participants to produce
- 383 compensatory reductions in variability. One possibility for this behavior is that speech
- 384 movements are already produced at or near the lower limit of an individual speaker's precision
- ability. **Experiment 4 (inward-outward pushing perturbation)** aimed to test this possibility by
- examining whether an outward-pushing perturbation can reduce produced variability of
- 387 participants *after* their variability has increased above baseline levels due to exposure to an
- inward-pushing perturbation as seen in Experiment 1. Participants significantly changed their
- 389 produced variability during the course of Experiment 4, reflected by a main effect of phase
- 390 (Figure 2E, F(2,38) = 9.71, p < 0.001, $\eta_p^2 = 0.34$). As expected given the results of Experiment 1,
- variability increased when the inward-pushing perturbation was applied (+4.1 mels, t(59) = 4.77, p < 0.001, d = 0.62). However, participants did not change their produced variability back to the
- baseline when receiving the outward-pushing perturbation in the following phase (+4.1 mels,
- t(59) = 4.13, p < 0.001, d = 0.53). While this result replicates the increase in variability observed
- during the exposure phase in Experiments 1 and 2, it suggests the failure to find the expected
- reduction in variability in Experiments 2 and 3 was not caused solely by a "lower limit" on
- 397 variability.
- 398
- 399 Finally, while not the primary focus of the study, we evaluated whether participants adjusted
- 400 their variability differently along the major/minor axes of variation using three-way repeated
- 401 ANOVAs including three within-subject factors (phase, vowel, axis). This analysis replicated the
- 402 results of overall variability changes (distances in F1-F2 spaces): a significant main effect of
- 403 phase was found in Experiments 1, 2, 4, but not in the control data or in Experiment 3. Perhaps
- 404 more interestingly, no significant two-way interaction between phase and measure was found in
- 405 any of these experiments, suggesting participants adjusted their variability along the major- and
- 406 minor-axis similarly. Similar results were found from models of F1 and F2 variability. See
- 407 Supplemental Material, Figures S2, S3 and Tables S1, S2 for detailed results and statistics.
- 408

409 *Centering changes*

- 410 In order to determine whether participants adjusted their within-trial control of variability in
- 411 response to the perturbation, we additionally measured vowel centering (Niziolek & Guenther,

412 2013; Niziolek & Kiran, 2018; Niziolek & Parrell, 2021), the reduction in variability from vowel

- 413 onset (first 50 ms) to vowel midpoint (middle 50 ms). Similar to the analyses on variability, the
- 414 control group did not show any change in centering over the course of the experiment (Figure
- 415 3A, F(2,48) = 1.45, p = 0.244). However, unlike the overall variability changes observed above,
- 416 no change in centering was seen in participants who received the **inward-pushing perturbation**
- 417 (Experiment 1, Figure 3B, F(1.49, 34.27) = 0.06, p = 0.896). In contrast, centering did increase
- 418 when participants were exposed to the **outward-pushing perturbation** (Experiment 2, Figure 419 3C, main effect of phase: F(2,40) = 3.94, p = 0.027, $\eta_p^2 = 0.165$), suggesting these participants
- 419 3C, main effect of phase: F(2,40) = 3.94, p = 0.027, $\eta_p^2 = 0.165$), suggesting these participants 420 became more responsive to errors. This increase in centering during exposure (+ 2.2 mels, *t*(65))
- 421 = 3.33, p = 0.004, d = 0.41) was not retained during the washout phase (+ 0.1 mels, t(62) = 0.11.
- 422 p = 1.000). Contrary to the increase in centering observed in Experiment 2, participants who
- 423 received a large outward-pushing perturbation in Experiment 3 (i.e. 200% increase in distance
- 424 to the vowel target) did not show an increase in centering over the course of experiment (Figure
- 425 3D, F(2,40) = 0.87, p = 0.428), actually tending to slightly decrease centering during and after
- 426 exposure. In Experiment 4 (inward-outward pushing perturbation), participants showed
- 427 changes in centering over the course of the experiment, indicated by a marginally significant
- 428 main effect of phase (Figure 3E, F(1.4, 26.5) = 3.15, p = 0.075, $\eta_p^2 = 0.142$). More specifically,
- the results replicated the patterns observed in Experiments 1 and 2: the initial inward-pushing
- 430 perturbation did not induce any significant increase in centering (+ 0.53 mels, t(59) = 0.38, p = 1.
- 431 000), while the subsequent outward-pushing perturbation did (+ 2.7 mels, t(59) = 2.27, p = 0.05,
- 432 d = 0.29).



433

434

435 *Figure 3. Baseline-normalized centering changes. Individual (small transparent dots, thin*

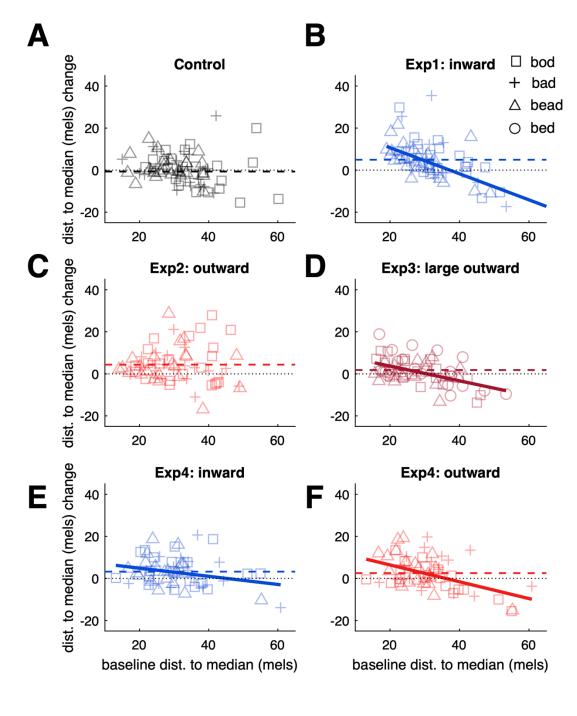
436 lines) and group means (large solid dots, thick lines) of baseline-normalized centering
437 (normalized by subtracting the average value in the baseline from the remaining trials) in the

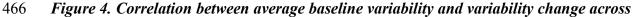
438 baseline, exposure and washout phases. Error bars show standard error. * indicates significant

439 change (p < 0.05) from baseline.

441 Correlation between variability change and baseline variability

- 442 Multiple regression was conducted in each experiment to determine whether changes in
- 443 produced variability could be predicted by baseline variability and vowel identity at the
- 444 individual level (see Figure 4). Results showed that baseline variability was not predictive of the
- 445 individual change in variability observed during the late exposure phase in either the control (β =
- 446 -0.18, p = 0.094) or Experiment 2 (outward-pushing perturbation, $\beta = -0.024$, p = 0.846).
- 447 However, this relationship was observed in the Experiment 1 (inward-pushing perturbation, β
- 448 = -0.44, p < 0.001), such that participants with lower variability in the baseline phase showed
- 449 larger variability increases. In Experiment 3 (large outward-pushing perturbation), where
- 450 there was no consistent change in variability over the course of the experiment, baseline
- 451 variability was nonetheless predictive of individual changes in variability ($\beta = -0.38$, p = 0.002):
- 452 participants with higher variability in the baseline phase tended to decrease variability, and vice
- 453 versa. Experiment 4 (inward-outward pushing perturbation) replicated the result from
- 454 Experiment 1: a significant correlation was observed between baseline variability and variability
- 455 change induced by inward-pushing perturbation ($\beta = -0.19$, p = 0.049). Perhaps surprisingly
- 456 given the results of Experiment 2, a similar relationship between baseline variability and
- 457 variability change was also observed during later outward-pushing perturbation ($\beta = -0.37$, p < -0.37)
- 458 0.001). However, it should be noted that there was a highly significant correlation in variability 459
- between the two perturbation phases ($\beta = 0.54$, p < 0.001), suggesting that the correlation
- 460 observed during the outward-pushing perturbation is likely a carry-over effect of the inward-
- 461 pushing perturbation which happened between baseline and outward-pushing phases.
- 462





⁴⁶⁷ *individuals*. Each data point represents the average production of one stimulus word, indicated

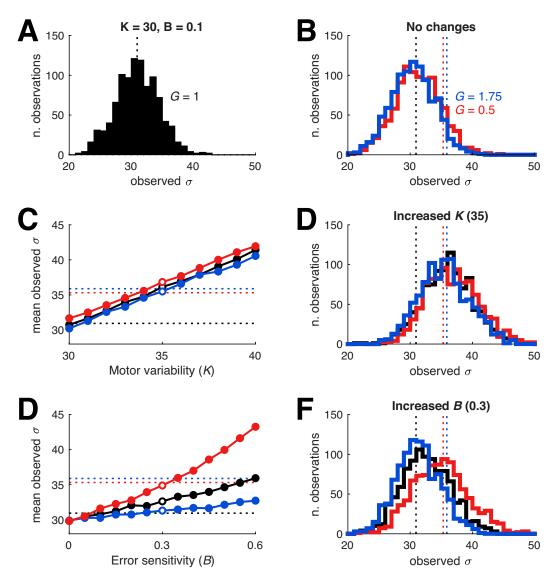
- 469 words were "bead", "bad", and "bed" in Experiment 3, and "bead", "bad", and "bod" in the
- 470 other experiments. Significant correlations are indicated by solid lines showing the least-squares
- 471 fit to the data points. The group-averaged (baseline-normalized) variability changes are
- 472 *indicated by colored dashed lines.*

⁴⁶⁸ by different markers. Each participant thus contributed three data points. Note that the stimulus

473 State space simulations

474 Using a modified version of the typical state space model that has been shown to account for

- 475 observed motor variability in reaching, we systematically varied the magnitude of motor
- 476 variability (K) and the sensitivity of the system to observed errors (B). Results of these
- 477 simulations are shown in Figure 5. We found that, predictably, increases in the underlying motor
- 478 variability increased the observed variability in motor production for both the inward- and
- 479 outward-pushing perturbations (Figure 5C). Values of *K* near 35 produced observed variability
- 480 measures consistent with those in both Experiments 1 and 2 (Figure 5D). Conversely, we found
- 481 that changes in error sensitivity had differential effects on motor variability depending on the
- 482 perturbation field. For the inward-pushing perturbation, variation in error sensitivity had very
- 483 minor effects on motor output. Conversely, for the outward-pushing perturbation, increases in
- 484 error sensitivity led to large increases in motor variability (Figure 5E). Values of *B* near 0.3
- resulted in a good match for the observed variability in Experiment 2, while no values of *B*
- 486 provided a good match for Experiment 1 (Figure 5F). In the latter case, the maximum increase in
- 487 observed variability over baseline was 3.7 where B = 1, still substantially less than the
- 488 experimentally observed value. These results indicate that the observed increase in Experiment 1
- 489 can only be explained by an increase in the underlying motor variability, while the increase
- 490 observed in Experiment 2 could arise through either an increase in controlled variability or an
- 491 increase in the sensitivity to auditory errors.





494 Figure 5. State space simulations of motor variability. For all panels, the dashed black line 495 represents the mean variability with model parameters set to match participant behavior in the 496 baseline phase, the dashed blue line represents the increase in variability observed in 497 *Experiment 1 (4.9 mels above baseline), and the dashed red line represents the increase in* 498 variability observed in Experiment 2 (4.4 mels above baseline). (A) shows distributions of 499 observed variability for 1000 simulations where the gain applied to the observed error is 1, 500 simulating the baseline phase in both Experiments 1 and 2. (B) shows similar distributions from 501 simulations with gains set to 0.5 (blue) and 1.75 (red), mirroring the perturbations applied in 502 *Experiment 1 and Experiment 2, respectively, with no changes to other model parameters. (C)* 503 shows the result of systematically varying underlying motor variability K on observed variability 504 with gains set to 1(black), 0.5 (blue), and 1.75 (red). The open circles in the left panel represent 505 the value for K used in the simulations shown in (D). (D) shows the distribution of observed 506 variability with K set to 35, chosen to roughly match the increase in variability observed in

507 *Experiments 1 and 2. (E) as for (C), showing the effect of varying the error sensitivity parameter*

- 508 B. Values of B greater that 0.6 (not shown) resulted in values observed variability > 50 where G
- 509 = 1.7 and < 34 where G = 0.5. (F) shows the distribution observed with B set to 0.3, chosen to
- 510 *match the increase in variability observed in Experiment 2.*
- 511

512 Awareness of perturbation

513 Most of the participants in Experiment 1, 2, and 4 (41/66) were not aware of the perturbation

514 applied to their vowels. Although 25/66 did indicate that they thought their speech was somehow

515 manipulated, only 1 participant correctly identified it as a change to their vowels/consonants. In

516 contrast, nearly all participants (19/21) in Experiment 3 (large outward-pushing) reported that

517 they thought they received a perturbation, and almost half (9/21) correctly identified it as a

518 manipulation to their vowels. No participants reported a strategy that aimed to address the

- 519 applied perturbation in any of the four experiments.
- 520

521 **Discussion**

522 In a set of four experiments, we examined whether variability can be actively regulated in a

523 complex, well-practiced motor task: speech production. Specifically, we examined whether

524 participants would adjust their produced variability when they were exposed to real-time

525 auditory perturbations that increased or decreased their perceived variability. Our results showed

526 that introducing a perturbation that reduces perceived variability (Experiment 1: inward-pushing)

527 leads to increases in produced vowel variability that remain even when normal feedback is

restored, suggesting that variability is monitored and regulated over relatively long time scales.

529 Perhaps surprisingly, a perturbation that increases perceived variability (Experiment 2: outward-

530 pushing) also increased produced variability, though such variability change was not maintained

solution was removed. In Experiment 3, participants who received a large outward-

- 532 pushing perturbation (i.e. a 200% increase in distance to the vowel target) did not change their
- 533 produced variability over the course of the experiment. This rules out the possibility that the

failure to find the hypothesized reduction in variability in response to the outward-pushing

535 perturbation (Experiment 2) is due to inadequate perturbation magnitude. Finally, we found that

an outward-pushing perturbation cannot reduce participants' produced variability even *after* their

537 variability has increased above baseline levels as a result of the inward-pushing perturbation

- 538 (Experiment 4: inward-outward pushing).
- 539

540 To our knowledge, this is the first study showing that variability in speech production can be

541 actively controlled, consistent with recent theories that have highlighted the adaptive value of

542 motor variability in other motor domains (Davids et al., 2003; Herzfeld & Shadmehr, 2014;

543 Tumer & Brainard, 2007). From this perspective, motor variability can be actively generated,

544 regulated and used by the brain to improve motor performance, reduce costs and explore new 545 solutions (Shadmehr et al., 2016). Early evidence shows that skilled performers are able to 546 upregulate the level of motor variability in each joint of the upper arm to meet the change of task 547 demands/constraints, while less skilled performers, in comparison, tend to have rigidly fixed 548 motor variability that is not fine-tuned with task constraints (Arutyunyan et al., 1968, see Newell 549 & Vaillancourt, 2001 for a review). More recent work using computational models also found 550 that force variability and the resulting kinematic variability are not generated primarily by 551 random "motor noise", and emphasize the importance of other sources of force variability which 552 can be tuned as needed by distributed sensorimotor systems (Nagamori et al., 2021). The results 553 from the current study extend previous work and provide support for this perspective by showing 554 the motor system closely monitors sensory variability and uses such information to actively 555 regulate the motor variability, even in complex and well-practiced behaviors such as natural 556 speech.

557

558 Surprisingly, participants exposed to both inward-pushing and outward-pushing perturbations 559 increased their produced variability. These results could be interpreted as a general variability 560 increase induced by either repetitive productions of many utterances or a non-specific auditory 561 perturbation (that is, any kind of auditory perturbation would lead to an increase in formant 562 variability). However, the results from our data as well as previous studies indicate that both of 563 the possibilities are unlikely. First, in analyzing an existing dataset where participants produced 564 460 utterances with normal auditory feedback (Parrell & Niziolek, 2021), we found that speakers did not significantly change their produced variability. This confirms that under normal 565 566 circumstances speakers produce vowels with a level of variability that is relatively stable over time. Second, previous work has shown that participants do not change their formant variability 567 in response to consistent auditory perturbation of both F1 and F2 (i.e. shifts of 240 Hz in F1 and 568 569 300 Hz in F2) (Nault & Munhall, 2020). Results from Experiment 3 are consistent with this 570 result, as participants who received a large outward-pushing perturbation did not exhibit any significant change in their variability. These results, taken together, rule out the possibility of a 571 572 general non-specific increase in variability induced by auditory perturbations. 573

574 In our experimental data, the increased variability induced by the auditory perturbation was 575 maintained even when normal feedback was restored in Experiment 1, but not in Experiment 2. 576 This difference suggests different mechanisms may have led to the increased variability observed 577 in the two experiments. As an attempt to disentangle these potential mechanisms, we conducted a 578 simulation using a state space model of error correction. Model simulations identified two 579 distinct mechanisms that could lead to the observed increase in produced variability: an increase 580 in controlled variability or an increase in the sensitivity to auditory errors. More specifically, 581 these simulations indicated that the observed increase in Experiment 1 (inward-pushing) can only 582 be explained by an increase in controlled variability, while the increase observed in Experiment 583 2 (outward-pushing) could arise through either of these two mechanisms. Importantly for

584 Experiment 2, a return to unperturbed auditory feedback in the washout phase would not 585 necessarily cause an immediate decrease in controlled variability, but would directly lead to a 586 change in variability related to trial-to-trial correction for errors even with a constant error 587 sensitivity (see Figure 5). These modeling results suggest the increase in observed variability in 588 response to the inward-pushing perturbation in Experiment 1 was likely driven by a relaxation of 589 controlled variability, as the perturbation "frees" the motor system to be more variable without 590 any loss in perceived accuracy. Conversely, the results from the Experiment 2 are most 591 consistent with an increase in error sensitivity caused by the outward-pushing field rather than a 592 change in controlled variability. Consistent with this difference, we found a significant 593 correlation between produced variability changes and baseline variability in Experiment 1 but 594 not in Experiment 2. One possible explanation for the pattern observed in Experiment 1 is that 595 participants who are naturally more variable may take advantage of the natural consequences of 596 the inward-pushing perturbation to reduce overall perceived variability, while less variable 597 individuals may relax their (presumably stricter) regulation of variability without negatively 598 affecting their perceived variability. In contrast, in Experiment 2, we would not expect that 599 changes in error sensitivity would be related to levels of baseline variability. In brief, the 600 combined results of behavioral and model simulation point to the two distinct mechanisms that 601 may have led to the observed increase in variability in response to inward-pushing and outward-602 pushing perturbation.

603

604 It is worth mentioning that while it would be ideal to compare the predictions generated by the

state space model to empirical estimates of error sensitivity, limitations of the experimental
 design prevent us from being able to estimate such parameters. Even with recent advances in this

regard (Blustein et al., 2021), accurate estimation of these parameters requires 100-200

608 sequential trials. In all experiments, participants produced 40-50 repetitions of each word per

609 phase, in a pseudo-randomized order. Thus, our protocol provides both an insufficient number of

610 trials as well as a potential confound of producing multiple intervening movements between

611 repetitions of the same item. Future work should explore whether current methods that are

612 known to provide accurate estimates of error sensitivity in reaching could be applied to speech

613 motor control with a more appropriate experimental design.

614

615 We additionally measured vowel centering, a measure of within-trial correction for variability

616 (Niziolek & Guenther, 2013; Niziolek & Kiran, 2018; Niziolek & Parrell, 2021). Unlike the

617 overall variability changes observed in both kinds of perturbation, an increase in centering was

618 only seen in participants who received the outward-pushing perturbation in Experiment 2 and in 619 the outward-pushing phase of Experiment 4. This suggests that participants exposed to outward-

620 pushing perturbations became more responsive to within-trial errors (i.e. larger within-trial

621 feedback gains). Although it is not clear that such an increased sensitivity to errors for within-

622 movement corrections is directly related to the error sensitivity related to cross-trial changes (i.e.

623 gains on trial to trial learning), it is possible error sensitivity is shared across both processes. This

would be consistent with the fact that we see increased centering only in Experiment 2, precisely where modeling results suggest an increase in trial-to-trial error sensitivity.

626

627 The only case where we did not see an increase in centering or variability was Experiment 3

628 (large outward-pushing perturbation). It is possible that the larger perturbations used in this

629 experiment were discounted by the sensorimotor system, such that they had limited effects on

630 speech production. This is consistent with previous studies that have similarly shown attenuated

responses to large auditory feedback perturbations (Burnett et al., 1998; Scheerer et al., 2013),

632 potentially because large perturbations are treated as externally induced, rather than self-

633 produced errors (Korzyukov et al., 2017). This is also in line with the perturbation awareness

results: almost half of the participants in Experiment 3 correctly recognized the perturbation

applied on vowels, while only one participant did across all other experiments.

636

637 Together, the results of Experiments 2-4 suggest that a sensory perturbation that increases

638 perceived variability does not drive participants to produce compensatory reductions in speech

639 variability, contrary to previous results in non-speech motor control which showed task-relevant

640 variability can be reduced when needed or after repeated practice (Kang et al., 2004; van Beers et

al., 2013; Wong et al., 2009). One potential explanation for our failure to observe the

642 hypothesized decrease in variability in response to the outward-pushing perturbation in

Experiment 2 is that speech is already produced at the lower limits of possible task-related

644 variability, consistent with the predictions of the Uncontrolled Manifold hypothesis and Optimal

645 Feedback Control (Harris & Wolpert, 1998; Scholz & Schöner, 1999; Todorov, 2004). This

646 could also explain the lack of change in produced variability when the outward-pushing

647 perturbation occurred after variability had increased above baseline levels (Experiment 4): it is

648 possible that controlled variability here returned to baseline levels (without reducing past that

649 point), but was counteracted by the increase of error sensitivity induced by outward-pushing

- 650 perturbations.
- 651

Another possibility is suggested by the fact that in reaching tasks, only task-relevant variability
 has been observed to reduce experimental tasks, while task-irrelevant variability remained high

654 (Robertson & Miall, 1997; Scholz & Schöner, 1999). Thus, it is possible that participants in the

655 current experiments reduced variability along a particular dimension, even if their overall

656 variability increased. To explore this possibility, we calculated changes in variability along

657 participant-specific major and minor axes of variability in the baseline phase, assuming that the

minor axis of variability may be more tightly controlled (Scholz & Schöner, 1999). However, we

659 found that participants produced similar changes in variability along the major- and minor-axis,

suggesting speech motor system might control variability more globally compared to the

selective regulation in certain components of movement variability observed in non-speech

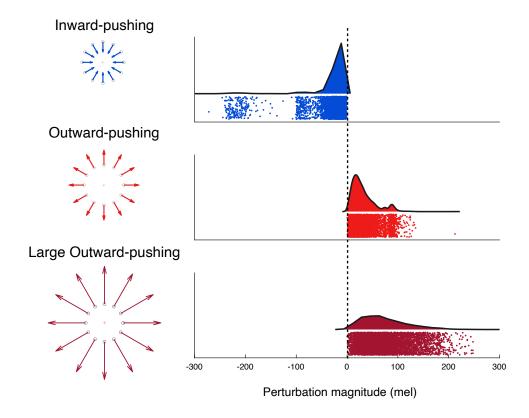
motor control (Abe & Sternad, 2013; Sternad et al., 2011). It is important to note, however, that

663 the major- and minor-axis in speech production are not necessarily equivalent to the task-

relevant and task-irrelevant dimensions in non-speech control, and indeed may both contribute to task performance. Further work is needed to clarify this point.

In summary, we have shown that individuals modify their produced variability when their perceived trial-to-trial variability is altered. Decreases in perceived variability lead to increases in produced variability, likely due to loosened restrictions on variability production, particularly in individuals with inherently low variability. These changes are retained even when the perturbation is removed, suggesting that the monitoring and regulation of variability acts relatively slowly. Conversely, variability also increases in response to perturbations which increase perceived variability, potentially due to increases in error sensitivity as participants try to correct for the perceived errors. Together, these results are consistent with recent evidence that suggests motor variability should be viewed as an important feature of how the sensorimotor system operates and learns rather than as the inevitable and unintended consequence of motor noise. Our results also highlight the importance of having a better understanding of motor variability during speech production, which has been largely overlooked in current theories and models of speech motor control. Acknowledgments This work was supported by NIH grant R01 DC019134 and a grant awarded through the University of Wisconsin-Madison Fall Research Competition.

- **Supplementary materials**



- 717

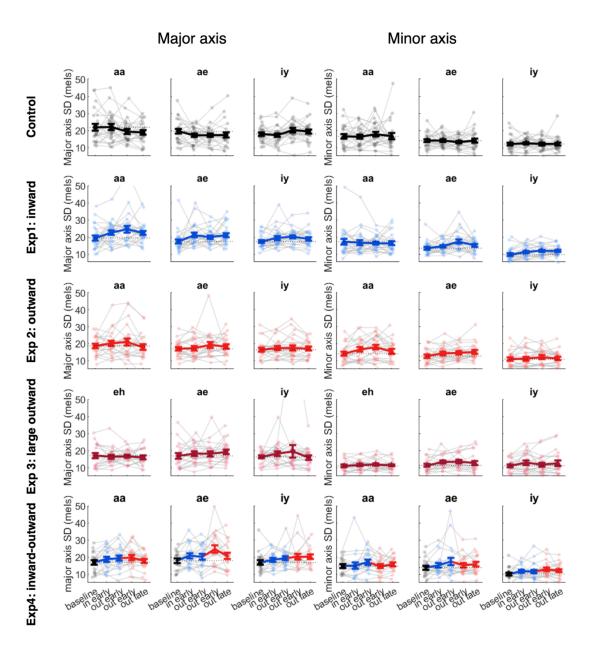
Figure S1. Schematic (left) and raincloud plot (right) of perturbation applied to speech vowel formants: inward-pushing pushing (Exp 1, top), outward-pushing (Exp 2, middle), and large outward-pushing (Exp 3, buttom). The raincloud plots show the magnitude of the applied perturbations both as a distribution (the 'cloud') and with jittered raw data (the 'rain').

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727	
728	

734 Table S1. Variability (SD) changes along major and minor axis

	Control	Experiment 1	Experiment 2	Experiment 3	Experiment 4
Main effect:					
Phase	F(2, 48) = 0.45,	F(2, 46) = 9.22,	F(2, 40) = 5.74,	F(1.5, 29.9) = 1.36,	F(2, 38) = 15.41,
	p = 0.642	p < 0.001**	p = 0.006*	p = 0.267	p < 0.001**
Vowel	F(2,48) = 5.39,	F(2, 46) = 17.31,	F(2, 40) = 17.82,	F(1.3, 25.2) = 1.28,	F(2, 38) = 7.47,
	p = 0.008*	p < 0.001**	p < 0.001**	p = 0.28	p = 0.002*
Axis	F(1, 24) = 110.13,	F(1, 23) = 116.54,	F(1, 20) = 40.02,	F(1, 20) = 61.5,	F(1, 19) = 77.23,
	p < 0.001**	p < 0.001**	p < 0.001**	p < 0.001**	p < 0.001**
Two-way intera	iction:				
Phase × Vowel	F(4, 96) = 1.90,	F(4, 92)=0.60,	F(4, 80)=2.01,	F(2.1, 41.4)=0.77,	F(4, 76)=1.06,
	p = 0.117	p = 0.662	p=0.101	p = 0.474	p = 0.385
Phase × Axis	F(2, 48) = 0.83,	F(2, 46) = 2.84,	F(1.6, 31.5)=0.33,	F(1.5, 29.4)=0.28,	F(2, 38)=0.78,
	p = 0.443	p = 0.069	p = 0.669	p = 0.693	p = 0.465
Vowel × Axis	F(2, 48) = 5.87,	F(2, 46) = 4.21,	F(1.5, 29.2)=0.1.83,	F(1.2, 24)=0.05,	F(2, 38)=8.93,
	p = 0.005*	p = 0.021*	p = 0.185	p = 0.858	p < 0.001*
Three-way inter	raction:				
Phase × Vowel ×	F(4, 96) = 1.69,	F(2.4, 54) = 3.07,	F(4, 80) = 0.58,	F(2.2, 44)=2.1,	F(4, 76)=0.771,
Axis	p = 0.160	p = 0.047*	p = 0.681	p=0.13	p = 0.547

Note. Significant three-way interaction was found only in Experiment 1. To follow up the significant three-way interaction, we grouped the data by vowel, and analysed the sample two-way interaction between phase and axis. There was no significant simple two-way interaction between phase and axis for any of the vowels (bod: p = 0.055, bad: p = 0.051, bead: p = 0.6). *p < 0.05 ** p < 0.001.



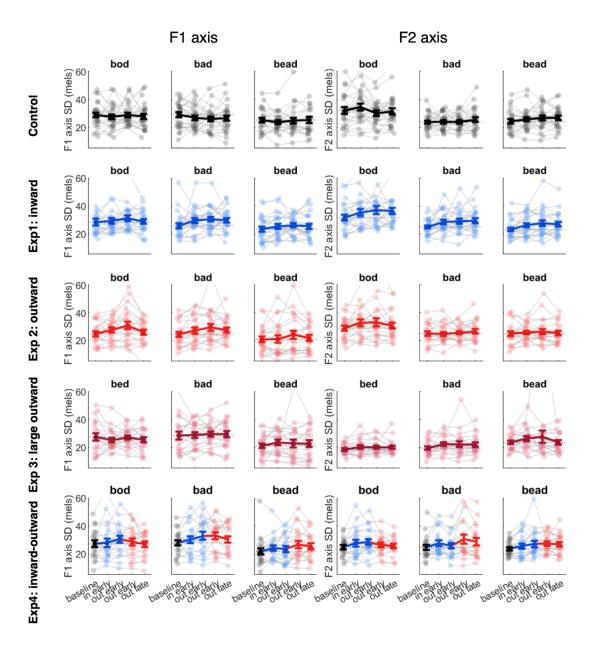
 $\begin{array}{c} 755\\ 756\\ 757\\ 758\\ 759\\ 760\\ 761\\ 762\\ 763\\ 764\\ 765\\ 766\\ 767\\ 768\\ 769\\ 770\\ 771\\ 772\end{array}$

Figure S2. Variability changes along major and minor axes in different words. *Individual (small transparent dots, thin lines) and group means (large solid dots, thick lines) of formant variability in the baseline, exposure and washout phases. Error bars show standard error.*

Table S2. Variability (SD) changes along F1 and F2 axis

	Control	Experiment 1	Experiment 2	Experiment 3	Experiment 4
Main effect:					
Phase	F(2, 48) = 0.25,	F(2, 46) = 7.38,	F(2, 40) = 7.26,	F(1.4, 28.1) = 1.30,	F(2, 38) = 12.02,
	p = 0.784	p = 0.002*	p = 0.002*	p = 0.278	p < 0.001**
Vowel	F(2,48) = 5.35,	F(2, 46) = 15.30,	F(2, 40) = 17.72,	F(1.3, 27.1) = 1.68,	F(2, 38) = 5.66,
	p = 0.008*	p < 0.001**	p < 0.001**	p = 0.209	p = 0.007*
Axis	F(1, 24) = 0.04,	F(1, 23) = 3.44,	F(1, 20) = 2.92,	F(1, 20) = 7.37,	F(1, 19) = 1.43,
	p = 0.837	p = 0.077	p = 0.103	p < 0.013*	p = 0.247
Two-way intera	iction:				
Phase × Vowel	F(4, 96) = 0.99,	F(4, 92) = 0.49,	F(4, 80) = 1.72,	F(2, 39.8) = 0.44,	F(4, 76) = 1.36,
	p = 0.417	p = 0.744	p = 0.153	p = 0.644	p = 0.256
Phase × Axis	F(1.6, 38) = 2.46,	F(2, 46) = 1.93,	F(2, 40) = 2.81,	F(2, 40) = 0.90,	F(2, 38) = 0.10,
	p = 0.110	p = 0.161	p = 0.072	p = 0.416	p = 0.907
Vowel × Axis	F(1.3, 32.8) = 2.40,	F(1.4, 31.5) = 3.30,	F(2, 40) = 3.35,	F(1.5, 30.7) = 27.85,	F(1.4, 27) = 1.73,
	p = 0.124	p = 0.067	p = 0.041*	p < 0.001 **	p = 0.200
Three-way inte	raction:		-	•	•
Phase × Vowel ×	F(4, 96) = 1.74,	F(2.4, 54) = 0.58,	F(4, 80) = 0.32,	F(4, 80) = 1.65,	F(4, 76) = 0.91,
Axis	p = 0.148	p = 0.678	p = 0.862	p = 0.17	p = 0.463

Note. *p < 0.05 ** p < 0.001.



785 786

Figure S3. Variability changes along F1 and F2 axes in different words. Individual (small
 transparent dots, thin lines) and group means (large solid dots, thick lines) of formant variability
 in the baseline, exposure and washout phases. Error bars show standard error.

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