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Converging toward a common speech code: imitative and perceptuo-motor recalibration processes in speech production

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Auditory and somatosensory systems play a key role in speech motor control. In the act of speaking, segmental speech movements are programmed to reach phonemic sensory goals, which in turn are used to estimate actual sensory feedback in order to further control production. The adult's tendency to automatically imitate a number of acoustic-phonetic characteristics in another speaker's speech however suggests that speech production not only relies on the intended phonemic sensory goals and actual sensory feedback but also on the processing of external speech inputs. These online adaptive changes in speech production, or phonetic convergence effects, are thought to facilitate conversational exchange by contributing to setting a common perceptuo-motor ground between the speaker and the listener. In line with previous studies on phonetic convergence, we here demonstrate, in a non-interactive situation of communication, online unintentional and voluntary imitative changes in relevant acoustic features of acoustic vowel targets (fundamental and first formant frequencies) during speech production and imitation. In addition, perceptuo-motor recalibration processes, or after-effects, occurred not only after vowel production and imitation but also after auditory categorization of the acoustic vowel targets. Altogether, these findings demonstrate adaptive plasticity of phonemic sensory-motor goals and suggest that, apart from sensory-motor knowledge, speech production continuously draws on perceptual learning from the external speech environment.

Keywords: phonetic convergence, imitation, speech production, speech perception, sensory-motor interactions, internal models, perceptual learning

INTRODUCTION

Speech production is a complex multistage motor process that requires phonetic encoding, initiation and coordination of sequences of supra-laryngeal and laryngeal movements produced by the combined actions of the pulmonary/respiratory system, the larynx and the vocal tract. Influential models of speech motor control postulate that auditory and somatosensory representations also play a key role in speech production. It is proposed that segmental speech movements are programmed to reach phonemic auditory and somatosensory goals, which in turn are used to estimate actual sensory inputs during speech production (for reviews, Perkell et al., 1997, 2000; Perrier, 2005, 2012; Guenther, 2006; Guenther and Vladusich, 2012; Perkell, 2012). The relationships between speech motor commands and sensory feedback are thought to be progressively learned by the central nervous system during native (and foreign) language acquisition, leading to the establishment of mature phonemic sensory-motor goals.

In adult/fluent speech production, a large number of studies employing manipulations of both somatosensory and auditory feedback also support the hypothesis that sensory feedback plays an important role in tuning speech motor control. For instance, transient transformations of both the auditory and somatosensory feedback, due to unexpected dynamical mechanical loading of supra-laryngeal articulators, result in on-line and rapid articulatory adjustments in speech production (Folkins and Abbs, 1975; Abbs and Gracco, 1984; Gracco and Abbs, 1985). Similarly, online modifications of the auditory feedback in its pitch (Elman, 1981; Burnett et al., 1998; Jones and Munhall, 2000), vowel formant frequencies (Houde and Jordan, 1998; Jones and Munhall, 2000; Houde et al., 2002; Purcell and Munhall, 2006a,b; Cai et al., 2011; Rochet-Capellan and Ostry, 2011, 2012) or fricative first spectral moment (Shiller et al., 2009, 2010) also induce compensatory changes in speech production. Finally, although auditory information is often assumed to be the dominant sensory modality, the integration of somatosensory information in

the achievement of speech movements has also been demonstrated (Tremblay et al., 2003; Nasir and Ostry, 2006; Feng et al., 2011; Lametti et al., 2012). Importantly, these studies not only demonstrate online motor corrections to counteract the effect of perturbations, but also a persistence of those corrections (i.e., an after-effect) once the perceptual manipulation is removed (Houde and Jordan, 1998; Jones and Munhall, 2000; Houde et al., 2002; Tremblay et al., 2003; Nasir and Ostry, 2006; Purcell and Munhall, 2006b; Shiller et al., 2009). The fact that motor compensatory adjustments do not disappear immediately likely reflects a global temporary remapping, or re-calibration, of the sensory-motor relationships.

Due to the intrinsic temporal limitations of the biological feedback systems, the concepts of efference copy (von Holst and Mittelstaedt, 1950) and internal models (Francis and Wonham, 1976; Kawato et al., 1987) have been introduced in order to explain how the central nervous system rapidly reacts to perturbations and adjusts fine-grained motor parameters (Guenther, 1995; Perkell et al., 1997; Guenther et al., 1998; Houde and Jordan, 1998; for recent reviews, see Perkell et al., 2000; Guenther, 2006; Hickok et al., 2011; Houde and Nagarajan, 2011; Guenther and Vladusich, 2012; Hickok, 2012; Perkell, 2012; Perrier, 2012).

During language acquisition, perceptuo-motor goals that define successful speech motor acts are thought to be gradually explored and acquired in interaction with adult speakers (Kuhl and Meltzoff, 1996; Kuhl et al., 1997; Kuhl, 2004). The relationships between speech motor commands and sensory feedback signals are then progressively learned by the central nervous system, and stored in the form of an internal *forward* model. The internal forward model allows for the prediction of the sensory consequences of speech motor movements in relation with the intended sensory speech goals. These internal sensory predictions, generated prior to the actual motor execution and sensory feedback, can assist in speech motor control. In case of discrepancy between the internal sensory predictions and the actual sensory feedback, corrective motor commands are estimated in order to further control production. Such corrective motor commands from the internal forward model allow refining and updating the relationships between the intended sensory speech goals and the relevant sequence of motor commands, which are then stored in an internal *inverse* model. Once the inverse model has been learned, it is hypothesized that speech production, in mature/fluent speech and in normal circumstances, operates almost entirely under the internal inverse model and feedforward control mechanisms (for recent reviews, see Guenther and Vladusich, 2012; Perkell, 2012; Perrier, 2012). From that view, the intended phonemic sensory goal allows the internal inverse model to internally specify the relevant speech motor sequences, without involvement of the internal forward model and sensory feedback control mechanisms, thus compensating for the delay inherent in sensory feedback. On the other hand, sensory feedback can still be used for online corrective motor adjustments, in case of external perturbations, in the comparison between internal sensory predictions from the forward model and actual sensory inputs.

The above-mentioned studies and models demonstrate a key role of on-line auditory and somatosensory feedback control

mechanisms in speech production and suggest that speech goals are defined in multi-dimensional motor, auditory and somatosensory spaces. However, for all their importance, these studies fail to reveal the extent to which speech perception and production systems may be truly integrated when speaking. First, individual differences in perceptual capacities may also act on speech production. From that view, a recent study on healthy adults, with no reported impairment of hearing or speech, demonstrates that individual differences in auditory discrimination abilities influence the degree to which speakers adapt to altered auditory feedback (Villacorta et al., 2007; but see Feng et al., 2011). Second, many studies of adaptation in speech production have focused primarily on the flexibility of motor processes, without regard for possible adaptive changes of phonemic sensory representations that are presumed to constitute the sensory goals of speech movements (except during language acquisition and the learning of internal models). However, two studies involving altered auditory or somatosensory feedback show compensatory changes not only in production of a speech sound, but also in its perception (Nasir and Ostry, 2009; Shiller et al., 2009). These results thus suggest plasticity of phonemic sensory representations in relation to adjustment of motor commands. Finally, the adult's tendency to automatically imitate a number of acoustic-phonetic characteristics in another speaker's speech suggests that speech production relies not only on the intended phonemic sensory goals and actual sensory feedback but also on the processing of external speech inputs.

In keeping with this later finding, the present study aimed at investigating adaptive plasticity of phonemic sensory-motor goals in speech production, based on either unintentional or voluntary vowel imitation. In addition to speech motor control, the working hypothesis of the present study capitalizes on previous studies on perceptual learning and speech imitation as well as on the theoretical proposal of a functional coupling between speech perception and action systems.

In this framework, it is worthwhile noting that speech and vocal imitation is one of the basic mechanisms governing the acquisition of spoken language by children (Kuhl and Meltzoff, 1996; Kuhl et al., 1997; Kuhl, 2004). In adults, unintentional speech imitation, or phonetic convergence, has been found to also occur in the course of a conversational interaction (for recent reviews, see Babel, 2009; Aubanel, 2011; Lelong, 2012). The behavior of each talker can evolve with respect to that of the other talker in two opposite directions: it may become more similar to the other talker's behavior (a phenomenon referred to as convergence) or more dissimilar. Convergence effects have been shown to be systematic and recurrent, and manifest themselves under many different forms, including posture (Shockley et al., 2003), head movements and facial expressions (Estow et al., 2007; Sato and Yoshikawa, 2007) and, regarding speech, vocal intensity (Natale, 1975; Gentilucci and Bernardis, 2007), speech rate (Giles et al., 1991; Bosshardt et al., 1997), voice onset time (Flege, 1987; Flege and Eefting, 1987; Sancier and Fowler, 1997; Fowler et al., 2008), fundamental frequency, and pitch curve (Gregory, 1986; Gregory et al., 1993; Bosshardt et al., 1997; Kappes et al., 2009; Babel and Bulatov, 2012), formant frequencies and spectral distributions (Gentilucci and Cattaneo, 2005; Delvaux and Soquet,

2007; Gentilucci and Bernardis, 2007; Aubanel and Nguyen, 2010; Lelong and Bailly, 2011). Apart from directly assessing phonetic convergence on acoustic parameters, other studies measured convergence by means of perceptual judgments, mostly using AXB tests (Goldinger, 1998; Goldinger and Azuma, 2004; Pardo, 2006; Pardo et al., 2010; Kim et al., 2011). Importantly, phonetic convergence has been shown to manifest in a variety of ways. Some involve natural settings, as during conversational exchange when exposure to the speech of others leads to phonetic convergence with that speech (Natale, 1975; Pardo, 2006; Aubanel and Nguyen, 2010; Pardo et al., 2010; Kim et al., 2011; Lelong and Bailly, 2011), or when exposure to a second language influences speech production of a native language, and vice-versa (Flege, 1987; Flege and Eefting, 1987; Sancier and Fowler, 1997; Fowler et al., 2008). Other involve non-interactive situations of communication, as when hearing and/or seeing a recorded speaker influences the production of similar or dissimilar speech sounds (Goldinger and Azuma, 2004; Gentilucci and Cattaneo, 2005; Delvaux and Soquet, 2007; Gentilucci and Bernardis, 2007; Kappes et al., 2009; Babel and Bulatov, 2012). Altogether, these phenomena of “speech accommodation” may facilitate conversational exchange by contributing to setting a common ground between speakers (Giles et al., 1991). In that respect, they may have the same effect as so-called alignment mechanisms, which are assumed to apply to linguistic representations at different levels between partners, in order for these partners to have a better joint understanding of what they are talking about (Garrod and Pickering, 2004; Pickering and Garrod, 2004, 2007).

Apart from social attunement, can phonetic convergence be also explained at a more basic sensory-motor level? In our view, phonetic convergence necessarily involves complex sensorimotor interactions that allow the speaker to compare or tune his/her own sensory and motor speech repertoire with the phonetic characteristics of the perceived utterance. Since phonetic convergence implies perception of speech sounds prior to actual speech production, phonetic convergence is likely to first rely on perceptual processing and learning from the external speech environment, leading to adaptive plasticity of phonemic sensory goals.

From that view, a significant body of speech perception research has demonstrated that sensory representations of speech sounds are flexible in response to changes in the sensory and linguistic aspects of speech input (e.g., Ladefoged and Broadbent, 1957; Miller and Liberman, 1979; Mann and Repp, 1980). In addition, studies on perceptual learning, or perceptual recalibration, have provided evidence for increased performance in speech perception/recognition and changes in perceptual representations after exposure to only a few speech sounds (e.g., Nygaard and Pisoni, 1998; Bertelson et al., 2003; Norris et al., 2003; Clarke and Garrett, 2004; Kraljic and Samuel, 2005, 2006, 2007; McQueen et al., 2006; Bradlow and Bent, 2008). In addition to perceptual learning, it is also to note that several psycholinguistic and neurobiological models of speech perception argue that phonetic interpretation of sensory speech inputs is determined, or at least partly constrained, by articulatory procedural knowledge (Liberman et al., 1967; Liberman and Mattingly, 1985; Fowler, 1986; Liberman and Whalen, 2000; Schwartz et al., 2002,

2012; Scott and Johnsruide, 2003; Callan et al., 2004; Galantucci et al., 2006; Wilson and Iacoboni, 2006; Skipper et al., 2007; Rauschecker and Scott, 2009). These models postulate that sensorimotor interactions play a key role in speech perception, with the motor system thought to partly constrain phonetic interpretation of the sensory inputs through the internal generation of candidate articulatory categories. Taken together, these studies and models thus suggest that listeners maintain perceptual and motor representations that incorporate fine-grained information about specific speech sounds, speakers, and situations. Hence, during speech production, phonetic convergence may arise from induced plasticity of phonemic sensory and motor representations, in relation to relevant adjustment of motor commands.

To extend the above-mentioned findings on phonetic convergence and to further test adaptive plasticity of phonemic sensory-motor goals in speech production, the present study aimed at investigating, in a non-interactive situation of communication, both unintentional and voluntary imitative changes in relevant acoustic features of acoustic vowel targets during speech production and imitation. A second goal of this study was to test offline perceptuo-motor recalibration processes (i.e., after-effects) after vowel production, imitation, and categorization.

METHODS

PARTICIPANTS

Three groups of twenty-four healthy adults, native French speakers, participated in the production, imitation and categorization experiments (12 females and 12 males per group). In order to test possible relationships between phonetic convergence and voluntary imitation, a subgroup of 12 subjects (6 females and 6 males) participated in both the production and imitation experiments (see Procedure). All participants had normal or corrected-to-normal vision, and reported no history of speaking, hearing or motor disorders.

STIMULI

Multiple utterances of /i/, /e/, and /ɛ/ steady-state French vowels were individually produced from a visual orthographic target and recorded by six native French speakers (3 females and 3 males) in a sound-attenuated room. In order to cover the typical range of F_0 values during vowel production for male and female speakers, the six speakers were selected with respect to their largely distinct fundamental frequency (F_0) values during vowel production (see below). None of the speakers participated in the three experiments.

Throughout this study, the focus was put on the main determinant of the voice characteristics that is F_0 , leaving aside a number of other possible acoustic parameters that could also provide targets for convergence phenomena (e.g., voice quality, F_0 variations inside the spoken utterances, intensity, duration, etc.). In the same vein, the focus was comparatively put on one of the main characteristic of vowels' phonetic quality that is F_1 , considering that in the set of unrounded front vowels here used, F_1 is both the basic cue to distinguishing these vowels from one another (see for example Ménard et al., 2002), and shows large variations from one French speaker to another (e.g., Ménard et al., 2008).

This also leaves aside a number of other acoustic determinants of phonetic quality such as F_2 , but also F_3 which is known to play an important role in the front unrounded region, particularly for /i/ and to a lesser extent for /e/. The choice to focus on acoustic variables a priori considered as the main characteristics in each domain seemed adequate in order to focus on major phenomena and escape from difficult—and largely unsolved—questions associated with the weighing of perceptual cues in a given perceptual domain.

One token of each vowel was selected per speaker and digitized in an individual sound file at a sampling rate of 44.1 kHz with 16-bit quantization recording. Using Praat software (Boersma and Weenink, 2013), each vowel was scaled to 75 dB and cut, at zero crossing points, from the vocalic onset to 250 ms following it. F_0 and first formant (F_1) values were then calculated for each vowel from a period defined as ± 25 ms of the maximum peak intensity (see Table 1). With this procedure, the stimuli differed in F_0 and F_1 values according to both gender and speaker (mean F_0 averaged across vowels: 100–120–136 Hz and 196–249–296 Hz for the three male and the three female speakers, respectively; mean F_1 for /i/, /e/, and /ɛ/ vowels: 258–314–496 Hz and 285–414–646 Hz for the three male and the three female speakers, respectively).

EXPERIMENTAL PROCEDURE

The three experiments were carried out in a sound-proof room. Participants sat in front of a computer monitor at a distance of approximately 50 cm. The acoustic stimuli were presented at a comfortable sound level through a loudspeaker, with the same sound level set for all participants. The Presentation software (Neurobehavioral Systems, Albany, CA) was used to control the stimulus presentation during all experiments, and to record key responses in the categorization experiment (see below). All participants' productions were recorded for off-line analyses. The experimental design and apparatus were identical in all experiments, except the task required during the presentation of the acoustic stimuli (i.e., vowel production, vowel imitation and vowel categorization; see Figure 1).

- Production experiment: The experiment was designed to test phonetic convergence on acoustically presented vowels

Table 1 | F_0 and F_1 values of /i/, /e/, /ɛ/ target vowels according to the six recorded speakers (3 females/males).

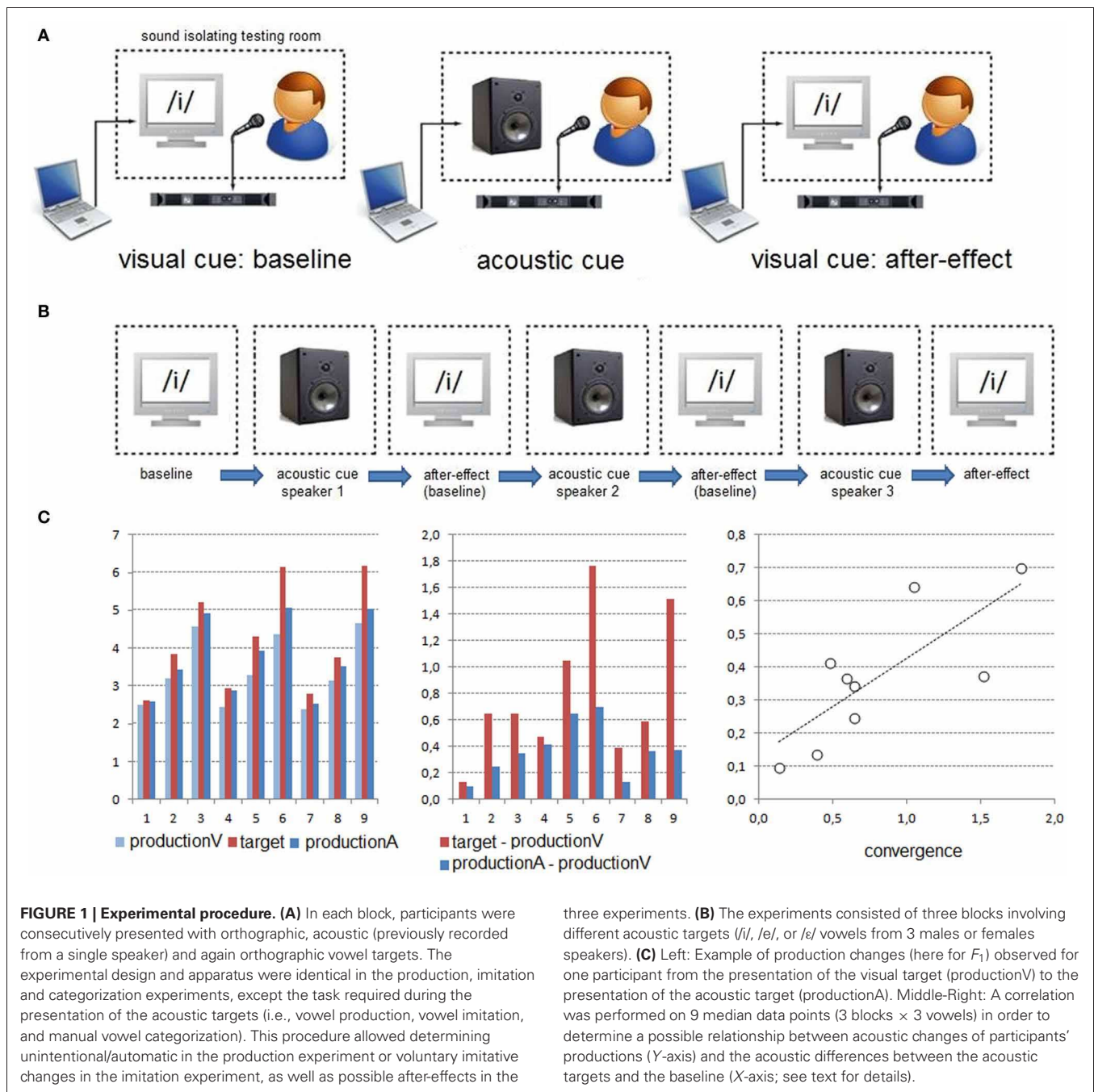
Vowel	Gender	F_0			F_1		
		S1	S2	S3	S1	S2	S3
/i/	Female	210	251	288	285	269	301
/e/	Female	190	248	290	389	399	453
/ɛ/	Female	187	249	284	693	577	668
		S4	S5	S6	S4	S5	S6
/i/	Male	137	120	103	278	248	247
/e/	Male	139	120	98	390	324	228
ɛ/	Male	132	121	100	510	440	538

and to measure the magnitude of such online automatic imitative changes as well as possible offline perceptuo-motor recalibration due to phonetic convergence (after-effects). To this aim, participants were instructed to produce distinct vowels (/i/, /e/, or /ɛ/), one at a time, according to either a visual orthographic or an acoustic vowel target. Importantly, no instructions to “repeat” or to “imitate” the acoustic targets were given to the participants. Moreover, all participants were naive as to the purpose of the experiment. A block design was used where participants produced vowels according first to orthographic targets (baseline), then to acoustic targets (phonetic convergence) and finally to orthographic targets (after-effect). This procedure allowed comparing participants' productions 1) between the first presentation of the orthographic targets and the following presentation of the acoustic targets in order to determine possible convergence effects on F_0 and F_1 values according to the acoustic targets and 2) between the first and last presentations of the orthographic targets in order to determine possible after-effects.

- Imitation experiment: To compare phonetic convergence and voluntary imitation of the acoustic vowels, the second group of participants performed the same experiment except that they were explicitly asked to imitate the acoustic targets. The only indication given to the participants was to imitate the voice characteristics of the perceived speaker.
- Categorization experiment: The third experiment was designed to test whether after-effects can occur without prior unintentional/automatic or voluntary vowel imitation but after auditory categorization of the acoustic targets. To this aim, participants were instructed to produce vowels according to the orthographic targets and to manually categorize the acoustic vowel targets, without overt production. During the categorization task, participants were instructed to produce a motor response by pressing with their right hand, one of three keys corresponding to the /i/, /e/, or /ɛ/ vowels, respectively.

Each experiment consisted of three experimental blocks, involving the acoustic targets previously recorded by either the three female or the three male speakers. In each block, the /i/, /e/, and /ɛ/ acoustic targets were related to a single speaker. With this procedure, F_0 values of the vowel targets remained similar within each block while F_1 varied according to each vowel type. The block order (across the three speakers) was fully counterbalanced across participants. In each experiment, six female and six male participants were presented with acoustic targets from the female speakers and six female and six male participants were presented with acoustic targets from the male speakers. This procedure allowed testing possible differences in imitative changes and after-effects depending on participant's and speaker's acoustic space congruency (i.e., female/female and male/male vs. female/male and male/female participants/speakers).

Each experimental block consisted of the orthographic presentation of the three vowels (presented 5 times in a random order) then the acoustic presentation of the three vowels (randomly presented 10 times) and finally the orthographic presentation of the three vowels (randomly presented 5 times).



Since perceptual learning from the external speech environment likely operated throughout the experiment, the last orthographic presentation of the vowels served as the first sub-block in the following experimental block. In each sub-block, each trial started with an orthographic or an acoustic target for 250 ms, a blank screen for 500 ms, a fixation cue (the “+” symbol) presented in the middle of the screen for 250 ms, and ended with a blank screen for 2000 ms. In order to limit possible close-shadowing effects (Porter and Lubker, 1980), participants were instructed to produce their response only after the

presentation of the “+” symbol. Hence, the intertrial interval was 3 s.

The total duration of each experiment was around 10 min. The experiments were preceded by a brief training session. A debriefing was carried out at the end of each experiment. Importantly, none of the participants reported having voluntarily imitated the acoustic stimuli in the production experiment. Note that the subgroup of subjects who participated in both the production and imitation experiments, always first performed the production experiment first.

ACOUSTIC ANALYSES

All acoustic analyses were performed using Praat software. A semi-automatic procedure was first devised for segmenting participants' recorded vowels (8640 utterances). For each participant, the procedure involved the automatic segmentation of each vowel based on an intensity and duration algorithm detection. Based on minimal duration and low intensity energy parameters, the algorithm automatically identified pauses between each vowel and set the vowel's boundaries on that basis. If necessary, these boundaries were hand-corrected, based on waveform and spectrogram information. Omissions, wrong productions and hesitations were manually identified and removed from the analyses. Finally, for each vowel, F_0 and F_1 values were calculated from a period defined as ± 25 ms of the maximum peak intensity of the sound file.

The mean percentage of errors was 2.8, 1.2, and 1.2% in the production, imitation, and categorization experiments, respectively, with no participant exceeding the error limit of 10%. For each experiment, median F_0 and F_1 values calculated on all participants' productions confirmed a standard distribution for the /i/, /e/, and /ɛ/ French vowels, with differences mainly due to gender (see Table 2).

RESULTS

For each participant and each sub-block, median F_0 and F_1 values were first computed for the /i/, /e/, and /ɛ/ vowels and expressed in bark [i.e., $\arctan(0.00076f) + 3.5 \arctan((f/7500)^2)$; Zwicker and Fastl, 1990]. For each experiment, median F_0 and F_1 exceeding ± 2 standard deviations (SD ; computed on the set of median values for the 24 participants) were removed from the analyses.

PHONETIC CONVERGENCE AND VOLUNTARY IMITATION (PRODUCTION AND IMITATION EXPERIMENTS, SEE FIGURE 2)

We here tested whether unintentional and voluntary imitation would result in shifting F_0 and/or F_1 toward the corresponding value for the acoustic target. To this aim, we first calculated acoustic changes of participants' productions between the presentation of acoustic targets and visual targets (baseline). For each participant and block, median F_0 and F_1 values produced in the baseline (i.e., median F_0 and F_1 values produced in the preceding sub-block during the presentation of the corresponding orthographic targets) were subtracted from those produced during the

presentation of each type of acoustic targets (i.e., /i/, /e/, or /ɛ/). Next, we calculated acoustic changes between the acoustic targets and the baseline. These two sets of data, calculated on both F_0 and F_1 values, were then correlated in order to determine a possible relationship between acoustic changes of participants' productions and the acoustic differences between the acoustic targets and the baseline (see Figure 1C). For each participant, one set of 9 correlation-points (from 3 blocks and 3 vowels) was therefore calculated for both F_0 and F_1 and one single subject slope coefficient for each acoustic parameter was estimated from these values by means of linear regressions. In order to keep the data sets homogeneous, slope coefficients exceeding ± 2 SD were removed from the following analyses (corresponding to one participant in both the production and imitation experiments for F_0 , and two and one participants in the production and imitation experiments, respectively, for F_1 , see Figure 2).

For both F_0 and F_1 slope coefficients, the remaining data were entered into analyses of variance (ANOVA) with the experiment (phonetic convergence, imitation) and the acoustic space congruency (same vs. different gender of the model speaker and the participant) as between-subject variables. In addition, individual one-tailed t -tests were performed for each experiment in order to test whether the mean slope coefficient was significantly superior to zero. Finally, in order to test whether imitative changes on F_0 and F_1 may correlate, a Pearson's correlation analysis was performed between single subject slope coefficients on F_0 and F_1 for each experiment.

For F_0 , ANOVA on single subject slope coefficients showed a significant effect of the task [$F_{(1, 42)} = 27.16$, $p < 0.001$], with stronger imitative changes according to the acoustic targets during the imitation task compared to the production task (mean slope coefficients of 0.08 and 0.48 in the production and imitation experiments). No effect of the acoustic space congruency [$F_{(1, 42)} = 0.05$] nor task \times acoustic-space congruency interaction [$F_{(1, 42)} = 0.01$] were however observed. In addition, slope coefficients differed significantly from zero in both the production [$t_{(22)} = 3.99$, $p < 0.001$] and imitation [$t_{(22)} = 7.11$, $p < 0.001$] experiments.

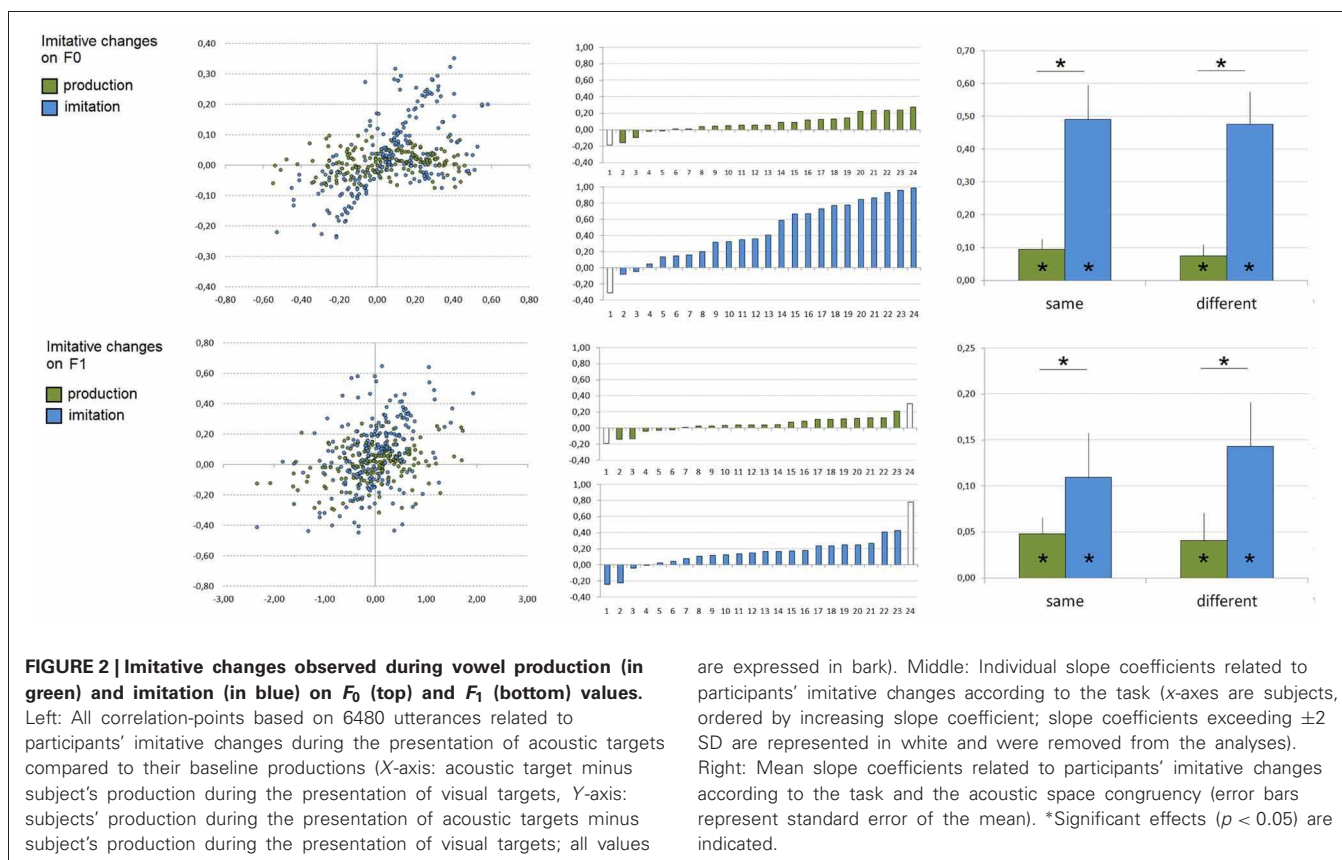
For F_1 , there was also a significant effect of the task [$F_{(1, 41)} = 4.95$, $p < 0.04$], with stronger imitative changes during the imitation task compared to the production task (mean slope coefficients of 0.04 and 0.13 in the production and imitation experiments). As for F_0 , no effect of the acoustic space congruency [$F_{(1, 41)} = 0.24$] nor task \times acoustic-space congruency interaction [$F_{(1, 41)} = 0.45$] were observed. Slope coefficients also differed significantly from zero in both the production [$t_{(21)} = 2.78$, $p < 0.02$] and imitation [$t_{(22)} = 4.21$, $p < 0.001$] experiments.

In addition, Pearson's correlation analyses showed no significant correlation between single subject slope coefficients observed for imitative changes on F_0 and F_1 in both the production ($r = 0.08$, slope = 0.06) and imitation ($r = 0.03$, slope = 0.01) experiments.

In sum, for both F_0 and F_1 values, these results demonstrate online imitative changes according to the acoustic vowel targets during production and imitation tasks, with stronger imitative changes in the voluntary vowel imitation task and a lower, albeit significant, phonetic convergence effect in the vowel production

Table 2 | Median F_0 and F_1 values of /i/, /e/, /ɛ/ produced vowels averaged over all participants' productions according to gender in Experiments A–C.

Vowel	Gender	Experiment A		Experiment B		Experiment C	
		F_0	F_1	F_0	F_1	F_0	F_1
/i/	Female	225	277	221	295	222	276
/e/	Female	220	416	216	417	215	407
/ɛ/	Female	214	613	211	610	210	607
/i/	Male	128	277	124	270	130	269
/e/	Male	125	372	120	366	126	365
/ɛ/	Male	123	508	119	522	125	545



task. Interestingly, these effects were observed independently of the participant and speaker acoustic space congruency. Finally, it is worthwhile noting the large variability across participants, especially in the production task.

AFTER-EFFECTS (PRODUCTION, IMITATION AND CATEGORIZATION EXPERIMENTS, SEE FIGURE 3)

We also tested possible perceptuo-motor recalibration, i.e., after-effects, compared to the participant's baseline. For each participant, block and vowel, median F_0 and F_1 values produced during the preceding baseline were subtracted from those produced during the second presentation of the orthographic targets. As previously, for each participant, one set of 9 correlation-points (from 3 blocks and 3 vowels) were therefore calculated for both F_0 and F_1 (see Figure 3) and single subject slope coefficients were estimated from these values by means of linear regressions. Slope coefficients exceeding ± 2 SD were removed from the following analyses (corresponding to one, two and two participants in the production, imitation, and categorization experiments, respectively, for F_0 , and two participants in the production, imitation, and categorization experiments for F_1 , see Figure 3).

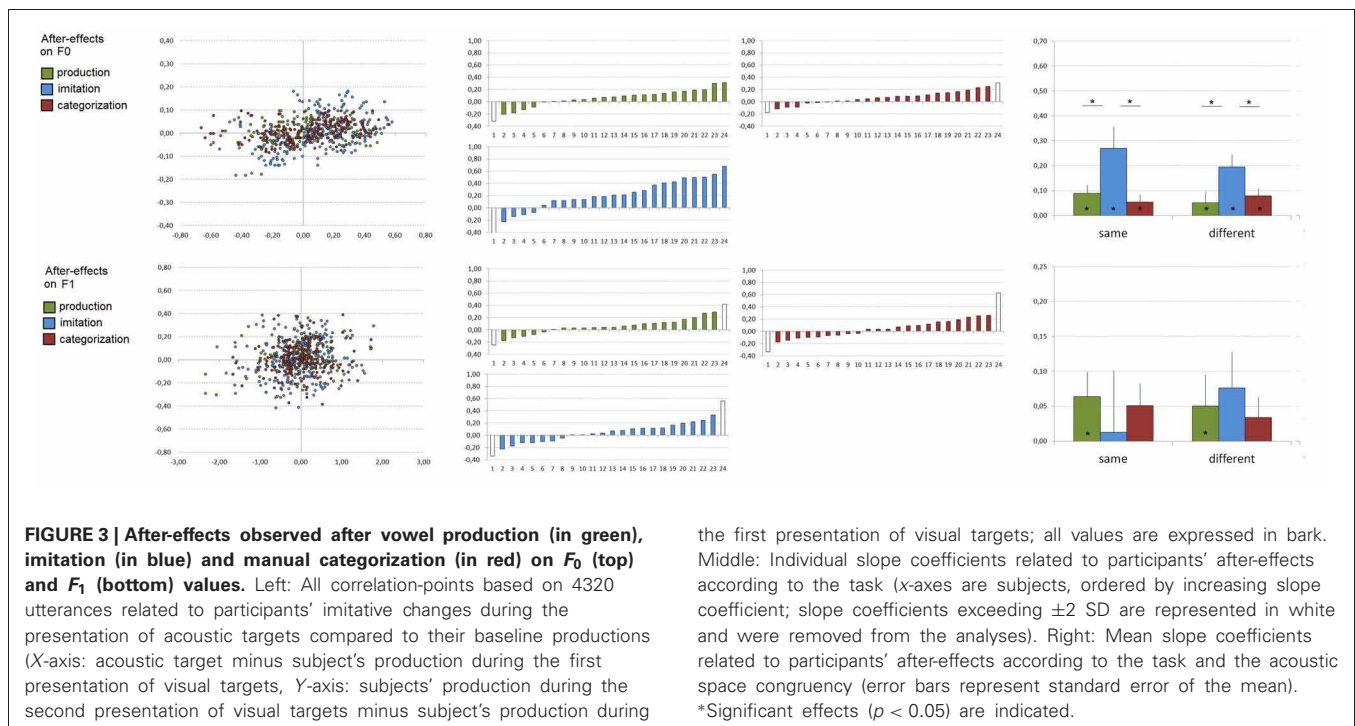
For both F_0 and F_1 slope coefficients, the remaining data were entered into ANOVA with the experiment (phonetic convergence, imitation, and auditory categorization) and the acoustic space congruency (same, different) as between-subject variables. In addition, individual one-tailed t -tests were performed for each experiment in order to test whether the mean slope coefficient was significantly superior to zero. As previously, in order to test

whether after-effects on F_0 and F_1 may correlate, a Pearson's correlation analysis was performed between single subject slope coefficients on F_0 and F_1 for each experiment.

For F_0 , ANOVA on single subject slope coefficients showed a significant effect of the task [$F_{(1, 42)} = 6.98, p < 0.005$], with stronger after-effects related to the acoustic targets after the imitation task compared to the production and categorization tasks (mean slope coefficients of 0.07, 0.23, and 0.07 in the production, imitation, and categorization experiments). No effect of the acoustic space congruency [$F_{(1, 42)} = 0.50$] nor task \times acoustic-space congruency interaction [$F_{(1, 42)} = 0.49$] were however observed. In addition, slope coefficients differed significantly from zero in both the production [$t_{(22)} = 2.85, p < 0.01$], imitation [$t_{(22)} = 4.92, p < 0.001$] and categorization [$t_{(21)} = 3.44, p < 0.005$] experiments.

For F_1 , no significant effect of the task [$F_{(1, 41)} = 0.08$], of the acoustic space congruency [$F_{(1, 41)} = 0.11$] nor interaction [$F_{(1, 41)} = 0.63$] were observed. Slope coefficients differed significantly from zero in the production experiment [mean slope coefficient of 0.06; $t_{(21)} = 2.59, p < 0.02$] but not in the imitation [mean slope coefficient of 0.04; $t_{(21)} = 1.83, p = 0.07$] and categorization [mean slope coefficient of 0.04; $t_{(21)} = 1.88, p = 0.07$] experiments.

In addition, Pearson's correlation analyses showed no significant correlation between single subject slope coefficients observed for after-effects on F_0 and F_1 in both the production ($r = -0.08$, slope = -0.07), imitation ($r = 0.10$, slope = 0.06) and categorization ($r = 0.11$, slope = 0.18) experiments.



Hence, for F_0 , offline perceptuo-motor recalibration processes were observed after vowel production, imitation, and categorization of the acoustic targets, with a stronger after-effect after voluntary vowel imitation and lower, albeit significant, after-effects after vowel production and categorization. Furthermore, these effects were observed independently of the participant and speaker acoustic space congruency. For F_1 , a small after-effect was only observed after vowel production, although there was also a trend in the same direction after vowel imitation and categorization. Finally, as for online adaptive changes, there was a large variability across participants in all tasks.

RELATIONSHIPS BETWEEN IMITATIVE CHANGES AND AFTER-EFFECTS (PRODUCTION AND IMITATION EXPERIMENTS, SEE FIGURE 4)

In order to test whether imitative changes and after-effects in the production and imitation experiments may correlate, Pearson's correlation analyses were performed for both F_0 and F_1 between single subject slope coefficients corresponding to the imitative changes and to the after-effects (see Figure 4). As previously, slope coefficients exceeding ± 2 SD were removed from the analyses (corresponding to two participants in both experiments for F_0 , and four and two participants in the production and imitation experiments for F_1 , see Figure 4).

For F_0 , the Pearson's correlation analysis showed a significant correlation between single subject slope coefficients observed for imitative changes and for after-effects in both the production ($r = 0.64$, slope = 0.71, $p < 0.005$) and imitation ($r = 0.78$, slope = 0.52, $p < 0.001$) experiments.

For F_1 , the Pearson's correlation analysis also showed a significant correlation between single subject slope coefficients observed for imitative changes and for after-effects in the production

the first presentation of visual targets; all values are expressed in bark. Middle: Individual slope coefficients related to participants' after-effects according to the task (x-axes are subjects, ordered by increasing slope coefficient; slope coefficients exceeding ± 2 SD are represented in white and were removed from the analyses). Right: Mean slope coefficients related to participants' after-effects according to the task and the acoustic space congruency (error bars represent standard error of the mean). *Significant effects ($p < 0.05$) are indicated.

experiment ($r = 0.53$, slope = 0.85, $p < 0.03$) but not in the imitation experiment ($r = 0.31$, slope = 0.27).

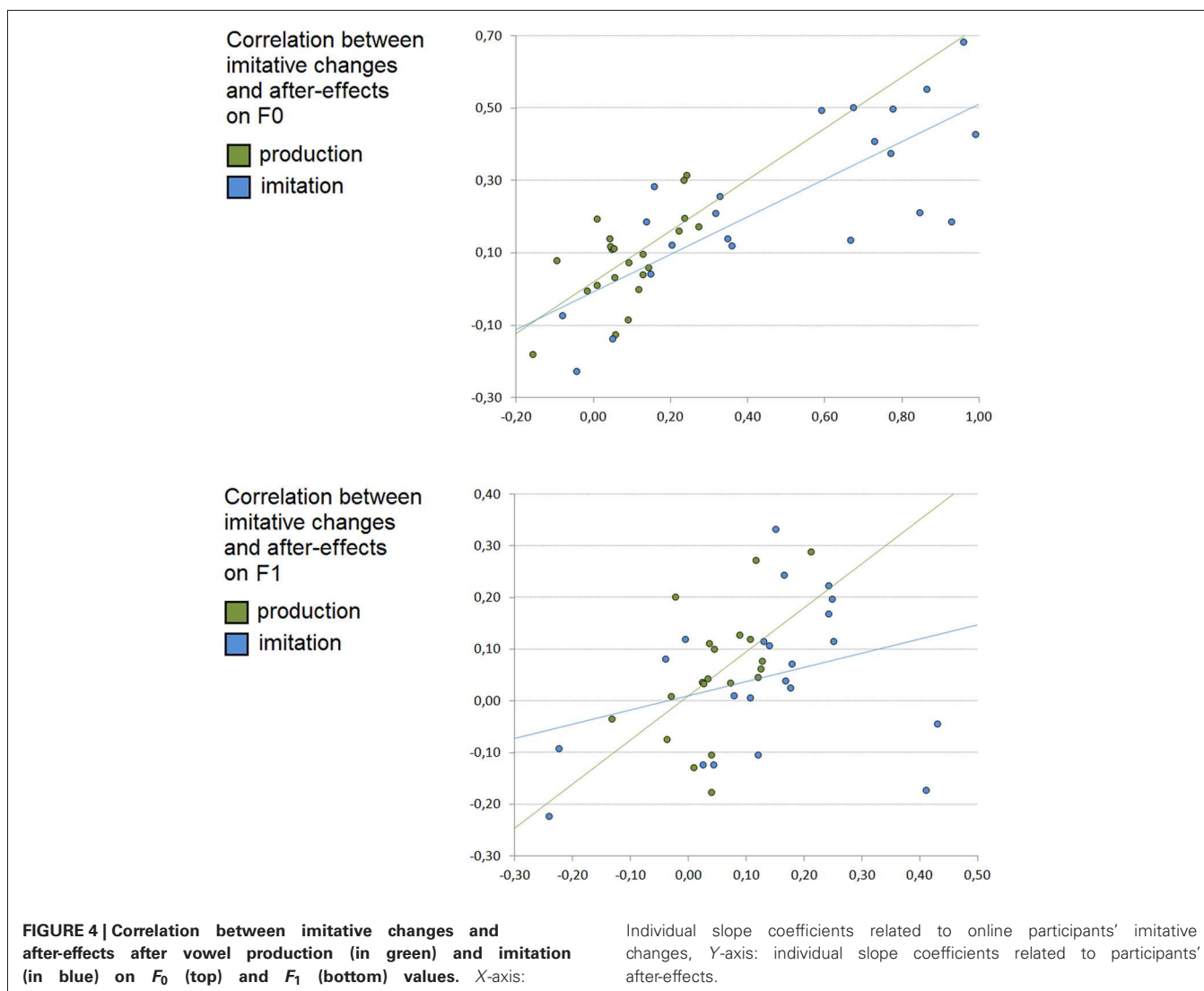
RELATIONSHIPS BETWEEN PHONETIC CONVERGENCE AND VOLUNTARY IMITATION (PRODUCTION AND IMITATION EXPERIMENTS)

In order to test whether phonetic convergence and voluntary imitation in the production and imitation experiments may correlate for the subgroup of subjects who participated in both experiments, Pearson's correlation analyses were performed for both F_0 and F_1 between single subject slope coefficients corresponding to the convergence and imitative changes in the two experiments (see Figure 4). As previously, slope coefficients exceeding ± 2 SD were removed from the analyses (corresponding to two participants for F_0 , and one for F_1 , see Figure 4).

The Pearson's correlation analysis showed no significant correlation between single subject slope coefficients observed for imitative changes in the two experiments for F_0 ($r = -0.24$, slope = -0.55) and F_1 ($r = 0.19$, slope = 0.38).

DISCUSSION

Influential models of speech motor control postulate a key role for on-line auditory and somatosensory feedback control mechanisms in speech production and highlight the sensory-motor nature of speech representations. However, studies on phonetic convergence suggest that speech production relies not only on phonemic sensory goals and actual sensory feedback but also on the processing of external speech inputs. In line with these findings, the present study demonstrates, in a non-interactive situation of communication, both unintentional and voluntary imitative changes in fundamental and first formant



frequencies of acoustic vowel targets during speech production and imitation tasks. Offline perceptuo-motor recalibration processes on fundamental frequency—and possibly, marginally, for first formant frequency—were also observed after vowel production, imitation, and categorization of the acoustic targets. In addition, while a significant correlation was observed between imitative changes and after-effects in both vowel production and imitation tasks, no correlation occurred between phonetic convergence effects and voluntary imitative changes for the subgroup of subjects who participated in both experiments on vowel production and imitation. Altogether, these results demonstrate adaptive plasticity of phonemic sensory-motor goals and suggest that speech production draws on both sensory-motor knowledge and perceptual learning of the external speech environment.

ONLINE UNINTENTIONAL AND VOLUNTARY IMITATIVE CHANGES

Phonetic convergence effects have been initially explored during natural and interactive settings, notably during conversational

exchanges between two speaking partners (Pardo, 2006; Aubanel and Nguyen, 2010; Pardo et al., 2010; Kim et al., 2011; Lelong and Bailly, 2011). This led to the hypothesis that “speech accommodation” may facilitate conversational exchange by contributing to setting a common ground between speakers (Giles et al., 1991; see also Garrod and Pickering, 2004; Pickering and Garrod, 2004, 2007). However, other studies conducted in a non-interactive laboratory setting, as when hearing and/or seeing a recorded speaker influences the production of similar or dissimilar speech sounds (Goldinger and Azuma, 2004; Gentilucci and Cattaneo, 2005; Delvaux and Soquet, 2007; Gentilucci and Bernardis, 2007; Kappes et al., 2009; Babel and Bulatov, 2012), indicate that convergence mechanisms do not depend on mutual adjustments and social attunement only. In our view, these later studies provide powerful evidence that, unless hindered by higher-order socio-psychological factors, phonetic convergence is a highly automatized process (for a review, see Delvaux and Soquet, 2007) that may also be triggered by low-level sensory and motor adaptive processes.

Based on F_0 and F_1 acoustic analyses of a large corpus of recorded vowels, the present study replicates and extends phonetic convergence effects previously observed on fundamental frequency (Gregory, 1986; Gregory et al., 1993; Bosshardt et al., 1997; Kappes et al., 2009; Babel and Bulatov, 2012) and on formant frequencies and spectral distributions (Gentilucci and Cattaneo, 2005; Delvaux and Soquet, 2007; Gentilucci and Bernardis, 2007; Aubanel and Nguyen, 2010; Lelong and Bailly, 2011). First, online imitative changes on both F_0 and F_1 in relation to the acoustic vowel targets were observed in a non-interactive situation of communication during the production task, with none of the participants reporting having voluntarily imitated the acoustic stimuli. Second, although previous studies usually involved the production of words or sentences (Goldinger, 1998; Goldinger and Azuma, 2004; Pardo, 2006; Delvaux and Soquet, 2007; Kappes et al., 2009; Aubanel and Nguyen, 2010; Pardo et al., 2010; Kim et al., 2011; Lelong and Bailly, 2011; Babel and Bulatov, 2012), adaptive changes were here observed during vowel production thus minimizing lexical/semantic processing (for phonetic convergence effects on F_0 and/or F_1 during syllable or non-word production, see Gentilucci and Cattaneo, 2005; Gentilucci and Bernardis, 2007; Kappes et al., 2009). Altogether, these findings thus suggest that phonetic convergence may also derive from unintentional and automatic adaptive sensory-motor speech mechanisms. However, it is worthwhile noting that, although significant at the group level, the magnitude of these adaptive changes was rather small (mean slope coefficients of 0.08 and of 0.04 for F_0 and F_1 , respectively) and quite variable across participants (individual slope coefficients ranging from -0.16 to 0.27 and from -0.14 to 0.21 for F_0 and F_1 , respectively). In addition, although phonetic convergence was attested for both F_0 and F_1 , adaptive changes were twice lower for F_1 . In the experiments, however, F_0 values of the vowel targets remained similar within each block while F_1 varied according to each vowel type. Although sensory-motor and convergence mechanisms are likely to differ for these acoustic parameters at the acoustical, biomechanical and neurobiological levels, it appears difficult to speculate on these observed differences. Finally, although gender effects have been previously observed on phonetic convergence (Pardo, 2006; Pardo et al., 2010; Babel and Bulatov, 2012), the exact nature of this mediation remains unclear and may depend on both specific experimental designs and/or “macro” social mechanisms, out of the scope of this study. Given the limited number of participants in each sub-experimental group condition (i.e., six female and six male participants presented with acoustic targets from the female speakers, and six female and six male participants presented with acoustic targets from the male speakers), we rather focused on the participant and speaker acoustic space congruency. Phonetic convergence was observed independently of the participant and speaker acoustic space congruency, a result suggesting that phonetic convergence on vowels and in a non-interactive situation of communication is pervasive and not strongly influenced by the acoustic distance between the participant and the model speaker.

To compare phonetic convergence and voluntary imitation of the acoustic vowels, a second group of participants performed the same experiment except that they were explicitly asked to imitate the acoustic targets. As expected, stronger online imitative

changes according to the acoustic vowel targets were observed during voluntary imitation (mean slope coefficients of 0.48 vs. 0.08 for F_0 and 0.13 vs. 0.04 for F_1 , for the imitation and production tasks, respectively). As in the production tasks, imitative changes were however quite variable across participants (individual slope coefficients ranging from -0.8 to 0.99 and from -0.24 to 0.43 for F_0 and F_1 , respectively). In addition, no significant correlation between phonetic convergence and voluntary imitation on both F_0 and F_1 were observed for the subgroup of subjects who participated in both the production and imitation task. Interestingly, although not significant, the slope coefficient for F_0 appears nevertheless quite high (mean slope coefficients of -0.55). Hence, although this last result does not indicate any significant correlation, possible dependencies between phonetic convergence and voluntary imitation have to be further investigated in future studies.

PERCEPTUO-MOTOR RECALIBRATION PROCESSES

Interestingly, previous studies showed clear evidence of post-exposure imitation, with experimental designs and long-lasting effects that preclude strategic explanations (Goldinger and Azuma, 2004; Pardo, 2006; Delvaux and Soquet, 2007). In these studies, phonetic convergence was first attested during the production of auditorily presented words in a non-interactive situation of communication. Offline adaptation to the acoustic targets was however observed in post-tests occurring either immediately (Pardo, 2006; Delvaux and Soquet, 2007) or even conducted one week after the production task (Goldinger and Azuma, 2004; see also Goldinger, 1998 using a close-shadowing task). These latter findings suggest that long-term memory to some extent preserves detailed traces of the auditorily presented words and thus support episodic/exemplar theories of word processing assuming that paralinguistic details of a spoken word are stored together as a memory trace (e.g., Nygaard et al., 1994; Goldinger, 1996, 1998; Nygaard and Pisoni, 1998), although hybrid models combining abstract phonological representations with episodic memory traces are also consistent with these results (e.g., McQueen et al., 2006; Pierrehumbert, 2006). Importantly, Pardo (2006) and Delvaux and Soquet (2007) also propose that these observed phonetic convergence and associated long-term adaptive changes may be at the source of gradual diachronic changes of a phonological system in a community.

In line with these studies, offline perceptuo-motor recalibration processes were here observed for F_0 after vowel production, imitation and auditory categorization of the acoustic targets, with a stronger after-effect observed after voluntary vowel imitation. The fact that after-effects equally occurred following prior vowel production and perceptual categorization of the acoustic targets likely suggests that these effects rely on perceptual processing and learning from the acoustic targets, without the need for a specific motor learning stage. As for online imitative changes, these effects were observed independently of the participant and speaker acoustic space congruency and, although significant at the group level, the magnitude of these after-effects was rather small (mean slope coefficients of 0.07, 0.23, and 0.07 for the production, imitation and categorization tasks, respectively) and quite variable across participants (individual slope coefficients

ranging from -0.20 to 0.32 , from -0.23 to 0.68 and from -0.12 to 0.25 for the production, imitation and categorization tasks, respectively). As expected, a significant correlation between single subject slope coefficients for imitative changes and after-effects was also observed in both the production and imitation tasks.

For F_1 , a small after-effect was only observed after vowel production (although there was a trend after vowel imitation and categorization), with a significant correlation between single subject slope coefficients for imitative changes and after-effects. The after-effect for F_1 in the production task and the trend found in the imitation and categorization tasks were therefore observed despite F_1 values of the acoustic targets varying according to each vowel type in each block. Finally, it is also interesting to note that for F_1 the imitation task did not provide stronger after-effects as compared to the other tasks. More intriguing is the very low after-effect observed in the imitation tasks when subjects and targets were of the same gender, a phenomenon for which we do have no clear explanation yet.

PERCEPTUO-MOTOR LEARNING AND INTERNAL MODELS OF SPEECH PRODUCTION

Altogether, our results demonstrate adaptive plasticity of phonemic sensory-motor goals in a non-interactive situation of communication, without lexical/semantic processing of the acoustic targets. Although they appear in line with previous studies on phonetic convergence and do not contradict the theoretical proposal that adaptive changes in speech production facilitate conversational exchanges between speaking partners, these results demonstrate that, in addition to social attunement and lexical/semantic processing, convergence effects may also be triggered by low-level sensory and motor adaptive speech processes. From that point of view, future studies on phonetic convergence contrasting interactive and non-interactive laboratory settings will be of great interest to further determine whether social interactions might enhance imitative changes.

Together with previous studies on phonetic convergence and imitation, the observed adaptive plasticity of phonemic sensory-motor goals sheds an important light on speech motor control and internal models of speech production (for reviews, Perkell et al., 1997, 2000; Perrier, 2005, 2012; Guenther, 2006; Guenther and Vladusich, 2012; Perkell, 2012). As previously noted, these models postulate that auditory and somatosensory systems play a key role in speech motor control and that speech goals are defined in multi-dimensional motor, auditory, and somatosensory spaces. However, they mainly focus on the flexibility of motor processes, without regard for possible adaptive changes of phonemic sensory representations that are presumed to constitute the sensory goals of speech movements. Convergence and perceptuo-motor recalibration processes however demonstrate that speech production relies not only on the intended phonemic sensory goals and actual sensory feedback but also on the processing of external speech inputs. In our view, these effects are based on complex sensorimotor interactions, allowing the speaker to compare or tune his/her own sensory and motor speech repertoire with the phonetic characteristics of the perceived utterance, and leading to perceptuo-motor learning from the external speech environment. During speech production, phonetic convergence and

after-effects may therefore arise from induced plasticity of phonemic sensory and motor representations, in relation to relevant adjustment of motor commands. Convergence effects are thus of considerable interest since they suggest that speech motor goals are continuously updated in response to changes in the sensory and linguistic aspects of speech inputs. Hence, as also advocated by Perkell (2012), adaptive processes, likely to modify online, to a certain extent, sensory speech representations, will have to be taken into account in future versions of speech motor control models.

From that view, there is now considerable neurobiological evidence that sensorimotor interactions play a key role in both speech perception and speech production. In line with internal models of speech production, modulation of neural responses observed within the auditory and somatosensory cortices when speaking are thought to reflect feedback control mechanisms in which predicted sensory consequences of the speech-motor act are compared with actual sensory input in order to further control production (Guenther, 2006; Tian and Poeppel, 2010; Hickok et al., 2011; Houde and Nagarajan, 2011; Price et al., 2011; Guenther and Vladusich, 2012; Hickok, 2012). In addition, it has been suggested that motor activity during speech perception partly constrains phonetic interpretation of the sensory inputs through the internal generation of candidate articulatory categories (Callan et al., 2004; Wilson and Iacoboni, 2006; Skipper et al., 2007; Poeppel et al., 2008; Rauschecker and Scott, 2009; Hickok et al., 2011; Rauschecker, 2011). From these models, perceptuo-motor learning and plasticity of phonemic goals induced by convergence and sensory-motor adaptive processes might depend on both a ventral and dorsal stream (Guenther, 2006; Hickok and Poeppel, 2007; Rauschecker and Scott, 2009; Hickok et al., 2011; Rauschecker, 2011; Guenther and Vladusich, 2012; Hickok, 2012; see also Grabski et al., 2013 for recent brain-imaging evidence that vowel production and perception both rely on these dorsal and ventral streams). The ventral stream (“what”) is supposed to be in charge for phonological and lexical processing, and thought to be localized in the anterior part of the superior temporal gyrus/sulcus (Scott and Johnsrude, 2003; Rauschecker and Scott, 2009; Rauschecker, 2011) or in the posterior part of the middle temporal gyrus and superior temporal sulcus (Hickok and Poeppel, 2007). The dorsal stream (“how”) would deal with sensory-motor mapping between sensory speech representations in the auditory temporal and somatosensory parietal cortices and articulatory representations in the ventral pre-motor cortex and the posterior part of the inferior frontal gyrus, with sensorimotor interaction converging in the supramarginal gyrus (Rauschecker and Scott, 2009; Rauschecker, 2011) or in area SPT (a brain region within the planum temporale near the parieto-temporal junction; Hickok and Poeppel, 2007). In line with the involvement of both the dorsal and ventral streams in imitative changes in speech production, recent studies using repetition, shadowing or voluntary imitation tasks have provided evidence for a neuro-functional/neuro-anatomical signature of speech imitation ability, mostly relying on the superior temporal gyrus, the premotor cortex and the inferior parietal lobule (Peschke et al., 2009; Irwin et al., 2011; Reiterer et al., 2011; Mashal et al., 2012). From these findings, the neural basis of

low-level sensory and motor adaptive speech processes involved in phonetic convergence and perceptuo-motor recalibration processes remains to be investigated in future studies.

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