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Original Article

ORIGINAL ARTICLE

Neural Basis of Sensorimotor Plasticity in Speech Motor Adaptation

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Abstract

When we speak, we get correlated sensory feedback from speech sounds and from the muscles and soft tissues of the vocal tract. Here we dissociate the contributions of auditory and somatosensory feedback to identify brain networks that underlie the somatic contribution to speech motor learning. The technique uses a robotic device that selectively alters somatosensory inputs in combination with resting-state fMRI scans that reveal learning-related changes in functional connectivity. A partial correlation analysis is used to identify connectivity changes that are not explained by the time course of activity in any other learning-related areas. This analysis revealed changes related to behavioral improvements in movement and separately, to changes in auditory perception: Speech motor adaptation itself was associated with connectivity changes that were primarily in non-motor areas of brain, specifically, to a strengthening of connectivity between auditory and somatosensory cortex and between presupplementary motor area and the inferior parietal lobule. In contrast, connectively changes associated with alterations to auditory perception were restricted to speech motor areas, specifically, primary motor cortex and inferior frontal gyrus. Overall, our findings show that during adaptation, somatosensory inputs result in a broad range of changes in connectivity in areas associated with speech motor control and learning.

Key words: human motor learning, neuroplasticity, speech

Introduction

The role played by the somatosensory system in speech production is evident when one considers that individuals who lose their hearing as adults are typically able to produce intelligible speech for years after hearing loss. This ability is consistent with the involvement of orofacial somatosensory inputs in the control of speech movements and suggests they may likewise play a role in speech motor learning (Nasir and Ostry 2008). Previous behavioral studies have pointed to the involvement of the somatosensory system in speech motor learning (Houde and Jordan 1998; Savariaux et al. 1999; Jones and Munhall 2000; Tremblay et al. 2003; Feng et al. 2011), and individual differences in reliance on auditory and somatosensory feedback in speech have been reported (Lametti et al. 2012). Brain areas that are active during speech motor learning and adaptation have been described (Adank and Devlin 2010; Shum et al. 2011; Mollaei et al. 2013; Segawa et al. 2015; Berken et al. 2016). However, because auditory and somatosensory signals are correlated during normal speech movements, the extent of the contribution of the somatosensory system to learning has not been isolated.

We have developed a way to identify the brain networks that underlie the somatic contribution to speech motor learning. We use a robotic device which selectively alters somatosensory input in speech but has no measurable effect on speech acoustics (Tremblay et al. 2003; Nasir and Ostry 2008). Participant's responses to this mechanical perturbation result in adaptive changes to speech movements and to the

perceptual classification of speech sounds. We inter-leave behavioral testing with a resting-state neuroimaging analysis. This latter technique uses a partial correlation procedure to identity from among the areas that encode learning those whose functional connectivity is both strengthened with learning and cannot be attributed to activity elsewhere in the learning-related network (Marrelec et al. 2006; Vahdat et al. 2014). The rationale for this approach is that even under resting-state conditions, many areas show activity changes with learning. We expect that a subset of these regions whose connectivity is strengthened by learning contribute to secondary changes in the remainder due to extensive connections between brain areas. The partial correlation technique enables us to identify those patterns of connectivity that are not attributable to activity elsewhere in the speech motor learning network.

We consider 2 questions, one concerning learning-related changes to speech movements and the other to perceptual change. First, since our behavioral manipulation involves changes to both somatosensory inputs and to motor commands, we asked whether the resulting changes to movement are primarily a consequence of changes to brain motor areas, or whether adaptation induces changes in sensory areas which lead to a secondary change in the output of motor areas and motor commands; that is, are changes to motor areas a byproduct of sensory change? Second, in previous work using somatosensory perturbations, changes were observed in the perceptual classification of speech sounds even though auditory inputs themselves did not change. It is unclear whether the somatic perturbation nevertheless induces changes in auditory cortical regions to bring about the perceptual adjustments, or whether these auditory perceptual adjustments are mainly accommodated by changes in motor areas, such that changes to auditory areas (if any) are byproducts of changes to regions within the motor network.

The present study extends previous behavioral work in that it identifies a somatic circuit in speech motor adaptation. However, the approach to studying plasticity differs. Rather than obtaining an aggregate measure of learning-related brain activity, the present techniques separate the contribution to speech motor learning of plasticity in sensory systems from that of motor areas of the brain. In addition, by examining changes in sensorimotor networks under resting-state conditions rather than during the performance of the behavioral task (Vahdat et al. 2011), one can eliminate the contribution of non-learning-related factors such as changes in movement execution or to changes in attention.

Materials and Methods

Subjects

Nineteen English speakers (12 female) between the ages of 19 and 34 participated in the study. Participants were healthy adults with no prior neurological or speech motor disorders. The participants were naïve with regards to the experimental conditions. The McGill University Institutional Review Board approved all experimental procedures.

Experimental Setup

In the behavioral sessions, participants were seated in front of a small robotic device (Phantom 1.5, SensAble Technologies, Fig. 1A). Custom-build acrylic and metal dental appliances were used to connect the participant's jaw to the experimental setup. A dental adhesive was used to attach the appliances to the upper and lower jaw. The upper jaw appliance was connected to 2 articulated arms, which fixed the upper jaw in place and kept the head motionless during the experiment. The lower jaw appliance was attached to a rotary connector, which in turn was connected to the robot. The lower jaw was able to move freely in all directions in the absence of applied load. A force torque sensor (Nano, ATI Industries) measured forces applied to the robot while robot encoders recorded jaw movement. The robot was also programmed to apply forces to the lower jaw. A computer monitor was placed to one side of the robot to visually present the words that were to be spoken aloud by participants. A unidirectional microphone (Sennheiser) was placed to the other side to record the participant's speech.

Behavioral Task

There was one familiarization session followed by 2 experimental sessions. The main experimental sessions were generally held on 2 consecutive days and always at the same time of the day (Fig. 1B). In the familiarization session subjects tried the dental appliances and then completed 2 practice blocks of the experiment. In the first block, they were instructed to repeat words that were displayed visually on a computer monitor (sensorimotor task, 200 trials). In the second practice block, participants' perception of speech sound stimuli was assessed using the same two-alternative forced-choice procedure and same stimuli as in the main experiment (perceptual test, 80 trials). The familiarization session served to control for the novelty of the dental appliances and word repetition task and for the experimental perceptual task.

The main experimental sessions each began with a block of sensorimotor trials in which subjects read aloud words that were displayed on a computer monitor. On the first day subjects experienced no forces due to the robot during these trials whereas on the second day forces were applied. This was followed in each case by MRI scans at the Brain Imaging Centre at the Montreal Neurological Institute, and then a final block of perceptual tests, back in the laboratory. The participants wore the dental appliances for both the sensorimotor tests and perceptual tests. The scans began approximately 45 min following the end of the sensorimotor sessions.

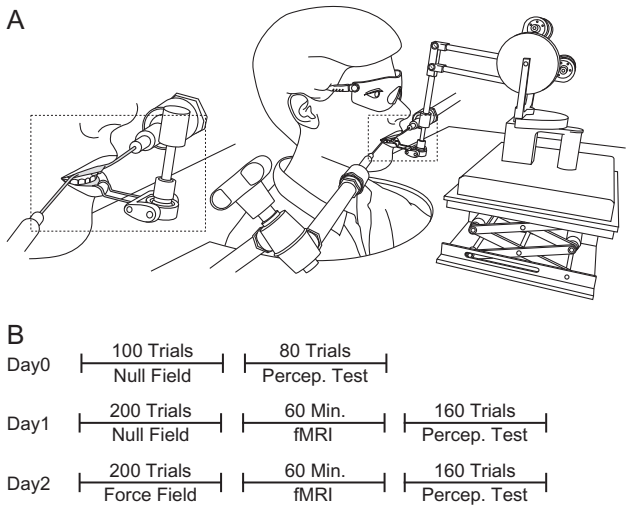

Figure 1. Schematic of experimental setup and experimental time-line. (*A*) The subject's lower jaw is connected to a small robotic device while the upper jaw is held in place with 2 articulated arms. (*B*) Experimental sequence during familiarization session and 2 days of experimental testing.

Sensorimotor Task

The 2 main experimental sessions each started with the sensorimotor task. Participants were instructed to repeat aloud, once each, words that were shown visually on the monitor. A random delay of one to 2 seconds was added between utterances. On each trial the test utterance was randomly selected from a set of 4 words: *head, said, ted, bed*. We chose words that involved the vowel *e*, as in *head*, because it provided for the possibility that, in perceptual tests, adaptation might result in a perceptual shift towards either a lower or higher frequency vowel sound, *hid* or *had*, respectively. In each session participants completed 200 trials. Subjects were given a 2 min rest after the first 100 trials.

In the first session of the experiment (and the familiarization session) the robot applied no forces to the jaw. In the second experimental session, the robotic device was programmed to apply mechanical loads to the jaw in the protrusion direction (outwards). The applied force followed the equation $F = k|v|$, where F is the force in Newtons, v is instantaneous jaw velocity in millimeters per second and k is a constant which was set to 0.02. The values for force application were obtained empirically and are the same as those that have been used in our previous studies. On average, maximum applied forces were 3.32 N.

fMRI Acquisition

fMRI data were acquired using a 3 Tesla Siemens Trio MR scanner at the Montreal Neurological Institute (MNI). Whole-brain functional data were acquired using a T2* weighted EPI sequence (32 head-coil channels, resolution 3 mm isotropic, 42 slices, 64 × 64 matrix; TE = 30 ms and TR = 2540 ms; flip angle 90). A T1 weighted structural image was obtained to provide anatomical data (1 mm^3 voxel size, 256 × 256 matrix). GRE field-maps were acquired to correct for geometric distortion of the EPI images.

Two 10 min resting-state fMRI scans were acquired in each session, with subjects' eyes closed. A GRE field-map was recorded between the 2 resting-state scans. A high-resolution anatomical scan was obtained following the second resting-state scan. In the second session, participants also completed a task-based functional scan at the end of scanning session. The task-based scan required that participants listen to random monosyllabic words (other than the test words *head, said, ted, bed*) thorough the ear-inserted headphones and repeat them aloud afterwards. We used a sparse sampling procedure with 2 s of data acquisition followed by 2 s of either silence or 2 s of a listen and repeat task. The stimulus words for the listen and repeat task were obtained from a male English speaker and had a duration of 700 ms. The Presentation software (Neurobehavioral System Inc.) controlled the timing of stimulus presentation. Words were presented at the start of each silent period which gave participants 1.3 s to repeat the word. Subjects were instructed to remain silent during data acquisition. We used a block design procedure in which 9 trials of 4 s each were presented during each task block. During the silent block, no stimulus was presented and participants remained silent. In total 6 blocks of listen and repeat and 7 blocks of silence were recorded.

Perceptual Tests

Participants' perceptual classification of speech stimuli was assessed using 2 sets of 8 auditory stimuli each. The first set of stimuli spanned the spectral continuum between *head* and *had*, the second set was between *head and hid*. The *head/had* continuum was generated by using an iterative linear predictive coding (LPC)-based Burg algorithm for estimating spectral parameters (Purcell and Munhall 2006). To build this continuum, the first 2 formants (F1 and F2) of *head* were shifted in equal steps towards that of *had* (Lametti et al. 2014). F1 and F2 for *head* were 519 and 1738 Hz, and F1 and F2 for *had* were 717 and 1563 Hz. The *head/hid* continuum was constructed in the same way, using the same pure *head* stimulus. F1 and F2 for hid were 434 and 1787 Hz, respectively. The original *head*, *had* and *hid* stimuli were obtained from a male Canadian English speaker. On each trial, the continuum that was to be tested was chosen at random. The 2 words at the ends of the continuum were displayed on the monitor and then the auditory stimulus was presented through headphones. The subject's task was to indicate which of the 2 displayed items had been presented. In total, each stimulus was presented 20 times in random order. Therefore, for each continuum subjects completed 160 trials in total. Subjects had a 2-min break after the first 160 stimuli. Subjects were also encouraged to take more breaks if desired.

Kinematic Data Analysis

Robot encoders sampled the jaw positional data in 3 dimensions at a 1 kHz rate with the resolution of 0.03 mm. These data were low-pass filtered at 10 Hz using a zero phase lag Butterworth filter in Matlab and numerically differentiated to estimate jaw velocity. The start and end of each trial were defined as the time at which jaw tangential velocity went above and fell below 5% of peak velocity. For analytical purposes the perpendicular deviation of the jaw (PD) in 3D from straight line connecting the start and end of movement was calculated at the maximum tangential jaw velocity. Since the robot applied the force in the protrusion direction and in proportion to the jaw velocity, the position at peak velocity is approximately the point at which subject experienced the maximum force. As in previous studies, the analyses are restricted to the downward movement of jaw (Tremblay et al. 2003; Lametti et al. 2012).

It was expected that participants would show adaptation to the force disturbances by reducing their movement curvature (PD) between early and late force field trials. This motor adaptation was scored in 2 ways. First, for every subject, a line was fit to all 200 PD values in the force field condition. Negative slopes indicate a reduction in perpendicular deviation and hence motor adaptation. We used the slope of the regression line r, which is an index of motor learning (MI), as of a regressor of interest in our fMRI analysis. Motor adaptation was also quantified by computing the difference between early and late PD values. To do so, for each subject, the average PD for trials 6–10 was compared to the mean PD of trials 195–200. The first 5 trials were not used as it was shown that there are transient increases in jaw stiffness in early force-field trials that limit movement curvature early in learning (Lametti et al. 2012).

An analysis of formant frequencies during baseline and training trials was conducted by computing first and second formant frequencies of the vowel /e/ in each test word production. A100 ms interval containing the steady-state portion of the vowel was selected by hand on a trial-by-trial basis. The formants in this interval were obtained with a formant-tracking algorithm that used standard LPC procedures implemented in Matlab. An analysis window of 25 ms was used for this purpose. The averages of the formant frequencies in the interval were used for subsequent analyses.

Perceptual Data Analysis

For every participant, 160 trials of auditory discrimination data in each of the *had* to *head* and *head* to *hid* continua were obtained. These tests were conducted twice, once before the sensorimotor learning task and once after. For each continuum, a logistic function was fit to the subjects' binary responses (dependent variable) and the associated first formant frequency (F1) values for the perceptual test stimuli (independent variable) to obtain the perceptual boundary between the 2 utterances. The 50% point of logistic function was taken as the boundary between the two. Two-way repeated measures ANOVA was used to compare changes in the boundary from before to after sensorimotor learning for the 2 perceptual continua. A composite measure of perceptual shift was also calculated on a per subject basis based on the average of these 2 changes in the boundary. This composite perceptual change index (PI) was used as a regressor of interest in our fMRI analyses.

fMRI Data Analysis

Image processing was performed in the FSL software environment version 5.0 (FMRIB Software Library). The same preprocessing pipeline as in Vahdat et al. (2011) was used. In short, (1) the first 2 volumes of each image acquisition were removed, (2) slice timing correction for each voxel's time series was carried out using Hanning-windowed sinc interpolation, (3) the Brain Extraction Tool of FSL was used to remove non-brain tissues, (4) FMRIB's Linear Registration Tool was used for motion correction, (5) B0 field-map images were used to correct for B0 inhomogeneity, and (6) images were spatially smoothed using a Gaussian kernel of 6 mm of FWHM. For the resting-state data, we also used a bandpass filter (fifth-order Butterworth with zero time-lag) to retain the signal frequencies in the range of 0.009–0.08 Hz (Fox et al. 2005). Two transformations were used to transfer the functional data to standard space (MNI space). Boundary-Based Registration was used to transfer the functional data to the T1 weighted structural image and from there non-linear registration (10 mm warp resolution) was used to transfer the T1 weighted image to the MNI standard space.

Listen and Repeat Task

The preprocessing pipeline was the same as in the resting-state data analysis. A block design (alternating blocks of rest and task) was used in which a boxcar function convolved with a double-gamma hemodynamic response function (HRF) served as the regressor of interest. The temporal derivative of this regressor was added to the model as well (Vahdat et al. 2011). These regressors were used in a subject level GLM analysis that was performed in FSL. The subject-level regression coefficients and their variance maps were then input to a group-level analysis, which used a mixed-effects general linear model ($Z > 3.5$, corrected for family-wise error using Gaussian random field theory, cluster significance threshold of $P < 0.01$). The resulting activity map was used to locate Region of Interests (ROIs) for a seed-based functional connectivity analysis of the resting-state data. The selection of ROIs in this fashion merits comment. By using areas that are active during speech production and listening, it is assumed that changes in resting state connectivity that survive beyond movement execution originate in neural activations that occur during listening and speaking.

In total 10 areas that were activated during speech listening and repetition were considered as regions of interest (ROIs) for subsequent functional connectivity analyses: primary motor cortex (M1), ventral premotor cortex (PMv), presupplementary motor cortex (preSMA), primary somatosensory cortex (S1), second somatosensory cortex (S2), Heschl's gyrus (HG), superior temporal gyrus (STG), inferior frontal gyrus (IFG), the supramarginal gyrus (SMG), all in the left hemisphere, and cerebellar cortex in the right hemisphere (CB). The Juelich histological and Harvard-Oxford cortical atlases were used in conjunction with the activity map obtained from the listen and repeat task to select the peaks of activity, which corresponded to each of these regions of interest. A sphere of 6 mm in radius around each peak of activity was used to specify the seed mask. Since the activation map for the listen and repeat task was often bilateral, in a control analysis, we investigated the contribution of the right cerebral cortex by defining the same set of ROIs in the right hemisphere and left cerebellar cortex (see Table 1).

Functional Connectivity Analysis with Behavioral Measures of Learning

Two resting-state scans were acquired in each session of the experiment. As in Vahdat et al. (2011), physiological artifact was removed from the fMRI data by using the average signals taken over white matter (WM), CSF and global signal. To extract WM and CSF from the rest of brain we used the FSL automated segmentation tool on the T1 weighted image. Only parts of segmented maps with a probability of 90% or above were considered. These maps were then transferred to the functional space of each subject to calculate the average time series of WM and CSF. These average time series (WM, CSF, and global signal) along with 6 motion parameters comprised 9 nuisance regressors.

After data preprocessing for each subject, the mean time series of activity in each seed region was used as predictor in a subject level general linear model (GLM) to find the functional

Table 1 Regions on interest corresponding to the peak of activity in a listen and repeat localizer task.

ROI	Anatomical label	MNI coordinates		
		X	Y	Z
LS1	Left primary somatosensory cortex	−56	−12	44
LM1	Left primary motor cortex	−48	−10	42
LPMv	Left premotor	−56	0	22
LSMG	Left supramarginal gyrus	−54	−40	32
LHG	Left Heschl's gyrus	−46	−18	6
LSTG	Left superior temporal gyrus	−54	−34	2
LS2	Left second somatosensory cortex	−60	−12	20
LIFG	Left Broca's area BA44	−56	8	8
RCB	Right cerebellar cortex	24	−68	−50
preSMA	presupplementary motor cortex	2	6	60
RS1	Right primary somatosensory cortex	50	−14	34
RM1	Right primary motor cortex	54	−8	44
RPMv	Right premotor	58	4	20
RSMG	Right supramarginal gyrus	56	−32	20
RHG	Right Heschl's gyrus	48	−22	8
RSTG	Right superior temporal gyrus	56	−30	2
RS2	Right second somatosensory cortex	60	−10	20
RIFG	Right Broca's area BA44	48	10	2
LCB	Left cerebellar cortex	−24	−68	−52

These seeds were used for resting state connectivity analysis. The table lists the ROIs, their anatomical label and their coordinates in MNI space.

connectivity of that ROI with all other voxels. We included the time derivative of each ROI's signal as a regressor in the GLM to account for possible time differences in the hemodynamic response function (HRF) of different cortical areas, as well as the latency for signal propagation from one cortical area to another (Vahdat et al. 2011). As noted above, the time series of nuisance signals, including the global signal, were used as confound regressors in this analysis. Since it has been reported that the global signal is associated with a negative bias in connectivity maps (Fox et al. 2009; Murphy et al. 2009), these analyses were repeated excluding the global signal as a confound in the GLM. This later procedure was only used to calculate the magnitude of connectivity in the pre- and post-adaptation resting-state sessions which are shown as bar plots in Figures 3 and 4. In the group level analysis, multiple comparison correction was performed using Gaussian random field theory ($Z > 2.7$; cluster significant level of $P < 0.05$ corrected).

The 4 functional connectivity maps of each subject (2 resting state scans in each day) were input to a mid-level fixed-effect GLM. Two regressors were used in the mid-level analysis; one modeled the difference in connectivity from Day 1 to Day 2 (Day 2–Day 1), and the other modeled the overall mean effect across all runs for each subject (+1 for all 4 runs). Finally, a group level analysis was performed using a mixed-effects model (FLAME). As in Vahdat et al. (2011), learning-related changes in movement and perceptual classification (MI and PI) were used as regressors in separate GLMs to obtain weighted averages of the connectivity change between days. This enabled the identification of changes in functional connectivity between 2 sessions, which are related to either the magnitude of speech motor adaptation or the magnitude of perceptual change that occurred in conjunction with adaptation.

The correspondence between the magnitude of each behavioral regressor and the unweighted change in functional connectivity was also assessed. We constructed a vector for each connection between an ROI and target cluster whose elements were each subjects' change in functional connectivity. This vector was correlated with both behavioral measures of learning, MI and PI, as shown below in the scatter plots of Figures 4 and 5. Note that in this analysis the unweighted change in connectivity was correlated with the magnitude of behavioral change.

Partial Correlation Analysis

Seed-based functional connectivity analyses using each of the behavioral factors (MI or PI) result in a network of brain structures that show significant changes in connectivity from pre- to post-learning sessions, that are related to the magnitude of learning. A limitation of functional connectivity analysis is that changes in functional connectivity between any 2 brain areas can arise as a byproduct of changes in activity in other areas that are functionally linked to both. This could include cases where changes in connectivity could be influenced by multiple combinations of inputs. For example, area A could influence area B directly and area C via areas D and E. To account for these possibilities, a partial correlation analysis was applied to the functional connectivity data in order to specifically calculate the correlation between the time series of 2 areas that cannot be accounted for by any of the other areas that are activated in the speech sensorimotor network (Marrelec et al. 2006, 2009). To calculate the partial correlations, we restricted the analyses to the set of seed regions and the corresponding clusters of activation that showed learning-related changes in connectivity which were correlated with either the MI or PI behavioral index (Fig. 6). We conducted 2 separate partial correlation analyses, one for the set of regions that showed changes in connectivity associated with perceptual learning, and a second that showed connectivity changes associated with motor learning (adaptation). The partial correlation analysis for PI was restricted to those areas related to perceptual change. None of the regions in the MI network were part of this analysis. The same was the case for the MI analysis, which was restricted to those areas whose connectivity change was related to motor learning.

The partial correlation analysis involved computing correlations between all pairs of areas (both ROIs and associated activation clusters) associated with either PI or MI. For the activation clusters, a sphere of 6 mm in radius around the peak of activity was considered and the mean time series within each sphere was calculated. The partial correlation provides a measure of functional connectivity between 2 areas that cannot be accounted for by the time series of activity in the other areas in the MI or PI associated networks. Therefore, in a network of n areas, $N = n(n-1)/2$ partial correlation coefficients were calculated. For each subject and each pair of areas, partial correlation estimates were computed for each day of the experiment. T-tests were used to identify those partial correlations which changed significantly between the first and second days of the experiment (corrected for multiple comparisons by the Bonferroni correction, $P < 0.05/N$). This procedure identified those changes in connectivity between pre- and post-learning sessions that survived the partial correlation test.

As noted above, areas in the seed-based whole-brain analysis that were found to have learning-related changes in connectivity served as inputs for the partial correlation analysis. The individual ROIs came from localizer scans which identified those areas that were active during listening to and repeating words. The target clusters came from whole brain analyses and accordingly were not limited to the preselected ROIs identified in the localizer scans.

To rule out the possibility that some sort of learning during baseline affects our neuroimaging results, we required participants to come to the lab for a familiarization day, before the day in which the baseline condition was tested. During familiarization training, the participant produced the test utterances 200 times, exactly as in baseline testing. The same was true for perceptual test in which subjects performed one block of perceptual test trials. Furthermore, the analyses of the neuroimaging data specifically focused on learning-related changes in connectivity and hence non-specific changes between days were excluded.

Results

Participants read aloud words that appeared on a computer screen. The testing was carried on 2 consecutive days. On Day 1, participants were connected to the robot but experienced no external forces as they repeated the utterances. Following these baseline or null-field utterances, resting-state functional images were acquired and afterwards participants were tested in an auditory perceptual classification task. The sequence on Day 2 was similar to that of Day 1 with the exception that this time the robot applied outwards forces to the jaw, that is, in the protrusion direction, as participants read the same utterances from a computer screen.

Behavioral Results

Figure 2A shows a representative example of a jaw opening movement in the sagittal plane. Under null field conditions, the movement is typically straight. On Day 2, early in force-field adaptation, the forces applied to the jaw resulted in outward trajectories in the protrusion direction (trial 2). As participants gradually learned the new dynamics, the jaw deviation declined until, late in this phase (third last trial was shown), when subjects successfully compensated for the effect of the force field, jaw trajectories approached those in null field conditions.

Jaw trajectories were quantified in 3D, using as a measure of movement curvature, the perpendicular distance of the jaw at maximum tangential velocity from a line connecting the start and end of each jaw opening movement (PD). Figure 2B shows the mean PD, averaged over subjects on a trial by trial basis, during movements in both null and force-field conditions. It is seen that under null conditions, jaw opening movements were

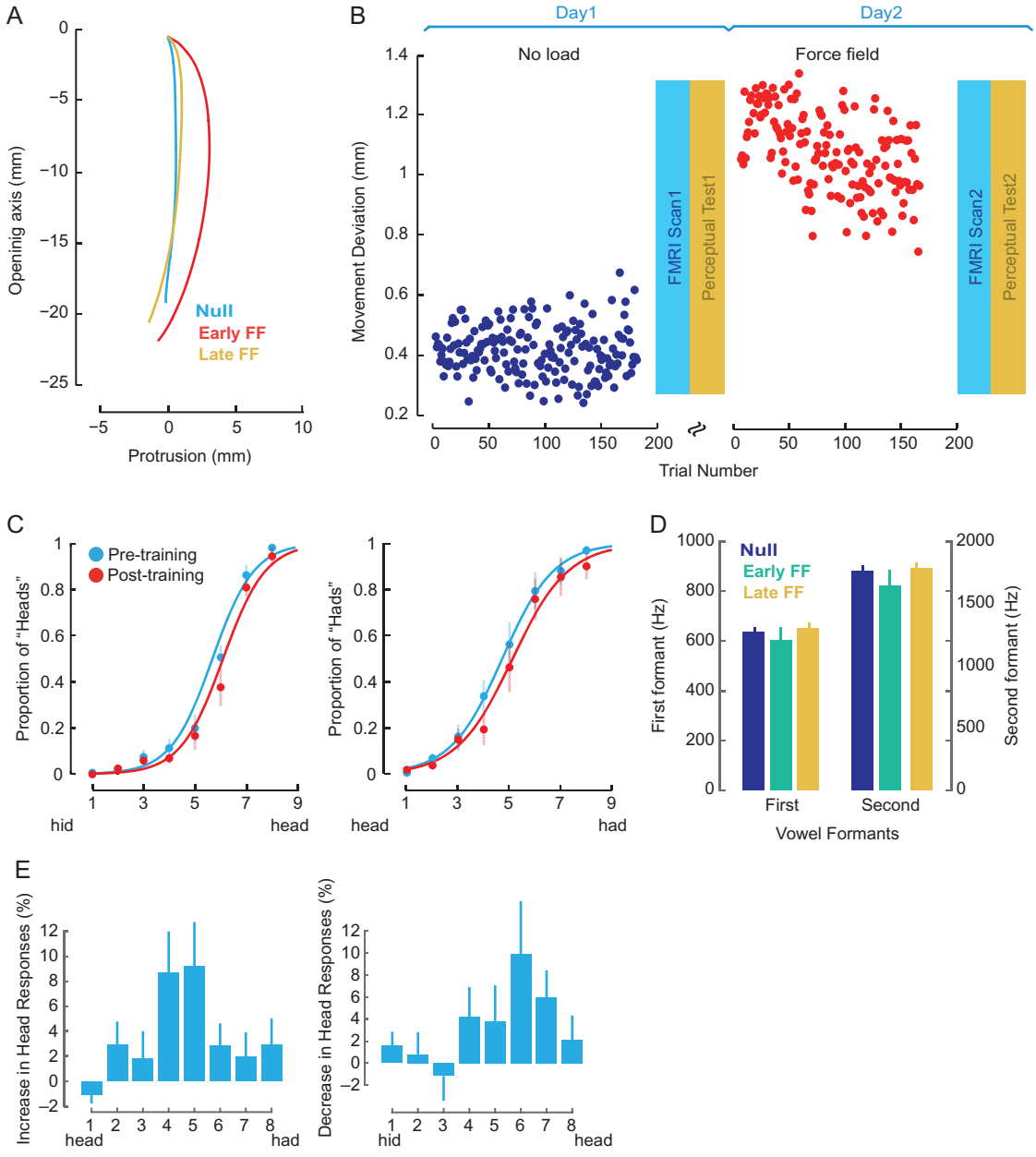

Figure 2. Somatosensory perturbations result in changes to speech movements and auditory perceptual classification, even though the perturbation has no measurable effect on speech acoustics (*A*) Forces in the protrusion direction alter the path of the jaw during speech. Participants adapt to the perturbation over the course of 200 test utterances. (*B*) The mean perpendicular deviation of the jaw (at the maximum tangential velocity) from a straight line joining movement start and end points. In the first session, subjects repeated the test utterances under no load conditions. Group PD was small with little deflection in the protrusion direction. Following fMRI scans subjects returned to lab for perceptual testing. In the second session, the robot applied velocity dependent forces in the protrusion direction. The initial jaw deflection was partially compensated for over the course of training. (*C*) Participant's classification of speech stimuli was measured before and after force field adaptation on *head-had* and a *hid-head* continuum. Perceptual boundaries between stimuli shifted after force field adaptation. (*D*) Mean first and second formant frequencies during the production of test utterances under null conditions, early and late in force field training. (*E*) Percentage change in the proportion of *head* responses at each point in the *head-had* and *hid-head* continuum.

slightly curved in the protrusion direction. When the robot applied forces to the jaw, movement curvature increased. With practice, the deflection was reduced although it never reached that observed under null field conditions. Jaw displacement is small due to the mechanical behavior of the jaw, which is stiffest in the direction of the perturbation (Shiller et al. 2002). It is noteworthy that there is compensation at all, given the limited displacement.

Force-field learning was assessed in 2 ways. First, for each subject, we calculated the mean jaw deviation early and late in force-field adaptation. *T*-statistics revealed a significant decrease in jaw deflection between early and late in learning ($t(18) = 2.12$, $P < 0.05$). Linear regression was also used to model changes in PD over the course of force-field trials. Negative slopes indicate a reduction in protrusion and hence motor learning. The average slope was negative and reliably different than zero ($t(18) = -2.43$, $P < 0.05$). These 2 measures, changes in PD from early to late in learning and the slope of regression line, both provide estimates of adaptation-related changes to movement. The 2 estimates are correlated ($r(17) = -0.78$, $P < 0.01$) and produce similar results in the neuroimaging analyses. The results shown below use the slope of the regression line for individual participants as the regressor of interest in the fMRI data analysis (MI).

Changes in perceptual function that occur in conjunction with adaptation are shown in Figure 2*C*. For each subject and for each perceptual continuum separately, a psychometric function was fit to the set of formant frequency values and associated binary responses. The formant frequency associated with the 50% probability point on this function was used as the perceptual boundary between the 2 stimuli.

Changes in the boundary from before to after force-field learning were assessed using a 2 way repeated measures ANOVA. ANOVA found a significant shift in the perceptual boundary from before to after force field adaptation ($F(1,18) = 9.237$, $P < 0.01$), however there was no indication of an interaction ($F(1,18) = 0.04$, $P > 0.8$). The perceptual boundary between *hid* and *head* shifted in the *hid* direction (towards lower F1 values) and resulted in a decrease in the proportion of *head* responses. Similarly, the perceptual boundary between *head* and *had* moved in the head direction (likewise towards lower F1 values), which means that the proportion of *had* responses decreased with force-field learning. For each subject, since the changes for both continua were in the same direction, the magnitude of the change in the perceptual boundary was averaged to obtain an aggregate measure of perceptual change following motor learning. This perceptual index (PI) was used on an individual basis as a regressor of interest in our fMRI data analysis.

Figure 2*E* shows a further analysis of the observed perceptual change in which learning-related differences in the classification of stimuli are shown at different points along the perceptual continuum. As would be expected, the changes observed in perceptual judgements are non-uniform, with the greatest differences in classification observed at mid-way positions along each perceptual continuum.

The perceptual testing procedure involved a total of 160 perceptual judgments. To test for the possibility that the observed effects were related to fatigue, the data for each of the perceptual tests was split in half to assess possible changes in acuity over the course of testing, which might indicate fatigue. ANOVA indicated that there was, if anything, a marginally significant increase in acuity in the second half of the test, as evaluated using the distance between the 25th and 75th percentile of the fitted psychometric function, $F(1,18) = 3.34$, $P = 0.08$. Hence, perceptual fatigue is unlikely to account for the observed perceptual change.

To assess the possibility that observed changes in the kinematics of jaw movement or in the auditory perceptual boundary were due to alterations in speech acoustics and hence auditory feedback as a result of the presence of the force-field, the first and second formant frequencies of the vowels were calculated for both null and force field conditions. For each participant, the mean first and second formant frequencies in the null field and also early and late in the force field condition (average of first and last 5 trials) were calculated (Fig. 2*D*). A 2-way repeated measures ANOVA indicated, as expected, that there were reliable overall differences in F1 and F2 frequencies ($F(1,17) = 935.27$, $P < 0.01$). However, no significant differences in frequency were observed between acoustical recordings done under null field conditions and those at the start and end of force field training ($F(2,34) = 0.82$, $P > 0.4$), nor was there a significant interaction ($F(2,34) = 1.52$, $P > 0.2$). Thus, there is no indication that adaptation produced measurable changes to speech acoustics.

Neuroimaging Results

As a first step, we used a listen and repeat task in the scanner to identify areas of activation for subsequent connectivity analyses (Fig. 3). Widespread activity was observed in this task in sensorimotor and auditory regions and in cerebellar cortex. In most cases the activation was bilateral, with the exception

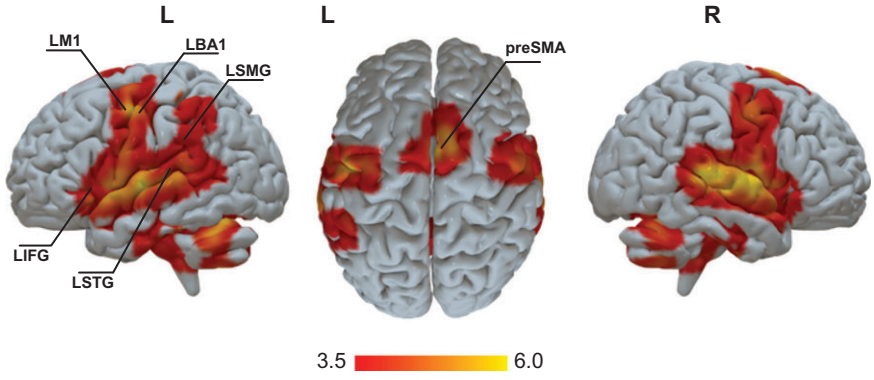

Figure 3. Three-dimensional surface rendering of statistical activation map of the listen and repeat task. Activation map shows the left and right hemispheres and an axial view from above. The location of seed regions for resting-state connectivity analyses is indicated.

that activity in the supramarginal and angular gyrus was limited to the left hemisphere. These areas of activation are similar to those in the Raucshecker and Scott (Rauschecker and Scott 2009) model linking speech perception and production.

Resting state fMRI scans were obtained following baseline utterances and then again following a sensorimotor learning task in which subjects repeated words as a robot applied loads to the jaw. The resting-state neuroimaging data were analyzed using a seed-based functional connectivity analysis. Based on peaks of activity in the activation maps extracted from a listen and repeat task performed in the scanner (Fig. 3), along with previous results on sensorimotor adaptation (Bohland and Guenther 2006), 10 regions of interest (ROIs) were identified in areas which are involved in either speech perception or production (Table 1). These included primary somatosensory cortex (S1), primary motor cortex (M1), second somatosensory cortex (S2), superior temporal gyrus (STG), Heschl's gyrus (HG), supramarginal gyrus (SMG), inferior frontal gyrus (IFG), presupplementary motor area (preSMA), all in the left hemisphere, and right cerebellar cortex (CB). Two separate group-level functional connectivity analyses were conducted. A first analysis focused on brain networks that were specifically related to the change in perceptual classification that occurs in conjunction with speech motor adaptation (PI). A second analysis identified regions whose changes in connectivity were specifically related to changes in movements that accompany speech motor adaptation (MI).

Figure 4 shows learning-related changes in connectivity that are associated with the perceptual change (PI). The left column shows the location of the ROI in red, the middle column shows the brain clusters whose connectivity with the ROI changes significantly with learning and in proportion to PI. The bar graphs show the amount of functional connectivity between the ROI and its corresponding cluster on Day 1 and Day 2. The scatter plots show the relationship between unweighted connectivity changes and behavioral measures of perceptual change (PI). As shown in the figure, there is an increase in functional connectivity between primary somatosensory cortex and each of bilateral inferior frontal gyrus, inferior parietal lobule and the superior temporal gyrus. Moreover, there are increases in connectivity between primary motor cortex and bilateral inferior frontal gyrus and between supramargional gyrus and cerebellar cortex (see Table 1). As shown in the scatter plots, subjects with greater change in connectivity from Day 1 to 2 also had greater perceptual change (PI). Table 2 presents a summary of functional connectivity changes from Day 1 to 2, which includes the ROIs (first column), MNI coordinates of peak of activity in the associated area (second column), corrected cluster level *P*-values (third column), Z-scores associated with the peak of activity in each cluster (forth column) and finally the last column shows the anatomical label of cluster. In summary, a network comprising primary motor and somatosensory cortex, IFG, STG, IPL and cerebellar cortex showed connectivity changes from Day 1 to Day 2 which were related to the perceptual changes associated with speech sensorimotor adaptation.

The same tests were conducted to assess speech motor learning-related changes in connectivity using MI as the regressor of interest in whole brain fMRI analyses. Figure 5 shows changes in functional connectivity from Day 1 to Day 2 that are specifically related to motoric changes (MI) during sensorimotor adaptation. An increase in connectivity was identified between primary somatosensory cortex (S1) and superior temporal gyrus (STG). Note that this connectivity increase was also observed in the previous analysis with respect to PI as the regressor of interest, and therefore this connection is part of the conjunction map between MI and PI. Changes in connectivity were also identified between Heschl's gyrus and STG, preSMA and IPL, STG and primary motor cortex and finally between STG and bilateral second somatosensory cortex (see Table 1). All of these changes in connectivity were significantly related to the improvement in movement involved in sensorimotor learning as shown in scatter plots in Figure 5. Table 3 presents a summary of these results with the same format as Table 2. Overall, a network comprising of primary motor and somatosensory cortex, STG, IPL, S2, preSMA and Heschl's gyrus revealed connectivity changes from Day 1 to Day 2 which were related to the motoric changes associated with adaptation.

The functional connectivity analyses described immediately above were repeated using same seed regions in the right hemisphere and left cerebellar cortex. We obtained no reliable changes in connectivity for either behavioral factor (MI or PI) using right hemisphere seed regions.

In the analyses reported above, all brain-wide changes in connectivity with each seed region were identified that showed a relationship with either speech motor adaptation or associated perceptual changes. However, 2 regions may show changes in connectivity due to a mutual dependency on other areas. To account for this possibility, a partial correlation analysis was conducted with the goal of identifying a subset of connections whose functional connectivity changes could not be explained by concomitant activity in the other parts of the network associated with MI or PI, respectively. Two analyses were carried out, one to identify the pattern of connectivity change associated with changes in speech perception (PI) and a second associated with changes to movement over the course of speech motor adaptation (MI). In each case, the network nodes were defined at the peak of activity of the identified clusters and their associated seed regions (refer to Figs 4 and 5), and the mean time series within a sphere of 6 mm were calculated for each experimental day. For each day, the partial correlation coefficient between each pair of areas was calculated, by removing their shared activity with respect to the other areas in that network (Marrelec et al. 2006). Changes in partial correlation coefficients from Day 1 to Day 2 were evaluated using pairwise *t*-statistics. To account for multiple comparisons, $P < 0.05/n$ was considered statistically significant, where n is the total number of connections (comparisons) in a given network.

Figure 6A shows the result of the partial correlation analysis in the perceptual network, comprising all of the 6 brain regions shown in Figure 4. The solid lines (both yellow and blue) indicate areas for which connectivity changed as result of learning and was correlated with the measured perceptual change (PI). Although all of the 15 possible pairings of the set of 6 areas implicated in perceptual change were considered, only the partial correlation between the primary motor cortex and the inferior frontal gyrus significantly changed from Day 1 to Day 2 ($t(18) = 3.72$, $P < 0.002$). This is shown in yellow in Figure 6. The remaining learning-related changes in connectivity (which did not survive the partial correlation test) are shown in blue. Thus, adaptation-related changes in connectivity between primary motor cortex and the inferior frontal gyrus could not be explained by activity in other nodes, while changes in connectivity of all the other links were dependent upon the activity of these or other nodes in this network. When the time-course of activity in primary motor cortex and the inferior frontal gyrus was regressed out, there were no remaining reliable changes in connectivity that were associated with perceptual change. This

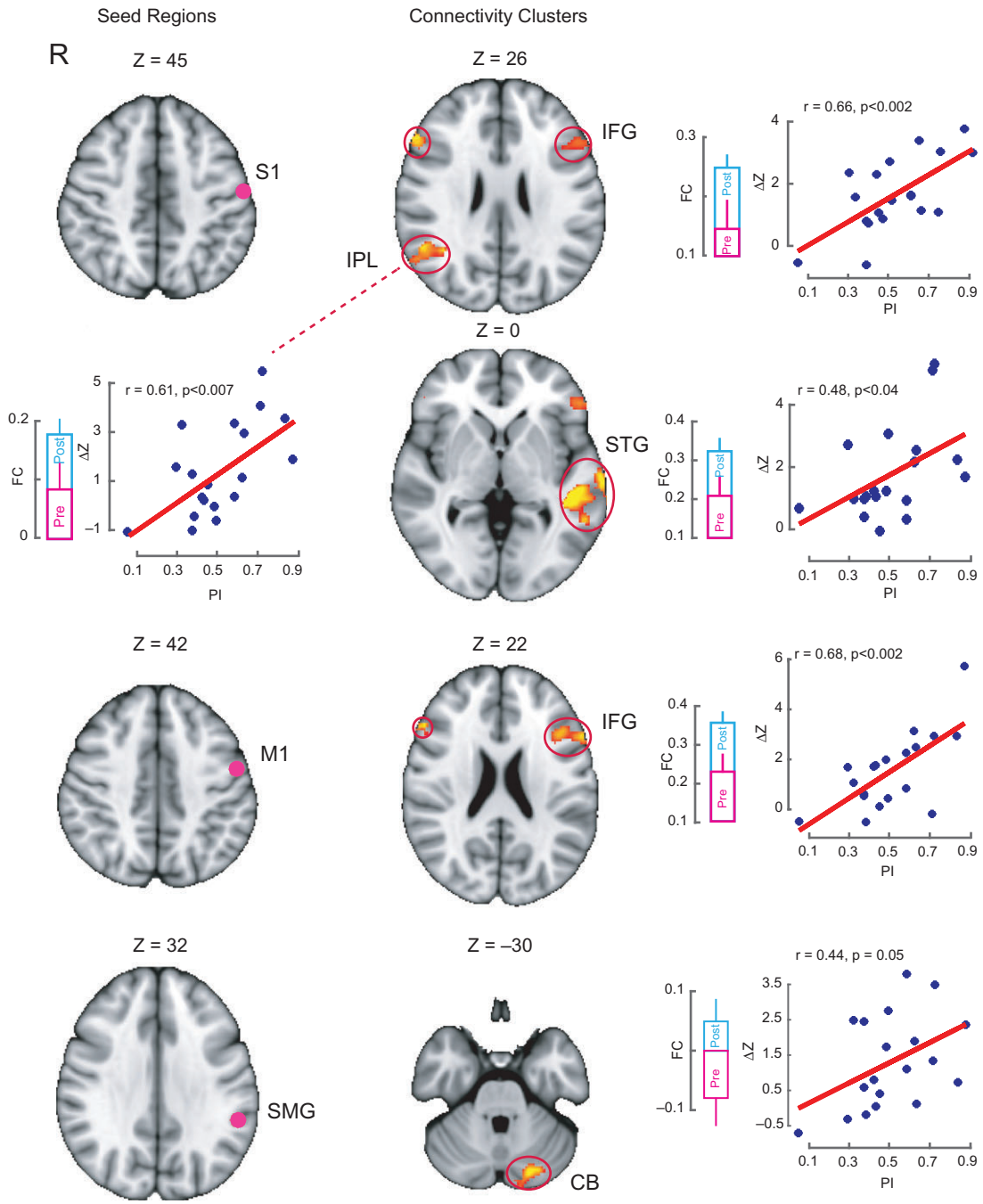

Figure 4. Changes in functional connectivity associated with changes in perceptual classification of speech sounds following sensorimotor learning. Left column shows the seed region; middle column shows clusters of voxels for which connectivity with the seed region increased following speech motor adaptation; bar graphs show functional connectivity measures before and after adaptation; scatter plots at the right show that greater changes in connectivity are observed for subjects with larger values of the perceptual index (PI), indicating greater perceptual change.

suggests that changes in connectivity in areas that are largely motoric can explain the perceptual changes that are observed following sensorimotor adaptation.

A second partial correlation analysis was performed for the motor learning network, comprising the 7 brain areas whose functional connectivity changed in relationship to relation to behavioral measures of learning, that is, MI (Fig. 5). Again, Bonferroni correction was used to correct for multiple comparisons (in total 21 possible pairings). Figure 6*B* gives the result of this analysis. The yellow and blue solid lines again summarize all the connectivity changes that are related to improvements in movement following motor learning. Out of these 21 possible connections among these 7 areas, only 2 showed a significant change in partial correlation over test days. Specifically, the connections shown in yellow between the primary somatosensory cortex and the superior temporal gyrus ($t(18) = 3.70$, $P < 0.002$), as well as the connection between the inferior parietal lobule and presupplementary motor area ($t(18) = 4.51$, $P < 0.000$) were the only links in this network that survive the partial correlation test. When the time-course of activity in sensory areas

Table 2 Results summary with PI used as a regressor of interest in functional connectivity analyses.

ROI	MNI coordinates			P_{cor}	Z_{value}	Anatomical Lable
	X	Y	Z			
S1	58	28	14	0.002	5.11	R Inferior Frontal Gyrus
	−40	20	18	0.008	3.69	L Inferior Frontal Gyrus
	52	−52	26	0.020	3.89	R Inferior Parietal Lobule
	−44	−36	2	0.000	4.51	L Superior Temporal Gyrus
M1	−40	20	18	0.000	3.78	L Inferior Frontal Gyrus
	56	28	18	0.002	4.31	R Inferior Parietal Lobule
SMG	−20	−80	−30	0.010	4.15	L cerebellar cortex

Each row reports the MNI coordinates of the peaks of activity for clusters that changed their connectivity with the ROI between the first and second day of the study and whose changes were related to the magnitude of the perceptual change (PI). The left column reports the corresponding ROI (seed region). The reported *P*-value (P_{cor}) is the corrected cluster-level value. The reported Z score shows changes in Z from Day 1 to Day 2.

was regressed out, there were no remaining reliable changes in connectivity in frontal motor areas related to motor learning. This suggests that changes in functional connectivity in a predominantly sensory network can explain the movement adjustments that are observed in conjunction with speech motor adaptation.

Discussion

We used a procedure that dissociates the contribution of somatosensory from auditory feedback in speech motor learning, and found that adaptation to altered somatosensory feedback results in adaptive changes to both speech movements and to the perceptual classification of speech sounds. In an analysis of accompanying resting-state neuroimaging data we used a partial correlation statistical technique to identify from among areas that showed learning-related changes in connectivity, the subset whose connectivity changes were not explained by activity elsewhere in the learning network. Using this technique, we found that speech motor adaptation was accounted for, not by frontal motor regions, but instead by changes in connectivity in non-motor areas of the brain, specifically, between auditory and somatosensory cortex, as well as between the inferior parietal lobule and preSMA. In addition, using the same technique it was seen that the observed speech perceptual changes were related to connectivity changes in cortical motor regions, specifically between M1 and IFG.

The learning-related changes to the speech motor network that are observed here with resting-state imaging extend previous reports. Learning-related effects in speech motor and perceptual learning studies have been found in M1 and SMA as well as in auditory association areas, S1, cerebellar cortex, and SMG (Adank and Devlin 2010; Shum et al. 2011; Grabski et al. 2012; Guediche et al. 2015; Segawa et al. 2015; Berken et al. 2016). The present results differ from previous findings in 2 specific ways. First, the partial correlation procedure isolates those changes in connectivity that are not explained by the time course of activity in any other learning-related areas. It thus results in the identification of a subset of areas whose connectivity changes are presumably responsible for other observed changes in resting-state activity following learning. Second, neuroimaging results that are obtained over the course of learning are confounded by the presence of behavioral changes. It is difficult using task-based scans to rule out the possibility that any observed changes have occurred because participants are performing the task differently rather than to learning. This confound is removed in resting-state scans as the behavioral task is absent.

One of the main results of the present study is that once the contribution to connectivity from remote regions of the speech motor network is removed, the remaining connectivity changes associated with kinematic improvements over the course of adaptation are not in motor areas of the brain but between auditory and somatosensory cortex and between the inferior parietal lobule and preSMA. When the contribution of activity in sensory areas is regressed out, we find no movement related changes in connectivity that are strictly within the motor network. This finding supports the hypothesis that in speech motor adaptation, changes to motor areas are a byproduct of changes in sensory areas of the brain. It should be noted that the connectivity changes do not indicate an absence of activity in the resting-state cortical motor network following learning. Indeed, we observe activity in M1 and PMv as well as SMA. However, the activity is not found to be learning-related.

Activity in each of auditory and somatosensory cortices occurs in the context of speech production (Bohland and Guenther 2006). The present observation that connectivity between these regions is strengthened in proportion to motor learning presumably reflects an update to the auditory–somatosensory map that is needed to correct for the somatic perturbation. This would serve to produce better sensory targets and in turn account for improvements in movement following learning. The possibility, as suggested by the results of the partial correlation analysis, that sensory systems drive adaptive changes in motor output is consistent with models of error-based control and adaptation. The idea that movements are planned and updated in sensory units is central to position control hypotheses (Feldman 1986; Gribble and Ostry 2000) and to recent accounts which postulate that adaptation occurs in response to the sensory prediction associated with a given motor command (Shadmehr et al. 2010; Hickok et al. 2011; Houde and Nagarajan 2011). In recent work on visuomotor rotation (during pointing movements) or altered auditory feedback (during speech), it is postulated that incorrect movements give rise to sensory prediction errors that are used to update the sensory prediction. This change in sensory prediction then causes the motor output to be different on the next trial.

It is notable that changes in resting-state functional connectivity are observed after brief periods of training. However, this is consistent with previous work involving visuomotor adaptation (Della-Maggiore et al. 2017) in which a single training session resulted in changes in resting-state connectivity that were measurable at a delay of 24 h. Possible neuroanatomical changes following short periods of learning have also been reported using DTI measures (Sagi et al. 2012).

The learning-related change to the perceptual classification of speech sounds is likely because the orofacial perturbation results in a sensory misalignment between somatosensory input, which arises from the perturbed orofacial configuration, and auditory feedback, which is unaltered. The auditory perceptual change is presumably an adjustment aimed at bringing audition and somatosensation back into register. The basic phenomenon observed here accords well with the extensive literature on audiovisual integration such as the McGurk effect in speech in which a mismatch between an image of a speaker's face and the sound of the speaker's voice results in changes to auditory perception (McGurk and MacDonald 1976). It is also consistent with examples of multisensory integration involving

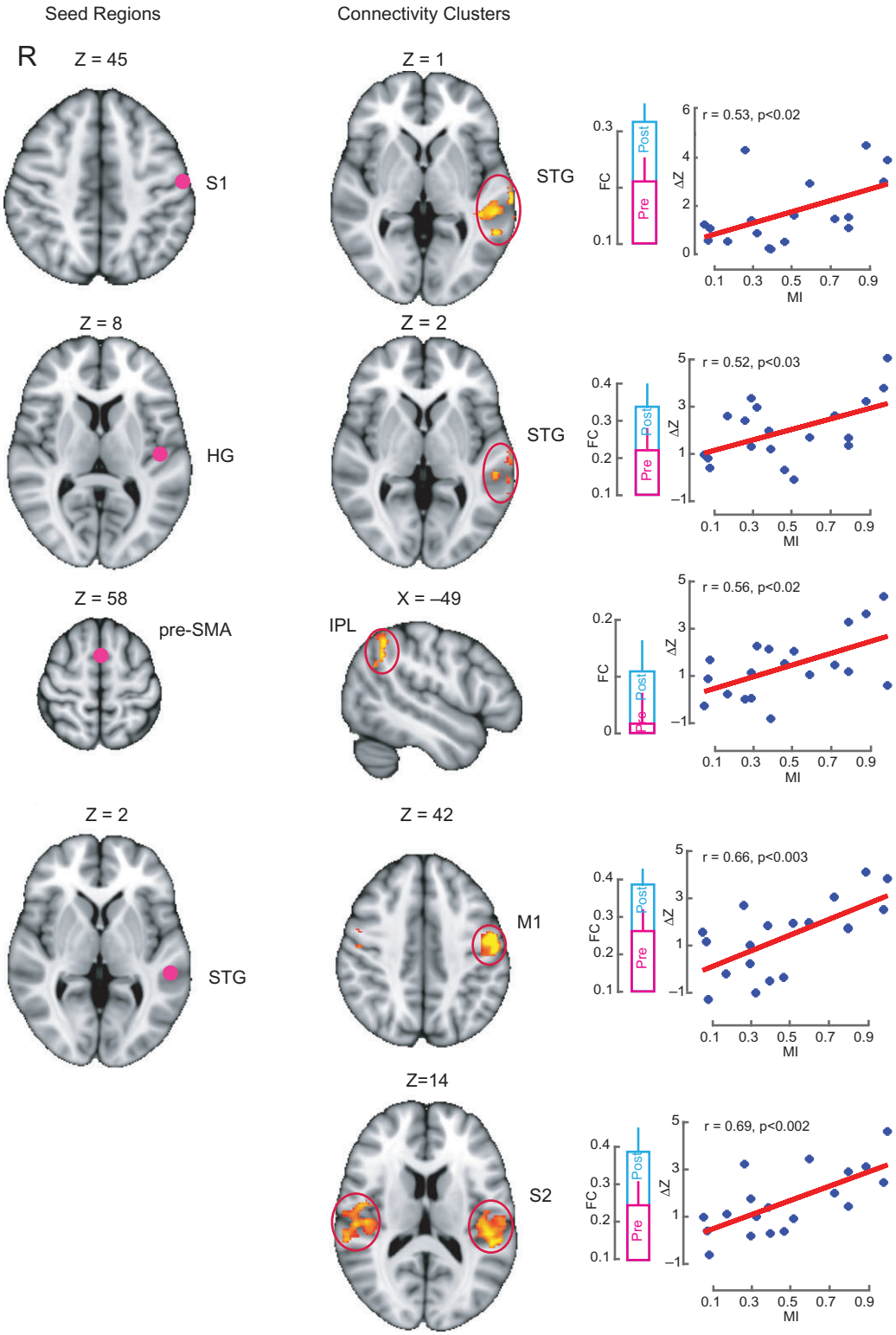

Figure 5. Changes in functional connectivity related to kinematic adaptation associated with speech motor adaptation. Left column represents the seed regions; the middle column shows voxels in which connectivity to the seed region increased following speech motor adaptation; the right column has 2 components: the bar graph shows functional connectivity before and after learning, the scatter plot shows that greater kinematic adaptation, as assessed by the motor index (MI), is associated with greater connectivity change.

audition and somatosensation in speech. Specifically, it has been shown that somatosensory stimulation affects the auditory perception of speech sounds. Somatosensory inputs due to speech-like skin stretch (Ito et al. 2009) and orofacial airpuffs (Gick and Derrick 2009) both produce changes to the auditory classification of speech. Anatomically, there are inputs in

macaques to areas of auditory cortex from regions within somatosensory cortex as well as from multisensory areas (Hackett et al. 2007). Responses to somatosensory inputs have been recorded in areas immediately caudomedial to primary auditory cortex (Schroeder et al. 2001; Fu et al. 2003). Similarly, in humans, tactile pulses and vibration are observed to activate the posterior auditory belt area (Schurmann et al. 2006). Pathways such as these presumably mediate both the behavioral effect of somatosensory adaptation on auditory perception as well as the improvement in functional connectivity between auditory and somatosensory cortex that is observed in the present study.

A strengthening of connectivity in proportion to perceptual change was observed between M1 and IFG. The finding is consistent with the involvement of frontal motor area in speech perceptual processing (Fadiga et al. 2002; Watkins et al. 2003; Watkins and Paus 2004; Wilson et al. 2004; Schomers and Pulvermuller 2016) and speech motor learning (Rauschecker et al. 2008) and with the presence of reciprocal connections between orofacial M1 and the presumed homolog of Broca's area in macaques (Simonyan and Jurgens 2005). It is also consistent with the presence of evoked responses in orofacial motor cortex in humans to electrical stimulation of the inferior frontal gyrus and to similar responses in IFG following motor cortex stimulation (Greenlee et al. 2004). The fact that the changes in connectivity between motor cortex and IFG are related to perceptual change rather than movement fits with recent reports that like IFG, frontal motor areas are involved in the auditory coding of speech sounds (Cheung et al. 2016). The present finding that there are learning-related change in connectivity between IFG and M1 explicitly links the change in perception to motor areas of the brain. In the context of models of speech production and perception (Rauschecker and Scott 2009; Hickok et al. 2011; Tourville and Guenther 2011; Houde and Chang 2015) the change in connectivity might be viewed as an element of an inverse perceptual model that maps sensory inputs to associated motor commands.

A strengthening of connectivity in relation to speech motor adaptation was observed between preSMA and the inferior parietal lobule, specifically, in a region between the angular and the supramarginal gyrus. PreSMA appears to play a role in movement sequencing and timing but has quite different patterns of anatomical connectivity than SMA proper (Luppino et al. 1993; Liu et al. 2002; Johansen-Berg et al. 2004). PreSMA does not project to the spinal cord (Dum and Strick 1991), it is weakly connected with SMA and receives strong inputs from area 46 in prefrontal cortex, which is implicated in working memory and attention. PreSMA also receives some input from the inferior parietal lobe regions PG and PFG, which in humans corresponds to the angular gyrus and the supramarginal gyrus respectively (Luppino et al. 1993; Yagmurlu et al. 2016). This same region of parietal cortex is seen to change in functional connectivity with preSMA in the present study and has also been previously implicated in speech motor adaptation (Shum et al. 2011).

Cerebellar cortex is widely implicated in studies of sensorimotor adaptation (Gilbert and Thach 1977). Consistent with this literature, adaptation-related changes in connectivity were observed in the present study between cerebellar cortex and the supramarginal gyrus. However, connectivity changes involving the cerebellum were not reliable following the partial correlation analysis. It is possible that further adaptation-related changes in connectivity involving cerebellum might

Table 3 Results summary using MI as a regressor of interest in the functional connectivity analyses.

ROI	MNI coordinates			P_{cor}	Z_{value}	Anatomical lable
	X	Y	Z			
S1	−52	−34	2	0.000	4.20	L Superior Temporal Gyrus
HG	−62	−42	−6	0.040	3.51	L Superior Temporal Gyrus
Pre-SMA	−36	−58	38	0.002	4.07	L Inferior Parietal Lobule
STG	−48	−10	42	0.001	4.75	L primary motor cortex
	−48	−30	16	0.000	4.09	L second somatosensory cortex
	46	−26	20	0.000	4.36	R second somatosensory cortex

The table gives the MNI coordinates of the peak of activity in each of the clusters that changed their connectivity to the seed region between the first and second day of the experiment and whose changes in connectivity were related to improvement in movement (MI). Conventions are as in Table 2.

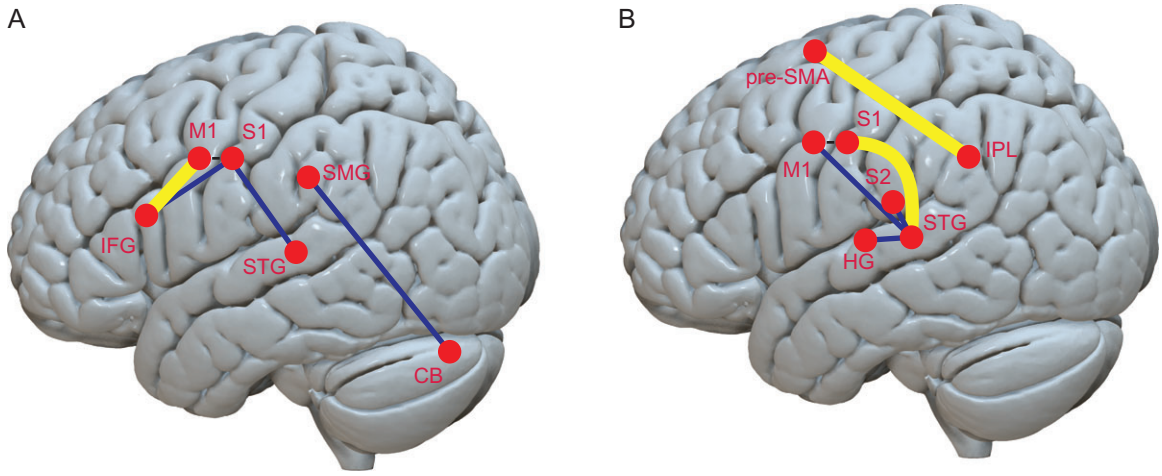

Figure 6. Partial correlation was used to identify from the set of areas in which functional connectivity changed with learning, the subset whose connectivity change was not accounted for by the activity in other areas in this set. The thin blue lines show areas in which learning was associated with connectivity increases that were related to changes in perceptual classification (*A*), kinematic adaptation (*B*). The thick yellow shows those connections that survived the partial correlation analysis.

have been detected had the analyses been based on smaller seed regions. However, as the present study presented a whole brain analysis, the number of seeds must be limited in order to perform multiple comparisons. Networks related to sub-regions of cerebellum might have been explored had the analysis been able to devote more seeds to individual regions.

The current perceptual shift involves a tendency to classify auditory stimuli as corresponding to words with globally lower F1 frequencies. That is, following adaptation subjects are more likely to classify sounds on a *head* to *hid* continuum as *hid* (in which the F1 frequency of *hid* is lower) and likewise to classify sounds on a *head* to *had* continuum as *head* (where F1 for *head* is lower). This result can be contrasted with that of (Lametti et al. 2014), in which perceptual changes following adaptation to auditory feedback were restricted to one part of this continuum. The reason for the difference is not presently known but several factors merit investigation. One difference between the manipulations is that the perturbation in the present study is wholly somatic whereas, in the Lametti manipulation, the perturbation is auditory and compensation requires that subjects tolerate somatosensory error in order to achieve desired sounds. Another consideration is the direction of the perturbation. Perturbations and compensation in the present study were in the jaw protrusion/retraction direction whereas the auditory perceptual changes were on a low to high continuum with respect to jaw or tongue position.

As in Lametti et al. (2014) no correlation was observed between the amount of movement adaptation and the observed perceptual change. In both speech and limb movement, correlations between movement and perceptual change have been reported in some studies, while in other studies in which perceptual change has been observed in conjunction with movement, no correlation between the magnitudes of these variables has been seen (see Ostry and Gribble (2016) for summary). Correlations have been reported more consistently in limb movement studies than in speech. This may be a consequence of the more complex mapping in speech between articulatory movements and perception, or of individual differences in the reliance on auditory versus somatosensory information in speech, either of which could result in a less tightly coupled relation between speech movement adaption and perceptual change.

A limitation of the present study is that it was conducted using behavioral regressors to find learning-related brain networks rather than a control group against which the experimental group might be evaluated. This latter analysis would have enabled the identification of differences in connectivity between the experimental and control group however we decided against this approach for 2 reasons. First, a no perturbation control condition may not provide a neutral baseline. Even simple repetition of test utterance without perturbations might result in use-dependent learning (Diedrichsen et al. 2010). Moreover, an analysis that is restricted to differences between the experimental and control conditions, would not address networks that are associated with perceptual versus motor aspects of sensorimotor learning.

Another limitation of the present study is that behavioral and resting-state measures were obtained in the same experimental sessions. Little is presently known about the relationship between resting state measures obtained immediately after adaptation trials and long-term motor memory (but see Della-Maggiore et al. (2017)). It will be important for future work to systematically explore the extent to which resting-state changes predict retention of learning.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

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Notes

Conflict of Interest: None declared.

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