

Cerebro-Cerebellar Connectivity Implicated with Perceptual Learning of the English /r-l/ Phonetic Contrast by Native Japanese Speakers

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ABSTRACT

This study investigates the pattern of cerebro-cerebellar functional connectivity implicated with both processing and learning of the English /r-l/ phonetic contrast by native Japanese speakers. The data used in the study was from fMRI recordings of nine Japanese individuals during a /r-l/ phoneme identification task both before and after one month of feedback-based perceptual identification training. Activity patterns in the right and left cerebellum related to contrasts of interest were determined by independent component analysis. Functional networks were identified via “seed-voxel PLS,” showing significant covariation between bilateral cortical speech regions and the pattern of activity identified in 1) the right cerebellum - reflecting processes present both before and after training, and 2) the left cerebellum - reflecting processes related to learning of the phonetic contrast. The results are consistent with the hypothesis that cerebro-cerebellar connectivity may facilitate /r-l/ identification performance by establishing auditory-articulatory representational mappings that constrain perception.

1. INTRODUCTION

Adult native Japanese speakers have difficulty reliably identifying and discriminating the English /r-l/ phonetic contrast (e.g. *rake* and *lake*) even after years of exposure [1]. However, after extensive feedback-based perceptual training, improvement in identification performance can be attained [2] that generalizes to novel stimuli, is long lasting [3] and also improves speech production performance, even though no formal production training is given [3].

Brain regions involved with learning the /r-l/ contrast by native Japanese speakers have recently been identified [4]. Figure 1 depicts the brain regions that have significantly greater activity after relative to before training. The study consisted of functional magnetic resonance imaging fMRI of nine native Japanese speakers both before and after one month of perceptual identification training using feedback. The task for the subject during the fMRI experiment was to listen to minimal-pairs of words and identify via button press whether the word started with a /r/ or a /l/. The control task consisted of randomly pressing a button when presented with signal-correlated-noise stimuli. All subjects

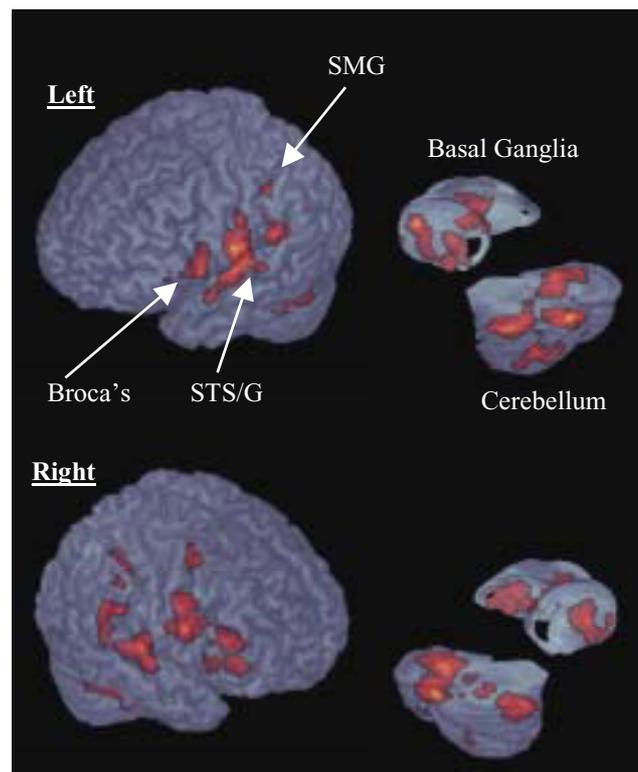


Figure 1. Brain regions showing an enhancement in neural activity during an /r-l/ identification task for native Japanese speakers after relative to before training. Activity is significant at $P < 0.05$ corrected for multiple comparisons. Adapted from data reported in [4]. Supramarginal gyrus SMG. Superior temporal sulcus/gyrus STS/G.

included in the study showed significant behavioral improvement over the course of training. The results indicate a considerable enhancement in activity thought to reflect changes in the manner in which these areas of the brain process the English phonemes /r/ and /l/ after relative to before training. Brain regions showing enhancement in activity include areas typically thought to be involved with speech processing, both perception and production (superior temporal sulcus/gyrus STS/G, supramarginal gyrus SMG, and Broca's area). It is also interesting to point out that many subcortical areas also show enhancement in activity after relative to before training. These areas include the basal ganglia and the cerebellum. Both of these areas have been implicated with feedback-based learning.

There is considerable evidence [5] suggesting that the cerebellum is involved with higher cognitive processes as well as with perception and motor control. The cerebellum is known to have reciprocal connections with the areas found to show enhancement in activity after /r-l/ training including the STS/G, SMG, and Broca's area [6]. The cerebellum is thought to be involved with the instantiation of both forward and inverse internal models that map between perceptual and motor representations [7]. It is possible that during acquisition of a difficult second-language phonetic contrast the cerebellum may be implicated with instantiation of auditory-articulatory mappings ('internal models') concerned with facilitating phoneme identification performance by allowing perception to be made in reference to potential action. It is hypothesized that the formation of auditory-articulatory mappings will be reflected by enhanced functional connectivity between the cerebellum and areas of the brain involved with speech perception and production. The purpose of this study is to determine changes in the pattern of cerebro-cerebellar functional connectivity related to acquisition of the English /r-l/ phonetic contrast by native Japanese speakers. Also of interest are patterns of cerebro-cerebellar functional connectivity that are present both before and after training.

2. METHODS

Functional connectivity between the cerebellum and the rest of the brain was determined by multivariate analysis of the respective patterns of covariance across brain imaging scans. The first step utilized independent component analysis ICA to determine the pattern across scans separately in the left and right cerebellum. ICA is able to maximally separate the fMRI data into component maps (spatial distribution of voxel values) and their associated time course of activation [8]. The coordinates of the Voxels included in the analysis consisted of those in the right and left cerebellum that were found to be active after training relative to the control condition as assessed by a statistical parametric analysis (SPM99b, Wellcome Department of Cognitive Neurology, University College - London) and reported in [4]. The pattern of scans in the experiment consisted of four control scans (during which signal correlated noise stimuli were presented) followed by four experimental scans (during which /r/ and /l/ minimal word pairs were presented). This pattern was repeated eight times for a total of 32 scans per condition. The normalized scans from both the before and after training sessions were included for each of the nine subjects, for a total of 1152 scans. The resolution of the scans included in the analysis was 2x2x2mm smoothed with an 8 mm FWHM Gaussian kernel and normalized to a standard brain. ICA [9] was conducted separately for the 5430 voxels in the left cerebellum and the 5613 voxels in the right cerebellum. Principle component analysis reduction was used to constrain the number of independent components to 32.

The next step consists of determining the independent components that show a significant pattern of activity

across scans relating to the contrasts of interest. The contrasts of interest in this study include: 1) (before training: experimental > control) as well as (after training: experimental > control) coding for activity greater for experimental than control both before and after training; and 2) (after training: experimental – control) > (before training: experimental – control) coding for activity greater after relative to before training taking into account the control condition. Independent components significantly related to the contrasts of interest are then used to determine the functional connectivity with the rest of the brain using "seed-voxel partial least-squares PLS" [10]. In this case, instead of using the pattern of activity from a single voxel as the seed, the pattern of activity of the independent component is used as the seed. It is maintained that selection of the activity pattern by ICA is more valid than arbitrarily selecting the voxel (which may or may not be characteristic of the neighboring voxels in the region) with the highest correspondence to the contrast of interest. An additional advantage of ICA is that it provides for a spatial projection onto the brain so that one can assess the localized pattern of activity. The coordinates of the brain voxels included in the analysis consisted of those in the entire brain (excluding voxels from the right or left cerebellum depending on the independent component being used as a seed) that were found to be active after training relative to the control condition and reported in [4]. There were 22902 voxels in maps excluding the right cerebellum and 23085 voxels in maps excluding the left cerebellum. "Seed-voxel PLS" was used to determine covariation patterns (latent variables) between the cerebellar independent component of interest and the rest of the brain. This technique involves determining the correlation pattern of the seed and the 128 scans for the 9 subjects and then subjecting the resulting matrix to PLS at the level of the entire image (1152x22902 excluding right cerebellum and 1152x23085 excluding left cerebellum). Permutation tests [11] were used to assess the inferential significance of a latent variable and bootstrap estimation of standard errors was used to assess the reliability of the voxel weights within the latent variable. "Seed-voxel PLS" was conducted using a Matlab toolbox developed by A. R. McIntosh.

3. RESULTS

The results of the ICA identified patterns of activity across scans related to the contrasts of interest. A single component was found in the right cerebellum that significantly related to the contrast coding for activity greater for experimental than control both before and after training (before: $T(8)=2.3$, $P<0.05$; after: $T(8)=3.2$, $P<0.05$; random effects analysis). The "seed-voxel PLS" analysis revealed two latent variables whose scores significantly related to the independent component of interest ($T(8)=2.6$, $P<0.05$; and $T(8)=2.9$, $P<0.5$) and were found to be reliable by permutation test (permutation $P<0.005$). The projected weights of the latent variables on to the brain assessed to be reliable by bootstrap estimation (weights to standard error

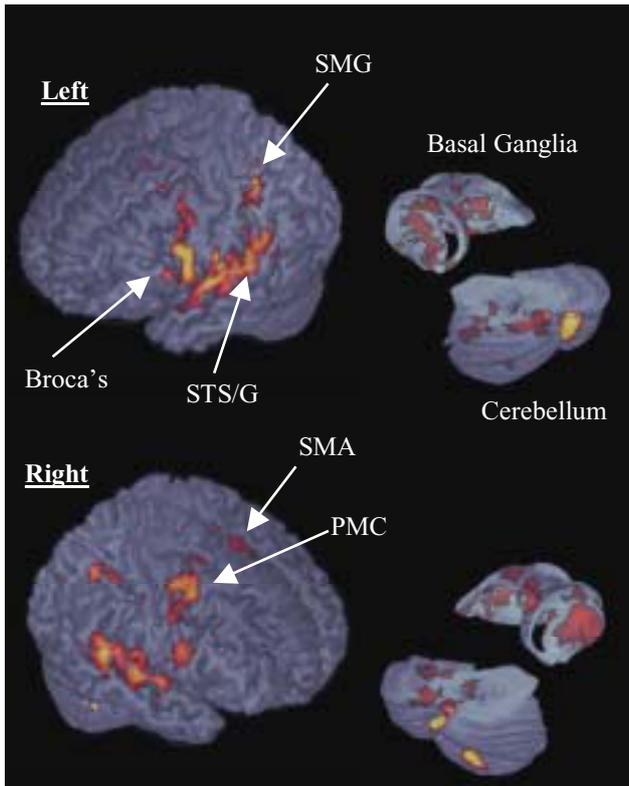


Figure 2. Latent variable showing significant covariance pattern in left and right speech processing regions with the right cerebellar independent component. The independent component coded activity that was significantly greater for experimental than control both before and after training. Supramarginal gyrus SMG, superior temporal sulcus/gyrus STS/G, premotor cortex PMC, supplementary motor area SMA.

ratio > 2) as well as the standardized ($Z > 1.645$) projected independent component pattern of the right cerebellum are shown in figures 2 and 3 for the two latent variables respectively. It can be seen in figure 2 that this latent variable shows covariance patterns with the right cerebellar independent component in both left and right speech processing regions as well as the basal ganglia. Figure 3 shows a covariance pattern for the latent variable in left SMG with the right cerebellar independent component. A single component was found in the left cerebellum that significantly related to the contrast coding for greater activity after relative to before training taking into account the control condition ($T(8)=2.5$, $P < 0.05$). This component also showed significantly greater activity for experimental than control for after training only ($T(8)=2.4$, $P < 0.05$). The “seed-voxel PLS” analysis revealed one latent variable whose scores significantly related to the component of interest ($T(8)=3.3$, $P < 0.05$) and was found to be reliable by permutation test (permutation $P < 0.005$). The projected weights of the latent variable on to the brain assessed to be reliable by bootstrap estimation as well as the standardized projected independent component pattern of the left cerebellum are shown in figure 4. It can be seen that this latent variable has a covariance pattern in both left and right speech processing regions as well as the basal ganglia with the left cerebellar independent component.

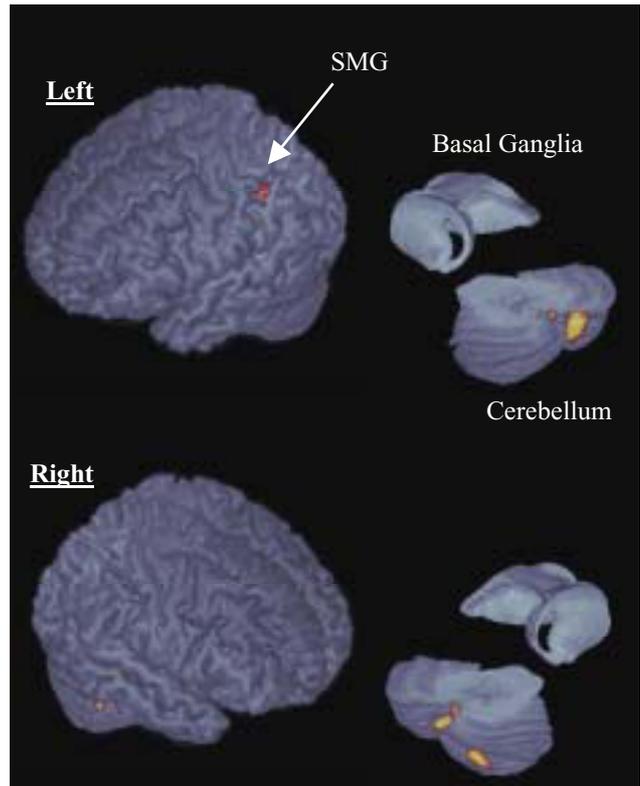


Figure 3. Latent variable showing significant covariance pattern in left SMG with the right cerebellar independent component. The independent component coded activity that was significantly greater for experimental than control both before and after training. Supramarginal gyrus SMG.

4. CONCLUSIONS

The results of the “seed-voxel PLS” analysis revealed that there are significant task related patterns of functional connectivity between the cerebellum and speech processing regions of the brain. The ICA identified activity in the right cerebellum that was significant both before and after training as well as activity in the left cerebellum that was greater after relative to before training. Given the crossed pattern of connectivity from the cerebellum to the cortex this finding is interesting in that activity in the right cerebellum, that projects predominantly to the left language dominant cortex, was significant both before and after training, suggesting that this activity may represent general processes for second-language phonetic identification of /r/ and /l/ that are maintained during training. Conversely, activity greater after than before training was identified with an independent component in the left cerebellum. This activity may represent the emergence of processes acquired as a result of learning the /r-l/ phonetic contrast.

The covariance patterns shown in figures 2 and 3 between the right cerebellum and the rest of the brain are thought to reflect functional networks relevant to second language /r-l/ phonetic identification that are present both before and after training. The functional network depicted in figure 2 includes both left and right regions of the cortex related to

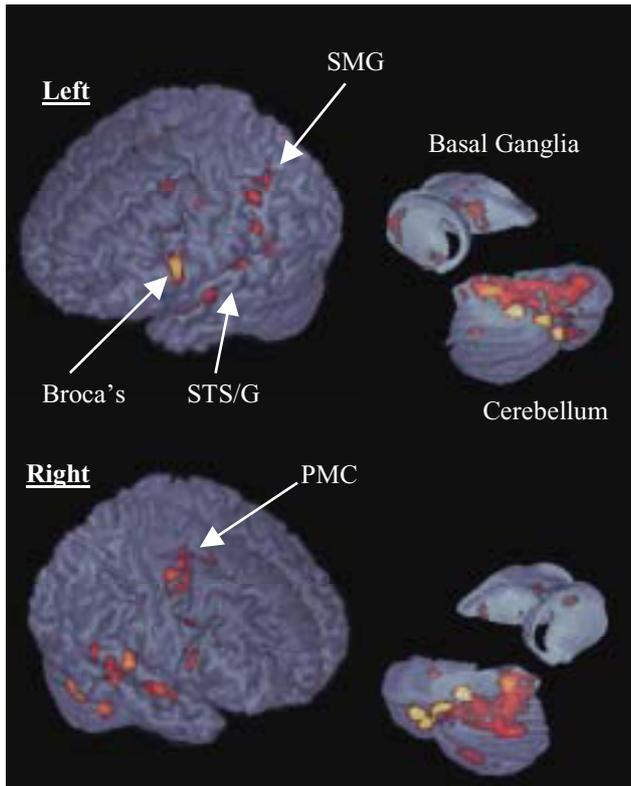


Figure 4. Latent variable showing significant covariance pattern in left and right speech processing regions with the right cerebellar independent component. The independent component coding for activity greater after relative to before training taking into account the control condition. Superior temporal sulcus/gyrus STS/G, supramarginal gyrus SMG, premotor cortex PMC.

speech processing as well as the basal ganglia and left cerebellum. This pattern of connectivity is consistent with findings [4] suggesting that second-language processing includes more bilateral activity than native language processing (considered left hemisphere dominant). The functional network depicted in figure 3 shows a crossed pattern between the right cerebellum and the left SMG. This is interesting in that the SMG is thought to be concerned with establishment of auditory-articulatory mapping involved with speech production acquisition as well as phonological working memory [12].

The covariance pattern shown in figure 4 between the left cerebellum and the rest of the brain is thought to reflect a functional network acquired as a result of learning the /r-l/ phonetic contrast. Similar to figure 2, the functional network depicted in figure 4 includes both left and right regions of the cortex related to speech processing as well as the basal ganglia and right cerebellum. This pattern of functional connectivity is consistent with the hypothesis that the cerebellum may acquire internal forward and inverse models that reciprocally map between auditory and articulatory speech representations that can be used to constrain phoneme selection to facilitate perception.

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