REVIEW

Predispositions and Plasticity in Music and Speech Learning: Neural Correlates and Implications

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Speech and music are remarkable aspects of human cognition and sensory-motor processing. Cognitive neuroscience has focused on them to understand how brain function and structure are modified by learning. Recent evidence indicates that individual differences in anatomical and functional properties of the neural architecture also affect learning and performance in these domains. Here, neuroimaging findings are reviewed that reiterate evidence of experience-dependent brain plasticity, but also point to the predictive validity of such data in relation to new learning in speech and music domains. Indices of neural sensitivity to certain stimulus features have been shown to predict individual rates of learning; individual network properties of brain activity are especially relevant in this regard, as they may reflect anatomical connectivity. Similarly, numerous studies have shown that anatomical features of auditory cortex and other structures, and their anatomical connectivity, are predictive of new sensory-motor learning ability. Implications of this growing body of literature are discussed.

The nervous system's remarkable capacity to learn has been a central concern of neuroscience since its origins. Manifestations of change, plasticity, or adaptation to environmental signals can be discerned at every level of analysis, from molecular to synaptic, to systems, to cognitive. What makes the problem intriguing is that changes in the nervous system must occur for an organism to optimize its behavior in relation to its environment; but the initial state of the nervous system when it is exposed to the learning situation is not identical for all individuals.

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Here, I consider this problem in the context of cognitive neuroscience of auditory-motor learning. Speech and music constitute the two most complex and characteristically human auditory-motor functions . These domains are interesting to compare (*1*) because they share some important similarities, while differing in critical ways as well. Recent advances in cognitive neuroscience have resulted in several related models of the interactions between auditory and motor systems that underlie performance and learning in both speech (*2*–*4*) and music (*5*–*7*). Furthermore, there are interesting individual differences in people's music and speech learning skills, whose neural correlates have recently begun to be investigated more. It is by now quite well established that various kinds of auditory-motor learning situations will engender changes in brain activity and also anatomical configuration; but the premise that I will defend is that there may also be important predisposing factors that influence the outcome of learning in both music and speech domains and that these factors can be discerned in terms of brain function and structure with neuroimaging techniques.

Functional Brain Activation Patterns Relevant to Learning: Effects and Causes

The pattern of changes in hemodynamic brain activity associated with learning is quite complex and includes both activity increases and decreases in various sensory and associative cortical

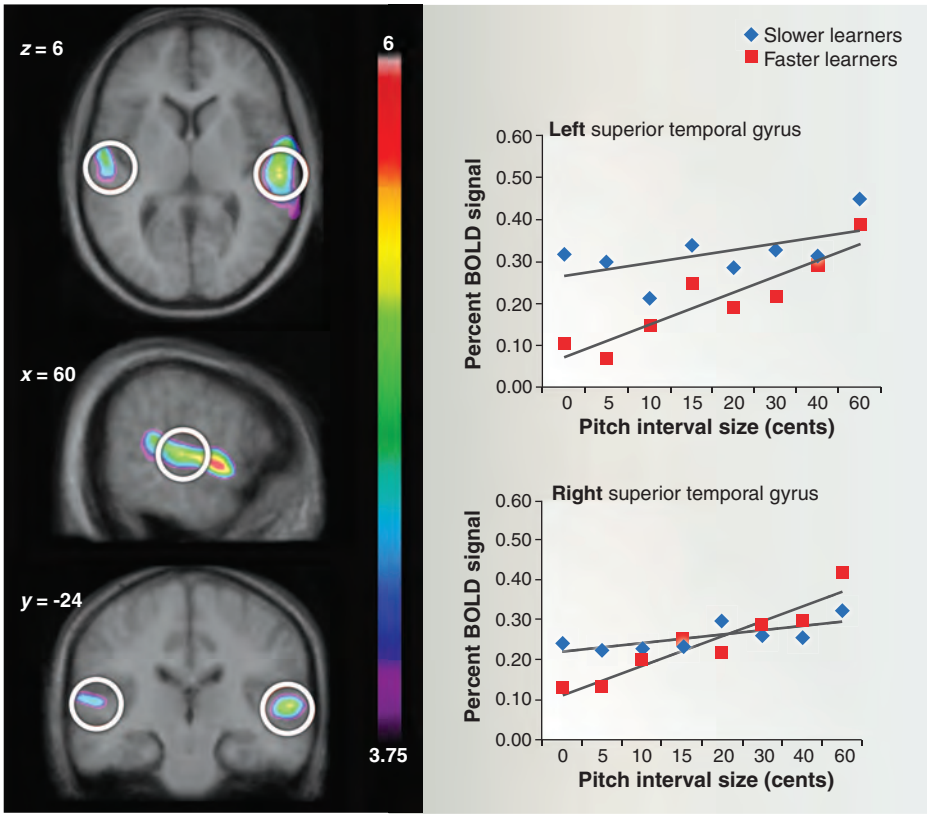

Fig. 1. Relationship between speed of learning in a microtonal pitch discrimination task and fMRI activity before start of training. The figure demonstrates that those who learned more quickly showed better initial encoding of pitch differences. (**Left panel**) fMRI data showing blood oxygen level–dependent (BOLD) activity increases as a function of increasing pitch-interval size in left and right auditory cortices. (**Right panels**) Function relating BOLD signal to increasing pitch-interval size, divided according to two subgroups of faster and slower learners; fMRI data were extracted from symmetrical left and right auditory cortical sites (white circles in left panel) on the basis of the pretraining data alone, independently of later group classification. Those individuals who subsequently showed more rapid pitch discrimination learning (red squares) had significantly higher slopes of this function than those who subsequently learned more slowly (blue diamonds), indicating an enhancement of pitch encoding in auditory cortex of faster compared to slower learners. [Adapted with permission from (*26*)]

regions, depending on the nature of the learning (*8*, *9*). Cross-sectional studies of musical training have shown that electrical and magnetic responses from auditory cortex are enhanced as a function of appropriate training (*10*–*12*). Electrical measures of brainstem responses have also shown enhanced fidelity of frequency encoding in musically trained individuals (*13*–*15*). A persistent question in these studies is whether such effects can be causally attributed to the training. In other words, because musical training is to some extent self-selected, it may be that those who seek out the training have some propensity. One argument in favor of experience-dependent effects is that the magnitude of the change is typically correlated with the age of commencement (*10*, *13*), suggesting a causal relationship. Stronger evidence for causality comes from longitudinal studies, which have demonstrated that after training, both in children (*16*) and in adults (*17*), there are clear changes in auditory cortical evoked responses and in the brainstem (*18*); however, these findings do not logically exclude the possibility that predispositions may also exist and interact with training.

The interpretation of an enhanced response originating in auditory cortex among musicians seems straightforward because musicians' training in an auditory domain presumably leads to more robust or higher-quality neural representations, which in turn are reflected in the evoked responses. Functional magnetic resonance imaging (fMRI) studies, however, show that in response to various musical task manipulations, musical training can also manifest itself in a variety of ways in extra-auditory regions, especially frontal and parietal areas (*19*–*23*). This heterogeneity may be related to many factors, especially as musical training itself is not unitary and the tasks used in the various studies probe many distinct cognitive abilities. But the outcome of training could also differ if individuals have different profiles before they begin learning. A few fMRI studies on auditory learning of tonal patterns using a longitudinal design have in fact noted the presence of subgroups who learn well or rapidly, versus those who learn poorly or slowly (*24*, *25*), but the origin of these differences is unknown.

These individual differences raise the question of how preexisting brain activity patterns might be relevant to explain the heterogeneous outcome of learning-related brain activity changes. We examined this factor using a task in which listeners had to learn, over a 2-week period, to distinguish tonal patterns using microtonal pitch intervals (i.e., much smaller than commonly used in musical scales) (*26*). Auditory cortices respond parametrically to increasing pitch-interval size (*27*), allowing the slope of the function relating activity to pitch change to serve as an index of cortical sensitivity to pitch processing. Learning was globally associated with a decrease in the magnitude of this function, which is consistent with a number of observations in other sensory domains (*8*) and can be understood in terms of fewer neural units being required for sensory encoding (*28*). But of greater relevance is that some individuals demonstrated very rapid learning, within the first day of training, whereas others showed much more gradual learning. When we examined the pitch-activation functions collected before the start of training, we discovered that those who subsequently went on to learn quickly initially had significantly steeper functions than those whose later learning was slower (Fig. 1). Thus, the faster learners could be thought of as having a finer-grained encoding of pitch information in auditory cortex, which in turn allowed them to learn more quickly.

These findings in the music domain are mirrored to some extent in the speech domain. Behaviorally, it is well known that certain speech contrasts are difficult to learn in adulthood if they are not part of one's native phonetic repertoire; however, certain people are better able to learn these features than others (*29*, *30*). Explicit training with novel speech contrasts of this sort has been shown to enhance evoked electrical or magnetic responses from auditory cortices (*31*, *32*). fMRI studies involving learning of these speech sounds also show effects comparable to those using musical training, to the extent that they show changes to auditory cortical responses as a function of learning, while others also implicate

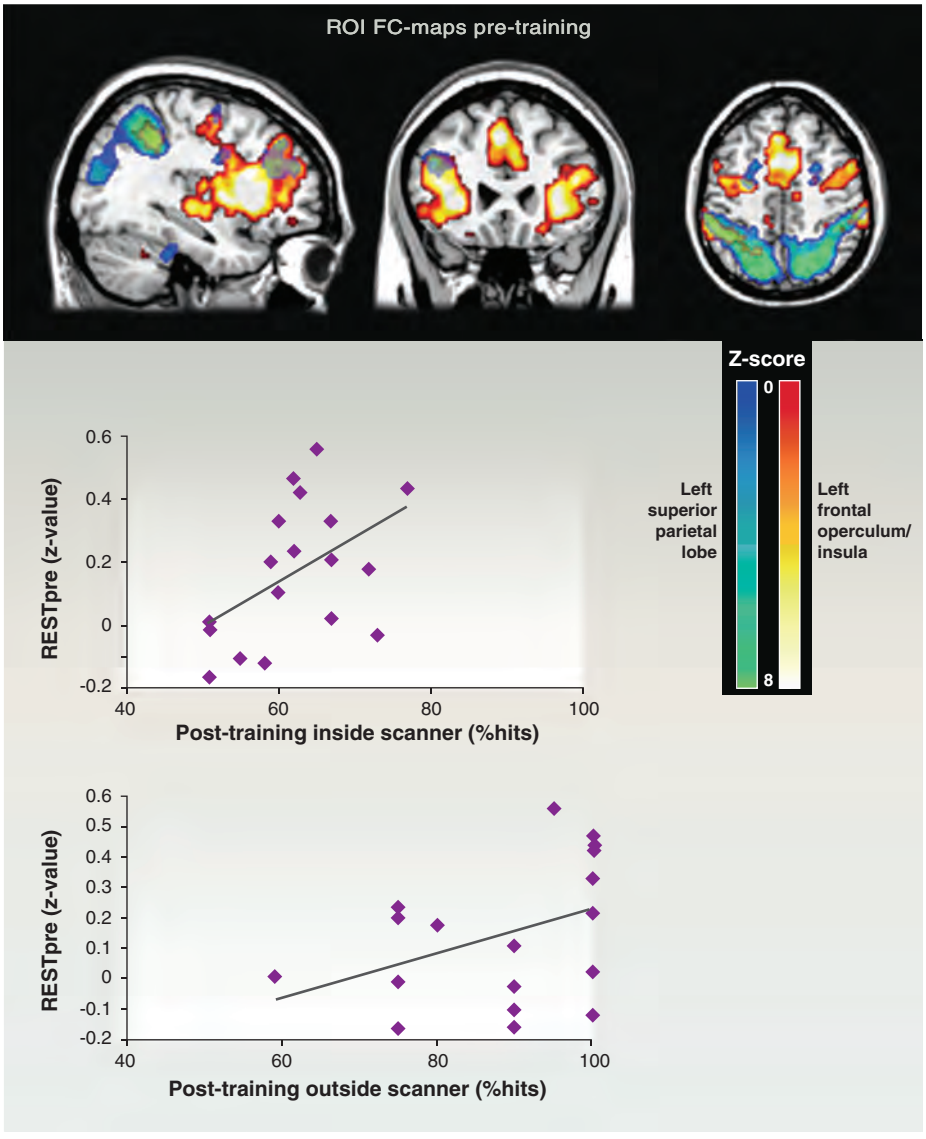

Fig. 2. Networks of resting-state fMRI activity and their relation to speech learning success. (**Top**) Temporal correlations in BOLD signal determine functional connectivity (FC) maps based on seed areas in the left frontal operculum/insula (red–orange bar) and the left superior parietal lobe (blue–green bar) before training. ROI, region of interest. (**Bottom**) Pretraining resting-state functional connectivity between the frontal and parietal regions was significantly correlated with subsequent speech-task identification performance for each individual, measured both inside and outside the scanner. [Adapted with permission from (*37*)]

nonsensory cortical areas, including especially classical language zones such as inferior frontal cortex and supramarginal gyrus (*33*–*35*).

Some intriguing predictive factors have recently been detected in functional properties of these neural systems. Paralleling some of the music-related findings, people who subsequently learn a linguistic pitch contour more quickly have a higher auditory cortical response at the outset than those who go on to learn less well (*36*). Resting-state connectivity networks may also serve as indicators of subsequent speech learning success (*37*). This fMRI measure has received much attention because it captures spontaneous fluctuations in brain activity that characterize the natural interactions across cortical regions, and that in turn form cognitively relevant networks (*38*). Those individuals who were better able to learn a nonnative speech contrast showed higher levels of functional connectivity between key components of a language-relevant network, especially inferior frontal and parietal nodes, compared to those who subsequently demonstrated poorer learning (Fig. 2). This effect was seen both in shorter- and longer-term training (*37*). This and other similar studies—for example, in the visual domain (*39*)—provide interesting information in terms of putative mechanisms underlying individual differences in learning potential. Specifically, one interpretation of the findings is that the spontaneous fluctuations between these regions might reflect variability in anatomical connectivity, a topic to which we now turn.

Anatomical Features Relevant to Learning: Effects and Causes

The development of whole-brain MRI-based anatomical measurement techniques, such as voxel-based morphometry, cortical thickness, and diffusion imaging, has spurred research showing that brain anatomy can change noticeably as a function of learning. The microstructural features that underlie effects visible to MRI are multifaceted, and so far largely unconfirmed, but likely include alterations in vascularization, synaptogenesis, and glial cells, as well as myelination and axonal sprouting, among others (*40*). Cross-sectional studies of musicians consistently show changes in auditory and motor cortical regions in gray-matter volume (*12*), concentration (*41*), and cortical thickness (*42*), and in the organization of related white-matter pathways (*43*, *44*), implying that musical training can effect changes at the anatomical level. Network analysis of cortical thickness correlation patterns also suggests a more focused organization between auditory cortical and inferior frontal cortex (*42*), a critical network for many aspects of auditory processing, particularly working memory.

The observation that certain anatomical features differ across groups of people who differ in their training or other background is useful but insufficient by itself to demonstrate that the feature is relevant to the training or that it is caused by the training. To address the first issue, it is necessary to show a relationship to a relevant behavior, which several studies have done. Gray-matter features in auditory cortex are predictive of task performance on certain pitch tasks (*12*, *45*), such that better performance is associated with greater gray-matter concentration or thickness in a pitch-sensitive region of auditory cortex. To address the second issue, some studies have shown that degree of anatomical change is related to amount of training (*43*, *45*) or to age of commencement (*44*), implying that experience is the cause of the change. However, this may not be the only factor at play because the relationship between anatomical features and behavior persists even after accounting for amount of training (*45*) and also exists in groups of people without training (*12*), suggesting that some individual differences are due to other factors, including perhaps predispositions.

Convincing evidence in favor of experience-dependent plasticity comes from longitudinal studies, which have shown changes in cortical morphology in both auditory and motor regions among children who received musical training (*46*); these anatomical effects were directly linked to improved performance because the degree of change correlated with behavioral measures. Similarly, in the speech domain there have been demonstrations that brain morphology is related to linguistic experience. Thus, differences in structural measures have been noted in auditory cortices in bilingual individuals (*47*) and also in simultaneous interpreters (*48*). As with the functional studies, however, such effects cannot be unambiguously attributed exclusively to training. Indeed, in the interpreters study, the difference observed was in the gyrification of auditory cortical regions, which is thought to mature early in development (*49*), raising the possibility that there may be some degree of predisposition involved.

To test specifically for the existence of anatomical predispositions, several studies have examined individual differences in learning novel speech-sound features. Anatomical MRI scans obtained before training show that white-matter features in left temporoparietal regions (*50*) and in left auditory cortex (*51*) are associated with faster learning (Fig. 3). These relationships were specific to speech learning, as they were not predictive of learning nonspeech sounds in control conditions. Related findings were provided in two studies examining how well individual listeners

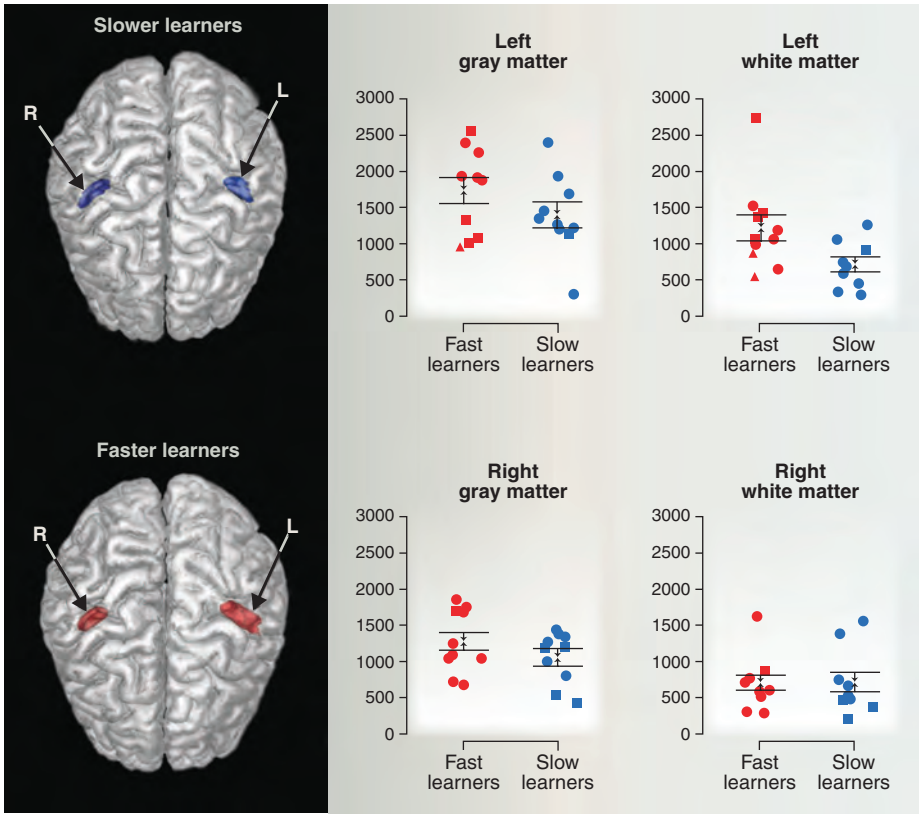

Fig. 3. Auditory cortex volume and its relation to speech perception learning ability. (Left panel) Renderings (view of brain from the top) of mean Heschl's gyrus volumes among individuals whose speed of learning to discriminate a foreign speech sound was relatively faster (red) or slower (blue). Note the relative size difference in the left Heschl's gyrus. **(Right panel)** Mean volume measures of segmented white and gray matter of Heschl's gyrus for faster and slower learners showing that the difference emerges primarily from the white matter on the left side. [Adapted with permission from (*51*)]

could learn to assign meaning to pseudowords that differed on the basis of acoustical features resembling those of a tone language. Those individuals who subsequently were better able to learn the words had larger volume of left auditory cortex (*52*), as well as enhanced white-matter organization in the left temporoparietal area (*53*). White-matter organization in left inferior frontal regions is also predictive of the ability to articulate speech sounds from a foreign language (*54*) and is associated with enhanced performance in an artificial grammar task (*55*).

Evidence is also mounting that the anatomical connectivity between specific cortical regions is a determinant of performance. Individual variability in white-matter organization of fiber tracts connecting frontal and temporal areas of the left hemisphere is associated with better learning of phoneme segmentation in an artificial language speech stream (*56*) (Fig. 4). This relationship is behaviorally specific, such that when rehearsal is blocked, a more ventral anatomical pathway correlates with learning, presumably reflecting access to an alternate route when the dorsal one is not accessible (*57*). The studies discussed in this section thus converge in demonstrating that interindividual variability in the distribution of various anatomical features is specifically predictive of subsequent performance or learning success. These relationships are relatively specific in that different components of the language network are dissociable in terms of their contributions to speech perception versus production, for instance.

Questions, Future Directions, and Implications

Variation is an essential feature of all biological populations; as Darwin observed, without it, selection and hence evolution would not be possible. In cognitive neuroscience, the nature and meaning of individual variability have begun to receive more attention (*58*, *59*). The related idea of neural predispositions for learning now appears to have sufficient empirical support to warrant concerted attention. The parallels that exist in the literature between structure and function, and

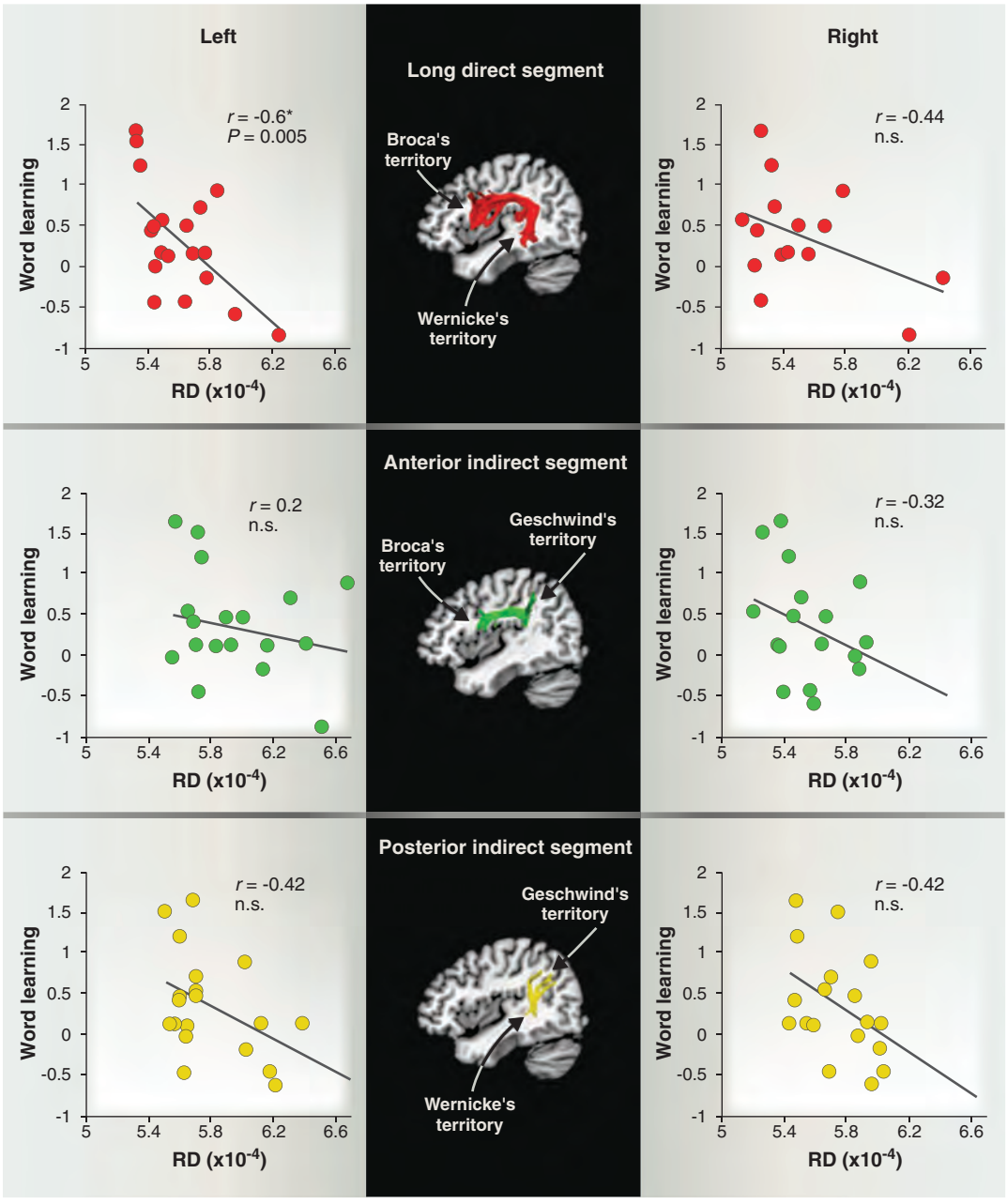

Fig. 4. Relation between individual ability to learn to segment new words from a speech stream and microstructure of the arcuate fasciculus. The latter is a fiber tract linking temporal cortex (Wernicke's territory) and inferior frontal cortex (Broca's territory), as well as premotor cortex. Each scatterplot represents individual word learning scores, expressed by d-prime measures, and the radial diffusivity (RD), a measure of white-matter structure. This anatomical feature is significantly predictive of word learning for the direct segment of the arcuate fasciculus (shown in red in top panel) in the left hemisphere. Indirect connections (middle and bottom panels) do not show a significant relationship. [Adapted with permission from (*56*)]

across domains, serve to motivate this question further. This brief review has provided a glimpse of how the concept may play out in two related domains, speech and music, which can serve as excellent model systems and which could profitably be studied in parallel to a greater extent. Many important questions remain that apply more generally beyond these domains. One obvious one is to identify the source of the individual differences, which in turn leads us to consider the interactions between genetic and epigenetic mechanisms with environmental factors, including the social environment. How these interactions play out with respect to ongoing maturational changes in the nervous system make the question all the more interesting, especially as sensitive periods have been described for both linguistic (*60*) and musical (*61*) functions. Another pertinent question is the extent to which individual differences are dissociable from one another; that is, do predispositions that favor one type of learning come at the expense of other abilities, or do they tend to be correlated? The evidence to date tends to indicate dissociations, but if we can identify the many separate predisposing factors that no doubt exist, we may also find that some of them cluster together. It also remains unclear whether predispositions for learning pertain to ultimate attainment potential, or merely speed of learning; the experimental evidence reviewed above suggests that both situations arise, and it is therefore important to not lump them together. An additional question is the extent to which the kinds of predispositions we have discussed represent traits or states; that is, are they stable over time, or do they reflect transient properties of a dynamically changing nervous system? Although much of the evidence seems to deal with the findings in terms of stable traits, given the evidence for experience dependency, it is also reasonable to assume that predispositions may themselves be affected by, or even be the consequence of, ongoing functional and structural changes.

The evidence reviewed here indicates that functional and structural properties of auditory and motor systems, and their interactions, can be construed as predictors of behavioral skill and learning in speech and music. But we do not yet fully understand the relationship between the functional and anatomical effects that are discussed above; nor is it clear how cortical and subcortical systems interact. Continued advances in neuroimaging will help us to understand what neural mechanisms underlie the phenomena under discussion. For example, variance in brain activity (*62*) may be a relevant indicator of the degree to which an individual nervous system can adapt to new circumstances and hence could help to explain individual proclivities. Similarly, pattern-analysis techniques are increasingly being applied to understand variability in neural activity (*63*) and could help to identify individual differences as well. Increasingly, both brain structure and function are being modeled as complex networks (*64*), and the organization of these networks will no doubt also shed light on the kinds of effects we are discussing here. The human connectome project (www.humanconnectomeproject.org/) will be of importance in this respect, particularly as genomic, phenomic, and cognitive information is added in to help understand variation.

Ultimately, the implications and applications of this knowledge will certainly lead to beneficial outcomes, but may also raise ethical questions. It may seem far-fetched to suppose that some neural measure could in the future be used to decide if someone should benefit from a certain learning opportunity, but we should prepare to ward off inappropriate uses of knowledge with appropriate discussion. On an optimistic note, I would hope that any kind of knowledge that could make predictions about outcomes would be immensely useful—in a rehabilitation or a pedagogical setting, for instance—in identifying the optimal type of training regime that might be most beneficial to a given individual. To the extent that different individuals have different perceptual, motor, or cognitive strengths and weaknesses, our ability to identify them and their neural bases should help to provide the right kind of training or remediation. Sensorymotor skills are essential for communication, so knowing more about how these skills vary across a population will be important clinically. Even knowing something about the speed with which one should expect learning to proceed could be helpful in this regard. We each have a unique brain, without which the world would be a very boring place indeed. It will be up to us to use our increasing knowledge of this uniqueness in productive ways.

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Acknowledgments: I thank all the authors who shared their materials for figures. I acknowledge support from the Canadian Institutes of Health Research, the Natural Sciences and Engineering Research Council of Canada, the Canada Fund for Innovation, and the Fonds de Recherche Nature et Technologies/Société et Culture via its funding of the Centre for Research in Brain, Language and Music.

10.1126/science.1238414