concepts. The presence of strong anisotropy in the lower crust induced by convergence-parallel shearing implies that there is deformation throughout the crust, as suggested by the thick-skinned model. On the other hand, the evidence for a sharp change in deformation geometry at a depth of ~10 to 15 km shares some aspects of the thin-skinned concept. The authors propose that this transition is not a décollement in the traditional sense, as there is mechanical coupling between the upper and lower crustal layers; however, their model does imply that compressional tectonics is active only in the upper layer.

These results reported by Huang et al. have important implications for our understanding of how the crust deforms in collisional orogens, and may prompt a reexamination of other mountain belts. A key question is whether there is widespread lower crustal anisotropy in other orogens, and whether a transition in deformation style in the mid-crust is a universal feature. The implications of such a sharp transition for our understanding of crustal rheology need to be explored. Another important question is to what extent the mantle lithosphere, in addition to the lower crust, participates in deformation. More generally, the observation and interpretation of crustal anisotropy, both in mountain belts and in other tectonic settings, represents an exciting frontier area, enabled by the increasing availability of data from dense seismic networks and the maturation of observational techniques that rely on the ambient noise field (1, 8) or on the analysis of converted waves (9). Furthermore, new constraints on the relationships between strain and anisotropy in crustal rocks (10, 11) are enhancing our ability to relate seismic observations to deformation geometry, opening the door to the detailed and quantitative testing of hypotheses related to the deformation of Earth's crust. ■

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DEVELOPMENT

Marmoset kids actually listen

Humans and other vertebrates may share a developmental program for vocal learning

By Daniel Margoliash^{1*} and Ofer Tchernichovski²

ndergraduate linguistics courses typically present language as unique to humans. Chomsky and others have postulated a language organ that evolved in hominids. This idea found modest support in the lack of evidence for vocal production learning (imitating sounds) in nonhuman primates. But did language suddenly emerge in the Homo lineage as a "hopeful monster" (1) who could learn new sounds and meanings? Evidence for vocal learning in nonhuman primates is now emerging (2, 3), and in hindsight, looking at vocal production learning as the sole evolutionary precursor of language might have been shortsighted. Similar developmental processes can lead to different end points, and minor modifications of a primitive developmental program can create very different creatures. On page 734 of this issue, Takahashi et al. (4) provide evidence for a developmental process, rather than its endpoint, which reveals a shared developmental program for animal communication and human language. This indicates an ancestral developmental program that is shared not only between humans and other primates but also across mammals and birds.

Vocal imitation was long thought to be common in birds but rare in mammals. In the past few decades, scientists have reported evidence for vocal production learning in marine mammals, bats, elephants, and primates (2). It is difficult to work with large mammals that breed slowly and require social interactions for normal development, which precludes their being reared in isolation. These difficulties are particularly acute for primate research. Nevertheless, recent results from field studies and in captivity demonstrate shared, learned group signatures in communication calls produced by monkeys and apes. For example, when two troops of adult chimpanzees were integrated in a zoo-an event that is improbable in nature-the referential food grunts of introduced members apparently

¹Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA. ²Department of Psychology, Hunter College, City University of New York, New York, NY 10065, USA.*E-mail: dan@bigbird.uchicago.edu changed to match those of the home territory group (3).

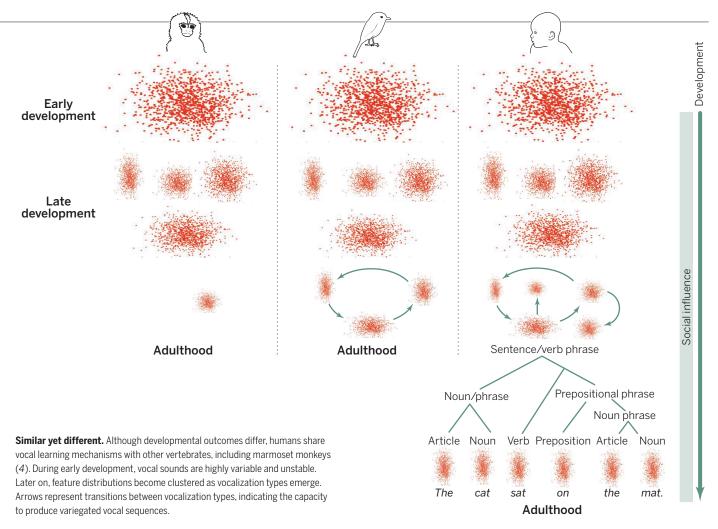
Given that there may be no evolutionary canyon separating human vocal learning from that of other primates, one can attempt to compare vocal development across species that vary strongly in their end points. Takahashi *et al.* did just that. They thoroughly investigated vocal development in common marmosets (*Callithrix jacchus*), tiny social primates that produce a limited number of call types. In captivity, their calls are dominated by whistlelike calls (phees). The authors report rapid changes in vocal devel-

"... Takahashi et al.'s findings point to an ancient substrate for vocal learning that an evolving large hominid brain could take advantage of ..."

opment driven by social (parent-infant) interactions. These vocal changes are similar to those previously described in human infants (5) and songbirds (6).

Takahashi et al. studied marmoset infants for 2 months from birth. By the end of this period, the juveniles were producing adultlike calls. Using a design that allowed dense sampling of thousands of vocalizations, the authors analyzed developmental changes in acoustic features previously shown to be useful for characterizing birdsong development. They observed significant vocal changes during development (see the figure). Early on, vocalizations were highly variable. Later, acoustic features of calls became clustered, indicating the emergence of ethologically meaningful call types. The numbers of clusters then declined, resulting in part from the transformation of immature call types into mature versions of phees.

To model the marmoset vocalizations, the authors used a nonlinear dynamical systems model of the vocal tract based on shared physical properties of vocal production in birds and mammals (7). Different calls occupied different regions of model parameters, which suggested that the changes are not ac-



counted for by growth alone. The biophysical model coupled with electromyographic measures of respiratory effort show that the marmoset infant cries, subharmonic phees, and mature phees are developmentally related. Infant cries arise from low respiratory pressure and laryngeal muscle tension. In contrast, adult phees are characterized by high pressure and tension. Interestingly, subharmonic phees occupy an intermediate regime.

These extensive analyses set the stage to address the critical question: Can infant-parent interactions help to explain the developmental trajectory of marmoset vocalizations? Takahashi et al. observed that infants rapidly transitioned to producing more adult than infant vocalizations. The timing of that transition varied considerably across individuals and was strongly correlated with the number of parental responses that each infant experienced.

How can we relate these behavioral results to an evolutionary process? Perhaps, just as evolution can be understood as a modification of a developmental program, we could think about vocal learning as a modification of a program for vocal development. The early stages of vocal development are remarkably similar across taxa (see the figure). The infant produces highly diverse but loosely structured vocalizations, a cloud of sounds from which distinct clusters gradually emerge. This indicates a transition from a continuous, graded signal to a weakly symbolic vocal performance. Call types then undergo further differentiation and selective attrition. A process for combinatorial capacity emerges.

The relative intensities of these processes vary across species. In the marmoset, there is modest attrition and differentiation of calls and little combinatorial capacity. In zebra finches, attrition and differentiation of syllable (learned-call) types are fairly balanced, which results in several syllable types and a moderate combinatorial capacity. In human infants, the differentiation of vocal types and combinatorial abilities are both extensive and prolonged and eventually lead to spoken language. From the perspective of neurobiology, the brainstemmidbrain systems for call production are common in vertebrates (8). Species-specific differentiation of vocal behavior might have evolved through gradual increase in the interactions between those primitive brain structures and the forebrain, driving species-specific variability in symbolic and combinatorial processes.

It has long been known that monkeys can learn during development to associate different vocalizations with different meanings (9). Takahashi et al. show that contingent social feedback also shapes the transition to adult vocal patterns, adding to the vocal learning processes that likely preceded the emergence of language. A single explanation for the complex factors influencing changes in vocal developmental patterns over evolutionary time is unlikely to emerge. However, Takahashi et al.'s findings point to an ancient substrate for vocal learning that an evolving large hominid brain could take advantage of, thus continuing the evolutionary process that has enabled communication in other animals (10). ■

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Daniel Margoliash and Öfer Tchernichovski *Science* **349**, 688 (2015);

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