

Animal Models of Speech and Vocal Communication Deficits Associated With Psychiatric Disorders

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ABSTRACT

Disruptions in speech, language, and vocal communication are hallmarks of several neuropsychiatric disorders, most notably autism spectrum disorders. Historically, the use of animal models to dissect molecular pathways and connect them to behavioral endophenotypes in cognitive disorders has proven to be an effective approach for developing and testing disease-relevant therapeutics. The unique aspects of human language compared with vocal behaviors in other animals make such an approach potentially more challenging. However, the study of vocal learning in species with analogous brain circuits to humans may provide entry points for understanding this human-specific phenotype and diseases. We review animal models of vocal learning and vocal communication and specifically link phenotypes of psychiatric disorders to relevant model systems. Evolutionary constraints in the organization of neural circuits and synaptic plasticity result in similarities in the brain mechanisms for vocal learning and vocal communication. Comparative approaches and careful consideration of the behavioral limitations among different animal models can provide critical avenues for dissecting the molecular pathways underlying cognitive disorders that disrupt speech, language, and vocal communication.

Keywords: Animal models, Autism, Language, Schizophrenia, Speech, Vocal communication

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Speech and language phenotypes are defining hallmarks of several psychiatric disorders, including autism spectrum disorders (ASD) and schizophrenia. The incidence of ASD in the United States is estimated to be 1 in 68 children (1), and ~30%–50% of patients with ASD achieve only a phrase-level command of language (2). The prevalence of schizophrenia is 1% worldwide, and disordered speech is one of three “positive” symptoms of schizophrenia that is diagnostic (3). Specific language impairment affects ~7% of young children (4). This disorder occurs in the absence of other neurodevelopmental symptoms and is limited to general problems with language syntax or phonology or both. Specific language impairment has a genetic component, and there appears to be some convergence of genes involved in specific language impairment and ASD (5). The prevalence of sustained stuttering worldwide is almost 1% (6), similar to schizophrenia, resulting in ~3 million people in the United States exhibiting stuttering. Together, these statistics underscore the importance of understanding the basic brain, molecular, and genetic mechanisms underlying speech and language. Besetting this goal is the availability of animal models that have conserved brain circuitry underlying phenotypes akin to speech.

As we rely on animal models for developing and testing drugs for the treatment of ASD or other psychiatric disorders, it is important to understand the uses and limitations of such models as they pertain to the speech-relevant aspects of these disorders.

In this review, we address the definition of speech and language and how forms of vocal learning in animal models can be appropriated for gaining insights into evolutionarily conserved brain circuits that form the basis for speech learning. We discuss the use of specific species and salient candidate gene models that have provided the most insight into language-related pathways to date. Finally, we consider which available animal models seem most relevant to specific psychiatric disorders.

VOCAL LEARNING: WHAT IS IT AND WHO HAS IT?

The use of vocalizations for signaling and social communication is common among vertebrates, and the structure, complexity, and plasticity associated with vocal behaviors range widely among species (7–12). Most forms of vocal communication involve innate emotive vocalizations (10). Although innate, these vocal behaviors are often context dependent and used to signal specific meanings to the receiver (7,13–15). For example, the purr and hiss of a cat are innate vocalizations produced under different contexts and used to convey very different signals. In contrast to these innate vocalizations, some species learn to produce complex vocalizations through imitation (9,12,13,16). This form of vocal production learning relies on auditory feedback and substantial specialized neural and peripheral motor circuitry that have not evolved in species without vocal learning (11). We distinguish between three forms of vocal learning in

this review (13): 1) production learning, in which animals learn their vocalizations by imitation; 2) usage learning, in which animals learn to use vocalizations in appropriate contexts; and 3) receptive learning, in which receivers learn appropriate behavioral responses to specific vocal signals. Although many species engage in usage and receptive learning, few species have also evolved central and peripheral apparatus for vocal imitation (11). For example, humans are the only primates that learn vocalizations through imitation (8). Vocal imitation is rare in extant mammals and has been identified only in humans, cetaceans (whales, dolphins, and porpoises), elephants, pinnipeds, and bats (11,12,16). In addition to these mammals, of >36 bird lineages, vocal learning has also evolved in three lineages, songbirds, hummingbirds, and parrots, which together comprise >4800 species (11).

How we define language may have implications for whether language is ultimately a uniquely human trait, but there is little argument that human language is a complex referential system of signaling that relies on specialized brain and vocal motor structures that evolved through natural selection. The referential capacity and syntax that define language allow ideas and thoughts to be constructed in an almost infinite number of ways (9,17,18). This magnitude of differential output to convey a matched number of exceedingly large associations, inferences, or meanings sets humans apart from other species. Human language can convey a wide range of information from the practical to the abstract. The output of human language can be in the form of vocal output (speech) or manual output (i.e., sign language or writing/typing). For relevance to psychiatric disorders, we focus strictly on vocal output. In addition, although there are many animals, as mentioned, that exhibit vocal learning, we focus on animals that are likely to be studied in the laboratory for the purposes of understanding psychiatric disorders either at the behavioral or at the neuroanatomic level.

Nonhuman Primates

Investigations into vocal learning in nonhuman primates revealed the extensive usage and receptive learning of vocal

behaviors, but little evidence of vocal imitation (8,11,12,19–22). The cognitive abilities of nonhuman primates, including the potential capacity for vocal learning, have fascinated scientists for decades. Extreme examples of this interest have been the integration of baby chimpanzees into human homes and the teaching of sign language to chimpanzees and gorillas. Although these animals are able to make associations between signs and objects (symbolic reference) and basic syntax, the primates failed to achieve a level of complex syntax indicative of language in all of the cases (23). Marmosets exhibit vocal communication that has a strong social component in that they take turns in calling to one another, reminiscent of the back and forth in conversational speech (24). Some data support the idea that marmosets learn this behavior over time, suggesting that usage-dependent learning may be involved in these vocal signals (25).

Rodents

There are two major types of rodent vocalizations: pup isolation calls and adult social and mating calls. All of these calls are in the ultrasonic range (hence the term ultrasonic vocalizations [USVs]) (26). These USVs have been primarily observed in the laboratory setting in either mice or rats. Pup isolation calls are experimentally elicited by isolating the pup from the dam; although it is still debatable, these calls may be used as a means of social communication between pup and dam (27,28). It is possible that the structure of the pup call may inform the dam as to the state of the pup and direct her retrieval behavior; however, such a correlation between isolation USV structure and behavior has yet to be directly examined. Adult USVs are frequently used to facilitate mating by males, although same-sex USVs also occur in nonaggressive social interactions (29). The structure of USVs changes with development from isolation to adult calls, as more complex calls are produced by adult animals than pups (Figure 1) (30). However, the interpretation of what kind of information these complex calls may be conveying compared with simple calls is currently debated (14,15). Perhaps the most controversial aspect of rodent USVs is whether this form of communication is innate or involves some learning component (14,31,32). Although

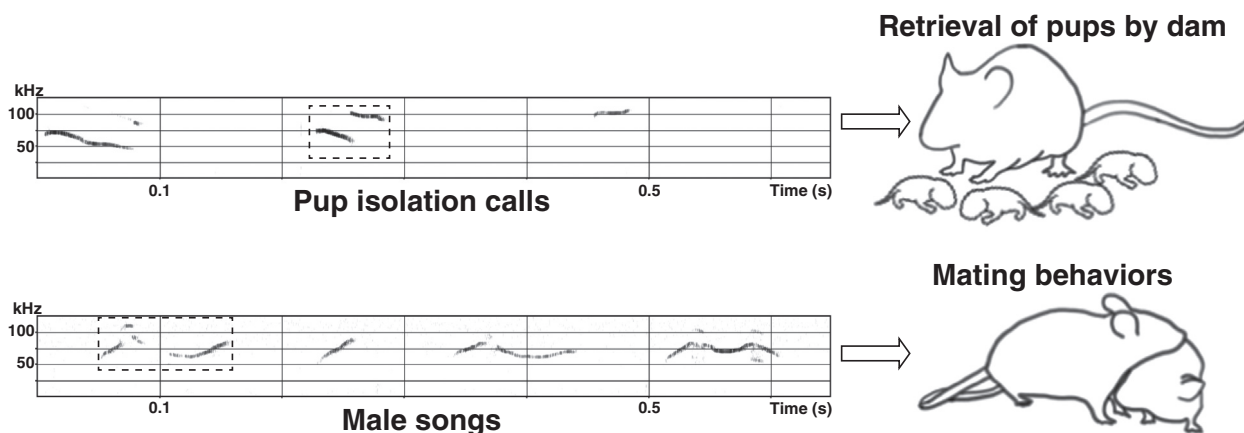


Figure 1. Rodent ultrasonic vocalizations (USVs). (Top panel) Rodents exhibit USVs as pups when isolated from the dam, and these calls assist in retrieval of the pups. (Bottom panel) Adult male rodents emit USVs when attracting a female for mating. Instances when males or females emit USVs in the presence of a rodent of the same sex are not shown. Example sonograms are depicted for each type of behavior. A representative complex call containing a frequency “jump” is boxed in each example. Adult USVs or songs typically have greater numbers of complex calls than seen in pup isolation calls.

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