Marmoset Vocal Communication: Behavior and Neurobiology

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Received 9 June 2016; revised 27 September 2016; accepted 8 October 2016

ABSTRACT: There has been recent increasing interest in the use of marmosets, a New World primate species, as a model in biomedical research. One of the principal advantages of marmosets as a research model is their rich vocal repertoire and communicative vocal behaviors displayed both in the wild and in captivity. Studies of this species' vocal communication system have the potential to reveal the evolutionary underpinnings of human speech, and therefore are of interest to the neuroscience and biology research communities. Here a recent research into the behavioral and neurobiological basis of marmoset vocal communication was reviewed and they argued for their broader value as a neuroscientific model. They discuss potential avenues for future research including developmental neurobiology and the application of modern molecular tools to the study of primate communication. © 2016 Wiley Periodicals, Inc. Develop Neurobiol 77: 286–299, 2017

Keywords: **marmoset; auditory cortex; pre-frontal cortex; vocalization; vocal communication**

INTRODUCTION

Marmosets have recently engendered significant interest as model organisms for neuroscience research. While the benefits of marmosets for implementing molecular approaches for the study of the primate brain have often been noted (Sasaki et al., 2009; Sadakane et al., 2015; MacDougall et al., 2016), their natural social behavior affords numerous opportunities for examining different aspects of primate brain function that have been largely overlooked in studies using other model species (Miller et al., 2016). Recent development of techniques to record neural activity in freely-moving marmosets has allowed scientists to begin exploring the neural basis of primate behavior beyond those conditioned behaviors more typical of past primate neurophysiology research. Coupled with quantitative characterizations of the species' natural vocal behavior and active social signaling paradigms, marmosets represent a potentially powerful model of primate vocal communication and language evolution.

Non-human primate communication has been of long-standing interest to biologists and neuroscientists due to their close phylogenetic relationship with humans and the hope that a better understanding will reveal important information about the evolutionary and physiological basis of human speech. Past efforts to understand the neural basis of primate communication have typically been limited to studies in which head-restrained animals are presented with static social stimuli (e.g., faces, vocalizations, etc.). Communication, however, is an inherently dynamic and interactive process involving the exchange of signals between conspecifics, and the social context in which signals are produced can have a profound effect on

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The authors have no conflicts of interest to disclose.

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Published online 14 October 2016 in Wiley Online Library (wileyonlinelibrary.com).

DOI 10.1002/dneu.22464

what is communicated (Engh et al., 2006; Seyfarth and Cheney, 2014). In order to study vocal communication effectively, it is important that neurobiological studies of natural communication take place, including a focus on the actual social interactions being mediated by the vocalizations. Moreover, because any communicative process requires the engagement of both production (sender) and perception (receiver), often acting in concert, a full understanding of the neural basis of communication, vocal or otherwise, should be based on an integrated approach to study all involved processes. However, because of the limited active communication in captivity exhibited by many species used in neurobiological research, including the popular macaque monkey, these species may not be ideally suited for studying communication in the laboratory. Instead such studies have been limited to constituent motor and sensory components, rather than the communicative process as a whole.

Here we present evidence of the significant value of marmosets in neuroscience as a model of social communication. We focus primarily on research using the common marmoset (*Callithrix jacchus*), as they have become the most frequently used marmoset species in scientific studies. We first briefly review past work from more traditional research models in rhesus and squirrel monkeys, followed by a discussion of how similar approaches in marmosets have yielded comparable results. We next extend our case for the marmoset vocal model by discussing several recent lines of work that highlight the unique insights that can be gained by studying the neural basis of vocal communication within the context of the marmoset natural behavioral repertoire: auditory feedback and antiphonal conversations. We conclude with a discussion of potential avenues for future research.

MARMOSET COMMUNICATION BEHAVIORS

Marmosets communicate with conspecifics using signals across multiple sensory modalities. Like all primates, however, social communication is dominated by visual and acoustic social signaling. Visually, marmosets acutely focus their attention on faces (Mitchell et al., 2014), as they can provide a wealth of communicative information to conspecifics. Marmosets produce several facial expressions, each of which communicates specific information to conspecifics related to the particular social context (Kemp and Kaplan, 2013). By attending to the face, marmosets not only gain information about facial expressions, but can follow the gaze of conspecifics to gain other valuable social information (Burkart and Heschl, 2006, 2007). For example, marmosets will follow a conspecific's gaze toward objects that are outside of their line of sight and use that cue to investigate (Burkart and Heschl, 2006). In addition to faces, marmosets also communicate visual information with body postures (Schiel and Huber, 2006). This importance of visual communication is evidenced by the presence of specialized processing at the neurobiological level. Like other human and nonhuman primates (Kanwisher et al., 1997; Tsao et al., 2006, 2008), the marmoset brain includes a network of "Face Patches" in the extrastriate visual cortex (Hung et al., 2015). More extensive reviews of marmoset visual communication can be found elsewhere (Mitchell and Leopold, 2015; Miller et al., 2016), here we focus on describing their vocal communication system.

Similar to many New World primate species, marmosets are remarkably voluble, engaging in nearly constant vocal communication. Their vocal repertoire comprises a diversity of signals that are produced depending on the particular social and ecological context (Epple 1968; Bezerra and Souto, 2008; Bezerra et al., 2009; Agamaite et al., 2015). These include calls that mediate social interactions, as well as predator alarm calls, mobbing calls and food calls (Bezerra and Souto, 2008). Both "Twitter" and "Trills," for example, appear to mediate particular interactions between conspecifics in relatively close proximity [Fig. 1(A)]. Twitters are characterized by a series of short, rapid frequency modulated pulses, while the spectro-temporal structure of trills shows sinusoidal frequency modulation. Behavioral descriptions from field observations describe trills being produced most commonly in the context of foraging, while twitters are often produced during intergroup encounters (Bezerra and Souto, 2008), though ascertaining the more explicit function of these vocalizations in those social contexts requires further study. Marmosets maintain these diverse vocalizations in captivity, avidly interacting vocally in laboratory colony environments [Fig. 1(B)].

The marmoset "Phee" call is, perhaps, the most extensively studied vocalization in the marmoset repertoire. This vocalization functions to maintain social contact between visually occluded group members (Miller and Wang, 2006; Bezerra and Souto, 2008), but are also produced during aggressive territorial encounters (Bezerra and Souto, 2008) suggestive of a more dynamic role in marmoset social interactions. This species-typical, long-distance contact call comprises one or more long slow-frequency modulated "whistle"-like pulses [Fig. 1(A)]. The acoustic

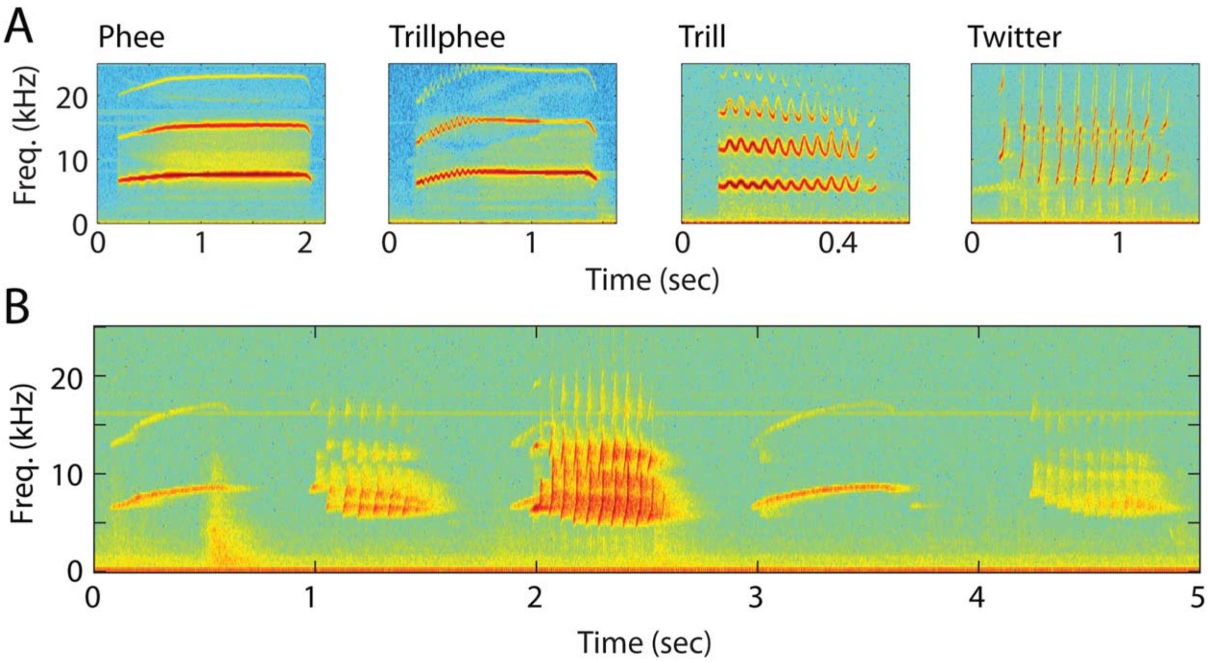

Figure 1 Illustration of marmoset vocalizations. Representative spectrograms are shown for the four most common classes of marmoset vocalizations (A), although marmoset exhibit numerous other types of vocalizations. Marmosets often vocalize interactively with multiple types of vocalizations in the colony environment (B). [Color figure can be viewed at wileyonlinelibrary.com]

structure of phee calls encodes a variety of social information that is relevant for aspects of social recognition, including the individual identity and sex of the caller (Norcross and Newman, 1993; Miller et al., 2010a,b). The phee call also encodes group-level dialects (Miller et al., 2010a,b), suggesting that at least some degree of vocal control and adaptive learning occurs for this vocalization similarly to other marmosets species (Elowson and Snowdon, 1994; Snowdon and Elowsen, 1999). Notably, these dialects develop even in captive colonies between groups in close proximity. This capacity for learning and plasticity may be supported by mechanisms of vocal control. Prior to producing a phee call, marmosets establish a motor plan that comprises the entire acoustic structure of the call, suggesting that specific acoustic features and are not random variations or errors, but instead potentially represent deliberate control over the vocal motor output (Miller et al., 2009b).

NEURAL BASIS OF VOCAL SIGNAL PROCESSING IN OTHER PRIMATE MODELS

Despite long-standing interest in the physiological basis of primate vocal communication, relatively little is known about the underlying neural processes. Much of the early research in vocal signal processing during the 1970s and 1980s focused on the squirrel monkey (*Saimiri sciureus)* model. Squirrel monkeys share a number of important features with marmosets and other New World primates that are advantageous for vocal research, including a rich vocal repertoire that is maintained in captivity. This early work first mapped the potential circuits involved in vocal motor control (Jürgens, 2002, 2009), as well as demonstrated sensory coding of vocal sounds in auditory brain areas (Newman and Wollberg, 1973; Symmes et al., 1980; Ploog, 1981). While this research revealed the presence of vocalization-related neural responses in the auditory system, in particular the auditory cortex, it failed to reveal a vocalization-specific brain region as had been hoped by some (Symmes, 1981). For various reasons, much of the pursuit of this line of work had ended by the mid-1980s.

Over the same period of time, rhesus macaques (*Macaca mulatta*) emerged as the dominant non-human primate model for neuroscience research. Macaques share many similar anatomical and physiological features of their auditory system with humans and other non-human primates, although with more developed cortical structures than marmosets or squirrel monkeys. Like other primates, macaques also exhibit a rich vocal repertoire in the wild (Hauser, 1998). Early acute neurophysiological experiments provided evidence suggestive of increased selectivity for complex sounds, including vocalizations, in non-primary auditory cortex (Rauschecker et al., 1995), particularly toward more rostral aspects of the superior temporal gyrus (Rauschecker and Tian, 2000). More recent experiments in awake macaques have identified a vocalization-selective region in rostral secondary auditory cortex that may be analogous to the human "voice" region (Perrodin et al., 2011; Petkov et al., 2008). The areas share direct reciprocal connections with ventrolateral prefrontal cortex (Romanski et al., 1999), where vocalization-related sensory responses have also been found (Romanski and Goldman-Rakic, 2002; Romanski et al., 2005), and may have a role in representing the semantic contents of vocal sounds (Gifford et al, 2005). Despite the importance of such findings, these experiments were performed in head-restrained animals either passively presented with vocalizations or engaged in a conditioned behavioral task and, as a result, we know little about how these brain regions might be involved in more active aspects of communication. Unfortunately, macaques are, by and large, not very vocal in captive laboratory environments, limiting their utility in studying active communication.

NEURAL BASIS OF VOCAL SIGNAL PROCESSING IN MARMOSETS

There appear to be many significant common features between the neural processing of vocal sounds in the auditory systems of marmosets and other non-human primate models. The ascending auditory pathway in marmosets is organized similarly to that of other mammalian and primate species (Aitkin and Park, 1993), including both a leminiscal, or primary-like pathway and a non-leminiscal pathway (De La Mothe et al, 2006). The sensory coding of simple sounds in these sub-cortical structures is similar to those of other mammals (Aitkin and Park, 1993), but relatively little is known about the coding of vocal sounds. Most marmoset auditory research has focused, instead, at the cortical level.

The marmoset auditory cortex exhibits a core-belt-parabelt organization with an anterior-posterior tonotopic organization that appears to be a conserved anatomical arrangement amongst primate species (Kaas and Hackett, 2000; Hackett et al. 2001). Several studies have examined the responses of neurons in marmoset primary auditory cortex (A1), a core auditory area, to species-specific vocal sounds. These studies have demonstrated a distributed representation of vocalizations in A1, with individual neurons responding to specific spectro-temporal features according to their frequency receptive field (Wang et al., 1995; Rajan et al., 2013; Lui et al, 2015). These A1 neurons do not appear to discriminate between natural vocal sounds and spectro-temporally matched synthetic or "virtual" vocalizations (DiMattina and Wang, 2006). However, degradation of these features, particularly in the temporal dimension, results in decreased neural responses (Nagarajan et al., 2002). Despite this apparently simple relationship in A1 between vocal coding and spectro-temporal features, there does appear to be a high degree of non-linearity both in the influence of temporal history (Luczak et al., 2004) and harmonic integration (Kadia and Wang, 2003) suggesting a more complex encoding scheme. What role these non-linearities play in vocal coding remain unknown.

Extending beyond A1, relatively less is known about the encoding of vocalizations in non-primary auditory areas. A few studies have shown vocalization responsive neurons in both the medial (Kajikawa et al., 2008) and lateral (Rajan et al., 2013) belts of marmoset auditory cortex. CM, the central-medial belt region, is a primary-like auditory area that appears to encode vocal sounds in a frequency and feature-dependent fashion similar to that of A1 (Kajikawa et al., 2008). The role of the lateral belt and parabelt are presumed to have a role in selectively encoding complex sounds, similar to what has been seen in macaques, but has not been rigorously explored. More recent work using fMRI in marmosets has found vocalization preferences, compared with degraded vocalizations, extending anteriorly along the superior temporal gyrus toward the temporal pole (Sadagopan et al., 2015). The roles of frontal brain areas, which have been implicated in vocal sensory perception in macaques (Romanski and Goldman-Rakic, 2002; Romanski et al., 2005), have not been explicitly studied in marmosets. However, immediate early gene (IEG) studies in which marmosets were presented recorded phee vocalizations, but failed to vocalize a response, have demonstrated increased expression in ventral prefrontal cortex (vPFC) consistent with local neural processing of vocal sounds (Miller et al., 2010a,b; Simoes et al., 2010). What specific role these diverse brain areas play in vocal coding and perception in marmosets remains unknown, particularly for the issue of vocal perception, as the majority of past physiological studies have been performed in passive or even anesthetized animals.

Another important open question about auditory coding in marmosets is to what extent their auditory cortex is acting as a specialist versus a generalist system. In a specialist system, for example, one might predict a brain region or group of neurons dedicated to encoding species-specific vocal sounds. The extreme extrapolation of this hypothesis would be an auditory equivalent of a "grandmother" cell. A previous search for such a specialization in squirrel monkeys was unsuccessful (Symmes, 1981), and to date no evidence has emerged for a specialized vocalization-coding area in marmosets. There is, however, some evidence suggesting that the marmoset auditory cortex is not a purely generalist system either. Presentation of natural and time-reversed marmoset Twitter calls evokes a stronger auditory cortical response to the natural call, a bias not present when presenting Twitter calls to cats (Wang and Kadia, 2001). Whether this represents some innate preference or specialization is unknown. On the other hand, experiments in which marmosets underwent surgical vocal tract modification, and had resulting atypical Twitter vocalizations, later found altered sensory coding of Twitter calls in A1 after several months (Cheung et al., 2005). These results suggest that any apparent specialization in marmoset auditory cortex may simply be a result of experience-dependent plasticity, especially given the degree of A1 plasticity observed in other mammalian species (Chang et al., 2005). Future work will be needed to resolve these ambiguities and to determine to the roles of acoustic features, experience, and active sensation on marmoset sensory coding and vocal perception.

VOCAL PRODUCTION AND SENSORY-MOTOR INTEGRATION

One of the key advances over the past few years that has allowed for more detailed studies of vocal production and natural vocal behaviors has been the development of free-roaming neurophysiological preparations. No matter how vocal a species is in the wild or laboratory colony, the physical restraints typically used in neurophysiological experiments often inhibit natural behaviors like vocal production. Although free-roaming recordings have long been used in rodents and other species, their application to non-human primates have been difficult due to their three dimensional movement and the ability to grasp with their hands. Over the past few years, this limitation has largely been overcome with new small micro-electrode arrays coupled with either tethered (Eliades and Wang, 2008a) or wireless (Mohseni et al., 2005; Roy and Wang, 2012) unrestrained recordings. These technologies have seen extensive use in marmosets and, to a lesser extent, squirrel monkeys (Grohrock et al., 1997; Tammer et al., 2004). When combined with either antiphonal vocal interactions (Miller et al., 2016) or experiments performed in the housing colony (Eliades and Wang, 2008b,), these methods have proven extremely effective at eliciting the full range of marmoset vocal behaviors while allowing chronic neural recordings from multiple brain areas.

Despite these recent technologic advances, relatively little is known about which brain areas are involved in generating and controlling vocal production in marmosets, although there is emerging evidence for the involvement of frontal cortical areas. Microstimulation studies in primary motor cortex have shown the presence of an expected somatotopic organization, however these studies have not examined laryngopharyngeal responses (Burish et al., 2008). Microelectrode studies of prefrontal (PFC) and premotor (PMC) cortical areas during antiphonal calling have found vocalization-related activity that often precedes or is phase locked to the onset of vocal production (Roy and Wang, 2012; Miller et al., 2015), results consistent with previous recordings in macaque monkeys (Gemba et al., 1999). Further evidence for frontal involvement in vocal control is found in IEG studies showing vocal production-related expression particularly in dorsal PFC/PMC (Miller et al., 2010a,b), although other studies have also found expression in ventral PFC (Simoes et al., 2010). Additionally, IEG expression from vocalization has been found in anterior cingulate cortex (Simoes et al., 2010), similar to locations of vocal modulation that have been reported in squirrel monkeys and macaques (Müller-Preuss et al, 1980; Gemba et al., 1995). To what extent cingulate function reflects vocal pre-motor control versus more non-specific motivation remains unknown. As far as subcortical structures that might be involved in vocal production, there have been no studies in marmosets, although it is assumed that this would be similar to the circuits that have been more extensively studied in squirrel monkeys (Jürgens, 2002, 2009).

As we have suggested, however, vocal production and perception should not be thought of as independent, isolated processes. For example, in order to ensure accurate communication of information, it is also necessary to listen to the sound of one's own produced vocalization, a process often referred to as feedback monitoring. Marmosets like many other species will increase their vocal loudness in the setting of feedback masking by background noise (Brumm et al, 2004; Eliades and Wang, 2012), and there has been a suggestion of more elaborate vocal changes when faced with frequency-altered vocal

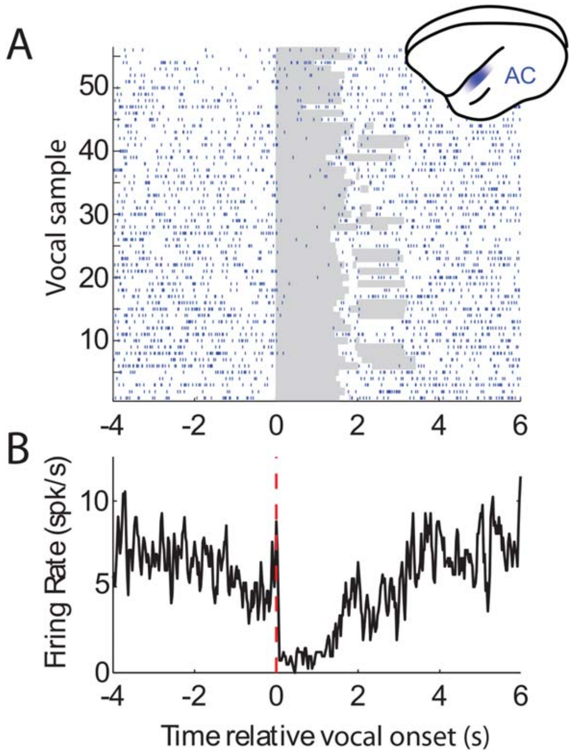

Figure 2 Vocalization-induced suppression in marmoset auditory cortex. A raster (A) and peri-stimulus time histogram (B) of a sample neuron are shown that illustrate the typical pattern of vocalization-induced suppression in auditory cortex. This neuron was nearly completely inhibited during phee vocalizations (shaded area) and exhibited the start of suppression prior to the onset of vocal production. [Color figure can be viewed at wileyonlinelibrary.com]

feedback (Eliades and Wang, 2008b). Similar feedback-dependent vocal control is even more pronounced in humans, where feedback control has been demonstrated in multiple aspects of speech (i.e., Lee, 1950; Lane and Tranel, 1971; Burnett et al, 1998; Houde and Jordan, 1998). Recent research in vocalizing marmosets has begun to reveal the neural basis of this vocal self-monitoring and feedback-dependent control.

Neural recordings in the auditory cortex of vocalizing marmosets have revealed the existence of two populations of cortical neurons. The first, which accounts for nearly 75% of neurons in auditory cortex, are neurons that are suppressed during vocal production (Eliades and Wang, 2003, 2005) (Fig. 2). This vocalization-induced suppression often begins prior to the onset of vocal production, in a pre-motor pattern, and continues throughout the duration of the vocalization, and contrasts with a more typical increased neural firing expected of a sensory response. This pattern of suppressed vocal responses, termed an auditory–vocal interaction, is suggestive of an internal modulator signal originating in vocal production centers (Fig. 3). In other sensory-motor systems, such signals are often termed efference copies or corollary discharges (Crapse and Sommer, 2008) and are thought to contain predictive information about the expected sensory consequences of a motor action, termed a forward model (Wolpert and Flanagan, 2001). Such models have proven valuable in understanding many aspects of motor control including speech (Hickok et al, 2011). During vocal production, such predictive information is thought to allow for accurate self-monitoring of vocal feedback. This pattern of vocalization-induced inhibition is not specific for a particular type of marmoset vocalization, but rather appears to be a generalized phenomenon during multiple vocalizations and contexts (Eliades and Wang, 2013).

The second population of neurons in the auditory cortex are neurons that exhibit vocalization-related excitation (Eliades and Wang, 2003). Unlike suppressed neurons, this vocal excitation does not begin until after the onset of vocal production, tends to be more specific for single types of vocalizations, and is thought to be un-modulated sensory responses to vocal feedback (Eliades and Wang, 2013). These neurons also respond normally to external sound during vocalization, in contrast to suppressed neurons, and are thought to play a role in maintaining environmental sound sensitivity during vocal production (Eliades and Wang, 2003).

More recent evidence has emerged that this vocalization-induced inhibition may play an

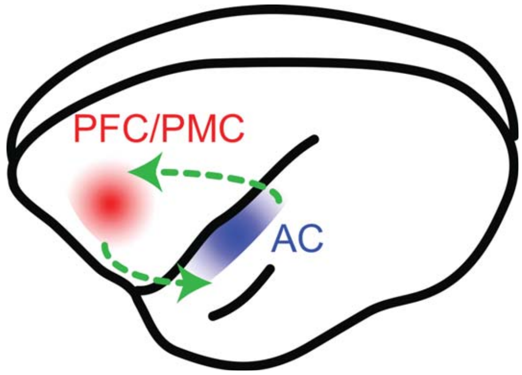

Figure 3 Schematic illustration of cortical auditory–vocal network. Because of the apparent interactions between vocal production and perception, a network is by which frontal vocal centers (PFC/PMC) influence auditory cortical (AC) processing during vocal production, and AC relays information to PFC to support vocal decision making and production. [Color figure can be viewed at wileyonlinelibrary.com]

important role in marmosets' self-monitoring and vocal control. Auditory cortex activity was recorded from vocalizing marmosets while they wore earphones that presented real-time frequency alterations of their vocal feedback (Eliades and Wang, 2008b). Despite the presence of inhibition, vocalization-suppressed neurons were found to be sensitive to this altered vocal feedback. In fact, these auditory neurons exhibited increased sensitivity to altered feedback when results were compared with predictions from passive auditory sensory responses, suggesting a role of vocal suppression in "tuning" the auditory cortex for self-monitoring. Further experiments have used masking noise during vocal production, a stimulus that has been shown to induce compensatory changes in vocal amplitude by marmosets (Brumm et al., 2004). Masking noise is thought to attenuate or block vocal feedback, thereby inducing a compensatory increase in vocal amplitude, a ubiquitous behavior commonly known as the Lombard effect. Similar to the effects of frequency-shifted feedback, masking noise-induced changes in the activities of auditory cortex neurons, particularly suppressed neurons (Eliades and Wang, 2012). Importantly, these changes in auditory cortex neural activity predicted subsequent compensatory changes in vocal amplitude. Together these results demonstrate a role for the marmoset auditory cortex in self-monitoring during vocalization, and suggest a possible role in feedback-dependent compensatory vocal control. This self-monitoring neural activity may potentially be relayed to frontal vocal-control centers to allow for vocal compensation, although further research is needed to better describe this auditory to motor transformation.

ANTIPHONAL CONVERSATIONS

Marmosets naturally engage in conversations. This vocal behavior, known as antiphonal calling, is characterized by the reciprocal exchange of Phee calls between conspecifics (Miller and Wang, 2006). Like human conversations, marmoset antiphonal conversations are characterized by individuals alternating their calling so as not to overlap their vocalizations in time (Miller and Wang, 2006), a behavior known as turn-taking (Takahashi et al., 2013). The periodicity of turn-taking is affected by nuances of the particular social scene, as the rate of calling changes depending on the sex and relatedness of the marmosets engaged in the interaction (Miller and Wang, 2006). The cooperative nature of these conversations is perhaps best evidenced by the degree to which individuals coordinate their interactions even in the face of acoustic interference. For example, a recent experiment in which pairs of marmosets were placed in a setting in which bursts of interfering broad-band noise were broadcast showed that subjects coordinated the timing of their antiphonal exchanges to avoid the noise and optimize signaling (Roy et al., 2011). These experiments suggest that marmosets closely monitor their respective social and acoustic landscape and can adjust their behavior accordingly to maximize communicative efficacy (Toarmino et al., 2016b).

Marmoset antiphonal conversations offer a unique opportunity to examine primate communication from the perspective of an active participant. Communication is an inherently interactive process, but many past vocal playback studies in primates have been limited to measuring subjects' reactions to presentations of a single vocalization or series of vocalizations (Waser, 1975; Seyfarth et al., 1980; Zuberbuhler et al., 1999). In contrast, interactive playback designs have been employed in studies of anurans and songbirds and offer the opportunity to directly engage subjects in their communicative exchanges (Dabelsteen, 1992; Dabelsteen and McGregor, 1996; Schwartz, 2001; King, 2015). The development of novel, interactive software that generates "Virtual Marmosets" (VMs), whose vocal behavior and signal structure can be experimentally manipulated (Miller and Wang, 2006), provides the opportunity to study primate vocal communication as a participant, rather than a third-party or passive observer. This approach has the clear advantage of not only directly engaging marmosets as an active participant in their natural conversations, but also allows experimenters to parametrically manipulate different dimensions of the behavior to test specific questions ranging from vocal signal recognition to social decision-making.

The VM paradigm has been used in several studies aimed at experimentally testing specific dimensions of marmoset conversations. For example, this natural antiphonal behavior is periodic, as callers alternate their vocalizations in sequences of reciprocal exchanges. To test the significance of this periodicity to antiphonal conversations, we tested subjects responses to VMs whose response latency varied from 1 to 15 s (Miller et al., 2009a). Results indicated that subjects were significantly less likely to engage in conversations with VMs with response latencies were over 10 s suggesting that the temporal characteristics are meaningful to the behavior. Other experiments have employed variants of the VM paradigm to examine social recognition and categorization. In one experiment, the caller identity was unexpectedly changed during the conversation and resulted in significantly decreased responses from marmosets, suggesting that the identification of the individuals in the conversation is particularly salient (Miller and Thomas, 2012). More recently, we implemented a paradigm in which subjects engage with multiple VMs in order to test social decision-making within the context of a communication network (Toarmino et al., 2016a). Each VM's vocal behavior was characterized by differences in response latency (Short|Long) and response probability (High|Low) in order to test the extent to which decisions to communicate were based on these behavioral characteristics and/or the behavior of the other VMs in the experiment. We found that subjects' decisions to engage a particular VM were not solely based on their vocal behavior. Instead, subjects compared the relative behavior of each VM in the immediate scene before deciding to exclusively engage one in a conversation. In other words, subjects responded differently to a VM with the same behavioral characteristics (e.g., short response latency and high response probability) depending on the behavior of the other VMs in the scene. Broadly, the VM paradigm offers the opportunity to examine aspects of primate communication that would be difficult with more traditional playback paradigms, and when combined with techniques to record neural activity in freely-moving marmosets, represent a powerful approach to study the neural basis of primate communication.

Such neurobiological studies of antiphonal conversations have yielded several notable insights into the neural mechanisms underlying natural communication in primates. One experiment sought to examine the functional neuroanatomy of the behavior by measuring expression of the immediate early gene (IEG), cFos (Miller et al., 2010a,b). Analyses revealed an increase in cFos expression in both auditory cortex and entorrhinal cortex, suggesting engagement of memory recall processes, during antiphonal conversations relative to controls, while expression in frontal cortex was more complex. Whereas an increase in IEG expression was evident in ventral premotor cortex (vPMC) during vocal production, vPMC and prefrontal cortex (PFC) exhibited a stronger response during vocal signal perception. This general pattern was also observed in a similar experiment performed by a separate laboratory (Simoes et al., 2010). These functional neuroanatomy data suggest that several neural substrates likely contribute to aspects of the antiphonal calling behavior, but more precise neurophysiological experiments are needed to identify their respective roles and contributions.

Subsequent neurophysiology experiments recorded neurons in prefrontal and premotor cortical areas while freely-moving marmosets engaged in antiphonal conversations with a VM (Miller et al., 2015). Although these frontal cortex neurons were responsive during antiphonal conversations, the pattern of responses was notably different than in analogous experiments in rhesus monkeys involving head-restrained rhesus monkeys (Coude et al., 2011; Hage and Nieder, 2013). The first difference was that neurons throughout marmoset frontal areas exhibited vocal motor-related changes in firing activity during vocal production. Neural responses were evident both in the 200 ms prior to vocal onset, as well as sustained changes in activity during call production, including neurons in putative Broca's homolog (Fig. 4). In contrast, neurons in PFC and vPMC cortex of rhesus monkeys trained to vocalize in response to a visual cue were responsive primarily 1000ms prior to vocal onset and only for vocalizations produced in response to the visual stimulus cue. Naturally produced vocalizations elicited no response from the same neurons (Coude et al., 2011; Hage and Nieder, 2013), suggesting the possibility of a cue or reward expectation-related response rather than one specific to vocal production and control.

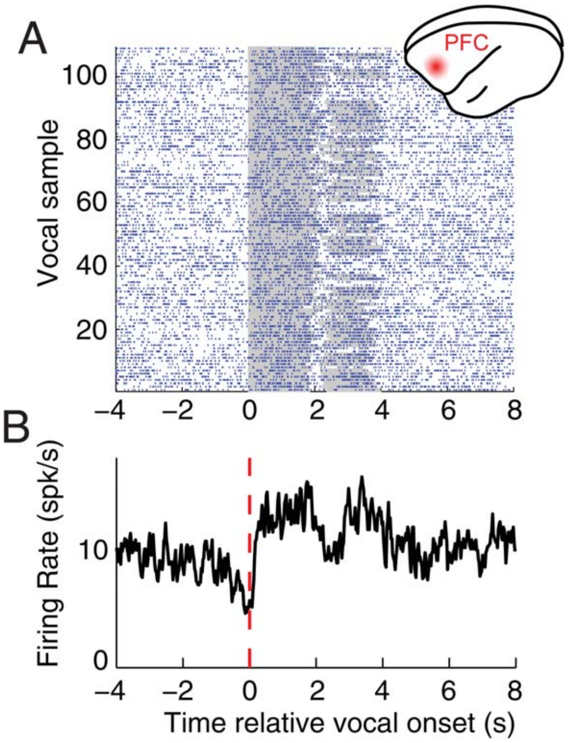

Figure 4 Vocal production-related responses in marmoset prefrontal cortex. Sample responses are shown from a prefrontal neuron recorded during antiphonal calling, and illustrate complex, dynamic activities before and during vocalization. [Color figure can be viewed at wileyonlinelibrary.com]

The second difference is that, although neurons in ventrolateral prefrontal cortex of head restrained rhesus monkeys exhibit responses to playback of vocalizations (Romanski and Goldman-Rakic, 2002; Romanski et al., 2005; Gifford et al, 2005), similar stimulus-driven activity does not occur in the analogous frontal population of neurons of freely-moving marmosets engaged in antiphonal conversations (Miller et al., 2015). However, further analysis using a population classifier was able to reliably distinguish between vocalizations produced by the VM that either did or did not elicit a behavioral response by subject marmosets. These results demonstrated that, as a population, marmoset frontal cortex is involved in sensory processing for antiphonal conversations, even though vocalization sounds elicited few strong firing-rate responses at the level of individual neurons. Such differences between studies involving freely-moving paradigms and those with more conventional, head-fixed preparations are notable and suggestive of the value that active social signaling paradigms, including the VM design, have for elucidating dimensions of primate brain function that would not be possible with more traditional approaches.

AVENUES FOR FUTURE RESEARCH

There has been a recent groundswell of interest in marmosets as a model species for neuroscientific research. Their appeal has been driven, in part, by their potential for implementing many of the molecular tools that have revolutionized studies of neural circuitry in mice (Belmonte et al., 2015; Miller et al., 2016). However, a number of characteristics of their natural communication system make the species notably valuable as a model of the neural basis of social signaling, particularly vocal communication. First, and foremost, is their maintenance of a vocal repertoire in captivity and their use of vocalizations within the context of dynamic social behaviors. As we have argued in this review, attempts to study vocalization by focusing exclusively on either production or perception, or by ignoring social context and interactive communication, will ignore the important co-dependence of these processes. Secondly, as a non-human primate, marmosets share may anatomical and physiological features with humans that potentially make marmoset vocal research more than an ethologic curiosity, as it can have direct implications for understanding homologous, rather than analogous, speech processes in humans. Third, because marmosets can be easily bred and raised in captivity, and housed in naturalistic familial and social groups, they provide a potential model for the study of developmental neurobiology, including behavior, genetics, and physiology. Here we briefly discuss several potential areas for future research to further our understanding of primate communication.

Developmental Neurobiology

The development of marmosets is relatively rapid compared with most other primates. Whereas rhesus monkeys reach adulthood at 4–5 years, marmosets are sexually mature within 18–24 months (Schultz-Darken et al., 2015). Because of this attribute, the opportunity for an expansive study of primate developmental neurobiology is possible in marmosets. While relatively little is known about the relationship between the development of specific neural circuits and observable behavior in marmosets, a growing body of work aims to rectify this issue (Bourne, this volume). Studies of marmoset vocal development highlight key changes in the ontogeny of natural communication with direct implications for understanding the underlying neural mechanisms (Chow et al., 2015). However, some of this work serves as a cautionary tale regarding the methodological challenges for this research.

Several recent studies of marmoset vocal development have sought to characterize the earliest stages of ontogeny, and have suggested evidence for early vocal learning (Takahashi et al., 2015, 2016; Zhang and Ghazanfar, 2016). Targeting the first few weeks of life is imminently valuable, as critical stages of development are likely to occur in this period. Some of these experiments, however, contain several flaws in their design that make interpretation of their results difficult. One key problem is that infants are separated from their mothers, a context that is stressful for the babies and likely affects aspects of vocal production and behavior. Such stress induced by separating infants from their mothers is evident in the presented results by the presence of tsik (alarm/stress) vocalizations (Takahashi et al., 2015), often produced by marmosets when placed in a new environment they find stressful. Not surprisingly, these calls are absent from the recordings that took place at later times. Indeed the presence of a conspecific caller can ameliorate the stress induced by isolating infant marmosets (Ruakstalis and French, 2005). Unfortunately, it is difficult to distinguish between changes in vocal acoustics and behavior that occur because of natural developmental changes and those that simply reflect an adaptation to the stressful environment. Without proper controls, interpreting the nature of the observed acoustic and behavioral changes over ontogeny is challenging.

These recent studies were not the first to employ the technique of removing infants from their parents for vocal recordings. Nearly a decade earlier, Pistorio et al. (2006) used a similar technique, and reported virtually identical changes in the acoustic structure of marmoset vocalizations early in development, though they were notably more measured in the interpretation of their data due to the limitations of the experimental design. The authors of these experiments are correct to target the very earliest stages of development in marmosets, a time which is likely key for vocal development. However, these experiments also serve as an important cautionary note for future experiments of this nature. In order to understand early development, effort should be made to not disrupt the species natural social behavior so that the effects of stress do not mask other aspects of development.

Identifying Functional Neural Circuitry with Molecular Approaches

One of the remarkable advances in biomedical research over the past decades has been the introduction of selectively genetically modified organisms, more commonly referred to as transgenic animals. Unfortunately, these advances have been largely limited to murine models and have been difficult to apply to non-human primates. Recent work, however, has seen the creation of transgenic marmosets, the first and only primate species so modified. This work began with simple fluorescent protein markers (Sasaki et al., 2009), but has since been broadened to a variety of disease lines (Belmonte et al., 2015). The potential for application of this technology to studying marmoset vocal communication is promising, particularly as it will allow the study of complex social behaviors that are not present in non-primate species. For example, there is evidence for specific genetic markers in the human speech motor system. FoxP2, a forkhead box gene, is one such speech-related gene and natural mutations have been associated with speech and language impairments (Vargha-Khadem et al, 2005). Patterns of FoxP2 expression have been found in thalamocortical-basal ganglia circuits in marmosets that are similar to those found in humans as well as songbirds (Kato et al., 2014). The ability for specific manipulation of this gene, coupled with extensive study of the resulting changes and vocal behavior and neurophysiology, has the potential to elucidate the specific role of this vocal-associated gene, and will result in a better understanding of the evolutionary origins and physiological basis for human speech. Other genetically and developmentally associated disorders can similarly be studied, particularly those human conditions in which vocal and social communication are affected, such as autism-spectrum disorders.

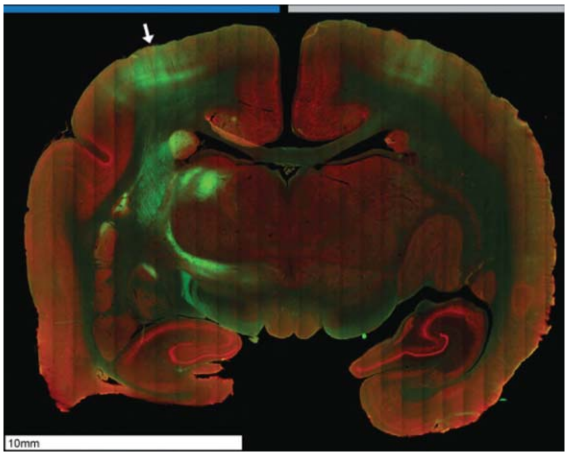

Figure 5 AAV tracer injection in marmoset cortex. Micrograph of a whole slice of marmoset brain showing viral expression following an injection of AAV9.hSyn.ChR2.eYFP at both the injection site (marked by white arrow) and contralateral cortex. Transfection is evident in white matter fiber bundles throughout subcortical areas and across corpus callosum. The ipsilateral hemisphere in which the injection was placed is marked by a blue bar, while the contralateral hemisphere is indicated with a light grey bar. [Color figure can be viewed at wileyonlinelibrary.com]

A second major advance in biomedical research over the past decade, that has largely bypassed non-human primates, has been the development of optogenetic and other optical techniques to study neural circuits (Deisseroth, 2015). These viral-based methods for gene editing can also be valuable for dissecting the neural circuits underlying communication in marmosets. Many adeno-associated viruses express robustly in the marmoset brain (Watakabe et al., 2015), including being useful for mapping long-range anterograde and retrograde projections (Fig. 5). The success of AAVs in the marmoset brain has laid the key foundation for recording and manipulating neuronal populations in marmosets. Because of their lissencephalic (smooth) cortex, marmosets are particularly well suited for multi-photon imaging. Yamamori and colleagues (Sadakane et al., 2015) recently reported remarkable GCaMP6f expression in marmoset cortex using a TET amplifier and were able to elicit stimulus-evoked changes in activity over several months from the same neural population. Likewise, a preparation for optogenetic stimulation in awake subjects has been recently developed in marmosets (MacDougall et al., 2016). Together these studies show that the tools for recording and manipulating neural circuits in the marmoset brain are becoming available and can be applied to a broad range of behavioral studies, including vocal communication. Such tools will allow for invaluable examination and manipulation of specific functional neural circuits supporting primate vocal communication.

CONCLUSIONS

The past few years have seen an emergence of the marmoset as an interesting and potentially invaluable model for biomedical and, in particular, neurobiological research. Marmosets have a number of advantages for neuroscience research. None of these, however, is more marmoset-specific than the ability to study the neurobiology of vocalization and social vocal communication. Studies of marmoset vocal production have the potential to reveal the neural basis of interactive communicative processes and to better understand human speech. In this review, we have summarized our current, limited understanding of the neurophysiology involved in both hearing and producing vocalizations. We make an argument that these processes cannot be studied in isolation, but must take into account the role of vocal production in perception, perception in production, and how social context and decision making can affect both. We further present upcoming research techniques that are just beginning to be applied in marmosets, and have the potential to revolutionize our understanding of human and nonhuman primate communication systems. At this point, the one thing we can say with certainty is that the future of marmoset research is bright.

REFERENCES

Agamaite JA, Chang CJ, Osmanski MS, Wang X. 2015. A quantitative acoustic analysis of the vocal repertoire of the common marmoset (Callithrix jacchus). J Acoust Soc Am 138:2906–2928.

Aitkin L, Park V. 1993. Audition and the auditory pathway of a vocal new world primate, the common marmoset. Prog Neurobiol 41:345–367.

Belmonte J, Callaway EM, Caddick SJ, Churchland P, Feng G, Homatics GE, Lee K, et al. 2015. Brains, genes and primates. Neuron 86:617–631.

Bezerra BM, Souto A. 2008. Structure and usage of the vocal repertoire of Callithrix jacchus. Int J Primatol 29: 671–701.

Bezerra BM, Souto A, Borstelmann de Oliveira MA, Halsey LG. 2009. Vocalizations of wild common marmosets are influenced by diurnal and ontogenetic factors. Primates 50:231–237.

Brumm H, Voss K, Kollmer I, Todt D. 2004. Acoustic communication in noise: Regulation of call characteristics in a New World monkey. J Exp Biol 207:443–448.

Burish MJ, Stepniewska I, Kaas JH. 2008. Microstimulation and architectonics of frontoparietal cortex in common marmosets (Callithrix jacchus). J Comp Neurol 507: 1151–1168.

Burkart JM, Heschl A. 2006. Geometrical gaze following in marmosets (Callithrix jacchus). J Comp Psych 120: 120–130.

Burkart JM, Heschl A. 2007. Understanding visual access in common marmosts (Callithrix jacchus): Perspective taking and other behaviour reading?. Anim Behav 73: 457–469.

Burnett TA, Freedland MB, Larson CR, Hain TC. 1998. Voice F0 responses to manipulations in pitch feedback. J Acoust Soc Am 103:3153–3161.

Chow C, Mitchell J, Miller CT. 2015. Vocal turn-taking in a nonhuman primate is learned during ontogeny. Proc R Soc B 282:210150069.

Chang EF, Bao S, Imaizumi K, Schreiner CE, Merzenich MM. 2005. Development of spectral and temporal response selectivity in the auditory cortex. Proc Natl Acad Sci U S A 102:16460–10465.

Cheung SW, Nagarajan SS, Schreiner CE, Bedenbaugh PH, Wong A. 2005. Plasticity in primary auditory cortex of monkeys with altered vocal production. J Neurosci 25: 2490–2503.

Crapse TB, Sommer MA. 2008. Corollary discharge circuits in the primate brain. Curr Opin Neurobiol 18:552–557.

Coude G, Ferrari PF, Roda F, Marensi M, Borelli E, Veroni V, Monti F, et al. 2011. Neurons controlling voluntary vocalization in the macaque ventral premotor cortex. PLoS ONE 6:e26822.

Dabelsteen T. 1992. Interactive playback: A finely tuned response. In: McGregor PK, editor. Playback and Studies of Animal Communication. London, UK: Plenum Press, pp 97–110.

Dabelsteen T, McGregor PK. 1996. Dynamic acoustic communication and interactive playback. In: Kroodsma DE, Miller EH, editors. Ecology and Evolution of Acoustic Communication in Birds. Ithaca, NY: Cornell University Press, pp 398–408.

De La Mothe LA, Blumell S, Kajikawa Y, Hackett TA. 2006. Thalamic connections of the auditory cortex in marmoset monkeys: Core and medial belt regions. J Comp Neurol 496:72–96.

Deisseroth K. 2015. Optogenetics: 10 years of microbial opsins in neuroscience. Nat Neurosci 18:1213–1225.

DiMattina C, Wang X. 2006. Virtual vocalization stimuli for investigating neural representations of species-specific vocalizations. J Neurophysiol 95:1244–1262.

Eliades SJ, Wang X. 2003. Sensory-motor interaction in the primate auditory cortex during self-initiated vocalizations. J Neurophysiol 89:2194–2207.

Eliades SJ, Wang X. 2005. Dynamics of auditory-vocal interaction in monkey auditory cortex. Cereb Cortex 15: 1510–1523.

Eliades SJ, Wang X. 2008a. Chronic multi-electrode neural recording in free-roaming monkeys. J Neurosci Methods 172:201–214.

Eliades SJ, Wang X. 2008b. Neural substrates of vocalization feedback monitoring in primate auditory cortex. Nature 453:1102–1106.

Eliades SJ, Wang X. 2012. Neural correlates of the lombard effect in primate auditory cortex. J Neurosci 32:10737–10748.

Eliades SJ, Wang X. 2013. Comparison of auditory-vocal interactions across multiple types of vocalizations in marmoset auditory cortex. J Neurophysiol 109:1638–1657.

Elowson AM, Snowdon CT. 1994. Pygmy marmosets, *Cebuella pygmaea*, modify vocal structure in response to changed social environment. Anim Behav 47:1267–1277.

Engh AL, Hoffeier RR, Cheney DL, Seyfarth RM. 2006. Who, me? Can baboons infer the target of vocalizations?. Anim Behav 71:381–387.

Epple G. 1968. Comparative studies on vocalization in marmoset monkeys (Hapalidae). Folia Primatol 8:1–40.

Gemba H, Miki N, Sasaki K. 1995. Cortical field potentials preceding vocalization and influences of cerebellar hemispherectomy upon them in monkeys. Brain Res 697:143–151.

Gemba H, Kyuhou S, Matsuzaki R, Amino Y. 1999. Cortical field potentials associated with audio-initiated vocalization in monkeys. Neurosci Lett 272:49–52.

Gifford GW, 3rd, MacLean KA, Hauser MD, Cohen YE. 2005. The neurophysiology of functionally meaningful categories: Macaque ventrolateral prefrontal cortex plays a critical role in spontaneous categorization of species-specific vocalizations. J Cogn Neurosci 17:1471–1482.

Grohrock P, Hausler U, Jurgens U. 1997. Dual-channel telemetry system for recording vocalization-correlated neuronal activity in freely moving squirrel monkeys. J Neurosci Methods 76:7–13.

Hackett TA, Preuss TM, Kaas JH. 2001. Architectonic identification of the core region in auditory cortex of macaques, chimpanzees, and humans. J Comp Neurol 441:197–222.

Hage SR, Nieder A. 2013. Singl neurons in monkey prefrontal cortex encode volitional initiation of vocalizations. Nat Commun 4:2409.

Hung C, Yen CC, Cluchta JL, Papoti D, Bock NA, Leopold DA, Silva AC. 2015. Functional mapping of Face-Selective Regions in the extrastriate visual cortex of the monkey. J Neurosci 35:1160–1172.

Hauser M. 1998. Functional referents and acoustic similarity: Field playback experiments with rhesus monkeys. Anim Behav 55:1647–1658.

Hickok G, Houde J, Rong F. 2011. Sensorimotor integration in speech processing: Computational basis and neural organization. Neuron 69:407–422.

Houde JF, Jordan MI. 1998. Sensorimotor adaptation in speech production. Science 279:1213–1216.

Jürgens U. 2002. Neural pathways underlying vocal control. Neurosci Biobehav Rev 26:235–258.

Jürgens U. 2009. The neural control of vocalization in mammals: A review. J Voice 23:1–10.

Kaas JH, Hackett TA. 2000. Subdivisions of auditory cortex and processing streams in primates. Proc Natl Acad Sci U S A 97:11793–11799.

Kadia SC, Wang X. 2003. Spectral integration in A1 of awake primates: Neurons with single- and multipeaked tuning characteristics. J Neurophysiol 89:1603–1622.

Kajikawa Y, de la Mothe LA, Blumell S, Sterbing-D'Angelo SJ, D'Angelo W, Camalier CR, Hackett TA. 2008. Coding of FM sweep trains and twitter calls in area CM of marmoset auditory cortex. Hear Res 239:107–125.

Kanwisher N, McDermott J, Chun MM. 1997. The fusiform face area: A module in human extrastriate cortex specialized for face perception. J Neurosci 17:4302–4311.

Kato M, Okanoya K, Koike T, Sasaki E, Okano H, Watanabe S, Iriki A. 2014. Human speech- and reading-related genes display partially overlapping expression patterns in the marmoset brain. Brain Lang 133:26–38.

Kemp C, Kaplan G. 2013. Facial expressions in common marmosets (Callithrix jacchus) and their use by conspecifics. Anim Cogn 16:773–788.

King SL. 2015. You talkin' to me? Interactive playback is a powerful yet underused tool in animal communication research. Biol Lett 11:20150403.

Lane H, Tranel B. 1971. The Lombard sign and the role of hearing in speech. J Speech Hear Res 14:677–709.

Lee BS. 1950. Effects of delayed speech feedback. J Acoust Soc Am 22:824–826.

Luczak A, Hackett TA, Kajikawa Y, Laubach M. 2004. Multivariate receptive field mapping in marmoset auditory cortex. J Neurosci Methods 136:77–85.

Lui LL, Mokri Y, Reser DH, Rosa MG, Rajan R. 2015. Responses of neurons in the marmoset primary auditory cortex to interaural level differences: Comparison of pure tones and vocalizations. Front Neurosci 9:132.

MacDougall M, Nummela SU, Coop S, Disney AA, Mitchell JF, Miller CT. 2016. Optogenetic photostimulation of neural circuits in awake marmosets. J. Neurophysiol 116:1284–1294.

Miller CT, Wang X. 2006. Sensory-motor interactions modulate a primate vocal behavior: Antiphonal calling in common marmosets. J Comp Physiol a 192:27–38.

Miller CT, Thomas AW. 2012. Individual recognition during bouts of antiphonal calling in common marmosets. J Comp Physiol a 198:337–346.

Miller CT, Beck K, Meade B, Wang X. 2009a. Antiphonal call timing in marmosets is behaviorally significant: Interactive playback experiments. J Comp Physiol a 195:783–789.

Miller CT, Eliades SJ, Wang X. 2009b. Motor-planning for vocal production in common marmosets. Anim Behav 78:1195–1203.

Miller CT, Dimauro A, Pistorio A, Hendry S, Wang X. 2010a. Vocalization induced cfos expression in marmoset cortex. Front Integr Neurosci 4:128.

Miller CT, Mandel K, Wang X. 2010b. The communicative content of the common marmoset phee call during antiphonal calling. Am J Primatol 72:974–980.

Miller CT, Thomas AW, Nummela SU, de la Mothe LA. 2015. Responses of primate frontal cortex neurons during natural vocal communication. J Neurophysiol 114:1158–1171.

Miller CT, Freiwald W, Leopold DA, Mitchell JF, Silva AC, Wang X. 2016. Marmosets: A neuroscientific model of human social behavior. Neuron 90:219–233.

Mitchell JF, Leopold DA. 2015. The marmoset monkey as a model for visual neuroscience. Neurosci Res 93:20–46.

Mitchell J, Reynolds J, Miller CT. 2014. Active vision in marmosets: A model for visual neuroscience. J Neurosci 34:1183–1194.

Mohseni P, Najafi K, Eliades SJ, Wang X. 2005. Wireless multichannel biopotential recording using an integrated FM telemetry circuit. IEEE Trans Neural Sys Rehab Eng 13:263–271.

Müller-Preuss P, Newman JD, Jurgens U. 1980. Anatomical and physiological evidence for a relationship between the ’cingular’ vocalization area and the auditory cortex in the squirrel monkey. Brain Res 202:307–315.

Nagarajan SS, Cheung SW, Bedenbaugh P, Beitel RE, Schreiner CE, Merzenich MM. 2002. Representation of spectral and temporal envelope of twitter vocalizations in common marmoset primary auditory cortex. J Neurophysiol 87:1723–1737.

Newman JD, Wollberg Z. 1973. Multiple coding of species-specific vocalizations in the auditory cortex of squirrel monkeys. Brain Res 54:287–304.

Norcross JL, Newman JD. 1993. Context and gender specific differences in the acoustic structure of common marmoset (Callithrix jacchus) phee calls. Am J Primatol 30: 37–54.

Perrodin C, Kayser C, Logothetis NK, Petkov C. 2011. Voice cells in primate temporal lobe. Curr Biol 21:1408–1415.

Petkov CI, Kayser C, Steudel T, Whittingstall K, Augath M, Logothetis NK. 2008. A voice region in the monkey brain. Nat Neurosci 11:367–374.

Pistorio AL, Vintch B, Wang X. 2006. Acoustic analysis of vocal development in a New World primate, the common marmoset (Callithrix jacchus). J Acoust Soc Am 120: 1655–1670.

Ploog D. 1981. Neurobiology of primate audio-vocal behavior. Brain Res 228:35–61.

Rajan R, Dubaj V, Reser DH, Rosa MG. 2013. Auditory cortex of the marmoset monkey - complex responses to tones and vocalizations under opiate anaesthesia in core and belt areas. Eur J Neurosci 37:924–941.

Rauschecker JP, Tian B. 2000. Mechanisms and streams for processing of “what” and “where” in auditory cortex. Proc Natl Acad Sci U S A 97:11800–11806.

Rauschecker JP, Tian B, Hauser M. 1995. Processing of complex sounds in the macaque nonprimary auditory cortex. Science 268:111–114.

Romanski LM, Goldman-Rakic PS. 2002. An auditory domain in primate prefrontal cortex. Nat Neurosci 5:15–16.

Romanski LM, Bates JF, Goldman-Rakic PS. 1999. Auditory belt and parabelt projections in the prefrontal cortex in the rhesus macaque. J Comp Neurol 403:141–157.

Romanski LM, Averbeck BB, Diltz M. 2005. Neural representation of vocalizations in the primate ventrolateral prefrontal cortex. J Neurophysiol 93:734–747.

Roy S, Wang X. 2012. Wireless multi-channel single unit recording in freely moving and vocalizing primates. J Neurosci Methods 203:28–40.

Roy S, Miller CT, Gottsch D, Wang X. 2011. Vocal control by the common marmoset in the presence of interfering noise. J Exp Biol 214:3619–3629.

Ruakstalis M, French JA. 2005. Vocal buffering of the stress response: Exposure to conspecfic vocalizations moderates urinary cortisol excretion in isolated marmosets. Horm Behav 47:1–7.

Sadagopan S, Temiz-Karayol NZ, Voss HU. 2015. High-field functional magnetic resonance imaging of vocalization processing in marmosets. Sci Rep 5:10950.

Sadakane O, Masamizu Y, Watakabe A, Terada S, Ohtsuka M, Takaji M, Mizukami H, et al. 2015. Long-term two-photon calcium imaging of neuronal populations with subcellular resolution in adult non-human primates. Cell Reports 13:11–11.

Sasaki E, Suemizu H, Shimada A, Hanazawa K, Oiwa R, Kamioka M, Tomioka I, et al. 2009. Generation of transgenic non-human primates with germline transmission. Nature 459:523–527.

Schiel N, Huber L. 2006. Social influences on the development of foraging beahvior in free-living common marmosets (Callithrix jacchus). Am J Primatol 68:1–11.

Schultz-Darken N, Braun KM, Emborg ME. 2015. Neurobehavioral development of common marmoset monkeys. Dev Psychobiol 58:141–158.

Schwartz JH. 2001. Call monitoring and interactive playback systems in the study of acoustic interactions among male anurans. In: Ryan MJ, editor. Anuran Communication. Washington, DC: Smithsonian Institution Press.

Seyfarth RM, Cheney DL. 2014. Evolution of language from social cognition. Curr Opin Neurobiol 28:5–9.

Seyfarth RM, Cheney DL, Marler P. 1980. Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. Science 210:801–803.

Simoes CS, Vianney PVR, Marcondes de Moura M, Freire MAM, Mello LE, Sameshima K, Araujo JF, et al. 2010. Activation of frontal neocortical areas by vocal production in marmosets. Front Integr Neurosci 4:1–12.

Snowdon CT, Elowsen AM. 1999. Pygmy marmosets modify call structure when paired. Ethology 105:893–908.

Symmes D. 1981. On the use of natural stimuli in neurophysiological studies of audition. Hear Res 4:203–214.

Symmes D, Alexander GE, Newman JD. 1980. Neural processing of vocalizations and artificial stimuli in the medial geniculate body of squirrel monkey. Hear Res 3: 133–146.

Takahashi D, Narayanan D, Ghazanfar AA. 2013. Coupled oscillator dynamics of vocal turn-taking in monkeys. Curr Biol 23:2162–2168.

Takahashi D, Fenley A, Teramoto Y, Narayanan D, Borjon J, Holmes P, Ghazanfar AA. 2015. The developmental dynamics of marmoset money vocal production. Science 349:734–738.

Takahashi D, Fenley A, Ghazanfar AA. 2016. Early development of turn-taking with parents shapes vocal acoustics in infant marmoset monkeys. Philos Trans R Soc B 371: 210150370.

Tammer R, Ehrenreich L, Jurgens U. 2004. Telemetrically recorded neuronal activity in the inferior colliculus and bordering tegmentum during vocal communication in squirrel monkeys (Saimiri sciureus). Behav Brain Res 151:331–336.

Toarmino C, Wong L, Miller CT. 2016a. Social context affects decision-making in a simulated marmoset communication network. In Review.

Toarmino CR, Jovanovic V, Miller CT. 2016b. Decisions to communicate in the primate ecological and social landscapes. In: Bee MA, Miller CT, editors. Psychological Mechanisms in Animal Communication. New York: Springer Verlag.

Tsao DY, Freiwald WA, Tootell RB, Livingstone MS. 2006. A cortical region consisting entirely of face-selective cells. Science 311:670–674.

Tsao DY, Moeller S, Freiwald W. 2008. Comparing face patch systems in macaques and humans. pnas 19514–19519.

Vargha-Khadem F, Gadian DG, Copp A, Mishkin M. 2005. FOXP2 and the neuroanatomy of speech and language. Nat Rev Neurosci 6:131–138.

Wang X, Kadia SC. 2001. Differential representation of species-specific primate vocalizations in the auditory cortices of marmoset and cat. J Neurophysiol 86:2616–2620.

Wang X, Merzenich MM, Beitel R, Schreiner CE. 1995. Representation of a species-specific vocalization in the primary auditory cortex of the common marmoset: Temporal and spectral characteristics. J Neurophysiol 74:2685–2706.

Waser PM. 1975. Experimental playbacks show vocal mediation of avoidance on a forest monkey. Nature 255:56–58.

Watakabe A, Ohtsuka M, Kinoshita M, Takaji M, Takaji M, Isa K, Mizukami H, et al. 2015. Comparative analyses of adeno-associated viral vector serotypes 1,2,5,8 and 9 in marmoset, mouse and macaque cerebral cortex. Neurosci Res 93:144–157.

Wolpert DM, Flanagan JR. 2001. Motor prediction. Curr Biol 11:R729–R732.

Zhang YS, Ghazanfar AA. 2016. Perinatally influenced autonomic system fluctuations drive infant vocal sequences. Curr Biol 26:1249–1260.

Zuberbuhler K, Cheney DL, Seyfarth RM. 1999. Conceptual semantics in a nonhuman primate. J Comp Psych 113: 33–42.