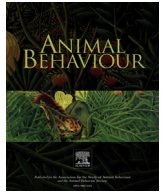




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Mechanisms and constraints underlying acoustic variation in rodents

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Like passerines among birds, rodents among mammals have experienced an enormous radiation. Similar to songbirds, this radiation is associated with the evolution of a critical innovation in how vocal signals are produced. Recent studies on the anatomical and physiological bases of vocal production provide an opportunity to understand how proximate mechanisms shape acoustic variation to influence signal function and evolution. Acoustic variation ranges from subtle changes within individuals in different social contexts to extreme divergence among closely related species. Despite increased appreciation of this modality, relatively few studies have assessed variability of acoustic features within individuals over time and/or the consequences of such variation. Moreover, our understanding of the mechanisms that promote and constrain acoustic variation is limited. Herein, we review ontogenetic, social and endocrine factors associated with intraspecific acoustic signal variation in murid and cricetid rodents, summarize the functional consequences of such variation and describe morphological and physiological adaptations underlying vocal displays. We then suggest a framework for developing mutually informative mechanistic and functional studies to explore the evolution of signal elaboration. Clarifying the causes and consequences of interspecific and intraspecific acoustic variation is critical to understanding the evolution and function of vocalizations in the largest radiation of mammals.

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Vocalizations used to attract mates or deter rivals are among the most diverse displays in the animal kingdom. The widespread importance of acoustic signals in mate and competitor recognition is especially celebrated in insects, birds and frogs (Bradbury & Vehrencamp, 2011). Indeed, acoustic divergence is associated with patterns of diversification in a variety of taxa, including songbirds (Passeriformes) whose radiation encompasses nearly two-thirds of avian diversity (e.g. Kochmer & Wagner, 1988; Raikow, 1988; but see Chen & Wiens, 2020; Wiens & Tuschhoff, 2020). Rodents similarly represent over 40% of mammalian diversity (Dent, 2018) and exhibit extreme variation in acoustic signal form, even among closely related species (Okanoya & Screven, 2018; Sales, 2010; Schleich & Francescoli, 2018; Shelley & Blumstein, 2005). In addition, individuals display dynamic changes in vocalizations over short and long timescales in reproductive contexts (Fernández-Vargas & Johnston, 2015; Pasch et al., 2017; Warren et al., 2020). Given the important role of a novel vocal organ (the syrinx) in bird diversification (Kingsley et al., 2018;

Riede et al., 2019), the origin of a new vocal production mechanism (high-frequency whistling) may have promoted rodent diversity. Yet, in contrast to birds, an understanding of the proximate and ultimate mechanisms underlying fundamental frequency (F0) regulation and intra- and interspecific acoustic variation in rodents is lacking. Integration of functional and mechanistic perspectives is needed to clarify the causes and consequences of signal variation.

In this review, we take a comparative approach to discuss evidence reported in several rodent species that produce vocalizations in the 'sonic' and 'ultrasonic' range. We focus on a subset of factors associated with signal variation in senders while acknowledging the underexplored importance of environmental transmission and receiver sensory systems on signal form (Charlton et al., 2019; Dent et al., 2018; Endler, 1992). In addition, we recognize that different selection pressures may exist on wild species versus laboratory-bred strains that could influence the extent of acoustic variation observed in each (Hoffmann et al., 2012; Kalcounis-Rueppell et al., 2010). First, we highlight the importance of considering acoustic variation within and among individuals and identify three factors that are associated with variation (ontogenetic, social, endocrine). Second, we review studies that assess the functional consequences of acoustic variation in reproductive and competitive contexts.

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Third, we synthesize recent findings on the physiological and anatomical basis of vocal production, underscoring two distinct mechanisms that are likely to constrain acoustic variation in different ways. In closing, we suggest how knowledge of sound production mechanisms can inform our understanding of signal function and evolution.

INTERSPECIFIC ACOUSTIC SIGNAL VARIATION AND DIVERSITY

Approximately 2100 of the 4660 described mammals are rodents, many of which produce some form of vocalization (e.g. Brudzynski, 2018; Dent et al., 2018). Muridae and Cricetidae represent the first and second largest families of mammals (Steppan & Schenk, 2017). Collectively, their vocal behaviour is diverse (Fig. 1), varying in context, rate, spectrotemporal parameters, call type diversity and complexity. Vocal repertoires consist of a single call (a continuous spectrographic contour; also termed 'syllable' or 'note' in other publications) or multiple calls. Multicall renditions can be considered more complex than single calls. However, complexity can also refer to calls with pronounced frequency modulation (e.g. a rat trill) and/or a call with frequency breaks or jumps separated by less than 10 ms of silence (Fig. 1).

Historically, acoustic signals in house mice, *Mus musculus*, and Norway rats, *Rattus norvegicus*, were categorized as either ultrasonic vocalizations (USVs) or audible vocalizations. The basis for the differentiation is a frequency cutoff at 20 kHz, the upper limit of the human hearing. We suggest that such an anthropomorphic cutoff is

not functionally useful and may impede progress in the field by conflating frequency content with underlying production mechanism. Light gas experiments indicate that rodent vocalizations are produced by either a whistle mechanism or airflow-induced vocal fold vibrations (Pasch et al., 2017; Riede & Pasch, 2020; Roberts, 1975). Often, the term 'USV' assumes that a laryngeal airflow generates a whistle, whereas 'audible vocalization' assumes that the same airflow induces vocal fold vibration. In reality, vocalizations with F0 (the lowest harmonic frequency component of a sound) near this threshold may be produced by either mechanism. For example, frequency-modulated calls produced by the northern pygmy mouse, *Baiomys taylori*, songs can fall below 20 kHz but are produced with a whistle mechanism (Riede & Pasch, 2020), whereas low-frequency vocalizations of grasshopper mice, genus *Onychomys*, with F0s approaching 17 kHz are produced using vocal fold vibrations (Pasch et al., 2017). Furthermore, some species are capable of dynamically switching between the two mechanisms depending on social context (Pasch et al., 2017). Throughout this review, we use the term 'high F0 whistle' in species where a whistle mechanism has been demonstrated (e.g. northern pygmy mice, house mice, grasshopper mice and Norway rats), and follow previous terminology (i.e. USV) if the vocal production mechanism is unknown. Similarly, we use the term 'vocal fold vibration sounds' where such a mechanism has been confirmed experimentally.

Although mechanisms of vocal production are unknown in most rodents, many species produce USVs during close contact inter- and intrasexual interactions. Lower-frequency sounds are produced

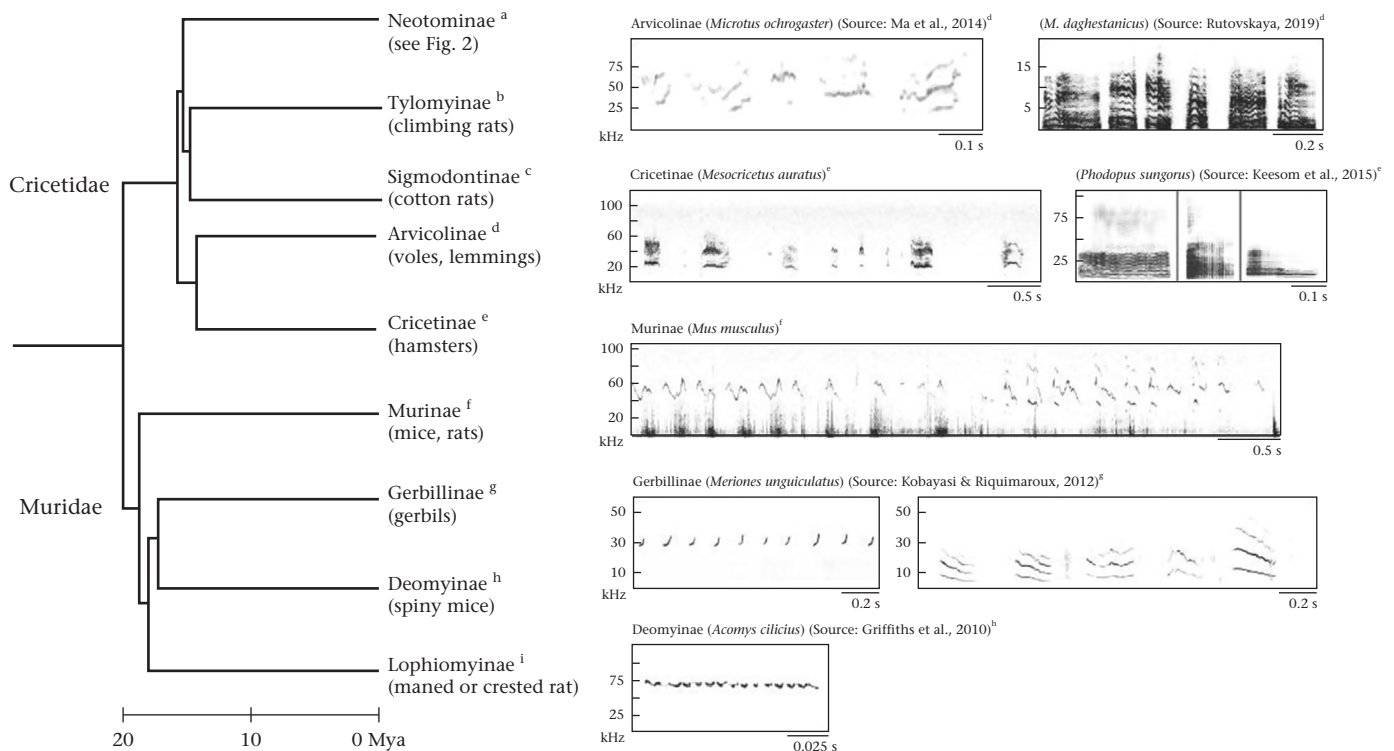


Figure 1. Phylogeny and acoustic diversity within and among murid and cricetid families. Subfamily phylogeny constructed after Steppan and Schenk (2017). Vocal behaviour has been reported in at least one species in all subfamilies of Cricetidae. ^aNeotominae (see Fig. 2). ^bTylomyinae: faint, rapid and high-pitched trills; and long-distance communication using 3.5 kHz chirps have been described in captive pairs of the tylomyine *Nyctomys sumichrasti* (Birkenholz & Wirtz, 1965; Timm & LaVal, 2000). ^cSigmodontinae: vocal behaviour has not been studied in detail in sigmodontines, but pup calls were described to range between 25 and 60 kHz in *Sigmodon hispidus* (Sales & Pye, 1974). ^dArvicolinae (voles and lemmings) (Ma et al., 2014; Rutovskaya, 2019; Terleph, 2011; Yurlova et al., 2020). ^eCricetinae (hamsters): vocalize low- and high-frequency calls during social contact (Fernández-Vargas & Johnston, 2015; Floody & Pfaff, 1977; Keesom et al., 2015). ^{f,g,h}Low- and high-frequency calling have been described during close-distance communication in all subfamilies of Muridae except in the monotypic subfamily Lophiomyinae (Dempster, 2018; Dempster & Perrin, 1994; Finton et al., 2017; Griffiths et al., 2010; Kobayasi & Riquimaroux, 2012; Simeonovska-Nikolova & Bogoev, 2008; spectrograms reproduced from Kobayasi & Riquimaroux, 2012, with the permission of the Acoustical Society of America, <https://doi.org/10.1121/1.3672693>). Notably, long-distance communication using low-frequency alarm calls has been reported and studied in great gerbils, *Rhombomys opimus*, in response to the presence of predators (Randall & Rogovin, 2002).

during close-distance agonistic interactions, distress or advertisement to potential mates or competitors over long distances ($>$ body length; Fig. 1) (Finton et al., 2017; Keesom et al., 2015; Kobayasi & Riquimaroux, 2012; Rutovskaya, 2019; Sales, 2010; Simeonovska-Nikolova & Bogoev, 2008). Members of the New World subfamily Neotominae, such as Neotropical singing mice (genus *Scotinomys*) and grasshopper mice, produce both variable and high-frequency vocalizations during close-distance social interactions, and loud, more stereotyped, lower-frequency vocalizations in long-distance communication (Fig. 2) (Miller & Engstrom, 2007, 2010, 2012; Pasch et al., 2017). Species in the genus *Peromyscus* (deer mice) also produce high-frequency calls (complex sweeps) and low-frequency calls (barks) during social interactions, including stereotyped calls with a $F_0 > 20$ kHz (sustained call) when mice are together or alone (Kalcounis-Rueppell et al., 2018). Thus, with the exception of the understudied golden mouse, *Ochrotomys nuttali*, all neotomines produce low- and high-frequency calls of variable structure. Although increased sampling of more species is required, close-distance, high-frequency and variable signals appear widely distributed across species, whereas long-distance, low-frequency and more stereotyped signals have only evolved in select lineages (Figs 1, 2).

INTRASPECIFIC ACOUSTIC SIGNAL VARIATION

Murid and cricetid species exhibit a great diversity of vocal signals. However, subtle to substantial patterns of acoustic variation exist within call types. High F0 whistles produced by house mice and Norway rats exhibit great variability within and across call types (Fig. 1) (Hertz et al., 2020; Liu et al., 2003; Rieger &

Dougherty, 2016). The low-frequency vocalizations of singing mice, pygmy mice (genus *Baiomys*), harvest mice (genus *Reithrodontomys*), grasshopper mice and deer mice are contrastingly more stereotyped (Miller & Engstrom, 2007, 2012) (Figs 1, 2) but still exhibit variation within and among individuals. What is the significance of these patterns of variation? To address this question, we highlight recent studies demonstrating that acoustic variation in low- and high-frequency vocalizations vary substantially within and among individuals in several species. We then describe how such variation is associated with changes with ontogenic, social and hormonal factors. We acknowledge that other factors (e.g. parasite load, immunity, nutritional state, fluctuating asymmetry or pathologies affecting vocal production) also contribute to acoustic variation and require further study.

Within- versus Among-individual Intraspecific Acoustic Variation

Understanding signal information content requires characterization of within- versus among-individual variation over time. Physiologically, vocal production is an intrinsically dynamic process that requires integration of numerous systems (Zhang & Ghazanfar, 2020). The resultant acoustic signals are composed of multiple spectral and temporal properties of variable consistency that provide different information to receivers. For example, classic studies in treefrogs showed that some acoustic properties (e.g. fundamental frequency; F_0) are 'static' and vary little within individuals to provide information on individual or species identity (Gerhardt, 1991). In contrast, 'dynamic' (e.g. call rate) properties vary greatly within individuals and are associated with changes in motivation, condition and/or arousal of the signaller (Gerhardt, 1991).

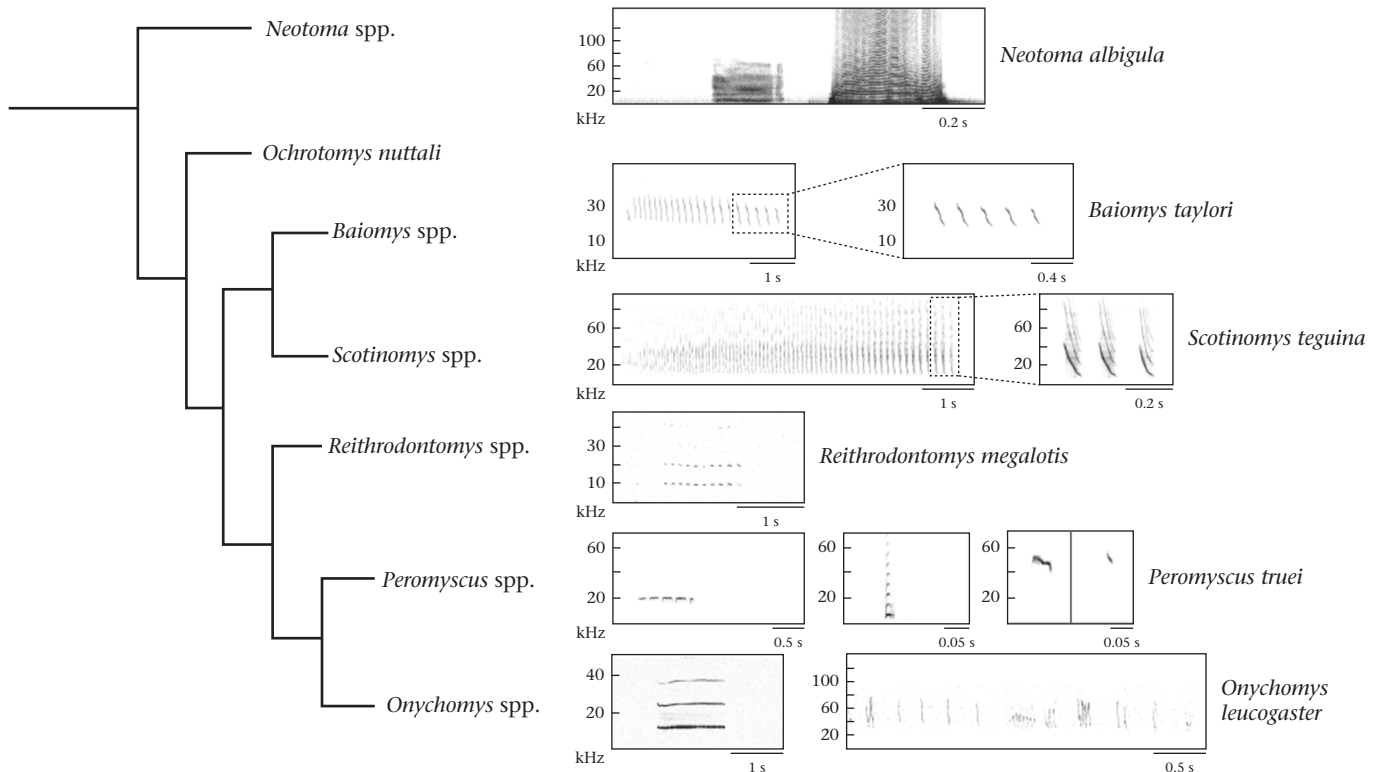


Figure 2. Phylogeny and acoustic diversity within the subfamily Neotominae. Low- and high-frequency vocalizations occur in neotomines during spontaneous advertisement (in the absence of nearby conspecifics) and during close-contact social interactions (Briggs & Kalcounis-Rueppell, 2011; Kalcounis-Rueppell et al., 2006; Kalcounis-Rueppell, Pultorak, & et al., 2018; Miller & Engstrom, 2007, 2010, 2012; Petric & Kalcounis-Rueppell, 2013; Pultorak et al., 2015; Pultorak et al., 2017; Rieger & Marler, 2018; Soltis et al., 2012). Low-frequency calls (loud squeaks) have been reported in pups of the semiarboreal golden mouse, *Ochrotomys nuttali*, but the species' vocal behaviour is largely understudied (Linzey & Packard, 1977).

Similar to those in treefrogs, the acoustic properties of vocalizations in rodents can vary greatly within individuals. However, no clear patterns emerge from the relatively sparse literature on variation and individual identity of different acoustic parameters, highlighting the continued need to document such phenomena. Spectral parameters (e.g. fundamental, maximum and minimum frequencies) in Neotropical singing mice and northern pygmy mice exhibit higher repeatability compared to temporal measures (e.g. song duration) (Burkhard et al., 2018; Riede & Pasch, 2020). Similarly, F0 is highly repeatable in grasshopper mice (Campbell et al., 2019). In contrast, house mice (strain C57BL/6J) exhibit dynamic spectral properties (e.g. frequency jumps, dominant frequency; Rieger & Dougherty, 2016) and static temporal properties (e.g. call rate and duration). In wild-derived house mice, both spectral (e.g. pitch of high- and low-frequency syllables) and temporal (e.g. duration) properties convey information on individual identity that is repeatable for at least 3 weeks (Hoffmann et al., 2012; Marconi et al., 2020). In contrast, most spectral and temporal properties of golden hamster, *Mesocricetus auratus*, USVs are highly dynamic following opposite-sex interactions (Fernández-Vargas & Johnston, 2015).

Researchers should incorporate acoustic measurements into identity metrics to better describe the full extent of acoustic variation. Numerous studies have traditionally reported within-individual variation in call rates or the propensity to even vocalize (e.g. Brunelli, 2005; Fernández-Vargas & Johnston, 2015; Marconi et al., 2020; Sangarapillai et al., 2021). However, metrics that integrate both within- and among-individual variation across acoustic properties can reveal the potential for specific properties to convey information on individual identity or motivation. Ideally, this should be assessed over multiple signalling events to estimate repeatability (i.e. consistency) over time. Examples of suitable metrics include the potential of individuality coding ((PIC) = ratio of within- to among-individual variation; Robison et al., 1993) and Beecher's information statistic (Hs; Beecher 1989). A recent review of individual identity metrics (Linhart et al., 2019) recommended adopting the robust Hs statistic (Beecher, 1989) to facilitate comparisons among studies and species. Importantly, detailed information about the conditions under which vocalizations are elicited and recorded must also be provided because significant acoustic variation is expected to be influenced by social and environmental conditions (see below).

Patterns of Intraspecific Acoustic Variation Across Postnatal and Prewaning Development

Many rodent pups produce isolation vocalizations to facilitate maternal contact. Call or syllable types produced by pups are similar to those produced by adults (Grimsley et al., 2011; Kalcounis-Rueppell et al., 2018; Liu et al., 2003). For example, house mouse pups produce all but one of the 11 syllable types produced by adults, but the proportion of syllable types changes over time (Grimsley et al., 2011). The most commonly produced syllables differ in mean peak frequency and duration between pups and adults. From postnatal day 5 to day 13, pup calls show a widespread range in frequency and duration that becomes reduced in adults (Grimsley et al., 2011; Liu et al., 2003). Moreover, patterns of within-individual variation revealed that most acoustic features are consistent within daily recording sessions but vary considerably across postnatal development (Rieger & Dougherty, 2016). A similar reduction in variation of peak frequencies also occurs between pup and adult Norway rat high F0 whistles (Boulanger-Bertolus et al., 2017). In Neotropical singing mice, within-individual variation of seven spectral and temporal variables increases from postnatal day 0 to postnatal day 15, and then decreases sharply in young adults

(Campbell et al., 2014), suggesting a similar pattern of variability in audible calls.

In adult rodents, vocal patterns appear to become more stereotyped after weaning. In house mice, intervals between syllables become shorter, there are fewer syllables within bouts and there is greater structural complexity in adult high F0 whistles (Grimsley et al., 2011; Liu et al., 2003). Across recording sessions, call duration and rate become more consistent in adults, while spectral or pitch-related features remain inconsistent (Rieger & Dougherty, 2016).

Whether auditory feedback or experience plays a role in rodent vocal development is contentious (Arriaga et al., 2012; Campbell et al., 2014; Kikusui et al., 2011; Mahrt et al., 2013; Pasch et al., 2016). However, acoustic variation within individuals can be partly explained by anatomical and physiological changes across development. The sound source, the larynx, is part of the upper respiratory system and functions in swallowing, respiration and vocal production. All three functions change across development. Pups do not develop a stable and adult-like breathing pattern until 10–14 days after birth; greater cycle-to-cycle variation during the first few days after birth is likely to contribute to larger acoustic variance (Dutschmann et al., 2014). Furthermore, dynamic post-natal changes in size and shape of the four cartilages that form the framework of the larynx are likely to cause shifts in biomechanical properties that affect acoustic output (Riede, Coyne, et al., 2020), but further study is needed.

Motivational and Social Factors Associated With Intraspecific Acoustic Variation

Internal physiological state, or affect, is an important factor of acoustic variation (Hurley & Kalcounis-Rueppell, 2018; Scherer, 2018). High F0 whistles in numerous rodents are believed to be reliable markers for motivational affect (e.g. Brudzynski, 2018). For example, in Norway rats, Siberian hamsters, *Phodopus sungorus*, and house mice, high F0 whistles are associated with positive affect (mating, reward, play) and lower-frequency whistles or calls are associated with negative affect (painful stimulus, aggression) (Burgdorf et al., 2008; Finton et al., 2017; Keesom et al., 2015; Kroes et al., 2007). Norway rat 50 kHz calls (a form of high F0 whistles) can provide a graded measure of a rat's positive state induced by human–rat interaction ('tickling') (Hinchcliffe et al., 2020). In female Norway rats, temporal acoustic features of 50 kHz whistles such as call duration and call repetition rate increase with positive affect (Gerson et al., 2019). In contrast, a decrease in call duration in California mice, *Peromyscus californicus*, is predictive of higher aggressive territorial defence (Rieger & Marler, 2018). Positive and negative emotions also have cardiovascular effects. In isolated female prairie voles, *Microtus ochrogaster*, a higher F0 and shorter call duration in USVs have been linked to increased heart rate (Stewart et al., 2015).

Rodent vocal behaviour is also particularly sensitive to changes in external social context (presence of conspecifics and eavesdroppers) of the sender (Hurley & Kalcounis-Rueppell, 2018). Social context can influence the physiological state of senders to cause changes in the multiparameter acoustic space (Wilkins et al., 2013). Differences in mean vocal parameters have been reported in calls produced in social versus nonsocial situations or during interactions with conspecifics of different sex, reproductive state or kinship (e.g. Briggs & Kalcounis-Rueppell, 2011; Chabout et al., 2012; Hanson & Hurley, 2012; Musolf et al., 2010; Petric & Kalcounis-Rueppell, 2013; Pultorak et al., 2017, 2018; von Merten et al., 2014).

The identity and familiarity of conspecific receivers can also affect the physiological state of a caller and modulate the caller's

vocal behaviour over short periods. For example, male golden hamsters produce USVs at higher rates following interactions with a female across a barrier (post-female calls). However, when such male–female interactions take place in the presence of a familiar male that previously won a fight against the male subject, the duration and energy of the subject's post-female calls decrease faster over time than when the stimulus male is a familiar neutral male (Fernández-Vargas, 2018a). Dominant males are known to copulate first with a receptive female and have greater reproductive success than subordinate males (Huck et al., 1985; Huck et al., 1986). Thus, a decreased vocal effort may be an adaptive response of a subordinate male in the presence of a dominant male. In Norway rats, odour cues from an unfamiliar male, but not from a familiar cagemate, decrease the duration of postejaculatory high F0 whistles. In contrast, mating cues such as the copulatory chamber increase call duration (Bialy et al., 2016). In California mice, call duration is positively correlated with pair bonding and with a female's interest in her mate's playback calls (Pultorak et al., 2017; Pultorak et al., 2018). Thus, the composition and familiarity of the social environment can change the acoustic parameter of calls and, in the case of the golden hamster, interact significantly with the timing of call occurrence.

Temporal acoustic parameters in low-frequency calls can also change dynamically with social context. Neotropical singing mice produce songs that consist of repeatable iterations of 15–30 stereotypic notes that increase in frequency bandwidth (range), internote interval and note duration over the course of the song (Campbell et al., 2010; Pasch, George, Hamlin, et al., 2011). During male–male competition, an intruding male increases his song repetition rate and song duration variability to avoid overlapping the resident male's song and generating 'countersinging' contests (Okobi et al., 2019). This suggests a certain plasticity in the temporal coordination of song production depending on the audience.

Male house mice are also capable of modifying vocal output depending on vocalizations and/or behaviour of females during courtship (Heckman et al., 2017; Neunuebel et al., 2015; Warren et al., 2020; Warren et al., 2018). During mounting, male mice produce longer and more complex spectral features (e.g. more frequency jumps) (Matsumoto & Okanoya, 2020), which may increase female receptivity (Asaba et al., 2017) and predict reproductive success (Nicolakis et al., 2020). Although female mice vocalize less than males during courtship, female calls can be distinguished from male calls based on different patterns of acoustic variation over time and can shape social interactions dynamically (Neunuebel et al., 2015; Warren et al., 2020; Warren et al., 2018). Female mice also produce low-frequency rejection calls (squeaks) during courtship that contain chaotic and noisy segments. The duration of those segments vary across interactions of the same female with different males and predict whether male mounting occurs (Finton et al., 2017).

Endocrine Mechanisms Associated With Intraspecific Acoustic Variation

Hormones are chemical signals that act on target organs in the body and the brain to modulate social behaviour. In particular, steroid hormones can influence the transcription of many genes early in development and later during reproduction and result in long-lasting behavioural changes (Adkins-Regan, 2005). However, rapid changes of steroid concentrations in the brain can induce nongenomic actions (e.g. influencing synaptic transmission) in specific neuronal populations and cause fast behavioural changes (Adkins-Regan, 2005; Balthazart et al., 2018; Cornil et al., 2012;

Remage-Healey et al., 2018). Here, we cover the long-term and short-term action of steroid hormones on vocal signalling. Additionally, we summarize recently discovered effects of nutritional hormones on rodent vocal display.

Long-term effects of steroid hormones

In rodents, the neural circuitry of vocal behaviour is organized during neonatal development and activated later in adulthood by gonadal hormones (see reviews Fernández-Vargas, 2018b; Marler & Monari, 2021). Gonadal hormones can affect vocal behaviour by modulating activity in different brain regions (e.g. limbic system, the midbrain periaqueductal grey (PAG)) or by affecting peripheral tissue structure such as mechanical properties or shape and size of the vocal organ (Adkins-Regan, 2005; Aufdemorte et al., 1983; Fernández-Vargas, 2018b; Marler & Monari, 2021; Rosenfeld & Hoffmann, 2020). More recently, endocrine disruptor chemicals have also been found to affect acoustic properties in California mice, like call duration in males (Johnson et al., 2018) and vocal activity in females (Marshall et al., 2019).

Endocrine effects on mechanical properties of the larynx are known in humans (e.g. Newman et al., 2000) and have been suggested in females of the genus *Rattus*. Ovariectomy may lead to an increase in thickness but simultaneously to a greater probability of inflammation processes of the lamina propria (an important structure of the vocal folds; see next section) (Kim et al., 2020; Oyarzún et al., 2011; Tatlipinar et al., 2011). Oestrogen replacement reverses the effects of a gonadectomy (Tatlipinar et al., 2011). The effects of gonadal hormones on peripheral structures of vocal production and on acoustic variation remain to be explored, but recent studies in birds are likely to elucidate the causal relationship (Alward, Madison, et al., 2016; Fuxjager et al., 2014).

Short-term effects of steroid hormones

Oestrogen levels in the brain can fluctuate by the local conversion of testosterone (T) into oestradiol by the enzyme aromatase, and this conversion takes place in response to social stimuli in several species of vertebrates (Remage-Healey et al., 2018). Social cues can also rapidly stimulate a transient surge of plasma T in house mice (Amstislavskaya & Popova, 2004), California mice (Oyegbile & Marler, 2005) and golden hamsters (Fernández-Vargas, 2017). These changes in the concentration of circulating gonadal T crossing the blood–brain barrier could sustain local fluctuation of oestrogen synthesis in the brain (Cornil et al., 2006).

Acute hormone injections in gonadally intact males rapidly change sexual behaviour in house mice (Taziaux et al., 2007), scent-marking behaviour in white-footed mice, *Peromyscus leucopus* (Fuxjager et al., 2015), and vocal behaviour in golden hamsters and California mice (Fernández-Vargas, 2017; Pultorak et al., 2015; Timonin et al., 2018). In golden hamsters, the temporal and energy parameters of post-female USVs change significantly over the course of a recording session after a single subcutaneous injection of T or oestrogen (Fernández-Vargas, 2017). These acoustic parameters are highly variable within callers, and these results suggest that they may be modulated by rapid changes in hormone level and motivational state (Fernández-Vargas & Johnston, 2015). This idea is plausible, given that blocking rapid synthesis of brain oestradiol has been demonstrated to modulate song motivation and song stereotypy in canaries (Alward, de Bournonville, et al., 2016). However, subtle but significant effects of T on signalling behaviour in white-footed and California mice are dependent upon whether males are subordinate or pair-bonded, respectively, supporting the idea that these rapid physiological changes can be tightly associated with nuances of social behaviour (Fuxjager et al., 2015; Pultorak et al., 2015).

Effects of nutritional hormones

Adipose tissue plays an important role in endocrine regulation. Hormonal products originating from adipose tissue include leptin and adiponectin, which inform the brain about current nutritional status and thereby stimulate or inhibit food intake. If we assume that vocal production in mating contexts incurs costs (metabolic costs, search costs, costs of predator attraction), such an investment would make sense only for the males in sufficient condition. Two studies in Alston's singing mice, *Scotinomys teguina*, tested the hypothesis that levels of metabolic hormones are related to male singing behaviour. Burkhard et al. (2018) found that song effort, but not frequency modulation, was predicted by adiponectin and leptin levels. Song effort was described by an axis of variation that was represented mostly by total singing and song duration. Interestingly, this axis of variation was variable within male callers (low repeatability), while the axis of frequency modulation was more consistent (high repeatability) (Burkhard et al., 2018). Giglio and Phelps (2020) followed up on the initial finding by manipulating leptin levels in male signing mice. Single leptin injections in ad libitum-fed animals induced an increase in singing effort and motivation. Thus, leptin levels can modulate a dynamic component of the acoustic display in a rodent.

In summary, steroid and nutritional hormones are implicated in modulating acoustic variation and display performance. This opens up new avenues of research focusing on how hormones can change vocal output in short and long timescales, together with exploration of the many possible sites of endocrine action (Table 1).

SIGNAL FUNCTION AND RECEIVER RESPONSES TO INTRASPECIFIC ACOUSTIC VARIATION

In the previous section, we reviewed factors associated with acoustic variation. How do receivers respond to such variation, and what could be the functional relevance? Signal function can be inferred from studies that correlate acoustic production with behavioural events, manipulative experiments that eliminate the acoustic modality, or playback experiments that examine the behavioural responses and fitness consequences of receivers.

Deafening and devocalizing experiments in murids (house mice and Norway rats) and cricetids (golden hamsters and desert woodrats, *Neotoma lepida*) indicate that hearing male vocalizations induces female lordosis and other proceptive behaviours (Floody & Bauer, 1987; Nomoto et al., 2018; Thomas et al., 1981; White & Barfield, 1987; White & Fleming, 1987). In house mice and Norway rats, playback of male high F0 whistles elicits female approach behaviour (Asaba et al., 2017; Hammerschmidt et al., 2009; Musolf et al., 2010; Willadsen et al., 2014). However, in Norway rats, whistles do not consistently elicit female approach (Snoeren & Ågmo, 2013, 2014b).

In aggressive contexts, social defeat reduces call rates in mice (Lumley et al., 1999) and dominant Norway rat males vocalize at higher rates than subordinates (D'amato, 1991; Nyby et al., 1976). Conversely, devocalizing resident or intruder male Norway rats had no effect on aggressive or defensive behaviour (Takahashi et al., 1983; Thomas et al., 1981). Such findings raise broader questions about the potential redundancy of acoustic and olfactory signals (Table 1). In murid and cricetid rodents, olfactory signals are important in mediating mate choice and dominance interactions (Fernández-Vargas et al., 2008; Snoeren & Ågmo, 2014a; Thonhauser et al., 2013; Zala et al., 2004). The multimodal nature of many courtship and aggressive displays (Partan & Marler, 2005) suggests that formal study of acoustic and olfactory interactions may elucidate the evolution of vocal communication in rodents (Table 1).

Playback experiments provide clearer insight into the variables important in mediating mating and aggressive interactions. In Norway rats, approach behaviour is dependent on concentration of broadcast

sound at the critical frequency band of 50 kHz (Wöhr & Schwarting, 2012). In house mice, females prefer playback of male high F0 whistles containing more frequency jumps (Chabout et al., 2015). In wild house mice, females exhibit preferences for playback of male high F0 whistles with distinct frequencies and amplitudes (Musolf et al., 2015). Female Alston's singing mice prefer synthetic male songs with higher note rates (Pasch, George, Campbell, et al., 2011). Interestingly, increased male call rate and complexity may facilitate stable partner affiliation in monogamous California mice (Pultorak et al., 2017), whereas paired females displayed agonistic territorial behaviours in response to playback of USVs of unfamiliar males (Pultorak et al., 2017).

In summary, receiver responses to acoustic variation in rodents mirror patterns found in other taxa like songbirds and frogs. Females prefer complex songs with diverse syllables or vocal performance traits that potentially indicate that a signaller's condition can bear the costs of producing physically challenging displays. Ultimately, identifying the mechanisms and mechanics of signal production can help identify constraints on signal elaboration.

ANATOMICAL AND PHYSIOLOGICAL BASIS OF SOUND PRODUCTION

Mechanistically, variation in acoustic signals is determined by integration of six variables: (1) morphological features of the sound source (Fig. 3a, b); (2) morphological features of the vocal tract filter (Fig. 3g); (3) changes in motor control of the source and filter (Fig. 3c–h, d, e); (4) selection on driving force (Fig. 3c–f); (5) the way sound radiates from mouth or nares (Fig. 3g); and (6) potential interactions between sound source and vocal tract filter (not discussed here, but see Riede et al., 2019 for a review of this effect in other taxa). Identifying the relative contributions of each component to acoustic variation is critical to understanding the function and evolution of vocal communication systems.

The Rodent Larynx as Sound Source

Species-specific laryngeal adaptations for vocal production are surprising given the essential role of the larynx in swallowing and breathing (Negus, 1949). Nevertheless, the laryngeal airway of many rodents is characterized by a small side branch inside the larynx termed the ventral pouch (e.g. Borgard et al., 2020; Riede et al., 2017; Smith, 1977). The ventral pouch is surrounded by the thyroid cartilage ventrally and laterally. Its entrance into the laryngeal lumen is reinforced by an alar cartilage, which is a rodent-specific cartilage inside the larynx and presumably derived from the epiglottis (Riede & Pasch, 2020). The distance between glottis and alar edge is actively regulated through intrinsic laryngeal muscles that pull on the alar cartilage. This movement is critical in regulating the F0 of rodent whistle vocalization (Riede et al., 2017).

In contrast, many rodent sounds are produced by airflow-induced vocal fold vibration. Vocal folds are multilayer structures consisting of an epithelium, a lamina propria (red in Fig. 3b) and the thyroarytenoid muscle. Vocal fold vibration rate, which determines F0, is dependent on multiple factors (see Collier & Riede, 2013), including size and mechanical properties of the vocal folds, specifically the lamina propria (Fig. 3b).

The Whistle

Rodents produce vocal signals through two distinct mechanisms: an aerodynamic whistle and flow-induced vocal fold vibration. Differentiation of the two mechanisms was demonstrated by light gas experiments (i.e. a mixture of helium and oxygen) (Pasch et al., 2017; Riede, 2011; Riede & Pasch, 2020; Roberts, 1975). Whistles are generated when an expiratory airflow through the

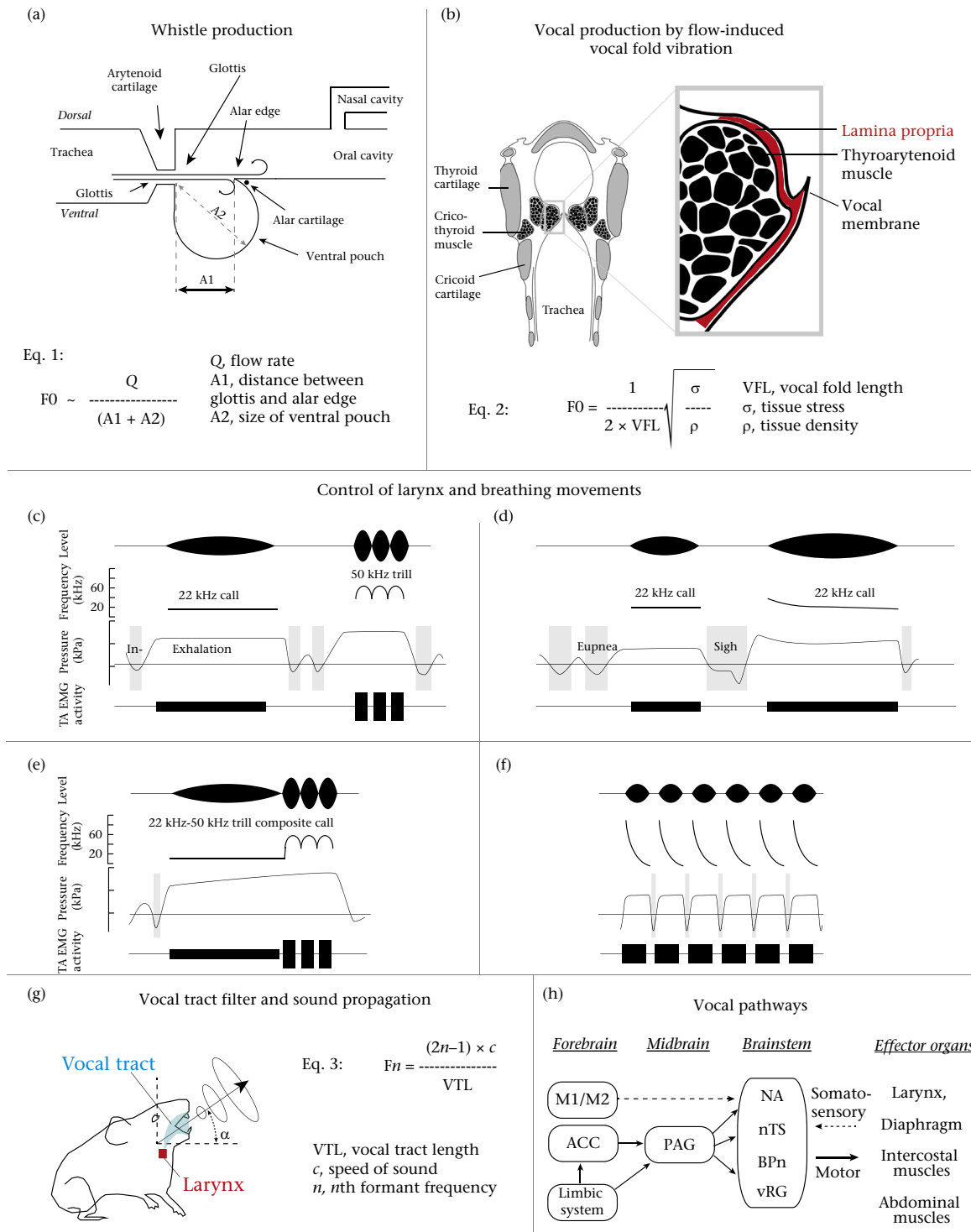


Figure 3. Sources of acoustic variation in murid and cricetid rodents. (a) Schematic of a midsagittal section of mouse laryngeal airway. Whistle production in mice is assumed to employ an edgetone mechanism. The glottal airflow passes over the opening of the ventral pouch and becomes deflected on the alar edge, generating pressure fluctuations. Fundamental frequency (F_0) depends on glottal flow rate (Q), the glottis–alar edge distance (A_1) and the size of the ventral pouch (A_2). (b) Flow-induced vocal fold vibrations is the second mechanism of vocal production for many sounds in rodent acoustic communication. The vibration rate of vocal folds, which determines the fundamental frequency (F_0), depends on mechanical properties (σ/ρ) of the lamina propria. (c) Breathing and laryngeal movements are controlled in a call type-specific fashion. (d) All three known breathing patterns in rodents (unlaboured normal breathing, sniffing and sighing) can be recruited for vocal production. (e) Rats have the capability of combining laryngeal movements into a single breath, generating the appearance of a vocal utterance consisting of a multiple spectral pattern, here a long flat component followed by a trill component. (f) Since both components can also be produced as stand-alone call types, this combination is referred to as ‘composite call’. Fast repetitions of syllables are likely to be based on the mouse’s ability for minibreaths, which replenish only the expended air volume and facilitate fast repletion rates. (g) Vocal tract resonances and sound propagation have not been studied in rodents but are likely to be under selection. (h) The neural pathways for vocal control in rodents has demonstrated the broadly established pathway between forebrain structures and brainstem motoneurons. The periaqueductal grey (PAG) plays an important gating function. Recent studies also suggest the presence of a direct motor cortex (M1/M2) – larynx motoneuron pathway (dashed line). The role of somatosensory feedback is little understood. ACC: Anterior cingulate cortex; NA: nucleus ambiguus; nTS: nucleus tractus solitarius; BPn: parabrachial nucleus; vRG: ventral respiratory group.

larynx interacts with a structure rostrally from the glottis (Fig. 3a). Whistles can be generated by different mechanisms, and the one in rodents has been compared to the 'edgetone model of whistle production' (Riede et al., 2017), a well-known concept for musical instruments (e.g. Coltman, 1976; Fletcher, 1979). The edgetone mechanism for rodent vocal production predicts that air in the ventral pouch cavity acts like a spring (Fig. 3a), wherein spectral properties of the resulting whistle sound (i.e. F0, F0 range and F0 modulation) are determined by (1) airflow rate through the glottal opening, (2) the size of the ventral pouch and (3) the distance between glottis and alar edge (Fig. 3b, equation 1) (Riede et al., 2017). Airflow rate through the glottis is determined by intrinsic laryngeal muscle activity and subglottal pressure (Riede, 2011, 2013). The geometry of the ventral pouch can be controlled through actively engaging intrinsic laryngeal muscles (Riede, 2011, 2013). A contraction of the thyroarytenoid muscle moves the alar cartilage closer to the glottis, thereby reducing the distance between glottis and alar edge and most likely reducing the volume of the ventral pouch simultaneously (Riede, 2013).

Recent work informed our understanding of the role of the ventral pouch in rodent whistle production. Among four ultrasonic whistle-producing rodents, ventral pouch size was inversely related to the F0 range of whistle sounds (Riede & Pasch, 2020). This suggests that laryngeal anatomy sets the foundation for vocal frequency range in whistle production across species. The role of the ventral pouch in sound amplification and modulation remains to be further explored.

Sound Produced by Airflow-induced Vocal Fold Vibrations

Airflow through the larynx causes vocal fold vibration, and the rate at which vocal folds vibrate determines the sound's F0. To a first approximation, vocal folds behave like a string (Fig. 3b, equation 2), whereby vocal folds that are larger or under less tension vibrate at a lower rate (Titze et al., 2016). Available studies on laryngeal anatomy of rodents indicate a close association between vocal fold size and body size (e.g. Riede et al., 2017; Riede, Coyne, et al., 2020; Riede & Pasch, 2020). Three different species of grasshopper mice produce surprisingly high F0 calls up to 16 kHz by airflow-induced vocal fold vibrations (Pasch et al., 2017), which are certainly at the upper limit or even above expectations for a 1 mm long vocal fold (Titze et al., 2016). Therefore, other mechanisms must facilitate variation in F0 produced by vocal fold vibrations. Besides active control of vocal fold length and tension, vocal fold mechanical properties are the most likely candidates. In Norway rats, the lamina propria is relatively thick and the fibrous proteins less organized (e.g. Tateya et al., 2005) compared with that in grasshopper mice, in which it is very thin and consists of densely packed collagen fibres (Pasch et al., 2017). We speculate that anatomical differences in lamina propria composition contribute to differences in mechanical properties and consequently to differences in the F0 range between Norway rats and grasshopper mice (up to 6 kHz in Norway rats; up to 15 kHz in grasshopper mice and between 7 and 12 kHz in house mice under stressful conditions; Grimsley et al., 2016). Indeed, Pasch et al. (2017) found that the vocal fold design in grasshopper mice differs dramatically from that in house mice (i.e. densely packed lamina propria and presence of vocal membranes) and proposed that such a design helps to raise the size-dependent upper frequency boundary.

Coordination of Laryngeal and Breathing Movements

Electrophysiological recordings in Norway rats (Sprague–Dawley) have demonstrated that both laryngeal muscle activity and subglottal pressure values are call type-specific (Riede, 2013).

Norway rats produce approximately 15 different call types (Wright et al., 2010), and each call type is associated with a characteristic coactivation of intrinsic laryngeal muscles. Fig. 3c exemplifies the activation of one intrinsic larynx muscle (TA, thyroarytenoid muscle) for two call types. The long flat call (22 kHz call) is associated with low-intensity and continuous muscle activity, but the 50 kHz trill is associated with burst-like high-intensity activations that match the trill pattern.

Laryngeal movements for vocal signal production are placed into the expiratory phase of the breathing cycle (Riede, 2011), i.e. high F0 whistles are produced during an exhalation (Fig. 3c). The subglottal pressure pattern is mostly call type-specific (Riede, 2013), but breathing patterns contribute to intraspecific acoustic variation. Breathing is a rhythmic behaviour with a characteristic rate. Three different breathing patterns in house mice and Norway rats are normal, unlaboured breaths (1–5 Hz), sniffing (5–10 Hz) and deep breaths (approximately 0.1 Hz; also known as 'sighing' or 'augmented breaths'), and are all used for vocal production. Associating a call type with one or another breath pattern generates acoustic variation. Riede, Schaefer et al. (2020) found that 22 kHz calls are longer in duration and that the fundamental frequency is more modulated following a deep inhalation than when the same call type follows an eupnea (Fig. 3d).

Vocal breath control studies have also revealed a capacity of rodents for combining call types into composite calls using a single breath (Fig. 3e), a phenomenon also known for bats and humans (Kanwal et al., 1994; Kershenbaum et al., 2016; Ravignani et al., 2019; Zuberbühler, 2020). Physiological recordings of laryngeal and respiratory activity in Sprague–Dawley rats suggested that rats combine two or more different call types into a single breath (Riede, 2014). Moreover, rats combine 22 kHz and 50 kHz trills into a single breath, so that the new call appears like a single uninterrupted composite call (Fig. 3e; Hernandez et al. (2017)). In nonhuman primates, call concatenation has been shown to be functionally relevant for communication (Zuberbühler, 2020), but the function in rodents is currently unknown.

High F0 whistles in male house mice have been labelled as songs for their high rates and diverse spectral appearance. Species like pygmy mice and Neotropical singing mice produce songs consisting of highly repeatable syllables uttered 10–20 times in short succession. The silent intersyllable intervals probably correspond to short inspirations (minibreaths) that allow time for larynx reconfiguration and replenishment of exhaled air used for sound production (Fig. 3f). How air supply and requirements for gas exchange dictate the temporal patterning of a mouse song remains to be explored. Comprehensive, synchronous recording of subglottal pressure, laryngeal muscle activity and vocal output in spontaneously behaving animals would open numerous avenues for exploration (e.g. Riede, 2011). For example, the call-to-call variation of call type-specific coactivation of intrinsic laryngeal and respiratory muscles has not yet been explored. How call type-specific coactivation of laryngeal and respiratory muscles occurs in other rodent species is also unstudied. For example, high F0 whistles that include frequency jumps are a spectral feature of great interest in house mice and Norway rats. Frequency jumps in Norway rats are not associated with measurable changes in subglottal pressure or laryngeal muscle activity (Riede, 2011, 2013). In the edgetone model of whistle production, frequency jumps can be generated by coupling mechanisms between the source and resonances of the attached vocal tract – a hypothesis to be further explored.

Contributions of Posture to Sound Radiation

The importance of the vocal tract filtering and sound radiation for high-frequency whistle production remains unclear (Fig. 3g)

Table 1
Open questions to be addressed in future investigations

Open questions	Approach
How does the ventral pouch contribute to acoustic variation	Comparative morphological work will elucidate the shape variation of vocal airways in rodents. Then interventional experiments can explain the relationship between ventral pouch geometry and acoustic features (e.g. spectral and amplitude range)
How is the neuromuscular system reconfigured across closely related taxa	Comprehensive physiological recording of laryngeal and breathing movements in spontaneously behaving animals of different species
What is the relationship between acoustic signals and diversification rates through time across the murid tree of life	Comprehensive sampling of phylogeny to characterize vocal behaviour and sound production, including the origins of the aerodynamic whistling mechanism
What is the functional relationship between olfactory and acoustic signals and are there redundancies or trade-offs in investment in olfactory versus acoustic signals	Characterization of multimodal nature of displays within species, assess major urinary protein (MUP) signal diversity versus acoustic signal diversity among species
Can receivers recognize different vocal signals or discriminate changes in acoustic variation	More studies using habituation–discrimination playback paradigms and operant conditioning procedures are necessary to examine how rodents discriminate and recognize different vocal signals, specific acoustic properties and patterns of acoustic variation
How do hormones modulate acoustic variation and what are the timescales and sites of action	Local pharmacological manipulations in steroid-sensitive brain regions involved in regulating the production of vocalizations can elucidate the role of steroids in modulating acoustic properties at short- and long-term scales. Treatment with drugs that do not cross the blood–brain barrier (e.g. androgen receptor blocker) will clarify steroid hormone actions in peripheral organs

(Riede, 2018). It is tempting to speculate that both variables play an important role and are under selection. Numerous species in the murid clade (e.g. grasshopper mice, Neotropical singing mice and northern pygmy mice) generate their vocalizations while the mouth is opened in a characteristic manner. Vocalizing animals often assume an upright posture (e.g. Bailey et al., 1929), affecting the angle between the ground and mouth of the sender (α in Fig. 3g). Body and head posture as well as mouth opening are likely to affect sound propagation patterns in rodents, as in other mammals (e.g. Hartley & Suthers, 1989; Olsen et al., 2020). Indeed, a flared mouth opening in grasshopper mice amplifies their long-distance signal by 20–30 dB (Pasch et al., 2017). Continued study of both variables deserves increased attention in future research.

Central Mechanisms for Vocalization

At a broader level, the brain represents an important source of acoustic variation in rodents (Krakauer et al., 2017). The investigation of central mechanisms for vocalizations in mice is an active field of research (Arriaga & Jarvis, 2013; Burgdorf et al., 2020; Mooney, 2020). The PAG is critical in gating forebrain information to brainstem circuitry (Jürgens, 2009; Tschida et al., 2019). The PAG receives inputs from different forebrain structures, some of which are implicated in regulating social behaviour (e.g. the hypothalamus, the extended amygdala and the nucleus accumbens; Newman, 1999; O'Connell & Hofmann, 2011). Forebrain areas (Fig. 3h) are also involved in mediating factors such as the presence of external sensory cues and the caller's internal state or experience, which can motivate the decision to vocalize. For example, efferent neurons from the limbic system are involved in either eliciting or inhibiting vocal signalling based on affective state (Bennett et al., 2019; Burgdorf et al., 2020). Vocal signal production depends on a pool of different brainstem motoneurons that activate laryngeal, respiratory and other facial/oral target organs. The PAG projects to this complex brainstem network and thereby facilitates rapid influence and coordination of vocal and respiratory activity.

A role for the rodent's motor cortex in vocal signal production has also been implicated. Tracing studies suggested direct or indirect projection from the motor (M1 and M2) cortex to brainstem nuclei which bypass the PAG (dashed line in Fig. 3h) (Arriaga & Jarvis, 2013; Van Daele & Cassell, 2009). Lesion studies in house mice (Arriaga et al., 2012) and local cooling experiments in Alston's singing mice (Okobi et al., 2019) support the hypothesis that motor cortex is involved in modulating brainstem vocal pattern generation.

In summary, recent findings suggest that rodent vocal production is complex and facilitated by integration of neural control with peripheral mechanisms. Studies that integrate how biomechanical properties, anatomy and neuromuscular systems interact to influence acoustic variation within and among species are needed to provide deeper insight into the evolution of vocal behaviour (Table 1).

CONCLUSIONS AND DIRECTIONS

Rodent acoustic signals vary considerably within and among species, and the degree of variation in spectral and temporal properties is species specific. Indeed, vocalizations should not be viewed solely as static but rather as highly dynamic and rapidly responsive to changes in context and motivational state. Analyses of intra- and interindividual variation should be included in future studies to identify the information content of various acoustic properties.

To date, functional studies implicate call rate, call duration, call diversity and performance trade-offs as important mediators of rodent social interactions. In parallel, mechanistic studies highlight the role of the brain, body and larynx, in particular, in shaping acoustic properties. The neurochemical pathways in which steroid and metabolic hormones modulate vocal pathways (indirectly on motivational centres or directly on pattern generators at brainstem level) remain to be studied. Furthermore, understanding the constraints inherent to each mode of laryngeal sound production is critical to informing the trajectories of acoustic variation and signal diversity. Although rates of frequency modulation or call duration are likely to be circumscribed by maximum rates of respiration, muscle activity or even neural control (Sirotin et al., 2014), how each system interacts differentially with the larynx during whistling versus vocal fold vibration is unknown. Similarly, biomechanical constraints unique to whistling are likely to require extreme modifications of the vocal tract to permit louder signal amplitudes. Thus, identifying the origins of the aerodynamic whistling mechanism in the rodent phylogeny is of high priority. Ultimately, understanding the nature of acoustic variation will require integration of mechanistic and functional studies to better understand diversification of rodent voices (Table 1).

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