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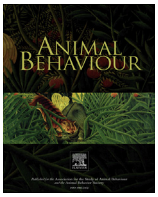

What's in a squeak? Female vocal signals predict the sexual behaviour of male house mice during courtship

Caitlyn J. Finton [1], Sarah M. Keesom [1], Kayleigh E. Hood, Laura M. Hurley*

Department of Biology, Indiana University, Bloomington, IN, U.S.A.

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Vocal production can be a two-way channel for the exchange of information between males and females during courtship. Although the ultrasonic vocalizations (USVs) of male house mice, *Mus musculus*, during interactions with females have been a focus of communication research, the vocalizations of females in this context remain poorly understood. During interactions with males, female mice produce audible vocalizations with a broadband harmonic structure (‘broadband vocalizations’, or BBVs) that are often described by human listeners as ‘squeaks’. We tested the hypothesis that the production of BBVs corresponds to male and female behaviours, as well as to contextual variables like oestrous phase, by measuring BBVs, USVs and nonvocal behaviours during 39 unique male–female pairings. We found that the relationship of BBVs to other behaviours depends on the phase of courtship. A high incidence of BBVs accompanied by male-directed kicks and lunges early in interactions predicted a lack of later male mounting and male-produced ‘50 kHz harmonic’ USVs. In contrast, there was significant temporal overlap between BBVs and 50 kHz harmonic USVs at later stages of courtship, potentially driven by mounting events. The duration of acoustically nonlinear segments of BBVs varied significantly among females, even across interactions with different males, but also varied across oestrous phase within females. These findings suggest that vocalizations could play a role in signalling acute female motivational state, identity or oestrous state during opposite-sex interactions. Since the information-bearing features of BBVs are relatively easily measured, they are potentially a useful readout of negative motivational state suitable for many research and educational applications.

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Vocalizations produced by house mice, *Mus musculus*, are an increasingly useful model for studying both the context dependence of vocal communication signals, and the bases of communication disorders (Chabout et al., 2012; Fischer & Hammerschmidt, 2011; Grimsley, Hazlett, & Wenstrup, 2013; Hanson & Hurley, 2012; Portfors & Perkel, 2014; Seagraves, Arthur, & Egnor, 2016). Mouse vocalizations have been categorized based on converging criteria including their spectrotemporal structure, the context in which they are produced, the identity of vocalizing mice and their association with nonvocal behaviours. Two major types of vocalizations that meet these criteria are ultrasonic isolation calls produced by pups and ultrasonic vocalizations produced during social interactions among adults (Egnor & Seagraves, 2016; Ehret & Haack, 1981; Heckman, McGuinness, Celikel, & Englitz, 2016; Lahvis, Alleva, & Scattoni, 2011; Liu, Miller, Merzenich, & Schreiner, 2003; Portfors & Perkel, 2014; Scattoni, Crawley, & Ricceri, 2009). Approaching vocalizations from this structural-functional perspective has allowed productive experimentation on the mechanistic bases of vocal communication in mice at behavioural, neural and genetic levels of analysis (Fischer & Hammerschmidt, 2011; Holfoth, Neilans, & Dent, 2014; Liu et al., 2003; Neilans, Holfoth, Radziwon, Portfors, & Dent, 2014; Portfors & Perkel, 2014; Roy, Watkins, & Heck, 2012; Scattoni, Ricceri, & Crawley, 2011). A third category of vocalizations about which much less is understood consists of human-audible broadband vocalizations, or ‘BBVs’ (Lupanova & Egorova, 2015).

Audible mouse vocalizations have been variously named ‘squeaks’, ‘low-frequency harmonic’ calls (LFHs), ‘squeals’, ‘clicks’ or ‘broadband vocalizations’ (Grimsley et al., 2013; Hanson & Hurley, 2016; Irwin, Kinoi, Van Sloten, & Workman, 1971; Nyby, 2001; Sugimoto et al., 2011). These vocalizations are characterized by a harmonic structure resembling that seen in the vocalizations of many other vertebrate species, including other rodents, other mammals and nonmammalian vertebrates, and that are even a feature of human speech (Bednářová, Hrouzková-Knotková, Burda,

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* Correspondence: L. M. Hurley, Department of Biology, Indiana University, 1001 E. Third Street, Bloomington, IN 47405, U.S.A.

E-mail address: lhurley@indiana.edu (L. M. Hurley).

[1] Co-equal authors.

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Sedláček, & Šumbera, 2013; Keesom, Rendon, Demas, & Hurley, 2015; Micheyl & Oxenham, 2010; Riede, Mitchell, Tokuda, & Owren, 2005, Riede, Arcadi, & Owren, 2007; Ryan & Guerra, 2014; Suta, Kvasnak, Popelar, & Syka, 2003; Suthers & Zollinger, 2004). BBVs are produced by both female and male mice in distress, as well as during conspecific interaction (Irwin et al., 1971; Lupanova & Egorova, 2015; Matthews et al., 2008; Wang, Liang, Burgdorf, Wess, & Yeomans, 2008; White, Prasad, Barfield, & Nyby, 1998). During opposite-sex interactions, BBVs are predominantly produced by females, as demonstrated by selectively preventing either male or female social partners from vocalizing (Wang et al., 2008; White et al., 1998). In physically and socially complex environments, female mice may also produce ultrasonic vocalizations (USVs) during pursuit by males, with males and females producing USVs in close proximity (Neunuebel, Taylor, Arthur, & Egnor, 2015). Female-produced BBVs during opposite-sex interactions are often tightly coupled in number and time with other female behaviours such as kicking or lunging at males, or darting away from males (Keesom & Hurley, 2016; Sugimoto et al., 2011). In contrast to the prosocial function of USVs, BBVs are therefore postulated to be acute signals of female rejection that may slow the progression of a sexual interaction (Johansen, Clemens, & Nunez, 2008). Reflecting the usage of these vocalizations in multiple contexts, male responses to playbacks of BBVs are context dependent. In the presence of olfactory cues of a predator, male mice avoid playbacks of BBVs more than when BBVs are paired with olfactory cues of females (Grimsley et al., 2013).

Although BBVs in general have been associated with specific behavioural contexts, the spectrotemporal structure of BBVs within even single contexts is highly variable (Lupanova & Egorova, 2015), raising the possibility that structural variation could carry behaviourally salient information. A prominent structural characteristic of female BBVs produced in opposite-sex interactions is the presence of spectral nonlinearity. Nonlinearities are commonly encountered features of vertebrate vocalizations that are thought to be caused by abrupt transition of vocal cords into irregular modes of vibration (Fee, Shraiman, Pesaran, & Mitra, 1998; Fitch, Neubauer, & Herzel, 2002; Fuamenya, Robb, & Wermke, 2015; Titze, Riede, & Popolo, 2008; Tokuda, Riede, Neubauer, Owren, & Herzel, 2002; Wilden, Herzel, Peters, & Tembrock, 1998). There are multiple categories of nonlinearity including subharmonics, in which a doubling or tripling of harmonics occurs, and deterministic chaos, or structured noise. In a range of species, nonlinearities convey important information. Nonlinearities may attract attention from conspecifics with high efficacy, reduce habituation to alarm calls, correspond to the physical quality of vocally advertising males or signal individual identity (Blumstein & Récapet, 2009; Blumstein, Richardson, Cooley, Winternitz, & Daniel, 2008; Fitch et al., 2002; Hauser, 1993; Karp, Manser, Wiley, & Townsend, 2014; Riede et al., 2007; Wilden et al., 1998). Nonlinearities and other structural characteristics of female mouse BBVs therefore have the potential to not only serve as a general signal of motivational state, but also to signal specific information to male partners of female mice.

To assess this potential, we characterized multiple characteristics of BBVs, including vocal nonlinearities, during interactions of female mice with males. We allowed females to freely cycle through oestrous phases to further determine whether vocal structure relates to reproductive state. Structural variation in female BBVs was compared to variation in vocal and nonvocal behaviours of both partners. We predicted that (1) BBVs would be coproduced with nonvocal female behaviours, as previously reported (Sugimoto et al., 2011), (2) structural variation in BBVs would correspond to behavioural variation by females or males and (3) the characteristics of BBV structure would be influenced by female reproductive state. All three of these predictions were confirmed. We additionally discovered that the relationships between BBVs and reproductive behaviours varied across different phases of social interactions, and that BBVs in the early phase of an interaction predicted sexual behaviour by males in a later phase.

METHODS

Animals

Focal subjects consisted of 13 female CBA/J mice (the Jackson Laboratory, Bar Harbor, ME, U.S.A.) paired with males. An additional 13 male mice of the same strain served as social partners for females. All female mice were aged 7–8 weeks at the time of the focal interactions, and were previously housed individually for 2 weeks on a 14:10 h light:dark cycle, with food and water provided ad libitum. Mice were housed in standard plastic caging for laboratory mice (28.5 × 17.5 cm and 12.5 cm tall), with pine bedding and supplemental nesting material. One week before behavioural recordings, females were given opposite-sex experience through three 10 min interactions with unfamiliar males on three consecutive days. Likewise, males used as social partners in experiments were given opposite-sex experience through three 10 min interactions with unfamiliar females on three consecutive days. Male and female mice used to give experience to experimental subjects were not used in experiments after these interactions.

Ethical Note

Care was taken to ensure compliance with guidelines on animal welfare in reducing the number of mice used in these studies and minimizing their pain or suffering. Mice were monitored during interactions to ensure that aggressive behaviour did not result in injury. Interactions resulting in injury would have been halted, but no interactions resulted in any injury. The balanced design, in which females were used in multiple interactions, allowed us to assess individual differences while collecting data from the same females across oestrous phase and across interactions with different males, resulting in efficient use of females. Finally, mice in the study were later used in different studies in our laboratory, as permitted by our animal welfare protocol. At the conclusion of all studies, mice were euthanized according to standard veterinary guidelines for the euthanization of small animals. All procedures were approved by the Bloomington Institutional Animal Care and Use Committee (protocol 15-021).

Experimental Design

Each female subject and male partner mouse participated in three unique social interactions, with one interaction per day and a novel partner for each interaction. Mice were transported to the recording room between 0800 and 0900 hours to allow habituation to the testing room. Interactions began between 1100 and 1400 hours. For 10 female mice, the 20 min interaction took place in the female's home cage (28.5 × 17.5 cm and 12.5 cm tall) inside a sound-attenuated recording chamber. Before the interaction, females in their home cages were placed in the recording chamber for 5 min. After habituation, a male of 7–8 weeks of age was added to the female's home cage and the interaction began. At the end of a 20 min interaction, the male was removed from the female's cage and returned to his home cage. From the 10 females and 10 males interacting in the home cages of females, a total of 30 unique male–female pairings were recorded.

For three separate female subjects, 20 min recordings took place in a mesh butterfly cage (~30.5 cm^3), which was empty except for

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