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Ultrasonic vocalizations as a tool for research on emotion and motivation in rodents

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Mice and rats are the most common laboratory animals utilised in biomedical research, neuroscience and experimental psychology. These species have extensively been used to study basic mechanisms underlying emotional and motivational functions. Such research usually relies on overt behavioural measures, like approaching (or working for) an appetitive stimulus, or avoiding or fleeing from an aversive one. Besides, the presumed motivational and affective state is usually inferred from physiological measures, like heart rate, corticosterone excretion, or brain activity. In addition, or even extension to these measures, substantial information about the animal under study can also be obtained by gauging its vocalization, most of which often occurs in the ultrasonic range. Such ultrasonic vocalizations (USV) are behaviourally important for at least two aspects: For one, they can serve as a measure of its current state, and secondly, they seem to be an important communicative variable, which has to be taken into account when analysing social aspects of such species (mating, nursing, aggression, defence etc.).

Data on USV in rodents were reported as early as 1954. Anderson (Anderson, 1954) observed that adult laboratory rats emit calls at frequencies around 23-28 kHz when socially isolated. Two years later, Zippelius and Schleidt published their important discovery that infant mice produce USV when separated from their mother and litter (Zippelius et al., 1956). Since then, several studies were performed showing that measuring USV can provide new insights into emotion and motivation as well as communication in mice and rats.

Mouse

Three USV classes are currently known in mice. Their occurrence is dependent on the animal's age. Isolation-induced USV are emitted by mouse pups during the first two weeks of life when separated from mother and littermates. Interaction-induced USV occur during social investigation in juvenile mice aged three to four weeks. Finally, female-induced USV are uttered by adult male mice when exposed to females or female urine.

Isolation-induced ultrasonic vocalizations

Affective state: Following Konrad Lorenz Zippelius and Schleidt (1956) named isolation-induced USV "Pfeifen des Verlassenseins" ("whistles of loneliness"), implying a negative affective state. Despite the fact that a wealth of evidence in support of the affective hypothesis has been accumulated since then, there is an ongoing scientific dispute on whether such isolation-induced USV reflect a negative affective state or whether they are simply the byproduct of a thermoregulation process (Blumberg & Sokoloff, 2001). Strongest argument in favour of the affective hypothesis is the fact that anxiolytic compounds such as benzodiazepines and other positive modulators of GABA-receptors reduce the production of isolation-induced USV (Benton & Nastiti, 1988; Fish et al., 2000; Nastiti et al., 1991; Takahashi et al., 2009).

Communicative function: Zippelius and Schleidt (1956) suggested that isolation-induced USV serve communicative purposes, since they have observed that mothers leave the nest to retrieve vocalizing pups scattered outside the nest, whereas no retrieval behaviour was seen in response to pups that have been anesthetized and hence did not emit isolation-induced USV. Later, it shown by means of playback experiments that indeed isolation-induced ultrasonic vocalizations elicit maternal search and retrieval behaviour (Ehret, 1987; Ehret & Haack, 1981; Sewell, 1970; Smith, 1976; Wöhr et al., 2008a).

In line with their communicative function, isolation-induced USV are increasingly used as a measure for the quantification of communication deficits in mouse models of neuropsychiatric disorders characterized by social and communication deficits (Scattoni et al., 2009; Silverman et al., 2010). There are a number of genetic mouse models of autism, speech impairment and related disorders displaying a reduction of isolation-induced USV (Chadman et al., 2008; Enard et al., 2009; Fujita et al., 2008; Gaub et al., 2010; Groszer et al., 2008; Jiang et al., 2010; Kurz et al., 2010; Laviola et al., 2006; Moles et al., 2004; Nakatani et al., 2009; Shu et al., 2005; Winslow & Insel, 2002; Young et al., 2010), while other mouse models, e.g. the BTBR T+tf/J inbred strain mouse model of autism, are characterized by an unusual repertoire of isolation-induced USV (Scattoni et al., 2008).

Interaction-induced ultrasonic vocalizations

Affective state: Recently, Panksepp et al. (2007) reported that also juvenile mice produce USV. They found high rates of USV during social interactions of four week old mice. As the production of interaction-induced USV occurred during the play period and no aggressive behaviour was observed, it is tempting to speculate that they reflect a positive affective state alike rat 50-kHz USV that also occur during play behaviour (Knutson et al., 1998; Otterbein et al., 2005). It is remarkable that emission of interaction-induced USV declines rapidly with sexual maturity – at the time when male mice start to display aggressive behaviour. Then, male mice begin to emit female-induced USV. In females, however, interaction-induced USV persist into adulthood (Moles et al., 2007).

Communicative function: It was suggested that interaction-induced USV help to maintain social contact, since their occurrence is positively associated with social investigation behaviour (Panksepp et al., 2007). In line with an affiliative function, Scattoni et al. (in press) reported that the lack of social investigation behaviour in the BTBR T+tf/J autism model is paralleled by a lack of interaction-induced USV.

Female-induced ultrasonic vocalizations

Affective state: In adult mice, high rates of USV were found in males when courting and copulating with females (Sewell, 1967). As shown by Whitney et al. (1974), female urine alone, i.e. in the absence of a female, is sufficient for eliciting male USV. No vocalization response, however, was detected when male mice were exposed to male mouse urine or female urine from rats or humans (Wang et al., 2008; Whitney et al. 1974). The production of male USV in response to females has song-like characteristics, including different syllable types and a temporal sequencing that includes the emission of repeated phrases (Holy & Guo, 2005). Interestingly, female-induced USV are highly sensitive to important social factors such as social status (D'Amato, 1991; Nyby et al., 1976) and previous heterosexual contact (Dizinno et al., 1978; Maggio et al., 1983; Nyby et al., 1977; Nyby et al.1983; Roullet et al., 2011; Sipos et al., 1992; Sipos et al.,1995). The notion that female-induced USV reflect a positive affective state alike rat 50-kHz USV (Panksepp & Burgdorf, 2003) is supported by the fact that USV in adult male mice can also be induced by amphetamine (Wang et al., 2008).

Communicative function: As shown in devocalization and playback studies, female-induced USV serve an important communicative function, namely to attract females (Hammerschmidt et al., 2009; Pomerantz et al., 1983). As for isolation- and interaction-induced USV, reduced levels of female-induced USV were reported in mouse models of autism (Jaiman et al., 2008; Radyushkin et al., 2009; Wöhr et al., in press b).

Rat

Dependent on sound frequency, call lengths and frequency modulation, at least three different classes of USV can be identified in the rat. Their occurrence differs dependent on animal age, and physical, or psychological demands of the environment (Knutson et al., 2002).

Isolation-induced ultrasonic vocalizations

Affective state: Rat pups typically exhibit USV around the 40-kHz level in response to several distressing situations, like separation from their litter and mother (Hofer, 1996; Hofer et al., 1978), or when ambient temperature drops (Blumberg et al., 1996). Considering the affective value of such experiences it was postulated that infant calling reflects a negative affective state. Indeed, isolation-induced USV appear to be a valid index of pup anxiety, since the rate of calling can be attenuated by anxiolytic drugs (Hofer, 1996; Insel et al., 1986; Kehne et al., 2000; Olivier et al., 1998a; Olivier et al., 1998b; Vivian et al., 1997). Furthermore, these calls seem to have an important value for pup survival. Thus, 40-kHz-vocalization can elicit maternal care, like licking or search and retrieval behavior. Playback of USV can induce stimulus directed search behavior (Allin et al., 1972; Smotherman et al., 1974; Wöhr et al., 2006; for mice see: Ehret et al., 1981). Furthermore, distress calls also act as a main elicitor of anogenital licking (Brouette-Lahlou et al., 1992). Such licking serves a vital function, since non-licked pups cannot defecate, and do not survive. Interestingly, maternal care can affect the development of emotionality. Adult rats, which had been licked more often during infancy, show less anxiety-related behavior in response to aversive stimuli than less frequently licked rats (Caldji et al., 1998). In accordance with this finding, it was shown that frequently licked animals emitted less isolation-induced USV, i.e. less anxiety-related behavior, in infancy than rarely licked animals (Wöhr et al., 2008b).

In contrast to simple USV measures like occurrence and frequency range, much less is known about the sonographic structure of such calls. Until recently, most research on USV in rats has been conducted with simple bat detectors set on limited frequency ranges. Since the emission of these 40-kHz calls is characterized by a high variability, calls occurring at different frequency ranges might be missed. Therefore, researchers have begun to look at sonographic characteristics in more detail. Brudzynski et al., (1999) were able to classify infant calls according to ten categories by using a recording system that is capable of monitoring a wide range of frequencies. Sonographic analysis revealed a developmental trend emphasizing those call characteristics, which are important for pup survival (Brudzynski et al., 1999). More recently, detailed sonographic analysis provides evidence that pharmacological treatment can selectively affect certain call patterns rather than USV production in general (Barron et al., 2005). Furthermore, it was shown that call characteristics, like amplitude, frequency modulation and bout structure, are related to the amount of maternal care experienced during early life (Wöhr et al., 2008b).

Communicative function: Isolation-induced USV seem to have an important value for pup survival. As isolation-induced USV in mice, rat 40-kHz USV can elicit maternal search and retrieval behaviour as demonstrated by means of playback studies (Allin et al., 1972; Smotherman et al., 1974; Wöhr & Schwarting, 2008a).

Fear-induced ultrasonic vocalizations

Affective state: Adult rats produce two different types of USV. These calls have been classified primarily on the basis of their sound frequency as low and high frequency USV. Low frequency vocalizations, so called 22-kHz vocalizations, are within a frequency range of 18 – 32 kHz. The calls have a narrow bandwidth of 1–6 kHz, a sound pressure level of 65–85 dB, and call durations of approximately 300–4000 ms (Borta et al., 2005; Brudzynski, 2001; Sales et al., 1974; van der Poel et al., 1989; Wöhr et al., 2005). High frequency vocalizations, so called 50-kHz-vocalizations, are within a frequency range of 32–96 kHz, with short durations of 30–50 ms, and a narrow bandwidth of 5–7 kHz (Brudzynski & Pniak, 2002; Kaltwasser, 1990; Sales et al., 1974; White et al., 1990). Increasing evidence from ethological, pharmacological, and brain stimulation studies suggest that these vocalizations are critically dependent on situational factors and experience, and may represent distinct affective states of the subject. Low-frequency 22-kHz USV are emitted by adult rats when exposed to predators (Blanchard et al., 1991), or other aversive stimuli, like startling noises (Kaltwasser, 1991), or unescapable foot-shocks (Antoniadis et al., 1999; Borta et al., 2006; Vivian et al., 1993; Wöhr et al., 2005). Furthermore, 22-kHz vocalizations are emitted during intermale aggression (Vivian et al., 1993).

Such vocalizations are not only emitted during the actual aversive event, but also in response to stimuli associated with such experiences (Antoniadis et al., 1999; Borta et al., 2006; Cuomo et al., 1988; De Vry et al., 1993; Molewijk et al., 1995; van der Poel et al., 1989; Wöhr et al., 2005). Accordingly, it was assumed that these calls reflect a negative affective state akin to anxiety and depression.

However, little information is available upon which acoustic parameter is carrying the strength of the signal. Interestingly, it was shown that not only the number of calls emitted is related to the intensity of an emotional state in the rat, but that latencies to utter vocalizations, call-lengths and loudness can also reflect the intensity of an aversive emotional state (Wöhr et al., 2005). Furthermore, rats, which were defined as highly anxious based on the time spent in the open arms of the elevated plus maze, tended to vocalize more often than rats displaying low anxiety-like behavior, and exhibited a higher peak frequency (Borta et al., 2006).

Communicative function: Blanchard et al. (1991) suggested that 22-kHz USV serve as alarm calls to warn conspecifics about danger. They observed that 22-kHz USV production in response to a predator, a cat, is dependent on the presence of conspecifics. In absence of such an audience, no 22-kHz USV were observed when a rat was exposed to a cat. Although an audience effect was not replicated in standardized laboratory conditions (Wöhr & Schwarting, 2008b), there is evidence that 22-kHz USV can induce anxiety-related behavior such as freezing in the recipient, supporting the notion that 22-kHz USV indeed serve an alarm function. By means of playback experiments it was shown that 22-kHz USV induce locomotor inhibition (Wöhr & Schwarting, 2007) and neuronal activity in brain areas implicated in fear regulation such as amygdala and central grey (Sadananda et al., 2008). Recent findings even indicate that rats are predisposed to form memory associations between 22-kHz USV and aversive stimuli (Bang et al., 2008; Endres et al., 2007; Furtak et al., 2007) and that 22-kHz USV play an important role in the social transmission of fear (Kim et al., 2010).

Interaction-induced ultrasonic vocalizations

Affective state: High-frequency 50-kHz USV occur in naturalistic contexts including juvenile play (Knutson et al., 1998; Otterbein et al., 2005), tickling (Burgdorf & Panksepp, 2001; Mällo et al., 2007; Panksepp & Burgdorf, 2000; Panksepp & Burgdorf, 2003; Schwarting et al., 2007; Wöhr et al., 2009), social exploratory activity (Brudzynski & Pniak., 2002), and mating behviour (McGinnis et al., 2003; White et al., 1990). Since 50-kHz USV are also expressed during anticipation of copulation (Bialy et al., 2000), play (Knutson et al., 1998), food (Burgdorf et al., 2000), and electrical stimulation of the medial forebrain bundle (Burgdorf et al., 2000), it has been postulated that these calls are sensitive marker for unconditioned and conditioned reward states (Knutson et al., 1999) and Panksepp and Burgdorf (2003) assumed that these calls reflect a positive affective state akin to joy.

On the basis of these findings, 50-kHz USV are increasingly used as a measure of positive affect in drug studies. It was repeatedly shown that administration of amphetamine elicits high rates of 50 kHz USV in a dose-dependent manner (Ahrens et al., 2009; Burgdorf et al., 2001; Knutson et al., 1999; Natusch & Schwarting, 2010; Wintink et al., 2001; Wright et al., 2010). Amphetamine-induced 50-kHz USV emission is affected by the test context. Higher call rates are emitted when testing is performed in test environments with fresh bedding material (Natusch & Schwarting, 2010). Also, social context has an impact on amphetamine-induced 50-kHz USV production (Wright et al., 2010). Wright et al. (2010) performed a detailed spectrographic analysis of 50-kHz USV elicited by amphetamine and identified 14 categories of 50-kHz USV. They found that pair-tested rats produce a higher proportion of frequency-modulated 50-kHz USV than individually-tested rats under both amphetamine and saline conditions, and that amphetamine treatment alters the call profile such that frequency-modulated 50-kHz USV became more prominent while flat 50-kHz USV occurred less often. Recently, it was demonstrated by means of cocaine self-administration experiments that 50-kHz USV can also serve as a useful marker for affective responses to cocaine administration, anticipation and craving (Barker et al., 2010; Maier et al., 2010).

As the production of aversive 22-kHz USV, emission of 50-kHz USV is characterized by huge inter-individual differences (Mällo et al., 2007; Schwarting et al., 2007; Wöhr et al., 2009). In tickling experiments, it was found that not all rats emit 50-kHz USV – some rats do not emit USV at all, others even emit 22-kHz USV (Mällo et al., 2007; Schwarting et al., 2007; Wöhr et al., 2009). Such inter-individual differences are considered predictive of stable individual traits in tests for social behaviour, anxiety and depression. Indeed, rats can be selectively bred for low and high rates of 50-kHz USV emission and such breeding is affecting social behaviour as well as anxiety- and depression-related behaviour. Rats bred for low levels of 50-kHz USV spent less time in contact with conspecifics in adulthood (Burgdorf et al., 2009) and do not show a preference for maternally associated stimuli in infancy (Harmon et al., 2008). Conversly, rats bred for high rates of 50-kHz USV display less anxiety-related behaviour as indicated by more center entries in an open field in adulthood (Burgdorf et al., 2009) and fewer isolation-induced USV in infancy (Harmon et al., 2008).

Recently, inter-individual differences in the production of 50-kHz USV were found to be linked with neurogenesis in the dentate gyrus of the hippocampus (Wöhr et al., 2009; Yamamuro et al., 2010). While the number of 50-kHz USV emitted during tickling was highly positively correlated with hippocampal cell proliferation, a highly negative correlation between 22-kHz USV and hippocampal cell proliferation was obtained. Interestingly, neurogenesis in the hippocampus has been repeatedly associated with affect regulation and psychopathology such as depression. Thus, it is well known that aversive stimuli and events like social defeat reduce hippocampal cell proliferation and that hippocampal cell proliferation is necessary for the antidepressant effects of selective serotonin reuptake inhibitors (Santarelli et al., 2003). It is therefore remarkable that neurogenesis in the dentate gyrus of the hippocampus is enhanced by tickling in rats that experienced the tickling stimulation presumably as appetitive as indicated by high numbers of 50-kHz USV (Wöhr et al., 2009; Yamamuro et al., 2010). Hippocampal cell proliferation levels in rats that emitted high rates of 50-kHz USV during tickling were almost as double as high than in non-tickled controls or in rats that emitted only some very few 50-kHz USV during tickling (Wöhr et al., 2009).

Communicative function: Besides appetitive situations, 50-kHz USV also occur after separation from conspecifics during short social isolation. Rats taken out from their home cage and individually exposed to a clean cage emit 50-kHz USV (Schwarting et al., 2007; Wöhr et al., 2008b). Typically, 50-kHz USV emission is highest during the very first minutes after separation from conspecifics (Wöhr et al., 2008b). For at least two reasons it appears to be unlikely that the emission of 50-kHz USV is novelty-induced. Firstly, 50-kHz USV emission is stable across testing days, i.e. no habituation occurs (Wöhr et al., 2008b). Secondly, not only the rat that has been taken out from the homecage starts to emit 50-kHz USV, but also the rat that stays alone in the homecage after the conspecific has been removed (Wöhr et al., 2008b). The fact that separation from conspecifics elicits 50-kHz USV indicates an affiliative communicative function of 50-kHz USV, namely to (re)establish or to maintain social contact.

An affiliative communicative function of 50-kHz USV is also in line with the observation that rats spent more time with conspecifics that vocalize a lot, than with those that display little emission of 50-kHz USV (Panksepp et al., 2002). Furthermore, Siviy and Panksepp (1987) showed that devocalizing or deafening rats affects rough and tumble play. Finally, Brudzynski and Pniak (2002) found that rats emit 50-kHz USV in a dose-dependent manner when exposed to odor of conspecifics, indicating that 50-kHz USV utterance is driven by potential social contact.

Subsequent playback studies further support the notion that 50-kHz USV serve as social contact calls. While aversive 22-kHz USV induce behavioural inhibition in the recipient, appetitive 50-kHz USV induce social exploratory behaviour (Wöhr & Schwarting, 2007; Wöhr & Schwarting, 2009). Exposure of rats to 50-kHz USV induce a three-fold increase in locomotor activity in comparison to that induced in test phases without acoustic playback or phases where an acoustic control stimulus was presented. Remarkably, the induced locomotor activity was directed towards the loudspeaker. During the 60 s period of 50-kHz USV playback, juvenile rats spent on average less than 5 s away form the speaker, while more than 40 s near to it. Such a preference was not observed during test phases without USV playback or when an acoustic control stimulus was presented. Noteworthy, social approach behaviour was weaker in adult rats, probably due to lower levels of social motivation.

The opposite behavioural responses elicited by playback of aversive 22-kHz USV and appetitive 50-kHz USV is paralleled by distinct patterns of brain activation (Sadananda et al., 2008). While playback of aversive 22-kHz USV is followed by an increase of neuronal activity in brain areas implicated in the regulation of anxiety and fears, such as amygdala and central grey, 50-kHz USV elicit activity in the nucleus accumbens, a key area for reward processing.

A first pharmacological study shows that social approach displayed in response to playback of 50-kHz USV can be used for studying neurochemical mechanisms underlying social motivation and interest (Wöhr et al., 2009). Endogenous opioids play an important role in the regulation of social behaviors. In rats, particularly rough and tumble play is affected by the administration of exogenous opioids. It was consistently shown that the administration of low doses of µ-opioid-receptor-agonists, such as morphine, increases rough and tumble play, while a decrease in rough and tumble play was observed after administration of µ-opioid-receptor-antagonists, such as naloxone (Vanderschuren et al., 1997). In line with these findings it was found that also social approach behaviour in response to playback of 50-kHz USV is affected by the administration of exogenous opioids. In juvenile as well as in adult rats, social approach behaviour was reduced after naloxone treatment, but enhanced with morphine (Wöhr et al., 2009). In addition to overt behavioural changes, ultrasonic calling in response to playback of 50-kHz USV was affected by opioid ligands in juvenile rats. While saline- and morphine-treated rats vocalized, no vocalization response was detected in rats treated with naloxone (Wöhr et al., 2009). This finding is in line with a study on ultrasonic communication in µ-opioid-receptor-knockout mice. Typically, male mice display social exploratory activity when exposed to interaction-induced USV emitted by females (Wöhr et al., in press a). Remarkably, adult male mice lacking the µ-opioid-receptor, however, do not display social exploratory behaviour under such conditions (Wöhr et al., in press a). Together, this indicates that an important feature of rodent social behaviour, namely ultrasonic communication, is at least partially regulated by endogenous opioids.

Conclusion

Production of USV can be utilized to study the neuroanatomical and pharmacological basis of motivation and emotion. Behavioural responses to playback of USV can provide important insights into the social brain and help to elucidate genetic, neurochemical and neuroanatomical factors underlying neuropsychiatric disorders characterized by social deficits such as autism. The application of new, more sophisticated recording systems and sound analysis tools which enables the researcher to create detailed spectrograms provides a clear improvement for research on USV. By using these tools the investigator can detect critical differences between treatments or individual animals, which may not be detectable with standard behavioural measurements.

Further reading

For more detailed overviews on ultrasonic communication in rodents please see: Wöhr & Schwarting, 2010a; Wöhr & Schwarting, 2010b, and Wöhr et al., 2010. There is also an overview in German available: Wöhr & Schwarting, 2010c.

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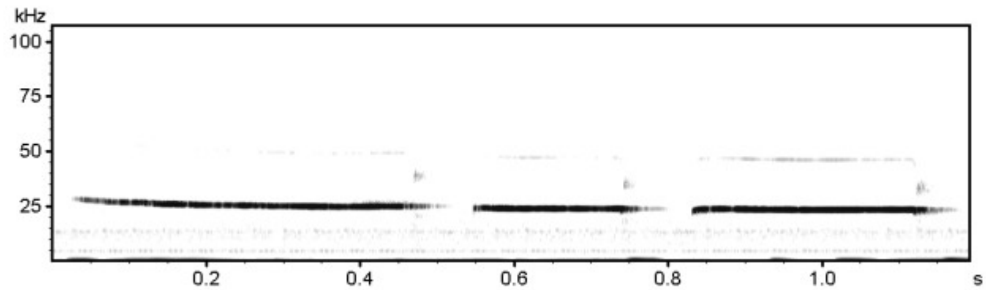
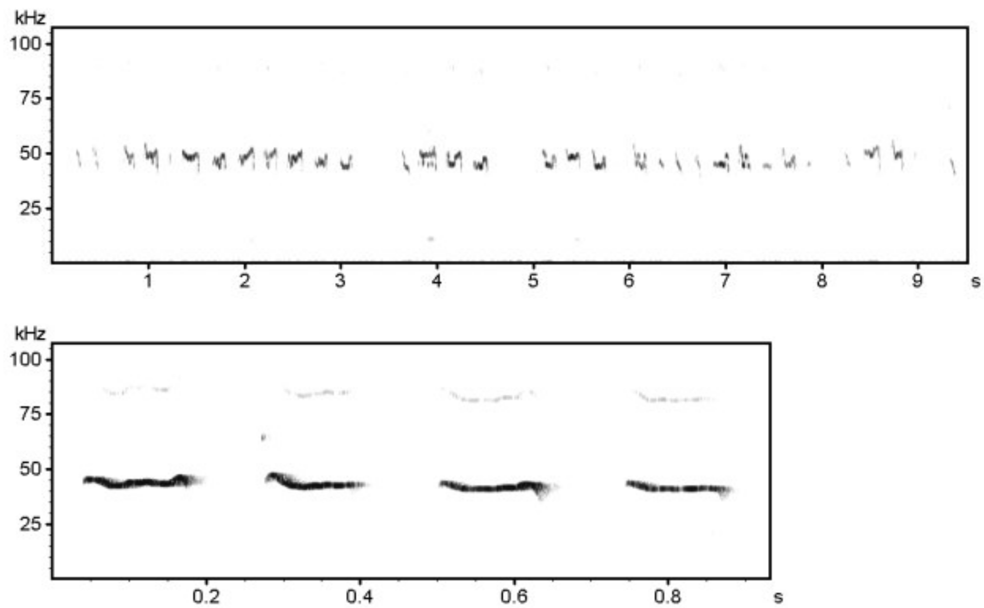
Examples of rat ultrasonic vocalizations (USV)
Norwegian Rat (*Rattus norvegicus*), Wistar albino strain, Males

The following recordings have been made with Avisoft-UltraSoundGate 116-200 at a sample rate of 214.285 kHz. In order to make the recordings audible, the sample rate of the original wav files has been set to 11.025 kHz (providing a time expansion factor of 19.44).

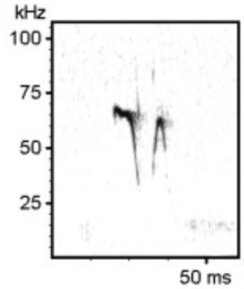


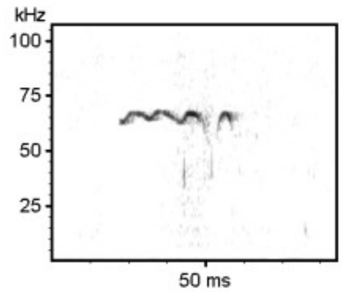
22 kHz rat calls ('distress' calls). Listen to the time-expanded wav file.



40 kHz rat calls (note the different time scales of the two spectrograms). Listen to the time-expanded wav file.

Various 50 kHz rat calls :





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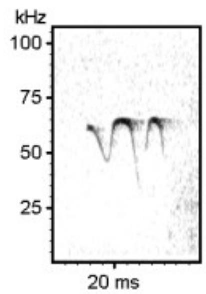

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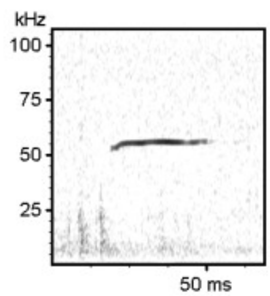

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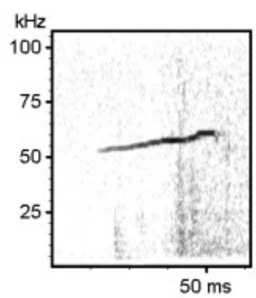

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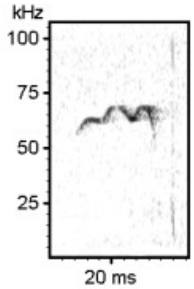

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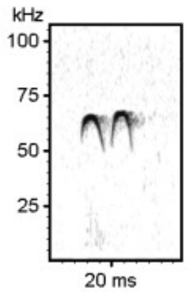

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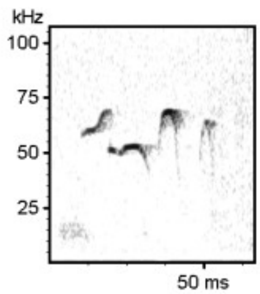

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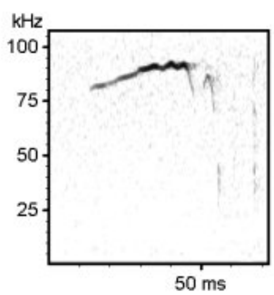

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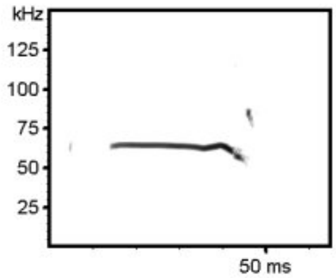
Examples of mouse ultrasonic vocalizations (USV)
Laboratory mouse (*Mus musculus*), C57BL/6JOlaHSd strain, infant male, 7 days old, separation-induced vocalizations

The following recordings have been made with Avisoft-UltraSoundGate 116-200 at a sample rate of 300 kHz. In order to make the recordings audible, the sample rate of the original wav files has been set to 22.05 kHz (providing a time expansion factor of 13.6).



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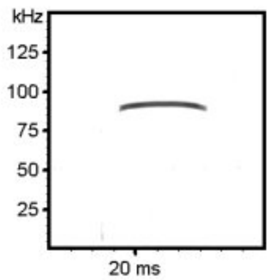

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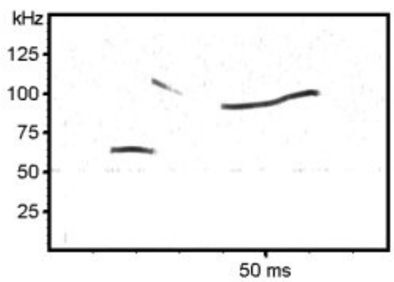

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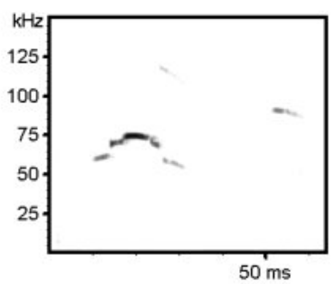

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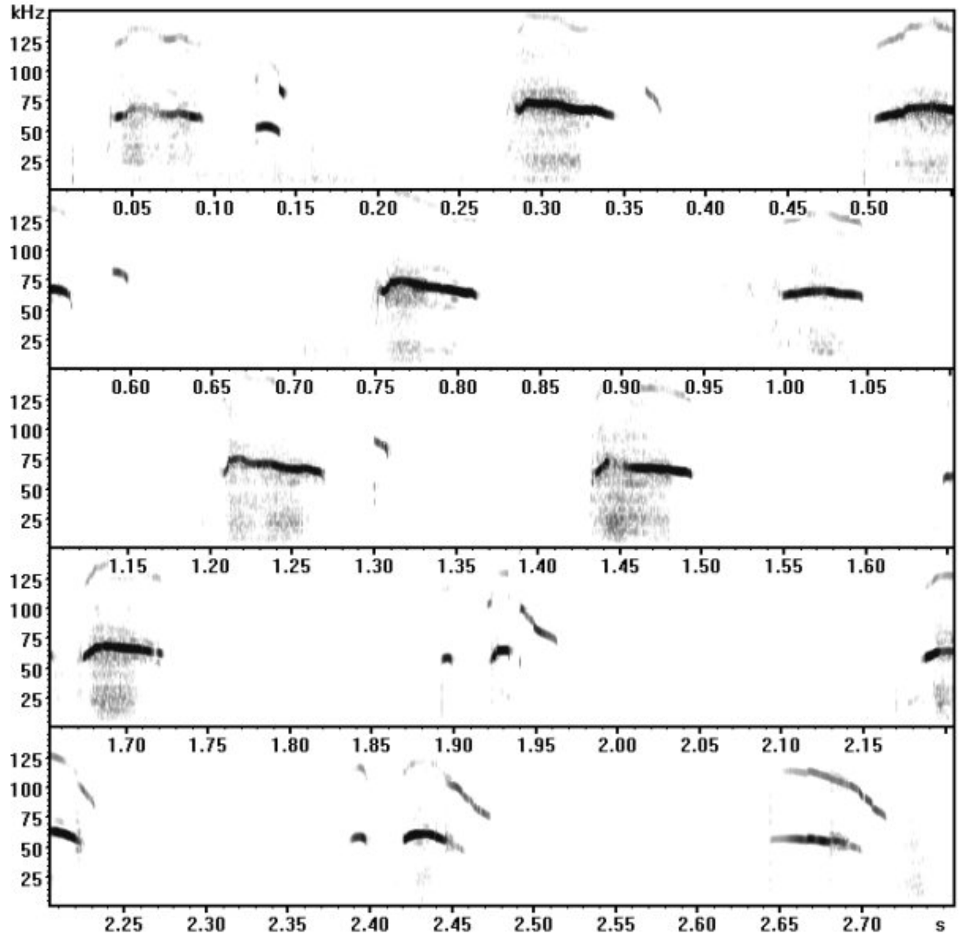

wav file

All sound recordings by Markus Wöhr (Philipps-University of Marburg, Germany).

An overview on the Avisoft Bioacoustics products suited for recording and analyzing mice and rat USV is available at the USV products overview page.

 last modified on 23 December 2010, Raimund Specht