Chapter 149
Effects of Previous Acoustic Experience on Behavioral Responses to Experimental Sound Stimuli and Implications for Research

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Abstract Ambient noise differs considerably between habitats. Increased ambient noise can affect the physiology and behavior in a variety of taxa. Previous acoustic experience can modify behavior and potentially affect research conclusions in natural and laboratory environments. Acoustic conditions should thus be accounted for, especially in experiments involving experimental sound stimuli. Methods sections should contain acoustic specifications, and a consensus should be achieved over which measurements to include for comparability between researchers. Further investigation of how previous and repeated exposure to sound affects behavior and research conclusions is needed to improve our knowledge of acoustic long-term effects in animal welfare and conservation.

Keywords Holding conditions • Aquarium noise • Anthropogenic noise • Ambient noise • Carryover

1 Ambient Noise Level Variability

Ambient noise varies greatly in terrestrial and aquatic environments. This variability arises from different sound-propagation characteristics modified by vegetation cover and density, substrate conditions, and abiotic and biotic sound sources (e.g., Marler and Slabbekoorn 2004; Popper and Hastings 2009a). Vegetation is a key factor that degrades and attenuates sound with increasing biomass and density (Martens 1980; Richards and Wiley 1980). Substrate characteristics mediate the amount of

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sound reflected or absorbed (e.g., Slabbekoorn et al. 2007). Abiotic sounds, such as those caused by rain, water currents, wind, earthquakes, and avalanches (e.g., Popper and Hastings 2009a), and biotic sound sources actively and passively emitted by living organisms (e.g., Bradbury and Vehrencamp 1998; Amorim 2006; Goerlitz et al. 2008) mediate the amount of signal interference and masking (e.g., Greenfield 1994; Bradbury and Vehrencamp 1998).

In terrestrial habitats, it has been long recognized that acoustic environments shape sensory ecology and evolution. In birds, for instance, song structures within and between species change with environmental conditions due to habitat-specific sound propagation and naturally occurring ambient noise (Morton 1975; Richards and Wiley 1980; Slabbekoorn and Smith 2002). Considerable work has investigated how acoustic experience can affect singing and mate choice behavior in birds (Riebel 2003; Marler and Slabbekoorn 2004; Woolley 2012), and previous acoustic experience has also been shown to modify reproductive behavior in crickets (*Gryllidae*; Wagner et al. 2001; Bailey et al. 2010).

Increasingly sophisticated underwater sound-recording equipment has moved research on underwater "soundscapes" forward and revealed considerable acoustic differences between and within aquatic habitats (Amoser and Ladich 2010; Radford et al. 2010; McWilliam and Hawkins 2013). A recent study has shown that previous acoustic experience can modify the behavioral response to sound stimuli in coral reef fish larvae (Simpson et al. 2010), organisms that have been shown to use acoustic cues to find their settlement sites (e.g., Simpson et al. 2005) and differentiate between different coral reef habitats (Radford et al. 2011). Moreover, a rapidly growing literature shows that increased noise levels can affect the physiology and behavior in animals of all taxa, including humans (e.g., Popper 2003; Barber et al. 2010; Radford et al. 2012).

The above examples indicate that a previous acoustic experience most likely also affects the physiology and behavior in research experiments. Responses to experimental stimuli may be modified by a variety of mechanisms, including increased hearing threshold levels as a physiological consequence to exposure to elevated sound levels (e.g., Codarin et al. 2009; Gutscher et al. 2011) or habituation or sensitization due to repeated previous exposure to specific sound sources or increased sound levels (Bejder et al. 2009). It is important to note that not only average sound levels of ambient noise can affect animal physiology and behavior but also sound level fluctuations and their predictability and frequency components (De Boer et al. 1989; Popper and Hastings 2009b).

2 Acoustic Variability in Captive Environments

Animals kept in captivity as pets, in zoos, or for food production and research are exposed to highly variable acoustic environments (Morgan and Tromborg 2007). Sound sources in captive environments range from continuous low-frequency noises caused by room ventilation and, in the case of aquatic animal facilities, by aquarium water filtration and aeration to ultrasonic sources arising from electronic equipment. In addition to continuous constant noise, sudden unpredictable noises can occur arising from maintenance activities (Milligan et al. 1993; Morgan and Tromborg 2007).

Elevated noise levels and the sudden onset of noises in animal facilities have been shown to elicit physiological responses such as increased blood pressure, plasma cortisol, heart rate, and metabolic rate (reviewed by Morgan and Tromborg 2007; Castelhano-Carlos and Baumans 2009). Sudden noises can also elicit behavioral responses such as increased agitation or startle responses, with potentially fatal consequences (Marai and Rashwan 2004; Leong et al. 2009; Gronquist and Berges 2013). Increased noise levels during the day caused by human activities can also lead to activity shifts of nocturnal animals to become more diurnal (reviewed by Morgan and Tromborg 2007).

Therefore, it is reasonable to predict that acoustic conditions in animal facilities may affect experimental findings. Dallman et al. (1999) showed that noise arising from nearby construction sites affected studies focusing on stress hormones in rodents. Because stress responses are involved in and affect a variety of physiological and behavioral mechanisms (Wendelaar Bonga 1997; Charmandari et al. 2005), previous exposure to elevated noise levels can have detrimental effects on a wide range of laboratory studies addressing questions beyond responses to experimental noise stimuli. Thus, controlling ambient-noise levels and minimizing the occurrence of sudden noises are not only issues of animal welfare but are also important for research design and planning.

Despite these known effects, acoustic environments in laboratories and animal facilities have not been considered systematically as a potential source of modification in experiments and are not monitored and reported in a standardized way. This is in contrast to light, temperature, feeding regimens, and elements of environmental enrichments (Baldwin et al. 2007; Turner et al. 2007). Recent studies showing the effects of acoustic test conditions on rat spatial learning and memory (Prior 2002, 2006) emphasize the necessity of reporting acoustic conditions in experimental areas, but ambient noise levels in holding cages have not been specified and as a consequence, any previous acoustic experience of the animals has not been monitored.

3 Implications for Research

The above examples illustrate the necessity of taking previous acoustic exposure into account, especially when designing and conducting research on the impact of experimental acute, repeated, or chronic sound stimuli as well as for experiments conducted in natural and laboratory conditions in general. It is therefore important to include in the Methods section of papers and research reports specifications of the noise levels and acoustic characteristics of natural habitats and laboratory holding conditions that animals were exposed to before experiments were conducted. To achieve comparability of acoustic quantifications, it is very important to find a consensus on which measurements to include to characterize the sufficiently relevant acoustic features (see also Popper and Hastings 2009b). Ideally, these measurements should include not only average noise levels but also frequency distributions using spectral level analyses and descriptions of noise level fluctuations or sound impulsiveness, such as counts of noise peaks within a given time frame; kurtosis, a statistical measure to quantify the extent waveform amplitudes deviate from a normal distribution over the duration of a signal; or the amount of sound above 50, 75, and 90% of the sound energy.

Clearly, more work is needed to investigate the effects of previous acoustic experience and exposure to different ambient noise levels on the physiology and behavior of animals (see Chapter 111 by Radford et al). However, testing animals at acoustically different field sites applying identical test procedures may be logistically difficult to conduct. Thus, laboratory environments could serve as highly valid alternatives because previous exposure to sound is highly controllable and acoustic environments differing in particular acoustic features, such as noise levels and fluctuations, could be specifically designed and their effects explored. This could be achieved by using different holding tank setups, one of which is designed to minimize filter and aerator vibration noise transmission into the tank (as in Voellmy 2013). Because these laboratory experiments are focusing on the previous experience of different ambient noise levels, principles of the effects found in these studies, for instance, indications of habituation or sensitization, may also apply to natural scenarios.

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