Psychophysical studies of auditory masking in marine mammals: key concepts and new directions

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1 Introduction

Auditory masking plays an important and nearly continuous role in the lives of marine mammals, as they inhabit ambient acoustic environments that generally limit their ability to perceive sounds. In recent years, growing awareness of the potentially harmful effects of human generated noise has led to concern over whether and how increasing noise levels may adversely affect marine mammals by interfering with detection of biologically important signals. Auditory masking occurs when the perception of a given signal is affected by the presence of another sound. Masking effects on perception may be manifested through spectral or temporal interference from noise which decreases the audibility of the signal relative to conditions when the masker is not present. The consequences of adding noise to an animal's environment may be studied in part by identifying and understanding the ways that noise alters normal or baseline hearing capabilities. In addition to auditory masking effects, it should be noted that other auditory effects—as well as non-auditory behavioral, physiological, or anatomical changes—can occur as a result of noise exposure. Further, marine mammals are not the only aquatic animals that may be vulnerable to these effects. However, the scope of this paper will be limited to consideration of the masking effects of background noise on the auditory perception of marine mammals. The aims are to briefly review key concepts and methods drawn from a psychophysical approach to the study of auditory masking; to examine how masking studies have been applied thus far to improve understanding of noise effects on marine mammals; and to consider how future laboratory studies with marine mammals may incorporate progressively more complex and realistic listening scenarios into psychophysical testing programs.

2 The psychophysical approach to auditory masking

Neural processing of auditory information in animals occurs at many levels, from the sensory receptors that receive sound cues from the external environment through progressively higher centers of the brain. As auditory masking is a perceptual phenomenon, it is clear that studies of masking must take into account the whole animal and not merely the physical environment and/or the primary receptor system. Psychophysics is the field of experimental psychology that uses specific behavioral methods to determine the relationship between the physical environment and an individual's subjective experience of that environment (Fechner 1860). Thus, psychoacoustic approaches, which describe the relationship between the lowest possible level of audition (the sound stimulus) and the highest possible level (the sensation of that stimulus), provide the most direct, complete, and effective perspectives on auditory processes such as masking (Fastl and Zwicker 2007).

Psychoacoustic parameters are not measured, but rather are approximated based on the subjective impression of an individual averaged over many stimulus presentations. For example, a hearing threshold for a sound of a given type, frequency, and duration is typically determined as the lowest sound pressure level that is detected by a subject in the absence of interfering noise over a specified percentage of experimental trials. A psychoacoustic threshold is therefore a probabilistic value, derived from observable responses that can be related to precisely measured stimulus variables. Reliable reporting responses must be produced by trained listeners in psychoacoustic tasks, because direct observation of perceptual events is possible only by introspection. Within a psychophysical paradigm, there are a few basic steps that are common to most studies of auditory masking: 1) determine the hearing threshold for a given signal, such as a tone, 2) add a potential masker, such as broadband noise, and 3) find the hearing threshold of the signal again, this time in the presence of the masking noise (Gelfand 2001). The difference between the initial and final hearing thresholds reveals how much of an effect the masker has had on the audibility of the signal.

Two of the most important metrics of auditory masking that can be derived from psychophysical experiments are critical bandwidths and the critical ratios. Both of these terms help to describe how the presence of noise may affect hearing. A critical band describes the frequency region over which masking noise may interfere with detection of a given signal. This is based on the bandwidth of the auditory filter in the listener's auditory receptor system. If a signal and masker are presented simultaneously, then only the masker frequencies falling within the critical bandwidth of the signal contribute to masking of the signal. Outside of this critical frequency band, the presence of noise does not alter the audibility of the signal. Therefore, understanding critical bandwidths as a function of signal frequency is essential for predicting the masking effects of noise. Generally, the frequency span of the critical band is proportional to the center frequency of the signal, so critical bandwidths increase in span with increasing frequency. Additionally, the shape of the auditory filter becomes asymmetrical with increasing masker level, generating an upward frequency spread of masking effects with increasing noise (Yost 2000). Critical ratios are related to critical bandwidths. A critical ratio is the minimum difference in dB between the sound pressure level of an audible pure tone signal and the spectrum level of background white noise (the power contained in each 1 Hz band of noise), when the frequency span of the noise matches or exceeds the critical band. For example, a 5 kHz tone with a level of 80 dB SPL might be just audible when the spectrum level of background noise is 60 dB, showing a critical ratio, or difference, of 20 dB; if the spectrum level of the noise should increase by 10 dB to 70 dB, then the level of the tone would need to increase to 90 dB SPL—still exceeding the noise by the critical ratio of 20 dB—to be audible to the same listener. Like critical bandwidths, critical ratios show a dependence on frequency, with critical ratios tending to increase with increasing frequencies, except at relatively low frequencies (Fletcher 1940). Because the ratios hold across a range of signal and noise levels, they can facilitate the prediction of masking effects when the critical bandwidth and the characteristics of the masking noise are known.

Psychoacoustic experiments which systematically explore various masking phenomena serve to reveal important details about auditory processing and the underlying physical and neural mechanisms of auditory systems. Comparative investigations of masking and auditory processing are essential because they highlight the generality of some effects and identify and quantify the relevant parameters that that differ amongst species and taxonomic groups. Both kinds of data are needed to establish a useful knowledge base from which informed assessments can be made.

3 Psychophysical studies of auditory masking in marine mammals

There have been many psychophysical studies of auditory masking in marine mammals since Johnson (1968) reported the first critical ratios measured for bottlenose dolphins. Most of these are reviewed by Richardson et al. (1995) with additional recent studies of odontocete cetaceans (Branstetter and Finneran 2008; Erbe 2000; Erbe and Farmer 1998; Kastelein and Wensveen 2008; Kastelein et al 2009; Lemonds 1999), sirenians (Gerstein 1999) and pinnipeds (Holt and Schusterman 2007; Southall et al. 2000, 2003; Turnbull 1994). The majority of these studies utilized pure tone or narrow-band signals and uniform masking noise to characterize masking effects on underwater hearing. As a result, the metrics of critical bandwidth and critical ratio are reasonably well understood for representative marine mammal species for which absolute auditory sensitivity has been measured.

Critical bandwidths in marine mammals follow the general mammalian trend of increasing with decreasing frequency, especially below 1 kHz. Functionally, this means that noise across a relatively wide span of frequencies contributes to masking of low frequency signals, while only relatively narrow bands of noise are effective in masking high frequency signals. While 1/3-octave bands of noise are typically considered reasonable minimum spans of the frequencies which contribute to masking in mammals, the available data indicate that critical bandwidths of some marine mammals may become wider at low and very high frequencies, while at intermediate frequencies, they are likely to be significantly narrower. Critical bandwidths may be measured directly in band-narrowing experiments, but more commonly, they are estimated from critical ratios obtained across the frequency range of hearing. While this practice produces reliable estimates of critical bandwidth for some species including humans, the discrepancy between the two approaches in some species, including some marine mammals, indicates that direct methods are required to determine accurate critical bandwidths (see Yost and Schnofer 2009) which can be reasonably used in models of potential noise effects.

The available data on critical ratios in marine mammals provide clear and useful indicators of how these animals hear in noise. As expected, critical ratios in all marine mammals tested thus far increase with increasing frequency, except at very low frequencies. There are no significant deviations to this trend, suggesting that marine mammals are generalists with respect to frequency resolution. The critical ratios of amphibious marine mammals including seals and sea lions are the same in air as they are underwater despite differences in absolute hearing sensitivity between the two media. Notably, marine mammals (with the exception of the sirenian *Trichechus manatus latirostis*) tend be better than most terrestrial mammals at detecting signals in noise. This may be due in part to their reliance on acoustic detection and frequency resolution in naturally noisy environments where the use of other sensory modalities is constrained.

These findings with marine mammals show how psychoacoustic studies using simple stimuli can improve understanding of how auditory systems operate to extract signals from interfering noise. The results are bolstered by complementary neurophysiological studies of masking, which provide additional insight into the general and species-typical characteristics of hearing, especially at the level of the peripheral auditory nervous system. While the metrics of critical bandwidths and critical ratios have been directly applied to model the auditory effects of anthropogenic noise on marine mammals living in natural environments, they are not sufficient to describe how noise interferes with the perception of sounds as the acoustic environment become progressively more realistic.

4 Auditory masking in progressively realistic hearing scenarios

In natural environments, the interactions between signals and noise are complex, and stimuli vary widely with respect to their temporal, spectral, and spatial characteristics. Marine mammals have adaptations on both the signal production side and the signal reception side to optimize their use of sound and to limit their susceptibility to auditory masking, and these include some higher order aspects of hearing that can only be accessed using psychoacoustic methods. Quantitative psychoacoustic approaches have been developed and refined to better understand acoustic communication in noise, including through studies of speech perception and birdsong. Many of these approaches have or can be expanded to marine mammal research in ways that will dramatically improve understanding of potential noise effects on hearing. Some concepts worthy of further development or consideration include the following:

(1) Release from masking. There are a variety of conditions where detection of signals in noise can be improved by auditory or behavioral "de-masking" processes. These include spatial release from masking (SRM), which occurs when masking effects of co-located signals and maskers are reduced when signals and maskers are spatially segregated and directional hearing is sufficient to support enhanced detection. These also include comodulation masking release (CMR), which occurs when the energy in masking noise is coherently modulated in time across frequency regions rather than randomly modulated, as often found in real noise environments (see Branstetter, this volume). The lower critical ratios obtained in contexts such as these can result in larger detection ranges for stimuli than would otherwise be predicted from simple models of noise effects.

(2) Complexity of signals. Complex signals, such as those often used as communication signals, are often easier to detect in noise than are tonal or narrow-band signals. Sounds with pulsed characteristics, harmonic elements, frequency modulation, or amplitude modulation may require lower signal-to-noise ratios for detection due to auditory processes such as loudness summation across critical bands. A few psychoacoustic studies have explored masking of complex signals in marine mammals, and there is one study with both natural signals and noise (Erbe and Farmer 1998). Masked hearing thresholds obtained for complex signals in noise can be productively compared to those predicted by pure tone critical ratio and broadband critical bandwidth data.

(3) Discussion of masking in marine mammals focuses almost exclusively on detection thresholds and corresponding potential communication distances. It is clear from studies of speech and birdsong, however, that progressively increasing signal-to-noise levels are required to progress

from mere detection of sounds in noise, to discrimination, recognition, and ultimately, effective communication (see Dooling this volume; Lohr et al. 2003). This issue truly gets at perception of acoustic signals and brings higher-level processes such as learning into the forefront. Marine mammals are especially good candidates for explorations of informational masking; the experiments are challenging for many reasons, but will yield invaluable insight into how noise constrains functional hearing in realistic listening scenarios.

5 Summary

Current models of auditory masking in marine mammals oversimplify hearing in realistic environments. Systematic and progressive experiments using psychoacoustic methods will help us move 'out of the ideal and into the real' in order to gain a more complete view of potential auditory masking effects in these animals.

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