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The jamming avoidance response in echolocating bats

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ABSTRACT

Bats face many sources of acoustic interference in their natural environments, including other bats and potential prey items that affect their ability to interpret the returning echoes of their biosonar signals. To be able to navigate and forage successfully, bats must be able to counteract this interference and one of the ways they achieve this is by altering the various parameters of their echolocation. We describe these changes in signal design within the context of a modified definition of the jamming avoidance response originally applied to the signal changes of weakly electric fish. Both of these groups use active sensory systems that exhibit similarities in function but we take this opportunity to highlight major differences each groups' response to signal interference. These discrepancies form the basis of our need for an expanded description of the jamming avoidance response in echolocating bats.

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Jamming and the jamming avoidance response (JAR) have long been a topic of inquiry in the domain of active sensory systems. JAR is a phenomenon first described in the weakly electric fish(es) (WEF) which use the electric organ discharge (EOD) in active electrolocation [1,2] and communication [3]. The later application of the same concept to biosonar in bats has resulted in considerable confusion. The goal of this paper is to briefly review JARs and to propose an adequate description of what constitutes a JAR in echolocating bats.

The traditional definition of JAR, originating with the WEF, asserts that when faced with the interfering signals of a nearby conspecific, individuals reflexively alter their EOD to minimize signal similarity [4] that would otherwise result in diminished electrolocation performance [5]. How the JAR is implemented depends on the type of WEF. Fishes that emit wave-like signals shift their discharge frequency to avoid spectral overlap with the signals of nearby conspecifics (Figure 1(a)), while those that emit pulse-like signals will change their inter-pulse interval to avoid temporal overlap (Figure 1(c)).

Following this convention, studies evaluating active sensing in bat models have maintained that a jamming stimulus must decrease task performance and a true JAR must act to increase signal disparity in the temporal and/or frequency domains. We believe it is not suitable to apply such constraining definitions to bat echolocation by virtue of the manner in which this modality operates. Bats are capable of adapting their biosonar emissions in a matter of milliseconds, which is three orders of magnitude faster than JARs seen in WEF [5]. Thus, bats could employ a JAR mechanism rapidly enough that a decrease in performance is not readily apparent in experiments. Also, numerous studies have illustrated the extensive capability of bats to adapt many parameters of their biosonar in the presence of acoustic interference and these changes appear to be highly context-dependent [9–14]. Just some of the documented changes include bidirectional shifts in echolocation frequencies away from a stimulus (Figure 1(b)) [15–17], changing the timing or rate of vocal emissions (Figure 1(d)) [18–20], and altering their peak signal frequencies, possibly to maximize individual differences [21–25].

The variability in bat vocal responses can be attributed to several factors such as the species, whether the study takes place in the field or lab, the potential jamming stimulus, and the type of task being performed. Measurement of biosonar features also varies. Some past studies claim to find evidence in support of a bat JAR, while others suggest the changes do not strictly fit into some definitions [26,27], and thus should not be considered as such.

There are two primary alternatives to the traditional JAR. The first, the Lombard effect, typically manifests as an increase in call amplitude in the presence of acoustic interference along with increases in frequency [28], signal duration and number of calls [29]. To achieve these changes, bats continuously monitor the ambient noise

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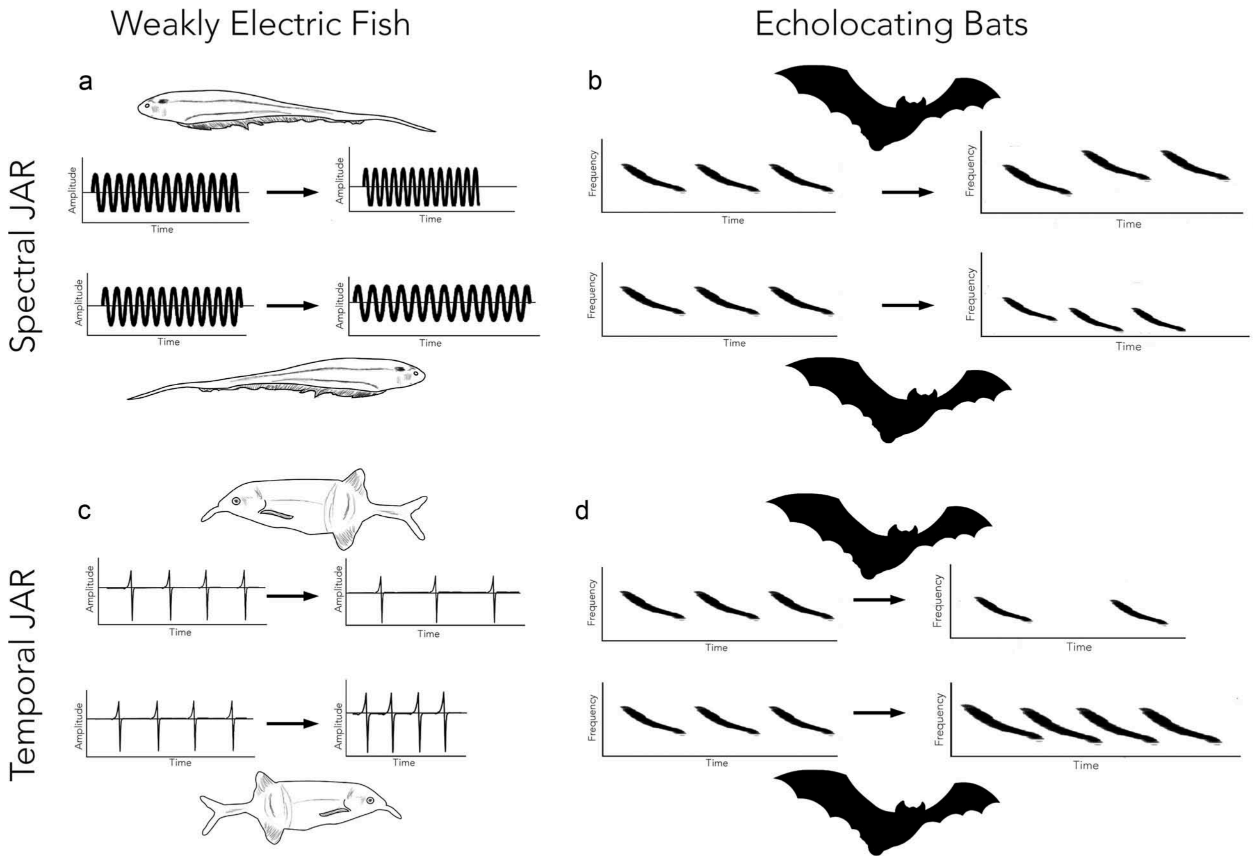

Figure 1. Hypothetical spectral (a,b) and temporal (c,d) JARs for WEF (a,c) and echolocating bats (b,d).
When two WEF are in close proximity and their EODs are very similar, wave-type fish will shift their EOD frequency in opposite directions while pulse-type fish alter the inter-pulse interval between EODs. We depict what this may look like in echolocating bats according to the traditional definition modelled after the WEF. Bats using frequency-modulated echolocation calls, as shown in the figure, would potentially face both spectral and temporal jamming. However, shifting frequencies or emission rates are not the only parameters that bats may alter. Bats using constant-frequency echolocation calls (a.k.a high duty-cycle bats) have not received as much attention, but would likely face challenges similar to the wave-type electric fish, who exhibit 100% duty cycle signals. These bats still exhibit changes in spectral [6,7,21,27] and non-spectral parameters [7,8,27]. For both WEF and bats, signal changes can be elicited with man-made stimuli and recordings of conspecifics.

level and this response occurs nearly instantaneously with only a 30 ms latency [30]. However, it is not clear whether this effect for bats is meant to increase the detectability of echoes, or is simply part of the audiovocal feedback loop used to construct signals. The second, the attention drawing hypothesis, states that bats change their echolocation in response to objects entering the acoustic field of view, causing a shift in attention from another task. In studies that support this explanation, bats always increase the spectral frequency of calls [26,27]. However, it is difficult, even in laboratory conditions, to know exactly what draws a bat's attention and if an attention drawing object happens to be one which itself produces sound (i.e. another bat), then it can be difficult to distinguish between acoustic interference and attention.

Many researchers have converged on the idea that neither traditional JARs nor the most common alternatives, fully explain the variation seen in bat echolocation when presented with jamming signals [15,26,27,31,32]. Given the studies to date, we believe that jamming in bats includes all forms of acoustic interference that make interpreting returning echoes more challenging and creating difficulty in completing vital tasks such as orienting or foraging. A JAR, therefore, is an umbrella term encompassing all the potential ways in which a bat may adapt their echolocation to reduce interference and subsequently negating the jamming effects on the bats' performance.

This is not to suggest that a JAR is necessary in every echolocation scenario. There are several inherent properties of echolocation that make it resistant to jamming. Bats make use of high redundancy, temporally patterned call sequences [33] with individual-level differences [11,34]. The brain also possesses neurons that are sensitive only to a range of pulse-echo delays [35,36], creating a particular time window during which the bat is most sensitive to returning echoes [37]. And lastly, there is directionality to the sonar beam and the sensitivity of the ears [38]. Nevertheless, there are scenarios in which these properties are not sufficient to reduce the effects of interference such as high-density bat emergences or foraging sites or when presented with active jamming signals [39], like those produced by insects in response to bat echolocation [40–43] or competing conspecifics [25]. In these instances, we would expect that individuals change some parameter of their biosonar.

Our modified description of JARs is useful firstly because it accounts for the vast array of responses reported in the literature and secondly because it does not constrain the biosonar response to only reducing spectral or temporal overlap. This allows us to fully encompass the flexibility of bat echolocation calls in our analyses and take into consideration the type of signal and context in which it occurs.

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