



OPEN Double stochastic resonance in stink bug sexual communication

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Stochastic resonance (SR) is a phenomenon where noise enhances the detection of weak signals in nonlinear systems. In this study, we investigate the role of environmental noise in facilitating acoustic communication during mating in the southern green stink bug, *Nezara viridula* (L.), a globally distributed and highly polyphagous pest species. Using behavioral experiments and the source-direction movement (SDM) ratio as a metric, we demonstrate that environmental noise can significantly improve signal recognition between individuals of opposite sex. Notably, the SDM ratio exhibits a nonmonotonic response with two distinct peaks, indicating the presence of a double behavioral stochastic resonance—a phenomenon previously predicted theoretically but not observed in biological systems. The noise intensity levels used in laboratory experiments closely match those recorded in natural habitats, reinforcing the ecological relevance of our findings. These results suggest that environmental noise may play a constructive role in enhancing mating communication in *N. viridula*, offering new insights into pest control strategies based on acoustic signaling.

Keywords Aperiodic stochastic resonance, Environmental noise, Stink bug, Acoustic communication, Double behavioral stochastic resonance

The phenomenon of stochastic resonance (SR) has emerged as one of the most intriguing and counterintuitive effects in noisy nonlinear dynamical systems, garnering growing attention in the literature on the physics of complex systems—an inherently interdisciplinary and rapidly evolving field^{1–9}. In complex systems, the interplay between stochastic and periodic excitations, coupled with the system's inherent nonlinearity, reveals the surprising and constructive role of noise in enhancing the coherence of the output. Remarkably, there exists an optimal noise intensity at which the system's output reaches a maximum. In other words, the addition of a certain amount of noise to a subthreshold signal is necessary to achieve an optimal, deterministic response from the system. The essence of SR lies in the system's response to the input signal, where the presence of noise causes a form of “resonance” in the system's transfer of the signal^{10–16}. Stochastic Resonance occurs not only in bistable, monostable, and multistable dynamical systems but also in systems with threshold-like properties, a phenomenon known as non-dynamical stochastic resonance. This broadens the scope of SR research and suggests that nature may exploit SR in biological systems to enhance sensitivity, enabling better discrimination of weak, information-carrying signals and optimizing neural signal transmission. This effect is reflected in metrics such as the signal-to-noise ratio (SNR), mutual information, coherence, and sensitivity index, as noise lowers the system's response threshold. At an optimal noise level, the system “resonates,” maximizing information transfer^{17–21}.

It is essential to highlight that SR has been widely documented in both human and animal perceptual systems, where the introduction of external noise can enhance behavioral performance across various sensory and motor tasks. Specifically, experimental studies have demonstrated that in humans, tactile perception and motor control benefit from stochastic facilitation, often following an inverted U-shaped relationship between the intensity of the applied noise and the behavioral response^{22–26}. These findings underscore the crucial role of stochastic resonance (SR) in biological systems as a physiologically essential and functionally beneficial mechanism, in addition to its already demonstrated importance as a powerful theoretical framework for multistable and threshold dynamical

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systems. Furthermore, neural modulation techniques such as transcranial random noise stimulation (tRNS) have demonstrated the ability to regulate cortical excitability and improve perceptual and cognitive performance^{27,28}, thereby reinforcing the translational potential of mechanisms based on stochastic resonance, as evidenced by clinical applications^{29,30}, neurorehabilitation strategies^{23,25}, and cognitive enhancement interventions^{24,26}.

Furthermore, a method for characterizing SR-type behavior in excitable systems with aperiodic and arbitrary inputs, such as broadband signals, has been developed and termed aperiodic stochastic resonance (ASR). It was discovered that noise can enhance the response of a sensory neuron to a subthreshold aperiodic input signal, suggesting a functional role for input noise in sensory systems^{31–33}.

Currently, the occurrence of stochastic resonance phenomena in biological and ecological systems is evidenced by the presence of a single peak, which represents the stochastic resonance effect at the optimal noise intensity^{19,34–40}. The possibility of observing two optimal noise intensity values at which the stochastic resonance phenomenon occurs was first predicted by Gailey et al.⁴¹. Subsequently, this phenomenon was demonstrated only mathematically in Refs.^{42–48} and has never been observed in a real biological system. In particular, in these theoretical studies, Gailey et al.⁴¹ examined the role of internal noise in nondynamical elements, such as two-state ion channels, and suggested that the second maximum might be observed in experimental studies only at noise intensities beyond the range of this class of systems.

Zeng et al.⁴⁴ investigated the transient and resonant properties of active Brownian particles in the Rayleigh–Helmholtz and Schweitzer–Ebeling–Tilch models driven by the simultaneous action of multiplicative and additive noise and periodic forcing. Double stochastic resonance has been shown in both models. Guo et al.⁴⁶ demonstrated that the phenomenon of multi-stochastic resonance occurs when the SNR varies with the intensities of multiplicative and additive noise. Qiao et al.⁴⁷ have identified and characterized double stochastic resonance as a function of potential-well depth and width. Finally, Palabas et al.⁴⁸ found double stochastic resonance in a theoretical model of astrocytes - the most abundant subtype of glial cells in the nervous system - with a second peak in the neuronal detection of weak signals depending on the noise intensity.

Taking into account the existing literature, our study was driven by the explicit hypothesis that *Nezara viridula* (L.) (Hemiptera: Pentatomidae) may exhibit a behavioral response characterized by two distinct peaks of stochastic resonance. This hypothesis is grounded in previous modeling studies that describe how the presence of multiple resonance peaks can arise from nonlinear interactions between noise and the intrinsic system dynamics^{42–45,48}. To test this hypothesis, we developed an experimental paradigm in which noise intensity was systematically varied within a biologically relevant range, while simultaneously measuring the insects' directional movement toward subthreshold vibrational signals, quantified through the source-direction movement (SDM) ratio. This approach allowed us to characterize the entire behavioral response curve, enabling the identification of two stochastic resonance peaks and thereby providing direct empirical support for our hypothesis. *N. viridula* is a highly polyphagous, cosmopolitan insect found across many tropical and subtropical regions. It is considered one of the most significant pentatomid insect pests worldwide^{49,50}. Acoustic communication plays a fundamental role in the mating behavior of this species and has been explored as a potential method for population control using traps that emit acoustic signals^{51–53}. Males and females of *N. viridula* communicate by transmitting mechanical vibrations through plants. These vibrations travel via the legs into the plant stem and are detected by vibroreceptors located in the legs of the receiving insect⁵⁴. Due to their critical role in mating behavior, the reception of these signals has been studied in *N. viridula* populations from Brazil, Florida, Italy, and Slovenia⁵⁵. The acoustic signals produced by the tymbal organ on the dorsum of fully developed adult bugs (see Fig. 1a)⁵², with a dominant frequency of approximately 100 Hz (see Fig. 1b), are captured by the membrane of a conic low-to-mid-frequency loudspeaker and stored on a computer for subsequent sound analysis.

Here, we report on experiments conducted on the response of *N. viridula* individuals to sub-threshold signals both in absence and presence of noise. In this study, we demonstrate how environmental noise enhances communication between males and females by examining their behavior using the source-direction movement (SDM) ratio. The source-direction movement ratio is defined as the proportion of insects moving toward the right apex of the Y-shaped dummy plant (see Fig. 2) relative to the total number of insects tested. Our analysis reveals a nonmonotonic pattern in SDM, characterized by two peaks, indicating a “double” behavioral aperiodic stochastic resonance.

This behavioral pattern exhibits two distinct peaks in response to varying noise intensities, partially resembling the inverted U-shaped function commonly observed in vertebrate sensory systems. This partial correspondence may reflect a generalization of the noise-enhanced signal detection mechanism seen in vertebrates, suggesting the existence of a shared underlying principle across phylogenetically distant taxa and potentially indicating a convergent or conserved strategy in sensory processing⁵⁶.

Furthermore, the noise intensity levels employed in laboratory experiments align with those observed in field conditions. These findings confirm and highlight the pivotal role of environmental noise in shaping acoustic communication between *N. viridula* individuals during mating, and suggest that similar SR-based mechanisms observed in vertebrate sensory systems may also be at play in invertebrate neuroethology. This comparative perspective reinforces the interdisciplinary relevance of our work and opens avenues for translational applications in both biological research and technological innovation.

Results

The experimental apparatus and setup are illustrated in Fig. 2. Vibrations of varying amplitudes significantly influence the directional choices of the bugs, which can either move toward the source of the female calling signal, located at the apex of the right branch, or along the left branch, where no vibrational sources are present. Mechanical oscillations applied at the right apex of the Y-shaped dummy plant allow for the observation of the behavior of individual males initially placed at the center of the vertical stem. The Y-shaped substrate consists of a wooden vertical stem and two wooden branches.

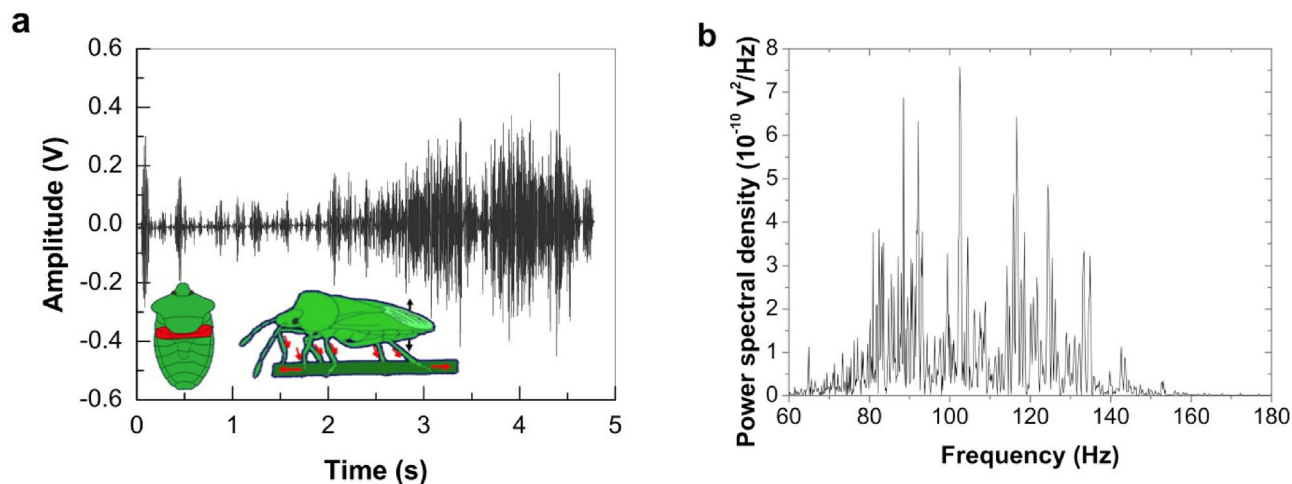


Fig. 1. Oscillogram (a) and power spectrum (b) of *N. viridula* female calling song. In this spectrum the dominant frequencies range from 70 to 170 Hz and the maximum peak occurs at 102.5 Hz. The inset of panel (a) shows that in adult bugs of *N. viridula* the vibrations are generated by the timbal organ across the back, transmitted through the legs into the plant stem.

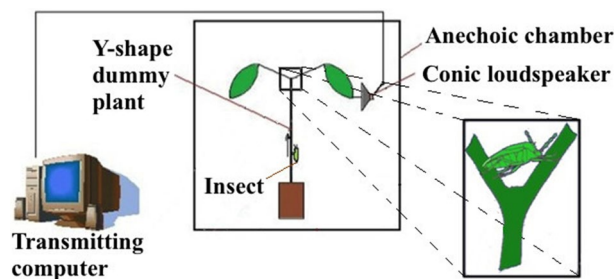


Fig. 2. Experimental apparatus and setup, including a transmitting computer and an anechoic chamber containing the Y-shaped dummy plant and a conic loudspeaker. Mechanical oscillations sent at the right apex of the Y-shaped dummy plant, allow to observe the behaviour of single male individuals initially placed at the centre of the vertical stem. The Y-shaped substrate is constituted by a wooden vertical stem 10 cm long and 0.8 – 0.9 cm thick, and two wooden branches 25 cm long and 0.4 cm thick. The angle between the oblique branches is 30° – 50° .

During a trial, when the insect chooses the right branch while walking, the female calling song is recorded and used as a signal for males^{57,58}. In nature, vibratory signaling is typically preceded by chemical signaling through male pheromones. However, the role of female pheromones -specifically, the potential influence of female chemical signaling- has not yet been described. Additionally, male chemical communication was not explored in our setup. Males usually respond to the female vibratory call when they are on the plant stem.

The behavioral response of male *N. viridula* to vibratory signals and noise was analyzed in detail (see Fig. 3), and the environmental noise conditions during the recording sessions are described at the end of the paragraph.

Behavioral response studies on male individuals were conducted by varying the amplitude of the female calling song to identify specific values that elicit a positive reaction, leading the males to choose the right branch of the Y-shaped substrate. This analysis revealed a bias in male insect behavior: for applied signal amplitudes greater than 0.06V, they chose the vibrating branch in at least 70 % of the trials (see Fig. 3a). The next step in the experimental study was to determine the threshold of the applied signal, V_{thr} , capable of activating the neurons of *N. viridula*. For signal amplitudes below 0.045 V, male insects exhibited random choice behavior, with the source-direction movement (SDM) ratio remaining around 0.5. Based on this observation, we conclude that male insects are not influenced by female calling signals with amplitudes smaller than $V_{thr} = 0.045$ V. This value thus represents the threshold of the insect's neuronal system, below which female calling signals fail to elicit vibrotaxis in males.

In Fig. 3a, we present the occurrences of the SDM ratio relative to the total number of trials. In particular, the first two stacked orange columns represent a total number of 64 trials performed for amplitude values of the vibration equal or less than 0.045 V. Correspondingly, the first two violet columns indicate a total number of 36 SDM ratio occurrences (positive responses) obtained for the same signal amplitudes. The corresponding percentage, equal to 56.25 %, indicates the presence of random choice behavior in the male insects. Vice versa,

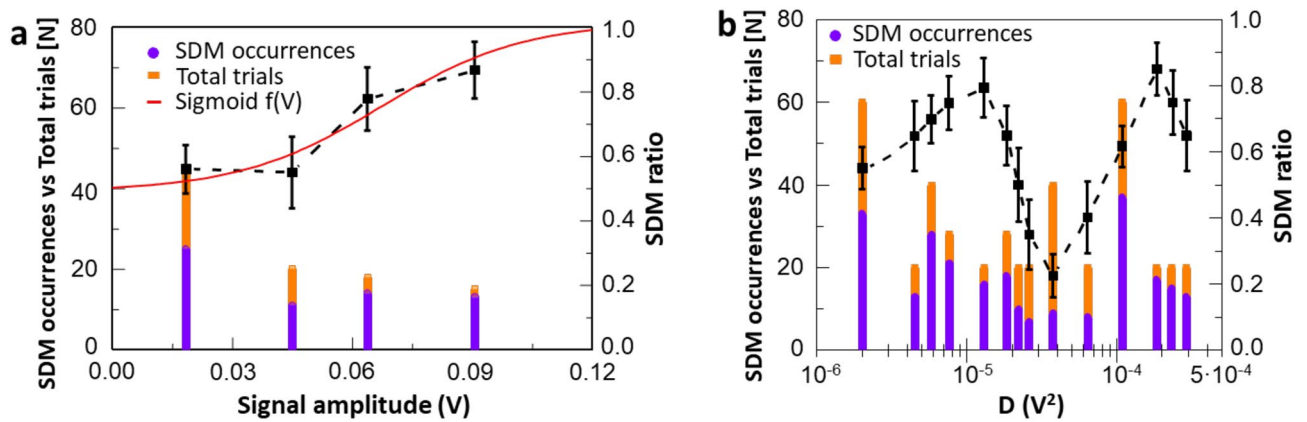


Fig. 3. Source-direction movement (SDM) occurrences vs Total trials (left scale) and SDM ratio (right scale) as a function of: **a** the amplitude of non-pulsed female calling song (noise-free signal); **b** the noise intensity D . Each plot shows both the SDM percentage with the related error bar and its number of occurrences (violet column) with respect to the total number of trials (orange column). The percentage of movements of the bugs towards the sound source approximately equal to the 50 % corresponds to the case in which the insects do not show a preferential choice, choosing randomly one of the two branches of the dummy plant. Vice versa, higher values of SDM ratio correspond to a biased choice of the branch carrying the transmitted vibrations. The SDM ratio, rescaled as $2(SDM - 1/2)$, is shown in the main panel and is best fitted by a sigmoidal function $f(V) = (1 + a \exp(-V/b))^{-1}$, where $a = 4.461105$ and $b = 0.0177468 V$. The fitted curve is displayed as a red line.

higher values of SDM ratio correspond to a biased choice of the branch carrying the transmitted vibrations. The behavior of SDM occurrences and the SDM ratio as a function of signal amplitude reveals a nonlinear dependence of the SDM response, which is well described by a sigmoid function (see inset of Fig. 3a).

Subsequent directionality experiments were conducted in the presence of a noise source. Specifically, we used a subthreshold female calling signal of 0.045 V combined with Gaussian white noise. Fig. 3b presents both the source-direction movement (SDM) occurrences versus total trials (left scale) and the SDM ratio (right scale) as a function of noise intensity D . These experiments reveal that the SDM ratio exhibits two distinct peaks in the presence of noise, indicating an enhancement in signal recognition due to the double SR phenomenon. The first peak occurs around $D \approx 10^{-5} V^2$, and the second around $D \approx 10^{-4} V^2$, reflecting an improvement in communication between *N. viridula* individuals of opposite sexes.

At very low noise intensities, male insects exhibit an unbiased behavior. As D increases, the SDM ratio rises, reaching a first maximum of approximately 80 % at $D \approx 10^{-5} V^2$. However, with further increases in D , *N. viridula*'s response to the noisy signal becomes less pronounced, causing the SDM ratio to decrease to a minimum value of about 20 % at $D \approx 4 \cdot 10^{-5} V^2$. Beyond this point, as D continues to rise, a second peak emerges at $D \approx 2 \cdot 10^{-4} V^2$, indicating another optimal noise level for enhanced signal detection.

These two peaks suggest that in a noisy environment, the presence of optimal noise levels can facilitate successful communication between individuals of opposite sex, further supporting the idea that noise can play a constructive role in biological communication systems.

The first resonant peak of double SR arises from the typical mechanism of non-dynamical stochastic resonance in threshold systems. Specifically, it corresponds to aperiodic stochastic resonance, which occurs in excitable systems exhibiting SR-type behavior in response to aperiodic and arbitrary inputs, such as broadband signals. The second resonance peak, observed at higher noise levels, has been attributed to the influence of internal background noise, as first hypothesized in Ref.⁴¹. Subsequent studies have shown that this background noise suppresses fluctuations in neural activity while increasing the neuronal response threshold^{48,59,60}. As a result, a greater noise intensity is required to overcome this noise-induced threshold increase, leading to the emergence of a second resonance peak. This completes the picture of a “double behavioral stochastic resonance” and provides a comprehensive understanding of how noise modulates signal detection in *N. viridula*. Overall, the behavioral responses observed in the laboratory are consistent with the environmental noise conditions recorded in the open field.

As shown in Fig. 4, the average environmental noise intensity fluctuated within the range $[5 \cdot 10^{-6}; 3 \cdot 10^{-3}] V^2$ over the course of the day, from midnight (00:00 AM) to midnight (24:00 PM). Specifically, between 00:00 AM and 10:00 AM, noise levels remained within $[5 \cdot 10^{-6}; 5 \cdot 10^{-4}] V^2$. During the rest of the day, the intensity increased, often exceeding $10^{-4} V^2$ and occasionally reaching peaks above $10^{-3} V^2$.

Cross-correlation

The experimental results in Fig. 3a show that the biological system constituted by *N. viridula* species manifests a nonlinear, amplitude-dependent SDM response which, rescaled as $2(SDM - 1/2)$, is best fitted by a sigmoidal function $f(V)$ that may represent the psychometric response of the insect to a sensory stimulus. We have simulated the response of our biological system by using the following threshold model

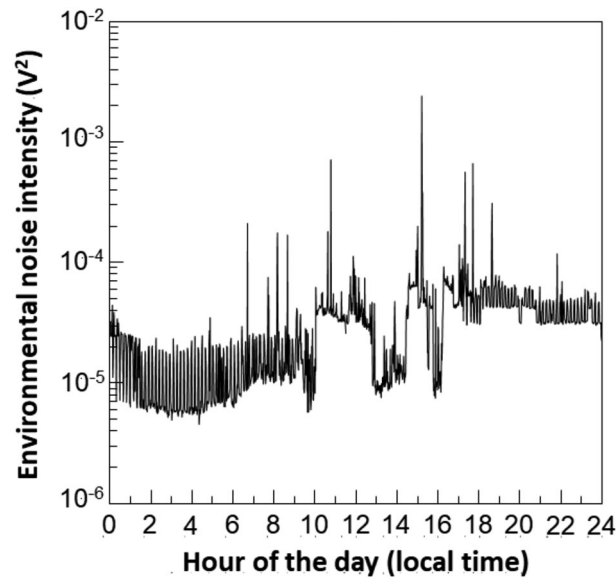


Fig. 4. Observational time series of the average intensity of environmental noise through all the hours of the day.

$$y(t) = \begin{cases} s(t)[Nf(s(t)) + g(s(t)) \sum_{k=1}^N \xi_k(t)], & s(t) \geq 0 \\ 0, & s(t) < 0 \end{cases} \quad (1)$$

with $s(t) = x(t) + n(t)$. Here, $x(t)$ represents the weak input signal, $n(t)$ is the external noise signal with intensity D , and $\xi_k(t)$ simulates the internal noise generated by the k -th element of an ensemble of N soft thresholds. The output signal is denoted as $y(t)$, while $g(V) = \sqrt{f(V)[1 - f(V)]}$ describes how the intensity of fluctuations $\xi_k(t)$ is modulated by the applied input signal and external noise through the psychometric function $f(V)$ ⁴¹. We used as psychometric function the logistic function:

$$f(\theta) = \frac{1}{1 + a \cdot e^{-\frac{(\theta - c)}{b}}} \quad (2)$$

where θ represents the stimulus amplitude, and the fitting parameters are given by $a = 2.00464$, $b = 0.0177468$, and $c = 0.055$.

Given the aperiodicity and broad spectrum of the input signal, we employed a cross-correlation measure, as introduced in Ref.³², as an appropriate metric for assessing stochastic resonance phenomena

$$\langle \rho \rangle = \left\langle \frac{\overline{x(t) \cdot y(t)}}{\sqrt{\overline{(x(t) - \bar{x})^2} \cdot \overline{(y(t) - \bar{y})^2}}} \right\rangle. \quad (3)$$

Here, the overline denotes an average over $T_s = 4.78$ s, which corresponds to the period of the female calling song used in our experiments, while the brackets indicate an ensemble average. The input-output cross-correlation coefficient $\langle \rho \rangle$ in Fig. 5 exhibits two peaks at $D \approx 1.3 \cdot 10^{-5} \text{ V}^2$ and $D \approx 1.8 \cdot 10^{-4} \text{ V}^2$, respectively. The presence of internal noise leads to the emergence of an additional peak in the plot of the correlation coefficient as a function of the external noise intensity. The noise levels at which these maxima occur closely match those observed for the SDM ratio (see Fig. 3b), consistently with the expected behavior of stochastic resonance. This agreement reinforces the idea that external noise of optimal intensity enhances the behavioral response of *N. viridula* to a repetitive weak vibratory signal.

Discussion

In our study, we aimed to determine whether the range of environmental noise intensities present in the habitat of *N. viridula* could facilitate communication through stochastic resonance. To this end, we recorded long time series of environmental noise in open fields near Palermo (Italy) during favorable periods of the species' mating season.

As detailed in the Results section (see Fig. 4), the environmental noise intensities measured in the habitat fall precisely within the range that facilitates stochastic resonance, thereby enhancing vibrational communication.

Notably, the measured environmental noise intensities were entirely within the range of D values associated with enhanced communication between individuals of opposite sex (see Fig. 3b).

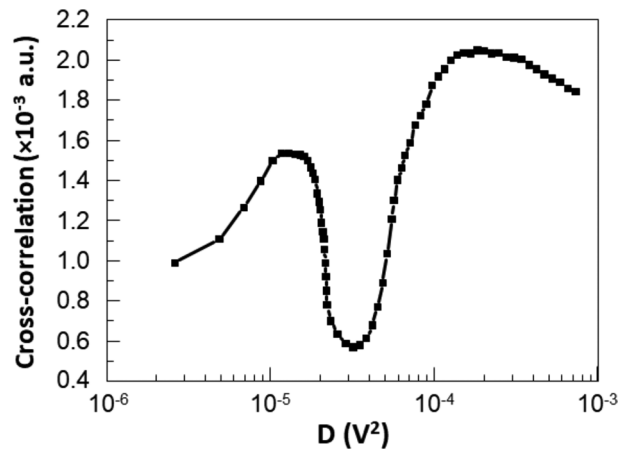


Fig. 5. Input-output cross-correlation $\langle \rho \rangle$ as a function of the noise intensity D .

These findings suggest that low levels of environmental noise may induce stochastic resonance, improving the detection of repetitive weak vibratory signals and thereby intraspecific communication.

Double behavioral aperiodic stochastic resonance may act as a beneficial mechanism for enhancing intraspecific communication in *N. viridula*, especially when signal transmission suffers from attenuation through signal propagation along plant branches. This advantage emerges at two distinct levels of environmental noise intensity, differing by an order of magnitude.

The strong agreement between experimental data and numerical simulations highlights the role of environmental noise in modulating internal noise within the ecological system where *N. viridula* lives and reproduces. This interaction seems to create a constructive interplay, ultimately giving rise to double aperiodic stochastic resonance peaks that facilitate communication between individuals of opposite sex.

Importantly, the presence of two distinct peaks in the behavioral response curve suggests the involvement of more than one underlying mechanism. The first peak, which occurs at lower noise intensity levels, aligns with the classical theory of non-dynamic stochastic resonance in threshold systems, where external noise facilitates subthreshold vibrational signals in crossing the activation threshold of peripheral sensory receptors⁶¹. The second peak, emerging at higher noise levels, is plausibly attributable to central processing adaptation -within the brain or other central neural structures beyond peripheral receptors-, whereby elevated internal background noise suppresses intrinsic variability -manifested as reduced neuronal membrane potential fluctuations- and concomitantly elevates the decision threshold, such that only sufficiently strong external noise can evoke a measurable behavioral response.

This interpretation is consistent with recent neurophysiological evidence demonstrating that white noise influences neuronal activity and reduces membrane potential fluctuations^{60,62,63}, as well as with studies showing that white noise can modulate cortical excitability and enhance signal discrimination via dopaminergic and cholinergic neuromodulatory pathways^{62,64,65}.

In this context, the presence of a second behavioral resonance peak may plausibly reflect a shift from peripheral sensory facilitation to central processing adaptation. This dual-mechanism hypothesis is consistent with evidence of stochastic resonance in cortical neurons, where low-level noise enhances the signal-to-noise ratio and facilitates perceptual discrimination^{66–68}. Moreover, it aligns with psychophysical models in humans, in which noise-induced facilitation exhibits an inverted U-shaped dependence⁵⁶, as well as with ecological studies showing that noise can modulate attention and learning in complex, naturalistic environments^{69,70}.

Beyond the immediate behavioral implications, the observed dual-peak resonance pattern may also hold ontogenetic and phylogenetic relevance. Although our current data do not distinguish between age groups or stages of sexual maturity, it is plausible that sexually immature individuals may exhibit different sensitivity profiles, either due to the presence of sensory structures still in development or to the incomplete maturation of central neural processing mechanisms. This hypothesis is consistent with developmental studies in other insect species, where sensory responsiveness and mating-related behaviors evolve with age and hormonal status⁷¹. Future research could investigate whether dual-peak sensitivity emerges gradually during maturation or is present from early developmental stages, potentially reflecting a phenomenon that is either learned or hormonally modulated. From a phylogenetic perspective, the presence of double stochastic resonance peaks may represent either a lineage-specific specialization in *N. viridula*, or a more generalizable feature among heteropteran insects that rely on substrate-borne vibrational communication. Vibrational signaling is widely distributed across insect taxa, with over 70% of families using vibrational signals either exclusively or in combination with other modalities⁷². Comparative studies have shown that vibroacoustic mechanisms have evolved independently multiple times across lineages^{71,73}, suggesting that nonlinear threshold-based processing may be a conserved feature in taxa exposed to complex vibrational environments.

It is worth emphasizing that the observed double resonance may reflect an evolutionary adaptation to the insect's complex noisy acoustic environment, where both low and high levels of ecologically relevant noise occur. In open habitats, environmental noise arises from the stochastic and nonstationary interplay of abiotic

factors such as wind, biotic sources including vegetation dynamics, and diverse anthropogenic disturbances and activities. A dual-peak system could enable *N. viridula* to maintain effective communication despite this environmental variability, thereby enhancing reproductive success under diverse conditions. This interpretation supports the view that stochastic resonance is not merely a passive byproduct of noise, but rather a functional adaptation shaped by ecological constraints and the dynamics of sensory systems^{74,75}. Therefore, our findings not only highlight the ecological relevance of environmental noise in insect communication, but also suggest that *N. viridula* may exploit noise-sensitive mechanisms at both peripheral and central levels to optimize signal detection and decision-making in acoustically complex environments, thereby enhancing mating success under diverse conditions^{71–73}. This comparative perspective underscores the interdisciplinary significance of our study and opens new avenues for investigating conserved principles of noise-enhanced perception across species and sensory systems.

Methods

Nezara viridula and sexual calling song

The mechanical signal examined in our study is the non-pulsed female calling song (NPFCS) (see Fig. 1a). To investigate the role of noise in the *N. viridula* mating behavior, we have designed an experimental setup to assess the ability of male individuals to locate the source of vibratory signals produced by female. Specifically, to perform directionality tests, we constructed a Y-shaped dummy plant inside an anechoic chamber. This Y-shaped substrate consists of a vertical wooden stem, 10 cm in length and 0.8 – 0.9 cm in thickness, with two wooden branches at the top, each measuring 25 cm in length and 0.4 cm in thickness, and the angle between the oblique branches ranges from 30° to 50° as illustrated in Fig. 2.

As a first step in each experimental trial, we placed a male insect at the center of the vertical stem and generated a mechanical signal on one of the branches of the Y-shaped dummy plant. At this stage of the experiment, a cone has been used as an electro-acoustic transducer to deliver the signal. A response was considered successful if the insect reacted to the stimulus. Following this procedure, we performed multiple trials for each fixed signal intensity, recording and counting the insects' left and right choices. Under these conditions, we observed the insects' behavioral responses to signals with amplitudes in the 0.015 – 0.1 V r.m.s. range, considering each movement towards the signal source as a positive response (see Fig. 2).

Experimental data were collected from *N. viridula* males captured in fields around Palermo (Italy) and reared in the laboratory under controlled conditions⁷⁶. Experiments were conducted in the late morning and early afternoon, aligning with the peak sexual activity of adult bugs. Adult males were tested at least ten days after their final molt to ensure full sexual maturity and after three days of seclusion from females^{53,55}. The non-pulsed female calling song was recorded using the membrane of a conical low-mid frequency loudspeaker with a diameter of 16.5 cm, carefully selected for its adequate frequency response in the range of 20 Hz to 20 kHz. The recorded signal was stored on a computer for subsequent sound analysis. The loudspeaker functioned as an electro-acoustic transducer, capturing sounds from its membrane. Sound recordings were conducted inside an anechoic chamber under controlled conditions - temperature: 22 – 26 °C, relative humidity: 70 – 80 % - and artificial lighting. The audio signal was sampled at 44, 100 samples per second with 16-bit resolution and subsequently filtered using an 18th order Type I Chebyshev band-pass filter with a frequency range of 60 – 400 Hz.

Applied noise

During the experiments, the noise applied via the loudspeaker was Gaussian and time-correlated, generated numerically using Matlab[®]. The noise signal featured a flat spectrum up to 22,050 Hz, with a correlation time of approximately 45 μs. The loudspeaker cone reproduced vibrations with a cut-off frequency of 20 kHz, which is more than two orders of magnitude higher than the highest frequency emitted by adult *N. viridula*. As a result, the insect perceives the noise effectively as white noise.

Experimental protocol

The experiment involved transmitting a vibratory signal along one branch of the Y-shaped dummy plant and observing the behavior of individual males initially placed at the center of the vertical stem⁵¹. The block diagram of our experimental setup is shown in Fig. 2.

The vibrational signal was transmitted to the right apex of the Y-shaped plant using the loudspeaker cone, which functioned as an electro-acoustic transducer. A response to the directionality test was recorded when the insect, before selecting a direction, touched the lower ends of both branches (see the zoomed-in section of Fig. 2).

For each fixed noise intensity, multiple trials were conducted, counting the number of times the insect chose either the left or right branch. Data analysis was performed using the statistical properties of a Bernoulli-distributed variable⁷⁷.

Data analysis

We estimated the *Source-direction movement* (SDM) ratio \hat{r} using its maximum likelihood estimator:

$$\hat{r} = \frac{x}{n} \quad (4)$$

where n is the size of the sample and x is the number of individuals that moved towards the sound source. We estimated the error bars of the ratio \hat{r} by the standard error:

$$SE = \sqrt{\frac{\hat{r}(1-\hat{r})}{n}} \quad (5)$$

for a sample of size n from a Bernoulli distribution.

We conducted the inferential statistical test:

$$z = \frac{\hat{r} - r_0}{\sqrt{\frac{r_0(1-r_0)}{n}}} \quad (6)$$

at the 5% level of significance. We assumed z to be normally distributed with mean 0 and standard deviation 1, under the null hypothesis $H_0 : r = r_0 = 0.5$, and the alternative hypothesis $H_A : r \neq r_0 = 0.5$ ⁷⁸.

We best fitted the data of Fig. 3a with a logistic (sigmoid) function of the form:

$$f(x) = (1 + ae^{-x/b})^{-1} \quad (7)$$

where x denotes the stimulus level or amplitude. The function in Equation (2) is equivalent to this form as long as the factor $e^{c/b}$ can be absorbed into the parameter a .

This function is commonly used in probabilistic models of detection and decision, as in the phenomenon studied here. It is also computationally more convenient than alternatives like the cumulative Gaussian, especially for software-based fitting. Moreover, it appropriately models low response rates at low stimulus levels and high response rates at high stimulus levels, while accounting for the gradual change around a threshold—a behavior observed even in simple organisms like insects⁷⁹.

We performed the best fitting using the nonlinear least-squares Marquardt-Levenberg algorithm on a rescaled SDM ratio ($2 \cdot r - 1$). The rescaling allows the model to produce values close to 0 at low stimulus levels and close to 1 at high stimulus levels.

Measurement of environmental noise

Long time series of environmental noise were recorded using the membrane of a conical low-middle frequency loudspeaker with a diameter of 16.5 cm and a bandwidth of 20 Hz – 20 kHz. The recorded signals were then stored on a computer for sound analysis. Noise acquisition was conducted outdoors in fields around Palermo (Italy), amidst the region's natural flora. The vibrations were sampled at a rate of 44,100 samples per second with 16-bit resolution.

Data availability

All data generated or analyzed during this study are included in this published article. Specifically, all datasets underlying the findings can be extracted from the figures and graphs presented within the manuscript.

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Author contributions

B.S. administered the project, supervised research; B.S. and D.V. conceptualized and devised the project; B.S., D.V., L.C., S.S. and S.M. developed the methodology; B.S., D.V. and L.C. conducted investigations; B.S., S.C., G.D. and E.P. conducted formal analysis; B.S. and S.M. secured funding; B.S., D.V., G.M. and S.S. interpreted data; L.C. and S.S. drafted the original manuscript; E.P. and S.C. provided resources and biological samples; L. C. conceptualized the experimental study; S.S. implemented software. All authors reviewed and edited the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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