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Vibrotaxis in slime molds – Exploring a previously unknown positive reaction to vibrational stimuli in *Physarum polycephalum*

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Abstract: Slime molds rely on diverse sensory mechanisms to navigate and explore their environments. The acellular slime mold *Physarum polycephalum* has been shown to respond to light, chemicals, gravity, and magnetic fields, but its sensitivity to vibration has only recently been suggested. Here, we tested whether *Physarum* exhibits positive taxis toward vibration. Using two experimental setups, we exposed plasmodia to vibration motors operating at different frequencies and controlled for possible electromagnetic side effects. Plasmodial spread was quantified by image analysis across quadrants relative to the vibration source. In different setups, *Physarum* consistently moved toward vibration at 200 Hz, while no attraction was observed when motors were inactive, blocked, or running at 100 Hz or 300 Hz. These results suggest that *Physarum polycephalum* is capable of vibrotaxis, adding vibration to its repertoire of sensory modalities. The ecological significance of this behavior remains unclear, but vibration may serve as a cue to favorable environmental conditions such as rainfall or fungal growth.

Keywords: behavior, myxogastrids, plasmodia, vibrational stimulus

Introduction

To explore and forage in an ever-changing environment, organisms must be able to detect relevant information and respond appropriately. While this ability has been studied primarily in animals, it is also evident in other forms of life. The true slime mold *Physarum polycephalum* is a myxomycete that spends its vegetative phase as a plasmodium, a macroscopic multinucleate amoeboid cell. It is best known for its spatial optimization strategies, such as solving mazes (Nakagaki et al. 2000), but it is also capable of complex decision-making (Dussutour et al. 2010) and even habituation to aversive stimuli (Boisseau et al. 2016). Despite being unicellular, *Physarum* exhibits remarkable sensory capabilities, enabling it to respond to a wide range of stimuli. Like most protists, *Physarum* responds to a variety of chemical cues, some of which are nutritive (Carlile 1970), others harmful (Adamatzky 2010), and some of yet undetermined relevance, such as valerian (Adamatzky 2011). A particular form of chemotaxis involves the extracellular slime produced by plasmodia, which can serve as an externalized memory or provide

information about the nutritional status of conspecifics (Reid et al. 2012). *Physarum* also responds to light, showing negative phototaxis to ultraviolet and short wavelengths (Nakagaki et al. 1996), positive phototaxis to certain longer wavelengths (Hato et al. 1976), and oscillatory responses to intermediate wavelengths (Adamatzky 2013). In addition, plasmodia actively seek optimal temperatures (Tso and Mansour 1975; Wolf et al. 1997), sense gravity (Block et al. 1992; Wolke et al. 1987), and even respond to magnetic fields (Shirakawa et al. 2012, 2020).

Many of these sensory capabilities have only been discovered in recent decades, as *Physarum* has become a widely used model organism. The mechanisms underlying its complex behavior remains poorly understood, and likely not all stimuli that influence its movement have yet been identified. In a recent study, we found evidence that *Physarum* responds to vibration by moving toward it in a T-maze (Gehrke and Freiberg 2025).

Outside of the animal kingdom, reports of vibrational sensitivity are sparse. In the fungus *Botrytis cinerea*, high-frequency vibrations (>5000 Hz) promote colony growth, whereas lower frequencies (<165 Hz) appear to reduce growth rates (Hofstetter et al. 2020). More recently, Kobayashi et al. (2023) demonstrated that vibration can promote the growth of shiitake mushrooms (*Lentinula edodes*). They proposed that vibration may have ecological relevance for fungal survival: natural sources such as rainfall and falling trees provide both humidity and decaying wood as resources. The vibrations caused by falling trees, in particular, may trigger sporulation, facilitating rapid colonization of new substrates. Although *Physarum polycephalum* belongs to the Amoebozoa and is unrelated to fungi, it shares many of their habitats and ecological niches. It thrives in humid environments and feeds on decaying wood, fungal spores, and fungal fruiting bodies (Rojas and Stephenson 2021). Thus, it not only exploits the same habitats and resources as fungi but also preys upon them, suggesting that it may share similar ecological preferences.

Following the findings of Kobayashi and collaborators (Kobayashi et al. 2023), we hypothesized that *Physarum* may also actively seek out sources of vibration. In this study, we aim to test this hypothesis by examining whether *Physarum polycephalum* exhibits positive taxis toward vibration—a behavior that, to the best of our knowledge, has outside of our earlier publication not yet been reported in the literature.

Materials and methods

Biological Material

The slime mold used in all experiments originated from a single dried sclerotium of *Physarum polycephalum* obtained from a commercial supplier. According to the provider, the specimen was collected in France. The plasmodium was cultivated and regularly subdivided to establish a clonal line of genetically identical individuals. Species identity was confirmed by inducing sporulation in one clone and examining sporocarp and spores following standard keys (Nannenga-Bremekamp 2022). Outside of experiments, plasmodia were maintained in complete darkness at 20 °C in 12×12 cm Petri dishes containing nutrient-free 2% water agar (20 g agar agar (CarlRoth GmbH) per 1000 ml tap water). Cultures were transferred to fresh agar every two days, sprayed with demineralized water, and provided with rolled oat flakes (Koelln-Flocken, Peter Kölln GmbH & Co. KGaA) as food.

Experimental Design

All experiments were conducted inside a custom-made wooden box to stabilize environmental conditions and minimize external influences. The box was kept in a climate-controlled room at 20 °C. The substrate in all experiments was nutrient-free 2% water agar, which provided moisture similar to the maintenance cultures. Waterproof, coreless vibration motors (25 mm length, 7 mm diameter, VM-0724A2.4-WP EKULIT, Elektrotechnik Karl-Heinz Mauz Gmbh, Ostfildern, Germany) were used as the vibration source. To avoid interference, the voltage source powering the motors was placed on a separate table 120 cm away. Two different setups were used for a total of seven experiments. The first three experiments were conducted on 12 plasmodia each, the last four experiments on 25 plasmodia each. Overall, 136 plasmodia were tested.

Experimental Setup 1

The aim of the first Experimental Setup was to control for any effects caused by the presence of a vibration motor itself. Since *Physarum* is also very sensitive to magnetic fields (Gehrke and Freiberg 2025; Shirakawa et al. 2012, 2020), any reaction to vibration might be a byproduct of using electromagnetism in vibration motors. Therefore, in this setup, the aim was to allow *Physarum* to get close to the motor if it was attracted to it. Three experiments were conducted using this experimental setup, which is illustrated in Fig. 1. We used a custom designed 3D-printed dish with inside dimensions of 13x13cm, with a depth of 3.5cm. This dish was filled with 2%-nutrient-free water agar to provide water to the slime mold. Submerged inside the agar without contact to the walls or ground the vibration motor was placed close to one wall. Two isolated wires were led outside of the agar to provide current to the motor. In the middle of the dish, a 1 cm^2-cut of *Physarum* was placed together with a single oat flake providing nutrition to the plasmodia. The experiments were recorded with a high-definition document camera (Optoma DC455, Optoma Europe Ltd., London) from above, taking a picture every 30 minutes to account for the movement speed of *Physarum*. For recording purposes, a white light LED providing 250 lux was installed directly over the experimental dish, using a spectrum and intensity that is known to not influence the movement of the slime mold (Nakagaki et al. 1996). Every individual plasmodium was tested for 48 hours, allowing them to explore the agar surface.

In this setup, three experiments were conducted to test for the reaction of the slime mold to the vibrational stimulus and to control for side effects produced by the properties of the used materials. In Experiment 1, the vibration motor was constantly running and creating vibrations of ca. 200 Hz, creating a source of vibration in the substrate with a clear direction in relation to the plasmodia. In Experiment 2, the motor was present but did not receive any current and was therefore inactive. This was done to control for the effects of residual magnetic fields in the parts of the motor or other effects caused by the presence of the motor. This, however, did not fully control for the effects of a running motor, therefore, Experiment 3 was conducted. In this experiment, the motors were opened up, blocked inside to stop them from creating vibration, and then resealed. This was done because the electrical current creates electromagnetic fields inside the motors to create the vibration, stronger than the intrinsic magnetic field in the parts of the motor. Furthermore, it has been shown that electric current influences the movement of *Physarum* plasmodia (Kato, 2012). Therefore, to account for the presence of electrical current in a running motor and the magnetic field created, these blocked motors were constantly under current during Experiment 3, therefore

being active without creating vibration. For each experiment, 12 plasmodia were observed for up to 48 hours, leading to a total of 36 plasmodia for experimental setup 1.

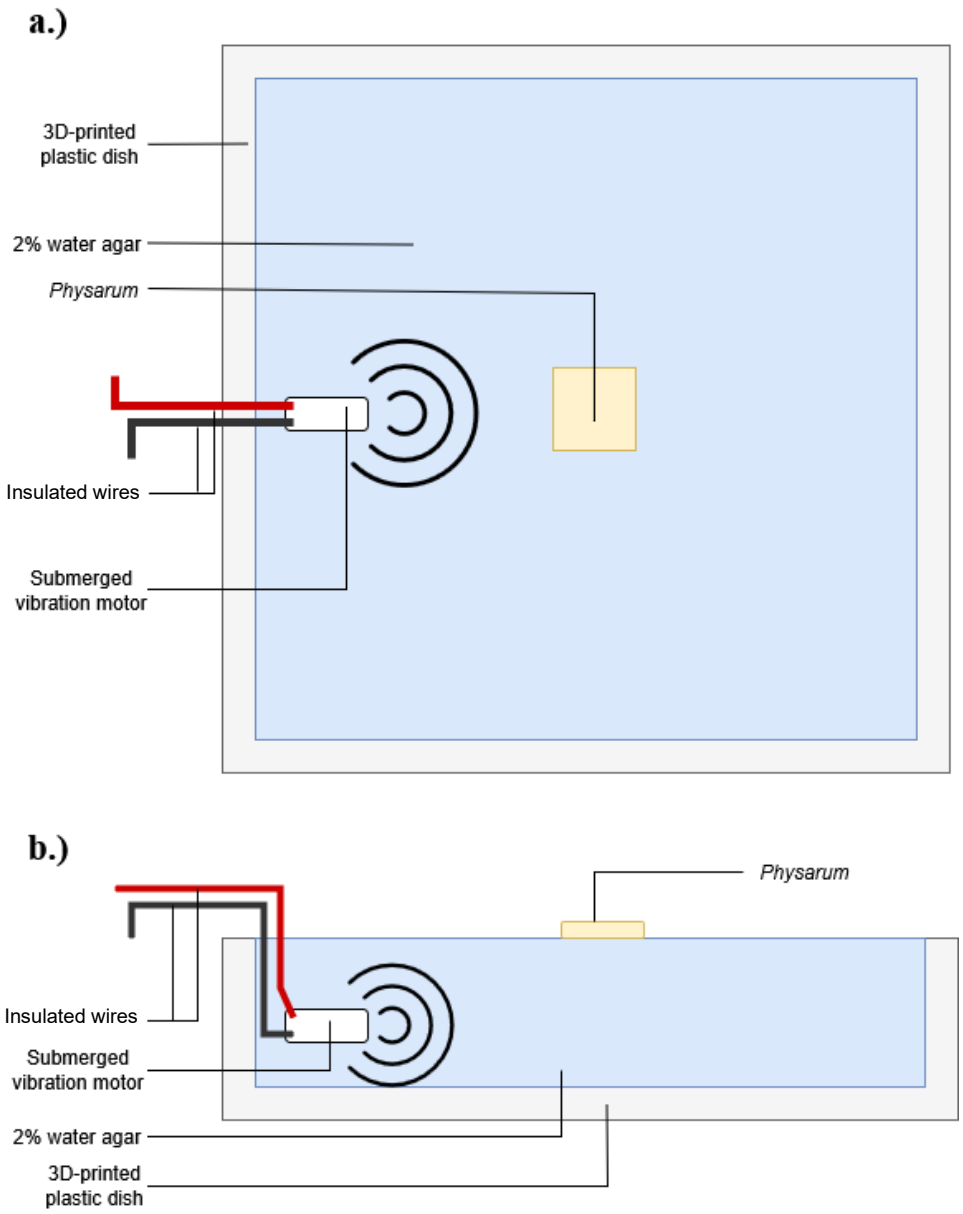

Figure 1. Visual representation of the first experimental setup. a.) shows the experimental setup as viewed from above, while b.) provides a side view.

Experimental Setup 2

The aim of the second experimental setup was to imitate the setup that led to the initial findings. In our initial study, the source of vibration was submerged in agar but not in direct contact with the plasmodia. Instead, it was placed on the table, reducing the intensity of the vibration reaching the slime mold (Gehrke and Freiberg 2025). To emulate this, in this setup the motor was submerged in 2% water

agar in a 5x5x5cm cubic plastic dish and placed on the table next to a square Petri-dish, at 5cm distance between them (as shown in Fig. 2). In this setup, four experiments were conducted on 25 plasmodia respectively to test the effect of different vibration frequencies: 0 Hz (motor off), 100 Hz, 200 Hz and 300 Hz. All tests were performed in the complete absence of light, all plasmodia were tested for 24 hours to avoid movement along the edge of the plate. After the test, images of the Petri-dishes were acquired with a high-resolution document camera (Optoma DC455, Optoma Europe Ltd., London) to assess the spread of the plasmodium. For each of the four frequencies 25 plasmodia were tested, leading to a total of 100 plasmodia tested.

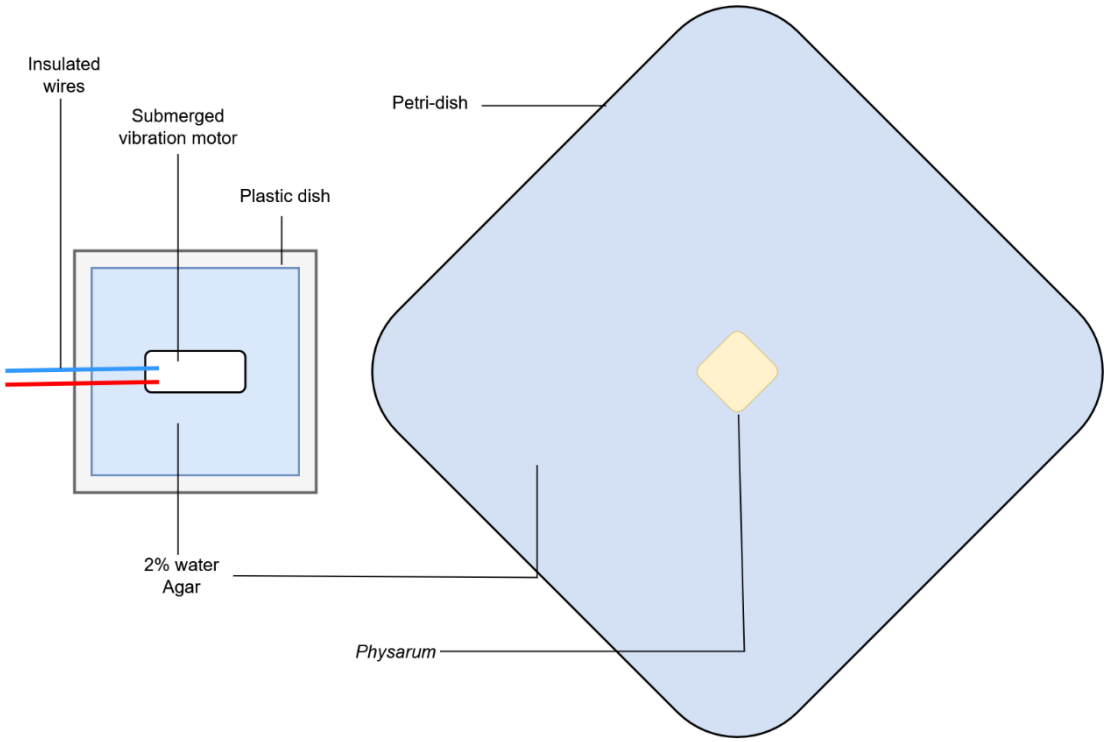

Figure 2. Visual representation of the second experimental setup as viewed from above.

Data analysis

The pictures taken during the experiment were analyzed using the open-source image analysis platform FIJI (Schindelin et al. 2012). The program was used to quantify the slime mold spread across the Petri-dish by determining the number of pixels that showed part of the plasmodium. To account for the movement direction the pictures were then broken up into 4 quadrants (V+, V-, S_l and S_r) with the starting point of the slime mold in the center. Fig. 3 shows the schematic after which the images were analyzed. For each quadrant and each image, the percentage of pixels of the plasmodium was calculated to evaluate the distribution of the plasmodium into the quadrant. Quadrant V+ was interpreted as movement towards the vibrational stimulus, while Quadrant V- was considered as movement away from the stimulus. Quadrants S_l and S_r accounted for movement to the left or the right, respectively. For the

first experimental setup, the image where the plasmodium first touched one of the walls of the dish was chosen for evaluation. In the second setup, an image was obtained after 24 hours. Both setups allowed to effectively eliminate wall-following behavior.

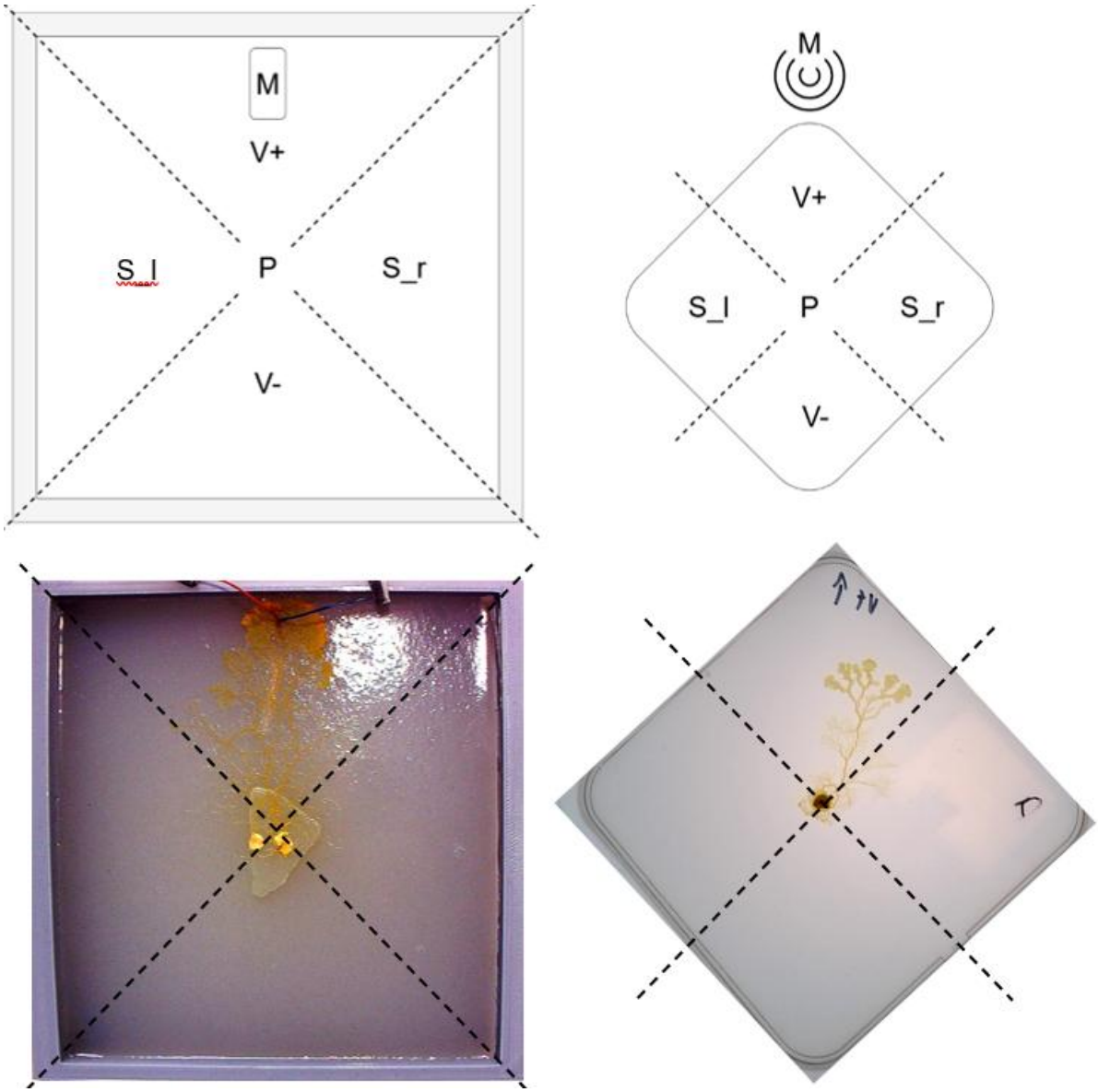

Figure 3. Upper row: visualization of the quadrants for evaluation of the plasmodium spread in both experimental setups. Experimental setup 1 is shown on the left, experimental setup 2 is shown on the right. In both setups, the plasmodium starts in the middle and can move either towards (V+) or away from the vibration (V-), or to one of the sides (S_l for left, S_r for right). Lower row: Pictures from the experimental data, divided after the quadrants shown in the upper row. Photo credit: J. Freiberg

Results

For each plasmodium, using the method described above, the percentage of spread into each quadrant at the moment the plasmodium first touched the wall of the Petri-dish was calculated. The mean spread of the plasmodia for all experiments can be found in Table 1, grouped by experimental setup. It was assumed that, if no influence of the vibration motor exists and the plasmodium would move at random, the mean spread to each quadrant would be close to 25%. Therefore, to test if a positive taxis towards vibration exists, one-tailed one-sample-t-tests were conducted to test for mean values significantly higher than 25%. The results of the t-tests are also shown in Table 1.

Table 1. Mean percentage of plasmodia spread into the four quadrants for all experiments in both experimental setups. Additionally, for the quadrant V+ the standard deviation (SD), standard error of the mean (SEM) and the t-value with the corresponding p-value for the t-tests are provided.

	V+	**V-**	**S_l**	**S_r**	**$SD_{\%V+}$**	**$SEM_{\%V+}$**	***n***	***t*$_{V+}$**	***p***
Setup 1									
On (200Hz)	44.64%	10.05%	34.91%	10.39%	34.32	9.91	12	1.983	**.029**
Off (0 Hz)	17.30%	27.17%	34.10%	21.43%	24.03	6.94	12	-1.110	.861
Broken (0 Hz)	20.61%	35.46%	27.63%	16.31%	29.39	8.48	12	-0.518	.695
Setup 2									
0 Hz	24.42%	25.60%	32.69%	17.29%	31.65	6.33	25	-0.091	.536
100 Hz	26.22%	20.46%	21.66%	31.66%	37.15	7.43	25	0.164	.436
200 Hz	39.53%	23.92%	11.14%	25.41%	37.64	7.53	25	1.931	**.033**
300 Hz	28.72%	21.31%	19.73%	30.24%	33.23	6.65	25	0.559	.291

Overall, the majority of the data is spread around 25% for each quadrant. A visualization of the spread can be found in Fig. 4. Significantly higher spread towards the vibration can be found in Experimental Setup 1 for the running, intact vibration motor ($p = .029$), and in Experimental Setup 2 for the motor running at 200 Hz ($p = .033$). No significant movement towards the source of vibration was found in either setups for the controls (motor off / broken), and in Setup 2 also not for the vibration frequencies of 100 Hz and 300 Hz ($p > \alpha = 0.05$). However, results have to be interpreted with caution as they would not be significant in a two-tailed test. Furthermore, Shapiro-Wilk-tests conducted showed that some groups differed significantly from normality.

Therefore, to further test for attraction toward vibration, two-tailed non-parametrical Mann-Whitney-U-Tests were performed. First, in Setup 1, the median percentage of quadrant V+ in the first condition (On (200Hz)) was tested against the median percentage of quadrant V+ in the second condition (Off (0Hz)). The results showed a significant group difference ($U = 108$, $z = 2.0514$, $n_1=n_2=12$, $p = .040$). Second, another Mann-Whitney-U-Test was performed to test the first condition (On (200Hz)) against the third condition (Broken (0Hz)). This test yielded no significant result ($U = 98$, $z = 1.4641$, $n_1=n_2=12$, $p = .143$).

Discussion

The acellular slime mold *Physarum polycephalum* is known to respond to a wide range of stimuli. Its response to vibration, however, has only recently been documented, when it was shown to move toward a vibration source in a T-maze (Gehrke and Freiberg 2025). Although the ecological or physiological basis of this behavior remains unclear, similar positive effects of vibration have been reported in fungi that share the same environment as *Physarum* (Kobayashi et al. 2023). The present study therefore aimed to replicate the initial findings, control for potential confounding factors, and examine the effect of different vibration frequencies.

The results of Experimental Setup 1 demonstrate that the observed behavior is not simply an artifact of electromagnetic fields produced by the motors. Neither an inactive motor nor a motor receiving current without producing vibration elicited significant movement. Only a functional motor vibrating at 200 Hz produced a clear response. A similar pattern was observed in Experimental Setup 2: no significant movement occurred when the motor was turned off, or at frequencies of 100 Hz or 300 Hz, whereas vibration at 200 Hz again elicited a significant response.

These results indicate that frequency, rather than vibration intensity, is the key factor. In both experimental setups, attraction occurred specifically at 200 Hz, despite differences in how the vibration was transmitted to the plasmodia. Nevertheless, the effect size was modest: the mean spread toward the vibration source was close to 40%, considerably weaker than responses to many other known stimuli. This suggests that vibration may act as a relatively weak cue in isolation, but could play a more important role when combined with other environmental signals.

The ecological significance of vibrotaxis in *Physarum* remains uncertain. Potential natural sources of vibration in its habitat include animals, fungi, falling trees, wind, and rain. Predation by beetles (Wheeler 1979) or springtails (Hoskins et al. 2015) could produce vibrations, but attraction toward predators would not represent an adaptive strategy. A more plausible explanation is that vibration guides Physarum toward food resources. Fungal growth, for example, may be associated with vibrational activity. While Kobayashi et al. (2023) suggested that fungi use vibrations from falling trees to induce sporulation, it seems unlikely that *Physarum* would respond in the same way. In our experiments, vibration did not induce sporulation, but it may facilitate movement toward potential food sources during the plasmodial stage.

Abiotic factors such as wind and rain also merit consideration. Wind disperses *Physarum* spores, while rainfall provides the humidity essential for its survival. Vibration may therefore serve as an indirect cue to conditions favorable for growth or reproduction. A recent study on caterpillars associated frequencies near 100 Hz with wind and those near 175 Hz with rain (Turchen et al. 2023). The fact that *Physarum* responded to 200 Hz but not 100 Hz suggests that it may be tuned to vibrations resembling those produced by rainfall, rather than by wind. This could explain why the observed response, while statistically significant, was not particularly strong- the experimental frequency may not have matched natural sources closely enough to fully elicit the behavior.

Physiological explanations should also be considered. Plasmodial movement and information processing depend on rhythmic oscillations within the tubular network (Boussard et al. 2021). It has been proposed that external vibrations or changes in substrate stiffness can interfere with these oscillations (Murugan et al. 2021). In our earlier work, vibration not only induced movement toward the source in a

T-maze, but also lateralized movement in plasmodia unable to approach the source of vibration directly (Gehrke and Freiberg 2025).

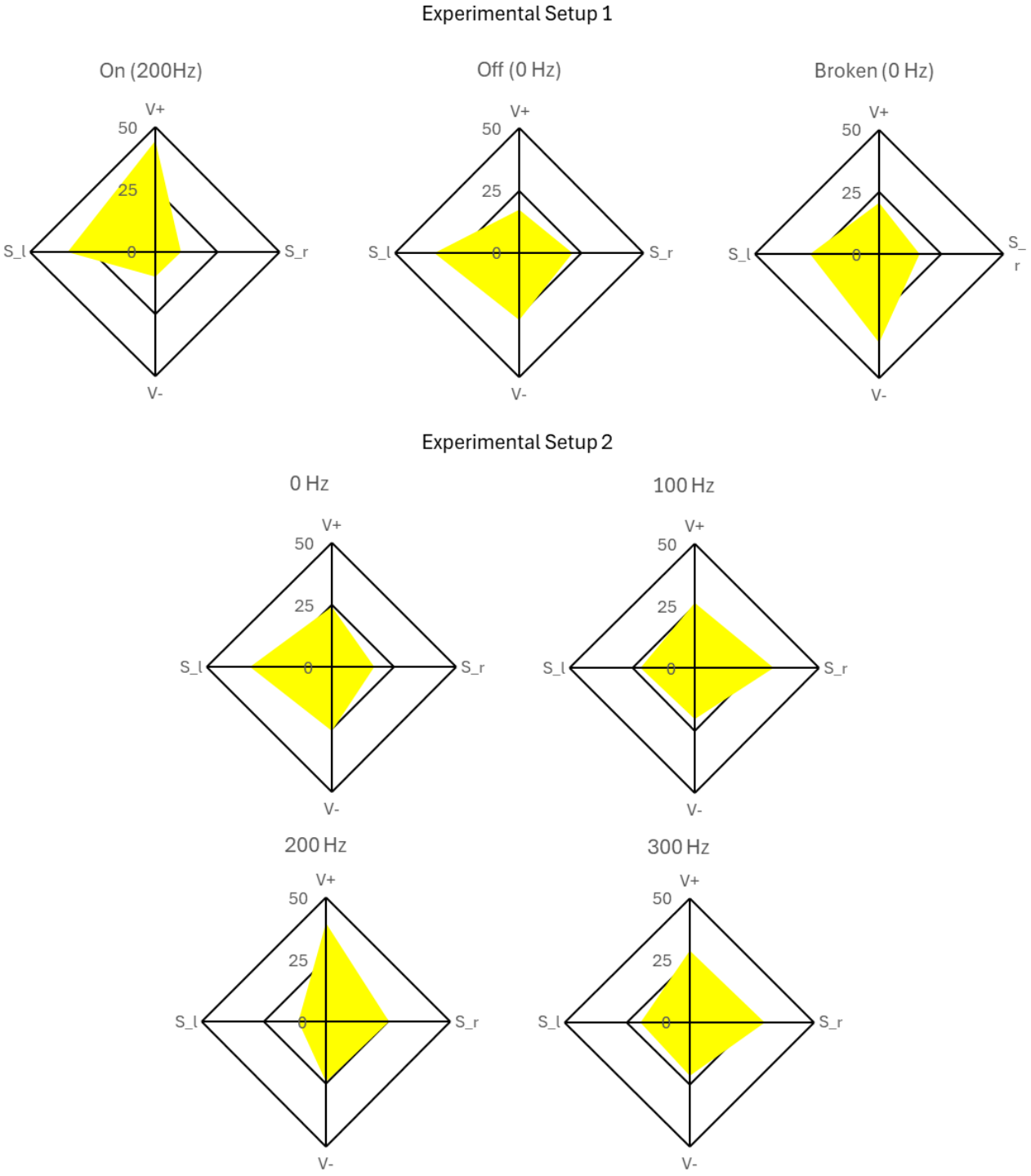

Figure 4. Visualization of the mean percentual spread of the plasmodia across both experimental setups into the quadrants of the respective Petri-dishes. In experimental setup 1, 12 plasmodia were tested per experimental condition, with a total of 36. In experimental setup 2, 25 plasmodia were tested with a total of 25.

In the present study, lateralized movement was not observed, but attraction toward the vibration source remained. This indicates that vibration does not completely disrupt normal motility, as occurs with galvanotaxis in an electric field, where movement is strongly biased toward the anode (Anderson 1951; Kato 2012). Instead, vibration may act as a subtle modulator of oscillatory dynamics, influencing directional movement without fully overriding other cues.

Overall, the ecological role and physiological mechanisms underlying vibrotaxis in *Physarum* remain unresolved. Nevertheless, our findings suggest that vibrations around 200 Hz attract plasmodia, and that this effect cannot be attributed to experimental artifacts. Future research should test frequencies more closely aligned with those produced by rainfall or fungal growth, to evaluate whether stronger or more consistent responses can be elicited. While the adaptive significance of vibrotaxis is not yet clear, it can be added to the expanding repertoire of sensory capabilites observed in *Physarum polycephalum*.

The original data presented in this study are openly available in OSF at https://doi.org/10.17605/osf.io/jgbhx (accessed on 05 September 2025). The experiments were not preregistered.

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