

A mobile trackball system for studying phonotaxis of insects in the field

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Abstract

Here we introduce a mobile trackball system for measuring phonotactic behaviour of insects in the field. The trackball system allows generating quantitative behavioural data in the field. Experiments for determination of the phonotactic threshold of two insect species of a parasitoid-host system proofed the utility and usability of this method. The threshold of the parasitoid fly *Emblemasoma auditrix* (Shewell, 1976) in response to the calling song of the host cicada *Okanagana rimosa* (Say, 1830) could be confirmed with 61 dB SPL. The behavioural threshold of female cicadas *O. rimosa* could be determined for the first time to 62 dB SPL. Thus, the mobile system allowed testing of the cicada in the field, which was not possible in laboratory environment. Generally, it was possible to test animals that exhibit certain behaviours only outdoors and to test intact animals and to release them immediately after completion of the experiment. With this method, it will also be possible to test animals under real environmental conditions, for example, in respect to noise.

Key Words

Behaviour, bioacoustics, cicada, Diptera, Homoptera

Introduction

The perception of the world by animals can only be addressed indirectly through observation of their behaviour and by experimental testing. The controlled and restricted environment in laboratories allows a detailed analysis of the animal's behaviour and physiology. Such experiments often reveal astonishing capabilities of their sensory and neural systems. However, animals in the wild might be more motivated and furthermore, they are exposed to a multitude of uncontrolled environmental influences. It is essential to use a multitude of different approaches and to study behaviour in both the laboratory and the field. In some cases, it might be possible and useful transferring laboratory methods to the natural environment. For example, it was possible to study the neuronal responses in crickets and grasshoppers to acoustic stimuli in the field (Rheinländer and Römer 1986; Gilbert and Elsner 2000; Pfeiffer et al. 2012; Römer 2021). In crickets it could be analysed how a specific nerve cell, the omega cell, is involved in auditory information processing in natural field conditions, for example, in respect to environmental noise (Rheinländer and Römer 1986; Schmidt and Römer 2011; Römer 2021).

Among insects, phonotactic behaviour is relatively well studied in the laboratory. The importance of different acoustic parameters, such as temporal pattern or carrier frequency for response or for orientation has been unravelled to detail (review: Hedwig 2006). For example, it has been shown that grasshoppers detect pauses of a few milliseconds in the calling song (von Helversen and von Helversen 1997) and that crickets can discriminate sound directions with less than 3° difference in azimuth (Hedwig 2006). In comparison, behavioural studies in the field are rarer but show that vegetation might diminish the high directional precision observed in an undisturbed sound field (Hirtenlechner and Römer 2014).

For testing orientation behaviours or to evaluate neuronal properties, a trackball or treadmill system is standard in many laboratories. For phonotaxis experiments in insects, different open loop systems are used in soundproofed rooms that have minimal sound reflections or external noises. One of the first systems was the “Kramer” treadmill, a large sphere which electronically turns to compensate the walking of an insect on top (Weber et al. 1981; Schul et al. 1998). Subsequently, fast trackball systems with smaller spheres were established (Mason et al. 2001; Hedwig and

Poulet 2005; Baden and Hedwig 2008; Römer 2020). With the latter systems, it could be shown that crickets make rapid steering movements and that they can detect sound differences of 1 dB SPL in intensity (Hedwig and Poulet 2004). Orminii flies have in such ideal test situations an auditory spatial resolution of only 2° in azimuth (Mason et al. 2001).

However, the behaviour of species might be difficult to analyse in the laboratory as some species do not show the studied behaviour in the enclosure. For example, cicadas (Auchenorrhyncha) are not only difficult to rear, but the adults rarely exhibit phonotactic behaviour indoors. Only for the cicada *Cystosoma saundersii* Westwood, 1842 a phonotactic reaction has been shown in the laboratory (Doolan and Young 1989). Furthermore, quantitative reports on cicada phonotaxis are rare (Huber et al. 1990; Daws et al. 1997) despite their well-known and elaborate bioacoustics. Therefore, the need for a test system for cicada phonotaxis seems obvious.

In order to combine precise behavioural recordings and outdoor conditions, we tested a mobile trackball system in the field. This approach has several advantages:

- It allows testing of animals that only exhibit specific behaviours outdoors.
- It allows testing of intact animals and their immediate release afterwards.
- It allows testing under natural environmental conditions (e.g. for the influence of noise).

We used the trackball system for two insect species that are part of a parasitoid-host system. Male cicadas of the species *Okanagana rimosa* (Say, 1830) (Homoptera: Cicadidae, Tibicininae) produce a calling song to attract females (Stölting et al. 2004). In addition to female cicadas, parasitoid flies of the species *Emblemasoma auditrix* (Shewell, 1976) (Diptera: Sarcophagidae) overhear the song and home in on the male cicadas (Soper et al. 1976; Lakes-Harlan et al. 1999). For this task the fly has an evolutionarily adapted hearing organ and specifically infects male cicadas at their sound producing organ, the timbal (Lakes-Harlan et al. 1999; Tron et al. 2016). Female flies and female cicadas have the same acoustic target and the phonotactic behaviour of both species depends on good weather conditions with sunny skies and warm temperatures (Stölting et al. 2004). The phonotaxis of the fly *E. auditrix* has been tested in the laboratory, although with restricted conditions (Köhler and Lakes-Harlan 2001; de Vries and Lakes-Harlan 2005). For the experiments, the animals had their wings clipped and a large proportion of individuals did not show phonotactic behaviour in the laboratory. With intact wings, the flies always flew to the next light source, such as a window or a ceiling lamp, ignoring the acoustic stimulus. Nevertheless, behavioural thresholds and preferences for temporal parameters were successfully evaluated (Köhler and Lakes-Harlan 2001; de Vries and Lakes-Harlan 2005). Female cicadas did not react to acoustic stimuli in the laboratory. Therefore, the mobile trackball system could be a solution for addressing behavioural questions.

Material and methods

We used an air-supported trackball system with a Styrofoam ball (from local shops) of 50 mm diameter, which fitted in a custom-made metal base (Fig. 1, workshop of the institute). The airflow was provided by a battery driven air pump (“Battery Air Pump, Q7-HQ-102”, intended for aquarium air supply, CHN; for a list of equipment used see Suppl. material 4) connected with fitting tubes (6 mm diameter) to the metal base. Air pressure pulses from the pump were smoothed with an elastic dilation (a small plastic bag) fitted in the tube system. Underneath of the trackball an optical movement sensor from a computer mouse (“USB Optical mouse”, Pixart Imaging Inc., TWN) was embedded. This sensor was connected to a laptop and the signals were collected with software “grille_paint Trackball”, developed by R. Schuster and generously provided free of cost by Dr. M. Hartbauer, both University Graz, AUT and which runs on a virtual LINUX machine. The trackball movements were calibrated by mechanically turning the Styrofoam ball for distinct distances. Data were exported as xy-position data per time point and further processed in Excel (Microsoft Corp., USA) for direction, distance and velocity.

In front of the trackball setup a loudspeaker (“Boomer mobile”, 2 W, Ultron AG, GER) was placed in 30 cm distance in a holder. Different sound files were prepared with Audacity software (audacityteam.org, USA). Here we report data on a test for behavioural threshold. Therefore, a pre-recorded calling song of *O. rimosa* (Stölting et al. 2004) was played for 10 s at 80 dB SPL to ensure responsiveness of the tested animal (Fig. 2). Thereafter the test file contained a sequence of six calling songs of 10 s duration and pauses of 2 s in between. In the sequence, the intensity was increased stepwise, starting at 50 dB SPL with 6 dB increments. Sound intensity was measured with a sound level meter (XL2, NTI Acoustic, GER; rel. 20 µPa).

The system was placed on a small outdoor table (50 cm × 50 cm × 70 cm) in a clearing of an open forest near Pellston, Michigan, USA (GPS 45°33'43.4"N, 84°44'39.1"W). Animals were caught nearby by phonotactic attraction with a loudspeaker (“Boomer chaka”, Ultron AG, GER) replaying a pre-recorded calling song of the cicada *O. rimosa*. Females of the parasitoid fly *E. auditrix* or of the cicada arrived often within a minute at the loudspeaker. Animals were cautiously captured with small vials. A caught animal was then processed within less than two minutes and positioned on the trackball. Therefore, a magnet was glued to the pronotum or scutum with a small drop of glue. We used a hot-melt adhesive (“Ultra Power Klebesticks”, Steinel, GER), which was more sticky and easier to apply than superglue or a colophonium-bee wax mixture. The tip of the adhesive stick was slightly melted with a cigarette lighter and then a small magnet (Neodym, 2 × 1 mm, 24 mg mass, Supermagnete.de, GER) was brought in contact with the glue. By moving the magnet slowly away from the melted glue, a thin thread of glue attached to it. The thin thread was cut

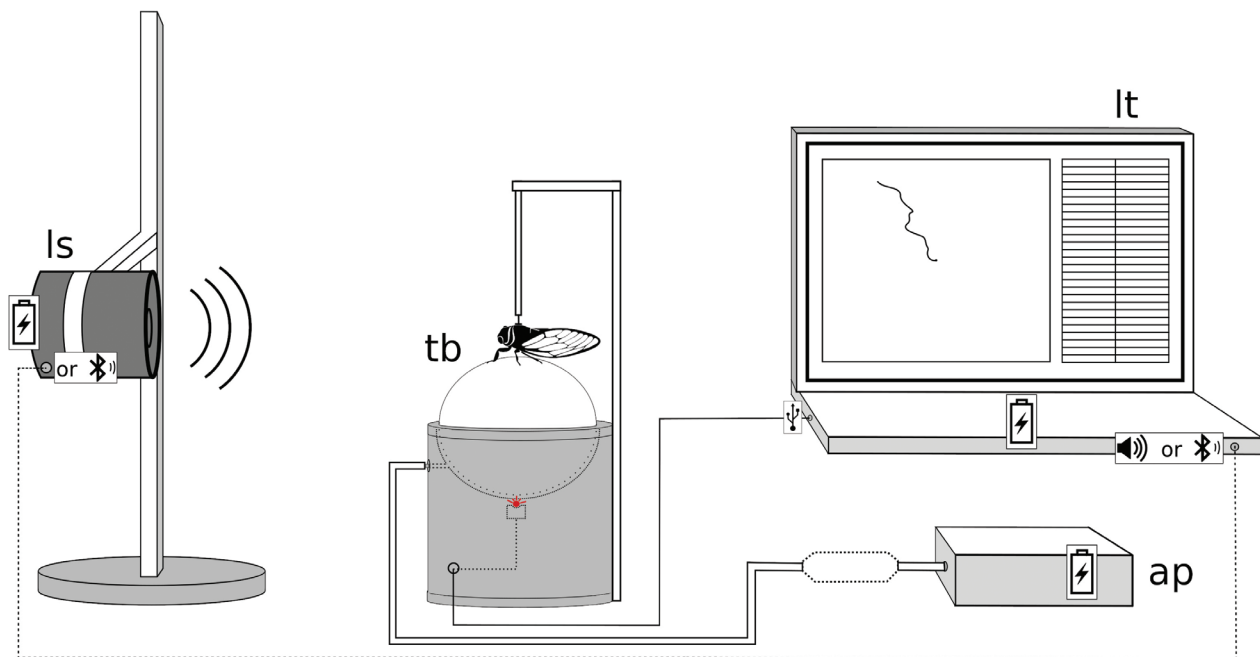


Figure 1. Schematic drawing of the mobile trackball system. All electric parts are battery-powered. The trackball (tb) is supported by an air-cushion from an air pump (ap). The connecting tube has a dilation to smooth air pressure pulses. The animal is attached with a magnet to a holder above the trackball. The movement of the trackball is registered via an optical mouse sensor and data are stored on the laptop (lt). Stimuli are provided by a loudspeaker (ls) with an internal amplifier connected to the laptop. Drawings not to scale.

near the magnet and melted again before approaching the animal and immediately placing the magnet on the scutum. Due to its small volume, the glue cooled very fast and without harming the animal.

Thereafter, the animal could be attached via the magnet to a steel needle fixed in a holder above the trackball (Fig. 1, Suppl. material 1). The steel needle in the holder could be adjusted to position the animal on top of the trackball. The magnetic attachment was relatively weak and the animal could make horizontal turns under the needle. The mass of the magnet was supported by the attachment to the needle and therefore the animal's motor behaviour was not impaired by the additional mass. However, the animals could support the mass of the magnet for a short period of time on their own – cicadas and even flies managed to fly with an attached magnet away from the experimental setup (in cases they escaped during handling).

After the tests, the magnet and the glue could be completely removed without reheating. The cuticle was not damaged and the animal could be released without further harm in its habitat. The animals were released at a different spot in the field to avoid pseudoreplication during an experiment series. For the threshold experiments 13 flies and 5 cicadas were tested.

Data resources

The data underpinning the analysis reported in this paper are permanently deposited in the Data Repository of the Justus-Liebig-University at <https://doi.org/10.22029/jlupub-20041>.

Results

The mobile trackball system was successfully used in the field (Suppl. material 1). Both species, the fly *E. auditrix* and the cicada *O. rimosa* showed phonotactic movements on the trackball in response to the cicada's calling song. All tested animals could be released after the experiments.

Female flies were very active on the trackball (Suppl. material 2). They sometimes rotated the trackball very fast without a stimulus. Flies have been tested in different experiments (only experiments on the threshold are described here) and they responded to the sound up to 30 minutes. Typically, a fly reacted strongly to the first stimulus of the series of callings songs used for determination of the threshold (80 dB SPL; Fig. 2). In the subsequent sequence of stimuli with increasing intensities, a threshold value was determined as the lowest sound intensity with a clear phonotactic behaviour (Fig. 2). The mean threshold was 61 dB SPL (SD 6.3, n = 10).

Female cicadas moved the trackball more slowly than the fly (Fig. 2, Suppl. material 3) and sometimes lifted the Styrofoam trackball. Cicadas were responsive to acoustic stimuli for several minutes only, but even in this relatively short period different tests could be performed. In the threshold experiments with increasing sound intensities, two cicadas (from 5) could be tested successfully. Both cicadas did not react to sound stimuli of 50 and 56 dB SPL, but showed phonotaxis to stimuli starting at 62 dB SPL with slow turns of the trackball (Fig. 2). Sometimes cicadas even exhibit flight behaviour with flapping of their wing while attached to the holder.

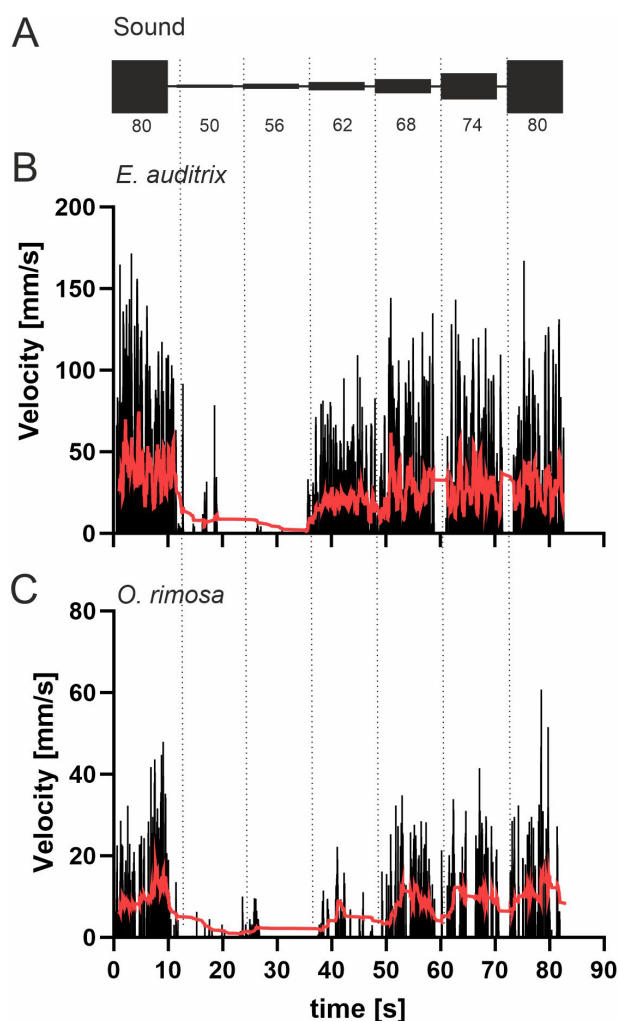


Figure 2. Exemplary phonotactic movement of the test animals on the trackball in response to the calling song of the cicada *O. rimosa* with different intensities. **A.** schematic oscillogram of the sound track, with a sequence of calling songs (CS) of 10 s and pauses of 2 s with increasing sound pressure levels after the first sequence. The sound pressure levels of 80, 50, 56, 62, 68, 74 and 80 dB SPL, respectively, at the trackball is indicated. **B, C.** Recordings of the velocity of the trackball rotation by the test animal. The black line represents the instantaneous velocity and the red curves represents a moving average of 20 data points. The fly *E. auditrix* reacted strongly to the CS, starting at 62 dB SPL (**B**). The cicada *O. rimosa* also reacted to the calling songs with 62 dB SPL and higher, but with a lower velocity than the fly (**C**).

Discussion

The trackball system was successfully implemented in field experiments. We demonstrated that females of both species, the fly *E. auditrix* and the cicada *O. rimosa*, exhibited phonotactic behaviour in response to calling song of the cicada while being tested on the trackball. It is not surprising that the animals were motivated to show the behaviour, as they were attracted with a loudspeaker in their habitat shortly before the experiments.

The threshold of *E. auditrix* on the trackball could be determined to 61 dB SPL. The threshold was previously

determined to be at 60 dB SPL for walking flies in the laboratory the calling song and for free flying flies (Köhler and Lakes-Harlan 2001; Tron and Lakes-Harlan 2017). Electrophysiologically, the threshold at 9 kHz, the peak carrier frequency of the calling song, was found to be about 65 dB SPL (Lakes-Harlan et al. 1999). Thus, these results indicate that the trackball experiments provide valid and useful data.

The threshold for phonotaxis of the cicada was 62 dB SPL. Although the threshold is only from two animals, it fits into the electrophysiologically determined threshold for pure tones of 9 kHz (peak frequency of the calling song) at about 67 dB SPL (Stölting et al. 2004). Of course, additional tests are needed. Unfortunately, our tests were made at the end of the season and only a few cicadas could be tested on the trackball. All responded to the sound, but a clear response in the threshold experiments was recorded only in the two animals. Nevertheless, the successful tests are encouraging, considering the lack of phonotactical behaviour under laboratory conditions. In two studies on Australian cicadas a phonotaxis behaviour was reported (Doolan and Young 1989; Daws et al. 1997). In one study a threshold around 70 dB SPL at 850 Hz carrier frequency was determined from flight posture in laboratory tests (Doolan and Young 1989). Female cicadas of *O. rimosa* exhibited a movement pattern with walks and flights on the trackball. Such a pattern is also observed when a cicada is attracted to a loudspeaker in the field. They fly towards the speaker, often land nearby, walk some distance and may start flying again (unpublished results).

Technique

The trackball technique is an established method (Mason et al. 2001; Hedwig and Poulet 2005) and as described here, field tests with the mobile trackball system were successful. Some animals showed a high spontaneous activity on the trackball, which typically decreased with time. Thereafter a stimulus correlated phonotactic reaction could clearly be distinguished in the data. For analysis, we used the parameters “distance” and “velocity” and species-specific differences in phonotaxis velocity were revealed. This corresponds to the walking behaviour on surfaces (vegetation) in the field, with cicadas moving rather slowly (unpublished observations).

We did not evaluate the parameter “direction” and the insects could rotate in the holder and the loudspeaker had only one position in azimuth. For analysis of phonotaxis direction or performance, the animal should be in a fixed position. Such approaches revealed the hyperacute directional hearing ability of the fly *Ormia ochracea* (Bigot, 1889) (Mason et al. 2001) and have been used to evaluate song preferences of different populations (Lee et al. 2019). Our experiments were intended as proof-of-concept with the maximal possible freedom for movement.

The trackball with 50 mm diameter worked for both species, as it is easily moveable on the air cushion.

However, it might also be useful to have a trackball with larger diameter for larger animals, although our experiments showed that cicadas can move a small trackball without notable limitations. The experimental setup was successfully used on the ground as well as on a small table in the habitat. It is also possible to use the trackball on a tripod which allows positioning it in different distances to abiotic or biotic noise sources, for example, like a chorus from cicadas in a tree (see below). Importantly, in our experiments no calling song of a cicada was heard or registered during the tests which might have influenced phonotaxis on the trackball.

The technique was used during dry, sunny weather conditions corresponding to the ecological preferences of the species (Stölting et al. 2004). Under these conditions it was a robust system and only the controlling laptop had to be placed in the shade.

Prospects

The use of a trackball setup in the habitat allows for testing in a realistic environment. This setup enables monitoring behaviour in relation to conspecific and abiotic noises. Testing of phonotactic behaviour in the field has been previously found to be useful (Rheinländer and Römer 1986; Römer 2021). For example, field experiments have demonstrated that crickets require higher amplitude differences for choice-making compared to laboratory conditions (Hirtenlechner and Römer 2014). Acoustic communication of insects can be disturbed by noise, e.g. anthropogenic noise (Costello and Symes 2014; Schmidt et al. 2014). The mobile trackball system allows for testing phonotaxis in various noise environments, ranging from natural areas to locations with high levels of anthropogenic noise.

Furthermore, the effect of natural soundscapes on the behaviour can be tested. The cicada *O. rimosus* is known as proto-periodic cicada, with large annual fluctuations in population density. The species is annually present, however, every seven to nine years mass emergences of adults occur resulting in a chorus of sound producing males (Stölting et al. 2004). Such years might provide the possibility to analyse the phonotactic behaviour in response to a chorus. A chorus has advantages for long-range signalling and probably diminish the risks for an individual to be attacked by a predator or parasitoid (Greenfield 2002; Lehmann and Lakes-Harlan 2019). But how can intraspecific females select an individually calling male within such a chorus? A chorus might set limitations to selective intraspecific phonotaxis (e.g. sexual selection), which has been tested often with relatively simple choice experiments in the laboratory. Similarly, the parasitoid fly must find a single host cicada in a potentially confusing acoustic environment. By moving the trackball on a tripod in between a group of calling males it might be seen, whether a female prefers one direction or rotates between the various directions of the sound sources.

Conclusion

The trackball setup enables testing animals with a potentially higher motivation than in the laboratory. One advantage is that motivated animals can be captured in the field and tested within minutes. Therefore, the internal state and external factors (light, temperature etc) should at least be permissive for positive testing of the behaviour. In contrast, motivation in the laboratory might decrease over time, and abiotic factors could be suboptimal. As mentioned above, the difference in behaviour between field and laboratory conditions is pronounced in the cicada species. This species did not exhibit phonotactic behaviour in the laboratory at all. However, it reacted to sounds while fixed on the mobile trackball system placed in the field. Furthermore, in respect to decreasing numbers of insects, it might also be important, that the animals could be released shortly after the tests. The animals remained intact and could be released unharmed after the test in their natural habitat.

In summary, it might be useful to apply the method to distinct species, especially species which do not exhibit the full behavioural repertoire under standard laboratory conditions.

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Supplementary material 1

Figure trackball system

Authors: Reinhard Lakes-Harlan, Marie-Sa Do, Joscha A. Alt

Data type: jpeg

Explanation note: Photo plate showing the parasitoid fly *Emblemasoma auditrix* (A) and the cicada *Okanagana rimosa* (B) on the trackball. The complete system can also be placed directly in the habitat (C; left: trackball with connections to the pump and the laptop; right: loudspeaker clamped to a metal stand).

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Link: <https://doi.org/10.3897/bull.insectology.164055.suppl1>

Supplementary material 2

Video Phonotaxis *Emblemasoma auditrix*

Authors: Reinhard Lakes-Harlan, Marie-Sa Do, Joscha A. Alt

Data type: mp4

Explanation note: A female fly *Emblemasoma auditrix* on top of the trackball. After onset of the calling song (indicated by a red dot) of the cicada *Okanagana rimosa*, it moves the trackball very fast in a phonotactic response.

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Link: <https://doi.org/10.3897/bull.insectology.164055.suppl2>

Supplementary material 3

Video Phonotaxis *Okanagana rimosa*

Authors: Reinhard Lakes-Harlan, Marie-Sa Do, Joscha A. Alt

Data type: mp4

Explanation note: A female cicada *Okanagana rimosa* on top of the trackball. After onset of the calling song (indicated by a red dot) of the cicada *Okanagana rimosa*, it moves the trackball rather slowly in a phonotactic response.

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Link: <https://doi.org/10.3897/bull.insectology.164055.suppl3>

Supplementary material 4

Data and method information

Authors: Reinhard Lakes-Harlan, Marie-Sa Do, Joscha A. Alt

Data type: xlsx

Explanation note: In an Excel sheet, the data used for Fig. 2 are provided. Furthermore, information about the parts necessary for the trackball system is provided.

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