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HOW TERMITES USE VIBRATION TO ASSESS POTENTIAL FOOD STRUCTURES

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Abstract

It has been long known that termites use vibration as a communication channel in a variety of ways. For example alarm signals produced by the soldiers, clearly audible to the unaided ear, elicit a programmed defensive response in the workers. It appears that they are also receptive to vibration through the substrate they inhabit and are able to use this information to some extent. Our recent work has shown that they are able to use information gained through structural vibration, not only to assess the volume, but also to determine a difference in material properties of the potential food source. This degree of sophistication in their vibratory assessment methods has not been shown before. This work raises questions as to the key vibratory property they use in managing their foraging preferences and suggests that they make use of features other than only the fundamental frequency of the food source, or its total mass.

1. INTRODUCTION

Vibration is a very important communication channel for insects and has been estimated to be utilised in some way by 90% of insect species [1-7]. It is well known that termites utilise vibration as an efficient and rapid communication channel [8-12]. More recently, it has been shown that termites are able to assess wood size for simple wood geometry using vibration [13]. How they sense this is most probably through the subgenual organ [14]. Electrophysiological studies show that termites are very sensitive to vibrations in the audio spectrum [15]. Although it is hypothesized by Evans *et al.* [13] that the termites respond to the frequency of the food source structures, this was not demonstrated directly. The key vibratory features that termites respond to while foraging are still unknown. Here, two simple hypotheses as to the primary vibratory feature the termites respond to, in assessing their food structures, are tested: the normal mode frequencies or the mass. The mechanism for the former may be that as described in [16-18], whilst that for the latter may be due to the response of the amplitude of acceleration, *via* Newton's second law of motion, **F**=m**a**, as a response to the force on the structures due to the wood fibres breaking. These hypotheses are tested through the use of paired bioassays, where the effective vibratory properties of test blocks are altered by exposing the termites to composite blocks designed to match the frequency or mass made of standard wooden blocks but with two materials having different properties: one with relatively high speed of sound and low damping (aluminium) and one with low speed of sound and high damping (rubber).

2. MATERIALS AND METHODS

2.1 Vibratory Measurement of Termite Feeding Activity

To measure the feeding behaviour of drywood termites, and to take recordings for a playback experiment, an accelerometer (Brüel & Kjær 4370, S/N:1360490, Nærum, Denmark) was stud-mounted with a grub-screw to the base of wooden blocks (air-dried *Pinus radiata*) held lightly by a retort stand with foam rubber in the clamp. The top end of the block had 15 drywood worker termites (*Cryptotermes secundus*, collected from Darwin, Australia) sealed into a cavity 10 mm deep with a diameter of 12.5 mm. The signal from the accelerometer was amplified by a charge amplifier (Brüel & Kjær 2635, Nærum, Denmark) and recorded onto a personal computer using the CoolEdit (Adobe Systems, Inc.) software. An artificial impulse was applied to the structure at the feeding site by hand using a pair of small stainless steel forceps.

2.2 Measurement of the Accelerance Functions of Composite Blocks

Using measured values of the properties of the materials used (Table 1), the length of aluminium and EPDM (ethylene propylene diene monomer) rubber with the same cross-section as the wood was calculated to give a composite block with the same effective speed of sound and mass.

Table 1: Properties of materials. The speed of sound in the longitudinal direction, c, and the mass density ρ were measured [19]. Nominal values of the damping factor d (equal to tan(δ) for a loss angle of δ) were obtained from [20-22]. All measurements were taken at approximately 25°C. As with most timber species, *Pinus radiata* shows great variation in material properties [20].

Material	Speed of sound, c	Density, ρ	Damping factor, d
	(m s^{-1})	(kg m^{-3})	
Aluminium	5040±103	2700±28	10^{-4}
Pinus radiata	4930±100	420±30	10^{-2}
EPDM rubber	45±1	504±30	10^{-1}

Measurements of the driving point accelerance functions (*i.e.* ratio of measured acceleration to applied force) of all test blocks were conducted. A white noise generator (Brüel & Kjær 1405, Nærum, Denmark, frequency range 0-20 kHz) was used to drive a shaker (Brüel & Kjær 4809, Nærum, Denmark) *via* a power amplifier (Brüel & Kjær 2706, Nærum, Denmark) and a force transducer (Brüel & Kjær 8200, S/N:1321629, Nærum, Denmark) was axially mounted to the shaker by a grub-screw, which was connected to the block at a point directly below its centre of mass. An accelerometer (Brüel & Kjær 4374, S/N:12939, Nærum, Denmark) was mounted above the centre of mass with beeswax. The force and acceleration signals were each amplified with Brüel & Kjær 2635 (Nærum, Denmark) charge amplifiers and captured to obtain the accelerance power spectrum using a portable FFT analyser (Ono

Sokki CF-350, Yokohama, Japan), from 128 averages with a Hanning window and maximum overlap, and a frequency resolution of 12.5 Hz (Figure 1).

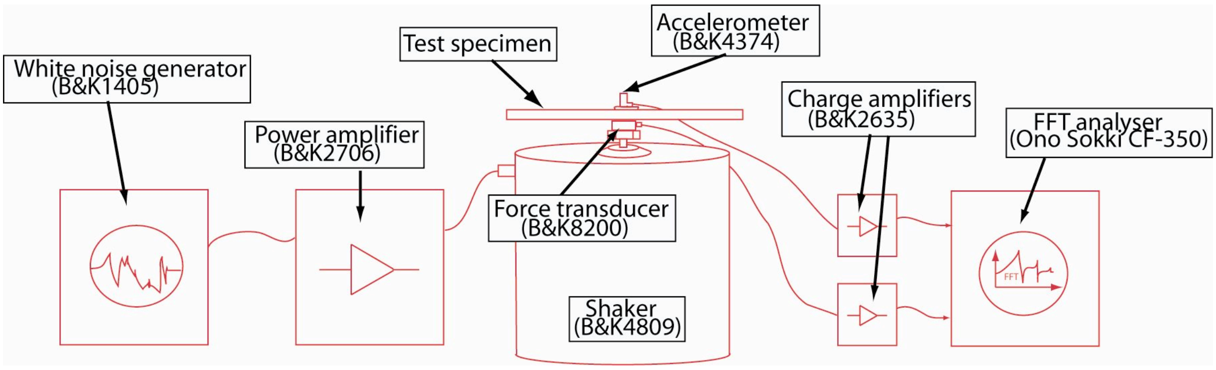

Figure 1: Experimental setup to measure accelerance transfer functions of composite and wooden beams.

2.3 Bioassays

A preliminary bioassay was performed to evaluate whether the adhesive used in the composite blocks affected the behaviour of *C. secundus*. Using paired 20 mm × 20 mm × 20 mm *P. radiata* wooden blocks. The adhesive was applied, as for the composite blocks, on the face of one block not exposed to the termites. Ten replicates were run, with 15 termite workers per replicate.

The test bioassays were choice experiments in which the termites were offered a choice of a standard 160 mm *P. radiata* wooden block and one of the other treatments. The wood in each pair was cut consecutively along the grain so that the surfaces of the wood were as identical as possible. The standard block and the test blocks were separated by 15 mm with the near-identical wooden surfaces facing each other, and then joined using aluminium foil and cellulose tape, on three sides so as to create a central space that could house the termites. A clear square of plastic was used on the top side, providing a window to observe the termites.

Fifteen *C. secundus* workers, from the same colony, were used in each replicate. A minimum of five different colonies were used for each treatment. The experiments were conducted in a controlled temperature of approximately 28°C and relative humidity of 80%. The experiments were conducted in the dark (except for a brief period every day for the first five days where the position of the 15 workers in each replicate was observed) for 14 days (the minimum length of time required by 15 individuals of *C. secundus* to tunnel 20 mm), after which the termites were removed and the number and lengths of tunnels were recorded. Data were compared using a one way ANOVA (between colonies) and paired t-tests (preferences for blocks in paired treatments).

There were eight treatments (Figure 2), each comprising a 160 mm × 20 mm × 20 mm wooden block paired with: 1: a control consisting of another 160 mm × 20 mm × 20 mm wooden block, 2: a wooden block measuring 20 mm × 20 mm × 20 mm, 3: a wooden block that had been cut into a 20 mm × 20 mm × 20 mm and a 140 mm × 20 mm × 20 mm block, and glued back together, 4: a 20 mm × 20 mm × 20 mm wooden block connected to a shaker (Phillip Harris, Leicestershire, England) playing a CD of the termite feeding signals on a wooden block 160 mm long (*q.v.* Section 4.1) through a portable CD player (Sony D-EJ100, Japan). Treatment 5 was a composite block made of wood and aluminium (Capral

Aluminium, Ltd) matched for frequency of the standard wooden blocks, Treatment 6 was made of wood and aluminium to match the mass of the standard blocks, Treatment 7 was made of wood and rubber (EPDM vibration damping rubber, Clark Rubber) to match the frequency, and Treatment 8 was made of wood and rubber to match the mass, of the standard wooden blocks. The lengths of the alternative material used in the composite blocks used to match frequency were calculated from the time-of-flight for the entire block.

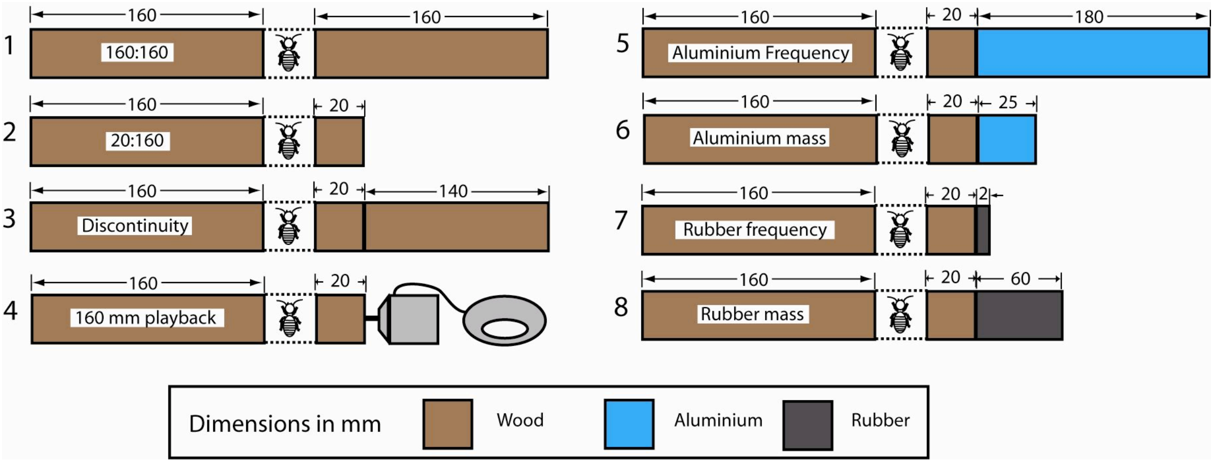

Figure 2: Schematic of the choice bioassays tested here. There were 12 replicates for each treatment, and 15 worker termites in each replicate.

3. RESULTS

3.1 Vibratory Measurements of Termite Feeding

The maximum force from breaking wood fibres was measured as about 20 mN (measured acceleration: 87.75 mms^{-2}, total mass of block and accelerometer 0.2339 kg).

The measured spectral responses of the blocks due to the termites feeding at the end of a block of wood are very similar in frequency to an artificial impulse at the feeding site. For example, a wooden block measuring 305 mm × 40 mm × 40 mm had a peak frequency of 3800 Hz for both (Figure 3).

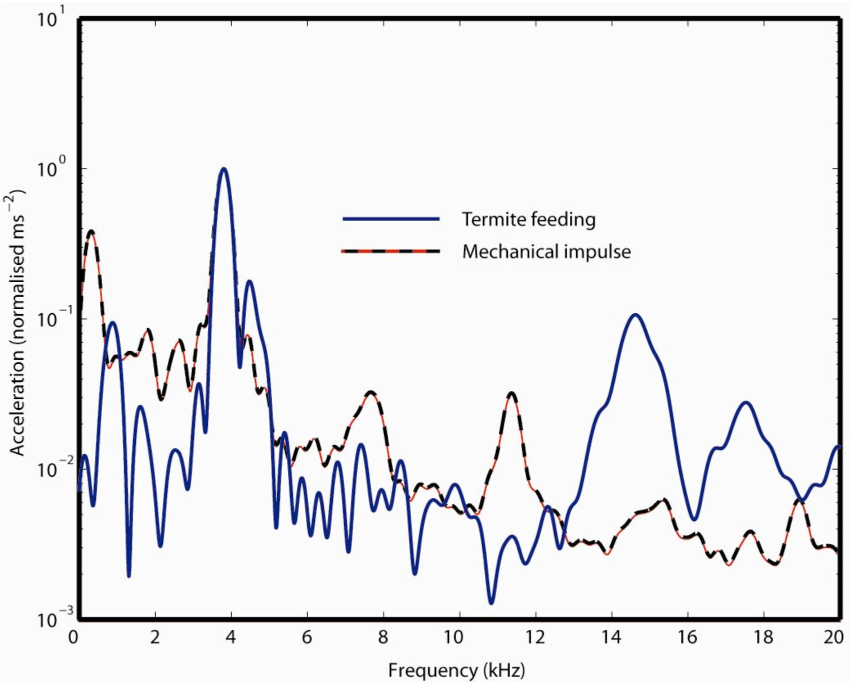

Figure 3: Measured acceleration spectra for a 305 mm × 40 mm × 40 mm block of wood. Shown is the response to natural feeding by *C. secundus* termites at one end, and the response due to an artificially induced impulse at the termite feeding site.

3.2 Frequency Response Functions of Test Blocks

In the frequency range 0-5 kHz, the test block with aluminium designed to have the same frequency as the standard 160 mm blocks (Treatment 5) and the discontinuity block (Treatment 3) have similar spectral features to the standard wooden block (Figure 4). The blocks with rubber have very low spectral features, including the test block in Treatment 7. This is because the motion of this beam is very different as it is very much shorter than those of the other treatments.

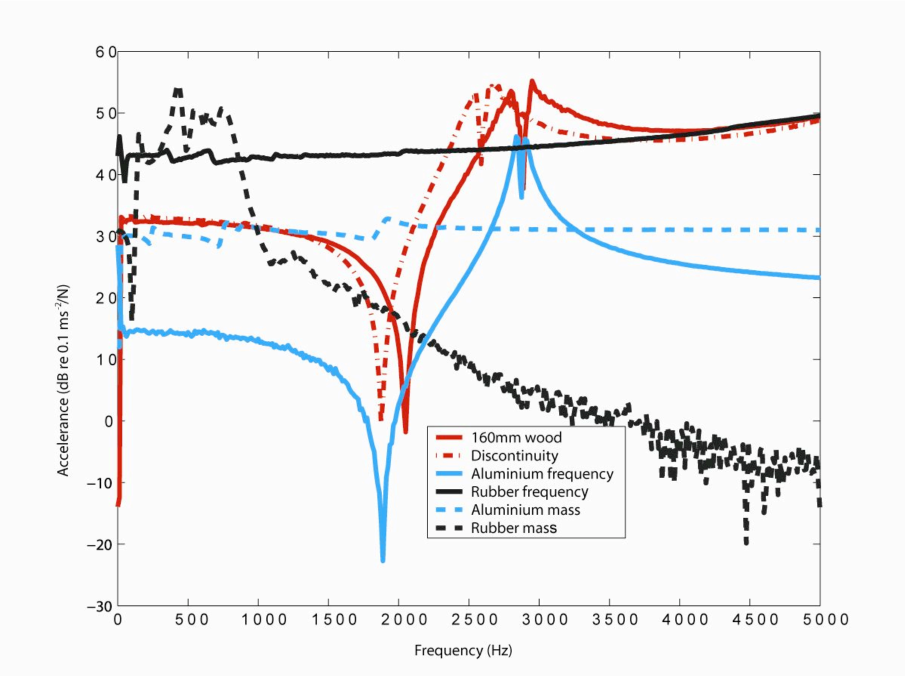

Figure 4: Measured accelerance functions of test blocks used in Treatments 1, 3 and 5-8.

3.3 Bioassays

The amount of tunnelling in blocks by termites from different colonies was highly variable; some replicates had no measurable tunnels at the end of the experiment (which were excluded from the analysis), whereas others had tunnels up to 20 mm in length. The total tunnelling of both blocks in each pair was compared between colonies and a significant difference between colonies was found for the total number of tunnels ($F_{12,94}=4.423$, $p < 0.001$) and for the total length of tunnels ($F_{12,94}=9.902$, $p < 0.001$). Consequently, tunnelling data were transformed into proportion of tunnelling in the 160 mm standard wooden block for each pair.

For the glue bioassay, no significant difference in tunnelling was observed on the paired 20 mm × 20 mm × 20 mm *P. radiata* wooden blocks in the number of tunnels (with adhesive 1.2±0.13, without adhesive 1.4±0.16; $t_4=1.630$, p=0.178) as well as in the length of tunnels (with adhesive 5.15±1.20, no adhesive 5.35±0.92; $t_4=1.472$, p=0.215). Therefore any observed effects in the test blocks are unlikely to be due to the adhesive.

For Treatments 1 and 3 (160:160 mm control and discontinuity) there was no significant difference in tunnelling between pairs of the blocks at the 95% level. For Treatment 2, there was significantly more tunnelling activity in the 160 mm block than the 20 mm block. However, if there were vibrations of the termites feeding on a 160 mm block played back through a 20 mm block, this preference was removed (Treatment 4). In Treatments 5-8 (all test blocks were composite blocks matched for frequency or mass of their paired standard block) there was significant preference for the 160 mm block, except in the case of number of tunnels for Treatment 8 (rubber mass) (Figure 5).

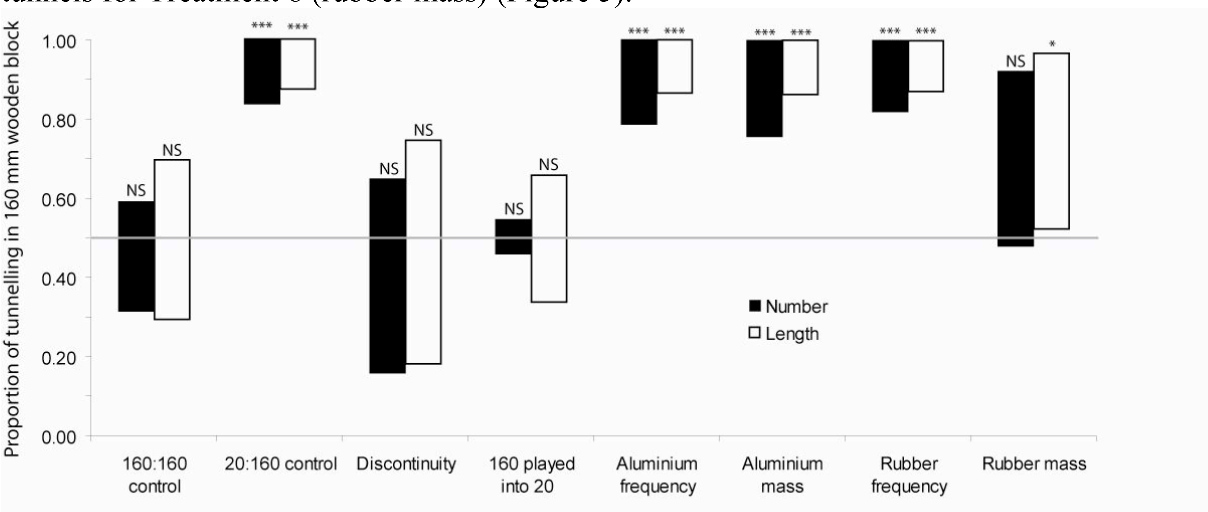

Figure 5: Proportion of measured tunnelling in standard 160 mm wooden block compared to test blocks. Shown are the numbers and total length of tunnels. The bars indicate the limits of the 95% confidence interval. NS means not significantly different to the null hypothesis (0.50), * indicates significance at the 95% level and *** indicates significance at the 99.9% level.

Also, the termites are able to assess the block rapidly: the observed movement of termites for the first five days of the experiment agree with the results of the tunnelling data (Figure 6).

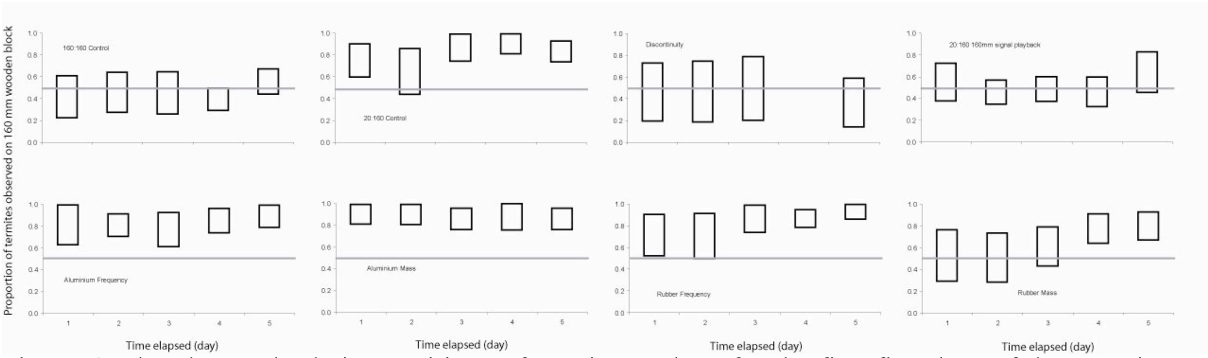

Figure 6: The observed relative positions of termite workers for the first five days of the experiment, as a proportion of numbers on the 160 mm wooden test blocks. In each case there is agreement with the tunnelling data.

4. CONCLUSIONS

This work demonstrates that the termite *C. secundus* responds to vibrations as a by-product of feeding on the structure, by playing the vibrations of their own feeding though a block of wood to alter their feeding preference. The dominant frequencies in the measured acceleration spectra produced through feeding are very similar to that produced by an artificial impulse, suggesting that there is no spectral signature transmitted though the structure in addition to that of the structure itself.

If the termites responded to spectral features of the structure alone, then we might expect them to show no preference for a composite block designed to have the same modal frequencies as a standard wooden block, yet this is not the case. This also applies to the mass of the food structure, where it is plausible that the amplitude of the acceleration may be used as a measure, which (assuming the amount of force from the wood fibres snapping is roughly the same for all wooden structures) decreases in proportion to the mass of the structure. It is plausible that structural damping, or the great mismatch in mechanical impedance at the boundary between materials in the blocks used here, may play an important role in the termite's assessment methods.

An obvious extension to this work is to more directly assess the role of damping and other properties in the feeding preferences of termites. This may be performed by directly measuring wood with a range of these properties and comparing to the amount of feeding on standard blocks of wood.

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