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TUNNEL ORIENTATION BY WORKERS OF *COPTOTERMES FORMOSANUS* (ISOPTERA: RHINOTERMITIDAE) SUBJECTED TO UNILATERAL ANTENNAL ABLATION

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Subterranean termites excavate tunnel networks to find resources (King & Spink 1969; Su et al. 2004). Tunnels are created by a rotation of individual excavators that travel towards the tip at the end of the tunnel to remove soil with their mouthparts, then reverse course and drop it along tunnel walls or into opened spaces (Bardunias & Su 2009a). Bardunias & Su (2009b) showed that the excavators are orienting the direction of tunnels by generating a vector through path integration that heads directly away from the origin of a tunnel. They follow a vector that intercepts both the tunnel's origin and their present location, termed a Global Away Vector (GAV) (Bardunias & Su 2009b), which is the opposite of a "global" or "homing" vector, leading directly back to a path's point of origin (Collett et al. 1998). Because bites of soil removed by the rotation of excavators in turn produce the tunnel heading, if successive termites at the tunnel tip excavate to the left and right in a haphazard fashion, the tunnel will tend to remain on course, with any change due to chance drift (Bardunias & Su 2009b). In order to turn a tunnel, the direction in which successive workers remove soil at the tip of a tunnel must coincide (Bardunias & Su 2009b).

In this study, groups of termites were subjected to unilateral antennal ablation prior to tunneling to investigate the role of antennae in determining where a termite removes soil from tunnel walls. If excavation was biased towards the intact antenna, then altered termites, forced to move through a right angle bend that places the GAV in the direction of the lost antennae, should have produced tunnels that failed to turn to match the GAV.

Individuals from 2 *Coptotermes formosanus* Shiraki colonies were collected in Broward County, FL, following Su & Scheffrahn (1986). Horizontal arenas consisted of 2 sheets of transparent Plexiglas (9 by 7.5 cm^2) (Fig. 1A, a), with a 0.2-cm inner Plexiglas spacer (Fig. 1A, b) surrounding an elongated hexagonal sand-filled space (6.5 cm width, 7.5 cm height). Sifted sand (Fig. 1A, c, 150-500-µm sieves, Play Sand Bonsal, Miami, FL) was moistened with deionized water

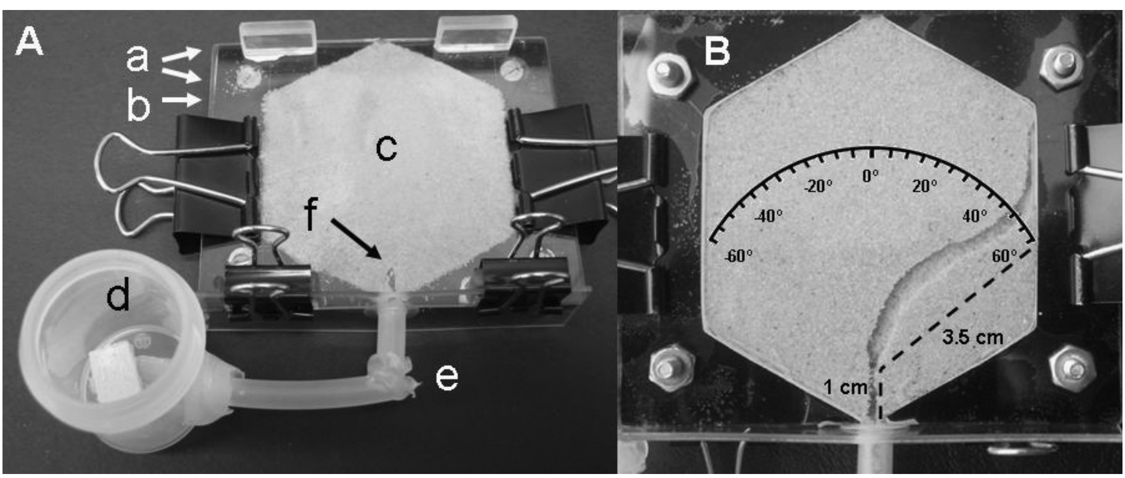

Fig. 1. A. Experimental arena with a single chamber and a forced 90º turn; a. Horizontal arenas consisted of 2 sheets of Plexiglas (9 by 7.5 cm^2); b. A 0.2-cm inner spacer; c. The elongated hexagonal sand-filled space (6.5 cm width by 7.5 cm length); d. Introduction chamber; e. Vinyl tubing, 4mm inner diameter, joining the introduction chamber to the arena via a 5-cm length, a 90º bend, and a further 2-cm length; f. Preformed tunnel (1 cm by 3mm) excavated in the arena sand to facilitate access to the arena. B. Tunnel excavated after moving through the forced 90º turn showing the superimposed arc used to measure the intercept. The dashed line shows the positioning of the arc, 3.5 cm from the end of the 1-cm preformed tunnel excavated in the sand of the arena.

to about 7% by weight. A 15-ml vial (Nalge Nunc International, Rochester, NY) was used as an introduction chamber (Fig. 1A, d, 3 cm diameter × 4 cm height). This was connected to the arena (Fig. 1A, e) through clear vinyl tubing (Watts, Andover, MA), 4 mm inner diameter, with an initial length of 5 cm, then a 90º turn and a 2-cm length connecting to the arena. The introduction chamber was loaded with a piece of wood (1 by 1 by 2 cm^3) as a food source and 80 termites in at least third instar, including 8 soldiers. A preformed tunnel (1 cm by 3 mm) was excavated within the sand at the coupling point to facilitate access to the arena (Fig 1A, f). Tunnels were allowed to elongate until they intercepted a 3.5-cm superimposed arc centered on the end point of the preformed tunnel (Fig. 1B). The angular intercept was determined as a deviation from the heading of the preformed tunnel by joining the point at which the tunnel intercepted the superimposed arc with the end of the preformed tunnel.

The termites were chilled in small batches at 4ºC to slow their movement and limit bleeding before the flagellum of an antenna was completely excised (Fig. 2). The termites were allowed to recover for 1h prior to placement within the introduction chamber. We conducted 12 trials, 6 with termites from each colony. We were only interested in situations where tactile or olfactory stimuli biased individuals to excavate from a side of the tunnel tip that was opposite the direction of the GAV. Thus, for each colony, half of the trials consisted of termites that had

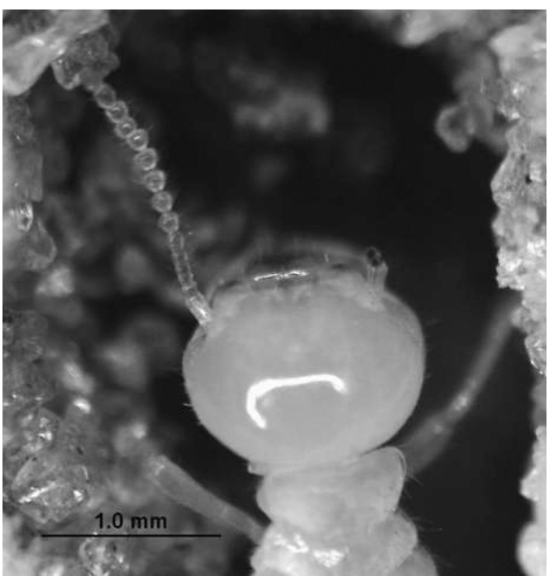

Fig. 2. Termite following antennectomy of the right antenna. The flagellum was excised at the pedicel. Note the moniliform structure of the antenna and the size of the termite relative to the width of the tunnel.

their left antenna removed, potentially biasing them towards the right side of the tunnel tip, who were forced to turn to the right, necessitating a turn to the left to reestablish a heading along the GAV, while the other half were the reverse situation. For comparison, 16 control groups of 80 unaltered termites, 8 from each colony, were forced to move through an equal number of right and left turns. The intercept angles of tunnels excavated by each of these 3 groups, left antennae excised, right antennae excised, and unaltered were subjected to an ANOVA at $\alpha = 0.05$ (SAS institute 1985).

The mean intercept angles (± SD) of tunnels excavated by termites were as follows: left antennae removed (46.16 ± 7.31), right antennae removed (44 ± 8.46), and unaltered (47.06 ± 6.08). An ANOVA ($F_{2, 25} = 0.43$, $P = 0.653$) failed to show significant differences among the 3 treatments. Termites with an antenna removed did not excavate more often towards the direction of their remaining antenna in a manner that produced a change in the orientation of tunnels relative to the controls. This may indicate that the response to tactile or olfactory stimuli at the tunnel tip is weak compared to the motivation to follow an internally generated GAV. It is also possible that the cues determining where a termite excavates are large and obvious, even to a termite with a single antenna, thus eliminating a true choice. Additionally, termites may behaviorally compensate for the loss of a single antenna by moving or turning their bodies in a manner not seen in other organisms, like crayfish (McMahan et al. 2005) that preferentially turn towards an intact antenna in choice tests. Observations of individuals following antennectomy are needed to determine the manner in which they use the remaining antennae and perhaps the maxillary and labial palps.

Summary

Subterranean termites subjected to unilateral antennectomy do not produce tunnels that differ in orientation from unaltered termites. Local cues at the tunnel tip may be weak releasers of excavation behavior in comparison to the motivation to tunnel away from the tunnel's origin. Alternately antennae may be important in determining where a termite excavates, but termites may be compensating for the loss of an antenna through changes in behavior.

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