Introduction

Myriapoda, like other terrestrial arthropods, is active at a particular time of day or night. Most centipede and millipede species are active at night (e.g. Cloudsley-Thompson 1951; Dondale et al. 1972; Hopkin & Read 1992; Koilraj et al. 1999; Lewis 1981; Tuf et al. 2006), though some species are active at dusk and before dawn (Bano & Krishnamoorthy 1979), though some species are active at dusk and before dawn (Bano & Krishnamoorthy 1979). The diel activity rhythm is controlled by endogenous (internal timer) and exogenous (a direct response to environmental changes) components; the rhythm is controlled by an endogenous circadian oscillator that is continuously modulated by environmental light and/or temperature (Saunders 2002). However, little is known about the mechanisms controlling the diel activity rhythm of Myriapoda. This study aims to investigate the mechanisms controlling the diel activity patterns of the common house centipede, Theruonema tuberculata (Wood), which is active at night, particularly in the early half of the dark period (Taguchi & Makiya 1982). In the present study, we address three objectives related to the centipede timing mechanism: 1) whether the locomotor activity rhythm can be entrained by a light-dark cycle, 2) whether an endogenous pacemaker is involved in the rhythm, and 3) how the centipede detects and interprets the photoperiod. Here, we present the locomotor activity rhythm of T. tuberculata under light-dark (LD), continuous dark (DD), and continuous light (LL) cycles, and a symmetrical skeleton photoperiod.

Materials and Methods

Four Theruonema tuberculata adults were collected on the campus of Miyagi Gakuin Women’s University, Sendai, Japan (38° 16’N) in May-August 2013. The centipedes were housed individually in 2-liter jar at 25 °C under a 15 h light:9 h dark (LD 15:9) photoperiod until testing. They were fed daily a nymph cricket, (Modicogryllus consobrinus), and a bottle (3 × 5 cm) of water plugged with cotton wool was inserted into the rearing box as a water source. The sex of the experimental animals could not be identified.

The locomotor activity rhythms of the centipedes were recorded individually in an activity chamber (plastic box of 10.5 × 19.5 × 2.5cm) flanked with an infrared light and detector (GT-1, Takenaka Electronic Industrial Co. Ltd. Japan). When the centipede intercepted the infrared light beam, the signal was fed to a computer that counted the movement in 6 min intervals. The entire recording apparatus was placed in an incubator (Nippon Medical and Chemical Instruments Co., Japan), where the temperature could be programmed within ±1.0 °C. The centipedes were illuminated by a 10 W fluorescent lamp that produced at least 400 lux at the level of the test animals. During the experiments, water was supplied, but not food.

The activity data were analyzed for rhythmicity using a chi-square periodogram analysis (Sokolove & Bushell 1978).

Results and Discussion

Locomotor activity was continuously monitored under an LD 15:9 photoperiod at 25 °C; Fig. 1 summarizes the locomotor activity patterns of the four centipedes. During illumination, activity was very low. After the transition from light to dark, locomotion initiated and the activity level peaked in the first half of the dark phase. Thus, T. tuberculata is nocturnal and the locomotor activity is entrained by the
light-dark cycle, as reported previously (Taguchi & Makiya 1982).

To confirm the involvement of a circadian pacemaker in the locomotor activity, the centipedes were allowed to free-run in DD at 25 °C. An example of the free-running locomotor activity is given in Fig. 2. When the centipedes were transferred from LD 15:9 to DD, a clear unimodal locomotor activity pattern persisted; all four individuals showed significant periodicity in their locomotor activity rhythm in DD (chi-square periodograms: $P < 0.001$ in all cases) and the calculated free-running period (mean ± s.d.) was 25.2 ± 0.6 hours (range 24.4 to 25.8). These results indicate that the locomotor activity peak of *T. tuberculata* is controlled by an endogenous pacemaker. The endogenous control of rest-activity rhythms has been also documented in other centipede species (e.g., Cloudsley-Thompson 1956, 1959; Cloudsley-Thompson & Crawford 1970).

In the next experiment, the centipedes were transferred from LD 15:9 to LL at 25 °C. Two of the four centipedes maintained a unimodal locomotor activity pattern in LL (see Fig. 3). The chi-square periodogram showed statistically significant periodicity in the locomotor activity rhythm ($P < 0.001$) with a free-running period of 25.1 and 25.2 hours, respectively. The free-running periods recorded in LL were similar to those recorded in DD. The other two centipedes ceased locomotor activity after being transferred to LL. We are unable to explain why the activity stopped, though the cessation of locomotor activity in LL has also been reported in *Scolopendra* sp. (Cloudsley-Thompson & Crawford 1970).

To further explore the photo-entrainment mechanisms of locomotor activity rhythm, two centipedes were first kept in DD and then introduced into a symmetrical skeleton photoperiod of two 1-hour pulses of white light at 25 °C. The first light pulse was from 04:00 – 05:00 and the second pulse was from 18:00 – 19:00 Japan Standard Time, thereby mimicking a complete LD 15:9 photoperiod. The centipedes entrained well to the skeleton photoperiod; activity was

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**Fig. 1.** Summarized activity of four *T. tuberculata* adults (#1, #2, #3 and #4) over 18 days in 6 min intervals under LD 15:9 at 25 °C. Black bars at the top of the figure indicate dark (D) and white bars indicate light (L).
Locomotor activity rhythm of *Thereuonema tuberculata*

Confined to the shorter dark intervals and an activity burst occurred ca. 1 hour after the second light pulse (Fig. 4). This suggests that the centipedes interpreted the first light pulse as “light-on” and the second pulse as “light-off”. The skeleton photoperiod almost perfectly mimics the action of a complete photoperiod, suggesting that the “light-on” and “light-off” signals play a vital role in the photo-entrainment of locomotor activity rhythms in *T. tuberculata*. This also suggests that the presence of continuous light between the signals is less important.

In conclusion, *T. tuberculata* is strictly nocturnal with a tendency to be most active in the first half of the night. The locomotor activity is controlled by an endogenous pacemaker and is entrained by the light-dark cycle, particularly the

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*Fig. 2.* Representative locomotor activity rhythm of a *T. tuberculata* adult transferred from LD 15:9 to DD at 25 °C. Triangle indicates the day of transfer to DD. Black bars at the top of the figure indicate dark (D) and white bars indicate light (L).

*Fig. 3.* Representative locomotor activity rhythm of a *T. tuberculata* adult transferred from LD 15:9 to LL at 25 °C. Triangle indicates the day of transfer to LL. Black bars at the top of the figure indicate dark (D) and white bars indicate light (L).
transitions between the light and dark phases. The observed centipede activity rhythms are similar to those reported in other arthropods (see Saunders 2002). *T. tuberculata* is easily reared and long-lived, so this species may be a useful model for long-term studies of diel activity rhythm.

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