

TACTILE CUES, BILATERALLY ASYMMETRICAL LEG MOVEMENTS AND BODY DISTORTION IN ISOPOD TURN ALTERNATION

Robert N. Hughes
University of Canterbury

ABSTRACT: Because woodlice (*Porcellio scaber*) and pillbugs (*Eluma purpurascens*) that traveled closer to the outer wall of alleys both before as well as after a 90° forced turn subsequently made sharper free turns in the opposite direction, it seemed possible that a quantitative relationship existed between tactile stimulation arising from wall contact and free-turn behavior. However, on emerging from straight runways, without any forced turns, pillbugs turned at sharper angles than woodlice but there was no relationship between the size of a turn and amount of wall contact apart from a very minor one for woodlice only. It was concluded that tactile stimuli played a negligible part in turn alternation of either species thereby supporting involvement of proprioceptive cues. By requiring woodlice to negotiate a forced turn lined with glass on the outer half of the floor, it became apparent that their alternation was determined by proprioceptive feedback from bilaterally asymmetrical leg movements rather than distortion of body segments.

Patterns of alternating turns at successive choice points and obstacles while free-moving have been described for a wide range of species (Hughes, 1989). In the absence of directional cues, such patterns provide a "correcting" influence (Barnwell, 1965; Dingle, 1964) which ensures relatively direct movement towards or away from significant environmental stimuli (Hughes, 1967, 1978). Sequential alternation should therefore facilitate foraging, exploratory and escape behavior as well as dispersal of the species (Hughes, 1978; Richman, Dember & Kim, 1987).

Since body turn alternation in most invertebrates depends mainly on response-generated proprioceptive rather than exteroceptive cues (Hughes, 1985), the phenomenon reflects an orientation reaction based on information about previous movement sequences. It has been proposed that the controlling mechanism in woodlice (*Porcellio scaber*) involves differential activity of legs on each side of the body during turning i.e., bilaterally asymmetrical leg movements (BALM, Hughes,

Address correspondence to Dr. R. N. Hughes, Department of Psychology, University of Canterbury, Christchurch 1, New Zealand.

1985). Alternation was seen to arise from the greater influence of legs on the side that had traveled the shorter distance or exerted less effort while negotiating a previous turn. Evidence for this view is found in turning to the same side as preceding unilateral forced walking (Beale & Webster, 1971), and traveling closer to the outer wall of an exit alley following sharper forced turns along with correlations between closeness to a wall and the size of a subsequent free turn (Hughes, 1985).

However, it has been recently shown that, while BALM influences appear to underly most woodlouse alternation, tactile cues can also be important for some individuals that come into close proximity with a vertical surface (Hughes, 1987). In spite of suggestions that, by itself, wall-following cannot account for the size of an alternating turn in either woodlice (Hughes, 1985) or centipedes (Schäfer, 1972), it is conceivable that exceptionally intense or prolonged tactile stimulation might modify the effects of a proprioceptive mechanism on alternation magnitude, particularly since slightly sharper turns may follow longer distances in contact with straight walls (Schäfer, 1976). In an attempt to clarify this issue, relationships between proximity to both pre- and post-forced turn outer walls and free turn angle size were examined in two isopod crustaceans, namely the woodlouse or sowbug (*P. scaber*) and a species of pillbug (*Eluma purpurascens*). As more recent isopod studies have been confined to *P. scaber* (Hughes, 1985, 1987), pillbugs were included for comparative purposes since the tendency of a related species (*Armadillidium vulgare*) to alternate is well established, e.g., Iwata and Watanabe (1957), Kupfermann (1966). *P. scaber*, a member of the family Porcellionidae, was introduced to New Zealand over 150 years ago presumably by ship from the British Isles where it is indigenous. It is widespread and generally prefers a cosmopolitan habitat living under stones and wood particularly in home gardens (Hurley, 1950). *E. purpurascens* belongs to the family Armadillidiidae noted for its ability to roll up into a ball (conglobate) when threatened. It is also an introduced species which is very rare in the British Isles (Sutton, 1972), but it is common in Christchurch gardens even though its presence in New Zealand has not yet been formally recognised (Johns, 1989).

Rather than leg movement cues, Schäfer (1982) has suggested that proprioceptive feedback from displaced body segments determines the size of a subsequent alternating turn in isopods. This proposal does not appear to explain relationships between proximity to the outer wall of a post-forced turn exit alley (and forced-turn angle size) which can however be accounted for by BALM effects (Hughes, 1985). Nevertheless, a direct test of the two explanations was thought desirable even though either or neither might apply to other species with different leg and tagmata characteristics.

EXPERIMENT 1

When woodlice travel along the exit-alley of a runway following a forced turn, distance from the outer wall appears to reflect the pre-choice operation of BALM effects rather than determine free-turn behavior (Hughes, 1985). If the amount of tactile stimulation provided by this wall does not affect the size of a free turn, there should be no relationship between free-turn angle and proximity to the outer wall of the start alley preceding a forced turn. Experiment 1 therefore investigated the importance of nearness to pre- as well as post-forced turn outer walls in alternation behavior of woodlice and pillbugs. The contribution of the type of response made while negotiating the forced turn was also considered.

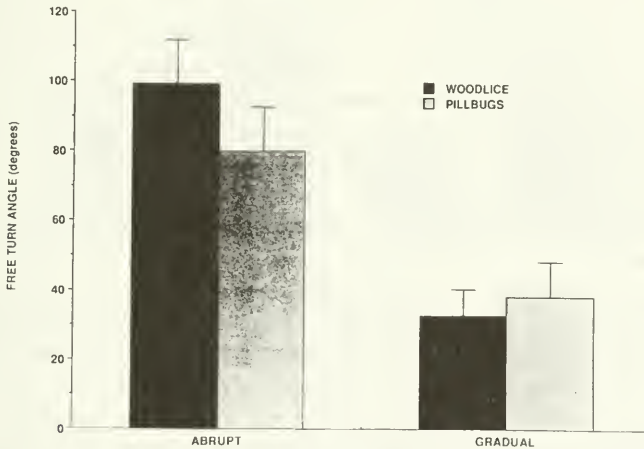


FIGURE 1

Mean + SE free-turn angle for abrupt and gradual turning woodlice and pillbugs following one 90° forced turn.

Method

Animals.—All woodlice and pillbugs used in this and later experiments were collected from beneath stones and decaying vegetation. They were kept in plastic receptacles containing damp soil, leaf litter and sliced carrot and potato. Only animals 4-6 mm in width were used. Fortyeight members of each species were observed in Experiment 1.

Apparatus.—For this experiment, the apparatus comprised a 10-mm-wide runway cut from 6-mm-thick clear Perspex with a 90° forced turn, a clear Perspex cover and an open-ended exit. The outer walls of the

start and exit alleys were 70 and 40 mm long respectively. The runway was positioned with the centre of a 200-mm-diameter circle (drawn on white paper) in the middle of the exit. To facilitate measurements of distances from the outer walls, there was a series of parallel lines drawn on the section of paper underlying the two alleys. At right angles to these, lines also appeared across the alleys at 10-mm intervals. A television camera (with a magnifying lens) and a VHS video-recorder were used to record behavior of the subjects while in the runway.

PROCEDURE

Each subject was gently lowered into the beginning of the start alley. The Perspex cover was replaced and the animal's progress from start to exit was video-recorded. On leaving the runway, the point where the subject crossed the circumference of the circle ($r = 100$ mm) was noted to enable subsequent determination of its free-turn angle of emergence. The video-record was later replayed and images frozen at distances of 30, 20, 10 and 0 mm from the forced turn to start and from the forced turn to exit. At each of these points, distances between the outer wall and the nearest part of each subject's thorax were measured. As the animal moved closer to this wall, greater numbers of those sense organs believed to be tactile receptors would have been stimulated. These organs comprise short bristles found on the dorsal and ventral surfaces, the legs and between the dorsal tergites, and in particular, long spines or "parking antennae" laterally positioned on each thoracic tergite (Jans & Ross, 1963). It was also noted whether the animal had collided with the exit alley outer wall before making its forced turn, thereby usually necessitating an "abrupt" right angle turn, or if it had begun turning into the exit alley before this wall had been encountered thus making a more "gradual" curved turn. Equal numbers of subjects were forced left and right.

RESULTS AND DISCUSSION

Numbers of abrupt and gradual turners were 11 and 37 respectively for woodlice and 19 and 29 for pillbugs. These proportions did not differ between the two species [$\chi^2 (1) = 2.38$].

Free-turn angles for abrupt and gradual turners of each species are outlined in Figure 1. As shown by an ANOVA, abrupt turners turned at significantly sharper angles than gradual turners [$F (1, 92) = 29.94, p < .001$]. There was no significant species differences [$F (1, 92) < 1$] or Species X Turner interaction [$F (1, 92) = 1.29$] for this measure.

Fortythree (90%) woodlice and 39 (81%) pillbugs alternated [$p < .0006$ in both cases, binomial test], but the difference between these

proportions was not significant [$\chi^2(1) < 1$]. However, significantly more abrupt turners alternated (100%) than gradual turners [83%, $\chi^2(1) = 4.12$, $p < .05$].

Average distances from the outer wall for the four measurements taken both before (pre) and after the forced turn (post) were calculated for each subject. Results for abrupt and gradual turners of each species can be seen in Figure 2.

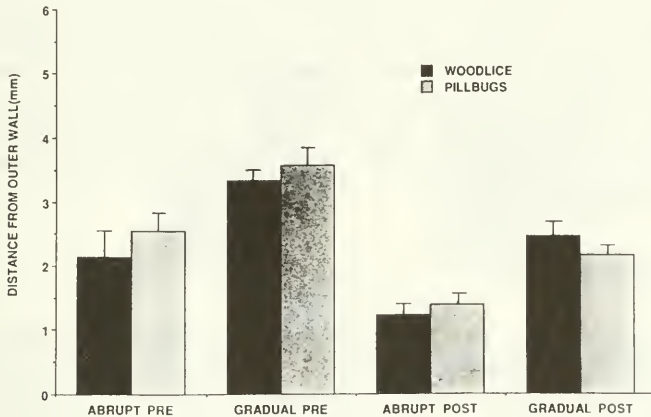


FIGURE 2

Mean + SE distance from the outer wall before (pre) and after (post) one 90° forced turn for abrupt and gradual turning woodlice and pillbugs.

While there was no significant species differences [$F(1,92) = 1.45$] abrupt turners traveled significantly closer to the two walls combined than gradual turners [$F(1, 92) = 25.06$, $p < .001$]. This difference characterised both the start [$t(92) = 7.79$, $p < .001$] and exit alley measurements [$t(92) = 5.79$, $p < .001$]. All subjects traveled closer to the outer wall of the exit alley than to that of the start alley [$F(1, 92) = 64.35$, $p < .001$]. No interactions were significant.

Correlations between free-turn angle and average distance from each outer wall were determined separately for abrupt and gradual turners. In view of the lack of species differences in either measure, no distinction was drawn between woodlice and pillbugs for this analysis. While neither correlation was significant for abrupt turners [pre/angle, $r(28) = .16$; post/angle, $r(28) = -.22$], both were significant for gradual turners [pre/angle, $r(64) = -.25$, $p < .05$; post/angle, $r(64) = -.38$, $p < .01$].

Since abrupt turners of both species traveled closer to the outer wall before as well as after the forced turn and then turned at sharper angles than gradual turners, it was possible that their free-choice behavior had

been at least partly determined by the amount of tactile stimulation experienced while following the two walls. This was supported by the small (but significant) negative correlation between free-turn angle and distance from the start-alley outer wall for gradual turners indicating that the closer subjects were to this wall the sharper they tended to subsequently turn. While a similar relationship observed for exit-alley behavior could be attributed to BALM effects (Hughes, 1985), this explanation would not account for the start-alley finding since no prior turning had occurred. The lack of significant correlations between those two measures for abrupt turners was probably due to ceiling (or wall!) effects arising from their much closer proximity to both outer walls. Abrupt turns were probably the inevitable result of restricted movement caused by traveling close to the start-alley outer wall. Overall the results suggested involvement of a graded responsiveness to tactile cues on the angle finally turned.

EXPERIMENT 2

In the next experiment, the effects of tactile stimulation (arising from contact with a vertical surface) on turning behavior were further investigated. If a graded responsiveness to tactile cues can influence the angle turned, the length of and thus duration of contact with a vertical surface should determine the angle turned on emerging from a straight runway. Isopods are thigmotactic (Pardi & Papi, 1961) and will turn in the same direction as a followed wall without having encountered any prior forced turn (Hughes, 1987).

Method

Animals and Apparatus.—The subjects were 40 woodlice and 40 pillbugs. The apparatus comprised two straight 10-mm-wide, 6-mm-thick clear Perspex runways. One was 60 mm long and the other was 180 mm long. As for Experiment 1, a series of parallel lines intersected by other lines at 10-mm intervals were drawn on the floor of each runway. Each exit was positioned in the centre of a circle and a TV camera and video-recorder was used to record runway behavior.

PROCEDURE

Twenty members of each species were individually introduced into the closed end of each runway for a single trial. Progress along the runway was video-recorded. On emerging from the exit, the direction turned and the point crossed on the circumference of the circle were noted. The video-record was later replayed and images frozen at 40, 30,

20, 10 and 0 mm from the exit to enable measurements of average distances from the wall on the same side as the direction subsequently turned.

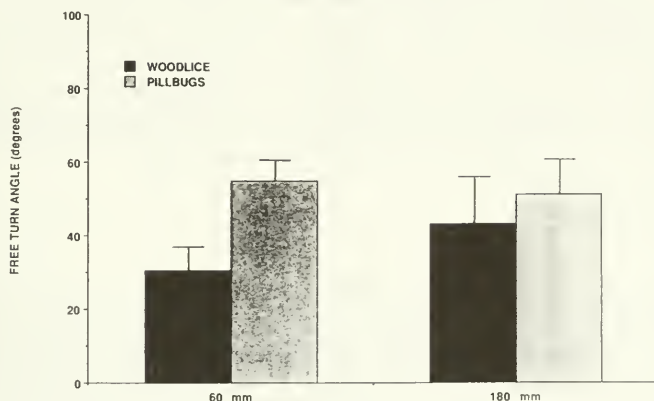


FIGURE 3

Mean + SE free-turn angle for woodlice and pillbugs emerging from 60- and 180-mm-long straight runways.

RESULTS AND DISCUSSION

Angles turned by each species after emerging from the two runways can be seen in Figure 3. While pillbugs emerged at sharper angles than woodlice [$F(1, 76) = 4.44, p < .05$], runway length did not affect turning behavior [$F(1, 76) < 1$] nor was the Species X Runway length interaction significant [$F(1, 76) = 1.17$].

Mean \pm SEM average distances (in mm) from the wall on the same side as the direction turned after emerging from the 60- and 180-mm runways respectively were, for woodlice, $2.54 \pm .21, 2.05 \pm .20$, and for pillbugs, $2.43 \pm .26$ and $2.35 \pm .19$. Neither species [$F(1, 76) < 1$] nor runway length [$F(1, 76) = 1.68$] or their interaction affected this measure [$F(1, 76) < 1$]. However, there was a small significant negative correlation between average distance from the followed wall and free-turn angle for woodlice in both runways combined [$r(38) = .35, p < .05$] but not for pillbugs [$r(38) = -.07$]. This suggested that the closer woodlice were to the wall, the sharper were their subsequent turns in its direction.

The lack of any relationship between wall length and free-turn angle for either species does not support any influence of a graded responsiveness to tactile cues on free-turn angle in the manner suggested for centipedes by Schäfer (1976). On the other hand, the negative correlation between distance from the followed wall and free-turn angle for

woodlice suggests, for this species, a weak quantitative relationship between tactile stimulation and turning behavior which is, however, independent of duration of such stimulation.

The sharper angles turned by pillbugs compared with woodlice cannot be readily accounted for apart from speculating that slight species differences in body shape or leg size and orientation were in some way responsible. *E. purpurascens* is narrower and less dorsoventrally flattened with shorter legs than *P. scaber*. Such factors might also account for the species difference in the relationship between average distance from a followed wall and free-turn angle.

EXPERIMENT 3

Because of the species differences observed in Experiment 2, it seemed desirable to partially replicate the study paying particular attention to possible quantitative relationships between distances from a followed wall and free-turn size. In order to achieve more accurate averages, distances from the wall were sampled at a greater number of points along the runway. Since it was suspected that, during each Experiment 2 trial, pillbugs but not woodlice gradually moved closer to the followed wall while progressing towards the exit, changes in this measure from the beginning to the end of the runway were also assessed.

Method

Thirty woodlice and 30 pillbugs were observed in a 120-mm-long runway. Other dimensions, means of measuring free-turn angles and video-recording equipment were the same as in Experiment 2. The procedure was the same as in Experiment 2 except that, when played back, video-recorded images were frozen at 9 points 10 mm apart ranging from 90 to 0 mm from the exit.

RESULTS AND DISCUSSION

The mean \pm SE free-turn angle was $29.57 \pm 5.03^\circ$ for woodlice and $45.77 \pm 5.21^\circ$ for pillbugs. This difference was significant [$t(58) = 2.24$, $p < .05$].

For each subject, average distances from the wall on the same side as the direction turned were calculated for points 80-60, 50-30 and 20-0 mm from the exit. The results for each species can be seen in Figure 4. Whereas the species effect was not significant [$F(1, 58) < 1$], there were significant differences between the points where measurements were taken [$F(2, 116) = 3.21$, $p < .05$]. However, this effect is more appropriately considered in the light of the significant interaction between

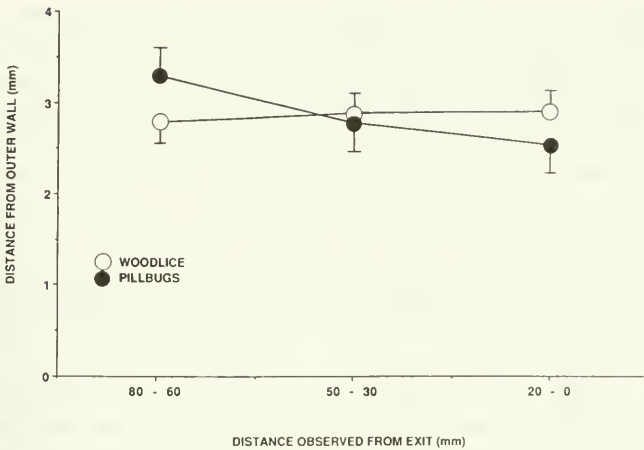


FIGURE 4

Mean + SE distance from the followed (outer) wall observed at three distances from the exit of a straight runway for woodlice and pillbugs.

the two factors [$F(2, 116) = 6.16, p < .01$] thereby confirming the obvious tendency outlined in Figure 4 for pillbugs but not woodlice to move closer to the followed wall as the exit was approached.

Average distances from the followed wall at 80-60, 50-30 and 20-0 mm from the exit were correlated with free-turn angle for each species separately. The results can be seen in Table 1. The only significant correlation was for woodlice when observed 20-0 mm from the exit.

As in Experiment 2, pillbugs turned at sharper angles than woodlice. The difference in free-turn angle between the two experiments was not significant for either species [$t(68) < 1$ in both cases]. The tendency for pillbugs but not woodlice to move closer to the followed wall as the

Table 1
Correlations Between Average Distances from the Followed Wall and Free-turn Angle for Woodlice and Pillbugs

Coefficients [r(28)] for distances (mm) from exit

<i>Species</i>	<i>80-60</i>	<i>50-30</i>	<i>20-0</i>
Woodlouse	-.05	-.10	-.43*
Pillbug	-.08	-.10	-.24

* $p < 0.05$

exit was approached reflected slight differences in locomotor styles. It was evident that both species began their runs with an obvious yawing motion but as they moved closer to the exit this pattern changed to a more stable attachment to the wall for pillbugs only, thereby producing shorter average distances for this species. This more consistent tactile stimulation for pillbugs might have accounted for their sharper free turns, in terms of a quantitative relationship between such stimulation and turning behavior, if it were not for the lack of any relationship between the angles they turned and their distances from the followed wall. On the other hand, the closer individual woodlice were to this wall when 20, 10 or 0 mm from the exit, the sharper were their subsequent turns.

However, a graded responsiveness to tactile cues seemed of minimal importance in determining the size of a subsequent free turn because of the ineffectiveness of wall length on free-turn angle, the nonsignificant distance-from-wall/free-turn-angle correlations for pillbugs and the lack of any relationship between the two measures for woodlice when further than 20 mm from the exit. Added to this is the small amount of variance accounted for by the two significant correlations for woodlice in Experiments 2 and 3, namely 15.21% and 18.49% respectively. It is therefore likely that the differences between abrupt and gradual turners observed in Experiment 1 were mainly due to BALM effects rather than to differing amounts of tactile stimulation. By initially traveling closer to the start-alley outer wall, abrupt turners were more likely to collide with the exit-alley outer wall than gradual turners thereby necessitating sharper forced turns. The generation of bilateral asymmetry in leg movements would have obviously been greater for abrupt turners thus causing them to travel closer to the exit-alley outer wall and emerge at more acute angles.

EXPERIMENT 4

Schäfer (1982) has proposed that the storage of information in isopods about previous turns (which is later used in determining the size of a free-turn) arises from the distortion of body segments. If such a mechanism rather than BALM effects were responsible for alternation, varied demands on different legs should have no effect on free-turn angle provided body distortion is kept constant. The final experiment aimed to distinguish between the two explanations.

It was reasoned that lining the outer half of a runway with smooth glass in the vicinity of a 90° forced turn should cause subjects' inner legs to grip a rougher surface more firmly than the outer thereby exerting proportionately more locomotor force than normal during the negotiation of a turn. Bilateral asymmetry in leg activity should be less and

free-turn angles smaller than if glass were not present because of the greater relative influence of outer legs worked less than normal. However, if distortion of body segments determined alternation, the presence of glass should have no effect since, while interfering with normal leg movements during turning, distortion would be the same whether or not glass were present.

Method

Subjects and Apparatus.—The subjects were 48 woodlice no narrower than 5 mm. (Pillbugs were not used since the nature of the experimental manipulation did not suit their shorter legs.) The runway was the same as for Experiment 1 except that, for half the subjects, the outer half of the paper floor was lined with 0.2-mm-thick glass from 27 mm before to 30 mm past the forced turn. The same video-recording equipment was used as in previous experiments.

PROCEDURE

Subjects were given one trial in the runway either with or without glass being present. For each animal, its progress along the exit alley was video-recorded, its free-turn angle noted and its video-record later replayed with images frozen at 30, 20, 10 and 0 mm from the exit to enable measurements of distance from the outer wall. Half the woodlice exposed to each type of floor were forced left and half were forced right.

RESULTS AND DISCUSSION

Some woodlice did not travel along the runway with legs from one side of the body consistently on glass and those from the other side on paper, while others turned around in the exit alley before emerging. Consequently data from 8 subjects exposed to glass (which appeared aversive) and 4 run on paper alone were excluded from statistical analyses.

Mean \pm SE free-turn angles for woodlice tested with and without glass were $17.13 \pm 10.55^\circ$ and $47.70 \pm 10.35^\circ$ respectively. The difference was significant [$t(34) = 2.07, p < .05$]. Only 11 of the 16 subjects (69%) run on glass alternated [$p < .2$] whereas 16 out of the 20 (80%) run on paper alone alternated [$p = .012$]. For woodlice run on either glass or paper alone, mean \pm SE average distances from the exit-alley outer wall were $2.95 \pm .17$ and $2.07 \pm .17$ mm respectively. The difference was significant [$t(34) = 3.64, p < .01$].

For reasons outlined earlier, it seems likely that the presence of glass lessened bilateral asymmetry in leg movements during the forced turn.

The greater distances from the exit-alley outer wall shown by woodlice run on glass indicates that their legs on this side had more relative influence on free-turn behavior than when glass was not present. Consequently, the results of this experiment are consistent with BALM effects rather than distortion of body segments being responsible for the size of free turns in the opposite direction to a forced turn.

GENERAL DISCUSSION

From the results of Experiments 2 and 3 it is clear that while tactile cues might determine the direction of a turn, they have minimal effects on its size in isopods. It is particularly notable that, following the results of these two experiments, enhancement of alternation by seemingly graded thigmotaxis-based wall following in Experiment 1 was later more satisfactorily explained by relationships between distances initially traveled from the start-alley outer wall and the nature of the subsequent turn required to move into the exit alley. Although at times under unusual circumstances they may replace the operation of proprioceptive mechanisms (Hughes, 1987), tactile stimuli are unlikely to play a significant part in determining the size of most alternating turns in the two isopod species investigated.

The results of Experiment 4 support the involvement of proprioceptive feedback from BALM effects (Hughes, 1985) rather than body distortions (Schäfer, 1982) in woodlouse alternation. However, it is unlikely that BALM effects alone will account for all cases of alternation since isopods still alternate when passively moved around a forced turn without leg movement (Schäfer, 1986). Although the amputation of one or both antennae does not affect isopod turn alternation (Hughes, 1978, 1985; Schäfer, 1986), Heggemann and Wendler (1981) have implicated asymmetrical stimulation of the antennae in the coordination of leg movements. It is therefore likely that no single mechanism is crucial. Depending on circumstances, BALM effects, body distortions, activity of the antennae and tactile cues may all contribute to the control of alternation but with proprioceptive feedback probably playing the major role. To avoid desiccation and predators, woodlice generally prefer to inhabit damp, protected environments (Sutton, 1972). If forced out into the open they may have to travel considerable distances as quickly as possible before encountering another suitable habitat. A combination of thigmotaxis and centrifugal swing is sufficient to maintain a pattern of alternating turns at successive physical objects. However, an ability to alternate by means of proprioceptive cues would be necessary for negotiating nontactile obstacles such as areas of dryness, heat or chemical contamination. Instead of this type of mechanism operating only in the absence of tactile cues, results of the present and earlier

studies (Hughes, 1985; Kupfermann, 1966) indicate its predominant importance for isopods negotiating turns both with and without tactile stimulation.

Provision of glass at the forced turn was more likely to have modified differences in effort exerted by legs on each side of the body rather than distance traveled during the forced turn. Accordingly, it was possible that a fatigue-related process was involved in the BALM effects, as suggested earlier (Hughes, 1985). However, it is maladaptive and thus unlikely for the large bilateral differences in fatigue that would be required for the production of an alternating turn to be generated by a single forced turn. It is also improbable that such differences would rapidly dissipate with continued effort as suggested by decreases in alternation with greater distances between forced and free turns (Hughes, 1967; Schäfer, 1982). Instead, it is more likely that isopod alternation mediated by leg movements arises from proprioceptive feedback from the legs to sites in the central nervous system responsible for the integration of inhibitory and excitatory influences in the control of turning behavior. In view of the elaborate array of proprioceptors found in the various joints of the crustacean limb and their importance in every aspect of movement (Evoy & Ayers, 1982), more detailed examinations of leg movements during turning at forced and free turns are clearly indicated.

ACKNOWLEDGEMENTS

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