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Sensitivity to tactile novelty in the terrestrial isopod, *Porcellio scaber*

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ABSTRACT

Invertebrates have been studied at biochemical, ecological, and behavioural levels, but current knowledge about the impact that learning may have on behaviour is rather sparse. The present study aimed to examine the sensitivity of isolated rough woodlice (*Porcellio scaber*, Latreille, 1804) to the tactile novelty of their environment. A simple way to test this issue was to refer to the place preference paradigm, traditionally used in vertebrates. In Experiment 1, woodlice were placed in a compartment for 30 min in order to assess their ability to develop habituation in the absence of reward. In Experiment 2, woodlice were exposed to a compartment for 20 min (habituation phase) and were then given free choice between that compartment and a novel compartment for 2 min (preference phase). Depending on test conditions, rewards (humidity and/or shelter) were present or absent in the familiar compartment. The familiar and novel compartments differed with respect to the texture of the floor. In Experiment 3, the floor texture was the same in the two compartments in order to control for a novelty effect. The main results indicate that woodlice exhibited increased locomotion time, increased distance travelled, and increased speed in the novel compartment compared to the familiar compartment. There was no preference for either compartment when the floor textures of both were identical.

1. Introduction

The propensity to explore novel environments has been extensively studied in rodents (Hughes, 2007), but also in a variety of invertebrate species (e.g. Lindauer, 1952, bee; Wilson and Fowler, 1976, cockroach; Mather and Anderson, 1999, octopus; Mailleux et al., 2010, ant; Huber et al., 2011, crayfish). An important problem that arises in the study of novelty-driven behaviours is to explain whether exploration is motivated by survival requirements (i.e. the individual merely attempts to escape a suboptimal situation) or by curiosity (i.e. the individual exhibits an interest in biologically insignificant stimuli). These two aspects can only be distinguished provided that appropriate testing conditions are used (Hughes, 1997). In this paper, I examined the sensitivity of woodlice (*Porcellio scaber*) to the tactile novelty of their environment and attempted to determine whether this sensitivity was influenced by the presence of rewards.

Among isopods, oniscidea consist of more than 4000 crustacean species and are composed of terrestrial families only. The ability to live outside the aquatic environment caused the well-known aggregation behaviour in woodlice, considered as an adaptation to struggle against desiccation (Edney, 1968) – a behaviour not observed in marine isopods (Takeda, 1984). The risk of desiccation also explains why woodlice exhibit a preference for moist, dark, and cool places (Sutton, 1972). Owing to the properties of their habitat, woodlice's ocular system might be limited to the perception of brightness changes and light contrasts (Schmalfuss, 1998). However, just as the blindness of cave species is often compensated for by overdeveloped tactile and olfactory organs (Ruffié, 1983), a large variety of sensory receptors are present on the entire body surface in woodlice (Holdich and Lincoln, 1974; Schmalfuss, 1998). These receptors allow them to capture mechanic, hygrometric, and chemical information in the environment. In particular, the ventral epimera contains sensilla and scale-like structures (or 'tricorns'), which are mechanoreceptors involved in the thigmokinetic responses of *P. scaber* (Holdich and Lincoln, 1974). Tricorns, as well as other structures (tubercles, plaques, pits, and eyes), are also present on the dorsal epimera and together enable woodlice to detect the contact of any part of their body with the surroundings. No sex differences are apparent (Holdich and Lincoln, 1974).

Empirical data have been collected with respect to humidity responses (Cloudsley-Thompson, 1956), reproduction (Linsenmair, 1984), feeding (Tuck and Hassall, 2004), sheltering (Hassall and Tuck, 2007), turn alternation (Hughes, 2008), and inter-individual attraction (Devigne et al., 2011) in several species of woodlice. Preferences seem to exist for stimuli usually defined as *rewards* in the rodent-related literature. For instance, woodlice are more likely to choose a location with a group of conspecifics rather than an empty location (Takeda, 1984) and they prefer papers marked with faeces rather than unmarked papers (Kuenen and Nooteboom, 1963). Also,

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humidity (sought throughout the year in the wild, Gupta, 1963) and shelter-induced darkness (more exploited under dry conditions, Dias et al., 2012) have been shown to act as important sources of reward as well.

The present study aimed to test the sensitivity of *P. scaber* to the tactile novelty of its environment through the place preference paradigm, traditionally used in rodents and other mammals. Novelty is not an objective property of a stimulus but depends on the extent to which the stimulus was previously experienced (Hughes, 2007). There is evidence that the narrower the ecological niches exploited by animals, the more pronounced is their aversion to novelty. For instance, song sparrows, *Melospiza melodia*, exploit a variety of habitats, while swamp sparrows, *M. georgiana*, live in a more confined environment. Greenberg (1990a) showed that when a novel object (e.g. a black box or a tube) was placed close to a feeding tray the birds of both species were used to visiting on a regular basis in the wild, the number of visits was not affected in *M. melodia* but dramatically reduced in *M. georgiana*. A similar tendency was observed between captive, younger individuals of the same two species when they were deprived of food beforehand (Greenberg, 1990b). If an aversion to novelty is more pronounced in 'specialist' species than in 'generalist' species, woodlice – whose conditions of life are narrow – should exhibit such an aversion. This paper is an attempt to determine (i) whether woodlice are able to show habituation to an environment, (ii) whether they exhibit an avoidance of, a preference for or an indifference to a novel environment, and (iii) whether their reaction to novelty can be altered by the presence of rewards.

2. Experiment 1

The ability of woodlice to develop habituation was assessed through a single 30 min session in 2 different tactile environments. This experiment served as a pretest in order to determine an optimal timing for the habituation phase in the next two experiments.

2.1. Materials and methods

2.1.1. Animals and housing conditions

Twelve woodlice (size: 11.7 ± 0.4 mm) were collected in the author's garden, irrespective of their sex. The individuals were maintained at the same time in a plastic container (20 cm × 12 cm × 8 cm) provided with earth, organic matter (leaves, small roots) in a decomposition phase, and pieces of bark for sheltering. The soil was humidified using rain water previously collected in order to avoid the desiccation of the woodlice. Small holes on the top allowed the container's ventilation. The container was placed in the room in which the animals were tested approximately 24 h later (temperature = 22.97 ± 0.16 °C; humidity = 48.75 ± 0.75% RH; brightness = 210 lx). Humidity inside the container, measured by means of a hygrometric captor introduced in the box a few minutes before testing, was higher than in the room (79.75 ± 5.14% RH). After testing, the woodlice were immediately released. No mortality occurred during housing and observations. This research complied with the Federal Public Service Health, Food Chain Safety, and Environment requirements.

2.1.2. Apparatus

The apparatus was constructed from fir tree wood and comprised 12 compartments (13 cm × 4 cm × 4 cm). As shown in Fig. 1, half of the compartments had their floor covered with large-grained sandpaper (grain size: 60), while the other half had their floor covered with smooth paper of the same colour (light brown). As woodlice have developed tactile organs on the entire body surface (Holdich and Lincoln, 1974), these two textures were expected to induce easily distinguishable environments. The inner walls in the middle of the apparatus consisted of removable wooden dividers (4 cm × 4 cm × 0.8 cm) – in Experiments 2 and 3, the dividers had to be removed for the free-choice task. The inner walls of the compartments, as well as the removable dividers, were covered with a transparent adhesive tape that provided a slippery surface preventing the tested animals from scaling and escaping from the apparatus – whose upper part remained open. There were no objects present in the compartments. An analogue camera (Canon® MV900) equipped with a stand and directed towards the room's floor – 80 cm above the experimental set-up – allowed the 12 compartments to be filmed simultaneously.

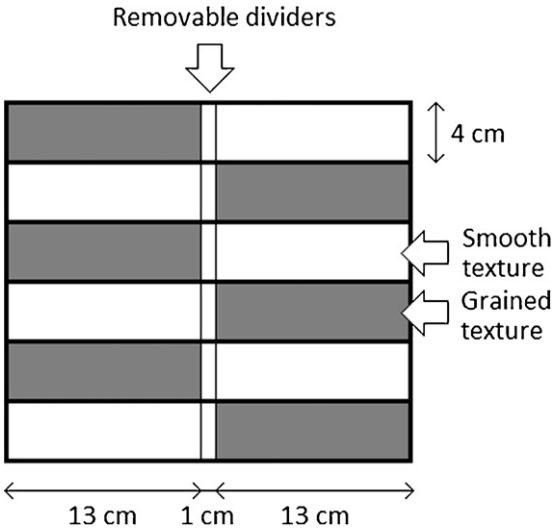

Fig. 1. Apparatus used to test habituation and free choice in woodlice. From box to box, the texture of the floor (smooth or gained) was alternated between the left and right compartments. The in-between zone was covered with paper of a different colour from that of both compartments. A removable divider was placed in this zone during woodlice habituation and the zone served as a neutral place (called 'buffer' zone) during the free-choice test.

2.1.3. Procedure

Once collected, the woodlice were measured using a ruler. Subjects whose body length was <10 mm were removed and directly released. The remaining individuals were kept in the plastic container for 24 h within the testing room in order to let them accustomed to the temperature, humidity and darkness conditions specified above which could differ from those experienced in the natural environment. This also increased the chance that all animals were in similar physiological conditions before testing. The woodlice were tested at 1400 (GMT + 1).

The 12 individuals (1 per compartment) were tested within a single 30 min session and their activity was tape-recorded every 10 min – i.e. 0-10-20-30. One woodlouse was placed in the middle of a compartment using a small plastic spoon. This operation was repeated in such a way that 6 individuals were simultaneously exposed to the grained floor and the other 6 to the smooth floor. The camera was turned on before introducing the first woodlouse, and animals were then filmed as mentioned above. The woodlice were not tested for a longer period of time than 30 min in order to avoid motor impairments caused by desiccation (Dailey et al., 2009). These animals were not reused.

2.1.4. Examined behaviours

- Locomotion time: an environment that becomes familiar as a result of learning should reduce exploratory activity, and hence the time spent running in this environment.
- Distance travelled.