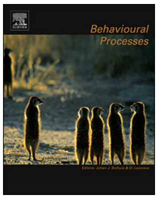
Behavioural Processes 159 (2019) 55–56

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Short report

Horizontal and vertical exploration in woodlice: A dual-process model

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ARTICLE INFO

Keywords:
Habituation
Sensitization
Woodlice
Exploration
Physiological stress

ABSTRACT

Woodlice placed in an unknown experimental enclosure typically run (horizontal exploration) and rear up on the enclosure's walls (vertical exploration). Previous findings with *Porcellio scaber* indicate that these two behaviors have an opposite temporal distribution and show differential sensitivity to rotation-induced physiological stress. It is argued that the dual-process theory of habituation and sensitization can serve as a basis to account for horizontal and vertical exploratory activities in woodlice. A model is presented. This model could help identify individual variability in "temperament" and to isolate its effects in various behavioral tasks in woodlice and perhaps other invertebrate species.

Horizontal and vertical exploratory activities have been well documented in rodents, but remain sparsely studied in invertebrates (e.g., Alcaro et al., 2011; Gharbawie et al., 2004; Thompson et al., 2018; Tirelli and Witkin, 1994). However, the question of whether these two behaviors depend on the same mechanism or on distinct mechanisms is unknown. The study of freely moving woodlice in small experimental enclosures (14 cm × 4 cm × 4 cm) without rewards – one individual per enclosure – reveals that the temporal distribution of horizontal (running) and vertical (rearing up) exploratory activities is different. After placement in the enclosures, the woodlice typically run and do not rear up on the vertical walls. But gradually, there is a habituation of (decrease in) running and a sensitization of (increase in) rearing up over time (Anselme, 2013, 2015, 2018). These effects are robust and clearly distinguishable following a 15–20 min exposure to the enclosure. After a time, the woodlice tend to stop any activity (immobilization). Recently, I showed that rotational stress reduces rearing up in a familiar and a novel environment, but alters running only in the novel environment (Anselme, 2018). So environmental familiarity seems to have some antistress protective effects on the habituated, but not the sensitized, behavior. Immobilization periods following the stress episode were indicative of stress because they were longer in the absence of environmental familiarity. Collectively, these results suggest that the horizontal and vertical exploration modes rely on distinct mechanisms relative to physiological stress.

Running and rearing up are likely to share the same functional purpose, which consists of trying to find better environmental conditions. Hence why should we believe that they are controlled by independent mechanisms? Because if they were not, one of these two scenarios would be expected: either their initial expression would be high and gradually decreased following repeated failures to escape, or their initial expression would be low and gradually increased as the need for vital resources (food, humidity, cool, etc.) becomes stronger. None of these scenarios happen. In contrast, the difference in their temporal distribution indicates the existence of a rule hardwired in the woodlouse's brain that establishes priorities in the activation of two distinct mechanisms. This rule could be this: "Run first and, if unsuccessful, rear up in the search of more favorable conditions". The "run first" strategy may help a woodlouse escape from physical disturbance, for example, induced by a bird or a hedgehog foraging on bugs in a forest. But this strategy is insufficient to allow the woodlouse to extract itself from a cavity in which it fell – a situation similar to our experimental enclosure. It needs a more sophisticated rule that includes rearing up in order to climb out of the cavity. As the "run first" strategy fails and results in habituation, the "then rear up" strategy takes over and is gradually sensitized since it represents the last option to quit the hostile environment. Thus, the former strategy should be less under stress control than the latter (Anselme, 2018).

I suggest that dual-process theory (Groves and Thompson, 1970) can overall explain horizontal and vertical exploration in woodlice. This theory posits that behavioral habituation and behavioral sensitization depend on two distinct processes (denoted by the same terms) that can be simultaneously activated, such that the behavioral outcome is the net effect of the two processes. The habituation *process* is assumed to activate the stimulus-response (S-R) system, a short neuronal path that links the eliciting stimulus with muscular response. Habituation is a stimulus-specific process that increases in proportion to the stimulus frequency. Habituation may occur between training sessions, but also within a session as shown with woodlice here (see also Leussis and Bolivar, 2006) – note that dual-process theory is especially relevant in the case of short-term habituation (Thompson, 2009). In contrast, the

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https://doi.org/10.1016/j.beproc.2018.12.019
Received 4 November 2018; Received in revised form 28 December 2018; Accepted 30 December 2018

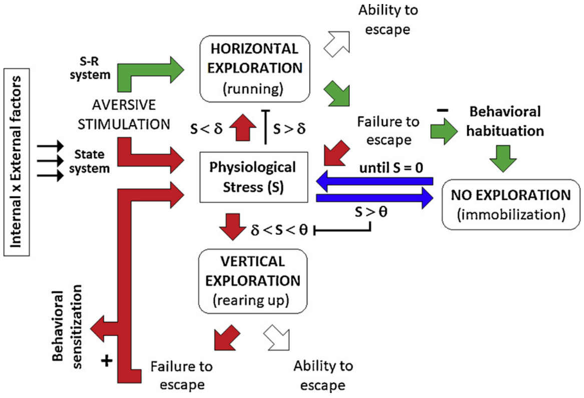

Fig. 1. Dual-process theory of Groves and Thompson (1970) applied to horizontal and vertical exploration in woodlice. The green pathway represents the habituation process, the red pathway the sensitization process, and the blue pathway a hypothetical "cool-down" process. Two fixed thresholds (δ and θ), whose value may differ from individual to individual, determine behavioral priorities on a continuum such that $\delta < \theta$. More details in the text.

sensitization *process* is assumed to occur in the state system, a part of the nervous system controlling the readiness to respond. Only arousing events such as the fear-potentiated startle response (Davis et al., 2008) can activate the state system, which determines the individual's alertness as a function of stimulus intensity.

A model of exploratory activity in woodlice in presented in Fig. 1. Exposure to a hostile environment – such as an experimental enclosure without rewards – is assumed to have two effects: producing horizontal exploration through automatic activation of the S-R system and arousing physiological stress as part of the state system. At this stage, physiological stress (S) may remain insufficient to elicit vertical exploration ($S < \delta$) – thus, the individual uses a "run first" strategy. Nevertheless, stress may boost running if $0 < S < \delta$. This strategy is subject to a stress-independent habituation process (green arrows, minus sign) if the aversive stimulation persists in time. However, as the inability to escape is prolonged, physiological stress increases and comes to elicit episodes of vertical exploration if $\delta < S < \theta$ – the individual uses the "then rear up" strategy, which inhibits running. At this stage, stress remains moderate and is assumed to fluctuate due to the influence of external and internal factors (relative humidity, temperature, food deprivation, etc. whose role is currently unknown), causing intermittent running episodes ($S < \delta$). After a time, stress reaches higher values that make running less and less likely to occur, despite their possible fluctuation. The inability to climb out or to find sheltering space in the vertical surfaces enhances activation of the physiological stress system, which causes gradual sensitization of vertical exploration (red arrows, plus sign) to the detriment of running. Retesting the woodlice five hours after rotational stress did not reveal any long-term behavioral sensitization (Anselme, 2018), but one session was perhaps insufficient to observe long-term effects on the physiological stress system. Finally, if too strong activation of the physiological stress system occurs ($S > \theta$), the woodlice gradually stop the "then rear up" strategy and enter into prolonged phases of immobility. In this context, immobilization is viewed as the consequence of intense stress, a behavior often observed after mechanical disturbance in the *Porcellio* genus (Schmalfuss, 1984) and other arthropod species (Acheampong and Mitchell, 1997). Immobility is hypothesized to "cool down" the overactive physiological stress system and reset the stress value ($S = 0$) before starting a new activity (blue arrows).

Like in many other arthropod species (e.g., Pamir et al., 2011; Planas-Sitjà et al., 2015), inter-individual differences exist in woodlice's behavior (Broly and Deneubourg, 2015; Devigne et al., 2011; Tuf et al., 2015). Not all individuals are therefore expected to strictly follow the same timing for these different steps. The model predicts that individuals that run without rearing up over a 20-min period show a low physiological stress response, while individuals that briefly run and then spend much time immobile show a strong physiological stress response. The individuals that slowly develop rearing-up behavior should have an intermediate stress level. Indeed, as mentioned in Fig. 1 legend, the values of the thresholds are fixed for a given individual but may differ between individuals – provided that $\delta < \theta$. In addition, some individuals may be more vulnerable to stress than others. As a result, at one extreme, reaching the θ threshold will be fast for some individuals, which typically run at a high speed for a few seconds and immobilize for several minutes following their placement in the enclosure. At the other extreme, some individuals seem to never reach the δ threshold, running at a low or normal speed for long periods of time. Intermediate individuals should follow the sequence of behaviors such as described in Fig. 1. Testing these predictions requires to measure and compare concentrations of the hyperglycemic hormone – the equivalent of corticosterone in crustaceans (e.g., Elwood et al., 2009) – in the hemolymph in these three categories of individuals. Establishing a positive correlation between physiological stress and behavioral reactions predicted by the present model could be useful to study the effects of "temperament" on processes such as decision-making, foraging, and social interactions in invertebrates. For example, preliminary observations in small enclosures could be used to identify stress-related behavioral profiles. The same individuals can then be used to study the effects of stress in many situations such as risk sensitivity in free-choice tasks involving effort and reward uncertainty, the propensity to explore vaster environment in the search of food, or the dynamics of inter-individual interactions in social and gregarious species. Finding behavioral indicators of internal states (such as physiological stress) in invertebrates offers a large panel of experimentations and is important in a comparative perspective with vertebrate species.

References

Acheampong, S., Mitchell, B.K., 1997. Quiescence in the Colorado potato beetle, *Leptinotarsa decemlineata*. Entomol. Exp. Appl. 82, 83–89.

Alcaro, A., Panksepp, J., Huber, R., 2011. D-amphetamine stimulates unconditioned exploration/approach behaviors in crayfish: towards a conserved evolutionary function of ancestral drug reward. Pharmacol. Biochem. Behav. 99, 75–80.

Anselme, P., 2013. Sensitivity to tactile novelty in the terrestrial isopod, *Porcellio scaber*. Behav. Process. 92, 52–59.

Anselme, P., 2015. Enhanced exploratory activity in woodlice exposed to random visuo-tactile patterns. Learn. Motiv. 50, 48–58.

Anselme, P., 2018. Rotational stress influences sensitized, but not habituated, exploratory behaviors in the woodlouse, *Porcellio scaber*. Learn. Behav. 46, 294–305.

Broly, P., Deneubourg, J.L., 2015. Behavioural contagion explains group cohesion in a social crustacean. PLoS Comput. Biol. 11, e1004290.

Davis, M., Antoniadis, E.A., Amaral, D.G., Winslow, J.T., 2008. Acoustic startle in rhesus monkeys: a review. Rev. Neurosci. 19, 171–185.

Devigne, C., Broly, P., Deneubourg, J.-L., 2011. Individual preferences and social interactions determine the aggregation of woodlice. PLoS One 6, e17389.

Elwood, R.W., Barr, S., Patterson, L., 2009. Pain and stress in crustaceans? Appl. Anim. Behav. Sci. 118, 128–136.

Gharbawie, O.A., Whishaw, P.A., Whishaw, I.Q., 2004. The topography of three-dimensional exploration: a new quantification of vertical and horizontal exploration postural support, and exploratory bouts in the cylinder test. Behav. Brain Res. 151, 125–135.

Groves, P.M., Thompson, R.F., 1970. Habituation: a dual-process theory. Psychol. Rev. 77, 419–450.

Leussis, M.P., Bolivar, V.J., 2006. Habituation in rodents: a review of behavior, neurobiology, and genetics. Neurosci. Biobehav. Rev. 30, 1045–1064.

Pamir, E., Chakroborty, N.K., Stollhoff, N., Gehring, K.B., Antemann, V., Morgenstern, L., et al., 2011. Average group behavior does not represent individual behavior in classical conditioning of the honeybee. Learn. Mem. 18, 733–741.

Planas-Sitjà, I., Deneubourg, J.-L., Gibon, C., Sempo, G., 2015. Group personality during collective decision-making: a multilevel approach. Proc. R. Soc. B 282.

Schmalfuss, H., 1984. Eco-morphological strategies in terrestrial isopods. In: Sutton, S.L., Holdich, D.M. (Eds.), The Biology of Terrestrial Isopods. Clarendon Press, Oxford, UK, pp. 49–64.

Thompson, R.F., 2009. Habituation: a history. Neurobiol. Learn. Mem. 92, 127–134.

Thompson, S.M., Berkowitz, L.E., Clark, B.J., 2018. Behavioral and neural subsystems of rodent exploration. Learn. Motiv. 61, 3–15.

Tirelli, E., Witkin, J.M., 1994. Verticalization of behavior elicited by dopaminergic mobilization is qualitatively different between C57BL/6J and DBA/2J mice. Psychopharmacology 116, 191–200.

Tuf, I.H., Drábková, L., Šipoš, J., 2015. Personality affects defensive behaviour of *Porcellio scaber* (Isopoda, Oniscidea). Zookeys 515, 159–171.