



Testing experience and environmental enrichment potentiated open-field habituation and grooming behaviour in rats

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In laboratory rats, one of the most used paradigms to assess habituation to novelty is the open-field test. Environmental enrichment has proved to be a reliable way to enhance open-field test habituation. Experiment 1, therefore, was designed to test whether grooming behaviour in the open-field test increases concomitantly with the habituation of exploratory behaviours (locomotion and rearing behaviour, an alert upright posture). To this aim, after a baseline measure, rats were raised in environmentally enriched and standard housing conditions and then tested 30 and 60 days later. As some grooming subtypes are differentially displayed in the open-field test, we hypothesized that only the grooming subtype that included longer and more complex sequences (e.g. body licking) would increase with habituation. We found that environmental enrichment enhanced short-term (within days) and long-term (between days) open-field test habituation, and increased grooming, particularly body licking. To provide evidence that grooming in the open-field test is part of the habituation process and not a by-product of environmental enrichment, habituation was promoted by exposing a different group of rats that had been reared in standard housing to four consecutive open-field tests in experiment 2. We supposed that the diminution of exploratory open-field test behaviours would be accompanied by an increase in body licking. We found that as locomotion and rearing behaviour decreased, body licking increased gradually both within and between days, suggesting that the appearance of more complex and longer grooming sequences are part of a de-arousal inhibition system subserving novelty habituation. A detailed analysis of grooming, therefore, may provide information about the emotional state of the rat that cannot otherwise be obtained from assessing exploratory activity.

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Grooming behaviour serves many purposes, which vary depending on the species. Cleaning is the most relevant purposes of grooming, since it allows organisms to remove accumulated dirt and keep their motor and sensory parts free from obstructions (Amador & Hu, 2015). Grooming is also implicated in thermoregulation (Almeida, Vizin, & Carrettiro, 2015; Roberts, 1988; Thiessen, 1988), pain relief (Spradley, Davoodi, Carstens, & Carstens, 2012), social interaction (Carter & Wilkinson, 2015; Seyfarth, 1980) and in stress and anxiety responses in natural (Molesti & Majolo, 2013) and non-natural contexts (Kalueff & Tuohimaa, 2005; Martin & Réale, 2008; Roth & Katz, 1980). Because some of the grooming components or subtypes seem to be related to emotionality (Delius, 1967; Doyle & Yule, 1959; Ewer,

1967; Kalueff et al., 2016; Moyaho, Eguibar, & Diaz, 1995; Spruijt, Van Hooff, & Gispén, 1992), the study of grooming in rodents has become a very useful strategy for modelling different mood and psychiatric disorders and for understanding neural circuitries underlying complex motor patterns (Kalueff et al., 2016). However, an old (Spruijt et al., 1992), but still open question (Fernández-Teruel & Estanislau, 2016; Kalueff et al., 2016; Song, Berridge, & Kalueff, 2016) is whether grooming should be interpreted as an indicator of stress and anxiety in the context of different testing procedures in laboratory rodents.

One strategy to assess stress-related grooming in rodents has been the study of novelty habituation in the context of the open-field test (Brenes, Padilla, & Fornaguera, 2009; Brenes, Rodríguez, & Fornaguera, 2006). Habituation is a form of nonassociative learning that is inferred from the progressive reduction of a behavioural response as a consequence of prolonged or repeated exposures to its eliciting factor (Groves & Thompson, 1970; Poon &

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Young, 2006). In this context, locomotion and rearing behaviour (rearing up on the hindlegs) are the most frequent behaviours displayed, which, at the same time, are the most sensitive responses to the effect of prolonged or repeated experience. Locomotion may be related to spatial and sensorimotor representation of the place being explored (Blanchard & Blanchard, 2008). Rearing behaviour, in contrast, has a different function related more to monitoring the surroundings in order to identify potential sources of danger (Brenes et al., 2006; Blanchard & Blanchard, 2008; Blanchard, Yang, Li, Gervacio, & Blanchard, 2001). At the beginning of the open-field test, exploratory and risk assessment behaviours are highly displayed, but as soon as the uncertainty about likely sources of threats starts to decline, these behaviours also gradually decline. Such a kinetics process is referred to as habituation (Blanchard & Blanchard, 2008; Brenes et al., 2009; Veloso, Filgueiras, Lorenzo, & Estanislau, 2016; Zhuang et al., 2001).

Previous reports showed that some grooming subtypes increase while habituation is taking place or has already occurred (Brenes et al., 2009; Zimmermann, Stauffacher, Langhans, & Würbel, 2001), suggesting that some of types of grooming behaviour could be implicated in the after-stress process rather than in the signalling of an ongoing stress event. Nevertheless, other reports have indicated the opposite phenomenon: grooming increases as a consequence of stress induction (Kalueff & Tuohimaa, 2005). In this regard, there are two general hypotheses that explain rodent grooming in conflicting or anxiogenic situations (Kalueff et al., 2016; Spruijt et al., 1992). First, the stress and anxiety hypothesis posits that grooming is a direct indicator of defensive emotional states, and second, the de-arousal hypothesis interpretes grooming as part of the emotional regulation process after stressing events (Brenes et al., 2009; Díaz-Morán et al., 2014; Fernández-Teruel & Estanislau, 2016; Kalueff et al., 2016; Song et al., 2016; Spruijt et al., 1992). Innovative approaches have revealed that artificially induced grooming after stressful events could reduce exploratory and risk assessment behaviours in a context-dependent manner (Füzesi, Daviu, Cusulin, Bonin, & Bains, 2016). In a safe environment, such as a home cage, laboratory mice show the greatest amount of grooming, but when tested in a novel context or in a place previously associated with stress, grooming is drastically reduced (Füzesi et al., 2016). The artificial induction of grooming also antagonizes other defensive responses such as conspecific attacks provoked by a territorial conflict (Hong, Kim, & Anderson, 2014). The artificial inhibition of such attacks, however, does not automatically induce grooming (Hong et al., 2014), suggesting that this behaviour is not a default response in conflicting situations. Instead, grooming may play an alternative role in stress and emotional de-arousal, probably in later stages when defensive behaviours are no longer required.

Environmental enrichment often provides animals with significantly greater physical stimulation (e.g. large cages with objects and devices to climb on and hide in) and/or social stimulation (2–15 cage-mates) than that in standard laboratory housing (Brenes et al., 2006, 2016). This environmental manipulation deeply affects different behavioural parameters in rodents and leads to several brain changes related to neural plasticity. Pioneering studies in rats showed that brain weight and cortical thickness increased as a consequence of environmental enrichment (Bennett, Rosenzweig, & Diamond, 1969; Diamond, Ingham, Johnson, Bennett, & Rosenzweig, 1976; Renner & Rosenzweig, 1986; Rosenzweig, Bennett, Hebert, & Morimoto, 1978). Later on, it was revealed that such gross brain effects may be attributed to augmented dendritic branching and length and to more dendritic spines and larger synapses (Faherty, Kerley, & Smeyne, 2003; Leggio et al., 2005; Rampon & Tang et al., 2000). It is well known that environmental enrichment promotes adult neurogenesis in the hippocampus (Brenes et al., 2016; Bruel-Jungerman, Laroche, &

Rampon, 2005; Kempermann, Kuhn, & Gage, 1997), induces changes in the expression of several genes (Rampon & Jiang et al., 2000) and impacts the availability of neurotrophic factors (Kuzumaki et al., 2011; Rampon & Jiang et al., 2000) and neurotransmitters in the brain (Bowling, Rowlett, & Bardo, 1993; Brenes & Fornaguera, 2008; Brenes et al., 2009; Neugebauer et al., 2004; Solinas, Thiriet, Chauvet, & Jaber, 2010).

At the behavioural level, environmental enrichment improves motor skills in healthy rodents and ameliorates motor deficits observed in animals with brain damage (Maegle et al., 2015; Marques et al., 2014; Matter, Folweiler, Curatolo, & Kline, 2011; Moritz, Geeck, Underly, Searles, & Smith, 2014; Schuch et al., 2016). Environmental enrichment also enhances learning and memory as assessed by means of spatial (Bennett, McRae, Levy, & Frick, 2006; Kempermann et al., 1997; Leggio et al., 2005; Mora-Gallegos et al., 2015; Moritz et al., 2014; Nilsson, Perfilieva, Johansson, Orwar, & Eriksson, 1999) and nonspatial learning tasks (Brenes et al., 2016; Bruel-Jungerman et al., 2005), but has no effects on olfactory social discrimination tests (Pena, Prunell, Dimitsantos, Nadal, & Escorihuela, 2006; Rampon & Tang et al., 2000), and it promotes exploratory behaviours in both vertebrates (rodents: Fernández-Teruel et al., 2002; Sampedro-Piquero, Begega, & Arias, 2014; Turner & Burne, 2014) and invertebrates (Bengston, Pruitt, & Riechert, 2014; Collymore, Tolwani, & Rasmussen, 2015). In fact, under certain reinforcement-based paradigms (e.g. a modified version of the hole-board test), exploratory activity of laboratory rats is somewhat enhanced by environmental enrichment (Sampedro-Piquero et al., 2014). However, when rats were allowed to freely explore the hole-board, those reared in enriched environments showed a reduced latency to explore the hole-board (i.e. began to head-dip earlier) than animals reared in standard housing, but they displayed less exploratory activity in general (Turner & Burne, 2014). In a comparable paradigm, environmentally enriched rats, but not controls or isolated counterparts, quickly reduced their exploratory activity and made fewer hole-pokes as the test progressed (Varty, Paulus, Braff, & Geyer, 2000). In the open-field test, a similar effect was observed, with environmental enrichment facilitating habituation learning (Brenes & Fornaguera, 2008; Brenes et al., 2009; Elliott & Grunberg, 2005; Mora-Gallegos et al., 2015; Moritz et al., 2014; Neugebauer et al., 2004; Pham et al., 1999; Schrijver, Bahr, Weiss, & Würbel, 2002; Varty et al., 2000; Zimmermann et al., 2001).

Since the understanding of grooming in stressful situations is still a work in progress, we aimed to study how habituation of novelty-evoked exploratory and defensive responses in the open-field test influences the occurrence of grooming and its different components. In these contexts, if grooming increases over time while active open-field test behaviours decline, we would take this as evidence in favour of the de-arousal hypothesis. We used environmental enrichment, therefore, as a reliable form of facilitating open-field test habituation, expecting that it would also enhance grooming behaviour. Here, in contrast to our previous studies, we assessed both short- and long-term habituation by analysing the behavioural changes occurring within and between tests, respectively. To this aim, in experiment 1, we assessed the behaviour of rats in the open-field test 30 and 60 days after environmental enrichment (EE) and standard laboratory housing (SH). As some grooming subtypes are known to be differentially displayed in the open-field test (Brenes et al., 2009; Rojas-Carvajal, Méndez, Fornaguera, & Brenes, 2016), we examined and analysed three grooming subtypes in this experiment. Here, we hypothesized that only the grooming subtype that included longer and more complex sequences (e.g. body licking) would increase concomitantly with habituation, especially in environmentally enriched rats. It is well known that consecutive exposures to testing apparatuses

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