

Research report

Early social and physical deprivation leads to reduced social motivation in adulthood in Wistar rats

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Abstract

Behavioural abnormalities in adulthood may have their origin in a disturbed interaction with the environment during postnatal development. We tested the consequences for adult social motivation of early deprivation (ED) of rat pups from mothers and littermates relative to nonhandled (NH) pups. Early deprivation was performed at room or warm ambient temperatures, cold-ED and warm-ED, respectively, and during either the dark or light phase of the daily cycle. In adulthood, rats that were unrelated and unfamiliar but of the same treatment group were introduced in pairs to an open field for a 30-min test. Social behaviour in home base and exploration modes was assessed using algorithmic analysis of the XY locations of the two rats. Findings revealed that Cold-ED induced a preference for a separate home base, which limited significantly the episodes of social interactions, in comparison to NH. Warm-ED had no comparable effect on the rats' social behaviour. These findings indicate that ED under ambient conditions that constitute severe thermal stress for rat pups leads to development of reduced social motivation in adulthood.

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1. Introduction

In mammals, the postnatal social environment is an important determinant of behavioural phenotype in adulthood. In rats, the most-studied species in this respect, maintenance of infant homeostasis is dependent on maternal care and on contact with littermates [11,12]. The dam and littermates provide each pup with thermal, nutritional and tactile stimulation, that regulate homeostasis in and maturation of metabolic systems, the autonomic nervous system, neuroendocrine axes, neurochemical systems, and the central nervous system and behaviour. The importance of maternal care and littermate contact for pup status have been demonstrated in studies based on deprivation of this "social buffer" and placement of the pup in specific physical environments during this deprivation (e.g. [17,19,22,40,42]). Furthermore, a number of studies have in-

vestigated the long-term effects of early life deprivation in the rat, in terms of physiological [13,28], behavioural [15,41] and neurobiological [13,20] parameters.

We have recently performed a number of studies investigating the long-term effects of daily, prolonged social isolation between birth and weaning (reviewed in [31]). This manipulation, which we refer to as early deprivation (ED), takes the form of deprivation of each pup from the dam and littermates for 4 h per day. As comparison groups we have studied early handling (EH), which involves social isolation for 15 min per day, and non-handling (NH), which involves complete non-disturbance of pups and dam. When ED is conducted at 30 °C and during the dark phase of the diurnal cycle, we have demonstrated that its long-term effects are, relative to NH, to reduce anxiety and fear responses to, and improve cognitive performance under, aversive challenge. As such, ED under these conditions exerts very similar long-term effects to those of EH, which is important given that the anxiety/fear-attenuating and cognitive-enhancing

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effects of EH relative to NH represents the most robust and informative model to date of the importance of the early environment for the adult phenotype [16,18,23,24]. For example, ED conducted at 30 °C and during the dark phase yielded adult offspring that demonstrated, relative to NH adults: more activity in an open field (EH were intermediate); attenuated acoustic startle reflex responding (EH were intermediate), reduced corticosterone responses to a restraint stressor (EH were intermediate); enhanced active avoidance conditioning (EH and ED were similar); and enhanced spatial navigation in the water maze (EH and NH were similar) [30–32].

Effects of ED in the direction obtained were unexpected. Although NH is probably a postnatal environment of sub-optimal stimulation [31] and although daily 3-h litter-dam separation has been demonstrated to be without effect relative to NH on a number of neurobehavioural parameters (e.g. [4,14,28,31]), it was nonetheless anticipated that daily 4-h complete social deprivation would impact negatively on the adulthood phenotype. Given that ED constitutes removal of the pup's social buffer, the conditions of the physical environment in which it is placed would be expected to be important determinants of the long-term effects of ED [6,43]. It is possible that the physical conditions of ED are critical in determining whether maternal and littermate deprivation exerts a negative long-term impact. The fact that ED was conducted at 30 °C meant that although pups were deprived of several forms of stimulation from dam and litter they were not thereby exposed to a severe thermal stressor [3], and it is possible that they were thereby protected from acute stress responses in some stress systems. In order to investigate this, ED has recently also been conducted at ambient colony room temperature. A second potentially important variable in ED studies is the stage of the daily cycle, and therefore the circadian status of the pup, at which ED is performed. In our original studies ED was performed during the dark, active phase, when levels of maternal care are relatively low [8,26], and it is possible that ED during the light phase when maternal care levels peak, would constitute a more severe deprivation. In siblings of the current subjects, we have recently demonstrated that when conducted at room temperature and relative to NH, ED yields adults that are less able to cope with aversive challenge (the forced swim test) and are also less responsive to positive reinforcement (motivation to obtain sucrose on a progressive ratio reinforcement schedule). In contrast to prediction, these effects of room temperature ED were obtained when the manipulation was conducted during the dark phase but not when conducted during the light phase [33].

Here, as a continuation of this investigation into the impact of specific forms of ED on adult emotionality, we describe a study of the effects of ED on social interactions in a mildly stressful environment. The rationale for developing and performing this challenge is as follows. Anxiety has, of course, a multifaceted nature and is expressed differentially under diverse conditions [21]. Clinical experience

also shows that expressions of abnormal emotionality are frequently context-related, with specific phobias being an example of this. Based on this reasoning, a search for altered emotionality may amount to a search for the contexts in which rats exposed to a specific form of ED are prone to show abnormal emotionality. The social context is particularly pertinent in this respect, as the very essence of ED is an interruption of pups' social interactions with mother and littermates. The open field is a useful test for the study of social interactions. In a familiar physical setting, pairs of unfamiliar (and non-manipulated) rats spend a high proportion of time in social interactions such as sniffing, grooming and following. Anxiogenic manipulations, including placement in a novel environment, decrease social interactions [7]. Therefore, it is possible that a social open field test will induce conflict between the motivations to be solitary versus social, and thereby reveal that the outcome of this conflict is dependent on early life experience. Indeed, a recent study reported that in a social interaction test conducted in a familiar open field, adults exposed to 8-h maternal separation (litter intact) on P 2–10 at 30–33 °C exhibited less social interaction than adults exposed to EH [21]. In the present study we use the social open field test to study the consequences of ED performed under specific conditions relative to the stringent comparison of NH. Behaviour in the open field is analyzed while considering rats' alternation between periods of restrictive motion at some preferred site termed a home base (HB) and periods of explorative excursions out of the HB [39]. Social attraction is assessed separately in each of the behavioural modes [9], following the demonstration that social proximity during common HB occupation but not social proximity during exploration is affected by antisocial pharmacological treatment [25].

2. Material and methods

2.1. Animals

Wistar rats (Swiss Federal Institute of Technology Zürich, Schwerzenbach) were maintained in standard polycarbonate cages of 59.0 cm × 38.5 cm × 20.0 cm with sawdust bedding, under a light/dark cycle with lights on from 07:00 to 19:00 or a reversed cycle with lights on from 19:00 to 07:00 (specified in the experiment), temperature at 21 ± 1 °C and humidity 55 ± 5%. Pellet feed (Universal feed 3430, Moulin Kliba, SA, Kaiseraugst, CH) and water were both available continuously and ad libitum.

2.2. Early deprivation

Adult nulliparous females were paired with males; half of the pairs were maintained on a normal light/dark cycle (light) and half on a reversed light/dark cycle (dark). The males were removed after 5 days and the females were allocated equally

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