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Research report

Early deprivation, but not maternal separation, attenuates rise in corticosterone levels after exposure to a novel environment in both juvenile and adult female rats

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Abstract

Separation from the maternal nest alters the hypothalamic-pituitary-adrenal (HPA) axis stress response in adult male rats, but little research has addressed how separation affects female rats. The following experiments investigated how early maternal separation from postnatal day (PND) 2 to 14 affected stress-induced corticosterone and ACTH after exposure to an open field in juvenile and adult female rats. Female rats were separated for 5 h daily from mother and littermates (early deprivation: ED), separated from mother but not littermates (maternal separation: MS), or animal facility reared (AFR). Male siblings were left with the mother rat during separation. Female rats were exposed to an open field arena either during the juvenile period (PND 30) or during adulthood (PND 80–100). Results show that ED juvenile female rats showed a lower corticosterone stress response than MS and AFR female rats when measured at 5 min post-stress, but no difference at 20 or 60 min post-stress. In adulthood, ED female rats showed comparable elevations of corticosterone as MS and AFR rats at 5 min post-stress but lower elevations at 20 min. In terms of behavior, there were no significant effects of early experience. However, in adulthood, ED and MS rats tended to show a decreased proportion of inner grid crossings of the open field compared to AFR rats, suggesting a tendency for increased anxiety in these two separation groups.
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Keywords: Separation; Juvenile; Adult; Female rat; Open field; HPA axis

1. Introduction

Early experience during the neonatal period can have effects on behavior and physiology that are evident at multiple developmental stages. For example, acute maternal deprivation during the stress hyporesponsive period (SHRP; postnatal days 2–14) increases corticosterone, an adrenal hormone released in response to stress, in pups and repeated deprivation further sensitizes this response during the neonatal period [38,61]. Being separated repeatedly from the mother rat but not littermates during the SHRP can lead to a hyperresponsive hypothalamic-pituitary-adrenal (HPA) response to stress in adulthood ([3,25,26,31,47]; other refs; also see Table 1). However, the effects of early repeated maternal separation on adult HPA axis response are inconsistent at best ([30,45,53]; also see Table 1). These inconsistencies may be due to the fact that maternal separation may have stressor-specific, manipulation-specific, age-specific, and/or gender-specific effects on the HPA stress response. At present, most maternal separation research has investigated effects on adult male rats. The purpose of the following experiments was to investigate the effects of early maternal separation on female rats in terms of behavioral and HPA responses to novelty (open field arena) at two different developmental periods, specifically during the pre-pubertal juvenile period and during adulthood.

In adult male rats, repeated maternal separation from mother and nest during the SHRP increases CRH mRNA, CRH content, ACTH, and corticosterone levels after stress ([3,25,26,31,47]; also see Table 1); however, the consistency of these effects depends on the type of stressor used, conditions of the separation procedure, and the age of testing [53]. For instance, in comparison to non-separated rats, male rats separated from the mother rat but not from littermates showed increased behavioral activity but lowered corticosterone in response to novelty during

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Table 1
A sample of the effects of early repeated maternal separation on corticosterone and anxiety-related behaviors in rats

Group	Gender	Effect	Reference (age of testing)
Corticosterone			
ED	Males	CORT: ED > H&NH basal and post-stress	3 (PND 45)
		No effect on CORT	25 (PND 105); 62 (∼PND 300)
ED	Males and females	Males, H > ED, NH&AFR for CORT post-stress, but no effect on females (restraint)	50 (∼PND 110)
		Males, no effect, but ED < NH for CORT post-stress (fear conditioned stimulus) for females	52 (adulthood)
MS	Males	MS > H for CORT post-stress	22 (PND 60–75); 24 (PND 90?); 31 (PND ∼90–120); 33 (∼PND 80); 48 (PND 60–75)
		MS > NH for CORT post-stress	31 (PND ∼90–120); 48 (PND 60–75); 58 (PND 40)
		MS < AFR for CORT post-stress	45 (PND 49)
		No effect on CORT	8 (PND 60); 28 (PND 600); 47 (∼PND 90–120)
MS	Males and females	Males, MS > AFR for CORT post-stress, no effect on females	74 (PND 120–150)
Anxiety-related behaviors			
ED	Males	ED&NH > H in exploratory test	3 (PND 45)
		No effect on OFA	43 (adulthood)
ED	Males and females	ED > NH activity in OFA in males	50 (∼PND 110)
		No effect of ED on males, but ED < NH anxiety in EPM for females	39 (PND 35)
		No effect on anxiety-related measures	62 (adulthood)
MS	Males	MS > AFR anxiety in EPM	8 (PND 60); 14 (PND 60); 22 (PND 60)
		MS < AFR anxiety in OFA	45 (PND 42)
		No effect on OFA	65 (∼PND 80)
MS	Males and females	Males, MS > NH&AFR anxiety in EPM, but females, MS < H&NH&AFR anxiety in EPM	24 (PND 90?); 74 (PND 120–150)
		Males, MS > NH activity in OFA, but females, only trend for same pattern	73 (∼PND 100)
		No effect on OFA	1 (PND 15); 28 (∼PND 85); 58 (PND 40)

Abbreviations: ED = early deprivation; separated from both mother and littermates. MS = maternal separation; separated from mother, but not littermates. H = handled; separated from mother, but not littermates for 15 min; also referred to as early handling. NH = non-handled; no handling/manipulations from birth to weaning. AFR = animal facility rearing; includes normal cage changing as per schedule within animal facility. PND: postnatal day. EPM = elevated plus maze. OFA = open field activity. CORT = corticosterone.

the juvenile period. In adulthood, similar increases in corticosterone after stress were seen for all groups [35]. This suggests an age-dependent effect of separation. In terms of anxiety-related behavior, the effects of repeated separation in male rats have been investigated using many tasks and are age-dependent, but generally, separation increases anxiety in the elevated plus maze and activity in the open field [1,8,14,24,28,39,60,65,73–75]. Some studies, however, have found no effect of separation on anxiety-related tasks [13,21,34,39,65,75] or a decrease in anxiety [46].

In terms of female rats, behavioral and endocrine effects are again inconsistent, but little research has addressed the effects of separation (from mother and nest, but not littermates; hence, 'maternal separation') or deprivation (of mother, nest and littermates; hence, 'early deprivation'). Early deprivation decreases the corticosterone response to some, but not all, stressors in female rats [50,52] while maternal separation has been found to be ineffective [67,74]. In female rats, maternal separation has been found to have no effect on anxiety-related behaviors [67], decrease anxiety-related behaviors [9,13,39,70], or increase anxiety-related behaviors [22,24,25,74].

Another factor that may contribute to these inconsistencies is the fact that corticosterone levels fluctuate over the estrus cycle with the highest levels seen during proestrus [2]. However, limited consideration has been given to fluctuations across the estrus cycle when looking at the effects of separation on the HPA axis and/or anxiety-related behavior in adult female rats [13,50,52,67,74].

As well as manipulation-specific effects, maternal separation may have effects that differ as a function of development. Male and female rats show an increase in gonadal hormones following puberty [7,10,54,72], with sex differences in open field activity appearing after puberty [36]. Responses to novelty also change with age [16,68,69]. Female rats, but not male rats, show an increase in basal corticosterone release and CRH mRNA levels with age [72] creating gender differences in HPA axis function [23,29,59,71,72]. Since maternal separation affects stress and the HPA axis changes with age, it is likely that the effects of separation will also change with age. This pattern was, in fact, found by Marin and Planeta [35] with separated male rats showing increased activity and lowered rise in corticosterone in

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