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Chronic stress effects on memory: sex differences in performance and monoaminergic activity

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Abstract

Increasing evidence suggests that the time course of advantageous versus deleterious effects of stress on physiologic function is also apparent in some brain functions, including learning and memory. This article reviews the effects of chronic stress on behavioral performance and, more importantly, shows that sex of the subject, as well as duration and intensity of stress, is an important determinant of the functional/behavioral, neurochemical, and anatomical consequences of the stress. Following chronic stress (7–28 days of restraint, 6 h/day), male and female rats were tested on a visual memory task (object recognition) and two spatial memory tasks (object placement and radial arm maze). At 21 days, stress impaired males on all tasks while females were either enhanced (spatial memory tasks) or not impaired (nonspatial memory tasks). Additionally, the influence of the hypothalamic–pituitary–adrenocortical axis in mediating the sex-specific responses to stress is considered. Behavioral and neurochemical assessments following chronic stress in ovariectomized females, with and without estradiol, suggest that estrogen exerts both organizational and activational influences on the observed sex differences in response to stress. Furthermore, stress differentially affected central transmitter levels in the frontal cortex, hippocampus, and amygdala depending on sex. The possible role of these sex-specific changes in neurotransmitter levels in mediating behavioral differences in response to stress is discussed. While these results are thus far limited to a few studies and require both further investigation and verification, chronic stress appears to be associated with distinct, sex-differentiated behavioral/cognitive and neurochemical responses. We conclude that sex differences must be taken into account when investigating or describing stress and associated sequelae.

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Introduction

The experience of stress is largely mediated by the hypothalamic–pituitary–adrenocortical (HPA) axis, and the HPA is sexually differentiated. Sex differences are evident in basal levels of HPA secretions; female rats have higher resting levels of corticosterone (CORT) (Critchlow et al., 1963) and display greater diurnal changes in both adreno-

corticotropin and CORT than males (Handa et al., 1994). A primary stress-induced physiological change in HPA activity is an increase in glucocorticoid (GC) levels. In comparison to males, female rats have higher GC levels following stress (Critchlow et al., 1963; Galea et al., 1997; Handa et al., 1994). These sex differences in CORT levels are responsive to the hypothalamic–pituitary–gonadal axis, as GC secretion fluctuates over the estrous cycle, with highest levels achieved on proestrus when ovarian secretions are high (Burgess and Handa, 1992; Carey et al., 1995; Viau and Meaney, 1991).

Sex differences are present not only in the HPA control of the stress response, but also in behavioral (Beck and

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Luine, 1999, 2002; Bowman et al., 2001; Luine et al., 1994, 1996), morphological (Galea et al., 1997; Watanabe et al., 1992a, b), and neurochemical (Beck and Luine, 1999, 2002; Luine et al., 2002; Mendelson and McEwen, 1991) responses to stress. In general, short periods of stress are adaptive and longer periods of stress prove maladaptive to male rats when tested on certain visual and spatial memory tasks (Conrad et al., 1996; Luine et al., 1994, 1996, 2002; McLay et al., 1998; Mizoguchi et al., 2000). Females appear less sensitive than males to the impairing effects of stress and show enhanced performance following the same stress duration that induces impairments in males (Bowman et al., 2001). While it is unclear what mechanisms are mediating these sex-specific stress responses, we have recently shown that circulating levels of estradiol are one important contributor to sex differences in the stress response (Bowman et al., 2002a).

Interestingly, differences among stress, sex, and memory extend beyond the rat model. Wolf and colleagues (2001) examined the influences of psychosocial stress and sex on memory in young adults and observed that stress-induced CORT enhancements were correlated with impaired memory performance for the stressed male, but not female, subjects (Wolf et al., 2001). In response to a psychosocial stressor, elderly men show larger HPA responses (e.g., ACTH, salivary free CORT, and plasma levels of total CORT) than elderly women (Kudielka et al., 1998). Furthermore, it has been observed that there is a sex-dependent lateralization of amygdala participation in emotionally influenced memory in men and women (Cahill et al., 2001).

This paper focuses on recent work from our laboratories demonstrating distinct sex differences in response to chronic stress on performance of both spatial and nonspatial memory tasks. Possible mechanisms, including hormonal and neurochemical substrates, as well as performance parameters underlying the sex-specific stress responses are presented and discussed.

Chronic restraint stress as a model for assessing functional effects of stress

Recent studies have considered how the stress response differs following various types of stressors. Broadly speaking, stressors can be categorized as either psychogenic, which are mainly psychological (e.g., exposure to a predator or a novel open field), or neurogenic, which are mainly physical but have psychological ramifications (e.g., foot shock, cold swim, immobilization). Some stressors, like restraint stress and overcrowding, have elements of both types. Restraint has psychogenic elements in that it is not physically painful, but unlike a purely psychogenic stressor, restraint involves a physical component that limits the response/defensive style of the subject (McIntyre et al., 1999). The combination of psycho- and neurogenic components suggests that overcrowding and restraint stress may result in

widespread morphological and neurochemical, and ultimately functional, changes in the brain.

In relation to CORT release after various stressors, there is no obvious trend for any one stressor type to cause greater release. It is, however, difficult to compare the intensity of the stimulus between all the types. Rivier (1999) found similar CORT levels following both footshock and alcohol: females had approximately 400 ng/ml of circulating CORT following each stressor while males ranged from 2 to 300 ng/ml. Likewise, Anisman et al. (2001) compared CORT levels in mice exposed to a rat, fox odor (psychogenic), restraint, footshock, coldswim, acoustic startle, or open field (neurogenic) and found more similarities than differences in circulating levels. Thus, a variety of commonly applied stressors are effective in causing release of CORT.

Studies in our laboratories have focused on the effects of chronic stress using daily restraint, which reliably activates the stress response through limbic forebrain circuits (Herman and Cullinan, 1997). Subjects are placed in a Plexiglas tube, 2 1/2 in in diameter and adjustable for body length, which allows only limited head and limb movement. Subjects stressed for 6 h daily remain active and healthy for a month without any physical symptoms or debilitations like those that are present in extended shock paradigms (Luine et al., 1994; Watanabe et al., 1992a). These considerations are critical when evaluating stress effects on cognitive function. Use of restraint stress to study learning and memory is also advantageous because it has been well characterized in terms of CORT secretion patterns, morphological and neurochemical correlates, and functional consequences (for review and discussion see Luine, 1994, 2002).

Stress, sex, and cognitive function

Both acute and chronic stress result in sex-dependent behavioral responses. For example, acute stress facilitates classical conditioning in male rats but is associated with impairments in females (Wood and Shors, 1998). Specifically, acute stress impairs acquisition of the conditioned response in females, but the stress-induced impairment can be blocked through either ovariectomy or administration of Tamoxifen, an estrogen antagonist (Wood and Shors, 1998). Furthermore, these sex differences are also apparent in trace conditioning performance, a hippocampus-dependent task (Wood et al., 2001). Basic nonassociative learning processes are also affected by stress. Male acoustic startle responses show a sensitized whole-body startle between 4 and 10 days following stress (Servatius et al., 1995), whereas female rats do not (Beck et al., 2002).

Chronic stress and spatial memory—Radial arm maze

Following application of the chronic stress paradigm as previously described, distinct patterns of sex differences in the performance of both spatial and nonspatial behavioral

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