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Gender-specific effects of prenatal stress on emotional reactivity and stress physiology of goat kids

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Abstract

The aims of this study were to investigate the effects of maternal stress during pregnancy on the emotional reactivity, the hypothalamo–pituitary–adrenocortical (HPA) axis, and the sympatho-adrenomedullary (SAM) system of goat offspring according to their gender, and to investigate the role of maternal cortisol in prenatal stress effects. Goats were exposed to ten transports in isolation or ten ACTH injections (0.125 IU/kg body weight) during the last third of pregnancy. Control goats remained undisturbed. No effect of repeated transport during the last third of pregnancy was found on basal cortisol concentrations of the offspring. However, an increase in phenylethanolamine N-methyl transferase activity in the adrenals was observed in prenatally stressed kids compared to control kids ($P = 0.031$). In the presence of novelty, prenatally stressed female kids were more active ($P = 0.049$) than control females; they also showed more signs of arousal ($P = 0.039$) and tended to explore more of their environment ($P = 0.053$) in reaction to a startling stimulus. On the contrary, prenatally stressed male kids tended to be less active ($P = 0.051$) than control male kids but showed more signs of distress ($P = 0.047$) in the presence of novelty. Intermediate effects were found on the emotional reactivity to novelty of kids born from dams given injections of ACTH. In conclusion, transport stress in pregnant goats affects the sympatho-adrenomedullary system and the emotional reactivity of their offspring in a gender-specific manner. Moreover, the effects of prenatal transport and ACTH injections showed some similarities but differed in some critical details.

Keywords: Prenatal stress; Transport; Isolation; Emotional reactivity; HPA axis; SAM system; PNMT; TH; Goats; ACTH

Introduction

Stress during pregnancy can modify the development of behavior and the hypothalamo–pituitary–adrenocortical (HPA) axis of the offspring. It has been found in previous studies that the offspring of female rats subjected to stress throughout pregnancy showed significant behavioral differences from those born to control dams. The former was characterized by increased emotional reactivity in both juvenile and adult rats (Fujioka et al., 2001; Thompson, 1957; Weinstock et al., 1992), delayed development (Fride and Weinstock, 1984), impaired sexual behavior (Velazquez-Moctezuma et al., 1993), and modified learning ability (Fujioka et al., 2001; Lordi et al., 1997). Moreover, an increase in basal corticosterone concentration was observed in prenatally stressed rodents (Weinstock et al., 1998) as well as an increased corticosterone response to stressors (Henry et al., 1994) and prolonged corticosterone secretion after acute stress (Maccari et al., 1997; Vallée et al., 1997). In comparison to studies on the HPA axis, very few studies have investigated the effects of prenatal stress on the sympatho-adrenomedullary (SAM) system. Weinstock et al. (1998) found that prenatally stressed rats displayed higher plasma norepinephrine and dihydroxyphenylglycol

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concentrations than control rats immediately after foot-shock, indicating a greater activation of the sympathetic component of the autonomic nervous system. In contrast, a study on prenatally stressed piglets did not show any differences in catecholamine concentrations after immobilization stress between prenatally stressed and control piglets (Otten et al., 2001).

Most of the reported effects of prenatal stress have been studied in males (Barbazanges et al., 1996; Fujioka et al., 2001; Henry et al., 1994; Maccari et al., 1995; Rimondini et al., 2003; Takahashi and Kalin, 1991; Takahashi et al., 1992; Vallée et al., 1996). However, some studies have shown that prenatal stress can have gender-specific effects. Early reports on gender variation in response to prenatal stress were reviewed by Archer and Blackman (1971), but they concluded that gender-specific effects were inconsistent. In more recent reports, whereas results are not always consistent due to variability in the species and tests studied, females appear to be more sensitive than males to various behavioral effects of prenatal stress (Braastad, 1998). Studies on the gender-specific effects of prenatal stress on the HPA axis are more prolific and consistent than studies on behavior. Several studies indicate that the female HPA axis is more susceptible to prenatal influences while little effect of prenatal stress occurs in male offspring (Koehl et al., 1999; McCormick et al., 1995; Osadchuk et al., 2001). The adrenal corticosterone responses to stressors or basal corticosterone concentrations are greater in prenatally stressed females than in males (McCormick et al., 1995; Szuran et al., 2000; Weinstock et al., 1992).

Maternal glucocorticoids are considered to be good candidates for programming of the fetal HPA axis during prenatal stress (Matthews, 2002). To study their role, several approaches have been used. These involved maternal adrenalectomy and corticosterone injections in dams (Barbazanges et al., 1996), or injections of CRF (Williams et al., 1995), ACTH (Fameli et al., 1994; Haussmann et al., 2000; Holson et al., 1995; Lay et al., 1997), and dexamethasone or betamethasone (Dodic et al., 2002; Sloboda et al., 2002; Welberg et al., 2001). Nevertheless, only a few studies have compared within the same experiment the effects of the above physiological approaches to those of psychological stressors during pregnancy on the offspring (Holson et al., 1995; Lay et al., 1997). In addition, in most physiological approaches, stress hormones were given at pharmacological doses similar to what is used in clinical practice (Matthews, 2002).

Most of the studies on prenatal stress have been performed on rodents (for a review, see Braastad, 1998; Matthews, 2002) while very few have been performed on farm species such as sheep and goats. The marked developmental differences between these neonates highlight the value of comparative studies on this topic. Neonatal kids or lambs are highly precocious in comparison to rat pups. In goats and more generally in ruminants, neurological and neuroendocrine development occurs mainly during fetal life (Dobbing and Sands, 1979; Richardson and Hebert, 1978). At birth, the HPA axis of lambs and goat kids is nearly mature and the onset of sensory functions occurs before birth as is the case for human fetuses (Pierson et al., 1995; Schaal et al., 1995; Vince and Armitage, 1980). Moreover, ruminants show a different placental structure compared to rats with a placentation characterized as epitheliochorial with caruncles separated by larger areas of endometrium (Faber et al., 1992; Silver, 1990) whereas that of the rodent is hemoendothelial. Therefore, the ruminant placenta offers a more significant barrier to maternal hormonal influences. In relation to this maturation and placenta structure, consequences of prenatal stress may differ between rodents and ruminants.

There were several aims in this study on the effects of prenatal stress in goat kids: to confirm that repeated exposure to prenatal stress results in alterations in the emotional reactivity and the HPA axis; to determine if prenatal stress also altered the SAM system; to investigate gender effects; and to investigate the role of maternal cortisol in prenatal stress effects on their offspring. ACTH injections were used at a physiological dose to simulate the maternal cortisol response to stress. Since transport and isolation are known to be very stressful experiences for farm animals, they were used as stressors in this study. Indeed, in the goat, an immediate increase in plasma concentrations of epinephrine after the start of transport has been observed together with a rise in cortisol which remains high throughout the duration of transport (Duvaux-Ponter et al., 2003; Nwe et al., 1996). Emotional reactivity was assessed in kids by exposing them to social isolation, novelty, and a startling stimulus. Social isolation is stressful to domestic ungulates, which have a strong tendency to flock (Fisher and Matthews, 2001). Likewise, the exposure to a novel environment or to a novel object elicits behavioral arousal which is similar to that induced by a nociceptive stimulation such as an electric shock (Dantzer and Mormède, 1983). Startling stimulus tests have also been widely used in farm animals to study their emotional reactivity (Boissy and Bouissou, 1995).

Materials and methods

Goats

Animals and treatments during gestation

Concerning animal welfare and the use of experimental animals, this work was conducted under the guidelines developed by the French Agriculture Ministry. Twenty-three Alpine and eighteen Saneen dairy female goats were selected for the experiment. They were synchronized prior to mating in order to give birth within a period of 7 days. Two months before parturition, the goats were assigned to one of three treatments according to their body weight, breed, parity, and the buck used for mating. The three treatments were transported (TRAN, n = 13), ACTH-