Maternal social stress modulates the development of prepulse inhibition of startle in infants

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ABSTRACT

Background: Stress during rearing has negative effects on the maturation of information processing in rodent offspring, but similar evidence in humans is absent. Prepulse inhibition (PPI) of startle is a measure reflecting the integrity of information processing. PPI does not depend on active cooperation, making it a suitable measure for studying newborns and infants. This study investigated whether postnatal development of infant PPI is influenced by self-reported stress in the mother.

Methods: 49 healthy term-born infants were studied twice, four days after birth and again at four months. PPI was assessed by presentation of acoustic startle stimuli (95 dB) either alone or preceded (SOA 120 ms) by a prepulse (75 dB). Mother’s social stress levels were assessed with the modified Trier Inventory for the Assessment of Chronic Stress (TICS). Cortisol saliva samples were collected from mothers and their children.

Results: ANOVA revealed a different development of PPI in infants whose mothers reported enhanced stress levels due to social isolation and reduced social recognition. Cortisol levels were related to mothers’ self-report stress, but not to PPI development in infants.

Conclusions: Maternal stress experience has an impact on the maturation of human infants’ information processing in the first four months after birth.

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1. Introduction

The ability to protect the processing of stimulus information from interruption by subsequent high intensity sensory input represents a fundamental cognitive skill. A deficiency in this ability may lead to disrupted and incomplete information processing, sensory flooding, and maladjusted behavior (Braff et al., 2001). Prepulse inhibition (PPI) of the startle reflex is an operational measure of sensorimotor gating, and it has been demonstrated in many animal species, including humans. Startle does not depend on a specific sensory modality, nor is it limited to a specific motor response. However, acoustic stimulation is most commonly used to elicit startle, and eyeblink EMG (electromyographic activity) is the measure that is most sensitive and resistant to habituation. The reflexive startle eyeblink response to an abrupt, and intense (e.g. 95–110 dB) acoustic noise burst (pulse) is inhibited when a weak (e.g. 60–85 dB) acoustic stimulus (prepulse) precedes the startle stimulus at a short (e.g. 60–300 ms) stimulus onset asynchrony. PPI is a reliable and robust finding in healthy humans (Graham, 1992), and can be assessed during sleep (Hoffman et al., 1987). PPI may be useful as an index of information processing in a wide

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variety of psychological disorders, but also across levels of personality characteristics, and other individual differences (Franklin et al., 2009a). An impaired inhibition of the startle blink reflex has repeatedly been reported in patients with schizophrenia (Bruff et al., 2005; Quednow et al., 2008); however, the PPI deficit is not specific to this disease, and is diminished in other psychiatric disorders (Franklin et al., 2009b), as well as in human newborns. It is known that PPI is already present in human neonates and children (Anday et al., 1988; Blumenthal et al., 1987; Ornitz et al., 1991) but that it is weak in neonates and children compared to adults (Graham et al., 1981; Ornitz et al., 1986, 1991). Under normal circumstances PPI will increase with age until about 10 years (Gebhardt et al., 2011).

Startle and PPI measurements are well established in animals. Indeed, the animal models serve to experimentally study stress and bio-social impact on PPI. Startle in rats is not measured by EMG but usually as a startle reaction of the entire body (ballistic movement). Animal studies have demonstrated that early life stress in the postnatal period, caused by reducing the quantity of mother-infant and infant-infant social interactions through maternal separation or isolation of rat pups from peers, may lead to PPI deficits (Cilia et al., 2005; Day-Wilson et al., 2006; Ellenbroek et al., 1998). Furthermore, maternal caregiver quality plays an important role, and rat pups of mothers with low caregiver behavior exhibited weaker PPI than pups of high caregiving mothers (Zhang et al., 2005). The caregiver behavior is worse in rat mothers who themselves experienced maternal deprivation (Lovic and Fleming, 2004), and crossfostering procedures confirm a negative impact of mother's own stress experience on PPI of their offspring (Ellenbroek and Cools, 2002).

However, to date, there are no human studies investigating the association between early life stress and PPI development. Since the newborn’s own coping strategies are still very limited, the principal caregiver, usually the mother, plays the most important role in buffering or aggravating early life stress. Not surprisingly, maternal parenting practice may be affected by stress. Indeed, human studies show a negative influence of emotional stress on mothers’ caregiver behavior, with less maternal warmth and less flexibility (Assel et al., 2002; Crnic et al., 2005). Also, adverse life events, daily hassles, and social conflicts have a negative impact on parenting and child development (Crnic et al., 2005; Webster-Stratton and Hammond, 1999).

After birth, mothers need to adapt to a new physically, emotionally and socially demanding situation. It is crucial to know how mothers appraise the specific demands of the postnatal period and the available social resources (Lazarus, 1993). On the one hand the social networks with partner, relatives, and friends have been shown to positively affect maternal stress experience, by providing emotional and material support, and thus, foster resources to deal with everyday stress and stabilize mood (Brugha et al., 1998; Quittner et al., 1990). On the other hand, the experience of overwhelming, overprotective, intrusive, or abusing relationships may be a source of social stress (Coyne and DeLongis, 1986; Wahler, 1980). In either case, social circumstances may have a major impact on the mothers’ stress level as well as, directly or indirectly, on mother-child interaction and thus, potentially, on child development (Adamakos et al., 1986; Wahler, 1980; Webster-Stratton and Hammond, 1999).

The present longitudinal investigation aimed to test whether the mothers’ self-reported chronic social stress is associated with impaired development of their infant’s PPI. For this purpose, infants’ PPI was measured twice; once a few days after birth and again four months later. We expected an increase in PPI from birth to four months due to maturation, and that maternal stress would affect this maturation. Maternal chronic stress experience was assessed twice by validated questionnaires. Additionally, we analyzed maternal and infant salivary cortisol concentration, as indicators of biological stress system activity.

2. Methods and materials
2.1. Participants

This study was approved by the local ethical Committee and 78 mothers gave their informed consent before delivery. All mothers were recruited in the Hospital of Bühlach, Switzerland. Prenatal exclusion criteria were maternal smoking, drinking (>57 g per week), eclampsia, diagnosed mental disorder, and requirement for regular medication because of a chronic illness or psychiatric disorder in the last two years. Participants with problematic physiological measurement, due to technical problems or excessive signal noise because of movements during both the first and the second PPI assessment, were excluded from analysis (not available for second test: n = 6; technical failure: n = 3; not sleeping during first or second test: n = 7). Further, participants defined as non-responders (startle response probability <.2) in the first or second PPI assessment were excluded from analysis (first test: n = 6; second test: n = 7). The final sample consisted of 49 mothers, and 19 girls and 30 boys. Mean age of mothers was 33.88 years (SD = 4.84 years), and for 17 mothers it was the first child. The babies were born at gestational week 39.64 (SD = 1.72), with a mean birth weight of 3481.22 g (SD = 578.36 g). All newborns had a normal adaptation after birth and were routinely checked for inner ear health in the hospital two days after birth by Otoacoustic Emissions (OAE).

2.2. Measurement and quantification of startle blink and PPI

Infants’ startle blink reflex and PPI were measured twice within four months, a few days after birth (mean: 4 days, range: 2–12 days) in a quiet hospital room, and again after four months (mean: 17 weeks, range: 15–19 weeks) at the participants’ home.

The babies were fed and lying in their sleep crib in a sleeping bag. After they fell asleep, the skin below the lower eyelid was cleaned with a dry towel. Electromyographic (EMG) electrodes (Ag/AgCl, 4 mm contact area) filled with conducting gel were placed below the right and left eye over the orbicularis oculi muscle. Two different acoustic stimulation sequences were unilaterally presented by holding a headphone over one ear. Presentation side was
randomized and counterbalanced between participants, and each participant heard the same sequences at the first and second assessment.

During a short habituation sequence, six startle stimuli (white noise, 95 dB, 50 ms duration, 0.1 ms rise and fall time) were presented with an average inter-trial interval of 15 s (range: 13–17 s). In the PPI sequence, twelve startle stimuli (95 dB, 50 ms duration, 0.1 ms rise and fall time), twelve prepulses (75 dB, 50 ms duration, 0.1 ms rise and fall time) and twelve pairs of prepulse-startle stimuli were presented alternately (inter-trial interval 13–17 s). In the prepulse–startle stimulus pair the prepulse preceded the startle stimulus with an onset to onset interval (stimulus onset asynchrony) of 120 ms. All stimuli were presented in blocks in which each stimulus condition was presented once. The order within and between blocks was counterbalanced. Both assessments were only done when babies were asleep. The measurement was stopped when the babies awoke and continued after they fell asleep again.

Dasylab 8.0 software was used to assess infants’ eyeblink responses. The raw EMG signal was sampled at a rate of 1000 Hz (16 bit resolution), band-pass filtered at 10–500 Hz (hardware), and then high-pass filtered at 20 Hz (cutoff) by software. After rectifying the raw signal, it was integrated with a time constant of 5 ms. A customized C++ based semi-automated PC-program running on a WinXP platform analyzed the eyeblink responses offline, which were then manually checked for artifacts. A response with an onset within a time window of 20–150 ms after stimulus onset was accepted. If the response was not in the typical time window of a participant, response magnitude was set to zero. In case of artifacts, such as excessive noise, movement, or other muscular activity, the trial was set to missing.

In the habituation sequence, magnitudes, including zero-responses (Blumenthal et al., 2005), of the ipsilateral recording side were log-transformed, and then averaged across trials. In the PPI sequence, the ipsilateral mean (not log-transformed) magnitudes to startle stimuli alone and prepulse–startle stimuli pairs, respectively, were calculated. In order to detect an inhibitory effect, a minimum number of responses to startle stimuli alone were necessary. Therefore, participants with a response probability to startle stimuli alone below 0.2 were excluded from the analysis (see above). Percent PPI was calculated by the formula: (magnitude prepulse–startle stimulus pair – magnitude startle stimulus alone)/magnitude startle stimulus alone * 100.

2.3. Assessment of chronic stress: TICS

Two months (mean 9 weeks, range 6–14 weeks), and four months (mean 16 weeks, range 14–20 weeks) after birth, mothers filled in the Trier Inventory for the Assessment of Chronic Stress (TICS) (Schulz et al., 2004). The original questionnaire includes 57 items on nine scales. The TICS is a reliable and valid questionnaire to assess different aspects of chronic stress. It has been used in different age groups, and it was found to be related to cortisol responses in adults (Rieger et al., 2004; Wust et al., 2000). It has also been used in pregnant women, but was not designed for the special demands of labor and delivery. Thus, the scale ‘chronic worries’ was a priori deleted from analysis. For the remaining scales mothers had to appraise, on a five-point rating scale, how often they experienced different stress situations within the last two months, for the first and second assessment separately in order to cover the time between birth and four months postpartum. All mothers were on maternity leave. However, the duration of the maternity leave was variable, and ranged between 8 weeks and several months. Therefore, the four TICS scales directly related to the work situation: ‘work overload’, ‘work discontent’, ‘pressure to succeed’, and ‘excessive work demand’ were deleted from analysis. The four remaining scales were all related to social stress: ‘social overload’ (overinvolvement in others’ concerns), ‘lack of social recognition’ (absence of recognition and reward for engagement), ‘social conflicts’, and ‘social isolation’ (lack of social contacts and loneliness). TICS scale values were averaged over both assessments.

2.4. Salivary cortisol sampling and quantification

At two months after birth, mothers were sent the material for salivary cortisol sampling at home. Mothers were asked to collect their own and their infants’ saliva samples at home on three consecutive days according to a prescribed time schedule. Mothers were instructed to take their first saliva sample immediately after awakening, then 30 min, 45 min, and 60 min thereafter, and again at 3 p.m. and 8 p.m., using Salivette tubes (Sarstedt, Germany). Sampling of infants’ saliva had to be 30 min after awakening of the baby and before feeding at any time of the day, but on the same day of mothers’ sampling. Mothers were instructed to use disposable cotton swabs (Visisponge Eye Sponge, Becton Dickinson, USA), and then to put them into Salivettes. Sampling of saliva from mothers and infants was done nine weeks after birth (range: 7–14 weeks), and infants’ sampling most often in the morning (day one: 79%, day two: 68%, day three: 61%). Morning and afternoon cortisol concentrations of the infants did not differ. Cortisol concentration was determined by immunoassay with fluorescence detection (Dressendorfer et al., 1992). Because of insufficient saliva or deviation from instructions, samples of eight mothers and twelve infants could not be analyzed. Maternal daytime (all 6 samples of the day) and awakening (samples 1–4) cortisol levels were aggregated to calculate the area under the curve with respect to ground (AUCG, with time in minutes) for each day (Pruessner et al., 2003) and then averaged across the days. The AUCG informs about the average cortisol level and not about the time course over the day. Cortisol concentrations of the infant samples were averaged across the three days.

2.5. Statistical analysis

The aim of this study was to identify statistical interactions of postnatal stress factors with infant PPI development. Therefore, mother–child pairs were selected according to the median stress factor level (split-half) yielding ‘high’ and ‘low’ stress factor groups (GROUP classification factor). This was done for each of the four
psychometric TICS stress scales 'social overload', 'lack of social recognition', 'social conflicts', and 'social isolation', respectively. The dependent variable 'infant PPI' was subjected to mixed design ANOVAs suitable for repeated measures (within factor TIME: four days after birth vs. four months; between factor GROUP: high vs. low stress), and TIME main effects, GROUP main effects, and TIME × GROUP interactions were tested. Because of the limited number of a priori defined statistical tests no adjustments (e.g. Bonferroni corrections) due to multiple testing were performed. In a similar way, the influence of mother and child cortisol values on PPI development was tested. Gestational age was always assigned as a covariate to control for prenatal maturation. Pearson’s correlations were used to analyze TICS and cortisol stability, as well as associations between TICS scales and cortisol data. Paired t tests and repeated measures ANOVAs were used to test time trends of the TICS scales and cortisol, as well as the significance of infant PPI data at each assessment time point (four days and four months). Analyses were performed with SPSS 16.0 (SPSS, Inc., Chicago, IL, USA), and the significance level was set to p < .05.

3. Results

3.1. PPI development and impact of stress factors

Mean results of PPI and startle data are presented in Table 1. PPI was significant both four days after birth (t = −2.03, p = .048) and at four months (t = −4.74, p = .001). PPI significantly increased from near birth to four months, F(1,47) = 4.23, p = .045, with no difference between girls and boys at any time point, nor a gender × time interaction. Startle significantly decreased in the first four months, F(1, 45) = 49.83, p = .001, with no gender effect or gender × time interaction.

For the TICS scale 'lack of social recognition' ANOVA of time (within factor: 4 days after birth vs. four months) and group (high vs. low 'lack of social recognition') revealed a group × time interaction F(1,46) = 5.24, p = .027, η²partial = 0.10, indicating that infants of mothers reporting more social recognition developed more PPI than infants of mothers having less social recognition (Fig. 1). There was no group main effect. Post hoc group comparisons between the group of more and less stressed mothers at four days and four months after birth separately did not show significant differences of infant PPI. Post hoc t-test revealed a significant time effect within the group of less-stressed mothers (t = −3.24, p = .004), but no time effect for the group of more stressed mothers.

For the TICS scale 'social isolation' ANOVA of time (within factor: 4 days after birth vs. at four months) and group (high vs. low 'social isolation') revealed a group × time interaction F(1,46) = 5.06, p = .029, η²partial = 0.10, indicating that infants of mothers reporting less social isolation developed more PPI than infants of mothers having more social isolation (Fig. 2). There was no group main effect. Post hoc group comparisons between the group of more and less stressed mothers at four days and four months after birth separately did not show significant differences of infant PPI. Post hoc t-test confirm a significant time effect within the group of less-stressed mothers (t = −2.87, p = .009), and did not show a time effect for the group of more stressed mothers again.

There were no time × group interaction effects nor main effects for the TICS scales 'social overload' and 'social conflicts', nor for maternal and infant cortisol data.

Table 1
Startrle eyelink analysis. Means and standard error (SE) of startle eyelink magnitude (µV) and probability in the habituation sequence, and of magnitude (µV) and percent PPI in the prepulse inhibition assessment sequence. Results are shown for the assessment shortly after birth and at four months separately.

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<td>Magnitude (µV)</td>
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<td>Probability</td>
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<td>Assessment PPI</td>
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<tr>
<td>Magnitude startle alone (µV)</td>
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<td>Percent PPI</td>
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Fig. 1. Social recognition and PPI development. Interaction between percent prepulse inhibition four days after birth and at four months (with standard error) × mothers with more and less social recognition.

Fig. 2. Social isolation and PPI development. Interaction between percent prepulse inhibition four days after birth and at four months (with standard error) × mothers with low and high social isolation.
3.2. TICS and maternal and infant cortisol levels

Pearson correlation showed that all TICS scales at two months after birth were significantly correlated with the corresponding scales at four months \((r > 0.6, p = .001)\). The scores of the scale ‘social overload’ decreased over time \((t = 2.71, p = .009)\), whereas all other scales remained unchanged. The score averaged over the two time points for the scale ‘social overload’ was \(M = 10.4 (SD = 3.5)\), ‘lack of social recognition’ \(M = 4.1 (SD = 2.8)\), ‘social conflicts’ \(M = 4 (SD = 3.2)\), and ‘social isolation’ \(M = 6.1 (SD = 4.1)\).

Maternal and infant cortisol levels for all sampling days are presented in Table 2. Maternal cortisol concentrations showed the expected diurnal rhythm with high morning and low evening values, \(F(5,36) = 212.49, p = .001\).

Maternal awakening cortisol levels were positively related to infant mean cortisol levels averaged over the three days \((r = .33, p = .047)\), and there was only a weak positive statistical association for a positive relation between maternal mean daytime cortisol level and infant mean cortisol level \((r = .31, p = .065)\).

The TICS scale ‘lack of social recognition’ was positively related to maternal mean daytime cortisol level, \(r = .34, p = .028\), but other scales were not. TICS scales did not correlate with infant cortisol levels.

4. Discussion

This study is the first to demonstrate in humans that mothers’ stress experience is linked to a different development course of their infants’ PPI. We compared infants of mothers who reported higher stress experience to infants whose mothers reported lower stress experience. The resulting PPI increase in the infants of mothers who reported higher stress experience was smaller than of infants from the unstrressed group.

Animal studies have demonstrated impaired PPI after disturbance of the mother–infant interaction or poor maternal caregiver behavior during the postnatal period (Ellenbrook et al., 1998; Zhang et al., 2005). The present results extend these findings in that human mothers’ chronic social stress was related to a different development of infants’ PPI. Infants of mothers reporting less ‘social recognition’ and higher ‘social isolation’ developed less PPI during the four months after birth than did infants of mothers with higher ‘social recognition’ and less ‘social isolation’. However, in this study, PPI did not significantly differ between groups shortly after birth or at four months. This has to be investigated in future studies with more participants and additional PPI assessment time points. Also, the animal development during the postnatal period is not directly transferable to human development. In rats, the first days and weeks after birth may correspond rather to a prenatal developmental stage in humans (Ellenbrook et al., 2004). Hence, from a developmental perspective, postnatal rat pup stress may be comparable to prenatal human fetal stress.

The quality and quantity of a mother’s social network are important predictors of parenting behavior (Adamakos et al., 1986; Goldstein et al., 1996), which is generally linked to child development (Webster-Stratton and Hammond, 1999). The birth of a child is a joyful event for many parents, yet the first months after birth are characterized by several adaptation and readjustment processes and can be perceived as stressful. Supportive relationships may indirectly influence parenting, and thereby the development of the child, by reducing maternal depression and parental stress (Adamakos et al., 1986; Brugha et al., 1998; Quitner et al., 1990). The recognition of the mother’s engagement and effort are part of an emotional support system and may enhance the mother’s sense of self-efficacy, a central component of parenting competence (Jones and Prinz, 2005). Parental self-efficacy has been shown to be influenced by the quality of the marital relationship and to mediate the influence of social support on parenting (Teti and Gelfand, 1991). On the other hand, the negative effect of social isolation does not only reflect the lack of support but may also be a cause of stress. It has been shown that on days when mothers had less frequent social contacts, they behaved more aversively towards their children, and the children behaved more oppositionally than on days with more social contacts (Wahler, 1980).

Previous research has shown that PPI increases during childhood as the individual matures (Blumenthal et al., 1987; Hoffman et al., 1987; Ornitz et al., 1991). The present study corroborates these findings and indicates a significant increase of PPI from 11% four days after birth to 26% at four months. The inhibition found at four months of age is comparable to that of other studies which found PPI of about 25% in infants aged four to six months (Graham et al., 1981), but it is still less than the corresponding values in adults (Ornitz et al., 1991).
Mothers’ cortisol levels were positively correlated to the TICS scale ‘lack of social recognition’, supporting results from previous research (Wust et al., 2000). There was a correlation between mothers’ awakening and infants’ cortisol levels, and no significant correlation between the mothers’ TICS scales and infants’ cortisol levels. In this study neither maternal nor infant’s cortisol levels were related to PPI development. However, an increase in sample size and/or more frequent assessment of maternal and infant cortisol data may be necessary to study cortisol effects in greater detail. Furthermore, the short time window we used in this study may have made it difficult to detect a modulating effect of cortisol levels on PPI. Infants in the first few months do not yet have a circadian cortisol rhythm and display great variability between days and weeks, possibly contributing to a weak mother–infant correlation (De Weerth and Van Geert, 2002). Nevertheless, there is some evidence that children growing up in an adverse environment exhibit less daytime variability in cortisol secretion than when growing up in a ‘regular’ family (Carlson and Earls, 1997; Gunnar et al., 2001), and have elevated cortisol levels (Essex et al., 2002). Mother-deprived rats have increased release of corticotropin releasing hormone (CRH) (Plotksy et al., 2005), and an increase in CRH may diminish PPI (Conti et al., 2002). There is evidence that PPI and the HPA axis are altered in patients with schizophrenia (Quednow et al., 2008; Walder et al., 2000). However, there are also conflicting results (Czyrak et al., 2003), and other endocrinological systems may play a role as well (Swerdlow et al., 2001).

The present study found a decrease in startle magnitude in the first four months. The startle eyeblink reflex is a brainstem response, and in the first months after birth some brainstem related reflexes weaken, e.g. the grasping reflex (Lantz et al., 1996). The disappearance of these behaviors has been discussed in terms of midbrain, limbic, or cortical structures and pathways that show dramatic increases in maturation in this time span and inhibit brainstem functioning (Herschkowitz et al., 1997). It has been suggested that the startle reflex is also modulated by higher brain structures (Koch, 1999). For example, lesions of the amygdala result in an increased startle response and lesions of the medial prefrontal cortex or the hippocampus may impair PPI of the startle reflex (Bast and Feldon, 2003; Daenen et al., 2003; Koch and Bubser, 1994; Swerdlow et al., 2001). These forebrain structures may also contribute to the startle magnitude reduction during PPI (Swerdlow and Geyer, 1999). The fact that higher structures can modulate startle is supported by the present reduction in startle magnitude over the first four months of life, since PPI increases and startle magnitude decreases, suggesting that maturation of higher structures result in tonic inhibition of the lower brainstem structures.

Animal studies have linked early disadvantageous environments to later PPI deficits (Cilia et al., 2005; Zhang et al., 2005), and thereby provide a model, in which early environmental conditions may influence neurodevelopment with long-term consequences. Our study corroborates these findings in showing that maternal stress indeed influences the development of this commonly used measure of sensorimotor gating. Sensorimotor gating deficits have been shown in psychiatric disorders, such as schizophrenia and behavior problems (Braff et al., 2001). It is tempting to conclude, that our results link maternal stress to behavioral disorders in humans. However, long-term studies, integrating prenatal and perinatal factors, are needed to disentangle the role of early maternal stress on behavior problems and cognitive processing in later years.

4.1. Conclusion

In summary, the present study showed that mother’s social stress experience is linked to the development of PPI in infants from near birth to four months. During this time PPI increases as a result of maturing inhibitory brain structures. Our data may suggest that the maternal perception of ‘social isolation’ and ‘social recognition’ could have consequences on these maturation processes, or that the neurological development in an infant is in some way related to susceptibility to stress in mothers. It remains to be investigated whether these effects are long-lasting.

Conflicts of interest

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