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The impact of maternal cafeteria diet on anxiety-related behaviour and exploration in the offspring

Thomas Wright [a], Simon C. Langley-Evans [b], Jörg-Peter Voigt [a,*]

[a] School of Veterinary Medicine and Science, University of Nottingham, Sutton Bonington, Loughborough, LE12 5RD, United Kingdom
[b] School of Biosciences, University of Nottingham, Sutton Bonington, Loughborough, LE12 5RD, United Kingdom

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ABSTRACT

Contemporary trends in obesity mean that research into whether unbalanced diets could impact on behavioural traits became increasingly important. The timing of exposure to obesity is particularly important, as sensitive periods during development have been identified where dietary extremes play a critical role in determining adult risk of physiological dysfunction. To this end, female Wistar rats were fed on chow or cafeteria diet (CD) for 8 weeks from weaning until mating. Half of the mated animals within each group were crossed-over to the alternative diet. This generated four treatment groups, differing in their pre-gestational and gestational diets. After birth, offspring of dams from each of the 4 pregnancy groups were further divided into groups, either being fed chow or CD throughout lactation. Anxiety-related behaviour and exploration in the offspring were tested in the Elevated Plus Maze (EMP) and the Open Field (OF) at 10 weeks of age. Maternal obesity significantly reduced the EPM locomotor activity in male and female offspring and grooming in males. Lactational CD had an anxiolytic effect in male offspring as shown in the EPM (increased entries into and more time on open arms) and the OF (shorter latency to enter the centre). In both sexes, lactational CD reduced grooming upon exposure to the EPM and the OF. Post mortem analysis revealed a stimulant effect of lactational CD on adipose tissue growth. The present study demonstrates that pre-gestational, gestational and lactational maternal CD programme behaviour in the offspring with lactational CD reducing anxiety in the male offspring.

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1. Introduction

Research over recent decades has provided evidence for a dietary impact on brain neurotransmitter synthesis and release. In particular, this research focused on the role of amino acid precursor molecules of nutritional origin, as the aromatic amino acids tryptophan and tyrosine which give rise to serotonin and the catecholamines, respectively [1]. Augmented serotonin synthesis following carbohydrate intake exemplifies how nutritive supply can possibly relate to brain functions. Although the biochemistry of this process is well understood and described elsewhere [2], for a discussion of the behavioural effects of dietary precursor molecules it might be particularly important that test meals usually consist of carbohydrates, fats, proteins and micronutrients, in variable proportions. In fact, microdialysis experiments in rats revealed that all differ in their effects on postprandial brain serotonin release [3]. The example of serotonin demonstrates that the composition of diet matters with regard to neurotransmitter release and suggests that unbalanced low caloric or high fat/high caloric diets could bring about variable neurochemical and behavioural effects.

Contemporary trends in obesity mean that research into whether unbalanced diets could impact on behavioural traits became increasingly important. Studies that have demonstrated the impact of hyperenergetic diets on the central nervous system [4] mean that investigating the behavioural implications of obesity has become an important priority. In this context the timing of exposure to obesity becomes important. An extensive literature has identified that fetal or early neonatal exposures to dietary extremes play a critical role in determining adult risk of metabolic and physiological dysfunction [5]. Relatively little attention has been paid so far to the impact of overfeeding during early development on emotional behaviour later in life.

Reflecting the human literature, many of the early animal studies modelling the developmental origins of disease focused on nutrient restriction during pregnancy [5]. As maternal food restriction can programme obesity in the offspring [5–8], it can also induce behavioural changes. Pre- and postnatal caloric restriction increases anxiety in the elevated plus maze and the open field test and also depressive-like behaviour in the swim behavioural despair test [9]. Caloric restriction prior to and during gestation as well as during lactation augmented maternal behaviour [10–12]. Although augmented maternal care may reduce anxiety in the offspring [13,14], this was not found in a study with only moderate caloric restriction [10].

More recent work has shown that maternal high-fat feeding during pregnancy can have postnatal metabolic consequences similar

* Corresponding author. Tel.: +44 115 951 6408.
E-mail address: peter.voigt@nottingham.ac.uk (J.-P. Voigt).

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to those seen after caloric restriction. Offspring from dams fed a maternal obesity-inducing, hyperenergetic diet before and during pregnancy have been shown to exhibit disturbed glucose and lipid homeostasis and greater adiposity in both the mouse [15] and the rat [16]. Collectively, these studies demonstrate that feeding high-fat, obesity-inducing diets during pregnancy in rodent models can lead to permanent alterations in postnatal physiological function, promoting adiposity and cardiovascular disease risk. Such a process through which exposure to environmental stimuli or insults, in this case feeding a hyperenergetic diet, during critical phases of development brings about permanent changes to the physiology or metabolism of the organism can be described as programming [17]. Despite this programming effect of maternal high caloric/high fat diets on metabolism and food preference [6–8], little is known so far about the possible consequences of such diets on emotional behaviour in the offspring.

There are a number of means of inducing obesity in animals through manipulation of the early environment. In addition to feeding hyperenergetic diets, obesity can also be programmed in rats by litter size reduction and subsequent early postnatal overfeeding [18]. Wistar rats, raised in such small litters, show increased exploratory behaviour and reduced anxiety in the elevated plus maze [19]. However, this approach to early life programming of obesity by postnatal overfeeding does not allow for the study of the effect of maternal obesity and gestational overfeeding. This is particularly important given the fact that up to 47% of women of childbearing age in the UK are expected to be obese by 2050 [20]. To model the impact of maternal obesity, dietary overfeeding at different stages of pre- and postnatal development will provide a useful approach. Feeding a cafeteria diet (CD) is a recognised approach for the induction of obesity in rodents and modelling the western diet in humans. CD consists of multiple highly palatable human food items that are offered to rodents in addition to normal chow. Feeding animals a CD, originally pioneered in the 1970s by Rothwell and Stock [21], has been one of many approaches used to study the development of obesity within laboratory rodents. Although there is accumulating evidence for nutritional effects on anxiety-related behaviour, it is important to address questions around contributions of maternal diet and obesity to the development of emotional behaviours and the significance of specific sensitive developmental periods. The present study was therefore designed to investigate the possible pre-gestational, gestational and lactational effects of a high caloric CD on anxiety-related behaviour in rat offspring.

2. Methods

2.1. Animals and feeding procedure

The experiments were performed under licence from the Home Office in accordance with the 1986 Animals (Scientific Procedures) Act. All animals were housed in plastic cages and subjected to a 12 h light–dark cycle at a temperature of 20–22 °C and 45% humidity. The rats were housed on shavings and had *ad libitum* access to food and water at all times.

Virgin female outbred Wistar rats (HsdHan:WIST, Harlan UK) aged 3 weeks were randomly allocated to be fed either a control chow diet (B&K Universal Ltd, Hull, UK) alone or in conjunction with a random selection of highly energetic and palatable human foods (cafeteria diet; CD). The CD included biscuits, potato crisps, fruit and chocolate, Mars bars, cheddar cheese, golden syrup cake, pork pie, cocktail sausages, liver and bacon pâté, strawberry jam and peanuts. The foods provided were altered daily, to maintain variety, by replacing two of the foods with new items; hence the animals did not receive the same foods for more than two consecutive days at a time. The body weights of the animals were measured between 09.00 and 10.00 h daily.

CD was introduced from weaning to allow a sufficient period of CD feeding to induce obesity before mating at age of 11 weeks. After 8 weeks of control or CD feeding, all females were mated with a Wistar male. Rats that were fed CD from weaning (CD pre-gestation; PG) exhibited excess weight gain and in keeping with our earlier report [22] were deemed to be obese. In order to separate the effects of maternal cafeteria feeding from the effects of maternal obesity, rats from both pre-mating groups were divided into a chow feeding group or a CD group during gestation. Rats initiating CD only at mating represent a group that was overfed but not obese (CD gestation; G). After birth offspring of dams from each of the 4 pregnancy groups were further divided into 2 groups, either being fed to control chow or CD throughout. Thus a set of non-obese animals exposed to CD in lactation only (L) was generated. A total of 8 groups were included in the study (Fig. 1). Litter size (8–12) was not significantly different between experimental conditions. After weaning animals were group housed with littermates of the same sex, with all 8 groups being maintained on a control chow for the duration of the behavioural study. Due to the main focus on effects of the diet during three distinct phases (pre-gestation, gestation and lactation) in the analysis, data is presented accordingly, resulting therefore in three exposure periods and the corresponding controls (see Section 2.3, Statistical analysis). A total of 128 male and female offspring were tested.

2.2. Analysis of behaviour

Behavioural testing of offspring started at the age of 10 weeks. Experiments took place between 0900 and 1300 h with animals placed in the room of testing 30 min before the beginning of the observation period to become acclimatized to the testing room. The behaviour was observed using a video camera mounted under the ceiling and was tracked and analysed using Ethovision 3.1 (Noldus, Netherlands) software. The animals were first tested in the elevated-plus maze and were exposed to the open field test one week later.

2.2.1. Elevated plus maze

The elevated plus maze consisted of 2 closed arms (60 cm × 10 cm × 35 cm), 2 open arms (60 cm × 10 cm), and a central zone (10 cm × 10 cm), elevated 69 cm above the ground. The light intensity on the open arms of the maze was 130 lx, and in the closed arms was 70 lx. Each rat was placed into the centre of the maze facing a corner to give an equal chance of the rat entering an open or a closed arm.

Rats were exposed to the elevated plus maze for a total of 5 min. The plus maze was thoroughly cleaned between animals. The data were analysed for the parameters of time spent in the open and closed arms of the maze, entries into the arms, and the total distance travelled. An entry was defined by crossing the dividing line between an arm and the centre platform with all four feet. In addition, the frequencies (total number/5 min test) of rearing and grooming were analysed.

2.2.2. Open field

The open field test apparatus consisted of a grey open plastic box (100 cm × 100 × 30 cm) virtually divided into an outer zone and an inner zone (50 cm × 50 cm). The light intensity in the centre of the maze was 130 lx. Animals were exposed to the open field for 5 min, with the test apparatus being disinfected after each animal. The data were analysed for the parameters of distance travelled and frequencies (total number/5 min test) of rearing and grooming. In addition, the latency to enter the inner zone and the time spent in the inner zone were analysed.

2.2.3. Body fat content

After the animals had been culled at the age of 5 months, gonadal, perirenal and intrascapular (white and brown) depositions of the

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