Hormones and Behavior 85 (2016) 56–66

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Behavioral consequences of exposure to a high fat diet during the post-weaning period in rats

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ARTICLE INFO

Article history:
Received 4 December 2015
Revised 4 July 2016
Accepted 27 July 2016
Available online 31 July 2016

Keywords:
High fat diet
Dopamine
Saccharin
Sucrose
Early life
Food reward
Condition place preference
Anxiety
Food preference

ABSTRACT

We explored the impact of exposure to an obesogenic diet (High Fat–High Sucrose; HFS) during the post-weaning period on sweet preference and behaviors linked to reward and anxiety. All rats were fed chow. In addition a HFS-transient group had access to this diet for 10 days from post-natal (PN) day 22 and a HFS-continuous group continued access until adult. Behavioral tests were conducted immediately after PN 32 (adolescence) or after PN 60 (adult) and included: the condition place preference (CPP) test for chocolate, sugar and saccharin preference (anhedonia), the elevated plus maze (anxiety-like behavior) and the locomotor response to quinpirole in the open field. Behavior was unaltered in adult rats in the HFS-transient group, suggesting that a short exposure to this obesogenic food does not induce long-term effects in food preferences, reward perception and value of palatable food, anxiety or locomotor activity. Nevertheless, rats that continued to have access to HFS ate less chocolate during CPP training and consumed less saccharin and sucrose when tested in adolescence, effects that were attenuated when these rats became adult. Moreover, behavioral effects linked to transient HFS exposure in adolescence were not sustained if the rats did not remain on that diet until adult. Collectively our data demonstrate that exposure to fat and sucrose in adolescence can induce immediate reward hypofunction after only 10 days on the diet. Moreover, this effect is attenuated when the diet is extended until the adult period, and completely reversed when the HFS diet is removed.

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1. Introduction

It has become increasingly evident that the early life environment, including nutrition, plays a pivotal role in determining the subsequent body weight and metabolic phenotype when adult. It is known, for example, that under- or over-nutrition in utero predisposes individuals to overweight and obesity, including increased risk of cardiometabolic disease. The impact of different diets in the early life period has been widely studied, especially during the gestation and lactation periods. In rodents, the offspring of mothers consuming a high fat diet have an increased risk of obesity and insulin resistance in adulthood (Ainge et al., 2011). What has been much less studied is the impact of the composition of the food environment during that critical post-weaning period, when individual food preferences are first expressed by the offspring and when many of the key pathways important for subsequent dietary choice and associated behaviors are established. Although we do not yet have a clear view of the brain pathways critical for food choice, we can follow food-linked (including homeostatic and reward-driven) behaviors that would seem critical for individuals to make favourable decisions for one food over another.

By the time weaning takes place, which usually occurs around post-natal days (PN) 21–22 in rats and mice, neurogenesis of many of the key pathways important for energy balance and non-homeostatic feeding will already have occurred, although the fine tuning of their connections continues for some time afterwards. Thus, neurogenesis in the hypothalamus is estimated to occur between embryonic days 13–15 (Markakis, 2002), with the circuitry of the arcuate nucleus, a pivotal site for energy balance integration, estimated to happen between PN 7–18 (Bouret et al., 2004). Of the non-homeostatic networks, the midbrain dopamine system that confers reward from natural and artificial reinforcers, including food, is a candidate target for programming of early life appetitive behavior. The neurogenesis of the dopamine circuitry in the striatum and projections to cortical regions are mostly developed between PN 7–21 in rats (Van den Heuvel and Pasterkamp, 2008), although during the peri-adolescent period (PN 21–42), a lot of rearrangements in dopaminergic systems occur (Andersen, 2003; Bernheim et al., 2013). This rearrangement of the dopamine system has been linked to risk-taking behaviors during the peri-adolescent period (Bernheim et al., 2013). Therefore, the stimulation of these structures when eating palatable food will have different effects depending on which period in development this occurs. Moreover, there is

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http://dx.doi.org/10.1016/j.yhbeh.2016.07.008
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evidence in humans that exposure to different types of food and the habits acquired early in life can influence our decisions and preferences for different diets (Beauchamp and Mennella, 2009; Schwartz et al., 2011).

Adult rats that are offspring to mothers consuming cafeteria diet (high in fat, sugar and salt) display altered reward-based behaviors due to an altered development of the mesolimbic reward pathway (Ong and Muhlhausler, 2011). They also have an increased preference for foods high in fat, sugar and salt (Bayol et al., 2007), indicative of metabolic imprinting (i.e. epigenetic modulation of metabolic and neurologic responses to food in the adult offspring). Mice fed high fat diet from weaning (PN 21) that continue on this diet for at least 15 weeks, displayed decreased expression of a number of dopamine-related genes in the mesolimbic reward circuit and increased expression of these genes in the hypothalamus (Vucetic et al., 2012), and decreased μ-opioid receptor expression in the mesolimbic reward circuits together with a decreased preference for saccharin (Vucetic et al., 2011), suggesting a state of reward hypofunction. Supportively, in pathological obese human subjects, a reduction in striatal dopamine D2-receptors, similar to that seen in individuals with substance abuse, has been reported (Volkow et al., 2013), a finding interpreted to indicate that the reward circuits are under-stimulated, predisposing these individuals to compensate for this "reward-deficiency" by overeating.

However, after the intrauterine and nursing period, very little is known about potential long-term effects of a short-transient exposure to obesogenic diets, during the post-weaning and adolescent period, on behaviors linked to appetite control, such as food motivation and anxiety-like behavior. Teegarden and colleagues demonstrated that mice given access to a high fat diet for 1 week after the weaning, subsequently showed higher preference for it (when adult) and this was accompanied by epigenetic changes in the ventral striatum (Teegarden et al., 2009). This supports the idea that exposure to an obesogenic diet in the post-weaning period can impact on adult food preferences and on the reward system.

In the present study, we sought to determine whether exposure to an obesogenic palatable diet high in fat and sugar during the post-weaning period (either transiently for 10 days or continued for >40 days into adult life) can alter behaviors linked to feeding control, including reward-linked and anxiety-like behaviors in rats. We also explored whether such behaviors can be altered immediately after transient exposure to the high fat diet in early life, or indeed, whether it is necessary to sustain the animals on the high fat diet in order to see behavioral changes. Finally, we also sought to discover whether there is an impact of the diet in the post-weaning period (transient or continued until adult life) on expression of candidate genes in key brain areas.

2. Methods

2.1. Animals

Pregnant Sprague-Dawley rats (Charles-River, Germany) delivered their pups by 8–10 days after their arrival to the animal facility. The litters were reduced to eight pups each, with a balance kept between males and females where possible. After weaning, on postnatal day (PN 22), the rats were regrouped with 4–5 per cage and in a way that ensured the animals in the same group were not all from one dam. Only the males were included in the experiments described here.

The animal room was maintained on a 12/12 hour light/dark cycle (lights on at 6 am), at 20 °C and 50% humidity. Rats always had ad libitum access to food and water. All procedures took place at the Laboratory for Experimental Biomedicine, University of Gothenburg. All animal procedures were carried out with ethical permission and in accordance with the University of Gothenburg Institutional Animal Care and Use Committee guidelines.

2.2. General procedure

After weaning (PN 22), the rats were divided in 2 groups balanced in body weight: (1) Chow rats: fed normal chow only (Teklad Global 16% Protein Rodent Diet, Harlan; 3 kcal/g) and (2) HFS rats: fed an obesogenic diet high in fat and sucrose (Western diet, TD88137, Harlan: 4.5 kcal/g; 15.2% kcal from protein, 42.7% kcal from carbohydrates and 42% kcal from fat. Sucrose represents 341.4 g/kg.) in addition to normal chow. The HFS was never offered alone but always in combination with chow in all experiments. After 10 days, on PN 32, half of the rats in the HFS group were returned to normal chow feeding (HFS-transient, HFS-T), while the other half continued to have access to HFS until the end of the experiments (HFS-continuous, HFS-C). Food and water were available ad libitum throughout the experiments, except during the behavioral tests. Rats were never food or water restricted. Three different cohorts of rats were tested immediately after PN 32 (puberty) in several reward-linked behavioral tests (see below), while another two cohorts of rats were evaluated in the same tests after PN 58 (adulthood) to study the long-term effects of the HFS diet (Fig. 1). The rats were handled at least three times prior to starting the behavioral tests. They were also habituated to the common procedures in the experiments like body weight measurements and intraperitoneal (i.p.) injections in order to reduce the stress associated with these procedures. All the experimental procedures were done during the light phase. The behavioral apparatus was cleaned with 5% ethyl alcohol between each individual test.

2.3. Behavioral tests

2.3.1. Sucrose and saccharin preference test

Rats were allowed to drink a saccharin solution (0.1% w/v) or sucrose (1% w/v) (Sigma, Dorset, England) ad libitum for 3 h/day on two consecutive days, and 1 h/day on the third day. The reduction to 1 h instead of 3 h on the third day aimed to increase the sensitivity of the test, as those with high preference for the solutions would be expected to drink a large volume in a very short time period. The rats were placed in individual cages for 1 h before starting the test. Saccharin and water were stored in special bottles to prevent leakage. The two bottles were refilled and side-switched each day. To habituate the rats to the procedure, we introduced the two bottles filled with water for 24 h in the home-cage before the test. Rats exposed to saccharin were never exposed to sucrose. The measures taken were saccharin, sucrose and water consumption per body weight. Preference for the sweet solutions over water was calculated as follows: (ml of sucrose or saccharin/ml of sucrose or saccharin + ml of water) * 100. The first day of exposure to sucrose or saccharin is not shown in the results since it is considered a day for adaptation to the solutions.

2.3.2. Conditioned place preference (CPP) for assessing food reward

The CPP test was performed in an apparatus comprised of two connected chambers with distinct visual and tactile qualities (Med Associates Inc., St Albans, Vermont, USA). Initial preference for one chamber was assessed on two consecutive days (15 min/day). The second day was used to determine the preference (Pre-test). The least preferred compartment was subsequently paired with rewarding/palatable food (chocolate pellets; Ms, Marabou, Kraft Foods, Väsby, Sweden). The preferred chamber was paired with normal chow. The pre-test was followed by 20 conditioning sessions (two sessions per day, 20 min each). One day following the last conditioning session, rats were tested again for their preference in the CPP apparatus for 15 min. During the CPP test, rats did not have access to food, enabling dissociation of the intake of palatable food from the reward evaluation process. The behavior of the animals was recorded and time spent in each compartment was determined automatically.

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