The Effects of the Hypothalamus and Nucleus Accumbens on Orosensory Fat Preferences in Rats: A literature review

Steven D. Robinson

Department of Psychology
Wofford College

Submitted in partial fulfillment for the Bachelor of Science Degree in Psychology at Wofford College, Spartanburg, SC
Abstract
Human preferences for fat are yet to be fully understood. The purpose of the following review is to provide an evaluation of the empirical research on the effects of the peptide galanin (GAL) and nucleus accumbens on orosensory fat preferences in rats. The orosensory properties of fats are believed to be enough reinforcement for the ingestion of oils. Fats with a strong nutritive value are believed to be orosensory preferred over fats with less nutritive value. The nucleus accumbens is a basal forebrain structure is believed to regulate motivation and appetitive behavior. The shell of the nucleus accumbens has been shown to be involved in the control of ingestive behavior. GAL is expressed in the hypothalamus and is thought to aid in the control feeding and metabolism. GAL prefentially increases the ingestion of a fat diet, rather than carbohydrate or protein diets when infused in the hypothalamus.
The Effects of the Hypothalamus and Nucleus Accumbens on Orosensory Fat Preferences in Rats: A literature review

The amount of fat ingested by the average American is a major public health issue. Dietary fats have been associated with increased risk for obesity, noninsulin-dependent diabetes mellitus, cardiovascular disease, and some types of cancer (Rice et al., 2000). The diet of most Americans consists of 42% fat, which is considerably above the 30% recommended by the American Cancer Society (Rice et al., 2000). Human preferences for fat are yet to be fully understood. It is widely assumed that the metabolic effects of dietary fat are a major determinant of fat intake (Smith et al., 1991).

The orosensory and metabolic effects of fat suggest ample motivation for the ingestion of oils. Research has demonstrated that rats can detect and discriminate oils based on their nutritive value prior to ingestion (Graciela & Sclafani, 1990). Taste preference for corn oil over mineral oil has been specifically investigated to provide evidence for the assumption that oils with the most nutritive value would be the most preferred. Long chain fatty acids are also believed to be involved in pre-ingestional discrimination (Tsuruta et al., 1999). Vegetable oils have been preferentially ingested by rats and orosensory effects along with the recognition of long chain fatty acids have been demonstrated to play role in preferences of oil (Tsuruta et al., 1999). Appetite for fats in general, may be due to the combined action of unlearned and learned responses to the orosensory properties of the nutrients. Fat is usually accompanied by sugar and evaluating the combination in comparison to vegetable oil will reveal the role it may play in food preference.
It is well known that foods high in fat elicit a pleasurable response. The nucleus accumbens is a basal forebrain structure located in the ventral striatum and is believed to regulate motivation in addition to appetitive behavior. Specific areas of the nucleus accumbens have been shown to effect fat consumption when stimulated by a gamma aminobutyric acid (GABA) agonist (Basso & Kelley, 1999). The GABA pathway has been found to mediate food intake in free-feeding animals when the GABA agonist muscimol was injected into specific regions of the nucleus accumbens (Basso & Kelley, 1999). An increase in dopamine level has been speculated to increase fat consumption (Zhang & Kelly, 2000). A correlation between taste palatability and the control by the nucleus accumbens and endogenous opioid systems have been demonstrated to play a role in fat consumption (Zhang et al., 1998).

Studies in animals as well as in humans reveal that body fat is more closely related to the amount of fat ingested than to total caloric intake (Leibowitz et al., 1998). The neurobiology of these phenomena is yet to be fully understood. There is some evidence that the peptide galanin (GAL), which is expressed in the hypothalamus, is involved in the control of feeding and metabolism. Lesions in various hypothalamic structures have resulted in increased (hyperphagia) or decreased (hyperoraphagia) food intake and / or changes in body weight. Hypothalamic nuclei may be linked to fat ingestion (Leibowitz et al., 1992). When injected into the hypothalamus of satiated rats, GAL stimulates food intake and can elicit a preference for dietary fat in some conditions (Leibowitz et al., 1992).
Orosensory Fat Preference

Oily and fatty foods tend to have a good flavor and which is preferentially selected in diets. Obesity induced by the excessive intake of fats has quickly become an epidemic of worldwide proportions. However, it is difficult to decrease fat intake even though it is well known that obesity represents a risk factor in many diseases (Takeda et al., 2000). The relative contribution of the orosensory and metabolic effects of fat suggest sufficient stimuli for acceptance and ingestion of oils.

The orosensory and metabolic effects for the intake of fat is uncertain. The ingestion of noncaloric oils, such as mineral oil, by rats suggests that the orosensory properties of fats are enough stimuli for the ingestion of oils. The potency of oils on the orosensory effects of fat has been investigated. The sham-feeding responses of male rats to corn oil and mineral oil in a 1-bottle test and 2-bottle preference tests were used in the investigation (Mindell et al., 1990). Corn oil was predicted to have a stronger orosensory effect because it has a stronger nutritive value than mineral oil (Graciela, & Sclafani, 1990). All rats discriminated between the orosensory effects of corn oil and mineral oil and the rats preferred corn oil in all tests that were given. When mineral oil and corn oil where presented to separate rats they were both ingested at equal quantities. The similar intake of the oils during sham feeding is compelling evidence that ingestion can be stimulated by the orosensory effects of oil in the absence of postingestive metabolic effects. The similar quantities of ingestion are not due to the failure of rats to distinguish the orosensory effects of the oils because when the oils were switched the intake of the novel oil was much smaller than the intake of the familiar oil (Smith et al., 1991). The
findings demonstrate that rats have an orosensory mechanism for detecting and discrimination corn oil and mineral oil (Mindell et al., 1990). Corn oil has a high level of linoleic acid compare to mineral oil and this fact may attribute to its taste preference.

Fatty acids have been shown to effect oil preferences in rats (Tsurata et al., 1999). To determine if only fatty acid composition is necessary to affect oil preference, different preferences for oils with similar fatty acids were examined by Rice, Greenberg, and Corwin (2000). Extra light olive oil and virgin olive oil both rich in oleic acid but contain a difference in quality characteristic were compared to determine oil preference. When the rats were given each of the oils separately they did not demonstrate a difference in oil intake during overnight exposure. The rats did show a preference for extra light olive oil over the extra virgin olive oil when given a choice under a two-bowl test conditions. If fatty acid composition is necessary for oil preference then oils that have large amounts of oleic acid like extra light olive oil and virgin olive oil should be equally preferred. The findings do not support the idea that fats with similar fatty acid profiles are equally preferred. However, it is likely that fatty acid composition interacts with other properties of the oils to influence preference. Rats can discriminate oleic acid and linoleic acid (Tsurata et al., 1999). Linoleic acid has been show to increase taste sensitivity and may be one of the other influences on taste preference (Tsurata et al., 1999).

In a study by Eicalde and Sclagani (1990) arbitrary flavor cues were paired with nutritive corn oil and nonnutritive mineral oil. Rats displayed a strong preference for the cue flavor paired with corn oil (94%) compared to water over the flavor mixed into the mineral oil (78%) compared to water. The study indicates that the appetite for oils, and
presumably fats in general, is due to the combined action of unlearned and learned responses to the orosensory and postingestive properties of the nutrients.

Many palatable foods such as bread, doughnuts, cakes, cookies, ice cream, ect., contain sugars and fats. Takeda, Imaizumi, and Fushiki (2000) investigated the preference of sugar and vegetable oil mixture compare to oil or sugar alone. A total of 54 Male ddY mice (Japan SLC, Inc., Hamamatsu, Japan) were used. All rats were deprived of water and food one hour prior to testing. The rats were divided into groups (control, sucrose, corn oil, and mixture groups) and tested for oil preference. The finding suggests that mice elicit a preference for vegetable oil over sucrose. Mice preferred the mixture of oil and sugar over the individual components (Takeda et al., 2000).

In general, the orosensory properties of fats are enough reinforcement for the ingestion of oils. Corn oil, which has a stronger nutritive value, is in general preferred over mineral oil. Research suggests that fats with a stronger nutritive value play a role in orosensory preference (Mindell et al., 1990). The appetite for oils, and presumably fats in general, is due to the combined action of unlearned and learned responses to the orosensory properties of the nutrients. Fatty acid composition alone does not account for oil preferences in rats but it may be indirectly involved. Foods that are high in fat are usually accompanied by sugar and mice elicit a preference for the mixture of oil and sugar over the individual components.

Nucleus Accumbens

The nucleus accumbens is a brain region considered important in the regulation of motivation and appetite as well as the reinforcement of drug abuse. It is essential in goal-
directed behaviors. It is hypothesized as a neural interface between motivational or emotional inputs arising from limbic structures and effectors motor systems.

Anatomical analysis of the nucleus accumbens indicates three major territories: core, shell, and rostral pole. Within the nucleus accumbens shell excitatory amino acids and a gamma aminobutyric acid (GABA) pathway mediate food intake in free-feeding animals (Basso & Kelley, 1999). The inhibition of the shell neurons with GABA agonists inhibited GABAergic accumbens-lateral hypothalamic pathway. The inhibition of GABA resulted in the disinhibition of the lateral hypothalamic neurons which increased feeding (Wise, 1974). The findings suggest that the shell of the nucleus accumbens is involved in the control of ingestive behavior, by means of direct or indirect anatomical connections with the lateral hypothalamus.

Basso and Kelley (1999) used the GABA agonist muscimol to investigate the subregions within the nucleus accumbens shell to map feeding responses. A total of 77 male rats were used and cannulas were implanted. The cannulas were aimed at five different sites within the medial nucleus accumbens shell: anterior-lateral, posterior-lateral, ventral, anterior-medial and posterior-medial. The effect of 20 and 50 ng muscimol infusion within the nucleus accumbens shell was examined to specify the intake of specific macronutrient diets in free-feeding rats. Saline solution was used as the control. A high Carbohydrate diet along with a high fat diet was presented individually and simultaneously.

Basso and Kelley (1999) found that muscimol elicited a significant feeding response only when infused in the anterior- or posterior-medial nucleus accumbens shell. The anterior-medial nuclease accumbens shell revealed a significant effect along with the
Mechanisms for Fat Preferences in Rats

posterior-medial nuclease accumbens shell. The injection of muscimol in either the ventral, anterior-lateral, or posterior-lateral accumbens shell did not increase food intake in satiated rats. When compared to saline solution, muscimol significantly increased the dose-related intake of high fat diet and carbohydrate diet. The greatest effect was apparent during the first 60 min after administration of muscimol. Rats did not show a macronutrient diet preference for either fat or carbohydrates when both diets were presented simultaneously.

Basso and Kelley (1999) findings support the involvement of GABA pathway within the nucleus accumbens shell on regulating ingestive behavior. The posterior-medial accumbens is somewhat more sensitive to the effect muscimol than the anterior-medial accumbens shell. The macronutrient and taste preference study indicates that the GABA-mediated feeding increases caloric intake and has no influence on taste or macronutrient selection (Basso & Kelley, 1999).

Zhang, Gosnell, and Kelley (1998) suggested a correlation between taste palatability, which is controlled by the nucleus accumbens, and endogenous opioid systems. Basso and Kelley (1999) used saline, sucrose, and saccharin solutions to test the GABAergic mechanisms in the nucleus accumbens. The three solutions were considered highly palatable to rats, because the baseline intake for the three solutions in satiated rats were higher than for water. However, the sucrose solution represents an important energy source along with being highly palatable. The results showed that an infusion of muscimol into the medial accumbens shell elicited a significant increase in intake for the sucrose solution compared with the infusions of saline. The muscimol infusion did not have a significant effect on the other two solutions. The results indicate that GABAergic
mechanisms within the medial shell of the nucleus accumbens are not involved with palatability, but are important in regulating caloric intake.

Recent studies have characterized feeding induced by stimulation of opioid receptors within the nucleus accumbens, using the same macronutrient diets as those used in Basso and Kelley (1999) study. Stimulation of mu-opiod receptor in the nucleus accumbens enhanced the feeding of high-fat food in a choice test between a high fat diet and standard laboratory chow (Zhang & Kelly, 2000). The mu-opiod receptor agonist, D-Aala², Nme-Phe⁴, Glyol⁵-enkephalin (DAMGO), and the general opioid receptor antagonist naltrecone were used to stimulate the nucleus accumbens. Fat intake was increased by 153% in the medial shell, 253% in the core, 231% in the ventrolateral striatum and 365% in the lateral shell. DAMGO stimulated feeding was not restricted to particular subregions of the nucleus accumbens compared to the GABA agonist muscimol. Muscimol increased feeding when infused with the medial shell but not the core, ventral or lateral shell, nor any dorsal striatal regions. The mapping differences suggest that the difference in anatomical connectivity between subregions of the nucleus accumbens may reflect specificity for GABAergic and glutamatergic, but not control of feeding for opioidic mechanisms (Zhang & Kelly, 2000).

With two macronutrient-specific diets simultaneously available, free-feeding rats given an infusion of DAMGO displayed a strong preference for fat compared with the carbohydrate diet. A significant influence of DAMGO on fat intake was demonstrated (Zhang & Kelly, 2000).

Several studies support the theory that central dopamine systems mediate the rewarding effects of sugar and fats in rats. It has been hypothesized that a more
Mechanisms for Fat Preferences in Rats

A reinforcing stimulus would cause more dopamine (DA) to be released at relevant receptor sites (Weatherford et al., 1991). Weatherford et al (1991) tried to detect an increase in dopamine by sham feeding rats sucrose and oil. The ratio of dihydroxyphenylacetic acid (DOPAC) to DA was used to measure DA metabolism. 6% sucrose, 10% sucrose, and 100% corn oil was used as the macronutrient stimuli. DA, DOPAC and the ratio of DOPAC/DA did not increase in any group of sham-feeding rats relative to non-sham feeding controls. The finding does not support the idea that a more reinforcing stimulus would cause more dopamine. Weatherford, Greenberg, Melville, Jerome, Gibbs, and Smith (1991) noted that 10% sucrose appears to be the “threshold” concentration for increasing the ratio of DOPAC/DA in sham-feeding paradigm. Corn oil along with sucrose failed to elicit an increase in dopamine. Weatherford et al (1991) stated that the reward value of corn oil relative to 40% sucrose is not known, it is not possible to determine if the negative results were because the reward value of corn oil is “subthreshold” or because the orosensory qualities of corn oil are not a stimulus for dopamine release.

The nucleus accumbens shell controls feeding by its connection with the lateral hypothalamic pathway. Basso and Kelly (1999) proclaim that electrical or excitatory amino acid stimulation of the lateral hypothalamus results in increased feeding, whereas lesions of this structure result in severe impairment of ingestive behavior and loss of body weight. It has been shown that certain neural inputs like $\alpha$-amino-3-hydroxy-5-methylisoxazole-4-proionic acid (AMPA) normally exert a tonic excitatory effect on shell neurons (Maldonado-Irizarry et al., 1995). Temporary removal of the excitatory effect of the neural inputs using 6,7-dinitroquinoxaline-2,3-dione (DNQX) causes shell-
hypothalamic neurons to become inactive, thereby disinhibiting lateral hypothalamic neurons. The disinhibiton is believed to cause animals to eat. Maldonado-Irizarry (1995) proclaims that neurons arising in the shell exert an inhibitory influence on lateral hypothalamic neurons, via a GABAergic mechanism. The nucleus accumbens shell displays neuroanatomical connectivity to several regions in the brain that are involved in the control of feeding behavior, such as the lateral hypothalamus, extended amygdala, and brainstem autonomic nuclei. The role of the nucleus accumbens on the lateral hypothalamus could be affected by other brain regions.

The nucleus accumbens is important in the regulation of fat intake. The GABA agonist muscimol was used to determine areas of the nucleus accumbens that stimulated a fat intake response. The mapping of the nucleus accumbens has demonstrated that the shell of the nucleus accumbens is involved in the control of ingestive behavior, by means of direct or indirect anatomical connections with the lateral hypothalamus (Basso & Kelley, 1999). The nucleus accumbens has no influence on taste or macronutrient selection or any involvement in palatability (Zhang & Kelly, 2000). Stimulation of mu-opiod receptor in the nucleus accumbens plays a significant role in caloric intake (Basso & Kelley, 1999).

Hypothalamus

The hypothalamus aids in the regulation of feeding and metabolism. Galanin (GAL), a 29-amino acid peptide is widely dispersed in the gut and brain. It has the highest concentration in the hypothalamus. The paraventricular nucleus (PVN) is a region of the hypothalamus found to have GAL receptor binding sites (Leibowitz et al., 1992).
Microinjection of GAL directly into the PVN stimulates the consumption of food in satiated rats (Leibowitz et al., 1992). The importance of the PVN in the feeding of stimulatory action of the GAL is demonstrated by the finding that GAL has generally little impact on food consumption when microinjected into other hypothalamic nuclei and certain extrahypothalamic areas (Kyrkouli et al., 1990). Electrolytic lesions of the PVN have been shown to abolish GAL induced feeding (Leibowitz et al., 1992). Research by Leibowitz and Wang (1992) has demonstrated that GAL aids in the specific control of macronutrients. The findings support the idea that an injection of GAL in the PVN increases the ingestion of a fat diet, rather than carbohydrate or protein diets. The research has been strengthened by the fact that specific macronutrient effects of GAL occur in all rats regardless of their natural macronutrient preferences (Leibowitz et al., 1992).

Leibowitz and Wang (1992) used the GAL antagonists M40 to precisely define the physiological role the GAL receptors have in the PVN. A total of 28 adult male Sprague-Dawley rats where used and cannulas were implanted into the PVN. The rats where maintained on a self-selection-feeding paradigm with three macronutrient diets, protein, carbohydrate and fat. The animals were tested with the peptide M40 or saline vehicle in counterbalanced order. The antagonist M40 or the saline solution was injected immediately prior to the onset of the nocturnal feeding period in rats. A second experiment injected the M40 or saline solution 30 min prior to a previous injection of 300pmol of GAL. The infections were administered immediately before the onset to the dark period (Leibowitz et al., 1992).
In the first experiment by Leibowitz and Wang (1992) the GAL antagonist caused a selective reduction in fat intake prior to the onset of the nocturnal feeding period. The phenomenon occurred at the three highest doses (18, 54 & 108 pmoles), which reduced intake by 50-70%. The selectivity of the M40 for fat is supported by the finding that carbohydrate and protein intake were relatively unaffected by the administration of M40 into the PVN.

In the second experiment by Leibowitz and Wang (1992) feeding responses produced by an injection of 300pmol of GAL was totally blocked by a prior injection of M40 into the PVN. The increased fat intake after GAL was significantly attenuated by M40. A total blockage of GAL occurred at the two lowest doses of M40, 2 and 6 pmol. The findings demonstrated that the injection of M40 into the PVN by itself reduces spontaneous ingestion of fat, an effect that is very behaviorally specific and opposite to that produced by GAL. The feeding stimulatory effect of PVN GAL, characterized by a selective enhancement of fat intake, occurred even in rats that strongly preferred carbohydrates or protein.

Leibowitz, Akabayashi, and Wang (1998) demonstrated that two specific hypothalamic sites have a rise in GAL activity in direct relation to the amount of fat consumed. The two areas are the PVN and the Median Eminence (ME) they both are on the infundibular hypothalamus. Research supports the idea that the two hypothalamic sites are anatomically linked by a projection from the PVN to the ME. The findings are demonstrated by the fact that GAL mRNA or peptide levels in the anterior parvocellular part of the paraventricular nucleus (aPVN) are positively correlated with GAL in the ME but not in other hypothalamic regions. The evidence indicates that GAL, in the aPVN and
Mechanisms for Fat Preferences in Rats

Galanin is co-produced with arginine-vasopressin (AVP) in the hypothalamus. Brattleboro rats are unable to synthesize AVP, because of a single base deletion in the gene encoding for AVP (Odorizzi et al, 1999). The genetic deficit of the central AVP synthesis is responsible for the polyuro-polydipsic syndrome, diabetes insipidus (DI) which leads to the chronic stimulation of hypothalamo-nerurohypophysial system (HNHS). Compared to the Long Evans (LE) rats, which are the wild counterpart of the Brattleboro rats, the Brattleboro rats have a much higher level of GAL in the PVN (Odorizzi et al, 1999). The Brattleboro rats ingest 60% more fat than LE rats. When the Brattleboro rats are treated with peripheral infusion of vasopressin V2 receptor agonist to correct the DI and the stimulation of HNHS, neither the GAL over expression or fat preferences disappear (Odorizzi et al, 1999). Ordorizzi et al (2002) demonstrated that GAL participates in the stimulation of the consumption for fat which is spontaneously observed in the Brattleboro rat. GAL receptor antagonists were used to demonstrate the macronutrient preference and the LE rat was used as the control. The injection of GAL antagonist into the PVN did not modify carbohydrate or protein selection but it reduced fat consumption.

Research has been found that demonstrates no effect of galanin on fat intake in a fat-chow paradigm (Corwin et al., 1995). Rats were given a choice between standard laboratory chow and fat (Crisco, Procter and Gamble, Cincinnati, OH; hydrogenated...
Mechanisms for Fat Preferences in Rats

vegetable shortening). Galanin did significantly increase chow consumption but total caloric food intake was not affected. M40 was tested at 2-500 pmol and had no effect on fat intake.

Corwin, Rowe, and Crawley (1995) stated that Leibowitz and Taewan (1992) macronutrient research used similar methods “in several regards:

1) Male Sprague-Dawley rats were used in both studies.
2) M40 was synthesized and provided by the same source.
3) Both studies were conducted in the early dark cycle.
4) The ingestion period in both studies was 2h.
5) The ingestion test was performed in the home cage.
6) The same injection volume (0.3 µl) was used.
7) Microinjection of the same does of galanin (300 pmol) and M40 (2-108 pmol) were administered into the PVN in both studies”.

The differences between the two experiments may be crucial. The differences included the type of fat used, the amount of time the fat was administered, and the food that was provided in addition to the fat. Lard fortified with vitamins was used in the macronutrient study (Leibowitz et al., 1992), whereas unfortified hydrogenated vegetable shortening was use with chow available ad libitum (Corwin et al., 1995). Differences in fat type and availability could have generated difference in the studies.

Smith, et al (1997) demonstrated that galanin injected into the PVN stimulated the intake of carbohydrate only in rats the preferred carbohydrates. Galanin induced equivalent intake of fat and carbohydrate relative to control injections. The experiments where conducted during the daylight period. The idea that the daylight period is when
minimal spontaneous feeding occurs could attribute to the findings. More research needs to be done confirm galanin effects on the hypothalamus.

Galanin which is expressed in the hypothalamus is involved in the control of feeding and metabolism. Microinjection of galanin directly into the paraventricular nucleus has been shown to aids in the specific control of macronutrients. Galanin in the paraventricular nucleus prefentially increases the ingestion of a fat diet, rather than carbohydrate or protein diets. Two specific hypothalamic sites the paraventricular nucleus and the Median Eminence (ME) are part of a positive feedback loop related to dietary fat. Brattleboro rats are unable to synthesize arginine-vasopression (AVP). A comparison of the Long Evans (LE) rats with the Brattleboro rats demonstrated that GAL participates in the stimulation of the consumption for fat.

Discussion

In modern western societies in which the food supply is abundant and obesity runs throughout the country it is essential to identify mechanisms that contribute to binge eating and uncontrollable cravings for sweet and high-fat foods. Research suggests that preference for fat in general, is due to the combined action of unlearned and learned responses to the orosensory and postingestive properties of nutrients. Mice elicit a preference for fats with strongest nutritive value (Takeda at el., 2000). The demonstrated contribution of the orosenory and postingestive metabolic effects of fat suggest sufficient evidence for the orosensory control of fat. Rats have an orosensory mechanism for detecting and discriminating corn oil and mineral oil (Mindell et al., 1990), but fatty acid composition alone does not account for oil preferences (Rice et al., 2000).
The nucleus accumbens is essential in goal-directed behaviors. The mapping of the nucleus accumbens has demonstrated that the shell of the nucleus accumbens is involved in the control of ingestive behavior, by means of direct or indirect anatomical connections with the lateral hypothalamus (Basso & Kelley, 1999). Research has demonstrated that GABA-mediated feeding increases caloric intake and has no influence on taste or macronutrient selection (Basso & Kelley, 1999). GABAergic mechanisms within the medial shell of the nucleus accumbens are not involved with palatability, but control caloric intake. Stimulation of mu-opiod receptors in the nucleus accumbens are also found to enhanced the feeding of high-fat food in rats (Zhang & Kelly, 2000).

The hypothalamus has been shown to elicit feeding responses in rats. Microinjection of GAL directly into the PVN of the hypothalamus stimulates the consumption of food in satiated rats (Leibowitz et al., 1992). GAL prefentially increases the ingestion of a fat diet, rather than carbohydrate or protein diets. Contrary research has demonstrated no effect of galanin on fat intake in a fat-chow paradigm (Corwin et al., 1995). Further research is needed to precisely dictate galanins role in macronutrient fat preferences.

Although research in the effects of mechanisms controlling fat preferences has grown tremendously in recent years, there still remains a number of important issues that need to be addressed. Takeda, Imaicumi, and Fushiki (2000) has proposed a number of areas where research has room to be feasibly improved. The following recommendations have been made to suggest ways that our knowledge can be expanded in the areas of orosensory fat preferences:
1) Sensitivity to basic tastes varies among different animal species and further research is needed to investigate different taste sensitivity among rats.

2) The effects of galanin and galanin antagonist need to be systematically investigated with a variety of fat sources.

3) Galanin production in the PVN needs to be examined during and after puberty to associate with body weight control.

4) Energy expenditure and galanin production in the PVN needs to be investigated. The increase in fat can increase energy expenditure.

Following these suggestions should cultivate a more successful convergence for the search of the causal mechanisms of orosensory fat preferences.
References


Tsuruta, M., Kawada, T., Fukuwatarti, T., & Fushiki, T. (1999). The Orosensory


