Programming Food and Flavor Preferences: Impact of Early Experience

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Abstract
There has been an increased interest in how early experiences *in utero* and/or postnatally shape the brain, physiology and behavior of individuals. Infants are not born a blank slate but, rather, enter the world with information gathered *in utero* that helps to prepare them for challenges in their immediate environment. One such area is the role of the maternal diet in shaping the flavor and food preferences of the offspring. This review aims to share what is known about perinatal flavor learning in cats and dogs and whether this influences later flavor preferences.

Glossary of Abbreviations
ePHF: Extensive Protein Hydrolsate Formulas

Introduction
Pets' food preferences and subsequent food intake are largely drive by the sensory properties of the food. Flavor and food preferences can impact the health of individuals by determining whether they choose to eat healthful or unhealthful foods. It also can result in overselection of one or more types of food that could result in malnutrition. And lastly, individual flavor and food preferences can be so narrowly tuned that it becomes extremely difficult to foster liking or mere acceptance of new potentially healthful foods. It is well-known that domesticated cats and dogs can be quite selective in what they eat, and this can make it very difficult to transition them to new foods, such as therapeutic diets. As such, it is important to understand the origins of flavor preferences and how to positively influence such preferences, especially at an early age to help create habits of healthful food choices as well as increase the likelihood for acceptance of novel foods. This review will look at only one of the mechanisms by which flavor preferences develop, but it is not assumed that this is the only means by which flavor preferences develop in cats, dogs and other animals.

Flavors from the maternal diet are transmitted to the fetus via the amniotic fluid and to the infant via breast milk. For example, Nolte et al.[1] showed that human judges could detect garlic odor in amniotic fluid, allantoic fluid, fetal blood, and maternal blood collected 100 minutes after a pregnant ewe had ingested 6 ml of garlic oil. Similarly, odors added to queens' diets were detectable in their breast milk (by chemical analyses) two hours after ingestion.[2]

Young animals from a number of species, including humans, are capable of early flavor learning that influences flavor preferences at birth,[2-5] after weaning,[2,6-11] young adulthood,[2,12] and adulthood.[13] Early flavor learning in the context of this review refers to prenatal learning, or learning *in utero*, and postnatal learning, or learning that occurs during the nursing period. Learning that encompasses both periods is referred to as perinatal flavor learning. Early flavor learning is one mechanism for preparing the offspring for foods it will encounter in its ecological niche. Learning before and after birth may serve different adaptive functions for young animals as will be discussed later.

Although it has been known for some time that early flavor learning could alter food and flavor preferences, it was only recently that studies were carried out with cats and dogs to understand if early flavor exposure did, indeed, condition flavor preferences in the newborn and at other ages.

Early Flavor Learning in Dogs
Prenatal flavor learning has been demonstrated in dogs.[5,11] Wells and Hepper[5] conducted a study in which bitches were fed twice daily 5 ml aniseed oil in their diets 19-23 days prior to whelping. When tested 24 hours after birth, more puppies with prenatal exposure to aniseed significantly preferred (oriented toward that odor) aniseed odor over distilled water than puppies whose mothers did not receive aniseed during pregnancy. Puppies that had no prenatal flavor exposure did not show a preference for either distilled water or aniseed.

To rule out the possibility that the prenatal flavor learning was a generalized enhanced preference for odors, the researchers then tested a different group of puppies for their preference for an unfamiliar odor, vanilla (matching intensity to aniseed) versus distilled water. This time there was no difference between the puppies from the two groups for their preference for vanilla versus distilled water. Since the puppies were tested at 24 hours after birth, it was possible for postnatal flavor learning to occur since the puppies would have had the opportunity to nurse during that period. To rule out postnatal flavor learning, a further test was done with puppies before the opportunity to nurse for the first time. Puppies were tested 15 minutes after birth, and, again, it was shown that only the puppies in the prenatal aniseed exposure group showed a preference for the aniseed odor over distilled

From the Purina Companion Animal Nutrition Summit: *Nutrition for Life*; Austin, TX; March 27-29, 2014.

water. Interestingly, when tested at 15 minutes old, the control group that did not have prenatal exposure to aniseed preferentially oriented toward water than the aniseed odor, suggesting avoidance for an unfamiliar odor. These findings show that puppies' flavor preferences shortly after birth were influenced by what was ingested by the mother during late gestation. Moreover, the puppies were able to generalize the odor from the fetal environment to a novel environment (cotton swab), indicating some olfactory continuity. Prenatal learning may be one mechanism by which the neonate[11] is able to quickly identify what is food and to facilitate nursing.

Prenatal flavor learning alone, however, does not appear to be enough to see the persistence of learning over time in puppies. When puppies were tested at 10 weeks old, their preference for aniseed odor on top of cooked minced chicken versus unscented cooked minced chicken was no different from control puppies that did not have prenatal exposure to aniseed.[11]

Hepper and Wells also assessed postnatal and perinatal flavor learning in 10-week-old puppies.[11] To assess postnatal flavor learning, one group of puppies was exposed to aniseed odor only via their mothers' milk, while the other group of puppies did not receive aniseed odor. The exposure period was 20 days after birth. To assess perinatal flavor learning, one group of puppies received both prenatal (20-25 days, on average) and postnatal flavor exposure (20 days after whelping and only via nursing) to aniseed odor, while the control group received no aniseed odor exposure prior to testing. Perinatal learning, but not postnatal flavor learning, was shown to produce a significant preference for the aniseed-scented treat over the unscented control.

Early Flavor Learning in Cats

A long-term study was conducted in cats to study the effect of prenatal, postnatal and perinatal flavor learning on flavor preferences in newborn, weaned and young adult cats.[2] The basic design of the study is shown in Table 1. Three groups of kittens were exposed to an odor (familiar odor) in one of three conditions: before birth, after birth or at both periods. A fourth group of kittens served as the control and was not exposed to the odors before or after birth.

Kittens were tested at three different time periods. At each period, they were tested for their preference for the familiar odor versus an unscented control as well as with an unfamiliar odor versus the same unscented control. Kittens' preference for an unfamiliar odor was assessed as was also done in the dog study to ensure that learning was specific to the exposed odor. Newborn kittens were assessed for their preference for both the familiar odor and the unfamiliar odor versus water. Weaned kittens were similarly tested except this time the odor was presented on 2.5g portions of minced chicken (treat). Finally, kittens were tested at 6 months of age with their normal food. Table 2 shows the main findings.

Table 1. Queens, depending on the group, were fed diets containing vanillin, 4-ethylguaicaol or no odor 24-27 days prior to parturition and/or 26 days after parturition.

	Prenatal Exposure	Postnatal Exposure
Kitten Group	(24-27 days)	(26 days)
Prenatal Exposure	✓	
Postnatal Exposure		✓
Perinatal Exposure	✓	✓
Control		

Newborn kittens, like puppies, exhibited prenatal flavor learning. However, unlike puppies, kittens with only prenatal flavor exposure persisted in showing a preference for the familiar odor at 8-10 weeks as well as at 6 months of age. The cat is not unique in demonstrating a long-term persistence in prenatal flavor learning. For example, prenatal-only exposure (50-130th day of pregnancy) to oregano oil led to a preference for oregano-supplemented feed in lambs tested at 3, 4.5, 6, and 7.5 months of age.[15]

Interestingly, the tests of newborn kittens with an unfamiliar odor versus water showed active avoidance of unfamiliar odors similar to what was seen with puppies when they were tested at 15 minutes old.[5] Thus, prenatal flavor learning appears to condition preference away from avoidance and not merely a neutral response.[2]

Similar to puppies, kittens did not exhibit postnatal flavor learning after weaning. However, they did show a preference for the postnatal flavor at 6 months of age. The authors explained that this finding is not unlike that seen with other species in which postnatal flavor exposure via breast or bottle milk often leads to long-term flavor preferences, and it may be necessary for some time to elapse for generalization of the flavor to other contexts.[2] Weaning stress may also have contributed to a failure to observe a conditioned flavor preference at 8-10 weeks old.[2] Indeed, Oostindjer et al.[16,17] showed that perinatal flavor learning did not result in preference for the pre-exposed flavor in piglets at the time of weaning, but it did positively influence their growth, food intake, lower occurrence of diarrhea, and their ability to cope with the stress of weaning.

Finally, the largest effect on flavor preferences was due to the combined effects of pre- and postnatal learning.

Perinatal learning has also been demonstrated in kittens that had a cheese flavor 25 days prior to birth (*in utero*) and 2-25 days after birth (queen's milk).[14] Specifically, kittens with perinatal exposure to the cheese flavor significantly preferred the cheese flavor over water at 2 days old and a cheese-flavored food over the unflavored control food at 45 days old. The control group of kittens with no exposure to cheese flavor before and after birth did not exhibit a specific preference at either 2 days or 45 days old.

Sensitive Periods for Flavor Liking and Acceptance

At least one sensitive period for flavor liking and acceptance has been identified in humans. Extensive protein hydrolysate formulas (ePHF) are an option for infants with certain types of food allergy. These ePHF formulas are deemed unpalatable both by their smell and taste by human adults. Mennella and colleagues[19]

From the Purina Companion Animal Nutrition Summit: *Nutrition for Life*; Austin, TX; March 27-29, 2014.

Table 2.

	Newborn (48 hrs) N=27		Weaned (8-10 wks) N=98		6 Months N=63	
Exposure	**Familiar* Odor vs. Water**	**Unfamiliar Odor vs. Water**	**Familiar* Odor vs. No Odor Treat**	**Unfamiliar Odor vs. No Odor Treat**	**Familiar* Odor vs. No Odor Food**	**Unfamiliar Odor vs. No Odor Food**
Prenatal	Familiar odor	Water	Familiar odor	No preference	Familiar odor	No preference
Postnatal			No preference		Familiar odor	
Perinatal			Familiar odor		Familiar odor	
Control	Water	Water	No preference		No preference	

* The control kittens were never exposed to the odors until they were tested, thus all odors were unfamiliar to them.

have shown that if babies are not exposed to ePHF before 3.5 months old, it is much more difficult to promote acceptance. However, if infants are exposed to ePHF for at least one month before they are 3.5 months old, they not only accept and consume more of these formulas than infants fed after 3.5 months old but also their facial response while consuming ePHF does not indicate signs of rejection.[18,19] Moreover, infants who had experience with ePHF were more likely to like novel foods that shared a flavor profile to ePHF compared to infants fed a milk-based formula.[20]

In the studies on perinatal flavor learning in both dogs and cats, the stimuli used for pre- and/or postnatal exposure were always hedonically neutral as determined by adult cats[5,11] and dogs.[2,14] No formal study to assess for a sensitive period for flavor acceptance of an unpalatable food has been conducted with cats and dogs. However, Rogers[21] made the following observations from nutrition research in his laboratory where it was necessary to adapt cats to eat unpalatable semi-purified diets. According to Rogers:

> We were able to observe kittens that received our semi-purified diets before weaning and assimilated them well. In this way, we were able to exert a lasting influence on the feeding behavior of the adult animals. If one wants to adapt an animal that had never had to take such an unacceptable diet, then it will take approximately one to two months before a sufficient quantity is taken. Kittens that during and after the lactation period took a semi-synthetic diet showed no acceptance problems in later life, even though they have received a commercial diet for a fairly long period in between. Therefore, I believe that this phase of acceptance for particular foods plays a very important role. One practical application of this observation: If one wishes to feed an animal a ration that is not easily acceptable, then it should be given directly after weaning.[21]

Rogers' observations suggest that there is likely a sensitive period when cats can learn to like and accept even unpalatable nutritious foods and that this learning persists well into adulthood and even after sustained periods of no dietary exposure. It could be argued that the prenatal period may also be a sensitive period for cats to learn to accept novel odors as Hepper et al.[2] showed in their work that newborn kittens avoided unfamiliar odors.

Further evidence of a sensitive period for flavor preferences in cats comes from a pilot study[22] with kittens that either had perinatal flavor exposure to only a single food, tuna or beef wet cat food, or to a variety of foods, and then later trained on an operant task with both foods serving as the reinforcer. The results showed tuna was more rewarding than beef flavor regardless of the flavor of single flavor of food received perinatally but only for kittens exposed to only one food perinatally. Those kittens often refused to eat the beef-flavored food. Kittens that were offered a variety of foods perinatally showed no preference for one flavor over the other and accepted both products equally well. Thus, it is possible that depending on the early experience with one or more flavors, it may be more difficult to facilitate acceptance for less palatable flavors. Early variety feeding may result in less finicky behavior.[23]

Conclusion

Both cats and dogs demonstrate early flavor learning.[2,5,11,14] They join a long list of other animals that are capable of such learning, which indicates an important role for this type of learning in development. The observation of avoidance of a novel odor in newborns suggests that prenatal odor learning serves to teach the newborn what is safe to eat, and it also indicates that early flavor learning may not only influence flavor preferences and food intake, but also the ability of the young animal to cope with new and potentially stressful events.[1,16,17] The research to date indicates both pre- and postnatal learning is possible, but to influence long-term flavor and food preferences both types of learning are necessary. Furthermore, early flavor learning teaches the animal not only about what is safe to eat but also can result in affective learning in which the animal learns not merely to prefer but also to like the flavors to which it was exposed perinatally. It may be easier to engender acceptance for less palatable, but nutritious, foods by exposing cats and dogs to such foods while they are young.

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From the Purina Companion Animal Nutrition Summit: *Nutrition for Life*; Austin, TX; March 27-29, 2014.