

Dopamine and food reward: back to the elements

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BRAIN DOPAMINE HAS BEEN LINKED to reward function by its importance first for the habit-forming actions of addictive drugs, then for direct electrical stimulation of the brain, and finally for more natural rewards such as food and sexual contact. Whereas addictive drugs and brain stimulation reward present relatively well-defined rewards, with direct delivery to the circulation or the brain and with known principal ingredients and mechanisms of action, food is a complex, multidimensional category, and news of food reward reaches the brain by several avenues. Hajnal et al. (3) in this issue of the *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* have begun to resolve the basic components of food reward and examine their isolated effects on the release of brain dopamine.

The brain mechanisms by which animals forage for and consume food are, in all likelihood, the brain mechanisms that are involved in the foraging for and use of addictive drugs. It is well established that brain dopamine is important for the rewarding effects of amphetamine, cocaine, opiates, and several other (but not all) drugs of abuse. Dopamine levels are elevated not only by most drugs of abuse but also by natural rewards such as food or sexual contact. If the dopamine system is blocked, animals do not learn to lever press for these normally habit-forming substances. If the dopamine system is blocked, animals that have already been trained to lever press for food, amphetamine, or cocaine do not continue to do so.

In the case of food, however, the reward stimulus is not well defined. Food is a fuzzy category; some studies are done with laboratory chow, some with cheese treats, some with chocolate, and yet others with breakfast cereal. It is impossible to know whether any of these substances are innately recognized as food. Even sweet taste, which is presumed to be innately preferred in rats and humans (4, 9), soon becomes importantly associated with the rewarding postingestive consequences of mother's milk and other nutrients.

The first step in understanding the effects of food reward is to resolve the basic elements of food stimuli. Hajnal et al. (3) make a good start. They studied the effects of intraoral sucrose on nucleus accumbens dopamine levels. Their food stimulus is close to unidimensional [although even the temperature of an ingested solution can contribute to its rewarding properties (7)]. Because it is given intraorally, its effects are not confounded with food-associated visual, auditory, and tactile stimuli that can, themselves, elevate brain dopamine levels (6). Moreover, the work was done with an open gastric fistula, so that the postingestive effects of sucrose were not a contaminating factor. The postingestive effects of glucose are known to confer conditioned importance to otherwise neutral

tastes with which they become associated (5). Thus the Hajnal et al. study begins to dissect the food stimulus at a much finer level of analysis than prior studies of the effects of food on dopamine levels. The coupling of studies where the sensory properties of food are differentiated with studies where the subregions of the dopamine system are differentiated (1) will greatly advance our understanding of how some foods become sought compulsively, to the point, some suggest, of addiction (2).

This analysis is important for yet another reason: it facilitates the comparison of food reward to intravenous drug reward. Single-cell recordings from the dopamine neurons that project to nucleus accumbens have led to the view that dopamine is more important for the anticipation of reward than for the receipt of reward (8). This distinction is easy to make in the case of the rewards of drugs of abuse or of direct electrical stimulation of brain reward circuitry; in these cases, we know with some precision when the reward itself is received by the body. In the case of food reward, on the other hand, receipt of reward is not so easily defined. Consider the case of a monkey presented with a piece of apple. What constitutes receipt of reward? Is it the tasting of the sweetness of the apple after it is chewed? Is it the feel of the apple once it is grasped? The sight of the apple when the door opens and it becomes visible? Or the click of the latch that releases the door behind which the piece of apple resides? The use of intraoral presentation of a unidimensional reward with an open gastric fistula takes an important first step toward resolving the essential elements of food reward and toward isolating the receipt of reward from the sensing of otherwise neutral stimuli that have become significant because of their relation to food.

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