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Original Article

How pathogen cues shape impressions of foods: the omnivore's dilemma and functionally specialized conditioning

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ABSTRACT

When consumed, meats and plants have presented asymmetric threats to humans and their hominid ancestors for hundreds of thousands of years. Here, we test the hypothesis that human food learning mechanisms are functionally specialized to navigate these asymmetric threats. Specifically, we predict that pathogen cues condition evaluations of meat differently than they condition evaluations of plants. Data across three studies are consistent with this prediction. In each study, participants who first viewed images of meats paired with cues to pathogens subsequently reported less desire to eat those meats relative to participants in a control condition. In contrast, participants who first viewed plants paired with the same cues to pathogens did not report less desire to eat those plants. Further, a meta-analysis of effects across the three studies (total $N = 398$) indicated that pairings with cues to pathogens affected both desires to eat meats and anticipated tastes of meats, but not desires to eat plants or anticipated tastes of plants. These findings present novel evidence for functionally specialized, pathogen-based meat learning.

1. Introduction

Food selection has posed a consistent and, relative to many species, unique problem for humans and their hominid ancestors for millions of years. In contrast with organisms that eat a narrow range of foods ("specialists," such as koalas, who eat only eucalyptus leaves), humans can and do eat a wide variety of foods extracted from wide-ranging ecologies (Rozin, 1976). The consequences of eating vary across foods. Two foods that contain equally valuable calories and nutrients might vary in their likelihood of causing damage when eaten (e.g., via toxins or pathogens), and two foods that are equally likely to cause damage might contain different calories and/or nutrients. The variety of foods that could be eaten – and the variability in the consequences of eating them – underlies the so-called "omnivore's dilemma" (Rozin, 1976): how do organisms with wide-ranging dietary options select fitness-promoting foods?

Humans use several strategies to resolve the omnivore's dilemma. One such strategy involves observing and imitating others' diets. Because cuisines evolve culturally to incorporate the plants, animals, and food preparation techniques that are beneficial within the local ecology (Billing & Sherman, 1998; Fessler & Navarrete, 2003; Henrich & Henrich, 2010; Rozin, 1976; Sherman & Billing, 1999; Sherman & Hash, 2001), monitoring and copying others' diets allows individuals to narrow the pool of potential foods to those likely to be safe and beneficial. Hence, the psychological mechanisms responsible for shaping food preferences should have important social learning components. And indeed, critical periods in which food preferences are learned occur when children are dependent on adults for food (Cashdan, 1994), and behavioral genetics studies indicate that dietary preferences are influenced by environmental factors shared by twins (e.g., learning from parents; Breen, Plomin, & Wardle, 2006; Hasselbalch, Heitmann, Kyvik, & Sørensen, 2008).

That said, a food selection psychology that relies exclusively upon social learning would encounter multiple problems. Foods that are normatively consumed can have different consequences for different individuals. Some people are allergic to foods that are healthy and safe for others (e.g., in the case of peanuts and peanut allergies), and some people have difficulty digesting foods that others digest with ease (e.g., in the case of foods containing lactose). Dietary risks and requirements also shift within individuals across the lifespan. As one notable example, compounds within some foods (e.g., teratogens, pathogens) cause more damage during the first trimester of pregnancy (Fessler, 2001; Profet, 1992). Food selection strategies that contingently shift across conditions and life stages should have an advantage over those that rely exclusively on social learning. Further, as a semi-nomadic species, humans have consistently encountered new ecologies that present novel and potentially beneficial food sources. Eating only those objects that an individual has observed others eating would fail to take advantage of new food sources—food sources that might be necessary if previously consumed foods become scarce.

Consistent with these considerations, humans adjust dietary preferences and behaviors independent of social learning. Pregnant women, for example, find some previously appealing foods particularly aversive during the first trimester of pregnancy (Fessler, 2002; Flaxman &

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Sherman, 2000), and they report more disgust toward potentially contaminated foods (Fessler, Eng, & Navarrete, 2005). Preferences for specific foods also change based on experiences that have coincided with or followed eating that food. For instance, individuals who experience nausea or vomiting shortly after eating a food often develop an aversion to that food (Rozin, Wrzesniewski, & Byrnes, 1998; Rozin & Zellner, 1985; Seligman, 1970). Even without vomiting, aversions to a food might develop if the food is paired with the experience of disgust (Borg, Bosman, Engelhard, Olatunji, & de Jong, 2016; Rozin, 1986; Rozin & Zellner, 1985), an emotion that provides information regarding the pathogen consequences of contact with an object (Schaller, 2014; Tybur, Lieberman, Kurzban, & DeScioli, 2013).

The omnivore's dilemma, then, is resolved using a mix of social learning, experiential learning, and facultative changes mediated by internal states (e.g., hormones). Each of these strategies involves functional specialization for navigating the costs and benefits of food. Within these solutions, we might expect to observe evidence of further functional specialization for neutralizing distinct problems posed by different foods. Here, we investigate solutions to the problems posed by meat.

1.1. Consequences of consuming meats versus plants

Human diets, while still heavily composed of plants, are rich in meat relative to the diets of our closest primate relatives (Kaplan, Hill, Lancaster, & Hurtado, 2000). These two types of foods, plants and meat, pose unique challenges. Plants sometimes possess physical defenses (e.g., thorns) that damage tissue, and they sometimes contain chemicals that are toxic to humans (see Wertz & Wynn, 2014, for a brief overview). Although some meats can also be toxic to humans (e.g., high levels of vitamin A in liver; ciguatera toxins in fish), the primary threat posed by animal tissue is pathogenic rather than toxic. This threat exists for at least two reasons. First, meat is more biochemically similar to human tissue than plants are, and the pathogens specialized for infecting non-human animals are more likely to infect humans relative to pathogens specialized for infecting plants. Second, pathogens that can infect humans rapidly colonize deceased animals, whose immune systems are no longer able to resist microbes (Fessler & Navarrete, 2003; Sherman & Hash, 2001). Hence, contact with dead animals – especially via the mouth – presents a pathogen threat greater than does contact with plants. This difference in the threats posed by plants versus meat has been implicated as a key reason behind the greater frequency of culturally evolved meat taboos relative to plant taboos (Fessler & Navarrete, 2003; Henrich & Henrich, 2010).

Given that meat and plants present varied threats, people might use different strategies for detecting and neutralizing threats across these food types. Plants' physical defenses, such as thorns and spines, are often visually detectable, and the chemical signatures of their toxins are often detectable via taste. Many of the dangers posed by plants can thus be neutralized by visual inspection or immediate expulsion after an initial taste (Fallon & Rozin, 1983; Wertz & Wynn, 2014). Pathogens within meat are more difficult to detect. The nematode *Trichinella spiralis*, for instance, can be housed within the seemingly healthy muscle tissue of several mammals, and infectious bacteria colonizing a dead animal can be present before producing olfactory or gustatory cues to their presence. Some evidence suggests that pathogen asymmetries between plants and meat contribute to contingent shifts in food preferences. The food aversions experienced by pregnant women, for example, disproportionately concern meat, presumably because gestating mother and fetuses are especially vulnerable to pathogens (Fessler, 2002; Flaxman & Sherman, 2000). The distinct costs imposed by meat might have led to the evolution of another solution to the omnivore's dilemma: functionally specialized conditioning.

1.2. Prepared learning and meat

Many learning mechanisms take a narrow band of stimuli as input—that is, they more effectively produce learned associations when certain stimuli are paired with certain responses (Seligman, 1970). The types of pairings that condition associations are not random; they reflect the classes of stimuli and responses whose pairings had fitness consequences in ancestral environments (Barrett, 2014). In other words, learning mechanisms develop to be "prepared" to make certain associations more readily than others. Some of the first observations of prepared learning involved food (Garcia, Ervin, & Koelling, 1966; Garcia, Kimeldorf, & Koelling, 1955; Garcia & Koelling, 1966). Rats made to feel nauseous, either via radiation or drugs, developed aversions to the taste of flavored water they drank during or prior to the bout of nausea. In contrast, the same nausea did not condition an aversion to audiovisual stimuli. Electric shocks paired with the same stimuli, however, were able to condition aversions to the audiovisual stimuli but not the flavored water. As put straight-forwardly by Garcia and Koelling (1966), "stimuli are selected as cues dependent upon the nature of the subsequent reinforcer" (pp. 123).

Given the greater pathogen threat posed by meats relative to plants, the learning mechanisms underlying food evaluations might have evolved to more readily form associations between meat and pathogens than between plants and pathogens (Fessler & Navarrete, 2003). Consider two examples: (1) cutting open a hyena's intestines and detecting visual or olfactory cues to pathogens versus (2) pulling a tuber from the ground and detecting similar cues to pathogens on the tuber. The first example likely gives reliable information regarding the probability that most hyenas' intestines contain pathogens and, hence, that hyena intestine should be avoided as a food in the future. In contrast, a pairing between cues to pathogens and a tuber likely gives less reliable information regarding the pathogen content of most tubers, since pathogens typically must be transmitted to plants (e.g., by fecal material left from a passing animal). Learning mechanisms that produce preferences for or aversions to foods might thus differentially consider pathogen information for meats and plants. These learning mechanisms would need to take cues to pathogen presence as input—cues such as the visual, olfactory, gustatory, audio, or tactile features that tend to elicit pathogen disgust (Tybur et al., 2013). Emotional experiences often coordinate learning in a functional manner (Al-Shawaf, Conroy-Beam, Asao, & Buss, 2015; Tooby & Cosmides, 2008)—indeed, learning mechanisms investigated in humans generate associations based on fear in a functionally specific manner (Navarrete et al., 2009, 2012; Öhman & Mineka, 2001). By this account, the frequently disgust-eliciting cues to pathogens should more effectively condition evaluations of meats relative to evaluations of plants.

Some evidence is consistent with such a prepared learning account. Multiple studies (reviewed by Fessler & Navarrete, 2003) suggest that adults acquire aversions to meats more often than aversions to other foods. If food aversions are acquired by pairing a food with experiences of disgust (Rozin, 1986; Rozin et al., 1998), more frequently developed meat aversions could point to disgust-based prepared meat learning. Existing research is limited in two ways, though. First, food aversion acquisition has mostly been measured using retrospective reports, which are vulnerable to recall error and lack experimental control that can identify the process (e.g., pairing pathogen cues and visual images of foods versus something else) that led to aversions. Second, more frequently acquired meat aversions could reflect more frequent pairings between meats and pathogens rather than any meat learning mechanisms that take cues to pathogens as input more readily than plant learning mechanisms do.

We build upon existing research by testing whether visual cues to pathogens condition evaluations of meat more readily than they condition evaluations of other foods. Like other tests of functionally specific conditioning hypotheses (e.g., Navarrete et al., 2009, 2012; Olsson, Ebert, Banaji, & Phelps, 2005), we test for differential effects of conditioning when a theoretically pertinent unconditioned stimulus (here, cues to pathogens) is paired with stimuli from different categories (e.g., meats versus plants). In effect, we pair images of different foods with visual cues to pathogens, and we test whether the effects of such pairings differ across meats and other foods.