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Causal Explanations of Human Behavior: From Culture to Psychology or From Psychology to Culture?

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At the beginning of the 21st century, there continues to be much debate regarding the extent to which evolution by natural selection has shaped the diversity of human psychology in the same way it has shaped human physiology and other living systems (e.g., Lewontin, Rose, & Kamin, 1984; Pinker, 2002). There are many sides to this debate, two of which include (a) those who do not employ the principles of evolutionary biology to explain human behavior and, instead, adopt (more or less) the tenets of a standard social science model (SSSM) of psychology (Tooby & Cosmides, 1992) and (b) those who use the logic of natural selection to guide investigations of the human cognitive architecture and the diverse array of behavior it generates. Whereas the former position privileges culture and social structure as causal forces shaping human psychology, the lat-

ter position allows for investigations of how evolved psychological adaptations pattern individual behavior and cultural phenomena. What follows is a brief overview of these two perspectives leading into a discussion of another active front in the behavioral sciences in which causality is being debated: inbreeding avoidance in humans. In the same way cultural patterns of mate preferences reflect the operation of evolved psychological programs that calibrate according to specific environmental contingencies (see target article), culturally expressed sentiments relating to incest, the other side of mating, are also products of our evolved psychological architecture (Lieberman, Tooby, & Cosmides, 2003). Data discussed in the target article by Gangestad, Haselton, and Buss (this issue) as well as those discussed in this article suggest that, at least

for some aspects of human behavior, the arrow of causality points from evolved psychological adaptations to culturally manifest behaviors.

The SSSM of Human Psychology

According to Tooby and Cosmides (1992), the SSSM is a set of assumptions that has shaped (and isolated) the social sciences throughout the last century. Briefly, proponents of the SSSM view social and cultural factors as primary, if not sole, causal forces shaping human behavior (e.g., Frazer, 1908/1910; Geertz, 1973; White, 1948). That is, the diversity of human behavior is a product of few domain-general psychological processes such as “learning,” “imitation,” and “socialization” that guide the absorption and transmission of local rules and norms (i.e., culture; see Tooby & Cosmides [1992] and Pinker [2002] for a thorough discussion of this perspective and its assumptions about human nature). Though many researchers within psychology would not readily categorize themselves as proponents of the SSSM as defined (e.g., stating in objection that they believe the mind does contain specialized “hard-wired” systems for perception and language), many still assume that the arrow of causation regarding human social behavior—including any sex differences that may exist—points from the outer world (e.g., culture, social structure, norms, and so on) to individual behavior and preferences.

One modern instantiation of the SSSM is the biosocial perspective (also known as the social structural theory, social role theory, or social learning theory) discussed by Halpern (2000) and Eagly and Wood (1999). For example, according to Wood and Eagly (2002), “the origins of sex differences are best understood from a biosocial perspective that gives priority to the interaction between the bodily specialization of each sex and the attributes of societies’ economy, social structure, and ecology” (p. 718). The bodily specializations discussed include physiological processes such as placentation and lactation (e.g., Eagly & Wood, 1999) and neuronal pathways and associated neurochemical processes (e.g., Halpern, 2000).

Perhaps most scientists, evolutionary and social learning included, would agree that the production of any phenotype is an interaction between many components, including one’s ecology, social structure, hormonal condition, and sex. However, for bodily specializations (e.g., female specializations for childbearing and men’s greater size and strength) to impact behavior in specific ways as Wood and Eagly (2002) suggested, there have to be information-processing procedures that use this information (e.g., time and energy costs associated with childbearing), integrate it with specific information from the environment (e.g., pathogen load or indexes of effort and skill required for obtaining a

particular resource), and motivate certain behaviors over others (e.g., motivations for seeking a mate with resources). What is needed is a rigorous description of the kinds of cognitive programs and information-processing procedures involved in the production of behavior. This level of analysis (i.e., an algorithmic level of analysis [Marr, 1982]) is absent from biosocial accounts. Rather, proponents of this view rely on domain-general learning programs to describe how a function is achieved. And although it may be acknowledged that humans and other animals are equipped to learn certain contingencies faster than others, social learning theorists suggest that the

predisposition to learn some behaviors or concepts more easily than others is determined by *prior learning experiences* and the *neurochemical processes* that allow learning to occur (release of neurotransmitters) and change in response to learning. ... Thus, learning depends on what is already known and on the neural structures and processes that undergird the learning and remembering processes. (Halpern, 2000, p. 16, italics added)

That is, explanations are deferred to prior learning experiences, whatever they may be, and are framed in terms of the physical arrangement of our neural system—an important level of analysis, but by no means the only one necessary. Throwing together a bunch of neurons and neurotransmitters within a particular ecology does not a social creature create; social behavior is produced by virtue of the information-processing procedures that, for our species and many others, are instantiated in neuronal pathways and that allow for the interaction with specific components of the ecology, social structure, and so on.

Neural structures in the brain process information, and a complete explanation of a particular behavior requires a description of the kinds of information represented and processed. This can be done independent of any knowledge of the physical instantiation of such processes. It seems theorists who privilege the physical organization of neural structures (e.g., the kinds of hormones and neurotransmitters) and physiology to explain human social behavior jump right over an analysis of the information-processing programs required and in its stead insert placeholders such as “learning” or “socialization.” Any attempt to rigorously specify the kinds of information-processing structures required to perform a particular function (e.g., choosing a mate based on certain environmental and physiological contingencies) would quickly reveal that the processes of learning and socialization are severely underspecified and that specialized systems are required to reliably tailor behavioral responses to local conditions. Specialized systems, however, are highly improbable orderings of matter (e.g., see Tooby,

Cosmides, & Barrett, 2003) and require an explanation for their existence. Evolution by natural selection is the only known causal force that can build complex functional designs—the kind that would be required to “learn” complex behaviors or modify behavior based on environmental contingencies. And so this requires knowledge of how and why complex functional mechanisms come into existence.

An Adaptationist Perspective of Human Psychology

In contrast to the SSSM and more recent social structural models of human psychology, an evolutionary framework suggests the human mind consists of information processing neural circuitry that was selected due to the effects such neural circuitry had on the probability of reproduction and survival over our species' evolutionary history (Tooby & Cosmides, 1990). Recurring selection pressures (e.g., pathogens, individuals of the opposite sex, deleterious recessive mutations, patterns of parental investment, predators, and close genetic relatives) led to the evolution of specialized psychological as well as physiological structures and processes that conferred a selective advantage with respect to each pressure. For example, the presence of pathogens over our species' evolutionary history not only led to physiological processes (e.g., elements of the immune system) for rapid detection and elimination but also psychological processes for avoiding contact with substances that were reliably associated with disease causing organisms such as feces, rotten meat, and spoiled milk (e.g., the cognitive program of disgust).

Pathogens are also hypothesized to have exerted a selection pressure on our mating psychology in at least two ways. First, as discussed in the target article, pathogens are capable of perturbing evolutionary developmental programs, one visible result being a body plan that more greatly deviates from perfect bilateral symmetry (see Gangestad & Thornhill, 1997). Consequently, circuitry guiding mate selection is hypothesized to take this information into account and motivate mateships with individuals displaying fewer cues signaling the presence of pathogens (Gangestad & Buss, 1993). Second, pathogens are hypothesized to have been a selective force in shaping inbreeding avoidance mechanisms (i.e., negative mate preferences; Tooby, 1982). Individuals of close common descent are more likely to share similar internal biochemistries. That is, by virtue of having an increased probability of sharing underlying genes, the internal biochemistry of, say, a brother and sister are more similar than the biochemistry of the sister and an unrelated man. Because pathogens are better able to adapt to environments that remain constant from generation to generation (i.e., they become better able to

sequester resources, replicate, and evade components of the immune system), mating with a close genetic relative would have produced offspring that were more susceptible to the harmful effects of pathogens. This is one reason why inbreeding avoidance mechanisms are thought to have evolved (Tooby, 1982).

The purpose of this discussion is to demonstrate how an adaptationist perspective generates hypotheses regarding the kinds of phenotypes (physiological and psychological) that are likely to exist given recurring features of our ancestral past. Furthermore, it allows for the development of potential models of our cognitive architecture. For example, given that pathogens posed the adaptive problem of avoiding contact with and ingestion of substances associated with disease-causing organisms, how did our ancestors know which substances to avoid? What cues correlated with the presence of pathogens? What motivation systems used this information to direct food choice? In general, fleshing out the kinds of information-processing systems required to direct behavior away from random can fortify investigations of human behavior and any variation (e.g., individual or cultural variation) that may arise.

Explaining Individual and Cultural Variation From an Adaptationist Perspective

An understanding of our evolved cognitive architecture provides a legend for interpreting the kinds of variation found within and between groups. For example, many of our psychological adaptations are hypothesized to be sensitive to context and generate behavioral and physiological responses contingent on contextual information. One consequence is that different environments may produce different phenotypes. This has been termed *evoked culture* (Tooby & Cosmides, 1992), and two examples are discussed in the target article (see also Tooby & Cosmides [1992] on patterns of social exchange based on resource variance). As mentioned in the target article, another way groups can become different from one another is through cultural transmission, that is, the passing of information between individuals. But not all information is transmitted—only a subset of all possible beliefs, skills, practices and so forth are transmitted and retained. This narrow state space has led some researchers to suggest that the study of cultural transmission is akin to the study of the epidemiology of representations (Sperber, 1994). If cultural transmission relies on the kinds of representations humans generate and communicate, then an understanding of culture entails the investigation of our cognitive architecture, including the nature of the representations used to process information and guide behavior, a level of analysis not utilized by social learning theorists.

The debate over whether evolutionary principles can be applied to understanding patterns of human behavior seems to become more charged the closer one comes to social behavior (e.g., mating behavior and moral sentiments). For instance, few scientists would likely object to recent findings showing that cultural variation in food preparation is intimately tied to the pathogen load of the environment. Billing and Sherman (1998) sought to understand “why some like it hot” and investigated the use of 43 spices in the meat-based cuisines of 36 cultures. They reasoned that because spices vary in their antimicrobial effects, cultures exposed to greater pathogen loads would utilize a greater number of more potent spices and, specifically, those spices best able to combat the local pathogen composition. They found that as mean annual temperature increased (an index of environmental pathogen load), so too did the percentage of recipes including spices, the number of spices used in total and per recipe, as well as the use of the most potent antimicrobial spices. They tested many alternate hypotheses and concluded that spices help protect foods from pathogens, rendering them safer to eat, and that this is reflected in cross-cultural patterns of food preferences. This example demonstrates how evolutionary hypotheses regarding the kinds of selection pressure that affected human survival and reproduction can help generate hypotheses regarding behavioral variation at the cultural level. If it is possible to explain food choice using these principles, then surely it is possible to apply the same principles to understand other domains of human behavior such as mate choice and moral sentiments.

Summary

Social learning theorists and adaptationist-minded researchers approach the study of human behavior from radically different perspectives. Whereas social learning theorists privilege culture and social structure as the prime causal forces shaping human behavior, adaptationist-minded researchers start with the same biological principles used to study nonhuman behavior to investigate human psychology, including cultural patterns and individual differences. The target article by Gangestad et al. (this issue) discusses how cultural patterns of mate preferences can be explained by considering the kinds of selection pressures that shaped male and female mating psychology (e.g., patterns of parental investment and environmental pathogen load). Oddly, social learning theorists that have voiced strong opposition to this perspective (e.g., Wood & Eagly, 2002) privilege differences in bodily specializations as direct causal forces in shaping mating behavior yet deny the causal role of parental investment theory. But where do they think different bodily specializations came from? Parental investment patterns played a heavy hand in shaping physiological structures (e.g.,

see Trivers, 1972), and if natural selection can differentially shape physical structures in men and women, surely it can also differentially shape psychological processes. In any event, social learning theorists maintain that the culturally derived social roles of men and women shape mating preferences; where roles are more disparate, mating preferences should differ, and where roles are more equal, mating preferences should be more similar. However, Gangestad et al. found little support for this perspective in explaining patterns of cross-cultural mating preferences.

The remainder of this commentary looks at another aspect of mating that can open a window onto the causal factors that play a role in the generation of culturally expressed variation: inbreeding avoidance and the incest taboo. Where do our sentiments relating to incest come from? Does culture or social structure fashion our attitudes relating to incest in the same way proposed for mating preferences (e.g., see Eagly & Wood 1999), or does our evolved psychological architecture pattern moral sentiments and attitudes relating to incest?

Causal Explanations of Human Incest Avoidance: Social Learning or Evolved Psychology?

A Short History of Explanations of Inbreeding Avoidance and the Incest Taboo

At the end of the 19th century, Edward Westermarck (1891/1922), a Finnish social scientist, proposed an explanation for the commonplace observation that family members rarely find one another sexually appealing. Having noted the injurious effects of inbreeding in many species, Westermarck hypothesized that early childhood association, which typically occurs among genetic relatives, serves as an inbreeding avoidance mechanism by triggering the development of a sexual aversion that becomes manifest later during adulthood (Westermarck 1891/1922). This has come to be known as the Westermarck Hypothesis (WH).

In addition to proposing a specialized mechanism that functions to reduce the probability of choosing a close genetic relative as a sexual partner, Westermarck (1891/1922) also proposed an explanation for the origin of the culturally manifest incest taboo. He claimed that the biological systems responsible for the development of sexual aversions between close kin were also responsible for the culturally expressed incest taboo. That is, the explicit cultural prohibitions regarding incest were hypothesized to be a by-product of the natural sexual disinclination that develops between near relatives.

Westermarck's (1891/1922) explanation of the incest taboo differed drastically from the reigning social learning theories of his day, which privileged the cultural incest taboo as the origin, not the consequence, of sexual avoidance behaviors (e.g., Frazer, 1908/1910). In what has become a well-known quote, Westermarck addressed the shortcomings of this alternate explanation:

Moreover, the [social learning] theories in question imply that the home is kept free from incestuous intercourse by law, custom, or education. But even if social prohibitions might prevent unions between the nearest relatives, they could not prevent the desire for such unions. The sexual instinct can hardly be changed by prescriptions; I doubt whether all laws against homosexual intercourse, even the most draconic, have ever been able to extinguish the peculiar desire of anyone born with homosexual tendencies. Nevertheless, our laws against incest are scarcely felt as a restraint on individual feelings. And the simple reason for this is that in normal cases there is no desire for the acts that they forbid. Generally speaking, there is a remarkable absence of erotic feelings between persons living very closely together from childhood. Nay more, in this, as in many other cases, sexual indifference is combined with the positive feeling of aversion when the act is thought of. *This I take to be the fundamental cause of the exogamous prohibitions. Persons who have been living closely together from childhood are as a rule near relatives. Hence their aversion to sexual relations with one another displays itself in custom and law as a prohibition of intercourse between near kin.* (pp. 192–193; italics added)

Though initially well received, the WH and Westermarck's (1891/1922) explanation of the incest taboo gradually fell into disfavor. There were, perhaps, many reasons for this. One main reason was the widespread adoption of the SSSM of human psychology (see Tooby & Cosmides, 1992; Pinker 2002). Whereas the WH implies the existence of content-rich psychological mechanisms designed by natural selection to regulate behavior in adaptive ways, according to the SSSM, the mind is akin to a content-free blank tape that, through processes such as enculturation and socialization, records "relevant" ambient signals from the surrounding social environment, which, in turn, shape an individual's behaviors and attitudes. Applied to the domain of incest, the SSSM (which captures the social learning theories discussed by Westermarck and more recent authors [e.g., Eagly & Wood, 1999]) claims that mere exposure to norms relating to incest automatically generates feelings of sexual disinterest toward family members. The function of this taboo-generated sexual disinterest was thought to have less to do with the dangers of sexual relations within the family (as Westermarck proposed) than the establishment of cooperative relationships between families

via cultural practices such as exogamy (e.g., see Frazer, 1908/1910; Levi-Strauss, 1960; White, 1948).

An Adaptationist Perspective of the WH

From an adaptationist perspective, the WH makes good sense. Due to the selection pressures posed by deleterious recessive mutations and short generation pathogens (Bittles & Neel, 1994; Tooby, 1982), individuals who avoided mating with a close genetic relative and instead chose as a sexual partner someone who did not share a recent common ancestor would have produced healthier, more viable offspring. For this reason, inbreeding avoidance mechanisms are hypothesized to exist in species, including humans, in which close genetic relatives frequently interacted over the lifespan. Indeed, such mechanisms have been found in a number of nonhuman species (Fletcher & Michener, 1987; Hepper, 1991).

What might a human inbreeding avoidance system look like? At least two systems would be required: one that computed genetic relatedness (i.e., a kin detection system) and one that regulated sexual avoidance based on the computed estimates of relatedness. Because it is not possible to directly compare DNA (at least it was not ancestrally), evolution is hypothesized to have shaped kin-detection mechanisms that took as input cues that correlated with relatedness under ancestral conditions. One ancestrally reliable cue to relatedness would have been patterns of childhood coresidence, as the WH suggests. Another cue that would have signaled genetic relatedness is seeing one's biological mother pregnant and caring for (e.g., breastfeeding) a newborn. Indeed, recent investigations have found support for the WH showing that childhood coresidence duration predicts the development of sexual aversions as well as the incidence of sexual behaviors between siblings (e.g., Bevc & Silverman, 2000; Fessler & Navarrete, 2004; Lieberman et al., 2003; Walter & Buyske, 2003; Wolf, 2005). Furthermore, recent evidence suggests that exposure to one's mother caring for a newborn also serves as a cue to siblingship (Lieberman, Tooby, & Cosmides, 2006). Certainly, other cues to siblingship may exist (e.g., facial similarity [e.g., DeBruine, 2002], and olfactory cues based on major histocompatibility complex (MHC) composition [e.g., Wedekind & Furi, 1997]) and it is possible different cues may be used to detect different categories of kin.

The Incest Taboo: Cause or Consequence?

Was Westermarck (1891/1922) correct? Are culturally manifest attitudes (e.g., moral sentiments) relating to incest a by-product of systems guiding the develop-

ment of sexual aversions toward one's own family members? Or, as suggested by traditional SSSM accounts of incest prohibitions, are our moral sentiments a result of the unbiased adoption of ambient cultural norms? These are empirical questions, capable of being explored using the tools of modern behavioral science. If Westermarck was indeed correct and culturally expressed moral sentiments relating to incest are a reflection of underlying biological systems for inbreeding avoidance, then the cues the human mind uses to detect kin and to regulate sexual avoidance should explain the patterns of moral sentiments relating to incest. If, on the other hand, social learning theorists (e.g., Wood & Eagly, 2002) are correct and individuals "learn" preferences based on their social role, then these cues should not necessarily explain patterns of moral sentiments. Rather, culturally transmitted values, either from one's peers or from one's family members, should predict an individual's moral sentiments.

In recent studies, coresidence duration with an opposite-sex sibling has been found to predict the level of moral opposition to third-party sibling incest (Fessler & Navarrete, 2004; Lieberman et al., 2003). These findings support Westermarck's (1891/1922) original notion that the culturally manifest incest taboo and related sentiments are a product of the same mechanisms guiding the development of a sexual aversion toward one's own family members. However, this finding could be marshalled as support for social learning theories: Coresidence duration may predict moral sentiments not because it regulates the development of sexual aversions based on estimates of kinship, but rather because coresidence duration tracks opportunities for the cultural transmission of norms. An alternate hypothesis, then, is that the cultural transmission of sexual attitudes from parents and peers should predict moral sentiments relating to incest. However, as Lieberman et al. (2003) have shown, they do not: Parental attitudes regarding sexuality and an individual's own attitudes regarding sexuality, attitudes that may have been shaped by peers or family members, do not predict moral sentiments relating to incest. In contrast, coresidence duration does predict moral sentiments relating to incest, even after the effects of parental and personal attitudes are statistically removed.

Social learning theorists could suggest, however, that family social structure is the important dimension, not coresidence duration per se. Families with more traditional values and structures may be less likely to divorce, leading to greater coresidence periods for the children. If this is the case, then the sex of the children should not matter; traditional family structure or not, sex is determined by a genetic coin flip. Consequently, coresidence with same- and opposite-sex siblings should generate similar patterns of moral sentiments. They do not. Whereas coresidence duration with an opposite-sex sibling

predicts moral sentiments, coresidence duration with a same-sex sibling does not (see Lieberman et al., 2003). Although difficult to explain from a social learning perspective, this makes sense based on evolutionary hypotheses: Systems regulating sexual behavior should target members of the opposite sex (assuming heterosexuality).

One last possibility is that social learning theorists might suggest family composition matters such that, in families in which both sons and daughters exist, parents are communicating different rules about sexual behavior compared to families in which only sons or only daughters exist. If this is the case, then to the extent that coresidence tracks a separate variable having to do with the communication of norms, it should do so regardless of birth order. That is, coresidence, if truly a proxy for a "norm transmission" variable, should predict moral sentiments regardless of whether an individual in an opposite-sex sibling pair is older or younger. However, adaptationist hypotheses suggest that coresidence duration may be a cue used to detect older siblings and not, necessarily, younger ones. This is because other, more reliable cues may have been available for detecting younger siblings, namely, seeing one's mother pregnant and breastfeeding a newborn. Because the arrow of time forbids younger siblings from seeing their older siblings being born or breastfed, coresidence may be the best cue available for assessing the relatedness of older siblings. Therefore, coresidence duration with an older sibling should predict moral sentiments relating to incest whereas coresidence duration with a younger sibling should not. And this is exactly the pattern found. Moreover, it holds after controlling for sibling age to ensure that opposition is not a result of the presence of prepubescent siblings (see Lieberman et al., 2006). Taken together, these findings militate against social learning hypotheses and suggest that evolved psychological adaptations for guiding mating behavior pattern culturally expressed sentiments relating to incest and not the other way around.

Conclusion

From a social learning perspective (e.g., Eagly & Wood, 1999), mating preferences, including any sex differences that might arise, are due to interactions between physiological specializations and particular attributes of the environment. To the extent there is any scientific merit to this approach, this interaction should specify the entire scope of mate preferences, from those traits preferred in a mate (see target article) to those avoided. That is, the interaction between physiology and the environment (e.g., culture and local resources) should explain the patterns of sexual avoidance and related attitudes in the same way it explains

the patterns of sexual preferences and related attitudes. But, as the target article and this discussion suggest, social learning theories do not explain the patterns of variation found in mate preferences or moral sentiments relating to incest.

The structure of mate choice in humans as well as other social behaviors in humans will, of course, rely on a multitude of factors. However, specific hypotheses are required to rigorously investigate why and how various factors influence behavior and related attitudes. The principles outlined by an adaptationist framework provide a robust set of guidelines for the generation of specific hypothesis regarding ultimate causation as well as the generation of cognitive models specifying proximate procedures that give rise to the array of individual behaviors and, consequently, patterns of cultural variation.

Note

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