

In the Eye (and Ears) of the Beholder: Receiver Psychology and Human Signal Design

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Although the study of signals has been part of human behavioral ecology since the field's inception,¹ only recently has signaling theory become important to the evolutionary study of human behavior and culture.² Signaling theory's rise to prominence has been propelled mainly by applications of costly signaling theory,³ which has shed light on a wide variety of human behaviors ranging from hunting⁴ to religion.^{5,6} Costly signaling rests on the idea that wasteful but highly visible traits and behaviors can be explained as honest indicators of underlying qualities that are otherwise difficult to detect. For example, a laborious hunting technique may serve as a display of skill on the part of the hunter, who may then be favorably perceived by potential mates and allies.⁴ The costs of the activity ensure that the signal is honest, since unskilled hunters will not be able to perform as well. Despite the usefulness of this perspective, many such studies begin by documenting a costly behavior that is then explained with reference to costly signaling theory. Because such behaviors are easy to detect, they may be overemphasized in the literature.⁷ Moreover, costly signaling theory by itself can explain neither all signals nor all aspects of signal design. In this review, we argue that a focus on the role that the psychology of the intended receiver plays in signal design can expand the scope of signaling theory as a promising avenue to explain human behavior.

In fields like psychology and marketing, related concepts such as “perceptual bias,” “unconscious processing,” and “implicit cognition” are used to refer to aspects of human psychology that influence behavior but occur outside of conscious awareness (for example, buying a particular

soft drink and not realizing that we passed an advertisement for that same product a few minutes before). Different terminologies and conceptual frameworks mean that cross-disciplinary dialogue is practically nonexistent. Moreover, little attention is given to the evolutionary history, design, or function of signals. We aim to delineate receiver psychology as a distinct field of study firmly anchored in signaling theory.

The way in which selection shapes a signal is determined by two main factors: the sender's capacity to produce it and the receiver's ability to receive it (see Box 1 for our understanding of what constitutes a signal). Costly signaling theory primarily focuses on the former: Is the sender able to pay the cost of sending the signal? Receiver psychology, on the other hand, deals with the latter: What is the structure of a signal and how likely is an organism to detect and act on it? A focus on receiver psychology allows us to gain insights into two related processes that are difficult to assess within the framework of costly signaling theory: how signal design is constrained by the perceptual and cognitive systems of the receiver^{8,9} and how features of receivers' psychology can be exploited by signalers.^{10,11} Within this framework, costly signaling can be understood as an approach to signaling that focuses on a single subset of receiver psychology: the receiver's skepticism regarding the signaler's honesty.⁷ If a signal is costly, only individuals in good condition or those who are in greater need of receiving the benefits of the display will find it beneficial to produce it. Thus, receivers of such signals have reason

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Box 1. What is a Signal?

One challenge of using the framework of signaling theory is that “signal” has been defined in many different ways over the years. Most recently, considerable debate has hinged on whether animal signaling is best understood as information transfer or influence. “Informational” or “adaptationist” definitions rest on the assumption that true signaling or communication occurs when there is a transfer of information between senders and receivers that, on average, benefits both parties.^{15,83} In a provocative essay, Rendall, Owren, and Ryan¹⁶ argued that such definitions may be too restrictive because they cannot accommodate instances in which one party deceives or exploits the other. For example, a widely used three-part definition is that a signal is “i.) any act or structure which alters the behaviour of other organisms, ii.) which evolved because of that effect iii.) and which is effective because the receiver’s response has also evolved.”¹⁵ Instead, Owren, Rendall, and Ryan²⁰ propose to define signaling as the use of “specialized, species-typical morphology or behavior to influence the current or future behavior of

another individual.” In this view, only the signaler’s traits and actions are necessarily the product of biological evolution, while the receiver’s response may be due to other factors, such as inherent “sensibility” in its perceptual or sensory systems. In essence, this definition is very similar to the first two components of the adaptationist definition stated earlier. Our only caveat is that we need to relax the stipulation that a signal must be the product of biological evolution. Given the wide range of novel and constantly changing signals made possible by language, this is particularly important for the study of human signals. Thus, for our purposes, a signal is any act or structure that is designed to alter the behavior of other organisms, regardless of whether it is a product of natural or cultural selection.

While receivers are expected to evolve resistance to strongly exploitative signals, these may persist if they are sufficiently rare. Moreover, this definition allows us to recognize signals even in situations of disequilibrium. This may be particularly important in the case of humans, and perhaps other

species such as bottlenose dolphins, in which social learning can lead receivers to respond to novel signals in maladaptive ways. Arguments that defend the adaptationist view deal with the problem of deceptive or exploitative signals by qualifying definitions with adjectives, such as “communication” versus “deceptive communication”⁸⁴ or by considering such cases as something altogether different from signaling, such as “coercion.”⁸⁵ We find the addition of more terms to be confusing rather than illuminating, especially since there is no agreed-upon taxonomy of related terminology. Although it is correct that receivers are not always “prisoners” of their sensory systems,⁸⁶ it is also quite true that such systems will shape the range of signals that can be attended to. As humans, we are also, at least to some degree, prisoners of cultural systems that constrain the kinds of stimuli we are likely to respond to. Thus, we favor an influence-based definition of signaling that does not assume symmetrical benefits for senders and receivers and that can accommodate both cooperative and competitive interactions.

to set aside their doubts about the signaler’s honesty.

The animal communication literature includes many theoretical formulations and empirical applications of receiver psychology to the study of animal signals.^{12–14} Despite recent debates on whether deceptive signals constitute true communication (Box 1), all signals can be seen as manipulative in the sense that they are designed and sent in order to change the behavior or another organism.^{10,15,16} Such manipulation or influence may be advantageous for both signaler and receiver (for example, the teaching of skills by parents to offspring), sometimes used out of their usual context to preferentially benefit the signaler (for example,

“friendly” signals sent by con artists), or designed to appeal to receivers’ biases (for example, marketing campaigns). The first case represents instances of honest communication, including costly signaling. Here, however, we are particularly interested in situations where there is potential for exploitation to occur. In the second case, equilibrium can be reached if the costs of occasionally responding to an exploitative signal are lower than the costs of ignoring it over the long term (when used in the “correct” context). Thus, it is the use, rather than the design of the signal, that results in exploitation. In contrast, a third type of signals are produced to appeal to receivers’ inherent sensibil-

ities. As we shall discuss, this may result in mutual benefits, but also exploitation of receivers by senders.

Although selection should favor the evolution of skeptical receivers who ignore exploitative signals and signalers who then economize by not sending such signals at all, it is not always safe to assume that such an equilibrium has been reached. Moreover, because of the speed with which cultural change can occur among humans, situations of evolutionary disequilibrium may be particularly common in our own species.¹⁷ Thus, focusing on receiver psychology can lead to insights regarding deception and exploitation that are difficult to account for in models that assume equilibrium while also enabling us to

make predictions about features of signals other than their cost.

It should be emphasized that many transmission processes and design constraints apply equally well whether signals are a product of natural selection or learned during an individual's lifetime. For example, receivers should resist exploitative signals on an evolutionary time scale, yet may also learn to avoid reacting to novel, exploitative stimuli. Conversely, learned signals will be perceived and attended to only inasmuch as they engage aspects of receiver psychology. In turn, receiver psychology itself may be shaped by both intrinsic and learned biases.

SENSORY TRAPS AND HIDDEN PREFERENCES

Factors intrinsic to the receiver are crucial determinants of which aspects of signals are attended to, acted on, and ignored.^{8,12,13,18} While some features of sensory and perceptual systems are clearly evolved adaptations, others may result in responses that have no clear adaptive function. Arnqvist¹⁹ posits two possible channels by which such responses may arise. First, organisms may have an existing adaptive preference that is co-opted by conspecifics or predators that evolve traits to capitalize on it. These are sensory traps. Second, hidden preferences are by-products of other cognitive capacities or neural structures, "side-effects or contingencies of how the sensory system, defined in its widest sense, of the receiver is constructed."¹⁹ Note that, as mentioned earlier, if sensory traps or hidden preferences result in high costs to receivers, this process may represent the original stages of rapid signal evolution. Otherwise the exploited sex or species would become extinct.¹⁸ However, sensory traps and hidden preferences are not necessarily exploitative. They may simply represent an additional consideration of signal design. For example, some features of signals may take advantage of sensory biases in order to increase their perception over background noise.²⁰ In such cases, although the receiver's response did not evolve specifically as a response

to the signal, the function of the interaction may be beneficial for both sender and receiver.

While explicit applications of receiver psychology to human signals are rare,^{7,21–23} the literature is rich with evidence that both sensory traps and hidden preferences are present and, in some cases, exploited by other parties. Color provides some clues to how visual hidden preferences can have surprising effects on human behavior. Preferential attention to red, for example, may be partly shaped by its long evolutionary history as a sign of aggression.²⁴ Some evidence supports the idea that red is associated with hierarchical displays: Red has been shown to increase perceptions of dominance in men's faces.²⁵ Also, some research indicates that athletes wearing red uniforms tend to win more often than those wearing other colors.²⁶ Alternatively, a preference for red in primate mating displays has been hypothesized to be the result of a preexisting bias related to foraging efficiency.²⁷ In humans, it has been hypothesized that red is a phylogenetically ancient signal of female receptivity and thus mediates perceptions of attractiveness.²⁸ Men have been shown to choose to sit closer to and to ask more intimate questions of women in red versus blue shirts.²⁹ In another study that illustrates the manipulative possibilities of signal use, women preferred to wear a red shirt rather than a green or blue one when they were led to believe they would be meeting an attractive man, but not when they were told they would be meeting an average man or an attractive or average woman.³⁰

Aspects of our aesthetic preferences may also be due to perceptual and cognitive biases.²³ Adaptive biases may also be carried into other, unrelated domains. A preference for symmetrical mates may have evolved as a response to cues of developmental stability and genetic quality,³¹ but such bias may help explain the widespread occurrence of symmetry in pottery, lithics, and other manufactured objects.³² Since there has been little empirical work in this area, it is impossible to rule out alternative explanations of how such biases arise.

Symmetry may be a hard-to-fake signal of the maker's skill rather than the result of a hidden preference. It also may arise simply because symmetrical objects are more useful or easier to manipulate. Future work could address some of these alternatives by, for example, experimentally comparing assessments of highly complex, nonsymmetrical objects and less complex but symmetrical ones.

Several studies have demonstrated the impact of neoteny, or the retention of youthful features into adulthood, on the perceptions and behaviors of others. "Babyfaced" individuals are perceived as being physically weaker, but also more approachable, naive, and honest,³³ are more likely to be seen as having committed crimes through negligence rather than intentionally,³⁴ and are rated higher in job applications that require submissiveness and warmth.³⁵ A well-known example of the exploitation of our preference for neotenyous faces is Hinde and Barden's³⁶ examination of the evolution of teddy bears. The earliest teddies resembled real bears, with low foreheads and long snouts but, as manufacturers redesigned the toys in response to consumer demand, they eventually arrived at the appearance we see today: round faces, large eyes, and short snouts. A preference for neotenyous features may also explain other elements of popular culture, from the changing face of Mickey Mouse over the years³⁷ to the popularity of cartoons.³⁸ The presence of facial neoteny in some pets is another area where further work may reveal a similar bias. It is suggestive that such features appear to be more common in lapdogs such as Pekinese or King Charles Spaniels, which have been specifically bred for close companionship, than in working or sporting breeds.³⁹

Individuals may also change their own appearance in order to appear younger or older, depending on circumstances. It is widely believed, for example, that younger women use cosmetics to appear older while older women use them to appear younger, although we know of no studies that have examined this phenomenon

scientifically. The effect of facial hair on the perception of male faces has received more attention from scholars. Men with facial hair appear older, more masculine, more dominant, and less sociable than do clean-shaven men,^{40,41} and beards enhance the perception of aggressive facial expressions.⁴⁰ In addition, full-bearded men are viewed as being healthier and having better parenting abilities.⁴² It is still unclear under what circumstances men may use beards to influence others' perceptions, but it is certainly an open avenue for further investigation.

Another area in which hidden preferences have been documented is olfaction. Smell detection of human leukocyte antigen (HLA), the human version of the major histocompatibility complex (MHC), has been linked to mate choice and is thought to be an adaptive incest-avoidance mechanism.⁴³ HLA is highly diverse, and preferences for different types vary considerably across individuals. Such preferences may be an unacknowledged component of fragrance and flavor preferences. Milinski and Wedekind⁴⁴ found a significant correlation between individuals who possess similar HLA and their perfume choices for personal use, a relationship that remains consistent after two years. Importantly, preferences for perfume use on subjects' partners were not related to the raters' own HLA, suggesting that perfume choice is used to intensify olfactory signals related to one's own immunocompetence rather than a generalized liking for a particular fragrance.

Hidden preferences (and aversions) may also influence how we perceive auditory stimuli. More than thirty years ago, Morton⁴⁵ suggested that harsh, low-frequency sounds are associated with close-contact aggressive calls across species, whereas high-frequency sounds are associated with nonthreatening, submissive, and fearful positions. He argued that such "sound structures" are linked to the organism's present motivational state and serve as indications of commitment to a course of action (aggression or passiveness) that effectively prevent confrontations with others or

elicit care from parents. More recently, Blumstein and colleagues⁴⁶ have found that nonlinear sound elements, such as unpredictable changes in frequency, distorting noise, and harsh sounds, do indeed provoke arousal and negative valence in human subjects, which suggests an association with threatening situations in ancestral environments. These responses may be exploited in a variety of contexts. For example, an evaluation of the presence or absence of nonlinear analogues in film soundtracks revealed that horror films employ more noise than expected, evoking fearful responses, while dramatic films use more sudden changes in frequency to induce emotional reactions from audience members.⁴⁷

Language, although seemingly arbitrary, may also be influenced by unconscious associations between particular sounds and object shape. Nielsen and Rendall⁴⁸⁻⁵⁰ devised a series of experiments using randomly generated jagged or curved shapes and nonsense words containing stops, strident consonants (e.g., /t/, /k/, /p/); continuous, sonorous consonants (e.g., /l/, /m/, /n/) and both rounded vowels (e.g., /ah/, /oh/, /oo/) and unrounded vowels (e.g., /uh/, /ay/, /ee/). Their results indicate that subjects preferentially used strident consonants to name jagged objects and sonorous ones to name rounded ones when nonsense words were presented in both written or auditory formats.⁴⁸ In addition, subjects had more difficulty learning associations between words and shapes when these were incongruent with the strident-jagged or sonorous-curved rule,⁴⁹ and were more likely than chance to build nonsense words consisting of plosive, strident consonants to designate jagged shapes and rounded vowels to designate curved ones.⁵⁰ While the effects in these experiments are not always strong, the data suggest that the presence of innate biases plays a role in shaping the most important form of human communication. Further research in this area would benefit from standardized experiments across linguistic and cultural groups.

A special kind of hidden preference is peak shift. Peak shift refers to the way that an organism that has been trained to discriminate between rewarded and unrewarded stimuli that vary within the same dimension (such as wavelength, tone frequency, or space) will show the strongest reaction to a novel stimulus that is more extreme – that is, farther away from conditioned stimuli (see Ghirlanda and Enquist⁵¹ for a review of peak shift and related concepts). Thus, while a preference for exaggerated traits may be evolved, the context in which it is expressed can consist of learned associations. Experimental work has shown that a preference for exaggeration, even over a rewarded stimulus, is present in a variety of species, including pigeons⁵² and bees.⁵³ In humans, Spetch, Cheng, and Clifford⁵⁴ have shown that peak shift has an impact on facial recognition. Such a bias may explain how distinctive features of faces are mentally represented and remembered. In addition, a recent study found that viewers rate women wearing high heels as more attractive than those wearing flats. The authors propose that high heels represent "supernormal stimuli" that accentuate feminine characteristics of gait such as shorter strides and increased hip rotation.⁵⁵ Another possibility is that an evolved preference for low waist-to-hip ratios in females⁵⁶ has given rise to cultural phenomena, including the exaggerated features of Paleolithic Venus figurines⁵⁷ or items such as whalebone corsets, wide belts, and Barbie dolls. Although the exact nature and universality of such a preference has been questioned,⁵⁸ its prominence in Western esthetics may be partly explained as a peak shift response. While empirical research in this area is scarce, there may be many other aspects of human behavior that can be interpreted as peak shift responses to exaggerated stimuli.

COGNITIVE BIASES, LEARNING, AND CULTURE

Analogous to the hidden by-products of sensory and perceptual systems, there are also preferences

and biases that arise from more complex cognitive processes. Some of these biases may represent mental shortcuts that provide an advantage over evolutionary time even when they appear to be irrational (“error management theory”)⁵⁹ or heuristics that are no longer relevant in contemporary environments (the so-called “mismatch hypotheses” that underlie much of evolutionary psychology). Because these processes depend on rapid and automatic cognition rather than a cautious evaluation of the domains that activate them, they may be particularly prone to exploitation by others. One example is the use of kinship terminology to elicit altruistic tendencies. Recognizing kin members is important to determine where our cooperative efforts should lie. While there are many nonverbal ways of recognizing kin, humans have developed numerous terminologies that recognize such relationships but also use them in ways that do not correspond with biological ties. The exploitation of a kinship bias is evident in various forms of religious and political rhetoric, although the use of specific terms will surely depend on the intended audience. Qirko^{60,61} has argued that organizations that sponsor suicide terrorism and organizations that require celibacy (such as orders of monks) routinely use the language of kinship to motivate their recruits. Similarly, Salmon⁶² assessed the persuasive power of kin terms by having her subjects read one of three different versions of a political speech. One used terms such as “brothers and sisters,” another replaced those terms with “friends,” and the third used the phrase “fellow citizens.” The first version was more persuasive than either of the other two.

Not all cognitive biases are the direct result of evolutionary pressures. In the context of animal signaling, ten Cate and Rowe^{63,380} differentiate between sensory biases and what they call learning-based biases, defined as “arising from central information processing involving plasticity generated by learning.” In humans, learning is often concerned with arbitrary and abstract associations that have little discernible

adaptive value; in other words, humans have culture. Unsurprisingly, evolutionary approaches have been inconsistent in their understanding or use of the concept of culture.⁷ In our view, the most useful understanding of culture is one centered on its ideational rather than behavioral properties. Most concisely, culture can be viewed as “a system of socially transmitted information.”^{64:140} This definition allows us to consider innate and learned aspects of cognition independently and to examine behavior as a manifestation of either or both.

In the framework of receiver psychology, culture as information can be viewed as the result or source of implicit preferences. In the former case, innate cognitive biases shape the information we supply to others and frame the behavioral expressions that result from it (as in the kinship

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rhetoric examples mentioned earlier). In the latter case, acquiring information through learning may give rise to biases and preferences that are much more plastic in nature and that can vary across groups. For example, in the United States the word and color “green” have become signals of health and closeness to nature. A recent study found that subjects rated clearly nonnutritious foods such as candy bars as healthier if the nutrition label was green. Moreover, the effect was more pronounced in those who reported being particularly health-conscious and thus more likely to be attentive to such indicators.⁶⁵

From this perspective, culture is part of the milieu that determines the design, intensity, and use of signals. A suggestive ethnographic example of how language signals may be used to influence others is provided by Chag-

non’s⁶⁶ work on kin term selection among the Yanomamö. Because cross-cousins (that is, the offspring of siblings of different genders) are preferred marriage partners among the Yanomamö, their Iroquois-Dravidian kinship terminology helps determine a man’s pool of potential mates. Some flexibility is created by the fact that people are typically related to each other in multiple ways. Although one should use the kin term that refers to one’s closest tie to another individual, the rule is often bent. Adult male Yanomamö tend to distort the rule in a way that increases their numbers of female cross-cousins and mothers-in-law (thus making these women’s daughters the men’s female cross-cousins). An additional rule of this system is that same-sex siblings are referred to by the same term. For example, one refers to one’s mother and one’s mother’s sister by the same term. Thus, adolescent males used the terminology not to create more potential marriage partners but rather to create more mothers, which makes sense at an age where food and other forms of aid are more important than lining up potential mates.

As advertisers have long known, marketing offers many potential examples of exploitative cultural signals. There is growing interest in the various sensory and cognitive traps of consumerism.⁶⁷ An example of consumer manipulation via “menu psychology” was recently reported by the New York Times.⁶⁸ Restaurateurs and chefs are increasingly attentive to the presentation of their menus, down to the use of specific fonts, in order to get diners to pay more. For example, the use of descriptive labels that appeal to the senses (“buttery pasta”), evoke geographic locations (“Brooklyn-style pizza”), and those that remind us of kin connections (“grandma’s chicken noodle soup”) are more likely to sell. A study by Yang and colleagues⁶⁹ found that avoiding explicit reminders of pricing, such as using 9 rather than \$9, makes customers more likely to order the expensive items. The restaurant industry has already taken advantage of such biases, giving rise to careers such as “menu engineer” and “menu consultant.”

CONCLUSION AND FUTURE DIRECTIONS

An appreciation of the role that receiver psychology plays in signal design is clearly of value to human behavioral ecologists, but it may also be useful to other types of evolutionary anthropologists. Signaling theory may offer archeologists some insights into aspects of artifact design such as symmetry, pattern, and exaggeration. Such an approach may help paleoanthropologists explain not only features that humans share with many other species, such as a preference for symmetry, but features that are unique to us, such as the emergence of prehistoric art²³ or the origins of language.⁷⁰ Receiver psychology also provides a link between the study of signals and the study of cultural transmission. Understanding the direction of perceptual and cognitive biases can help us interpret the spread and features of various cultural phenomena even when adaptive benefits are unclear.⁷¹ Because memorability is a key to the longevity of culture traits, a focus on features of signals that enhance memory may be particularly fruitful. For example, Lieberman and colleagues⁷² found that frequently used English verbs are more likely to retain irregular past tense forms than are less frequently used verbs, presumably because it is easier to remember irregular forms if they are used often. Another interesting case is Boyer's work on the minimally counterintuitive nature of many religious concepts or MCIs.⁷³ By violating our intuitions about the world in limited ways, ideas such as ghosts and virgin birth have a way of attracting attention and staying in people's memories better than ideas that conform to our expectations or that violate those expectations in extreme ways (see Box 2 for a discussion of receiver psychology and religion).

A receiver-psychology perspective may be particularly illuminating in arenas that involve conflicts of interest. Whining by children has been shown to capture increased attention from listeners and cause physiological arousal in both parents and nonparents,⁷⁴ which may have implications

in modern contexts where nonrelatives are often responsible for much of infant care. Infant crying may be an honest signal of vigor or need, but it also has the potential to exploit parents and others into exceeding levels of investment that are optimal for themselves.⁷⁵ Another area that has yielded insights into the pressures acting on receivers' perceptions is competitive scenarios. Some types of smiles, for example, have been shown to be judged as indicating lower status and less physical dominance to observers, perhaps as a strategy to avoid aggression in potential conflicts.²² Conversely, features such as beards appear to heighten the perception of aggressiveness, and people across populations are accurate in their evaluations of physical strength from nonphysical signals like voices.⁷⁶

Much of what shapes receiver psychology is still largely unknown. For example, sensitivity to particular cues is expected to differ between the sexes and throughout the life cycle (Box 3), but other aspects of individual variation (such as attractiveness, height, or status) may also shape such biases. Recent work suggests that subtle aspects of communication, such as shared eye gaze direction or a similar posture, cue various forms of coordination.⁷⁷ Language style matching (LSM), for example, is a measure based on the unconscious use of function words, such as articles and pronouns, by dyads or groups during normal speech or writing. LSM has been shown to increase cohesiveness in small groups and improve group performance in an experimental task.⁷⁸ Ireland and coworkers⁷⁹ have also found that LSM predicts mutual initial romantic interest in people meeting for the first time, as well as relationship stability in couples independently of conscious measures of relationship quality. Receptivity to other tacit patterns in verbal and nonverbal communication may further explain the seemingly arbitrary preferences that underlie friendship or romantic attachment.

Another set of largely unexplored phenomena in humans are cases of "eavesdropping" that occur when a signal reaches an unintended party,

who then may react in a way that is detrimental to the signaler.^{12,20} Eavesdropping appears to be a factor in men's estimations of others' dominance ranks,⁸⁰ although it is not clear if this is costly to the signaler. Some aspects of language may represent solutions to the problem of eavesdropping. Pinker, Nowak, and Lee⁸¹ note that indirect speech, such as euphemisms and insinuations, may be a way of deterring eavesdroppers who lack the context to make sense of it. In cases where eavesdropping is particularly damaging, we should expect to see increasingly complex codes of indirect speech. Examples include organized crime syndicates such as the Mafia or the use of slang by teenagers and particular subcultures. Some evidence is provided by a recent study that modeled language dynamics and found that in the presence of eavesdroppers languages do tend to grow more complex.⁸² Some languages, such as the Eastern Nilotic Maa, are characterized by a great amount of indirect speech about people and events. Such natural settings may offer opportunities to test these ideas.

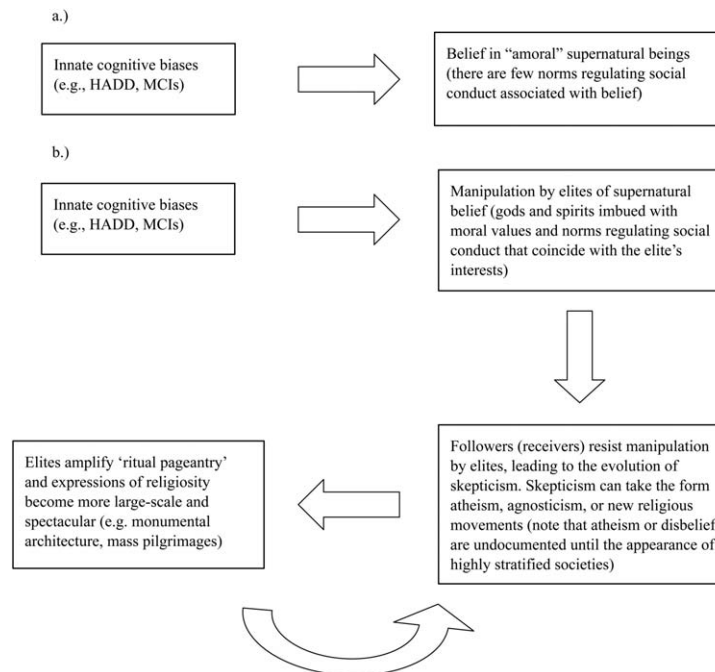
While applications of receiver psychology in humans are widespread in the literature, they come from a wide variety of fields that have little cross-fertilization between them. In addition, the role of sensory and perceptual biases is not always explicitly acknowledged. Signaling theory provides a coherent framework that can incorporate input from various disciplines to shed light on the nature of such biases, the structure and design of signals, the salience of specific signal features, and the consequences of variable signal use. Costly signaling is an important subset of such a framework, but theoretical and empirical work should expand to instances of communication that are exploitative as well as honest. In this regard, it is particularly important to pay attention to the insights and debates that have developed in the animal communication literature. Among humans, of course, the presence of culture means that there is an additional avenue through

Box 2. Culture and Receiver Psychology: Linking Religion and Morality

Recent cognitive approaches have emphasized the notion that religion is a by-product of other cognitive capacities. For example, our bias to infer intentional agents in situations where there are none through a cognitive “hyperactive agency detecting device” (HADD) may have given rise to belief in supernatural beings.⁸⁷ A receiver psychology perspective that centers on the memorability of minimally counterintuitive concepts or MCIs has helped explain why religious beliefs are widespread and easily transmitted.⁷³ Although these theories have shed new light on the study of religion, they explain neither the importance that religious ideas are granted across cultures nor why such beliefs are often linked to moral authority. Taking into account the interactions between senders and receivers may help illuminate this relationship.

The link between religion and morality can be viewed as an arms race between signalers that attempt to influence receivers and the latter’s attempts to resist those efforts.²¹ Evidence suggests that moralizing gods that enforce fixed codes of conduct and judgmental afterlife beliefs are more likely to be found in large, stratified societies than in smaller, more egalitarian ones.⁸⁸ As social stratification emerges, authorities and elites may use religious rhetoric and ritual to bolster unilaterally beneficial political and economic systems. One prediction is that this will result in increased preponderance of the visual, auditory, and even olfactory cues (for example, incense) that make ritual a good example of a multimodal signal.⁶ Multimodal signals (those transmitted through various sensory channels) may be more attention-

grabbing, memorable, and efficient at eliciting associative learning in receivers,⁸⁹ which makes such signals more likely to evolve in situations where the response has long-term or important effects.¹² In response, receivers should develop mechanisms to resist manipulative efforts, such as increased skepticism. Such skepticism make take the form of nonbelief (such as atheism or agnosticism), but may also stimulate the emergence of new religious movements. Skepticism is expected to lead to increasingly intense signaling by senders in efforts to maintain control (Figure 1). Focusing on the vulnerabilities of “follower” psychology may allow us to make predictions about the prevalence and design of rituals and beliefs,²¹ as well as the level of conformity and adherence to specific norms expected across societies independently of political stratification.



Box Figure 1. The cultural evolution of religious belief and morality. (a) Studies suggest that religious beliefs are by-products of innate cognitive adaptations. In small-scale societies and other non Judeo-Christian religious systems, supernatural entities are often amoral and their relationship with followers is pragmatic. (b) In stratified societies, religious beliefs may be manipulated by elites to force moralistic values on followers, who in turn are expected to resist by developing mechanisms of skepticism. As skepticism grows, elites should intensify efforts to manipulate by increasing the dramatic content of rituals and rhetoric, resulting in an arms’ race.

Box 3. Individual Differences in Receiver Psychology

Differences in signal perception within the same species may be found, given diversity in sex, age, or other qualities. In humans, one realm in which systematically divergent biases have been documented is voice perception. Low-pitched male voices are consistently rated as more attractive by women and are perceived as more dominant, while men prefer higher-pitched female voices (for a recent review of these findings, see Pisanski, Mishra, and Rendall⁹⁰). Since voice pitch can be modulated, it is a good candidate for a potentially deceptive signal. People can “disguise” their normal voice by altering its frequency, and such alterations are used consistently by criminals.⁹¹ Fraccaro and coworkers⁹² report that women increase the pitch of their voices when talking to more attractive males. Low voice pitch in males and high pitch in females has been associated with perceptions of likelihood to commit infidelity,⁹³ but the reverse scenario is easy to imagine in confrontations between couples when the suspected cheater is attempting to turn the situation in his or her favor. Recent studies have shown that subjects are more likely to attribute qualities like integrity and physical prowess to male voices that have been experimentally altered to a lower pitch⁹⁴ and expressed a voting preference for candidates of both genders with low-pitched voices.^{94,95} Thus, vocal qualities may have an impact on decisions regarding leadership.

The possibilities for individual variation in receiver psychology are practically endless. For example, Watkins and colleagues⁹⁶ found that taller men are less sensitive to cues of social dominance, such as low voice pitch and facial masculinity, in other men. Smaller individuals may be more vulnerable to physical intimidation and thus in greater need of paying attention to such cues. Fluctuating hormonal levels also affect how signal perception varies. Numerous studies have found that women’s preferences for a range of male facial traits change systematically across the menstrual cycle.⁹⁷ Finally, receptiveness to certain signals appears to change throughout an organism’s life history. While older children exhibit the common adult bias for infantilized teddy bear faces, very young children prefer more adult-featured ones, suggesting an adaptive tendency to find adult faces appealing.⁹⁸ Perhaps the best-known signal that results from development is the practice of “motherese,” or infant-directed speech.⁹⁹ Cross-cultural patterns such as simplified grammar and vocabulary, exaggerated pitch, slow speech, and repetitions appear to communicate adults’ intentions to infants and toddlers most effectively.¹⁰⁰

which our susceptibilities and expectations are shaped. An important strength of this approach is that it can encompass the role of evolved preferences as well as complex cultural phenomena.

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