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by

Sasha Lutz Winkler

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ABSTRACT OF THE DISSERTATION

Evolutionary Perspectives on Play and Laughter

by

Sasha Lutz Winkler

Doctor of Philosophy in Anthropology

University of California, Los Angeles, 2024

Professor Erica A. Cartmill, Co-Chair

Professor Susan Emily Perry, Co-Chair

Laughter is a universal human behavior that likely evolved from a play vocalization in the common ancestor of great apes. Comparative research on play signals, their associated emotions, and their cognitive effects can shed light on laughter's origins and on human sociality more broadly. This dissertation investigates the evolutionary roots of play and laughter through theoretical and empirical studies in humans and our primate relatives. Chapter 1 provides a general introduction to the evolution of play and laughter and their significance for our understanding of human emotion, cognition, and social bonding. I highlight the importance of social bonds in research I conducted on the development of sex differences in play in white-faced capuchins and on playful teasing behaviors in apes. Chapter 2 is a literature review synthesizing research on laughter and play vocalizations across the animal kingdom, adding support to the theory that human laughter likely evolved from a pant-like play signal. I present a

comprehensive review of species that vocalize during play, along with acoustic descriptions of the calls. I also discuss potentially unique aspects of human laughter and implications for the evolution of language.

Chapters 3 and 4 describe a set of cognitive bias experiments I conducted with humans and one of our closest ape relatives, the bonobos. I tested whether hearing laughter leads to optimism bias in judgements of ambiguous stimuli, which would indicate a positive affective response. The study in chapter 3 found that bonobos tended to approach ambiguous stimuli more often after hearing unfamiliar conspecific laughter. However, the study in chapter 4 did not find evidence that humans show greater optimism bias or more positive self-reported feelings after hearing infant laughter. In chapter 5, I conclude with a general discussion of these findings and future directions. While only apes produce human-like laughter, many animals have play vocalizations that appear to involve positive emotions. Laughter perception and contagion likely include ancient emotional mechanisms, and perhaps some derived ones. Further comparative research can illuminate the extent to which emotional and behavioral contagion underpin play vocalizations across species and the unique psychosocial mechanisms associated with human laughter. Overall, this dissertation grounds the study of laughter in evolutionary theory and research on animal play, using an interdisciplinary approach to tackle both proximate and ultimate explanations for this ubiquitous behavior.

The dissertation of Sasha Lutz Winkler is approved.

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2024

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

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1. Introduction

1.1 General introduction

In the quest to identify what makes us human, many have turned toward our species' sociality. Our seemingly unique social traits include our ability and eagerness to cooperate, our large and complexly layered social groups, our predilection for social learning, and our care for the young, old, and sick. In contrast to most other animals, humans enjoy the company of large groups and dedicate much of our time and effort to social life—including forming, assessing, and maintaining social bonds, the relationships that tie us to friends and family.

By researching the behavior of our animal relatives, we can investigate the evolution of these traits that seem to define our species. The comparative method can inform us about when various aspects of our sociality most likely evolved. In particular, comparative research on humans and our closest living relatives, the great apes, gives us specific insight about shared aspects of ape sociality that set humans up for success in the social domain, and derived aspects that evolved after humans split from a common ape ancestor.

Research on animal prosociality and social bonding has gained increasing momentum in recent decades. Historically, animal behavior research tended to focus more on negative or anti-social behaviors, such as aggression and stress-related behaviors. Nevertheless, the cognitive revolution and increased interest in positive psychology have trickled into animal research, with increasing attention given to studying animal emotions and positive social behaviors (Bekoff, 2008; Nelson et al., 2023; Rose, 2020). This is long overdue, as we know people are strongly motivated to play and laugh with others and spend large amounts of time and effort playing in

various forms (Pellegrini, 2009). A comparative focus on play and signaling during play has the potential to ground these tendencies in our evolutionary history.

Although there is a substantial scientific literature on animal play (e.g., Burghardt, 2005; Fagen, 1981), specific research on vocal signals of play and playful teasing behaviors is relatively rare (Eckert et al., 2020; Winkler & Bryant, 2021). More research in these specialized areas has the potential to shed new light on old problems about the evolutionary benefits of play. Both play signals and playful teasing offer rich opportunities for comparison to human laughter and teasing (especially nonverbal teasing in preverbal infants)—thus speaking to broader literatures in psychology and childhood development.

Research in this dissertation draws upon theories from comparative cognition, evolutionary anthropology, ethology, the psychology of emotion, signaling theory, and interdisciplinary research on the evolution of language and cooperation. I apply these diverse literatures to the study of play, communication, and positive emotion both in humans and animals. Specifically, these studies aim to improve our understanding of the evolutionary origins of human laughter, patterning of auditory play signals across animals, and the cognitive and emotional effects of laughter perception in humans and bonobos, one of our closest primate relatives. I approached these topics from both theoretical scholarship (Chapters 1-2) and by conducting a series of comparative experiments (Chapter 3-4). Chapter 2 represents my scholarship focused on ultimate questions about playful signaling across the animal kingdom and its relationship to human laughter. Chapters 3 and 4 discuss a set of experiments conducted in bonobo and human subjects, focused on proximate questions about the emotional and cognitive underpinnings of laughter.

For these studies, I assume the Complexity and Continuity Hypothesis developed by Davila-Ross and Dezecache (2021), which asserts that human laughter likely evolved from a play-specific signal that was already present in the ancestor to all great ape species (at least 10–16 million years ago). Using this framework, we can ask questions about the ways that humans have evolved derived features and functions for laughter, separate from those in extant great apes, including cognitive and perceptual features. The experiments in chapters 3 and 4 used a nonverbal test of emotion, which measures a subject's optimism bias when judging ambiguous stimuli (i.e., "cognitive bias test" or "ambiguous judgement test;" Harding et al., 2004; Rygula et al., 2012). By running a similar experiment in both humans and bonobos, I aimed to test whether human and bonobo laughter is underpinned by a similar emotional state. This paradigm is common in the animal welfare literature for assessing emotional valence but has only been rarely applied in research on human behavior. The study described in Chapter 3 is the first application of the paradigm in bonobos.

A common theme I explore throughout my research is the concept of ambiguity or uncertainty. Social play is highly ambiguous, as it involves cooperative interactions with elements of aggression, flexible behavioral forms, unclear immediate fitness benefits, and high risks of misinterpretation. Investigating *why* play behaviors are ambiguous may reveal insights about their function, especially in the case of playful teasing. Understanding *how* ambiguity is reduced, for example through acoustic signals, implicates the sociocognitive processes and other mechanisms that facilitate play. This in turn can help to contextualize human laughter as a signal with its evolutionary roots in play. Finally, in my experimental work, I deliberately introduce stimuli with uncertain outcomes to generate variation in behavioral responses. These ambiguous

stimuli allow me to measure the extent to which subjects exhibit optimism bias in their expectations of rewards.

Play and playful signals can be used as signs of positive welfare or well-being across species. Play is rare when animals are stressed or when basic homeostatic needs are not met (Burghardt, 2005). In humans, laughter and play are implicated in physical and emotional health. Laughter is associated with increased endorphin release, decreased stress hormones, and other cardiovascular health benefits (Dunbar et al., 2012; Manninen et al., 2017; Yim, 2016). Laughter and humor are also used in psychotherapy as tools for coping with stress (Yim, 2016). Basic research in these areas may ultimately improve our ability to promote health, welfare and positive mental well-being in both humans and animals.

1.2 Primate play and social bonding

To better situate the following research on signaling during play, it is helpful to first zoom out and consider evolutionary perspectives on play itself. Several lines of research I have conducted during my PhD have aimed to clarify functions of play, first by examining patterns of play across the lifespan as it relates to socioecological factors (Winkler & Perry, 2022) and secondly by describing and defining playful teasing as a unique class of behavior in great apes (Eckert et al., 2020; Laumer et al., 2024).

In Winkler and Perry (2022), I investigated the development of social play, solitary play, and grooming in wild white-faced capuchin monkeys (*Cebus capucinus*) over an 18-year period, using longitudinal data from the Lomas Barbudal Monkey Project in Costa Rica. We found that rates of both social and solitary play decreased with age, with the exception of social play in males, which increased in the early juvenile period before declining. Male and female capuchins

showed different patterns of social play over the lifespan, with males playing more than females during most of the juvenile period, but we did not find substantial sex differences in solitary play rates. Males and females also exhibited different patterns of grooming: males participated in grooming at low rates throughout their lives, while adult females participated in grooming at much higher rates, peaking in early adulthood around age 11 before declining. We argued that this could be evidence of male and female capuchins adopting alternative social bonding strategies, through the use of different behaviors (social play for males vs. grooming for females) and by varying the developmental timing of the behaviors to maximize fitness. For example, the peak in social play rates for male capuchins occurred right before one of the most dangerous periods in their life history, when they must leave their natal groups, band with other males, and attempt to join potentially hostile new groups. This emphasizes the importance of using longitudinal data and developmental perspectives on social behaviors, since these patterns would not be apparent from cross-sectional data alone (Winkler & Perry, 2022).

In short, Winkler and Perry (2022) found evidence to suggest that play is critical for the development of sex-specific social strategies in a wild primate. Our results were consistent with two functional hypotheses of play: the practice hypothesis, which posits that play allows young animals to practice physical and tactical skills needed in adulthood, and the bonding hypothesis, which posits that playing with others allows animals to form, test, and learn about social bonds. In particular, testing of social bonds might be elaborated in playful teasing, a cognitively rich form of play I have worked to define in great apes.

1.3 Testing bonds through play: the case of playful teasing in great apes

Defining playful teasing

Playful teasing is a type of dyadic interaction that exists on the border between play and aggression. It is characterized by provocative, mostly one-sided behaviors from the teaser directed toward a target, often accompanied by positive markers indicating playfulness or amusement on the part of the teaser (Eckert et al., 2020; Reddy & Mireault, 2015). While verbal teasing is perhaps more recognizable, nonverbal forms of playful teasing have been described in both preverbal infants and non-human primates. Playful teasing is interesting because it appears to be cognitively sophisticated. Teasers might intentionally surprise or violate the expectations of their targets as a way of playing with other's expectations. At the very minimum, teasers must engage in prediction and monitoring of the target's response to their highly ambiguous behaviors (Eckert et al., 2020; Reddy, 1991). Playful expectation violation is thought to be a key aspect of humor (McGraw & Warren, 2010). Therefore, playful teasing in preverbal infants and great apes could represent a form of proto-humor (Eckert et al., 2020).

Eckert, Winkler, and Cartmill (2020) reviewed the literature for evidence of playful teasing in great apes and other non-human primates. We looked for instances of three types of playful teasing that had previously been described in preverbal human infants: offer-and-withdrawal of objects, provocative non-compliance (i.e., provocatively doing a behavior that was requested incorrectly or refusing to do something), and disrupting others' activities (Reddy & Mireault, 2015). We found examples of all three types of interactions in the existing literature on great apes. Although playful teasing had been described most thoroughly in chimpanzees and other apes, reports of potential teasing behaviors had also been published in several monkey

species. Other animals might also engage in playful teasing, such as offer-and-withdrawal of toys in domestic dogs (Eckert et al., 2020).

Despite all this scattered evidence in the literature, previous research in apes had largely excluded playful forms of teasing from any systematic analysis and instead focused on quasi-aggressive "harassment" behaviors, such as repeated poking, hitting, or other potentially irritating behaviors. Eckert et al. (2020) hypothesized that playful forms of teasing are common in apes and may serve prosocial functions, such as learning about social rules or facilitating social bonding through positive shared experiences (Eckert et al., 2020).

Building upon this line of research, Laumer, Winkler, Rossano, and Cartmill (2024) took a more empirical approach to describe playful teasing from direct behavioral observations of great apes. Using a video dataset of four groups of zoo-housed great apes (chimpanzees, bonobos, gorillas, and orangutans), we developed a set of behavioral coding criteria for identifying playful teasing interactions. We additionally recorded behaviors that are typically used as signatures of play in animal research (Burghardt, 2005). The most common teasing behaviors we observed were generally provocative in nature, such as repeated poking, hitting, or swinging/dangling body parts in the target's field of vision (see Laumer et al., 2024 for a complete list of these behaviors). The behavioral forms suggest that teasing is designed to provoke attention or a response from the target, although there was a large degree of flexibility in the exact behaviors used. In contrast to typical rough-and-tumble play, playful teasing interactions were usually highly asymmetric and resulted in a variety of responses from the target, in ways that appeared mutually enjoyable in some cases but not others. Targets typically responded with ignoring, moving away, or mildly aversive behavior, or (less commonly) with play or affiliation. They almost never responded with aggression, fear or submission. Playful

teasing also exhibited markers of intentionality that are used in analyses of gestural communication, including response looking, elaboration, and repetition. It was mostly observed taking place in relaxed contexts, similar to playful teasing in human infants. Across the four great ape species we investigated, there were many similarities in how playful teasing manifested overall, but the frequency and the specific behaviors used (e.g., hitting versus swinging objects) appeared to vary across species and across different age classes. However, we were unable to measure comparable frequencies of behaviors across species, due to the limitations of using focal follow data from only one juvenile per group per species (with varied demographic compositions in each group).

The function of teasing behaviors is not well understood, although several have been proposed for less playful forms of teasing. Depending on the proportion of playful and aggressive elements, it is possible that there are multiple functions. De Waal (1996) proposed that teasing in chimpanzees was used to learn about authority and the social environment (de Waal, 1996). Similarly, Pusey (1990) and Kummer and Goodall (1985) proposed that the teasing behaviors they observed in chimpanzees were younger males "challenging" adult females (Kummer & Goodall, 1985; Pusey, 1990). This led some researchers to hypothesize that teasing is a way for chimpanzees to test or improve their rank (Adang, 1984, 1985; Nishida, 2003). More aggressive forms of teasing may simply offer an aggressive outlet or a means to reinforce the dominance hierarchy. On the other hand, playful teasing, especially instances with higher prevalence of play markers (e.g., play face) may be a complex form of social play—the function of which is also highly debated (Pellis & Pellis, 2017; Špinka et al., 2001; Symons, 1978). Teasing could be one-sided play (only enjoyable for the teaser) or an attempt at reciprocal play

with mutual enjoyment, in which case it may bring individuals closer together emotionally and serve a bond-strengthening function.

The possible functions of teasing so far discussed can be grouped into the following categories: (a) enjoyment/play, (b) learning about the social environment or social norms (relatedly, learning about other minds, see Eckert et al. 2020), (c) dominance rank improvement, (d) dominance rank enforcement, or (e) aggressive outlet.

Zahavi's "testing of a bond"

A novel function I propose for playful teasing is a bond-testing function. Teasing interactions include elements that would make them an effective way to test social bonds. Amotz Zahavi first described his "the testing of a bond" theory in a 1977 paper, which was later expanded into a chapter in Amotz and Avishag Zahavi's seminal book "The Handicap Principle" (Zahavi 1977; Zahavi and Zahavi 1997). Zahavi proposed that humans and some other animals might benefit from "tests" of their social bonds, in order to gain information about the quality and strength of the bond. In other words, certain behaviors could function to test the social commitment of the partner. The tester would benefit from information about their partner's likelihood of future cooperation, provisioning, nonviolence, mating, or some other fitness-relevant interaction.

Fittingly, as it is explained in a book about the handicap principle, Zahavi situates this theory on bond testing within theory about costly signaling in general. According to signaling theory, communication systems are difficult to evolve because they are vulnerable to cheaters who will send false or dishonest signals to gain marginal benefits over others. Using game theory, one can show that cheaters will always have an advantage in a population of honest

signalers, thus cheaters will become more frequent via natural selection and eventually the communication system will collapse as it ceases to be net beneficial for most individuals. However, if signals are sufficiently costly, they can become too difficult to fake. Having a cost to generating a signal is a way to guarantee the signal's honesty (Maynard Smith, 1994). Grafen (1990) strengthened Zahavi's handicap principle theory by using a game theoretic approach to show that strategic costs could create signal honesty and adding the requirement of differential cost, i.e., the requirement that low-quality individuals have to pay a higher cost than higher-quality individuals for giving high-quality signals (Higham, 2014).

According to Zahavi's bond testing hypothesis, an individual (A) who wishes to test their bond with a social partner (B) must behave in a way that imposes some cost for B in order to get a reliable signal from B about B's attitude toward A. If the cost of the "test" is too great compared to the value of the relationship to B (or at least, the benefit of not harming the relationship), B may act negatively in response to the test, for example, by disengaging or directing aggression toward A. However, if B strongly values the relationship, B will be willing to tolerate the cost. In assessing B's tolerance to this cost, A can therefore glean valuable information about the strength and quality of their social bond with B.

Put another way, the logic of this theory is that if the relationship is valuable to the receiver of the test, the receiver will tolerate some cost from the tester in terms of time, annoyance, distraction, or unpleasantness of the stimulus. This interaction may also be risky or costly for the tester because there is a chance that the receiver will not tolerate the unpleasant "test" behavior. The tester may receive aggression, social embarrassment, or some other unpleasant outcome (for example, increased risk of disease as in the case of capuchin eye-poking rituals described later). The key aspect of the bond test, however, is that the one receiving the test

incurs a cost. As summarized by Zahavi (1977), “my hypothesis requires that a reliable test of love should be stressful.”

Again borrowing from signaling theory, the distinction between a signal and a cue is helpful for understanding Zahavi’s bond testing hypothesis. As defined by Maynard Smith and Harper (2003), a signal is a behavior or structure that evolved for the purpose of altering the receiver’s behavior, and is adaptive for both the signaler and receiver. Signals are effective because the receiver has also evolved to be affected by the signal (Scott-Phillips, 2008). A cue, on the other hand, is a behavior or structure that contains information that may be used by the receiver to guide its behavior but did not evolve in the sender for that purpose. A cue is not typically adaptive for the sender to emit. If it were, it would likely evolve into a signal. According to this definition, any social behavior could act as a cue to give a social partner some information about the strength or quality of their bond. However, by definition, cues have not evolved for that purpose. Zahavi’s bond testing hypothesis therefore is most usefully applied to signals. It describes evolved behaviors in which the one being tested produces an honest signal of bond quality, benefitting both the signaler and the bond tester who receives the signal. Signaling the value of the relationship should benefit the signaler (on average) if it helps them coordinate or cooperate with the tester in the future. On the other hand, bond testing could be at risk of manipulation, as signalers might have an interest in obscuring their level of commitment if they can deceive their partners into undue social benefits.

Zahavi’s bond testing hypothesis did not gain as much traction as other aspects of the handicap principle, which is now a key tenet of signaling theory and spawned a substantial literature on costly signals of mate quality (Grafen, 1990; Higham, 2014; Johnstone, 1995; Maynard Smith & Harper, 2003). One reason for this is that there are methodological challenges

to measuring social bond quality or certainty, and difficulties with predicting what the outcome of these "bond-testing" behaviors should be (if all goes well, there may be no change in behavior, and the status quo should continue). Another element of difficulty is that bond testing may not be beneficial in many taxa. I would expect bond testing to be most beneficial for species in which dyads cooperate or help one another, and when the cost/benefit ratio to cooperation varies substantially across time within the same dyad. For example, mother-infant bonds are important for many animals, but it is unnecessary for the infant to test the mother's level of social commitment if that level is predictably high as a result of selection pressure.

Despite the methodological difficulties, there have been a number of studies in nonhuman primates that support the existence of Zahavian bond testing behaviors. A good example of this is greetings in male baboons. Smuts and Watanabe (1990) described olive baboon greeting rituals in which males present to and mount one another and handle each other's testicles ("diddling"). Because this is so risky and requires some element of tolerance or trust from the one who is "diddled," this is a good candidate for a bond-testing behavior. Smuts and Watanabe (1990) argued that greetings serve as a test of the social partner's willingness to provide future coalitional support because they observed more symmetrical greetings among older males with more stable and reciprocal coalitionary bonds. Dyads with more tense relationships appeared less likely to successfully execute greeting rituals (Smuts & Watanabe, 1990).

Whitham and Maestripieri (2003) studied similar greetings in Guinea baboons. Greeting (i.e., diddling) was correlated with high frequencies of grooming, contact, and proximity within the dyad, and not associated with aggression or reconciliation. Furthermore, rank could not explain the greeting patterning, except that low-ranking males received more greetings (i.e., they were more often the one being diddled). The authors interpreted this as an increased need for

low-ranking males to test other males' levels of tolerance and support (Whitham & Maestripieri, 2003). However, it is important to note that some of this literature lacks nuanced discussion of same-sex sexual behaviors, with more recent work by queer scientists criticizing the euphemistic or problematizing language in the research on baboon greetings (Cunningham & Benítez, 2024).

Another intriguing example of Zahavian bond testing is seen in the rituals performed by white-faced capuchin monkeys. These rituals are described by Perry and Smolla (2020) as idiosyncratic interactions between capuchin monkey dyads that involve long periods of repetitive behaviors, often including game-like elements or serious risk of bodily harm, while maintaining unusually high levels of attentional focus. Examples of these rituals include capuchins inserting their fingers into the eye, nose, mouth, or ear of a partner, inserting the partner's fingers into their own orifices, and plucking hair from the partner and passing it back and forth via the mouth.

Perry and Smolla tested three alternative hypotheses for the evolutionary function of these ritual behaviors (Perry & Smolla, 2020). Hypothesis 1 posited that the function of rituals is to establish or maintain social bonds. Hypothesis 2 proposed that they function to test social bonds (according to the Zahavian bond testing hypothesis). Hypothesis 3 proposed that rituals function to bolster cohesion across the entire social group. Each of these hypotheses offered different predictions about the types of behaviors that were expected to comprise the rituals, and the characteristics of the dyads that engage in them. According to hypothesis 1, rituals should be most common in dyads that are emotionally close and spend a lot of time in proximity, affiliation, or cooperation. According to hypothesis 2, rituals should be most common in dyads that have uncertain relationships but not such poor quality relationships that the rituals become too risky (such as dyads with intermediate to low levels of interaction and/or intermediate

relationship quality). As noted above, bond-testing behaviors should also involve some risk or discomfort for the social partner. Finally, the third hypothesis predicted that rituals should have consistent behavioral forms across the group and be performed by multiple individuals at once. The group cohesion hypothesis (hypothesis 3) was not supported because essentially all ritual interactions were dyadic, and between-dyad consistency in form was low. Instead, the authors found the strongest support for the bond-testing hypothesis (hypothesis 2), and modest support for the hypothesis that rituals establish and maintain bonds (hypothesis 1).

A final example of potential bond-testing behaviors are the "gargle" and "twargle" vocalizations of white-faced capuchins (Duchesneau et al., 2022). These are very loud and acoustically noisy vocalizations typically given at close range from infants or females, especially toward the alpha male of the group. Duchesneau et al. (2022) suggested that these vocalizations could function as a bond-testing mechanism, because the intrusive acoustic features appear designed to impose a cost on listeners (i.e., "loud, guttural stimuli that are extremely irritating to the human ear, and seemingly to monkeys as well, because they often elicit aggressive responses"). These impose attentional costs, as loud stimuli are difficult to ignore, and possibly physiological costs due to stress on cochlear cells (Casale et al., 2024). Responses vary widely from aggressive to affiliative, and therefore could provide the tester information about their partner's relationship investment. Infanticide from new alpha males is a major cause of infant mortality in white-faced capuchins. The patterns of senders and receivers suggested that these vocalizations may be used as a means for mothers and infants who are at the highest risk of infanticide to gain important relationship information from the alpha male about the probability of his future infanticidal behavior (Duchesneau et al., 2022).

Functions of playful teasing

The playful teasing behaviors of great apes are good candidates for Zahavian bond testing because they impose a cost on receivers. Annoying, attention-grabbing behavior, imposition on personal space, or quasi-aggressive displays are assumed to be unpleasant for the target. The willingness of the target to tolerate teasing may vary according to the value that the target places on his or her relationship with the teaser. The target's reaction (which can vary from tolerance to play to aggression) can therefore offer information to the teaser about the quality of their social bond. The bond-testing hypothesis for teasing behaviors predicts that teasing should be most common in dyads where the relationship is uncertain, but still secure enough to minimize the risk of retaliation to the tester (Perry & Smolla, 2020). The quality or tenor of the social bond could be operationalized as the level of affiliation (or level of affiliation relative to aggression). Intermediate quality relationships should be the most uncertain, and thus tested most often.

Other patterns may either rule out or offer support for the other functional hypotheses. For example, if teasing is most common in dyads with close, secure, and affiliative social bonds, that would lend support to the typical play/play initiation hypothesis but not to the bond testing, rank improvement, or aggressive outlet hypotheses. Under the rank improvement hypothesis, teasing is expected to be directed up the hierarchy, and most likely toward individuals closer in rank to the teaser (for example, it would be unlikely that a low-ranking chimpanzee female would seek to improve her rank by teasing the alpha female; rather, she should target someone who ranks just above her). In contrast, under the rank enforcement hypotheses, we would expect teasing to always be directed down the hierarchy. Under the aggressive outlet hypothesis, teasing should be contingent on having recently received aggression or experienced some other source of frustration (relatedly, it might correlate with cortisol or testosterone levels). The age of the

interactants could also be an informative variable. Under the hypothesis that teasing facilitates learning about the social environment, teasing is expected to be initiated most often by juveniles and decrease with age (as older individuals have already learned about appropriate social boundaries and other social information). Since rates of play tend to decrease with age in most species (Bateson & Martin, 2013), this might also lend support to the idea that teasing is merely a complex form of social play.

To clarify playful teasing functions in apes, future research should analyze the types of dyads that tend to engage in teasing interactions, particularly by looking at the patterning of age, sex, or dominance classes of the individuals involved. Another interesting future direction for this research would be to investigate the use of signals during playful teasing interactions. The timing of signals during behavioral sequences could give us a better understanding of when and why it is enjoyable to participate in teasing, thus showing possible cost/benefit tradeoffs for the interactants.

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2. Animal play signaling and its relationship to laughter

2.1 Play vocalisations and human laughter: a comparative review

Abstract

Complex social play is well-documented across many animals. During play, animals often use signals that facilitate beneficial interactions and reduce potential costs, such as escalation to aggression. Although greater focus has been given to visual play signals, here we demonstrate that vocalizations constitute a widespread mode of play signaling across species. Our review indicates that vocal play signals are usually inconspicuous, although loud vocalizations, which suggest a broadcast function, are present in humans and some other species. Spontaneous laughter in humans shares acoustic and functional characteristics with play vocalizations across many species, but most notably with other great apes. Play vocalizations in primates and other mammals often include sounds of panting, supporting the theory that human laughter evolved from an auditory cue of laboured breathing during play. Human social complexity allowed laughter to evolve from a play-specific vocalization into a sophisticated pragmatic signal that interacts with a large suite of other multimodal social behaviours in both intragroup and intergroup contexts. This review provides a foundation for detailed comparative analyses of play vocalizations across diverse taxa, which can shed light on the form and function

of human laughter and, in turn, help us better understand the evolution of human social interaction.

Introduction

Play is common in a few lineages of the animal kingdom, being especially prevalent among some birds and many mammals (Burghardt, 2005). Many theories of the function and types of play have been proposed, although difficulties exist, including but not limited to the basic problems of defining, identifying, and quantifying supposed play behaviour. Here we focus on social play—the most frequently described type of play in mammals. Despite its frequency, categorizing this behaviour can be problematic, even in humans. The playful laughs and screams of children during wrestling, tickling, and chasing can indicate a certain non-serious mode of interaction, but the less obvious examples of social play present challenges. Consider subtle joking between adult antagonists, or verbal, emotional jousting between close social partners—identifying components that constitute play and how they relate to other social dynamics can be complex (Gibbs et al., 2014). The same can be true for nonhuman animals as well, compounded by challenges in identifying mental states like playfulness, and the inability to use self-report.

Smaldino et al. (2019) explored the evolutionary dynamics of play behaviour, and using a simple formal model, argued that play can evolve into different types depending on various cost/benefit tradeoffs associated with life history factors. For modeling purposes, they categorized play as either simple or complex, while acknowledging that these types likely exist on a continuum. They provided preliminary evidence that complex play—which likely enhances sociocognitive and physical motor development—requires significant investment, but can confer long-term benefits. In many cases, complex play manifests as mock fighting, and is thought to

facilitate the practice and development of interactive fighting skill and calibrate defensive maneuvering (Byers & Walker, 1995; Symons, 1978). An important component of this collaborative activity is that while engaged in play fighting or chasing, animals need ways to signal that their actions are neither dangerous nor done with harmful intent (Bateson, 1955). Animals must also maintain fairness in order for play interaction to be evolutionarily stable (Dugatkin & Bekoff, 2003; Palagi, Cordoni, et al., 2016). For play fighting to remain playful, species have evolved various rules of combat that, if followed, ensure that the play fighting does not escalate to aggression (Pellis & Pellis, 2017). These rules managing play have co-evolved with communicative behaviours, including visual, auditory, and olfactory signals (Aldis, 1975; Bekoff, 1995; Palagi, Burghardt, et al., 2016; Pellis & Pellis, 1996; Wilson & Kleiman, 1974).

The most extensively studied play signals have been visual, especially the play face in primates and the play bow in canids, with vocal play signals mostly limited to reports of their occurrence and short descriptions. Here we attempt to systematize play vocalizations and develop a framework for understanding their use and evolution. We will draw explicit connections between variants of play vocalizations across nonhuman species and their corresponding socioecological contexts, with an eye toward a better understanding of the phenomenon of human laughter.

A challenge of studying play-associated vocalizations, and play signals more generally, has been the difficulty of identifying play in nonhuman animals with the usual guard against anthropomorphism. However, renewed interest in the evolution of play has led to improved methodologies for classifying it using specific behavioural conditions. For example, Burghardt (2005) proposed that for a behavioural sequence to be classified as play it must satisfy a set of five criteria. The behavior should be nonfunctional in the short term, rewarding, modified from

its ordinary functional form, repeated, and initiated by healthy animals in relatively unstressed contexts. In the wild, of course, categorizing animal behaviours according to these criteria can be extraordinarily difficult as activity patterns are fleeting, and sequences are integrated with one another in complex (and largely unknown) ways.

There are four main categories of play described in the comparative literature: locomotor, object, social, and fantasy play (Pellegrini & Smith 2005). Rough-and-tumble play, sometimes referred to as play fighting, is a subcategory of social play marked by wrestling, chasing, and gentle biting (Aldis, 1975). Play fighting is widespread across mammals and especially predominant in primates. Importantly, it constitutes the category of play most associated with vocalizations (Bekoff & Allen, 1998). The vocal channel is effective for signaling during play fighting because the partner's face may not always be visible. Rapid detectability is a crucial dimension in play signaling, and evidence suggests that visual signals, such as play bows in dogs (*Canis lupus familiaris*), occur at junctures in the play action that maximizes their salience (e.g., during moments of physical separation with face-to-face positioning; Cordoni et al. 2016). Vocal signals do not require special positioning to work, but still might be produced systematically in an attempt to optimize their effectiveness (e.g., with specific temporal relationships to upcoming behaviour).

The study of vocal signaling during play presents researchers with a classic problem, illustrative of not only more general problems concerning the meaning of animal signals (Fischer & Price, 2017; Rendall et al., 2009), but also the issue of redundancy (Wiley, 2006). Vocal play signals frequently accompany other non-vocal behaviours, such as the play face in primates (van Hooff, 1972) or the play bow in dogs (Bekoff, 1995). Play vocalizations may reinforce or emphasize the non-vocal signals, or add specific information not contained in other behaviours.

Moreover, vocalizations that are common during play often occur additionally in non-playful interactions (Pellis & Pellis, 1996). Thus, it becomes difficult to determine exactly how vocal signals are functioning across varying contexts, especially when the vocalizations are acoustically similar across them. Many constraints shape the evolution of context-specific signaling across taxa (Townsend & Manser, 2013). Some species might have one or more play-specific signals, while others use more general signaling behaviors in context-sensitive ways. A comparative analysis focusing on form and function relationships between signal characteristics and behavioural strategies allows theorists to evaluate how signals operate in context, as well as understand their phylogenetic history through identifying common ancestry (homology) or independent but convergent adaptations (homoplasy).

In evolutionary biology, structural characteristics of traits (i.e., their forms) can be understood with reference to their observed functions. This theoretical framework has proven invaluable across different areas of study including functional morphology, behavioural biology, and signal design. The idea applies to play in at least two ways. Behavioural analyses of play reveal clear connections between the recurrent action patterns of animals engaged in play and the ultimate functional benefits of those actions. For example, play fighting has characteristics that facilitate the development and calibration of adult fighting skills, such as nonaggressive fight simulation and turn-taking in role-play (i.e., being attacker versus victim). In the case of vocal signaling, acoustic features of vocalizations are inherently connected to their communicative functions, such as loud and noisy features of alarm calls that grab receivers' attention (Blumstein & Récapet, 2009; Owren & Rendall, 2001). Form and function logic has informed efforts to understand human vocal signaling as well (Bryant 2020b). For example, in infant-directed speech, loud and abrupt acoustic features of prohibitives (e.g., "No!") can function to redirect an

infant's attention and interrupt undesired behavior. Conversely, slow rising pitch intonations and lilting speech rhythms can encourage other behaviors (Bryant & Barrett, 2007; Fernald, 1992). The aversive sound qualities of infant crying are easily understood as shaped by selection to cause behaviour in caretakers that results in crying cessation (Soltis, 2004), and these features extend to distress calls in nonhuman species as well, indicating conserved structure (Lingle et al., 2012). As we describe below, the form–function approach can help us understand the communicative functions of play vocalizations, including human laughter.

Play vocalizations across species

We conducted an exhaustive literature review searching empirical reports that included descriptions of play vocalizations in any animal species. Our aim in this summary of the literature is not necessarily to identify every paper reporting such behaviour, but instead compile a reasonably complete survey of the animal behaviour literature to date in order to establish any pattern of structural features that can be plausibly linked to human play vocalizations, typically manifesting as laughter. Many of these descriptions appear in studies that focused on other aspects of animal social behaviour, and most only provide verbal descriptors of the vocal sound. We found reports of vocal play signals throughout the mammal literature, especially among primates, rodents, social carnivores, and (to a lesser extent) marine mammals. In the case of primates, play vocalizations are documented in the majority of species that have been studied extensively. Additionally, researchers have described at least three species of birds with play-specific calls.

Table 2.1 presents the list of species ($N = 65$) for which we found reports of play vocalizations, and we include information (if available) regarding whether there is evidence that

the vocalization is specific to play contexts, as well as verbal descriptors of the sound particularly concerning: a) noisy (i.e., broadband energy) versus tonal (harmonic structure), b) loud versus quiet, c) high versus low pitch, d) short versus long duration, and e) single calls versus regularity (i.e., rhythmic series).

While all of the vocal behaviours listed in Table 2.1 are explicitly described as having occurred during play interactions, some were described both in play and other behavioural contexts. Thus, 'play-specific' indicates vocalizations described as occurring *only* during play and not in any other context. Further research may reveal that some signals are characteristic of social play, but still manifest infrequently in other contexts—perhaps marking a playful mood outside of recognizable social play interactions. Alternatively, the vocalizations may have multiple subtypes, only some of which occur during play. For example, detailed analysis of dog growls reveals that playful growls have a different acoustic signature from aggressive growls; as such, labelling these two subtypes as 'growl' could misleadingly suggest non-specificity of the call context (Faragó et al., 2010). Additionally, many studies briefly mention vocalizations associated with play, without sufficient detail for determining whether they exclusively occur during play. Fagen's (1981) description of play in margays (*Leopardus wiedii*) is typical:

> '…their play is usually quiet as well, but there are exceptions to this rule. Vocalizations have the effect of controlling play, and it is always possible for an observer to detect that a margay play-bout is becoming rough when the animals begin making a low growling or rough purring sound whose intensity may rise if roughness continues' (p. 173).

That these vocalizations increase with play intensity and 'control' play suggests that they provide specific facilitative functions within play, similar to the laughter-like play vocalizations in the great apes. But the margay vocalizations could simply indicate pain or aggression that happens to occur in the course of rough play, rather than being play-specific. A more complete

understanding of the functional significance of vocalizations during play interactions is needed in order to determine the phylogenetic relationship of these signals across extant species.

Evidence for play vocalizations in non-mammal vertebrates (e.g., birds, reptiles, and fish) is extremely limited. Play is particularly difficult to identify in non-mammals, but some researchers have argued for its presence in birds and potentially even some reptiles (e.g., turtle object play) and fish, although this should be viewed as preliminary (Burghardt, 2005). To our knowledge, two bird species in the parrot group and Australian magpies (*Gymnorhina tibicen*) are currently the only non-mammals that have been clearly described using distinct vocalizations during social play (Diamond & Bond, 2003; Pellis, 1981; Schwing et al., 2017). Figure 2.1 shows a cladogram displaying the phylogenetic relationship between all species currently known to produce play vocalizations, based on NCBI taxonomy (Letunic, 2020; Letunic & Bork, 2007).

Vocal systems are subject to a number of constraints (e.g., predation risk, anatomical factors, sexual selection, etc.) that might have decoupled vocalizations from play in some species. Whether play behaviour itself is homologous across mammals, and possibly even across vertebrates, is yet to be determined (Burghardt & Pellis, 2019). One possibility is that the underlying (and sometimes latent) biological machinery proximately motivating play (such as an endogenous reward system triggered by positive social interaction) is homologous across mammals, but differences in play vocalizations arise from variation in the vocal repertoire and cost/benefit tradeoffs of play signaling across different species. Consequently, in a given comparison between two species with similar play behaviours, we might find homology in the physical play sequence, but homoplasy in the associated signaling, or in the specific attributes of that signaling. Indeed, research on play in rats (discussed in detail below) is suggestive of this pattern. To answer these evolutionary questions, we need better comparative data on the

variation in acoustic features of play vocalizations, and the ways that specific features covary with ecology and phylogenetic relatedness.

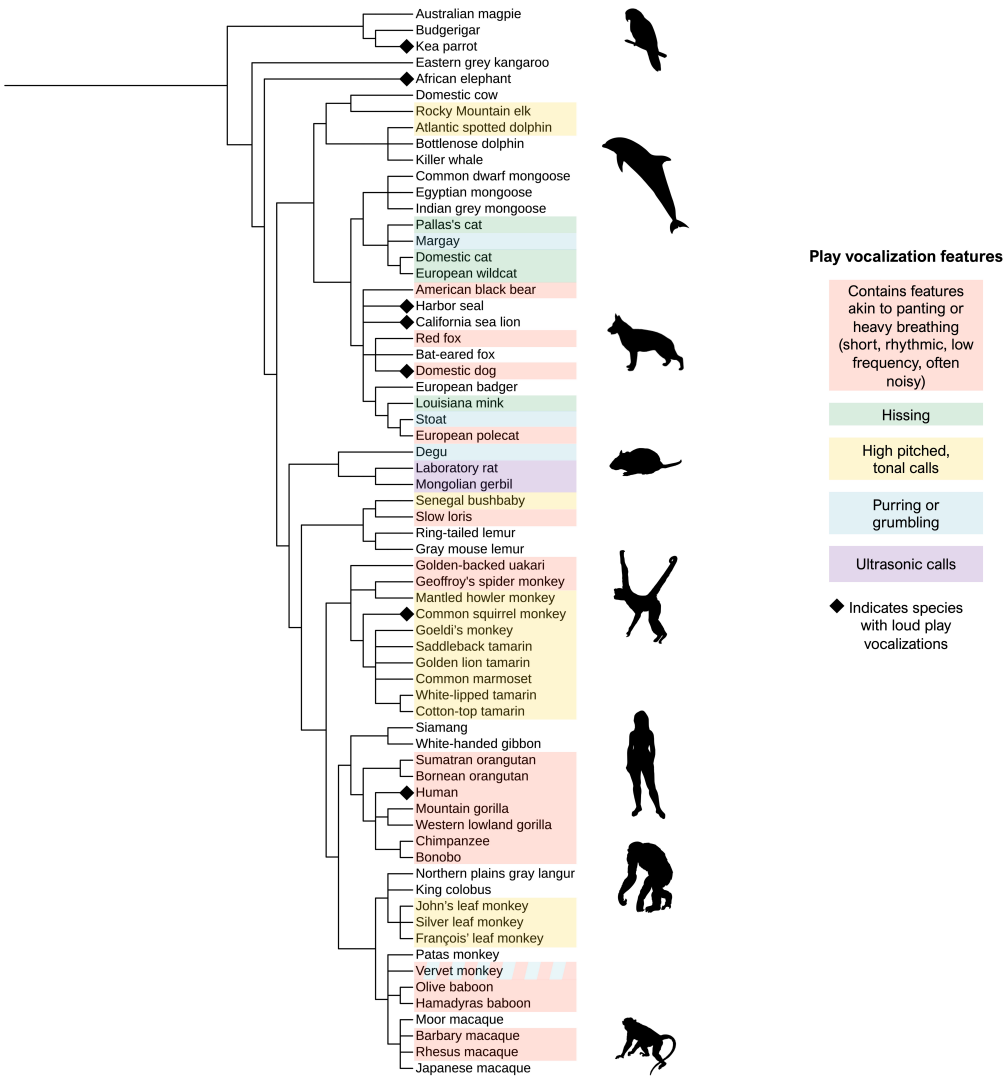

Figure 2.1. Cladogram illustrating the phylogenetic relationship between all species reported to have play vocalizations, including designations of vocal features across clades.

Acoustic features of play vocalizations

Many scholars have noted the similar forms of play vocalizations across the great apes, identifying them as variants of laughter (Darwin, 1872; Provine, 2000; van Hooff, 1972). Vettin and Todt (2005) examined play vocalizations in Barbary macaques (*Macaca sylvanus*), chimpanzees (*Pan troglodytes*), and adult humans, all occurring during tickling episodes, and found that in humans and chimpanzees, there was similar high intrabout variability in call interval duration and fundamental frequency—auditory features that seem to play an important role in making a vocalization sound like a laugh (Kipper & Todt, 2001). All species produced serially organized calls, and interval durations between expiratory and inspiratory elements were similar. However, macaque calls tended to lack harmonic structure and were significantly lower in amplitude.

Acoustic characteristics of play vocalizations can provide insight into their evolutionary history. Davila-Ross, Owren, and Zimmermann (2009) reconstructed the phylogeny of great ape play vocalizations through acoustic analysis and suggested that all ape 'laughter' can be traced to the play vocalization of a common ancestor that lived approximately 18 MYA. The evolutionary trajectory leading to current ape species appears to have shifted toward vocalizations with increased vibration regimes (i.e., greater voicing/more tonal), shorter bursts, and longer bouts. Airflow is also universally eggressive, with the exception of chimpanzees who more typically produce laughter calls with alternating airflow.

Existing research has uncovered acoustic similarities across primate species, but few other comparative studies have been conducted. Our extensive literature review, comprised of a variety of mammals and a few birds, reveals a general trend: play vocalizations are most commonly described as short, serially organized, low amplitude bursts. While these

commonalities are notable, there is still significant acoustic variation across species. Play vocalizations range from quiet hissing to harmonic barks, including tonal squeals, low-pitched grunts, noisy chattering, and ultrasonic trills. Figure 2.2 shows representative spectrograms of play vocalizations in different taxa as an example of this variation. Still, even in these different forms, play signals are usually quiet. The inconspicuous nature of the signals is generally attributed to predator avoidance—loud broadcasts of play behaviour can attract predators, and a quiet signal will suffice if the signalers are in close proximity to one another. Loud signals, such as human laughter, are exceptions to the rule, and we describe implications of this below.

Despite the profoundly incomplete record of play-associated vocal behavior across animals, as well as inconsistent reports of sound features in those that have been described, some lineages exhibit clearly divergent acoustic patterns. For example, in Old World monkeys, two subfamilies appear to have distinct vocal behaviours. In the subfamily *Cercopithecinae,* such as baboons and macaques, play vocalizations tend to be quiet, noisy, and rhythmic. But in close relatives from the subfamily *Colobinae,* such as several leaf monkey species, play vocalizations tend to be tonal, high-pitched peeps and squeals. New World monkeys, such as squirrel monkeys, howler monkeys, and spider monkeys, also often produce tonal, high-pitched peeps and chatters. As mentioned earlier, great ape play vocalizations share many properties with human laughter, and are usually described as panting or chuckling.

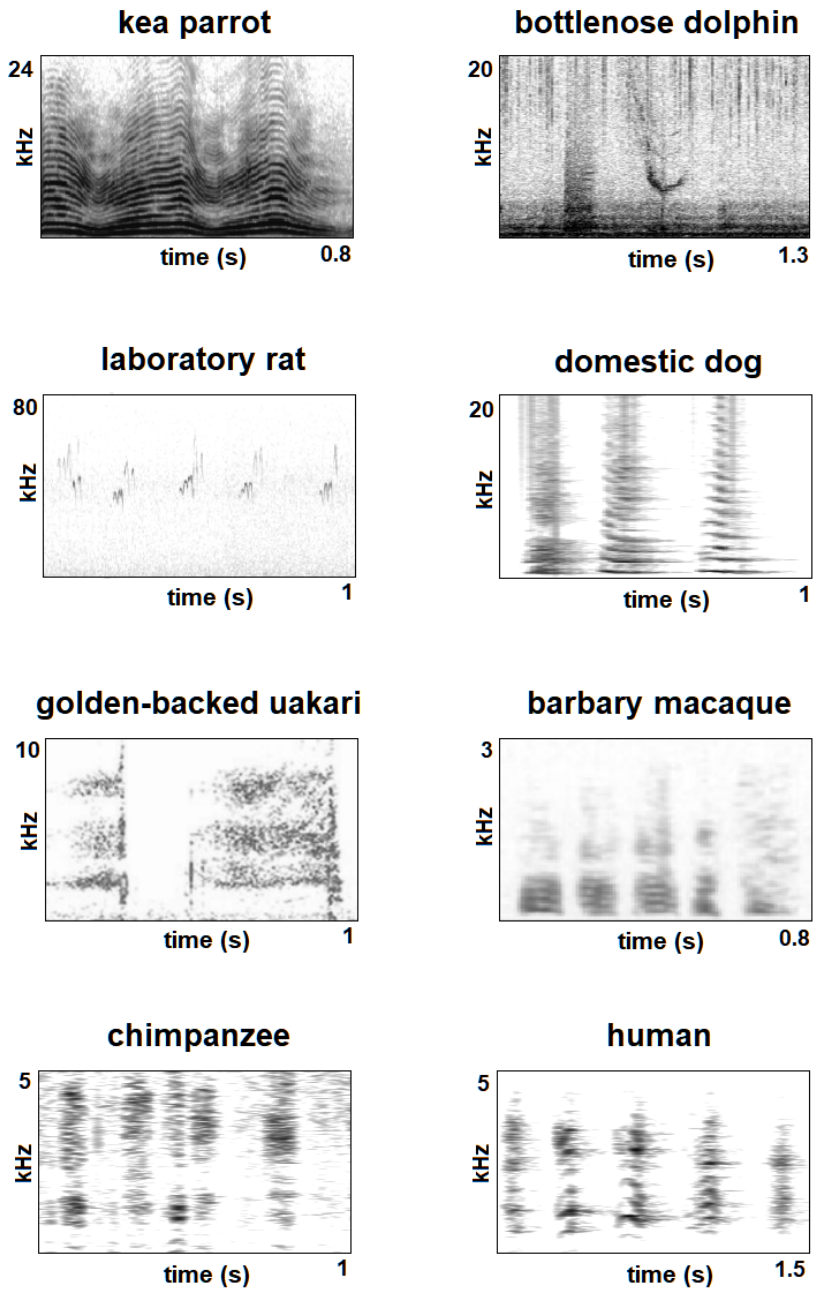

Figure 2.2. Spectrogram examples of play vocalizations across disparate species.

Indeed, many of the play vocalizations mentioned in Table 2.1, particularly among primates and carnivores, are described as 'panting,' or some form of laboured breathing. These pants are voiced in some species and unvoiced in others. Other types of play vocal signals have acoustic features similar to panting, in that they are described as rhythmic, staccato, chuckling, or chattering. These qualities are consistent with the notion that play vocalizations evolved from heavy breathing during play. Because rough-and-tumble play requires a high level of physical exertion, unvoiced rapid or heavy breathing during play likely originated as an acoustic cue of energy expenditure and investment in the play activity (Provine, 2000). Through a ritualization process (Tinbergen, 1952), the vocal pattern was then shaped into a communicative signal of benign intent that clarified mutual positive investment in the activity and induced positive affect, which helped prolong the play. This process potentially occurred in a mammalian common ancestor, meaning that all current mammalian play vocalizations are homologous. By this perspective, any variation in the acoustic features of play vocalizations across mammals evolved from an ancestral pant-like sound via species-specific vocal evolution. Convergence in similar, atypical acoustic traits across disparate species could constitute homoplasy (e.g., loud barking vocalizations in both sea lions and dogs), even if the underlying behavioural adaptation of producing play vocal signals is homologous. Alternatively, convergent evolutionary dynamics might have afforded the independent evolution of play vocalizations multiple times over mammalian evolutionary history.

Vocal signals of play in rats (*Rattus norvegicus*) illustrate this phylogenetic puzzle nicely. Knutson, Burgdorf, and Panksepp (1998) first documented ultrasonic vocalizations (USVs ~50 kHz) emitted by juvenile rats during play, and in a series of experiments, demonstrated that they were associated with positive affect. An earlier account associated similar vocalizations with

chasing and sexual activity (Sales, 1972). Since then, a fair amount of evidence has accumulated revealing that many vocalizations comprise the category of USVs and distinct subtypes are reliably associated with specific behaviours in the sender, and responses in receivers (for a review, see Burke et al. 2020). Interestingly, some USVs are potentially tied to breathing. Burke et al. (2017) described the *movement byproduct hypothesis*—an attempt to explain vocalizations as artifacts of particular jumping and exertion during high activity. As Burke et al. pointed out, this cannot explain the current vocal behaviour, but it could plausibly account for antecedent vocal cues that became ritualized, as described earlier. This presents a good case for convergent evolution in that USVs associated with play evolved in the context of a larger repertoire in rodent species (see also Sangiamo et al. 2020), but independently from primates that also have evolved play-associated vocal signaling. It is additionally worth noting that tickling of rats by human experimenters evokes these 50 kHz signals (Panksepp & Burgdorf 2000), which could point to deep homologies in the underlying neurological mechanisms, despite differences in the acoustic features of the calls and their evolutionary history.

While rat USVs clearly represent a unique form of mammalian play vocalizations, there are other acoustic distinctions across species' play vocalizations that suggest theoretical alternatives to being evolved from laboured breathing. For example, among several New World primates (*Platyrrhini*), play vocalizations are often described as high-pitched peeps, whistles, or squeals (Biben & Symmes, 1986; Cleveland & Snowdon, 1982; Masataka & Kohda, 1988). Masataka and Kohda (1988) argued that these vocalizations evolved from a location or contact call given by infants toward their mothers during allomothering, rather than from laboured breathing during play. In these species, evolutionary convergence could explain the independent evolution of play vocalizations derived from a unique, pre-existing vocal repertoire.

Other types of play vocalizations are more difficult to interpret. For example, 'nasal trumpets' given by elephants (*Loxodonta africana*) during play could plausibly be derived from a type of heavy breathing, as elephants expel bursts of air through their trunks during physical exertion (Poole, 2011; Soltis, 2010). However, the clicks, pulses, and whistles produced by marine mammals during play are unlikely to be intimately tied to breathing, due to the evolutionary constraints on marine mammals' breathing and vocal apparatus. Additionally, there are no candidates for evolutionary antecessors to the play-specific warble call in the kea parrot (*Nestor notabilis*; Schwing et al. 2017). As one of the few play-specific calls that have been extensively described in a non-mammal species, the kea's play vocalization most likely evolved independently. Comparative acoustic analyses across species similar to the methodology of Davila-Ross, Owren, and Zimmermann (2009) could shed light on questions of homology versus homoplasy in these signals.

To complicate matters further, not all play vocalizations are the same within a given species, and different vocal signals may have disparate functions within the play context. Many species are described as having several types of play-specific calls. For example, Stevenson and Poole (1982) reported three distinct types of play vocalizations in the common marmoset (*Callithrix jacchus*). Several researchers have described play-specific pants, growls, and barks in domestic dogs (*Canis lupus familiaris*; Bekoff, 1995; Faragó et al., 2010; Simonet et al., 2005; Yin & McCowan, 2004). Rat researchers have identified different 50 kHz calls that corresponded to specific tactical maneuvers in play fights (Burke et al., 2018). Future work should investigate which species have multiple types of play vocalizations, and attempt to identify specific functional roles across the types.

Functions of play vocal signals

Most generally, play signals likely evolved to help limit the costs of play. The signals realize this function by reducing costly misinterpretations of impending ambiguous signals and/or behaviours, thus sustaining positive affect, and maintaining or prolonging play bouts. One possible way this is achieved is through metacommunicative signaling—play signals create a context (i.e., indicating 'this is play') in which upcoming behaviours are properly interpreted as play rather than aggression (Bateson, 1956; Bekoff, 1975), though this viewpoint has been criticized as being unnecessarily complicated to explain many nonhuman phenomena (Symons, 1978). Play signals can be described as a special class of signals of benign intent. For example, in rhesus macaques (*Macaca mulatta*), a higher-ranking female approaching a lower-ranking female with offspring might signal, through a grunt or a soft vocalization known as a girney, that she intends no harm to the offspring. She may then approach and have a nonaggressive interaction with that offspring, without the mother acting defensively. These kinds of low-cost signals can be evolutionarily stable if there are repeated interactions between the individuals (Silk, Kaldor, & Boyd 2000). The primary distinction from play signals involves the nature of the behaviour following the signal—interpreting what would otherwise be construed as aggressive intent following the play signal could require sophisticated inhibitory control, if not metarepresentational reasoning.

Most theorists agree that play signals, at a minimum, facilitate play interaction. Research with devocalized rats have lent strong support to this approach. In one study, juvenile rats played more frequently if both partners could vocalize compared to when only one of the partners was devocalized, suggesting that the vocal signals function to encourage or enable play (Kisko, Himmler, Himmler, Euston, & Pellis 2015). Other work showed that adult rats were less likely to

escalate to aggression (e.g., deliver a bite) during play if both partners could vocalize (Kisko, Euston, & Pellis 2015). Research with adult rats has also demonstrated that certain types of USVs may function specifically to aid in coordination of complex reciprocal 'moves' in play, such as attacking and being attacked, while other types of calls appeared to facilitate particularly vigorous or risky behaviours, such as pinning, playful biting, or contact with the neck (Burke et al. 2018). Thus, play vocalizations often function to initiate and prolong playful interactions, and are likely crucial for the coordination of complex play-fighting as seen in rough-and-tumble play. Work with chimpanzees reveals similar functionality, and affords clear comparisons to human laughter. During play, chimpanzees produced laugh-like vocalizations in response to conspecific laughter, and the response laughs may have had unique acoustic features (Davila-Ross et al., 2011). Duration of play was positively associated with the occurrence of these vocalizations, suggesting that they functioned to facilitate play, similar to the way laughter prolongs play and conversation in humans (Schnurr & Chan, 2011).

As described earlier, play vocalizations are rather quiet, either as atonal, exaggerated pants or low-amplitude trills or peeps. Their inconspicuous nature is a primary reason they have not been extensively studied acoustically, and are not more thoroughly documented. There are methodological challenges in not only recording the vocalizations effectively, but also identifying signalers during close-contact play. The low-amplitude acoustic form is not surprising if the signals are functioning only within closely interacting dyads or groups. Moreover, there should be selection pressure to avoid risks of predation by not widely broadcasting playful encounters, especially given that interactants are often young, and play distracts from typical anti-predator vigilance (Goedeking 1988). Additionally, if play is an important bonding activity, advertising it may be costly if third-party conspecifics react

aggressively to intervene. These factors likely select for restrained acoustic features such that the play partner can unequivocally detect the signal even during scuffles or noisy chases, but not so noticeable as to attract undue attention from others. In social play such as chasing, there could be additional reasons we might expect quiet signaling. For example, stealth predators like cats might be expected to use quiet signaling as they calibrate pursuit behaviour. In fact, several species of cats have been observed using inconspicuous, hiss-like, atonal vocalizations as play signals (Fagen, 1981). Overall, quiet signaling during play makes it fairly clear that the signals are transmitted only between the interacting partners, suggesting a play facilitation function, without a broadcast function. That is, only the interactants are able to hear the signaling, and it benefits them by lengthening play time (Burke et al., 2020).

While play vocalizations tend to be quiet, 'conspiratorial whispers' (Krebs & Dawkins, 1984), there are exceptions. Even with selection for inconspicuousness, formal models suggest that signal detection costs must be considered for senders, receivers, and eavesdroppers, and that some circumstances can result in greater magnitude signals without selection for broadcasting (Johnstone, 1998). For example, play was more likely to escalate into aggression in adult rats when one play partner was devocalized, showing the high stakes of failing to perceive play vocalizations (Burke, Kisko, Pellis, et al., 2017; Kisko, Himmler, et al., 2015). Interestingly, 50 kHz USVs of rats during play may be uniquely suited to balance the competing costs of detection from predators and non-detection from conspecifics, as they dissipate rapidly (Brudzynski, 2019).

In other circumstances, there could be selection for wide broadcast. While clearly in the minority, some species generate conspicuous play signals, including the play peeps of squirrel monkeys (*Saimiri sciureus*), the barks of domestic dogs (*Canis lupus familiaris*), seals (*Phoca*

vitulina), and sea lions (*Zalophus californianus*), the play-trumpets of African elephants (*Loxodonta africana*), the warble of kea parrots (*Nestor notabilis*), and the loud laughter of humans (Peterson and Bartholomew 1969; Biben et al. 1989; Feddersen-Petersen 2000; Poole 2011; Bryant 2020a). There is no single account that likely explains loud play vocalizations across all of these species, but any explanation must address both the apparent low costs of broadcasting to potentially dangerous eavesdroppers and the possible benefits of signaling to third-party conspecifics. Notably, many species with loud play vocalizations are large-bodied, and are not particularly vulnerable to predation. While somewhat unique acoustically in the category of animal play vocalizations, we can obtain great insight into the nature of human laughter by identifying commonalities across species in acoustic form and communicative function. Moreover, form-function comparisons can help identify possible homoplasies, as particular acoustic features might serve similar specific play-related functions across disparate species due to evolutionary convergence. We will return to the issue of loudness in our discussion of human colaughter.

Laughter as a human play vocalization

> 'The anthropoid apes, as we have seen, likewise utter a reiterated sound, corresponding with our laughter, when they are tickled, especially under the armpits.'
>
> - Charles Darwin, 1872, p. 199

It has long been recognized that human laughter bears a strong resemblance to play vocalizations in the great apes (Darwin, 1872), but only fairly recently has the deeper connection been made to play vocalizations across mammals other than primates (Gervais & Wilson, 2005; Panksepp & Burgdorf, 2000; Provine, 2000). However, even compared to its counterparts in our

closest living relatives, laughter in people has evolved into a much more complex signal (Scott et al., 2014). People laugh in almost any possible situation, and in contexts associated with any identifiable emotional state. For instance, we have the potential to laugh when we are in despair, disgusted, joyous, or bewildered. Many philosophical works have focused on laughter's so-called dark side, with connections to teasing, taunting, and schadenfreude (for a review see Provine 2000). Despite this extreme flexibility, most instances of laughter can be reasonably classified as playful at some level. For example, if we consider the criteria of play described earlier (Burghardt 2005), cases of verbal taunting or teasing, while often construed as negative, certainly qualify. Teasing is nonfunctional in the short term, rewarding for the teasers (and potentially the target), modified from actual verbal aggression, repeated over time, and generally occurs during unstressed and ordinary moments. Laughter can help initiate and prolong a teasing attack, make it feel non-serious and playful, and can even elicit laughter in targets despite their lack of desired participation (Glenn 2003; Schnurr and Chan 2011; also see Eckert et al. 2020 for a comparative perspective on playful teasing).

The most obvious manifestations of playful human laughter occur in contexts associated with humor, such as tickling and joking. The case of tickling is, of course, the closest context that connects laughter to other primate play vocalizations—exaggerated panting mixed with squeaks and grunts, directly triggered by rough-and-tumble play—but its complexity is apparent even in this situation. During tickling, human laughter can be intermixed with other vocalizations that communicate distress, including screaming and crying—even unadulterated laughter does not necessarily index pleasure. In the case of ordinary conversational joking (as opposed to scripted jokes or formal comedy), laughter can act as a means for speakers to inform receivers of the presence of a joke, or for receivers to signal the recognition of one. The completion of a

natural (i.e., conversational) joke turn can be effectively conceptualized as a form of encryption-decryption. That is, the actual referent in an utterance, or set of utterances, is unstated, and spontaneous colaughter can act as a signal of mutual knowledge (T. Flamson & Barrett, 2008; T. J. Flamson & Bryant, 2013). The case of conversational joking might represent the point of departure for human laughter as a separate kind of vocal signal from its nonhuman play vocalization precursor.

As an emotional expression, spontaneous laughter is generated by a vocal production system shared across all mammals, as opposed to volitional laughter that is produced by a speech system unique to humans (Ackermann et al., 2014; Jürgens, 2002). The conserved nature of vocal emotions provides the best prima facie evidence that ape laughter evolved from a play vocalization in a mammalian common ancestor that lived at least 100 MYA. But humans are unique across the great apes in our capacity for speech, generated by a volitional vocal production system that other apes only reveal with debated limitations (e.g., Pisanski et al. 2016; Lameira 2017). We can control our vocal apparatus to produce an amazing range of sounds, and do so in ways that mimic, sometimes with dramatic accuracy, sounds around us. One of the targets of selection in the development of this ability was likely the imitation of genuine emotional vocalizations: deliberate crying, screaming, and laughing that is decoupled from the emotional triggers required for spontaneous production (Bryant et al., 2018; Bryant & Aktipis, 2014).

Volitional control over our vocal production co-evolved with language and many aspects of human culture and cooperation, though comparative data suggest some aspects trace back to before the appearance of modern humans (Pisanski et al., 2016). Laughter has certainly played an important role in our sophisticated communicative capacity. Within that complex milieu, the

ancestral function of play still looms large—volitional laughter retains some important characteristics of play vocalizations we see in other mammals. In humans, natural conversation can be an important context of play. Like teasing described earlier, many conversational structures satisfy Burghardt's (2005) criteria, and constitute playful interaction that requires particular play signaling. Laughter plays an important role in the timing and unfolding of conversational behaviour, including the signaling of turns during talk, backchanneling, signaling emotional investment in the interaction, and regulating conversational flow (Jefferson, 1979; Vettin & Todt, 2004).

Functionally, a controlled (i.e., volitional) form of laughter fulfills many pragmatic needs in conversation (Pisanski et al. 2016; Bryant 2020a). In contrast, spontaneous laughter can interrupt the speech production system and is thus not well-suited to operate during discourse (McGettigan & Scott, 2014). Volitional laughter is deployed strategically, in rule-governed ways around linguistic units (Provine, 1993), and in a manner quite similar to how play vocalizations operate in nonhuman animals, such as managing turn-taking, inducing positive affect, and regulating the flow of play. For example, when using indirect language (e.g., verbal irony, parody, and other figurative devices) that relies heavily on inferential communication, laughter can help listeners understand speakers' actual communicative intentions (Bryant 2011; Bryant 2020a). These instances are often experienced as humorous and are easily construed as verbal play, including role-playing and reciprocity. Laughter can mark an utterance as indirect, typically resulting in a relevant response that engages the speaker in a pretense-based, play-like bout (Gibbs, 2000), also often marked by responsive laughter (Bryant, 2011; Schnurr & Chan, 2011). Contrary to folk intuitions, speakers produce laughter much more frequently than receivers (Provine, 2000; Vettin & Todt, 2004). Speakers mark their own ambiguous speech with benign

or playful intent, mirroring the way that nonhumans produce play signals before an ambiguous play attack. More generally, laughter functions to limit the cost of indirect speech (Pinker et al., 2008; Sally, 2003), which is quite similar to the way that nonhumans use play signals to reduce the potential cost of an interaction escalating to aggression.

One consequence of ongoing verbal play between two or more people is the recurring colaughter that is readily audible to third parties. Most laughter occurs in group contexts, and this fact might help explain one of the unusual acoustic features of human spontaneous laughter: it is typically quite loud. As described in the introduction, children's play is accompanied by a familiar cacophony of laughter and screaming. Adults also frequently engage in loud colaughter, whether at parties, in bars and restaurants, or just during ordinary conversation. Human laughter has all the acoustic hallmarks of a signal designed for wide broadcast: alerting components (i.e., high amplitude and high frequency onset), conspicuousness, and repeated elements with small repertoires (Wiley, 1983). Additionally, it is contagious—hearing laughter is the best trigger for spontaneous laughter (Provine, 1992). Overall, the acoustic form of colaughter suggests a group chorusing function (Bryant et al., 2020). While few (if any) nonhuman play signals appear to have this chorusing function, some play signals are known to be contagious among dyads, as in the case of rapid facial mimicry of primate play faces or the contagion of play vocalizations in keas (Mancini et al., 2013; Palagi et al., 2019; Schwing et al., 2017).

What does it mean when people are laughing together in a group? As in our previous example of encryption and humor, when two or more people share an inside joke they are often triggered to laugh together. In doing so, the group is implicitly revealing that they have shared information, which may be due to strongly bonded relationships or, at a minimum, shared cultural references. The positive emotions and proximate physiological rewards associated with

successful humorous interaction and colaughing bouts (e.g., Manninen et al. 2017) drive what might be an honest signal of affiliation that is often broadcast fairly widely to others nearby. Research shows that people are sensitive to it. When presented with very brief (~ 1 s.) audio presentations of colaughter, listeners from around the world could distinguish between established friends and newly acquainted strangers (Bryant et al., 2016). Even infants as young as five months associated friendly colaughter with affiliative behaviour in others (Vouloumanos & Bryant, 2019). Colaughter also signaled affiliation more reliably than another kind of co-occurring vocalization—overlapping talk—even when the talk samples were over twice as long in duration (Bryant et al., 2020). Colaughter might comprise a derived signal of affiliation that allows groups of friends to communicate to other individuals. In our evolutionary past, there could have been positive selection for signaling group affiliation among large, interconnected social networks. Colaughter fulfills this function efficiently, possibly representing a unique turn in the evolution of primate play signals associated with the emergence of language and complex, cooperative sociality among humans.

Conclusion

The regulation of social play in many species often requires the use of visual and vocal signaling. These signals help animals clearly communicate intentions during interactions where misunderstandings could have costly consequences. In a play fight, for example, the ongoing negotiation of participants' roles facilitates continued interaction, ultimately helping to calibrate physical development and prepare animals for future aggressive encounters. Close examination of play vocalizations across disparate species helps illuminate the nature of human laughter, one of our most common and mysterious vocal behaviours. Laughter helps people negotiate

relationships, manage emotional experiences, and engage in complex social interactions both linguistically and nonverbally. The social uses of human laughter are innumerable, including ancestral functions associated with play, affiliation, and positive affect, as well as derived functions that occur during conversation. Volitional laughter can be used deceptively to induce affect in ways that manipulate receivers against their interest (Bryant et al., 2018; Bryant & Aktipis, 2014), but can also be used as a pragmatic device to help facilitate positive emotional connections between people. Additionally, people laugh in large groups, possibly as a means of intergroup signaling. Overall, human laughter contains contextual and acoustic features that make it somewhat unique across mammals, and even great apes.

Our comprehensive literature review reveals that vocal signals during social play are quite common across mammal species, and some birds, further challenging the once 'conventional wisdom' that animal play is silent (Fagen 1981, p. 149). Still, much more comparative research is needed to understand the phylogeny of play vocalizations. Different factors leading to the evolution of play signals might be associated with distinct evolutionary trajectories. For example, the capacity for social play and its appearance across animals might be the product of deep neurological and behavioural homologies that underpin social interaction more generally. But constraints on vocal signaling evolution could result in variable appearances of play-specific vocal signals across distant taxa. Even if play is homologous between any two given species, their play vocalizations might be convergent due to different vocal evolutionary histories, or changing ecologies that afford selection for particular kinds of vocalizations (or their absence altogether). More research examining the social and ecological contexts of species with play vocalizations will help shed light on the evolutionary factors that preclude selection for both the presence of play vocalizations and their particular acoustic features.

There are many methodological problems that must be overcome to properly study play vocalizations. As noted earlier, a high proportion of known play vocalizations are very quiet, so it is a certainty that many species generate these signals but the behavior has not been documented in the scientific literature. Fortunately, technology is improving and wireless audio recording possibilities are increasing (e.g., Gayk and Mennill 2020). Additionally, sensing technologies developed for animal welfare (for reviews see Jukan, Masip-Bruin, & Amla, 2017; Neethirajan, 2017) could be potentially adapted as a means of gathering continuous emotional and behavioral data for a more comprehensive approach to a variety of communication phenomena, including play signals. A large proportion of the studies we collected have descriptions of play vocalizations only as an aside, but greater focus on specific acoustic properties and behavioural patterning of play vocalizations will help answer outstanding questions about the evolution and function of these signals.

Further research is also needed on the sources of variation between species in the presence and frequency of play vocalizations. With more rigorous comparative criteria for identifying play, we should be able to include additional species, including taxa described here that have been commonly overlooked in discussions of laughter and play signaling. For instance, cetaceans, pinnipeds, and other marine mammals that rely heavily on acoustic communication are good candidates for the use of vocal play signals, but research to date is sparse. This is, in part, likely due to a common resistance to describe behaviours as ‘playful’ in these animals (Hill et al., 2017).

The study of play vocalizations is part of a much larger enterprise of understanding the nature of animal communication systems, and the related puzzle of human communication. Laughter might be one of the best examples of communicative behaviour that affords

comparative analysis, while remaining deeply embedded within our uniquely human language and culture. Recent developments in comparative neuroanatomy have provided fascinating insights into the origins of volitional voice modulation, and future research will undoubtedly lead to new discoveries regarding the many connections between human and nonhuman vocalizations. There is still much to learn, so keep laughing.

Table 2.1. List of species for which we found reports of play vocalizations.

Table 1. List of species for which we found reports of play vocalisations.

Taxa (common name)	Species (common name)	Scientific name	Reference	Play-specific	Name of vocalisation	Acoustic descriptors*
Great apes	Human	*Homo sapiens*	Bachorowski et al. (2001)	No	Laughter	Loud or quiet, tonal and noisy, high and low frequency, short, rhythmic and single
Great apes	Chimpanzee	*Pan troglodytes*	Van Lawick-Goodall (1968); Marler and Tenaza (1977); Van Hooff and Preuschoft (2003); Matsusaka (2004)	Yes	'staccato, throaty panting,' laughter	Quiet, tonal and noisy, short, low frequency, rhythmic
Great apes	Bonobo	*Pan paniscus*	de Waal (1988); Förderreuther and Zimmermann (2003)	Yes	Panting laugh; laughter	Quiet, noisy, low frequency, short, rhythmic (irregular)
Great apes	Western lowland gorilla	*Gorilla gorilla gorilla*	Salmi et al. (2013)	Yes	Panting chuckle	Quiet, low frequency, short, rhythmic
Great apes	Mountain gorilla	*Gorilla beringei beringei*	Schaller (1963); Fossey (1972)	Yes	Panting chuckle (a-a-a-a)	Quiet, noisy, low frequency, short, rhythmic
Great apes	Sumatran orangutan	*Pongo abelii*	Rijksen (1978)	Yes	'ahh,' play-grunt, laughter	Quiet, low frequency, short, rhythmic
Great apes	Bornean orangutan	*Pongo pygmaeus*	Chevalier-Skolnikoff (1982), Davila Ross (2007)	Yes	Laughter	Quiet, low frequency, short, rhythmic
Lesser apes	White-handed gibbon	*Hylobates lar*	Davila Ross (2007)	Unclear	Low frequency vocalisations	Low frequency
Lesser apes	Siamang	*Symphalangus syndactylus*	Davila Ross (2007)	Unclear	Low frequency vocalisations	Low frequency
Old world monkeys	Olive baboon	*Papio anubis*	Smuts (1985); Lewis (2005)	Yes	Voiceless chuckles; play chuckle	Quiet, noisy
Old world monkeys	Hamadyras baboon	*Papio hamadryas*	Kummer and Kurt (1965); Aldis (1975); Leresche (1976)	Yes	Coughs	Quiet, noisy, low frequency, short, rhythmic
Old world monkeys	Vervet monkey	*Chlorocebus aethiops*	Struhsaker (1967); Fedigan (1972); Masataka and Kohda (1988)	Yes	Panting; purr	Quiet, low frequency
Old world monkeys	Patas monkey	*Erythrocebus patas*	Hall (1965)	Unclear	Nickering	Quiet
Old world monkeys	Barbary macaque	*Macaca sylvanus*	Preuschoft (1992); Kipper and Todt (2002); Vettin and Todt (2005)	Yes	Low intensity voiced breathing; chuckle	Quiet, noisy, rhythmic
Old world monkeys	Rhesus macaque	*Macaca mulatta*	Symons (1978)	Yes	Panting	Quiet, noisy
Old world monkeys	Moor macaque	*Macaca maura*	Aldis (1975)	Unclear	Chattering	Quiet
Old world monkeys	Japanese macaque	Macaca fuscata	Itani (1965) as described in Goedeking and Immelmann (1986)	Unclear	N/A	N/A

(*Continued*)

Table 1. (Continued).

Taxa (common name)	Species (common name)	Scientific name	Reference	Play-specific	Name of vocalisation	Acoustic descriptors*
Old world monkeys	Northern plains grey langur/Hanuman langur	*Semnopithecus entellus*	Sugiyama (1965)	Unclear	Heavy breathing	Quiet, noisy
Old world monkeys	King colobus	*Colobus polykomos*	Kirchshofer (1960) as described in Aldis (1975)	Yes	Smacking	N/A
Old World Monkeys	Silver leaf monkey/ Silver lutung	*Trachypithecus cristatus*	Masataka and Kohda (1988)	yes	peep-like or squeal-like	tonal, high frequency
Old World Monkeys	François' leaf monkey/ François' langur	*Trachypithecus francoisi*	Masataka and Kohda (1988)	Yes	Peep-like or squeal-like	Tonal, high frequency
Old World Monkeys	John's leaf monkey/ Nilgiri langur	*Trachypithecus johnii*	Poirier (1970)	Unclear	Peep-like or squeal-like	Tonal, high frequency
New world monkeys	Golden-backed uakari	*Cacajao melanocephalus*	Bezerra et al. (2010)	Yes [reco]	Reco call, áhh call	Reco: short, single or series áhh: quiet, noisy, short, single
New world monkeys	Geoffroy's spider monkey	*Ateles geoffroyi*	Aldis (1975)	Unclear	Chattering	Quiet, noisy, rhythmic
New world monkeys	Mantled howler monkey	*Alouatta palliata*	Baldwin and Baldwin (1976)	Unclear	Whimpers	Tonal, high frequency
New world monkeys	Common squirrel monkey	*Saimiri sciureus*	Winter et al. (1966); Baldwin and Baldwin (1974); Biben and Symmes (1986); Masataka and Kohda (1988)	Yes	Cackles, peeps	Cackles: N/A peeps: high and increasing frequency
New world monkeys	Goeldi's monkey	*Callimico goeldii*	Masataka and Kohda (1988)	Yes	N/A	Tonal, high frequency
New world monkeys	Golden lion tamarin	*Leontopithecus rosalia*	McLanahan and Green (1977); de Oliveira et al. (2003)	Unclear	Rasp, trill, peep, chatter, squeal	Varies
New world monkeys	Saddleback tamarin	*Leontocebus fuscicollis*	Masataka and Kohda (1988)	Yes	N/A	Tonal, high frequency
New world monkeys	Common marmoset	*Callithrix jacchus*	Stevenson and Poole (1982); Masataka and Kohda (1988)	Yes	Whirr/phee, tsak/tsik, ngä	Varies
New world monkeys	White-lipped tamarin	*Saguinus labiatus*	Masataka and Kohda (1988)	Yes	N/A	Tonal, high frequency
New world monkeys	Cotton-top tamarin	*Saguinus oedipus*	Cleveland and Snowdon (1982); Goedeking and Immelmann (1986); Goedeking (1988)	Unclear	Whistles, squeals	Varies; unstable frequency
Strepsirrhines	Senegal bushbaby	*Galago senegalensis*	Zimmermann (1989a)	Unclear	Week, weeak, wak	Tonal

(*Continued*)

Table 1. (Continued).

Taxa (common name)	Species (common name)	Scientific name	Reference	Play-specific	Name of vocalisation	Acoustic descriptors*
Strepsirrhines	Slow loris	*Nycticebus coucang*	Zimmermann (1985); Zimmermann (1989b)	Unclear	Call type II.4, chro	Call type II.4: quiet, noisy and tonal, short, series chro: high frequency, short
Strepsirrhines	Ring-tailed lemur	*Lemur catta*	Macedonia (1993)	Unclear	Trills, hmms	Quiet
Strepsirrhines	Gray mouse lemur	*Microcebus murinus*	Zimmermann (1991); Scheumann et al. (2007)	Unclear	Trill, tsak	N/A
Rodents	Laboratory rat	*Rattus norvegicus*	Knutson et al. (1998); Burke et al. (2017a)	Yes	50 kHz calls with several subtypes	Short, high frequency, rhythmic
Rodents	Degu	*Octodon degus*	Wilson and Kleiman (1974); Long (2007)	Unclear	Purring/gurgling, warble	Purring/gurgling: quiet, long warble: quiet, high frequency, short, single
Rodents	Mongolian gerbil	*Meriones unguiculatus*	Holman and Seale (1991)	No	Ultrasonic vocalisations	High frequency
Carnivores (Canids)	Domestic dog	*Canis lupus familiaris*	Bekoff (1974); Bekoff (1995); Feddersen-Petersen (2000); Robbins and McCreery (2003); Simonet et al. (2005); Faragó et al. (2010)	Yes	Bark, panting, growl, yelp	barks: loud, tonal growls: quiet, noisy, variable duration, low frequency, series, panting: quiet, noisy, rhythmic yelp: loud, tonal, high frequency
Carnivores (Canids)	Red fox	*Vulpes vulpes*	Cohen and Fox (1976)	Unclear	Panting	Quiet, noisy, rhythmic
Carnivores (Canids)	Bat-eared fox	*Otocyon megalotis*	Lamprecht (1979)	No	Snarl	High frequency
Carnivores	European badger	*Meles meles*	Eibl-Eibesfeldt (1950) as described in Goedeking and Immelmann (1986)	Unclear	N/A	N/A
Carnivores (Mustela)	Louisiana mink	*Neovison vison*	Svihla (1931)	Unclear	Hissing, squealing, growling	Varies
Carnivores (Mustela)	European polecat	*Mustela putorius*	Poole (1966)	Unclear	Clucking, hissing	Quiet
Carnivores (Mustela)	Ferret/Domesticated polecat	*Mustela putorius furo*	Goethe (1940); Fagen (1981)	Unclear	Chattering, Klaffen	Quiet, noisy, rhythmic
Carnivores (Mustela)	Stoat/ermine	*Mustela erminea*	Fagen (1981)	Unclear	Mucker, grumble softly, purr, mutter	Quiet, low frequency

(*Continued*)

Table 1. (Continued).

Taxa (common name)	Species (common name)	Scientific name	Reference	Play-specific	Name of vocalisation	Acoustic descriptors*
Carnivores (Pinnipeds)	California sea lion	*Zalophus californianus*	Schusterman et al. (1966); Peterson and Bartholomew (1967); Peterson and Bartholomew (1969); Aldis (1975)	No	Barks, clicks, whinnies, bleats, unvoiced or voiced cough	Loud, short
Carnivores (Pinnipeds)	Harbour seal/Common seal	*Phoca vitulina*	Wilson (1974)	Unclear	Wooah	Loud
Carnivores	American black bear	*Ursus americanus*	Henry and Herrero (1974)	Unclear	Panting and breathing sounds	Quiet, noisy, rhythmic
Carnivores	Egyptian mongoose	*Herpestes ichneumon*	Rensch and Dücker (1959) as described in Goedeking and Immelmann (1986)	Unclear	N/A	N/A
Carnivores	Indian grey mongoose	*Urva edwardsii*	Rensch and Dücker (1959) as described in Goedeking and Immelmann (1986)	Unclear	N/A	N/A
Carnivores	Common dwarf mongoose	*Helogale parvula*	Rasa (1984)	Yes	Pulse	Short, high frequency, series
Carnivores (Cats)	Margay	*Leopardus wiedii*	Petersen (1979); Fagen (1981)	Unclear	Low growling/purring, harsh miaows and growls	Quiet, noisy, low frequency
Carnivores (Cats)	Pallas's cat	*Otocolobus manul*	Fagen (1981)	No	Hiss	Quiet, noisy
Carnivores (Cats)	Domestic cat	*Felis catus*	Fagen (1981)	No	Hiss	Quiet, noisy
Carnivores (Cats)	European wildcat	*Felis silvestris*	Fagen (1981)	No	Hiss	Quiet, noisy
Cetaceans	Bottlenose dolphin	*Tursiops truncatus*	Herzing (1996); Blomqvist et al. (2005)	Yes	Pulse burst, whistle, squawk	Varies
Cetaceans	Atlantic spotted dolphin	*Stenella frontalis*	Dudzinski (1998)	Unclear	Whistle	Tonal
Cetaceans	Killer whale	*Orcinus orca*	Rehn et al. (2007)	Unclear	V4 type calls, 'chatter'	Modulated frequency, series
Ungulates	Rocky Mountain elk	*Cervus canadensis nelsoni*	Altmann (1958)	Unclear	Squeal	High frequency
Ungulates	Domestic cow	*Bos taurus*	Schloeth (1961) as described in Bouissou et al. (2001)	Yes	N/A	N/A
Proboscids	African elephant	*Loxodonta africana*	Langbauer (2000); Poole (2011)	Yes	Nasal trumpet	Loud, tonal
Marsupials	Eastern grey kangaroo	*Macropus giganteus*	Watson (1998)	Unclear	Cough	Quiet, low frequency, short

(*Continued*)

Table 1. (Continued).

Taxa (common name)	Species (common name)	Scientific name	Reference	Play-specific	Name of vocalisation	Acoustic descriptors*
Birds (Parrots)	Kea parrot	*Nestor notabilis*	Schwing et al. (2017)	Yes	Warble	Loud
Birds (Parrots)	Budgerigar	*Melopsittacus undulatus*	Diamond and Bond (2003)	Unclear	Soft croaking	Quiet, low frequency
Birds	Australian magpie	*Gymnorhina tibicen*	Pellis (1981)	Yes	Gutteral sounding call	Quiet, low frequency, long

*This column indicates acoustic descriptors based on available reports in the literature. Acoustic dimensions include loudness (loud/quiet), harmonicity (tonal/noisy), frequency (low/high), call duration (short/long), and repetition (single, rhythmic, or series). N/A indicates a missing or ambiguous description.

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2.2 Further reflections: laughter and the evolution of language

Note: parts of the following section appeared in the 2024 proceedings of the Evolution of Language conference, as "From play pants to pragmatics: Laughter's linguistic leap," authored by Sasha Winkler, Erica Cartmill, and Gregory Bryant.

As described in the previous section, laughter is a signal that develops in infants pre-linguistically (Provine, 2000). It is homologous to the play vocalizations of other great apes and likely evolved from a play-specific, pant-like signal in our shared primate ancestors (Davila-Ross, Owren, & Zimmermann, 2010). However, in humans, laughter can also function as a pragmatic signal to facilitate turn taking and indicate speaker meaning in language use (Bryant & Bainbridge, 2022). Thus, laughter presents an intriguing case in which a pre-linguistic play vocalization became integrated into the speech system.

Our systematic review of play vocalizations (Winkler & Bryant, 2021) added support to the theory that human laughter and its precursor in primates could have initially evolved from a cue of heavy breathing during play. We found that acoustic signaling during social play is extensive across the animal kingdom. While animals used a wide variety of sounds to communicate during play, a commonality among many mammals was to use pant-like vocalizations (e.g., short, rhythmic, low-frequency, noisy calls linked to the breath). These vocalizations most likely function to initiate social play and reduce uncertainty in play interactions in order to avoid aggression. Proximately, play vocalizations appear to be mediated by positive affect (as shown in optimism bias experiments, e.g., Saito, Yuki, Seki, Kagawa, & Okanoya, 2016 and my experiments discussed in chapters 3 and 4).

How did a vocalization that is emotionally linked and context-dependent become a flexible feature of human communication? Since diverging from other apes, human laughter has evolved unique functions. It is routinely used outside of social play, within speech, and to broadcast social information. Unlike other types of nonlinguistic emotional vocalizations like crying and screaming, laughter is tightly integrated with speech. It occurs in specific, rule-governed patterns relative to other linguistic constituents to punctuate utterances, signal turn-taking, and indicate irony, humor, and other indirect meanings (Bryant, 2011; Provine, 2000; Vettin & Todt, 2004). A likely explanation for this is that humans have different vocal production modes allowing for volitional forms of all nonverbal vocalizations. In the case of laughter, spontaneous and volitional forms are acoustically distinct, perceived differently by listeners, and underpinned by independent neural circuits, with volitional laughter generated by the speech production system (Ackermann, Hage, & Ziegler, 2014; Bryant & Bainbridge, 2022; Gerbella et al., 2021). Volitional laughter became incorporated into our speech production,

suggesting that its signaling functions are interrelated with functions of language-based conversational interaction more generally.

With greater clarity on laughter's phylogenetic origins comes greater pressure for language evolution theories to account for the puzzle of laughter. Research on laughter—its evolutionary history, development, and neural control—can shed light on the ways that language co-evolved with our ancestors' existing repertoires of vocal communication. In turn, research on the origins of language may help clarify the routes by which laughter came to have pragmatic functions.

2.3 References for Chapter 2

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3. Effects of laughter on a cognitive bias test in bonobos

3.1 Bonobos tend to behave optimistically after hearing laughter

Note: the following is a preprint of a manuscript co-authored by Sasha L. Winkler (Department of Anthropology, UCLA, Los Angeles, California, USA), Isabelle Laumer (Max Planck Institute of Animal Behavior, Development and Evolution of Cognition, Konstanz, Germany), Heidi Lyn (Departments of Psychology and Marine Sciences, University of South Alabama, Mobile, Alabama, USA), Alex Taylor (Institute for Neuroscience, Universitat Autònoma de Barcelona), and Erica A. Cartmill (Department of Anthropology, Indiana University, Bloomington, Indiana, USA).

Abstract

Emotions can impact a wide range of cognitive functions, including memory, attention, and decision-making. So far, studies of emotion in non-human animals have typically focused on negative emotions—like fear—with clear behavioral correlates. Studies of positive emotion are needed to balance this one-sided understanding. In humans, laughter is often a clear behavioral marker of positive emotion. Non-human great apes produce similar vocalizations during play that likely evolved from a shared ancestral form of laughter. To determine the cognitive impacts of positive emotions in apes, we used a cognitive bias test to ask whether hearing conspecific laughter led apes to expect positive outcomes. We trained bonobos to approach rewarded (black) stimuli and to skip unrewarded (white) stimuli. We then presented them with occasional ambiguous (grey) stimuli. Bonobos approached the ambiguous stimuli more often after hearing laughter. Our results suggest that hearing laughter induces positive emotions and may therefore bias decision-making in bonobos. While only apes produce human-like laughter, many non-

human animals have play-specific vocalizations, some of which are also contagious. Play vocalizations may lead other species to anticipate positive outcomes, revealing commonalities in the role of positive emotion in behavior across species.

Introduction

Emotions can impact many aspects of cognition, including memory, attention, visual processing, and decision making (e.g., Mendl et al., 2009). Animal research has historically focused on negative emotions, but there is growing interest in positive affective states in animals (Nelson et al., 2023). Comparative studies are well-suited to answer questions about the biological basis of affect and cognition, but are in need of robust methods for experimentally inducing positive affect (Nelson et al., 2023).

One behavior consistently associated with positive affect in humans is laughter (Provine, 2000). While laughter is often thought of as a human trait related to humor, it has many commonalities with the signals animals make during play. Play-specific vocalizations in animals are common and likely evolved to reduce the risk of play being misinterpreted as aggression (Winkler & Bryant, 2021). Great apes produce vocalizations resembling human laughter during tickling and rough-and-tumble play. Phylogenetic analyses of their acoustic properties suggest that they share a close evolutionary history with human laughter (Davila-Ross et al., 2010).

Primate play vocalizations and their associated facial expression (play face) are contagious, underpinning the similarities to human laughter (Davila Ross et al., 2008; Davila-Ross et al., 2011; Mancini et al., 2013). In chimpanzees, contagious laughter correlates with longer periods of play (Davila-Ross et al., 2011), suggesting that play vocalizations might promote positive affective states. This aligns with comparative studies showing that hearing play

vocalizations induces play (in kea parrots; Schwing et al., 2017), leads subjects to expect positive outcomes (in rats; Saito et al., 2016), and reduces stress behaviors (in dogs; Simonet et al., 2005). These studies suggest that play vocalizations can initiate and prolong play, and that they might also impact cognition outside of play.

Measuring affect in animals is difficult since one cannot use self-report. One promising approach is to look for cognitive effects that accompany affect changes in humans. We employed this method to study positive affect in bonobos (*Pan paniscus*), an ape species closely related to humans. We used a cognitive bias test to assess the emotional and cognitive effects of listening to laughter. This paradigm, alternatively called a judgement bias or ambiguous cue interpretation test (Mendl et al., 2009; Rygula et al., 2012), draws on the finding that human and non-human animals, when faced with uncertain events, expect more positive outcomes when they are in positive affective states —in other words, they are more optimistic (Mendl et al., 2009). We hypothesized that *emotional* contagion is the proximal mechanism for the *behavioral* contagion of play faces and laughter in great apes (Davila-Ross et al., 2011), and that simply hearing laughter would induce a positive mood. We used a similar cognitive bias test design to those used in other species (Bateson & Nettle, 2015; McCoy et al., 2019; Saito et al., 2016). Subjects were first trained to produce different responses to positive and neutral stimuli. Then, their responses to ambiguous, intermediate stimuli indicated whether they anticipated positive or neutral outcomes (Hintze et al., 2018). We expected that animals in a positive mood would have greater optimism bias, and would therefore be more likely to respond to ambiguous stimuli as if they were positive.

Results

We used a within-subjects cognitive bias test design to determine whether bonobos would respond optimistically after hearing laughter. Subjects ($N = 4$ bonobos) listened to recordings of either bonobo laughter or a control sound for approximately seven minutes and then completed a cognitive bias test that assessed their likelihood to approach ambiguous stimuli. The laughter was compiled from clips of an unfamiliar bonobo infant provided by Dr. Marina Davila-Ross. The control recording was a synthetic "winter storm" soundtrack. We predicted that subjects would approach ambiguous stimuli more in the laughter condition.

To assess the impact of condition on the decision to approach (GO) or skip to the next trial (NO-GO), we used a generalized linear regression model with binomial error distribution and logit link function. Our outcome variable was the decision to approach the ambiguous stimuli. We included condition, box color, subject, session number, and date as fixed effects. After controlling for these variables, the effect of condition on the decision to approach had an odds ratio of 3.39 (95% confidence interval = 0.895 to 15.6, $p = 0.0878$). The effect of condition was marginally significant in a likelihood ratio test between the full and null model (nested model excluding condition; $\chi^2 = 3.207$, $p = 0.073$; see SI for additional models). Figure 3.3 shows the effect of condition on likelihood of approach.

Discussion

Bonobos tended to behave more optimistically following exposure to laughter compared to a control sound. The odds ratio for condition in our model was 3.39, meaning that bonobos in the laughter condition had more than three times greater odds of approaching the ambiguous stimulus (expecting a reward) than those in the control condition (after accounting for our control

variables; see Figure 3.3 for the average approach responses in the raw data). This implies that the sound of conspecific laughter induced a positive affective state in bonobos, consequently making them more optimistic.

To our knowledge, this study is the first to detect positive affect shift in non-human primates from a brief experimental intervention. However, our method was quite training-intensive and our final sample ($N = 4$) was even smaller than our target sample ($N = 7$) due to difficulties in training some individuals. This reduced our statistical power and was the main limitation of our study. Cognitive bias tests with response-time designs that require less training might be more practical in future research (e.g., Bateson & Nettle, 2015).

The positive emotional contagion that humans experience from laughter appears to have been present in the primate lineage long before the evolution of language. Further studies are needed to strengthen our understanding of positive affect. Specifically, comparative research on positive affect and cognition can provide insights into the evolutionary precursors of emotional contagion, empathy, cooperation, and ultimately, human prosociality.

Materials and Methods

Subjects were four bonobos (three male, one female) at the Ape Cognition and Conservation Initiative in Des Moines, Iowa, USA.

We applied a modified cognitive bias test design previously used in chimpanzees (Bateson & Nettle, 2015). Stimuli were five differently-colored boxes located approximately 3 meters from the subject. The positive box (black) always contained a food reward, while the neutral box (white) was always empty. Bonobos were first trained to approach the black box (GO) and to push an initiator button (similar to Hintze et al., 2018) to skip to the next box when

presented with a white box (NO-GO). Apes proceeded to testing if they approached the positive box and refrained from approaching the neutral box in at least 80% of trials in two consecutive training sessions of 20 trials each. Seven bonobos underwent initial training but only four met these testing criteria.

Each test subject received four laughter and four control sessions, in an alternating order counterbalanced across subjects. Test sessions consisted of four to ten refresher trials of anchor stimuli (positive and neutral), followed by a semi-randomized block of eight positive, eight neutral, and three ambiguous stimuli that apes had never seen before. The three ambiguous boxes (intermediate shades of grey) were rewarded 50% of the time to reduce learning. All sessions were videotaped, and the GO/NO-GO response was coded from video. To ensure that the paradigm worked we calculated approach rates for each of the five stimuli during testing. Apes almost always approached the black box, almost never approached the white box, and intermediate stimuli were approached in accordance with their perceptual closeness to these anchor stimuli (see Figure 3.2 and SI for more details).

This study was approved by the UCLA Animal Research Committee (ARC-2022-063) and the Ape Initiative IACUC (222505-01) and was carried out in accordance with relevant guidelines and US laws regarding animal care and use.

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Figures

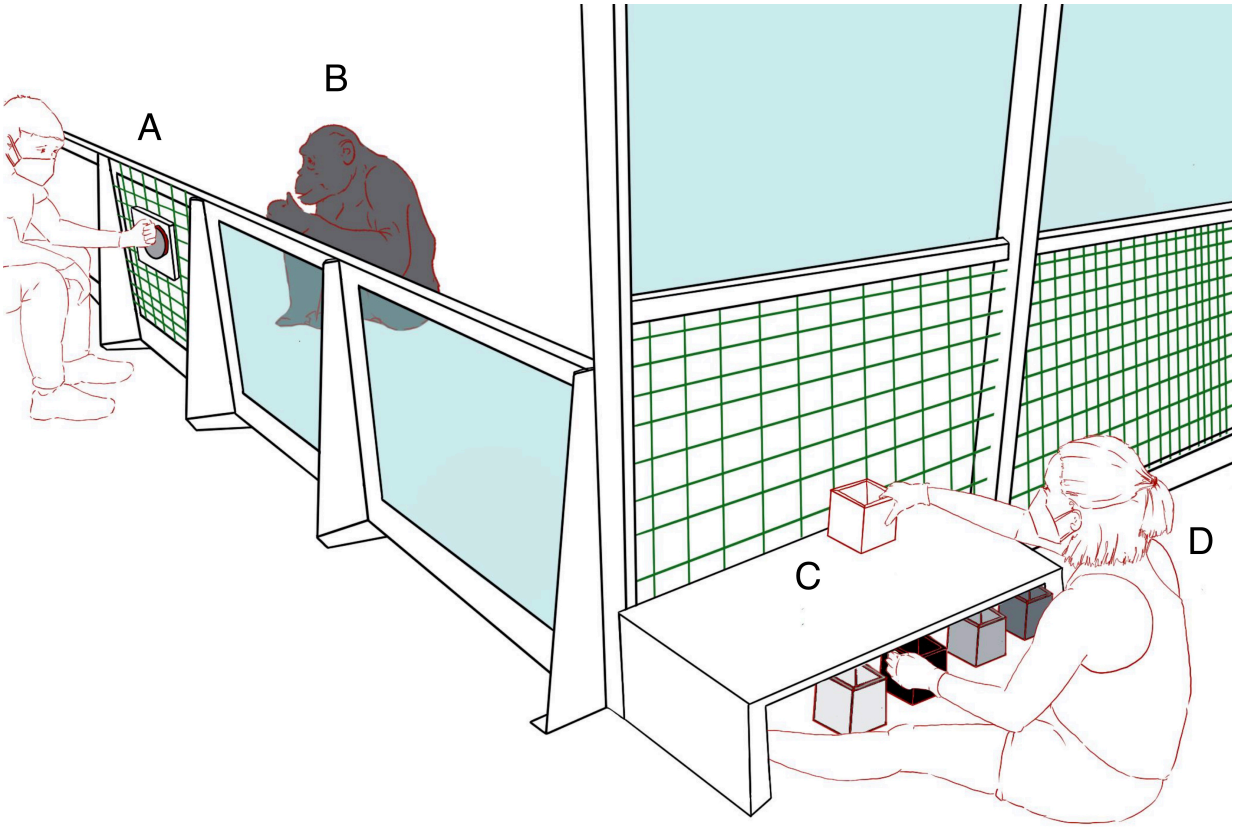

Figure 3.1. Experimental set-up. Subject (B) is pictured near the initiator button operated by experimenter (A). Pressing the button began a new trial: experimenter (D) presented a new box (C) and the subject either approached (GO) or pressed the button to skip (NO-GO).

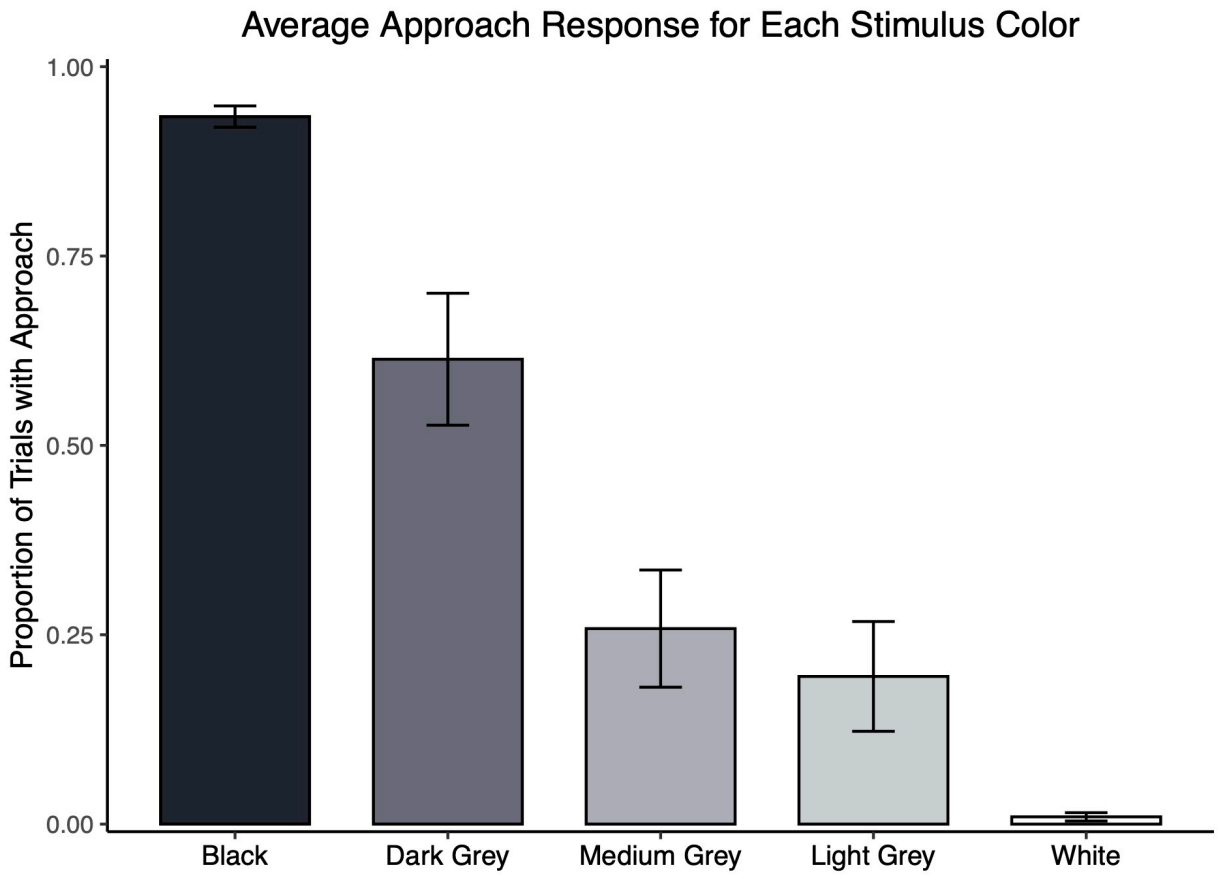

Figure 3.2. Mean proportion of testing trials with approach (GO) responses plotted against stimulus color. The black box (positive) always contained food, white box (neutral) never did, and grey boxes (ambiguous) did 50% of the time. Bars represent bootstrapped standard errors.

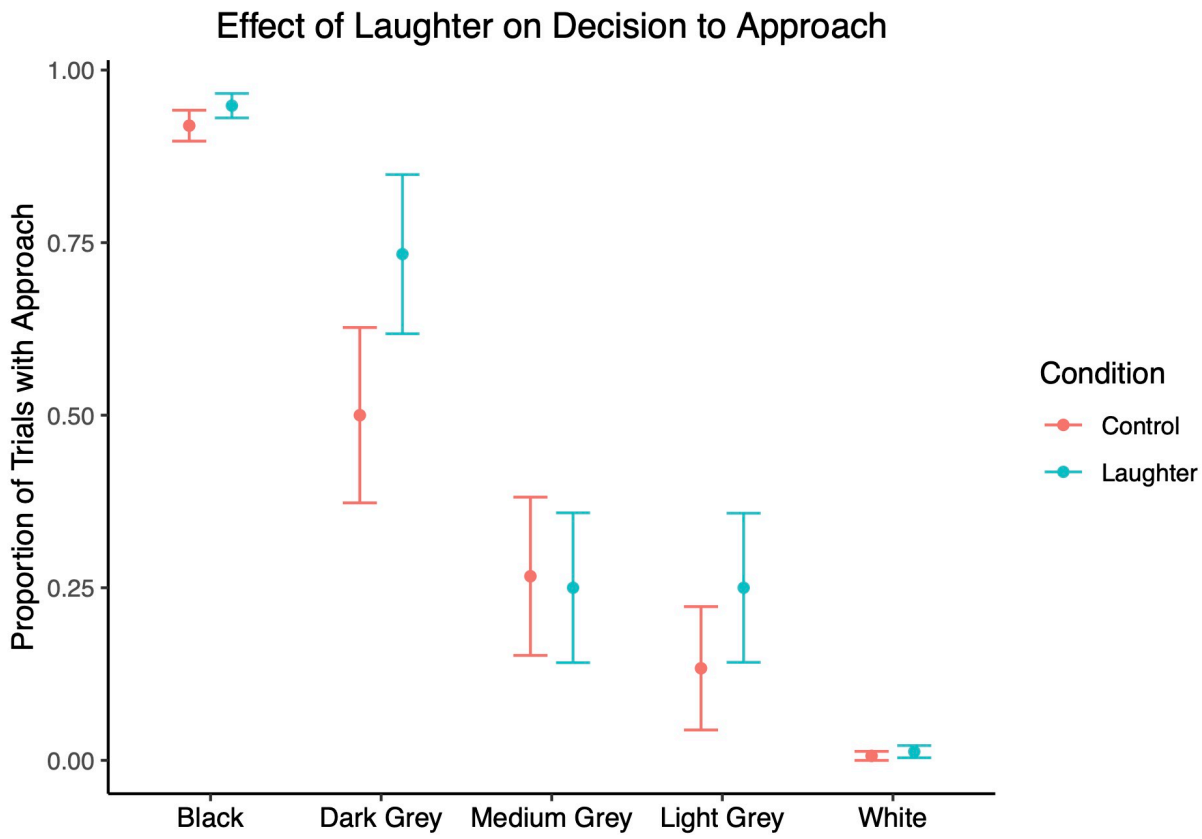

Figure 3.3. Mean proportion of testing trials with approach (GO) responses plotted against stimulus color, broken out by condition (red = control, blue = laughter). Bars represent bootstrapped standard errors.

3.2 Supplementary Information for "Bonobos tend to behave optimistically after hearing laughter"

Supporting Information

Extended details of the experimental methods are included below.

Subjects

Subjects were four adult bonobos living at the Ape Initiative in Des Moines, Iowa, USA: Mali, a 14-year-old female, Teco, a 12-year-old male, Kanzi, a 41-year-old male, and Nyota, a 24-year-old male. Testing took place August to December, 2022. All subjects had extensive experience interacting with human caretakers. Three of the subjects (Kanzi, Nyota, and Teco) also had experience using lexigrams (a keyboard language system), though proficiency varied greatly between apes. Lexigrams were not used in this study, but they illustrate the level of past experience these apes had with human interaction (see Lyn, 2017).

Training Information

Before testing, the bonobos were trained to anticipate positive and neutral outcomes for two anchor stimuli: a positive box (black) that always contained a food reward and a neutral box (white) that never contained a food reward. Apes were also trained to use an initiator button to begin a new trial (i.e., to have a new box presented), similar to Hintze et al. (2018). After subjects met our training accuracy threshold, they proceeded to testing sessions. Apes never saw the ambiguous stimuli (the three different shades of grey) until testing. Our accuracy threshold to qualify for testing was that a subject must: (1) approach the positive box in at least 80% of trials

(GO response) and (2) refrain from approaching the neutral box in at least 80% of trials (NO-GO response), in at least two consecutive sessions of 20 trials each (ten black and ten white, at minimum). Three of the seven bonobos were unable to reach this threshold due to lack of participation within the training timeframe (2 females) and inability to reach accuracy (1 male).

Study Design, Randomization and Counterbalancing

Order of testing sessions. All bonobos received laughter and control sessions on separate days in an alternating order, with two subjects starting with laughter and two subjects starting with control. However, due to an experimenter error, one bonobo (Mali) received the order (1) control, (2) laughter, (3) control, (4) laugher, (5) control, (6) control, (7) laughter, (8) laughter—the order of sessions 6 and 7 was swapped. All other sessions were counterbalanced, and we controlled for condition and session number in the statistical models. Each subject was always tested in the same location and with the same set of experimenters.

Order of trials within sessions. Each trial involved a single stimuli presentation (including the bonobo pressing the initiator button, the experimenter presenting a new box, and the bonobo's GO/NO-GO decision). Each testing session consisted of 23 trials total: ten positive/black trials, ten neutral/white trials, and three ambiguous/grey trials (each one a different shade of grey).

A block of four refresher trials always came first and involved presentations of two black boxes and two white boxes (pseudorandomized such that we always started with a black). The refreshers were designed this way to increase motivation at the start of the session and to refresh the bonobo's anchor stimuli training.

After the refreshers, the apes were presented with a block of 19 trials: eight black, eight white, one light grey, one medium grey, and one dark grey. These were pseudorandomized such that the ambiguous grey trials were not clustered together and no more than three trials of one type of anchor (or one type of anchor stimuli plus ambiguous stimuli) appeared in a row. This was to prevent learning of any heuristic responses and to sustain participation, because bonobos tended to lose motivation if too many unrewarded trials appeared in a row during training.

Additionally, one subject (Nyota) exhibited low motivation to participate in any research task on certain days. To assess his willingness to participate before we started the audio playback, we presented Nyota with an additional refresher block of 6 trials (3 black, 3 white) before testing started. If he refused to engage in these 6 probe trials, testing was postponed to the next available testing day.

Ambiguous trial rewarding. We randomized rewards for the ambiguous stimuli (the three grey boxes). Randomization was designed to reduce the possibility that subjects might learn any rules or heuristics for whether to approach the ambiguous boxes. Grey boxes were rewarded on average 50% across all the trials that each bonobo received. These were pseudorandomized such that the three ambiguous trials within a testing block were never all unrewarded or all rewarded. The reward rate was (1) 50% for *all* shades of grey in total across all sessions; (2) 50% for *each* shade of grey across all sessions; (3) 50% for *all* shades of grey in the laughter sessions and 50% in the control sessions; (4) either 33% or 66% across *all* the shades of grey *within* each session (since there were only three grey trials per session). Due to an experimenter error, there was one ambiguous trial that was unrewarded when it should have been rewarded (subject Mali, session 7, dark grey trial) resulting in 33% ambiguous trials rewarded in that session rather than 66%.

Excluded trials. In the final analyses, we did not include any trials where the bonobo or experimenters made mistakes with the testing paradigm (3.5% of trials). Mistakes were mostly trials in which the bonobos did not see the box color before making a decision: either the bonobo started to approach before the box was visible and the experimenter, not noticing this, still presented a box (i.e., false start; 1.8%), or the bonobo did not turn their head to look toward the box at any point before pressing the button for the next trial (1.2%). This ensured that all of the GO/NO-GO responses we analyzed were fully informed by the color of the box, which is key to the testing paradigm. Four trials were excluded due to human experimenter errors with the testing procedure (0.5%; two accidentally skipped trials and two trials with mistakes on the timing of the button replacement). One trial was mistakenly added at the end of a session (subject Teco, session 1, black trial) and was included in analyses of the anchor stimuli.

Audio Playback Information

Audio was played from an Anchor AN-Mini speaker connected to a laptop. The audio was controlled using either Windows Media Player or Apple Music software.

Laughter recordings. The laughter playback recording was compiled from clips of an unfamiliar infant bonobo laughing while being tickled by a human experimenter. The clips were provided by Dr. Marina Davila-Ross at the University of Portsmouth. The laughs were from the same bonobo, a male approximately eight months old. Several shorter laughter clips were edited and integrated into one 3:44 clip that was repeated with 1 s. of silence in between. The total duration of the playback recording was 7:28. A small amount of mechanical, percussive, and/or ambient noise was present in some of the clips used to produce the playback recording. All audible human vocal sounds were edited out. In cases where we could not remove the human-

generated sounds without affecting the bonobo laughter sounds, we did not include the entire clip in constructing the playback.

Control recording. The control recording was a time- and volume- matched recording of a sound similar to white noise. Instead of using true white noise, which can be aversive to some animals (Blumstein & Récapet, 2009; Saito et al., 2016), we used a synthetic "winter storm" noise obtained online (mp3 purchased on Soundcloud), similar to those available on commercial sleep machines. The duration was the same as the final laughter audio (7:28, including a short fade in and out to avoid a harsh onset/offset).

We were limited to one control condition due to the small sample size and experimental design. Having fewer conditions reduced the number of testing sessions and lowered the risk that bonobos would learn rules or heuristics for responding to the ambiguous stimuli. We opted to play a neutral environmental sound as the control condition to keep all the experimenters' behavior between the conditions as similar as possible (setting up the speaker, playing sounds from a laptop, etc.) between conditions. While a neutral vocalization would be an ideal control, we could not identify any bonobo vocalization that would be predicted to be meaningless or without affective relevance to the listener. Future research with larger sample sizes would benefit from additional controls to assess the effects of laughter compared to other vocalizations.

Statistical models

All statistical models were fitted in R version 4.3.1 (R Core Team, 2023). Our primary statistical model assessing the effect of condition on the likelihood of approaching was fit using the glm function in the stats package (Hastie & Pregibon, 1992; Venables & Ripley, 2002) using the binomial family and the following model formula: *Approach ~ Condition + Stimulus Color +*

Date + *Testing Session* + *Bonobo*. *Approach* was the decision to GO (coded as 1) or NO-GO (coded as 0). *Condition* was laughter (1) or control (0). *Stimulus Color* was a categorical variable for the color of the box (Dark Grey, Medium Grey, or Light Grey). *Date* was the day of testing, with 0 being the first day of testing, included to control for exogenous mood effects related to seasonality as testing began in summer and ended in winter. *Testing Session* was the session number as a categorical variable included to control for order effects. *Bonobo* was the subject's identifier, included as a fixed effect.

As we had no subject-level research questions we included *Bonobo* as a fixed effect. This is standard practice when there are fewer than five levels of the cluster variable (see Gomes, 2022 for a nuanced discussion of these modeling tradeoffs). A multilevel version of the same model with *Bonobo* as a random intercepts effect was fit using the glmer function in the lme4 package (Bates et al., 2015) using the binomial family with the optimizer "bobyqa" to aid in convergence. We used the following model formula: *Approach* ~ *Condition* + *Stimulus Color* + *Date* + *Testing Session* + (1 | *Bonobo*). After accounting for the control variables, the effect of condition in this model had an odds ratio of 2.79 (95% confidence interval = 0.795 to 9.77, p = 0.109). The likelihood ratio test between the full and null model (nested model excluding condition; see below) resulted in a χ^2 of 2.7051 (p = 0.100).

Model comparison. We conducted a likelihood ratio (chi-squared) test to estimate the effect of including *Condition* in the model reported in Section 3.1 and the multilevel model reported above. In both cases we compared the goodness of fit between two nested models, the full model including condition and a simpler model including the same predictors except for *Condition*, to evaluate whether the full model improved the fit to the data compared to the simpler model (Forstmeier & Schielzeth, 2011; Glover & Dixon, 2004).

Supporting Information for Figures

The standard errors for Figures 3.2 and 3.3 were calculated using a bootstrap method using the function boot() in the boot package in R. The original data was resampled with replacement to produce a distribution of 2000 bootstrapped sample means.

In Figure 3.2, the mean proportion of trials with approach for the **black box** across all testing conditions = 0.934, *SD* = 0.248, *SE* = 0.0141, number of trials = 304, 95% *CI* = [0.905, 0.961]. The mean approach proportion for the **dark grey box** across all testing conditions = 0.613, *SD* = 0.495, *SE* = 0.087, number of trials = 31, 95% *CI* = [0.452, 0.774]. The mean approach proportion for the **medium grey box** across all testing conditions = 0.258, *SD* = 0.445, *SE* = 0.077, number of trials = 31, 95% *CI* = [0.129, 0.419]. The mean approach proportion for the **light grey box** across all testing conditions = 0.194, *SD* = 0.402, *SE* = 0.073, number of trials = 31, 95% CI = [0.0645, 0.355]. The mean approach proportion for the **white box** across all testing conditions = 0.010, *SD* = 0.097, *SE* = 0.005, number of trials = 314, 95% *CI* = [0, 0.0223].

Note: this is the end of the preprint manuscript.

3.3 Analysis of response times

Introduction

In previous cognitive bias studies, response time is often used as the outcome variable. The primary benefit of this approach is reduced training. Unlike in the forced choice GO/NO-GO paradigm used in our study, response time designs require minimal training to establish differential response times to two anchor stimuli. In general, animals are faster to approach or

touch rewarded stimuli compared to unrewarded stimuli. Once this is established, approach times on trials with ambiguous stimuli can then be used as an indication that the animal is anticipating a reward. As examples of cognitive bias studies with response time outcomes, Adrianese et al. (2019) measured latency to peck in ravens; McCoy et al. (2019) measured latency to peck in New Caledonian crows; Bateson & Nettle (2015) measured latency to touch in chimpanzees; Doyle et al. (2011) measured latency to approach in sheep; Mendl et al. (2010) measured latency to approach in dogs; and Gordon & Rogers (2015) measured latency to inspect in marmosets.

In contrast, our GO/NO-GO paradigm was more similar to a forced-choice task, with animals trained to produce different responses to the anchor stimuli that were not comparable in time. The GO response required walking to another side of the cage while the NO-GO response merely required pushing a button. Because our task required different behavioral responses to the anchor stimuli, we did not establish during training that subjects produced reliable response time differences to approach the anchor stimuli. During the final training sessions, subjects almost always approached the black boxes (above 80% of the time) and almost never approached the white boxes (less than 20% percent of the time). Thus, approach times were difficult to calculate for the white box as they were rare and treated as errors during training.

Despite this, if the general phenomenon holds that rewards are associated with faster response times, we might still expect animals to be faster when they anticipate a reward. Thus, we predicted that bonobos in our study would have shorter approach times toward the black boxes than the white boxes. We also predicted that bonobos would approach gray stimuli faster in the laughter condition (treating them as more similar to the black box) than in the control condition. Finally, we speculated that bonobos might also respond to all stimuli faster in the

laughter versus control conditions due to increased reward anticipation or excitement (in contrast to response slowing under threat conditions, as in Marzouki et al., 2014 and Bethell et al., 2016).

Methods

We measured all response times during the cognitive bias test previously described in sections 3.1 and 3.2. Testing sessions were videotaped and behaviors were coded using the software program BORIS, which enabled precise time estimates (Friard & Gamba, 2016). The response times were calculated from the time that a new box was visible to the time the subject completed their GO/NO-GO decision: either when they pressed the button (for NO-GO) or reached the mesh in front of the box experimenter (for GO). In cases of a failed button press (see Table 3.1 for description) that was then followed by a successful button press, we coded the response time as the time from the box being visible to the first failed button press, as we can assume this was the moment they made the decision to NO-GO but had difficulty pressing the button.

To establish coding reliability, all behaviors were coded in BORIS by me and one other observer. Reliability was measured by calculating percentage agreement scores. Two coders were considered to be in agreement if the same behavior was coded within a certain time threshold. This threshold was one second for all the behaviors that were used to calculate response times. In other words, the coders were considered to be in agreement if they entered the same behavior within one second of one another. False starts were not used to calculate response times, so we used a less strict reliability threshold of three seconds.

Table 3.1. Ethogram and reliability information for bonobo response time analysis

Behavior	Description	Reliability threshold (seconds)	Number of observations	Percent agreement
Box is visible	The experimenter presented a new box; coded first frame when at least 50% of the box appeared to be visible to the bonobo.	1	755	94.2
Approach mesh	The bonobo approached the mesh within arm's reach of the box experimenter; coded the first frame that the bonobo appeared to stop moving toward the experimenter.	1	334	93.1
Press button	The bonobo successfully pressed the initiator button triggering an auditory cue ("start").	1	816	99.0
Failed button press	The bonobo clearly touched and tried to press the initiator button but did not trigger the full auditory cue ("start"). Experimenters may prompt the bonobo to press it again ("try again").	1	58	86.2
False start	The bonobo began to approach the box experimenter before a new box was visible. When this occurred, the bonobo was repositioned at the initiator and the trial was restarted. Coded the first frame that the bonobo appeared to stop moving toward the experimenter.	3 (not used for response times)	76	92.1

Note: for each observation, the two coders were considered to be in agreement if they both entered the same behavior within the reliability threshold time (e.g., with timestamps that differed by less than one second).

Results

Average approach times for anchor stimuli

Our predictions for approach times were generally not supported. In the few cases in which the white boxes were approached (3 times, all by the subject Nyota), they tended to be approached faster than the black boxes (mean GO time for white boxes = 2.92s, *SE* = 0.397, mean GO time for black boxes = 3.50s, *SE* = 0.045). This may be attributed to an error in decision making, leading any approach to signal anticipation of reward. If the bonobo did not anticipate a reward, they should have skipped to the next trial.

Average NO-GO response times for anchor stimuli

Interestingly, bonobos were faster to make NO-GO responses to the black boxes than the white boxes (mean NO-GO time for white boxes = 2.63s, *SE* = 0.188, mean NO-GO time for black boxes = 1.98s, *SE* = 0.178). However, it is difficult to interpret these results without more information. One possibility is that when bonobos made an error, by skipping the box that was actually rewarded, those errors were more impulsive and thus faster than the accurate NO-GO responses to the white boxes. Perhaps the faster reaction times to the black box were indicative of a lack of processing of the color, which might cause longer response times under correct decision making. It might also be an indication of lack of inhibitory control on the NO-GO response. Indeed, it appeared as though NO-GOs to black boxes were occasionally recognized as errors by the bonobos, who sometimes quickly rushed over to approach the box after first giving a NO-GO response—in other words, correcting their mistake (coded as false starts for the next trial, see Table 3.1).

Anecdotally, it also seemed that inhibitory control was an important part of the cognitive bias task training. As an example, one subject (Kanzi) began early in his training by always approaching all the boxes, even white ones. After learning to instead skip the white boxes by pressing the button, he then went through a training phase where he often pressed the button in response to black boxes but then still begged toward the experimenter afterward. His training therefore involved shaping his behavior to first inhibit the default approach, and then to inhibit the default button press.

Average response times for ambiguous stimuli

On average, when bonobos made a NO-GO response, the gray boxes were responded to in a somewhat intermediate pattern to the anchors based on perceptual similarity (see Figure 3.4 and Table 3.2). There was no clear pattern to the approach times toward the gray boxes in relation to the anchor stimuli approach times. An exception was the dark gray box, which had even longer approach times than the black boxes (mean response time = 3.82s, *SE* = 0.267). However, it is important to note that the variances were quite large in proportion to these differences.

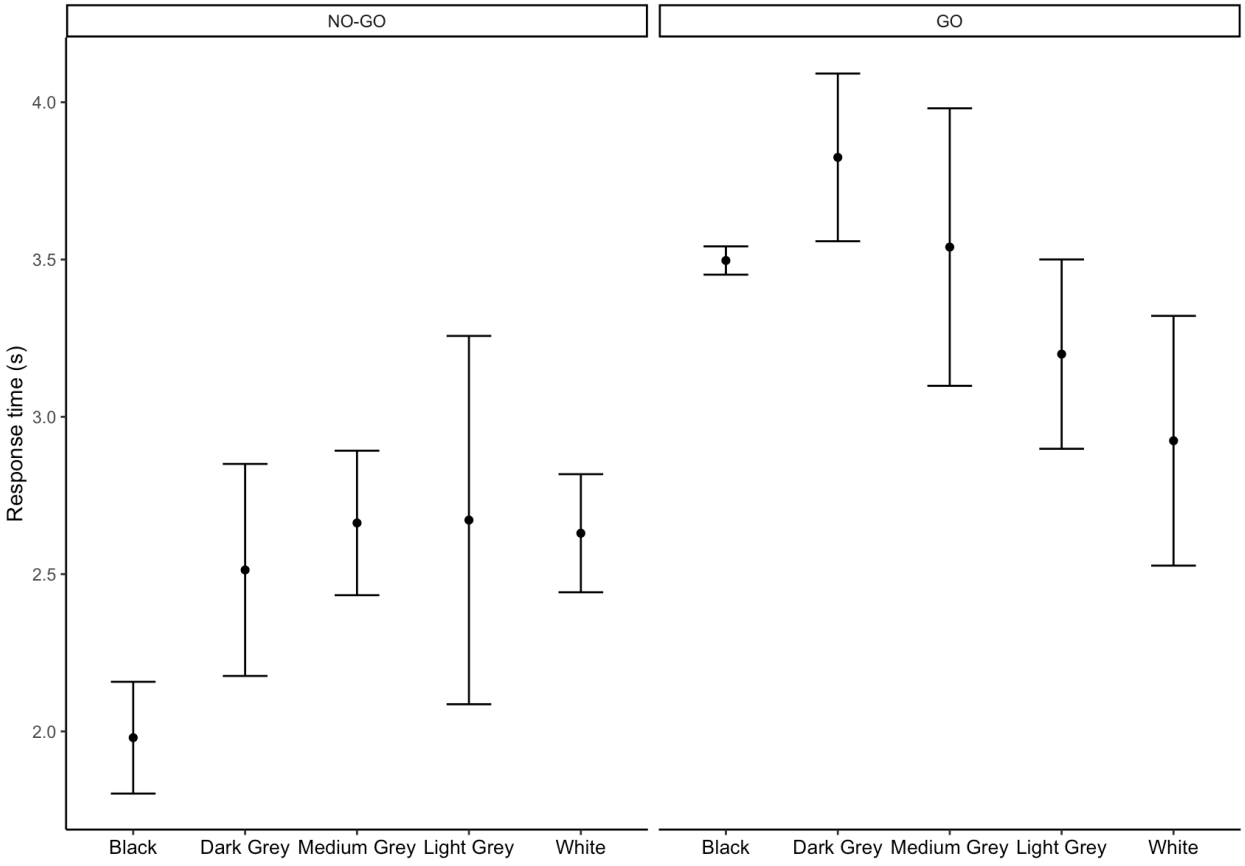

Figure 3.4. Average response times to different stimuli during testing.

Effect of laughter on approach response times

There were no clear patterns of the effect of laughter on approach times (see Figure 3.5). For the black stimuli, laughter appeared to have no effect on approach times (mean GO time in the control condition = 3.51s, *SE* = 0.055, mean GO time in the laughter condition = 3.48s, *SE* = 0.071). There were too few approach responses toward white boxes to detect any patterns, with only one approach to white boxes in the control condition (3.70s) compared to two in the laughter condition (mean = 2.53s, *SE* = 0.133). The ambiguous gray boxes produced inconsistent patterns in approach times. Approaches toward light gray boxes were faster in the laughter

condition, but approaches toward dark gray boxes were slower in the laughter condition and approach times toward medium gray boxes were similar between the two conditions.

Effect of laughter on NO-GO response times

Hearing laughter slightly decreased reaction times for all NO-GO responses. Because all NO-GO response times were slightly faster in the laughter compared to control condition, the ambiguous responses were more similar to the average black response than to the average white response, which is consistent with our general predictions about the effect of laughter on reward anticipation. Unexpectedly, the strongest effect of laughter was seen in the incorrect NO-GO responses to black boxes (see Figure 3.5). If these errors can be attributed to lack of processing of the color and/or lack of inhibitory control, it appears that laughter may have exacerbated the effects of those quick error-generating phenomena. However, this is merely speculative as laughter resulted in faster NO-GO response times for all colors.

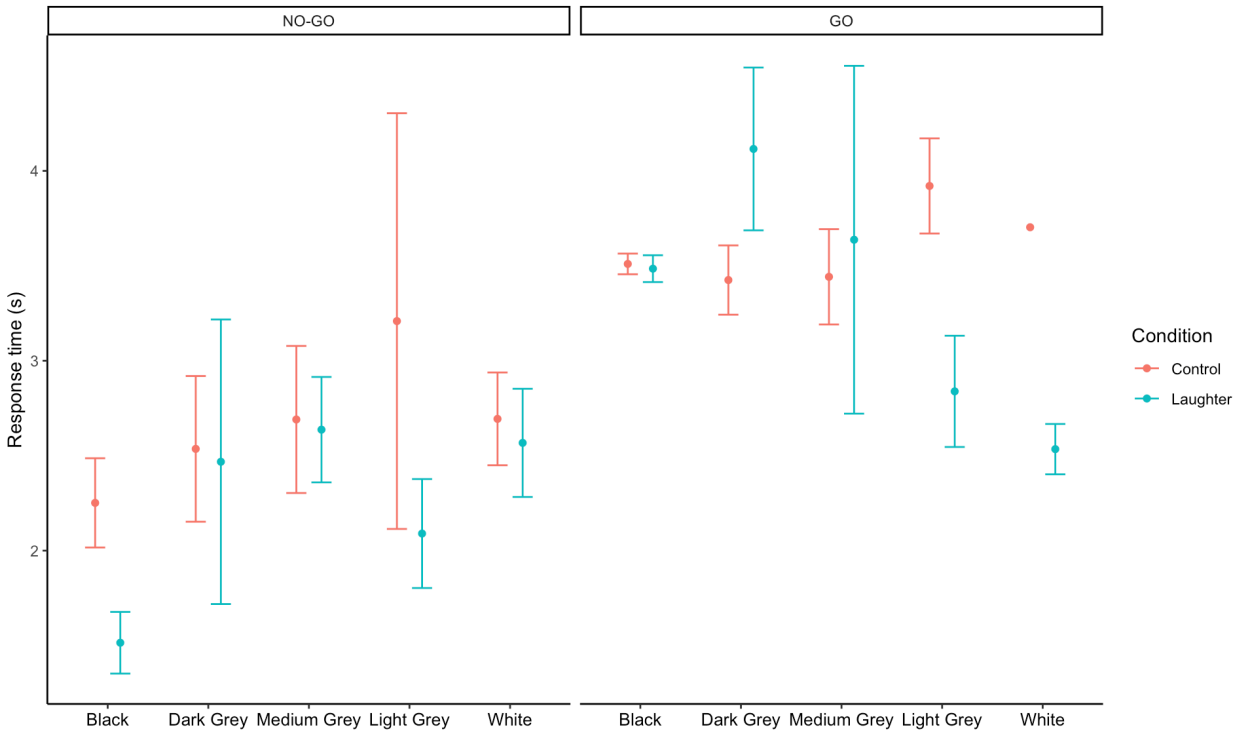

Figure 3.5. Average response times to different stimuli during testing, with effects of condition.

Table 3.2. Average response times in seconds by response type and stimulus color.

Color	GO/ NO-GO	Mean	*SE*	*n*
Black	NG	1.98	0.178	19
Dark Grey	NG	2.51	0.337	12
Medium Grey	NG	2.66	0.230	23
Light Grey	NG	2.67	0.585	25
White	NG	2.63	0.188	311
Black	G	3.50	0.045	284
Dark Grey	G	3.82	0.267	19
Medium Grey	G	3.54	0.441	8
Light Grey	G	3.20	0.301	6
White	G	2.92	0.397	3

Table 3.3. Average response times in seconds by response type, stimulus color, and condition.

Color	GO/ NO-GO	Control Mean	Control *SE*	Control *n*	Laughter Mean	Laughter *SE*	Laughter *n*
Black	NG	2.25	0.235	12	1.51	0.162	7
Dark Grey	NG	2.54	0.384	8	2.47	0.749	4
Medium Grey	NG	2.69	0.387	11	2.64	0.278	12
Light Grey	NG	3.21	1.09	13	2.09	0.287	12
White	NG	2.69	0.244	154	2.57	0.285	157
Black	G	3.51	0.055	137	3.48	0.071	147
Dark Grey	G	3.42	0.182	8	4.12	0.429	11
Medium Grey	G	3.44	0.251	4	2.84	0.293	4
Light Grey	G	3.92	0.250	2	3.64	0.916	4
White	G	3.70	*n/a*	1	2.53	0.133	2

Discussion

Caution should be taken in interpretations of reaction times in this study due to the overall high level of variation in response times and lack of variation in response type to the white anchor stimuli. Still, bonobos clearly made faster (presumably accidental) NO-GO responses toward the rewarded black stimuli than the (presumably not accidental) white or gray stimuli. This raises some interesting questions about the mental processes that could have generated these systematic errors in decision-making. Hearing laughter appeared to increase the rapidity of all NO-GO responses and the rapidity of all errors when errors were made on the anchor stimuli. Therefore, an interesting direction for future research would be to explore whether hearing laughter might systematically impair accuracy on cognitively demanding decisions, or impair inhibitory control more generally.

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4. Effects of laughter on a cognitive bias test in humans

4.1 Do humans behave optimistically after hearing laughter?

Introduction

Laughter is universal across human populations (Bryant & Bainbridge, 2022; Provine, 2000; Sauter et al., 2010). Babies laugh before they can speak, and adults laugh about 18 times every day (Martin & Kuiper, 1999). Laughter-like vocalizations are present in other animals, with comparative research over the last several decades helping to unveil laughter's deep evolutionary history rooted in play (Panksepp & Burgdorf, 2003; van Hooff, 1972; Vettin & Todt, 2005; Winkler & Bryant, 2021). The play vocalizations of other great apes share key acoustic features with human laughter. When coupled with known phylogenetic relationships, these acoustic similarities suggest that laughter evolved from a play-specific signal present in the great ape lineage at least 13 million years ago (Davila-Ross et al., 2009, 2010). As a ubiquitous and ancient nonverbal signal, laughter may provide an intriguing window into the origins of human communication. Studying laughter allows us to investigate how humans use and perceive vocal signals without the semantic connotations of language.

Previous scholarship has revealed two different types of laughter with unique production and perception systems. Volitional laughter is produced by neural systems similar to those used in speech, which may explain the remarkable flexibility we have to use laughter within conversation, and to use it intentionally to achieve pragmatic and social goals (Vettin & Todt, 2004). Meanwhile, spontaneous laughter relies on neural pathways homologous with those used in non-human communication, suggesting an evolutionarily older production system (Ackermann et al., 2014; Gerbella et al., 2021, Jürgens, 2002). Consistent with this, spontaneous

laughter is acoustically more similar to ape play vocalizations (Davila-Ross et al., 2009), and listeners perceive it as more similar to animal vocalizations than volitional laughter (Bryant & Aktipis, 2014).

Laughter occurs during a wide range of contexts in addition to speech and play, unlike the comparable vocalizations in animals that are play-specific (Winkler & Bryant, 2021). Despite this variability, laughter is generally associated with positive emotion and well-being. Several studies have linked laughter production to psychological and physiological benefits. For example, Dunbar et al. (2012) found that laughing increases pain thresholds, most likely by means of increasing endorphin production (Manninen et al., 2017). Laughing also decreases blood cortisol levels, a hormonal indicator of stress (Yim, 2016). Similarly, studies of humor suggest a range of positive physical and mental health outcomes from laughing, from improving one's ability to cope with stressors to possibly even extending the lifespan (Martin, 2002). However, many of these studies tend to combine or conflate laughter with humor, so it can be difficult to determine the effects of laughter itself separate from the effects of enjoying humorous stimuli.

Cross-cultural studies have also found a seemingly universal interpretation of laughter as an expression of positive emotion (Gendron et al., 2015; Sauter et al., 2015). Studies of laughter perception reveal that subtle social information is encoded in the sound. One study showed that listeners across 24 societies were able to detect affiliation strength (close friends versus acquaintances) from extremely short clips of their co-laughter (Bryant et al., 2016). Even 5-month-old infants are able to distinguish friends from acquaintances based on their co-laughter: infants preferentially listened to co-laughter between friends compared to laughter of

acquaintances, and were more surprised when the laughter clip did not match the social closeness in a video interaction scene (Vouloumanos & Bryant, 2019).

Laughter perception research has explored the contagiousness of laughter. In a classic study, Provine (1992) found that simply hearing canned laughter caused listeners to smile and laugh themselves. This study relied on self-report of the behaviors and only included students from a single undergraduate psychology class (Provine, 1992). A more recent study by Arévalo-Pachón and Cruz (2021) found evidence for contagion in the facial expressions and facial EMG muscle responses of participants when listening to laughter that had previously been rated by others as highly contagious. Neural studies have identified a common area in the pACC that is activated during both perception and production of laughter, suggesting a possible mirror mechanism (Caruana et al., 2020). In one study, infants as young as 5 months of age also had higher rates of smiling after listening to laughter (Jordan & Thomas, 2017). Contagion may be an evolutionary ancient aspect of laughter, as animals like chimpanzees, rats and kea parrots appear to display contagion in their play vocalizations (Davila-Ross et al., 2011; Saito et al., 2016; Schwing et al., 2017).

One plausible mechanism for the behavioral contagion of laughter is contagion of a positive or playful emotion: that simply hearing laughter puts the listener in a positive mood, causing them to display smiles and laughs as signals of their own affect. Indeed, Bachorowski and Owren (2001) argued for an affect-induction hypothesis of laughter based on their findings that listeners gave consistently positive or negative ratings of different types of laughs depending on their acoustic properties (e.g., voiced versus unvoiced). They argued that rather than being a stereotyped signal with context-dependent meanings, laughter can be used strategically (and unconsciously) to manipulate others' arousal and general affective state through its acoustic

properties alone (Bachorowski & Owren, 2001). Further support for shared positive emotions comes from a study by Manninen and colleagues, which found that people had increased opioid levels after co-laughter (although it was impossible to tease apart the effects of hearing laughter, sharing laughter, or simply sharing a positive and humorous experience with another person; Manninen et al., 2017). On the other hand, behavioral contagion could also be explained proximally without a need for any underlying emotional contagion—for example, by means of a more reflex-like mirror neuron system (Davila-Ross et al, 2011).

Social context certainly influences humor appreciation, and context could play an important role in the more basic processes of laughter perception and its associated emotion. In fact, psychological and social constructionist theories of emotion regard emotions themselves as fundamentally dependent on social contextual factors and appraisals (Gross & Barrett, 2011). Meanwhile, basic emotion theory (Ekman, 1992; Panksepp & Watt, 2011) is more compatible with a simple stimulus-response pattern, such that the perception of laughter (and perhaps even the perception of distinct acoustic signatures or components of laughter) triggers a basic emotion circuit for joy or play, which then guides future behavior such as the replication of the same signal. The latter is more similar to Bachorowski and Owren's (2001) affect-induction hypothesis. Due to the rapid contagion of the response, it is possible that simply hearing the sound of laughter might directly and automatically induce positive emotions in listeners, which are later modulated by social and contextual factors. Factors such as the relationship to the social partner, surrounding behavior, number of people present, and semantic or other contextual information, could all interact with laughter perception to produce different sociocognitive effects.

Cognitive effects of emotion

The effects of hearing laughter are likely both emotional and cognitive: it may change the behavior of perceivers, how they feel, how they react to others, or how they process linguistic and other social information. For example, laughter in speech aids understanding of statements as ironic or humorous (Bryant, 2011). The extent to which cognitive or behavioral effects of laughter may themselves be caused by emotion has not been explored.

Emotions are known to influence biases in attention, memory, and decision making (Hales et al., 2014; Lemaire, 2021). Optimism bias, for example, is the bias that people have when assessing the likelihood of positive or negative future events (Sharot, 2011). Optimism or its converse, pessimism, are influenced by both short-term emotions and more chronic moods and mood disorders. People experiencing more positive emotions tend to be more optimistic. In previous research, people with symptoms of depression had a higher expectation of negative future events (Strunk et al., 2006). People in negative moods were also more likely to interpret ambiguous homophones or sentences as negative in several studies (Eysenck et al., 1991; Mathews & MacLeod, 1994; Mogg et al., 2006). Aylward et al (2019) found that people with symptoms of pathological anxiety and mood disorders tended to have a more negative bias when interpreting ambiguous tone stimuli, when compared to asymptomatic participants. However, a short-term intervention to induce anxiety did not significantly increase negative bias on the same task (Aylward et al., 2019).

Optimism bias as a proxy for positive emotion has been validated by self-report studies. For example, low reported anticipation of future positive events was correlated with self-reported questions on the BDI-II (a 21-question scale for depressive symptoms) in Strunk et al. (2006). Additionally, in Paul et al. (2011), participants reported their current moods using the PANAS, a

20-question emotion scale. They then participated in a cognitive bias task that had subjects judge whether an X on a screen was closer to either a positive or negative anchor location. Positive outcomes were associated with gained points and a pleasant image, while negative outcomes were associated with lost points and an unpleasant/frightening image. They found that the PANAS positive affect score was positively correlated with optimism bias (the proportion of positive responses made to ambiguous stimuli) and the negative affect score was negatively correlated with optimism bias. Furthermore, response times to ambiguous stimuli correlated with PANAS scores: participants who reported stronger negative affect had slower response times when identifying negative outcomes ("hazards;" Paul et al., 2011).

Because there are known cognitive effects of emotion, we can use cognitive tasks to assess emotion without the need for a verbal self-report. In the current study, I used a cognitive bias test to infer the emotional effects of hearing laughter. In a typical cognitive bias test, subjects are first trained to associate positive and negative outcomes with two anchor stimuli. This could also be positive and neutral, or high positive/low positive outcomes—what matters is that there are differential rewards associated with the anchors (for a review of the paradigm, see Lagisz et al., 2020). Afterward, the subject's response toward an ambiguous stimulus is probed. The ambiguous stimulus is perceptually intermediate between the positive and negative anchors. The subject's response thus indicates whether they perceive the intermediate stimulus as more similar to the positive or negative anchor, measuring the subject's bias to anticipate a positive or negative outcome. In turn, this bias can be used to infer the underlying emotional state, because of the previously established association between emotion and optimism bias.

This type of cognitive bias test was originally developed for translational research in rats, but has since been applied successfully in many animal welfare studies and in human research

(Harding et al., 2004). In Daniel-Watanabe et al. (2020), there was an effect such that human participants in more positive moods (i.e., not depressed) were more likely to treat the ambiguous stimulus as if it were positive, by clicking a button associated with a high positive reward. In animals, the decision to approach and time to approach an ambiguous stimulus are reliable measures of cognitive bias (e.g., Hintze et al., 2018). Animals with greater optimism bias behave in ways consistent with higher expectations of reward (i.e.., a delicious food) when presented with ambiguous stimuli.

I used a nonverbal cognitive bias test to investigate whether people display positive cognitive changes after hearing laughter. My hypothesis was that simply perceiving laughter acts to produce positive affect in the listener. Thus, I predicted that people would behave more optimistically in the cognitive bias test after hearing laughter, compared to after hearing control sounds. I used laughter from unfamiliar infants and toddlers to ensure that the laughter was spontaneous, reduce culturally-specific or learned variants, and improve translatability of the study across species (as play vocalizations are typically easier to record from young animals). Studying this phenomenon using a non-verbal, translational tool allows greater opportunities for studying similar emotional phenomenon in preverbal children and non-human animals. For example, a study in rats found a positive bias in subjects after hearing recordings of prosocial laughter-like vocalizations (Saito et al., 2016). Establishment of a similar effect in adult humans would enable us to better understand the phylogenetic history and development of laughter perception.

Methods

Subjects

Participants were 202 undergraduate students (162 female, 36 male, 4 nonbinary or opted to not specify their gender), recruited from the UCLA Department of Communication subject pool between May 2022 and March 2023. All participants were native speakers of English and were at least 18 years old (M = 19.6 years, SD = 1.44). No participants reported having children. All received a course credit for their participation. Additionally, participants that scored within the top 10% in terms of accuracy on the cognitive bias task (not including the ambiguous stimuli) were offered a $5 bonus payment.

Participants were required to use headphones and have sufficient internet speeds to play audio and video during the experiment (>5 Mbps). Finally, they were instructed to only take the experiment on a laptop or desktop computer as they needed continual access to both a screen and keyboard.

Stimuli and design of the cognitive bias test

We used the Gorilla Experiment Builder to create and host our experiment (www.gorilla.sc; Anwyl-Irvine et al., 2019). Our experiment built upon open-source Gorilla designs that were previously validated in an online study of optimism bias (Daniel-Watanabe et al., 2020).

The entire study duration was approximately 15 minutes. Subjects played an online game and were instructed that their goal was to maximize points to qualify for a monetary bonus at the end of the task. Subjects were presented with solid black lines of varying orientation on the screen: 0, 45, and 90 degrees with respect to the bottom edge of the frame. During each trial, the

participant saw a single line and then pressed either the *z* or *m* button to respond. If they gave the incorrect response, a red X appeared along with a 3250ms delay, and if they failed to respond within 2750 ms, a timeout screen appeared that read "Too slow, timeout!" along with a 3250ms delay. The 90-degree line was associated with a high reward of 5 points (high positive stimulus) and the correct response was rewarded with a screen that said "Correct! + 5 points" along with a cartoon image of money for 750 ms. The 0-degree line was associated with a low reward of 1 point (low positive stimulus); the correct response triggered a screen that said "+1 point" for 750 ms, with no cartoon money. The 45-degree line was the ambiguous stimulus. This was randomly rewarded as high positive or low positive: 50% of the time the correct answer was *z* (leading to the high positive screen) and 50% of the time the correct answer was *m* (leading to the low positive screen).

Training phase

Subjects first participated in a training phase where they learned to respond appropriately to the anchor stimuli. The goal of this phase was for participants to learn to press the *z* button to gain 5 points when presented with the high reward stimulus and to press the *m* button to gain 1 point when presented with the low reward stimulus. Subjects were not given verbal instructions on these details, other than to try to maximize their points. In the first part of the training phase, subjects were presented each stimulus 5 times in a row, with no time limit, to scaffold them in learning the correct rule. They were then given the chance to practice responding to a seemingly random sequence of the two anchor stimuli under time pressure. This procedure was the same as the testing phase, except for that they were given longer to respond before the timeout screen (5550 ms). See Figure 4.1 for an example of the stimuli used in the training phase.

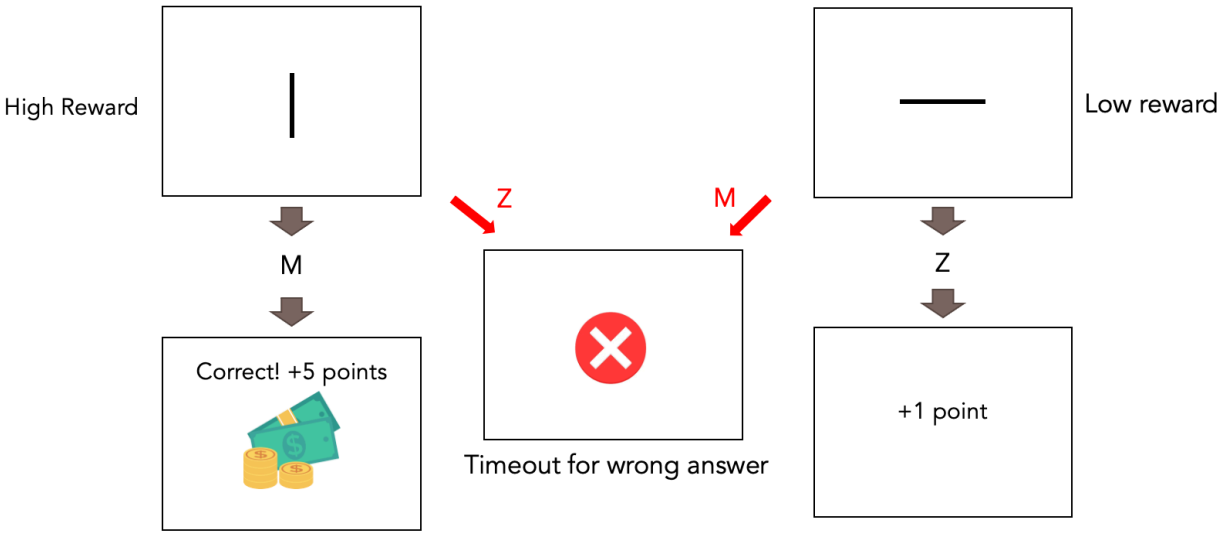

Figure 4.1. Anchor stimuli. Participants learned to press *m* in response to the vertical line to receive 5 points, or *z* in response to the horizontal line to receive 1 point. If they made the wrong key press, they were given a short timeout screen with a red X.

Testing phase

After the training phase, subjects proceeded to testing. They all received 10 blocks of 12 trials. In each block of 12 trials, subjects saw 4 high, 4 low, and 4 ambiguous trials in a pseudorandomized order. Figure 4.2 shows an example of the ambiguous test stimuli. In between each block, participants watched a 10-second neutral animated video of colorful bouncing balls (to keep attention on the screen) while listening to an audio clip. In the laughter condition, the video was accompanied by short clips of laughter. In the first control condition, participants instead listened to clips of nonword pronunciations (see below for more detail). In the second control condition, participants listened to a neutral environmental sound ("white noise," see below).

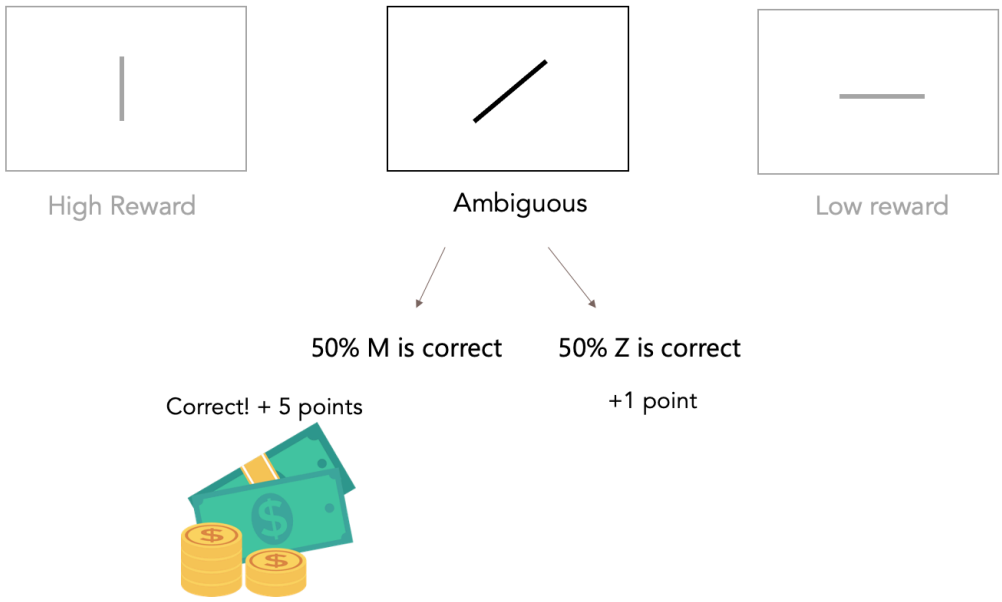

Figure 4.2. Ambiguous stimuli. During testing, participant emotion was probed with an ambiguous stimulus which was perceptually intermediate between the high and low anchor stimuli, i.e., a diagonal line. The ambiguous trials were rewarded at 50% so that it was difficult for participants to learn a rule. On average, we expected participants in more positive moods to be more likely to treat the ambiguous stimulus as the high reward stimulus (by pressing *m*) compared to those in more negative moods.

Audio stimuli

Laughter

Recordings of laughter were obtained from unfamiliar English-speaking infants and young children ages 1-4. Before each of the 10 blocks of the cognitive bias task, participants listened to laughter while watching an animated video of colorful bouncing balls. The videos

were 10 seconds long, with approximately 6-8.5 seconds of laughter and 2 distinct laughs per video.

Nonword pronunciations

Participants in the nonword condition listened to nonword pronunciations in between blocks, while watching the same video of colorful balls. The nonwords were four-syllable words cut from an audio recording of a 4-year-old boy performing a nonword repetition task. This task requires participants to repeat strings of nonsense syllables. This condition was to control for any possible responses that listeners may have had to simply hearing the voice of a young child, while not providing any semantic linguistic content that could trigger unintentional emotional responses.

White noise

Participants in the second control condition listened to white noise in between blocks, accompanied by the same ball video. Recordings of true white noise may be aversive to some listeners, so we used a simulated waterfall noise similar to one used by commercial white noise machines. This condition was to control for any possible effects of watching the video and listening to audio during the breaks between trial blocks.

Verbal measures of emotion and other questions

Assessment of emotion and mood

At the beginning and end of the main task, participants were asked to rate their current feelings on a 5-point scale (see Supplementary Item 4.2). At the end of the task participants were

also given the PANAS (Positive and Negative Affect Schedule), a 20-part questionnaire about their current emotions. The PANAS is scored such that there are two outcome scores: a positive affect score and a negative affect score (Watson, Clark, and Tellegen 1988; see Supplementary Item 4.1).

Screening for mood disorders

Participants were given the PHQ-4 (Patient Health Questionnaire-4) before the main task. This is a brief self-report questionnaire designed to screen for symptoms of depression and anxiety. The PHQ-4 includes two questions from the PHQ-9, a longer questionnaire designed to screen for depression, and two questions from the GAD-7, a longer questionnaire designed to screen for anxiety (see Supplementary Item 4.3). The subset of questions from each of the longer questionnaires have previously been validated as the PHQ-2 and GAD-2 (Kroenke et al., 2003, 2007). The PHQ-4 is scored on a 1-12 scale with 1-6 points each for depression (the PHQ-2 score) and anxiety (the GAD-2 score); higher scores indicate a higher likelihood of underlying depression or anxiety. The recommended threshold for further clinical assessment is a score of 3 out of 6 or higher on the depression and anxiety sub-scores (Kroenke et al., 2009).

Infant attitudes

To assess participant attitudes towards infants, participants were asked to rate their agreement with the statement, "I enjoy being around infants, including those that are unrelated to me," with the following options: strongly disagree, somewhat disagree, neutral, somewhat agree, and strongly agree. We expected that more positive feelings toward infants would result in more positive feelings and greater optimism bias in the laughter and nonword conditions.

Attention and audio checkpoints

To confirm that the participants' audio was working properly and that they paid attention throughout the experiment, there were a series of three checkpoints – once before testing began, once after the training period and before the cognitive bias test began, and once at the end of the cognitive bias test. During each checkpoint, participants heard three common words (chair, donkey, frog, lemon, pumpkin, tree, bird, kitten, number, or woman) and were asked to write down the word they had just heard. Any participants who answered more than one word incorrectly in the initial audio screening were automatically rejected from the study and did not proceed to testing (this was only the case for one person, not included in the original 202 participants). Participants who proceeded to testing but answered more than one word incorrectly in the pre- or post-test audio check were not included in any data analysis (with the exception of a few obvious typos, e.g., "pumkin" for pumpkin). Finally, because "frog" was the first word participants heard at the end of the cognitive bias test, those that responded to "frog" with blanks or odd words (e.g., "cheese") were likely to have had an audio failure, turned their audio off, stepped away from their computers, or otherwise had poor attention during the task. Those participants were also considered to have failed the audio check, even if they gave no other incorrect responses.

Analysis

All statistical analyses were performed in R version 4.3.1 (R Core Team, 2023).

Results

Participant selection

Several groups of participants were excluded from the final analyses: those that failed the audio and attention checks, those who reported not paying attention on the task, and those that got below 70% accuracy on the anchor stimuli.

Attention criteria

Forty participants were not included in analyses due to poor performance on the attention and audio checks (12 gave >1 incorrect answer, and 28 additional participants failed the first word after the cognitive bias task). Sixteen participants answered no to the direct question posed at the end of the experiment: “Did you pay attention throughout the game part of the study? Please answer honestly, as this will not affect your score or payment.” Those that answered no were also not included in analyses. Participants that got below 70% accuracy on the anchors were also not included (7 participants, including 2 that did not pass the audio check).

Some participants were excluded for multiple reasons. This yielded a final dataset of 146 participants (112 female, 31 male, 3 nonbinary; *M* age = 19.7 years, *SD* = 1.58).

Task performance criteria

Cognitive bias task data were not usable for an additional four participants, although their self-report data were included in analyses. One participant received an anomalous number of trials (more than 40 in each condition), suggesting a software error in administering the task. Three additional participants had to be excluded because in the debrief comments they reported an unexpected strategy for the ambiguous trials which was to hit both keys at the same time.

Since this prevented us from measuring optimism bias, these participants' cognitive task data could not be used. For example, this strategy resulted in one participant timing out of most of the ambiguous trials, skewing their response time and accuracy.

Descriptive statistics: Cognitive bias test

Performance on anchor stimuli trials

Subjects were overall highly accurate on their decisions about the anchor stimuli during testing trials (for original sample of 202: M correct = 92.8%, SD = 10.2%). After eliminating participants who did not meet the attention and task performance criteria, the mean accuracy on the anchor stimuli was 94.9% (n = 142, SD = 4.5%).

Performance on ambiguous trials

As expected, participant's accuracy on the ambiguous trials was not significantly different than 50% (M = 0.494, SD = 0.088, $t(141)$ = -0.963, p = 0.337). In other words, they did not use any unexpected rules to optimize accuracy on the ambiguous trials. Subjects varied quite a bit in how often they chose the more positive key for the ambiguous trials, but on average there was a slight optimism bias, which is consistent with the previous literature (average positive keypress to ambiguous = 0.528; significantly higher than 0.5, $t(141)$ = 2.597, p = 0.010).

Descriptive statistics: Self-reported feelings

Participants rated their current feelings before and after the experiment on a scale from 1 to 6, where a score of 1 indicates "very bad" feelings and a score of 6 represents "very good" feelings. The most common feeling reported before the task was "slightly bad," with an average

score of 3.945 (with 4 corresponding to "slightly good," *SD* = 1.19). Most participants reported no changes in their feelings from the beginning to the end of the task: the mode and median change in feelings score was 0. However, there was a slight skew such that on average, participants reported feeling slightly worse at the end of the experiment (overall mean change in feelings score = -0.562, *SD* = 1.162). This varied slightly by condition, with the greatest negative change reported in the laughter condition, and the least change reported in the white noise condition.

Table 4.1. Changes in self-reported feelings by condition.

Condition	Mean change in feelings	*SD*
Laughter	-0.630	1.25
Nonword Control	-0.564	1.03
White Noise	-0.489	1.24

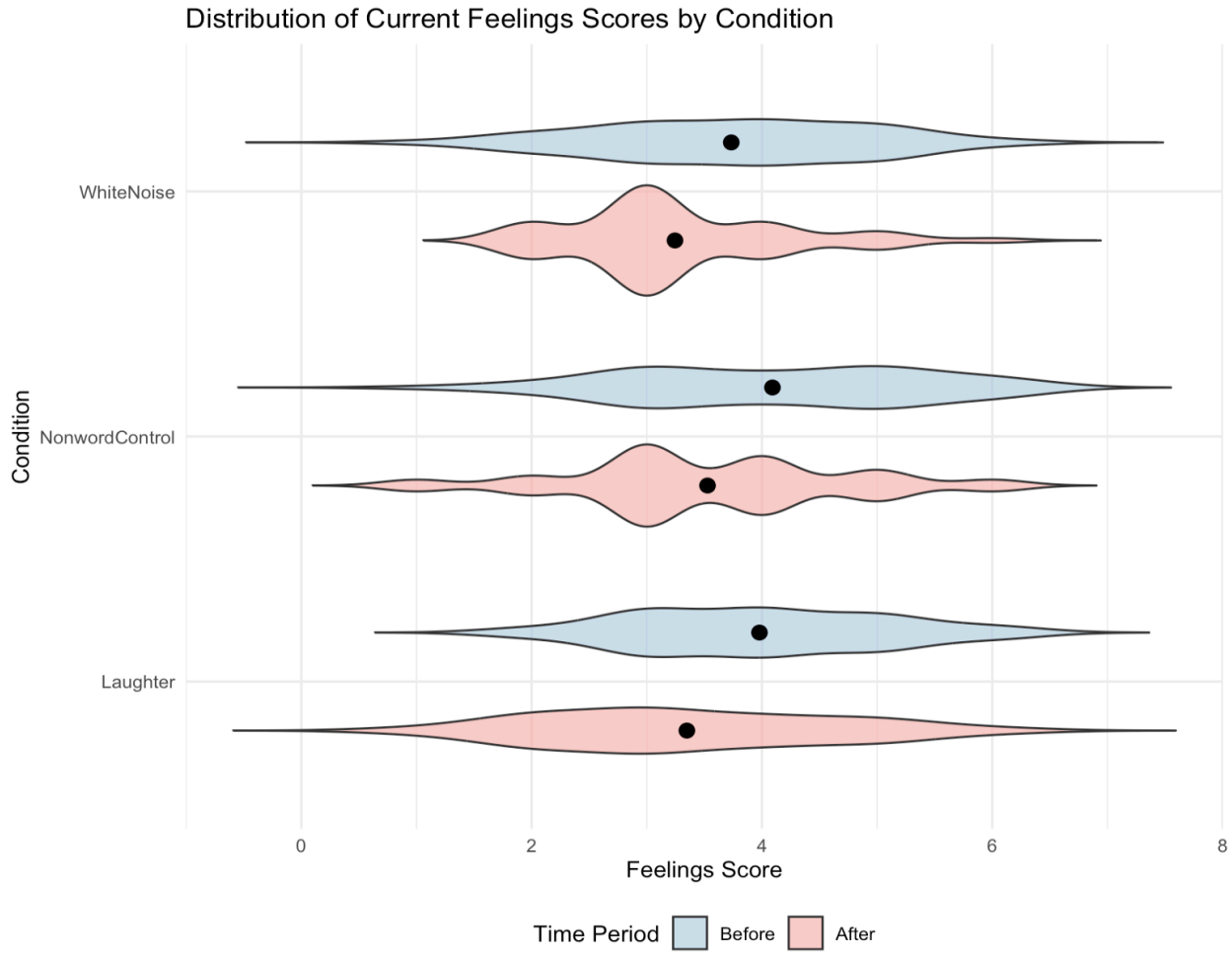

Figure 4.3. Distribution of current feelings scores by condition.

Male-identifying participants (hereafter: males) reported a greater negative change in feelings than female-identifying participants (hereafter: females), but this was not a significant difference when considering the effect of gender across all conditions or when gender was interacted with condition (glm, change in feelings ~ gender: estimate for male vs. female = -0.448, $p = 0.058$; glm, change in feelings ~ gender*condition: yielded $p > .05$ for all predictors). Additionally, the effect of gender on the change in feelings score was no longer trending toward significant after accounting for the baseline initial feelings score (glm, change in feelings ~

gender + feelings before: estimate for male vs. female = -0.283, $p = 0.165$). This is likely due to males reporting more positive feelings than females before the task started (see Table 4.2). Females reported liking unfamiliar infants more than males, although this did not appear to produce gender differences in the change in reported feelings by condition (glm, likes infants ~ gender, estimate for male vs. female = -0.626, $p = 0.015$).

Table 4.2. Self-reported feelings by condition and gender.

Condition	Gender	Mean (*SD*) feelings before task	Mean (*SD*) feelings after task	Mean (*SD*) change in feelings	*n*
Laughter	Female	**3.94** (1.08)	**3.37** (1.24)	**-0.571** (1.09)	35
Laughter	Male	**4.2** (1.14)	**3.3** (1.49)	**-0.9** (1.79)	10
Laughter	Other	**3** (*n/a*)	**3** (*n/a*)	**0** (*n/a*)	1
Nonwords	Female	**4** (1.3)	**3.61** (1.14)	**-0.39** (0.972)	41
Nonwords	Male	**4.31** (1.25)	**3.23** (1.36)	**-1.08** (1.12)	13
Nonwords	Other	**5** (*n/a*)	**4** (*n/a*)	**-1** (*n/a*)	1
White Noise	Female	**3.64** (1.15)	**3.22** (1.02)	**-0.417** (1.25)	36
White Noise	Male	**4** (1.31)	**3.38** (0.518)	**-0.625** (1.19)	8
White Noise	Other	**5** (n/a)	**3** (*n/a*)	**-2** (*n/a*)	1

Descriptive statistics: PANAS

Recall that the PANAS was a mood scale administered at the end of the task, therefore we expected it to correlate with the simpler self-reported mood score measured after the task and with their performance on the ambiguous trials.

The PANAS scale produces two mood scores: positive activation (PA) and negative activation (NA). PA scores can range from 10 to 50, with higher scores representing higher levels of positive affect. In previous research, the PANAS PA score has typically averaged around 31.3-33.3 (*SD* = 7.2-7.7; Crawford & Henry, 2004). In our final dataset, the mean PA score was lower than typical, with a mean of 19.42 (*SD* = 7.42). NA scores can range from 10 to 50, with lower scores representing lower levels of negative affect. In previous research, the PANAS NA score has typically averaged around 16.0-17.4 (*SD* = 5.9-6.2; Crawford & Henry, 2004). In our final dataset, the mean NA score was fairly typical, with a mean of 17.56 (*SD* = 5.82).

Did PANAS correlate with our current feelings measure?

The PANAS scores were correlated with the simpler measure of self-reported feelings after the task, in the expected directions for both the PA and NA scores. Higher (more positive) feeling scores corresponded to a higher PA score (Pearson's correlation using cor.test(): r = 0.421, $t(141) = 5.566$, $p < 0.000$, 95% *CI* = [0.277, 0.546]) and lower NA score (Pearson's correlation using cor.test(): r = -0.344, $t(144) = -4.402$, $p < 0.000$, 95% *CI* = -0.480, -0.193]).

Descriptive statistics: PHQ-4

Recall that PHQ-4 scores range from 1-12 scale with 1-6 points each for depression and anxiety; higher scores indicate a higher likelihood of underlying depression or anxiety. When used together the total score is a good measure of "caseness" for either depression or anxiety, with a score above 3 on depression or anxiety being the recommended cutoffs for further

screening (Kroenke et al., 2009). The average PHQ-4 score in our sample was 4.418 (*SD* = 2.784, *M* depression = 1.877, *M* anxiety = 2.541).

Did PHQ-4 correlate with our current feelings measure?

PHQ-4 score correlated negatively with self-reported feelings before the test ($r = -0.284$, $t(144) = -3.559$, $p < 0.001$, 95% *CI* = [-0.427, -0.128]). Participants who reported feeling worse tended to score higher on both the depression questions ($r = -0.218$, $p = 0.008$) and the anxiety questions ($r = -0.285$, $p < 0.001$) of the PHQ-4.

Optimism bias and self-reported emotions (current feelings, PANAS, PHQ-4)

Optimism bias was not significantly correlated with any self-reported temporary or chronic emotions. Pearson's correlation tests found no significant correlation between optimism bias and PANAS NA score, PA score, PHQ-4 total score, or self-reported feelings either before or after the test. Additionally, optimism bias did not correlate independently with the depression or anxiety sub-scores of the PHQ-4. See Figure 4.4 for details.

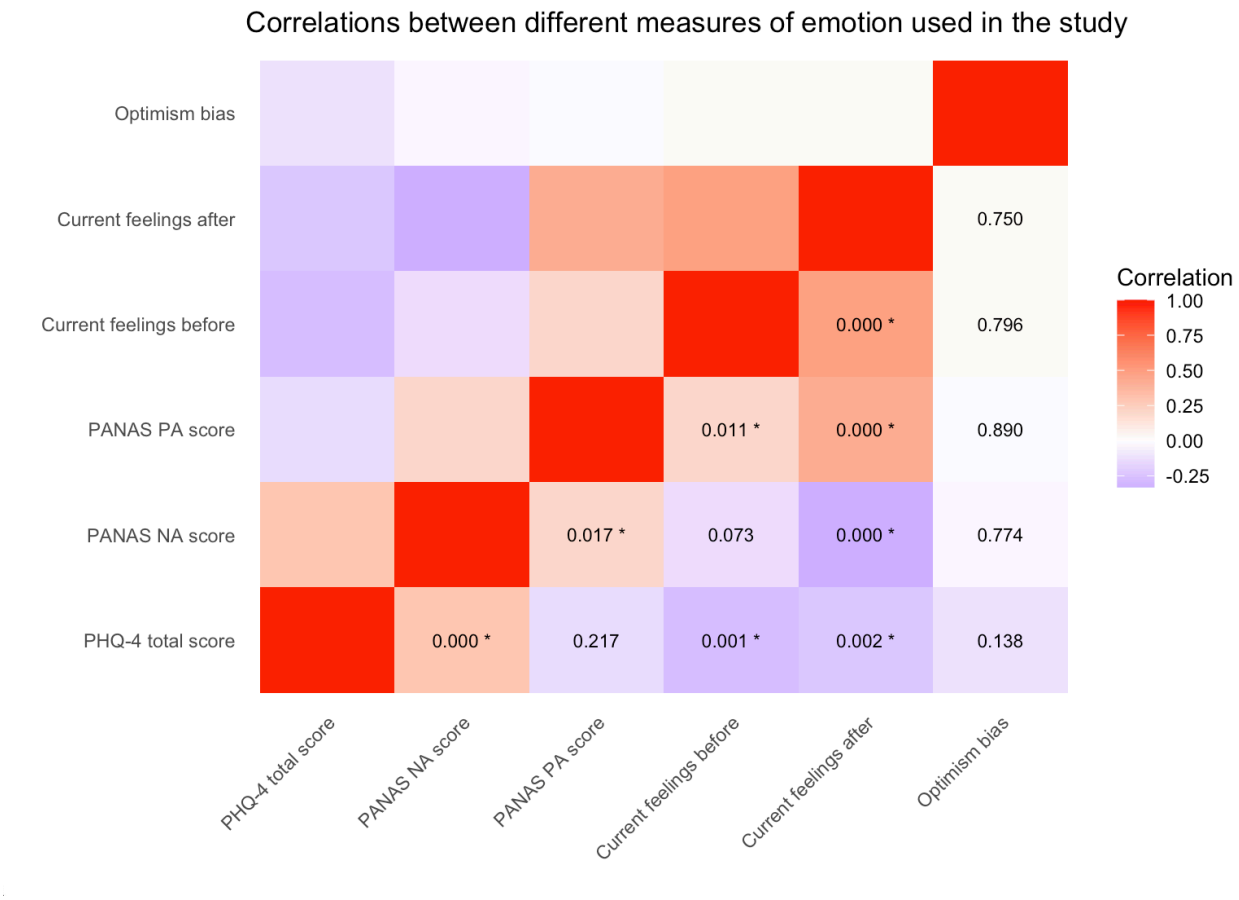

Figure 4.4. Correlations between different measures of emotion used in the study.

The color of the tile corresponds to the correlation coefficient estimate, while the text overlaid shows exact p-values for each pairwise comparison (no corrections were performed for multiple testing). Optimism bias was calculated as the proportion of ambiguous trials that the participant responded to by pressing the high positive key.

Laughter and self-reported feelings

The effect of laughter on the change in feelings score

An Analysis of Covariance (ANCOVA) on the feelings change score by condition, with no additional control variables, did not find any significant difference in the change score

(feelings after-feelings before) by condition, $F(2, 143) = 0.167$, $p = 0.847$). In other words, people did not report feeling any better or worse after hearing laughter compared to those in the other conditions.

We ran glm models with additional control variables: the "likes infants" variable interacted with condition, as well as gender, age, and PHQ-4 total score. The outcome was the change in feelings score. None of the predictors were significantly associated with the change in feelings score in this model. In a model with the same predictors but with the outcome being just the current feelings score after the task, the only significant predictor was the PHQ-4 score. However, the effect of PHQ-4 failed to reach significance when the current feelings before the task were included in the model, which could be interpreted as underlying depression and/or anxiety mediating the ratings of current feelings regardless of the experimental manipulation.

The effect of laughter on PANAS scores

We were curious if people would report feeling better after hearing laughter on the PANAS score afterwards, either through a higher positive affect or lower negative affect score. According to simple glm models including just the PANAS scores by condition, condition did not have a significant effect on the PANAS PA score (with laughter as the reference condition, nonword control estimate = -1.3957, $p = 0.350$; white noise estimate -0.7957, $p = 0.611$). The same was true for the NA score (with laughter as the reference, nonword control estimate = -0.222, $p = 0.85$; white noise estimate = -0.869, $p = 0.48$)

Laughter and optimism bias

Did people behave more optimistically after hearing laughter, compared to after hearing the control sounds of white noise or nonword pronunciations?

To assess the effect of condition on optimism bias, we ran a generalized linear model on the likelihood of choosing the positive key for the ambiguous stimulus. As control variables, we included the participants' age, gender, PHQ-4 depression and anxiety scores, their self-reported feelings at the beginning of the task, and their rating of agreement with the "likes infants" question. There were no significant differences in the estimates between the laughter condition and either control condition. This was true regardless of whether condition was assessed alone or as an interaction with the "likes infants" variable.

The "likes infants" variable was significantly associated with optimism bias when assessed in the model with no interaction, but not in the same model when included as an interaction term. No other variables were significant predictors of optimism bias.

Table 4.3. Coefficient estimates from glm with interaction.

Variable	Coefficient Estimate	*p*
Condition: White Noise	0.035	0.681
Condition: Nonwords	-0.012	0.875
Likes Infants	-0.021	0.15
White Noise*Likes Infants	-0.005	0.827
Nonwords*Likes Infants	0.007	0.735

Model formula: optimism bias ~ condition * likes infants + age + gender + PHQ-4 depression score + PHQ-4 anxiety score + current feelings before

Table 4.4. Coefficient estimates from glm with no interaction.

Variable	Coefficient Estimate	*p*
Condition: White Noise	0.017	0.542
Condition: Nonwords	0.013	0.622
Likes Infants	-0.02	**0.028**

Model formula: optimism bias ~ condition + likes infants + age + gender + PHQ-4 depression score + PHQ-4 anxiety score + current feelings before

Discussion

Laughter is generally thought to be a signal of positive emotion. People associate laughter with positive emotions across cultures, and laughter production results in biological markers of positive affect, such as decreased pain and lowered stress hormones (Dunbar et al., 2012; Gendron et al., 2015; Manninen et al., 2017; Sauter et al., 2015; Yim, 2016). We therefore predicted that people would report more positive emotions and behave more optimistically on a cognitive bias test, a nonverbal test of emotion, after hearing audio clips of laughter compared to after hearing control sounds of white noise or nonword pronunciations. Our results did not support these predictions, with little difference found between the three conditions on both optimism bias and self-reported feelings. This study found no evidence that the perception of laughter alone, devoid of the normal social context, directly induces a positive emotional state in listeners.

There are several potential explanations for these null results. It is possible that laughter and laughter contagion *are* underpinned by a positive emotion that was simply not detectable with our methods. Our study failed to replicate previous cognitive bias test experiments, suggesting possible methodological limitations. For example, in contrast to findings from Paul et

al. (2011), neither higher positive affect nor lower negative affect (as reported on the PANAS) predicted greater positive bias on the task. Furthermore, Daniel-Watanabe et al. (2020) and Aylward et al. (2019) found associations between depression and lower optimism bias toward ambiguous stimuli. However, in our study, overall PHQ-4 scores (combining depression and anxiety) and depression sub-scores did not correlate with a more negative bias. Optimism bias also did not track with self-reported current feelings before or after the task, despite the theoretical link between optimism bias and emotion. While PHQ-4 scores did correlate with self-reported feelings, neither measure related to optimism bias. Based on these findings, we cannot draw any definitive conclusions about the relationship between chronic mood disorders, transient affective states, and optimism bias.

The experimental design for the cognitive bias test is quite variable across studies (Lagisz et al., 2020). Studies using cognitive bias to measure temporary emotion interventions are rare, although some experiments have been successful at doing so (Paul et al., 2011). Several factors in our experimental design could have inadvertently reduced our ability to detect emotional effects of laughter. Very similar methods to the ones used here were adequate in a study of pathological emotions (Daniel-Watanabe et al 2020), but there were a few key differences. While we used nearly exactly the same software program, counterbalancing, and stimuli as Daniel-Watanabe et al. (2020), we used points instead of dollar amounts for rewards and tied points to future payment to avoid misleading participants. Paul et al. (2011), which detected temporary mood interventions, also used more points gained/lost for their anchor stimuli outcomes (+/- 10 points). Another difference was that we added an initial scaffolding block to improve learning of ambiguous stimuli, and broke the test trials up into several blocks with interspersed video and audio stimuli. Additionally, we used the shorter PHQ-4 to evaluate depression, rather than the

21-item Beck Depression Inventory used in Daniel-Watanabe et al. (2020). The PHQ-4 may not have been powerful enough to replicate effects established with this more in-depth survey of depression symptoms. We also used different modeling approaches than Daniel-Watanabe et al. (2020), who used a specialized drift diffusion model that incorporated both decision and reaction times. Finally, this was an online study conducted during the pandemic and may have been impacted by low participant attention, as suggested by the surprising number of participants who did not pass the attention checks. Multiple participants reported in our debrief questions that they were frustrated by not knowing the rules. However, this should theoretically have been the case in Daniel-Watanabe et al. (2020), which used the same stimuli and a similar reward structure. Compared to our study, Paul et al. (2011) might have had lower executive demands and greater emotional salience, since the experimenters labeled their keys with smiley and frowny faces. They also validated the emotionality of their stimuli beforehand through independent ratings and skin conductance.

Notably, some participants had strong negative reactions to the repeated laughter, which may have produced unexpected effects. Participants in the laughter condition reported things such as, “Hearing that laughter over and over again has me questioning whether or not I like kids;” “this was a painful experience and i [sic] would like to receive monetary compensation;” “I never thought torture could be this interesting;” and “I was confused by the baby sounds as well as the visual showing every single time. I did not understand what was happening and eventually got irritable with the sound of babies laughing.” These all point to nuanced and unexpected impacts of hearing laughter, with at least a few participants experiencing strong negative feelings.

The sound of unfamiliar children might induce negative emotions in listeners if it evolved to be a cue of potential costs on those listeners. Throughout our evolutionary history, unrelated infants and young children were typically costly in terms of social effort, attention, and other resources (Trevathan & Rosenberg, 2016). Our participants were all young adults without children themselves. Perhaps a cue of unrelated children nearby should be unpleasant if it has evolutionarily been associated with future caregiving costs. Due to social norms against disparaging others' children, this may not have been captured by our self-report question about attitudes toward infants.

Laughter alone might additionally have negative emotional effects due to evolved social associations, regardless of the age of the laugher. Unlike in our primate ancestors, human laughter occurs in many contexts, not just during play. Laughter encodes social information, for example indicating social bonds between co-laughers (Bryant et al., 2020). Laughter in conversations can also be a signal of shared knowledge or cultural background (Flamson and Barrett 2008; Flamson and Bryant 2013). Listeners are adept at picking up on this social information (Bryant et al., 2016). Thus, hearing ambient laughter without understanding the reason for it might be a signal or cue that one is being excluded from a social bond or group.

This exclusion could in some cases be directly threatening, if laughter is deployed strategically to communicate to eavesdroppers. Directed *schadenfreude* and taunting laughter could be a form of aggression that informs the listener of out-group membership and poor social valuation (Leach et al., 2003). Therefore, the emotional significance of hearing laughter is likely to depend heavily on the social context in which it occurs. We deliberately provided minimal social context in our study so that we could assess the impact of the sound alone. Consequently, laughter may have produced limited emotional responses or a range of different emotions in

different individuals. Because human laughter is not an honest signal of nonaggression, the way it appears to be in other great apes, perhaps receivers evolved additional perceptual defenses against the positive emotion induction seen in bonobo laughter as a safeguard against manipulation by signalers (Krebs & Dawkins, 1984). Indeed, the evolution of two kinds of laughter, spontaneous and volitional (as discussed earlier), makes the production of "fake" laughter relatively common and cost-free. It would be disadvantageous for listeners to automatically feel better and act more optimistically from this common signal as it could open them up to easy social exploitation.

In conclusion, further research is needed to investigate the extent to which emotional contagion is involved in laughter, which has important implications for understanding human social coordination and empathy. Future studies with methodological refinements may help illuminate these subtle effects.

4.3 Supplementary Information for "Effects of laughter on a cognitive bias test in humans"

Supplementary Item 4.1. The PANAS (from Watson, Clark, and Tellegen 1988)

Please read each item and then indicate to what extent you feel this way **right now**, at the present moment.

Interested

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Distressed

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Excited

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Upset

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Strong

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Guilty

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Scared

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Hostile

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Enthusiastic

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Proud

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Irritable

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Alert

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Ashamed

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Inspired

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Nervous

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Determined

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Attentive

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Jittery

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Active

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Afraid

Very slightly or not at all	A little	Moderately	Quite a bit	Extremely

Supplementary Item 4.2. Current feelings question

How do you feel **right now**?

Very bad	Somewhat bad	Slightly bad	Slightly good	Somewhat good	Very good

Supplementary Item 4.3. The PHQ-4 (from Kroenke et al., 2009)

Over the **last 2 weeks**, how often have you been bothered by any of the following problems?

Little interest or pleasure in doing things:

Not at all	Several days	More than half the days	Nearly every day

Feeling down, depressed, or hopeless:

Not at all	Several days	More than half the days	Nearly every day

Feeling nervous, anxious, or on edge:

Not at all	Several days	More than half the days	Nearly every day

Not being able to stop or control worrying:

Not at all	Several days	More than half the days	Nearly every day

4.2 References for Chapter 4

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5. Conclusion

5.1 General discussion

In this dissertation, I produced theoretical work on the evolution of human laughter from animal play signals, and conducted a series of experiments to investigate the emotional and cognitive mechanisms underlying laughter perception in humans and bonobos. In Chapter 1, I set the stage for my work on playful signaling by grounding it in research on the evolutionary origins of play and playful teasing. In Chapter 2, I presented a comprehensive theory for the evolution of human laughter from a pant-like play vocalization in our last common ancestor with great apes. I tied this to the literature on play vocalizations across the animal kingdom and to research on human laughter and its derived features.

Chapters 3 and 4 describe a series of comparative experiments in bonobos and humans to assess emotional responses to laughter and its impact on decision-making using a similar cognitive bias paradigm. The experiment in chapter 3 provides suggestive evidence for positive emotional responses to laughter in bonobos. Simply hearing conspecific infant laughter was associated with greater optimism bias on a go/no-go cognitive bias task. After listening to laughter, bonobos were more likely to treat an ambiguous stimulus as if it were a positive (rewarded) stimulus, compared to after they had heard a neutral environmental noise. This suggests that a play vocalization homologous to human laughter induced positive emotions in bonobos, one of our closest living relatives.

In contrast, the comparative study with human participants (chapter 4) did not find the same effect. Humans did not demonstrate greater optimism bias after hearing infant laughter, and there was no difference in performance between participants in the laughter condition compared to those who heard control sounds of white noise or nonword pronunciations. The failure of our

experiment to replicate previous correlations between optimism bias and self-reported emotions might indicate that there were methodological issues that did not allow us to fully measure optimism bias in our study. Despite this, participants also did not report more positive feelings in the laughter condition compared to the controls.

These findings may point to specialized cognition that co-evolved with human laughter after it diverged from the play vocalizations of our last common ancestor. The evolution of different types of laughter in humans, such as volitional laughter and taunting laughter, as well as the seemingly unique functions of human laughter to broadcast affiliation and group membership to others, likely resulted in laughter's meaning becoming much more dependent on context. As laughter production became decoupled with play, receivers likely co-evolved defenses against emotional manipulation and came to require additional information to evaluate the sound of others' laughter as positive, negative, or irrelevant depending on interactional and group dynamics. Together, these comparative experiments provide innovative methods and a launching point for further comparative research on human laughter and the emotional and cognitive effects of animal play vocalizations.

My future research will continue to explore the themes of emotion, communication, social cognition, and learning. One interesting question that remains is the role of play and playful signaling in cooperative tendencies. Does play or laughter increase the tendency to cooperate? The tendency to cooperate may depend on one's relationship with the cooperation partner—their history of past interactions, their trust that the other will cooperate or return the favor, and the value of the relationship and possible benefits received from cooperating. Other factors may determine whether one cooperates, such as the current emotions the individual is experiencing. If positive affect promotes cooperation, dyads will be more likely to cooperate

after playing or hearing conspecific laughter. This type of research could have important implications within the fields of human behavioral ecology, evolutionary psychology, child development, and comparative cognition.

Many animals, including humans, have play vocalizations that appear to similarly involve positive emotions. Laughter perception and contagion might involve shared basic mechanisms across distant phylogeny, as evidenced from studies in rats and kea parrots (see Chapter 2). Future comparative research should investigate the extent to which emotional and behavioral contagion underpin play vocalizations across species and the unique psychosocial mechanisms associated with human laughter. To probe the origins of human laughter, there is still much more research needed on play signals, their associated emotions, and their cognitive effects. Tinbergen (1952) famously advocated for the importance of merging of ontogenetic, mechanistic, functional, and phylogenetic perspectives on behavior, and I have attempted to do so in this body of work on play and laughter. These topics have promise for improving our understanding of positive emotions, social bonding, empathy, and cooperation. In short, studying the seemingly lighthearted topics of play and laughter can help us with a profound pursuit: figuring out what it means to be human.

5.2 Concluding references

Tinbergen, N. (1952). “Derived” activities; their causation, biological significance, origin, and emancipation during evolution. *The Quarterly Review of Biology, 27*, 1–32. https://doi.org/10.1086/398642