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RUNNING HEAD: Primate Social Psychology

A Melding of the Minds:

When Primatology Meets Personality and Social Psychology

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ABSTRACT

Social/personality psychology and behavioral primatology both enjoy long histories of research aimed at uncovering the proximate and ultimate determinants of primate--human and nonhuman--social behavior. Although they share research themes, methodologies and theories, and their studied species are closely related, there is currently very little interaction between the fields. This separation means that researchers in these disciplines miss out on opportunities to advance understanding by combining insights from both fields. Social/personality psychologists additionally miss the opportunity for a phylogenetic analysis. The time has come to integrate perspectives on primate social psychology. Here we provide a historical background and document the main similarities and differences in approaches. Next we present some examples of research programs that may benefit from an integrated primate perspective. Finally, we propose a framework for developing a social psychology inclusive of all primates. Such a melding of minds promises to greatly benefit those who undertake the challenge.

KEY WORDS: Primatology, Interdisciplinary, Personality, Sexual behavior, Equity and Justice, Intergroup behavior

If you want to know something about human social behavior you should consult the social and personality psychology literatures. For more than a century, social and personality psychologists have studied humans to pin down the proximate and ultimate causes of human social behavior.¹ However, not far away -- perhaps in another university building or, in the case of the first author, right down the hall – a different research group is interested in much the same thing. Although research practices may differ, the research themes, theories and hypotheses are often quite similar. Moreover, they study individuals who are extremely closely related to humans. These are the behavioral primatologists who study the same thing as social psychologists – the ultimate and proximal determinants of social behavior – except in nonhuman primates.

A plethora of social and cultural factors could explain the great divide that currently exists between the human and nonhuman primate literatures, but a little historical perspective indicates that this has not always been the case. Notably, Charles Darwin included humans alongside other primates (and non-primates) in his theory of evolution, and his “Expression of Emotions in Man and Animals” (Darwin, 1872; 3rd ed. 1998) is one of the first comprehensive works on personality psychology. As the title suggests, this work did not draw a line in the sand between humans and other species and, arguably, neither should our academic disciplines.

We propose that those who study human and nonhuman primates reconnect by reading and incorporating each other’s insights, models and methods. We recognize that this is not an easy process but believe that the ultimate benefits far outweigh the costs. Below, we first provide a rationale for social psychologists to study nonhuman primates and second give a brief historical sketch of the relationship between the disciplines.

Third, we discuss the potential obstacles and opportunities for an integrated primate social psychology by looking at similarities and differences in research approach and methodology. Fourth, we present four case studies, representing key themes in social psychology--individual differences and interpersonal, intragroup and intergroup relations--in which insights from human and primate research can be fruitfully combined. Two research programs, on personality and justice, already show the benefits of collaboration, whereas two other programs, on intergroup relations and sexual behavior, show promise for integration. We end with a discussion of the opportunities and challenges lying ahead, and our recommendations for a future field of primate social psychology.

Why Study Nonhuman Primates?

A brief taxonomy

Humans are primates, sharing a taxonomic Order (*Primates*) with all other primates and a Family (*Hominidae*) with the other great apes (see Figure 1).² Of these, we are most closely related to chimpanzees and bonobos, both members of our sister Genus, *Pan*. Generally, primates are divided into (1) Prosimians, which are the primates least closely related to humans, having diverged from the lineage that led to humans approximately 80 million years ago (e.g., lemurs and sifaka), (2) New World monkeys (Platyrrhines), which diverged approximately 40 million years ago (e.g., capuchins, howlers, marmosets, and tamarins), (3) Old World monkeys (Catarrhines), which diverged approximately 20 million years ago (e.g., macaques, baboons, and columbine monkeys), and (4) Great Apes, of which humans are a member, along with chimpanzees (*Pan troglodytes*), bonobos (*P. paniscus*), gorillas (*Gorilla gorilla* & *G. beringei*), and orangutans (*Pongo pygmaeus* & *P. abelii*).

Studies of nonhuman primates, our closest living evolutionary relatives, have been successfully used to extract the evolutionary history of our behaviors. These behaviors are difficult to study because they do not fossilize and often leave no material artifacts. However, a technique known as *behavioral phylogeny* allows comparisons to be made between different species to extrapolate the likelihood of common descent for any behavior (Boehm, 1999; Wrangham & Peterson, 1996). In behavioral phylogeny, species with different degrees of relatedness are evaluated for a behavior. If both species possess it, then it is assumed to have been present in their most recent common ancestor, and hence represents a *homologous* trait (one with a shared evolutionary history). If one species (species B) lacks the behavior, then it is assumed that the behavior arose in that species lineage *after* it diverged from the other species (species A). If two species possess a similar behavior, but other species intermediate to them (in evolutionary terms) do not, then the behavior is a homoplasy, or example of *convergent evolution* (Figure 2). These traits arise when two species face similar environmental conditions which lead to the emergence of similar traits (e.g., wings in birds, bats, and butterflies). Studying species which are more closely related yields a much more fine-grained analysis. This is why studying the other primates, particularly the apes, can give us so much information about the evolution of human behavior.

The wide diversity of social systems and behaviors in the primates allows us to compare behaviors which are similar by common descent and those which arose through convergent evolution, to better understand the pressures that caused a behavior to evolve. So, for instance, comparing behaviors in primates who are typically cooperative (e.g., callitrichids, capuchin monkeys and chimpanzees) may tell us about the pressures which

led different species to develop cooperation, as well as the suite of behaviors which correlate with complex cooperation. Similarly, studying closely related species, such as the great apes, may help us to better understand situations in which species in dissimilar environments share behaviors, presumably due to homology. Such comparisons can help our understanding of the origins and manifestations of behavior in human relationships.

An important side note, often neglected, is that in the evolutionary process each species has taken its own separate course, evolving from a common ancestor and not from each other. Thus, humans did not evolve from extant monkeys or apes, but from an ancestor common to us and them. Therefore, when comparing behavior what we are really trying to uncover is the behavior of the last common ancestor between us and the species we are studying, from which we can make conclusions about the evolution of our behaviors (see Figure 1).

Role of other species

An important ultimate goal is to create a truly comparative social psychology inclusive of all animals (Gosling, 2001; Zajonc, 1969). However, a review of all animal taxa is beyond the scope of the current paper; thus, our contribution focuses on primates because their shared evolutionary background offers a promising starting point for such an endeavor. Note, however, that other species, ranging from insects to mammals, share a wide variety of behaviors of interest to social psychologists. To give but a few examples, cleaner fish show high levels of cooperation and partner discrimination (Bshary, Grutter, Willener, & Leimar, 2008), vampire bats share food with hungry group-mates (Wilkinson, 1984), animals from rats to primates shows social learning (Heyes & Galef, 1996), elephants, dolphins, and magpies show evidence of a concept of self

(Plotnik, de Waal, & Reiss, 2006; Prior, Schwarz & Güntürkün, 2008; Reiss & Marino, 2001), goats reconcile (Schino, 1998), lions engage in coalitional aggression (Packer & Pusey, 1982), and individuals in all species must make critical decisions regarding the timing and direction of group movement (Boinski & Garber, 2000; Van Vugt, 2006).

It is important to examine evidence that is accruing from non-primate and primate species in tandem (Gosling, 2001). Specifically, these comparisons can be essential in teasing apart traits due to convergence versus those due to shared homology (for an example in the psychology literature, see Fraley, Brumbaugh & Marks, 2005). Below we include references to some non-primate studies; however, our focus here is on primates as a promising starting point for a cross-species comparison.

Behavioral primatology and social psychology

The field ‘primatology’ encompasses a broad range of interests, from ecology and conservation to molecular biology and medicine. Here we focus on a group of primatologists, sometimes referred to as behavioral primatologists, who typically study primate social behavior – in other words, the same questions that interest social psychologists. These individuals may be working in psychology, anthropology, ecology, or biology departments, study primates *in situ* in the field or in captive settings, and employ observational or experimental methods. Thus, it is truly a diverse group, connected by a deep interest in how the social environment affects primate behavior, and vice versa. Similarly, social/personality psychology is just one area within a large psychology discipline with an almost exclusive focus on the psychological underpinnings of social behavior. Of course, researchers from other areas of psychology as well as from

related disciplines such as anthropology, economics, neuroscience, philosophy, and sociology are interested in human social behavior.

Historical Perspective

Social psychologists and behavioral primatologists both try to understand the social behavior observed in their respective study animals, including personality, emotions, social relationships, culture, sexual behavior, theory of mind, self-concept, altruism, aggression, forgiveness, group dynamics, group decision-making, leadership, justice, and intergroup relations. With few exceptions, these questions are investigated on parallel tracks, with little cross-fertilization between the disciplines, departments, and species-of-interest. Behavioral primatologists and social psychologists tend not to attend each others' meetings or read each others' journals (see Appendix for suggestions to improve the dialogue), and there is little communication between these fields. Handbooks and textbooks in social psychology and primatology rarely cite each other, even though the topics discussed are similar. For instance, the most recent two-volume *Handbook of Social Psychology* (Gilbert, Fiske, & Lindzey, 1998) contains just a handful of citations to research on nonhuman primates, and it is not a great deal better on the other side, in primatology.

We are not the first people to notice the lack of communication or the potential benefits of cooperation. Eric Vanman has argued in the past that both primatology and social psychology suffer when we fail to pay attention to each other's work (Vanman, 2003). Sadly, this call has been largely ignored by researchers in both groups. The irony, of course, is that originally the human and nonhuman behavioral sciences were not mutually exclusive. Probably the most famous example is Charles Darwin's work.

Another early proponent of combining observations of humans and nonhuman primates (hereafter referred to as primates) for the purposes of understanding social interaction, was the oft-maligned Harry Harlow, whose groundbreaking work on infant primates helped redirect an entire generation of research on attachment and parenting and changed the way young children were treated (Blum, 2002).

Psychologists, too, have seen the utility of examining our nonhuman cousins. One of the pioneers of the field of behavioral primatology, Robert Yerkes, began his professional career studying humans, became interested in comparative psychology with studies on non-primate species (Yerkes, 1907), and ultimately ended up being one of the first scientists to study cognition and behavior in apes (Yerkes & Yerkes, 1929). William McDougall included primate behavior in his 1906 book on *Social Psychology*. John Bowlby was inspired by primate research in his seminal work on attachment and separation (Bowlby, 1969). Carl Murchison included a chapter on primates in his 1934 *Handbook of General Experimental Psychology* and in his explicitly comparative 1954 volume, *Child Behavior, Animal Behavior, and Comparative Psychology*. Robert Zajonc also explicitly combined the two disciplines in his 1969 classic *Animal Social Psychology*. Perhaps indicating a trend back in this direction, the recent *Handbook of Personality* does include a chapter on personality in animals (Weinstein, Capitanio & Gosling, 2008) and we hope the newest edition of the *Handbook of Social Psychology* will include nonhumans as well. Finally, the comparisons are becoming more common in popular writing as well, hopefully reflecting a change in attitudes within the disciplines (e.g., de Waal, 2005; Maestripieri, 2007).

In any review of these fields, it is necessary to note one early attempt to merge these fields, which went initially rather badly. In 1975, Edward O. Wilson published *Sociobiology*, a work intended to apply an integrated view of social behavior across the animal world. In contrast to Darwin, who simply alluded to humans and otherwise concentrated in the *Origins of Species* on the other animals, Wilson ended with a very brief chapter applying these same principles to humans. For both political and scientific reasons, Wilson was attacked by both his scientific colleagues (notably Richard Lewontin and Stephen Jay Gould) and the general public (see Alcock, 2001 and Segerstråle, 2000 for more details on the controversy). Although time has favored Wilson's interpretation, the response to these ideas undoubtedly set back the merger of these disciplines. Fortunately, there are researchers today who are once again bridging this gap. These are found primarily in the new field of evolutionary psychology, which can be regarded as a successor to the sociobiological approach to understanding human behaviour.

Some evolutionary-minded psychologists already compare research on humans and primates. For instance, Michael Tomasello and his research team compare human children with chimpanzees to examine the development of social learning and imitation (e.g. Tomasello, Savage-Rumbaugh, & Kruger, 1993) and cooperation and altruism (e.g., Warneken, Chen, & Tomasello, 2006). Sam Gosling examines personality in humans and nonhuman primates, as well as in other social animals such as canines and hyenas (Gosling, 2001). Robin Dunbar routinely uses data from human and nonhuman primates in tandem to investigate how sociality has shaped our brains (Dunbar, 2003; Hill & Dunbar, 2003). Andrew Whiten studies imitation and social learning in both humans and primates with the same experimental paradigms (Horner & Whiten, 2005; Whiten,

Custance, Gomez, Teixidor, & Bard, 1996). Despite some legitimate criticisms of evolutionary psychology, a focus on the evolutionary history and function of behaviors has lead psychologists to pay more attention to research on primates and other animals.

These examples are becoming less isolated and, perhaps because of their success, cross-species comparisons are becoming somewhat of a trend, even in social psychology. There has been a greater representation of primatologists at social psychology meetings and social psychologists at primatology conferences. For instance, a recent SPSP-meeting had a session on “Social psychology in the Wild”³ organized by Laurie Santos, who studies primates. For many of these scientists, the critical detail is examining the antecedents of social behavior, and the species involved is almost secondary. Past and current success stories indicate that a combined primate approach can be a very fruitful avenue to explore.

Similarities and Differences in Approaches

Any attempt at integrating social psychology and behavioral primatology will only succeed if it appreciates the similarities and differences in core aspects of each of the fields. Here we present a list of the key points of convergence and divergence (for an overview see Table 1). It will become clear that there is much overlap in critical areas and that the differences are real but surmountable.

We have already noted that these disciplines have very similar research foci. Like social psychologists, behavioral primatologists try to understand interactions between the individual organism and its social environment. For each of us, studying individuals in the context of important interpersonal, within, and between group relationships is paramount. Furthermore, both disciplines tend to examine these behaviors

at all levels of analysis, from individual characteristics to group and intergroup dynamics. Ultimately, what we all want to know is how the social context affects individual behavior and vice versa.

Beyond these proximate questions, there are questions regarding when and for what purpose these behaviors have evolved, the ultimate or evolutionary questions. For instance, what functions do a sense of justice or empathy serve for the individuals who display them? What were the environmental contexts which led to this specific suite of traits? And what can we learn about our present from studying our past? Such evolutionary questions have been a core focus in behavioral primatology for longer than in social psychology. However, recent developments such as the emergence of evolutionary social psychology have introduced evolutionary thinking (if, not always, practice) to social psychology as well. The focus on evolution provides disciplines with a common integrative framework for understanding how human sociality came about (e.g., Buss, 2005; Schaller, Simpson, & Kenrick, 2006; Van Vugt & Schaller, 2008).

The methods used by social psychologists and primatologists are often strikingly similar. Both rely heavily on a combination of observations to discover behavioral patterns and consistencies and experimental manipulations to understand the underlying causal mechanisms. Although surveys, very popular in social psychology, cannot be used in primates because of the absence of language, many other techniques and research paradigms such as economics games, theory of mind tasks, and computerized cognitive testing, can look remarkably similar across humans and primates. Carefully thought out and executed experiments – many examples of which exist – allow the researcher to bypass many of these problems and, at the very least, provide a close approximation.

Potential obstacles

Given that social psychology and behavioral primatology study different organisms and have long independent histories, there are clearly also some conceptual, methodological and practical obstacles to overcome (Table 1). One difficulty when any two disciplines interact is differing – and not always compatible – terminology. For instance, basic terms like “prosocial” and “altruism” often have different meanings in different disciplines (Brosnan, in press-a), and Bshary and Bergmüller (2007) identify at least four different ways in which the evolution of helping behavior is studied. A first step for any joint project is to carefully define terms used in their reports, with special attention paid to situations in which terminology is known to be incompatible. With time, a new, compatible terminology may emerge, but in the meantime, careful operational definitions can avoid misunderstandings.

A related issue is discipline-specific norms (such as authorship order, cutoff for statistical significance, and manuscript length). These cultural traits are often unknown to outsiders, making it difficult to ‘break in’ from the outside and complicating collaborations. The fact that many behavioral primatologists reside in or were trained in psychology departments tends to reduce these sorts of issues, but they exist nonetheless. Combined with the difficulty in gaining a fully nuanced, in-depth understanding of another discipline (while keeping up with one’s own journals), these issues may seem insurmountable. However, increasingly biology journals publish research with human data and psychology journals publish data from nonhumans.

A critical issue that arises specifically when comparing humans with other species, including primates, is the presence of uniquely human attributes, such as

language and culture. Language opens up new possibilities for methodologies and complex experiments in humans that are not available to primate researchers. For example, various social psychology methodologies that require complex instruction (e.g., some lab experiments) or rely heavily on linguistic framing (e.g., scenarios) are simply unavailable to primate researchers. Yet the same problems are encountered when studying human infants. Scientists have worked around this by creating excellent methodologies for comparing human infants and primates. For instance, Warneken & Tomasello (2006) designed a non-linguistic procedure examining prosocial behaviors in which experimenters pretended to be unable to reach items, and subjects, either chimpanzees or children, could assist them by returning the item.

The absence of language also means that there is no ability to debrief primate subjects, gather self-report data, ask about intentions or goals, or engage in other language-based data acquisition. This makes it more difficult to gather information on why individuals behaved in the ways that they did, or what their intentions were. Further, it limits the ability to perform post-experimental checks to verify that a manipulation was believable. Of course, this can be worked around, or even turned in to a benefit. Controlled primate experiments can elucidate some perceptions or intentions by gathering data on even very subtle behavioral changes across conditions. For instance, to investigate how monkeys perceived their reflection in a mirror, researchers measured increases in eye contact and decreases in anxiety-related behaviors when subjects were next to a mirror versus next to a piece of glass separating them from a stranger. The monkeys treated their mirror image with less anxiety and aggression than the stranger, indicating that they did not perceive the image as a stranger (de Waal, Dindo, Freeman &

Hall, 2005). A potential benefit to such non-linguistic examination is that the subject cannot intentionally or accidentally mislead the experimenter by reporting false motivations, which is a great concern in social psychological studies that use self-reports (social desirability bias: Crowne & Marlowe, 1960). Arguably there are also fewer concerns about inadvertent experimenter bias, such as hypothesis guessing, if no instructions are given to subjects prior to the study, simply because there is less opportunity to introduce bias during the interaction with participants.

Another key difference in comparing humans and primates is the importance of culture in humans. Human cultures include educational, legal, and religious institutions and the extensive development of art and symbolism, which exert strong influences on human social behavior (Baumeister, 2005). However, recent primate studies have revealed the importance of culture in chimpanzee, orangutan and even monkey behavior, and in these cases the same underlying mechanisms may explain cultural differences in both human and primate species (social learning, imitation, conformity; Huffman, 1996; McGrew, 2004; Perry et al., 2003; van Schaik et al., 2003; Whiten et al., 1999). Cultural variation in behavior is certain to be more evident in humans than nonhumans. However, this does not preclude the possibility of cross-culturally similar patterns, potentially relying upon mechanisms that are shared between species. It is important to remember that culture is not a topic that is separate from human evolution, and that other primates have a rudimentary cultural capacity as well.

A final issue to keep in mind is how to effectively utilize homology in studying behavior. Homology can be very useful in elucidating underlying mechanisms for behavior (Lorenz, 1973; Wenzel, 1992). If two behaviors in two closely related species

look similar, they are likely to utilize the same cognitive pathways. However, it is critical to be appropriately cautious (Fraley et al, 2005; Gosling & Graybeal, 2007); just because behavioral outcomes are the same, the underlying pathways which lead to those outcomes may not be. It may be particularly easy to make this error of assuming homology that does not exist when comparing primates with humans because they are so similar in appearance and behavior.

Nonetheless, it is also important to remember that just because species are highly different does not mean that there are not convergent similarities worth investigating. As an example, since brain structures differ it can be tempting to assume that cognition and behavior cannot be easily compared. However, it is known that behaviors such as mirror self-recognition and tool use are widespread across taxa such as dolphins, primates, and birds, indicating that similar behaviors do evolve, albeit via different pathways (Marino, 2002; Prior et al, 2008; Weir, Chappell, & Kacelnik, 2002). In other words, homology and convergence are both extremely useful tools when applied carefully and appropriately to the questions at hand

Combining research methods

Primateology and social psychology could benefit by adopting each other's research methods. The strengths of primatology are (1) a well-developed history of observational studies, (2) a longitudinal approach, (3) a comparative approach, and (4) the complementarity of different types of research, such as field vs. captive research or observational vs. experimental research. The strengths of social psychology are (1) a particularly strong emphasis on laboratory experimentation and (2) advanced statistical

models. Below we discuss each of these strengths, and how they could be effectively applied in the other field.

Primatology has a long history of observational studies, primarily in the field, but also in captive settings. Such studies allow the researcher to see how the animals interact in their own environment when they have free choice over what to do and with whom to do it. Watching behavior in such a natural situation often leads to important revelations as behaviors which were not suspected suddenly appear (e.g., inter-group attacks in chimpanzees, Goodall, 1986). On the other hand, observational studies cannot exist in isolation, as these conditions do not easily allow for access to the cognitive mechanisms underlying these behaviors. For instance, while nutcracking behavior in chimpanzees was first documented in the field (Boesch & Boesch 1981; Sugiyama & Koman, 1979), studies in the laboratory have focused on which factors are required for an individual to be able to learn this behavior (e.g., Hopper et al, in press).

Another contribution of primate studies to human social psychology is long-term engagement with the same participants. In primate research, an individual's entire life history can be known, including relatedness, social history, relationships with other individuals, previous experimental history, and even how physiological factors (reproductive status, health, etc.) vary over time. Moreover, it is easier to constantly monitor primates over extended periods. This is obviously fairly straightforward in captive populations, although there is the drawback that the sample sizes are fairly limited, and captive participants are typically used repeatedly, raising concerns about cross-test contamination. However, continuous monitoring has also been very successfully done with wild-living species, even though they are not under nearly the

degree of control as their captive counterparts. Some study sites have been continuously monitored for decades (e.g., Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1990). This extended relationship is not unknown in human studies; longitudinal designs can do this very successfully as well. Recruitment and retention of participants over a longer period of time is effortful and expensive, and even so, the tight degree of control usually cannot be matched. Yet the gains are great, and we argue that it is well worth the while of any scientist who undertakes it.

One of the hallmarks of primatology has always been the extensive reliance on the comparative approach. Ape and monkey species living in similar environments are compared with one another, comparisons are made between female-dominant and male-dominant species, apes are compared to humans, and so on. Such a comparative approach is not uncommon in social psychology either, of course; the cross-cultural approach is essentially the comparative approach within the same species. However, virtually all social psychologists are “single species” scientists, studying only humans. The benefit to any form of comparison, over whatever degree of phylogenetic relatedness, is that it allows the researcher to put existing behavioral patterns into an evolutionary context. This helps explain why certain patterns are more common than others, illuminates why different situations evoke different behavior patterns, and begins to explain odd or difficult to interpret behavior patterns. Thus, new, predictive, hypotheses can be formed (see Case Studies, below, for examples of this).

Of course, social psychology also has many advantages to offer primatology. One of the most obvious is adoption of more advanced statistical approaches, particularly those for analyzing multilevel data (e.g., individuals nested within groups; e.g., see

Kenny, Kashy, & Bolger, 1998). While it may not always be possible for primatologists to use these statistics, owing to much smaller sample sizes, the power they offer gives added incentive to those primatologists who can accrue a larger data set to do so. Clearly, there is much to be gained when the strengths of each approach to studying social behavior are combined. We now turn to some concrete examples of the fruitfulness of such an exchange.

Case Studies in Social Psychology and Behavioral Primatology

Here we present four case studies of major research programs in social/personality psychology and behavioral primatology to illustrate the benefits of an integrated approach. These case studies represent key areas in the study of social behavior in both humans and primates as seen in any introductory text, (1) personality and individual differences, (2) equity and social justice, (3) intergroup relations and (4) sexual behavior. Moreover, in two research programs (personality, social justice) there is already ongoing collaboration between social psychologists and behavioral primatologists, and these fields show some signs of integration. The other two programs (sexual behavior, intergroup relations) have developed on parallel tracks and, although there is little interaction yet, there is a great deal of scope for future collaboration.

Case 1: Personality and Individual Differences

In many respects, the integration of personality research in social psychology and primatology is a success story. Some of the earliest investigations into the psychology of nonhuman species studied personality (e.g., Pavlov, Yerkes), and there have been recent calls to fully re-integrate human and nonhuman personality research (Gosling, 2001; Nettle, 2006), up to the inclusion of a chapter on nonhumans in the most recent

Handbook of Personality (Weinstein et al, 2008). This research clearly shows how work from humans laid a framework – both theoretical and experimental – for studying nonhumans, and has ultimately led to investigations which may in turn inform human studies.

Much of the work on personality in primates explicitly begins by applying human research to the study of primates, and typically employs the same sorts of measures. There is, of course, some variation. Most commonly, researchers who study humans gather information on individuals' personalities using self-report questionnaires. Researchers who study nonhumans must rely on keepers, trainers, and other individuals with long-term familiarity with the primate subjects fill out these questionnaires, similar to research using young children who cannot answer on their own. Typically, multiple parties rate each subject.

The primate data on personality are quite consistent with the human data. For instance, there is quite a high trait reliability indicating that personalities are stable within and vary between participants. A study on chimpanzees had an inter-rater reliability (IRR) of .75, with IRRs for each adjective ranging between .55 and .81 (King & Figueredo, 1997). Observers scored each chimpanzee on 43 adjectives, drawn from a list used in human studies (Goldberg, 1990). Factor analysis revealed that chimpanzees roughly fit the five-factor model that has been proposed for humans (McCrae & Costa, 1987). The major difference is the addition of a 'dominance-submissiveness' factor, which is not included among humans (but probably should be; see King & Figueredo, 1997)

Other research goes even further, attempting to correlate personality with social behavior. For instance, personality variables in adult male rhesus monkeys (*Macaca mulatta*) are predictive of behavior across many different situations, and these variables remain predictive even over several years of study (Capitanio, 1999). A recent study in chimpanzees combined the questionnaire approach with the use of a novel stimulus to investigate how novelty-seeking behavior correlated with personality assessments (Freeman, Gosling, Lambeth, & Schapiro, 2007). Karate dummies (a novel and potentially threatening stimulus) were introduced to groups of chimpanzees and the subjects' behavior was monitored. Aggression towards the dummy correlated positively with aggression and injuries sustained over the past 3 years, and correlated negatively with caution and fearfulness.

As with humans, personality differences in nonhuman primates are affected by both genetic and environmental factors. For instance, rhesus macaque personalities are very stable, and they are manifest from a very young age (1 month; Higley & Suomi, 1989). However, there is malleability. When rhesus macaques are raised with older "tutors" of the closely related, but much more mild-tempered, stumptail macaques (*M. fascicularis*), they display stumptail-typical behaviors rather than those of their birth species (de Waal & Luttrell, 1989). In another example, after the death of several top-ranking adult males in a bout of bovine tuberculosis, the remaining individuals in this group of olive baboons (*Papio anubis*) became much less aggressive and more peaceful, possibly due to the females' influence on the behavior of newly arriving males (Sapolsky & Share, 2004).

Unlike in humans, a lot of personality research in primates has looked at differences in temperament. It is typically assessed through the subject's behavioral reaction to a novel stimulus (typically threatening, such as the aforementioned karate dummies). While temperament and personality are technically different, they are sufficiently similar that they are often measured together. In primates, as with humans, temperament tends to vary between individuals, populations, and species (Clarke & Boinski, 1995) and is affected by prenatal stress (Clarke & Schneider, 1992), early rearing environment (e.g., Mason, 1979; Novak & Harlow, 1975), and maternal behavior (Fairbanks & McGuire, 1993). The three factors most strongly associated with temperament often turn out to be rank, age, and sex, indicating that these are not personality factors *per se* (Buirski, Plutchik, & Kellerman, 1978; McGuire, Raleigh, & Pollack, 1994).

Stable personality and temperament differences have also been found in a number of other species. As one example, male guppies (*Poecilia reticulata*) respond very differently to predators, with some approaching and investigating and others hanging back (shyness vs. boldness; Godin & Dugatkin, 1997). The former, which researchers label as "bold" guppies, do have higher predation risk, but they are more likely to be preferred as mates by females. This tradeoff pattern suggests that guppies' personalities are a case of balancing selection, in which different personality styles dominate in different social or ecological contexts. A similar argument has been made in a number of other species, including humans (Dugatkin & Godin, 1998). These behavioral strategies are hypothesized to be adaptive, and may represent, for instance, specialization for different life history strategies (Bergmüller & Taborsky, 2007).

Summary and implications. Studies of personality and individual differences provide a prime example in which the human and nonhuman literatures have drawn from and inspired each other. One critical feature has been the incorporation of each other's literatures and ideas, and, where possible, methodologies. Creative work by primatologists has adapted human-subjects approaches to work with nonhuman subjects, and an understanding of personality and temperament as an evolved characteristic of the organism has rapidly emerged. This progress has been facilitated by researchers who study multiple species, including some who span humans, nonhuman primates, and nonprimates. The cross-species approach to personality is perhaps the best developed example of how primatology and social psychology can cross-fertilize and enhance each other.

Case 2: Equity and Social Justice

As with the example of personality, studies of inequity responses show how theory developed for humans can be applied to leverage the theoretical understanding of similar behaviors in nonhumans. Unlike with studies on personality, however, practical constraints required the development of significantly different procedures and protocols (e.g., the lack of language prohibits scenario research). Nonetheless, application of theory from social psychology (and economics) has led to a rapid development of theory and research in primates, and recent primate work is beginning to inform an evolutionary understanding of the phenomenon in humans as well.

Equity theory was developed in the 1970s, primarily by the work of Elaine Hatfield and colleagues (Walster [Hatfield], Walster, & Berscheid, 1978). Today there is a thriving literature studying many different forms of inequity in the fields of fairness and

social justice (see *Personality and Social Psychology Review*, Vol. 7, No. 4, 2003, a special issue on this topic). Independent from the social psychological literature, the study of inequity emerged in behavioral economics using economic games experiments (Fehr & Schmidt, 1999). This game methodology has been adapted to make it possible to study inequity responses in nonhuman primates, drawing substantially from both the social psychology and economics literatures.

Early work found that, like humans, nonhuman primates respond negatively to distributional inequity, refusing to continue participating in interactions in which they receive less than a partner does (Brosnan & de Waal, 2003; Brosnan, Schiff, & de Waal, 2005; Fletcher, 2008; van Wolkenten, Brosnan, & de Waal, 2007). The comparison between human and nonhuman species is interesting in and of itself, yet for our purposes the critical feature is the rapidity with which theory emerged to support the nonhuman data (Brosnan, 2006a, 2006b, 2009). Based on human data, it was not surprising to find that both monkeys and apes reacted strongly to inequity that was personally disadvantageous -- getting less than their partner for similar effort -- but rarely responded to situations of overcompensation -- getting more than their partner for similar effort (Brosnan, 2006b; Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005; Vonk et al., 2008). Previous work in both social psychology and economics (Loewenstein, Thompson, & Bazerman, 1989; Walster [Hatfield], Walster, & Berscheid, 1978) had suggested that responses to overcompensation should be weaker than responses to receiving a less beneficial outcome. In humans, these responses to overcompensation are often psychological leveling, or justification for one's receipt of the surfeit (Walster [Hatfield] et al, 1978). One practical limitation in analyzing the behavior of nonhumans is

that, due to the lack of language, it is much more difficult to tell if they, too, utilize psychological leveling techniques to justify their greater receipt.

Social psychological theory also helped to explain individual variations in chimpanzees' reactions to inequity (Brosnan, Schiff, & de Waal, 2005). The social psychology of relationships suggests that humans respond differently to fairness in close, versus distal relationships. In humans, the former generates a communal orientation, in which instances of inequity are more easily accepted, whereas the latter generates an exchange orientation in which inequity is not tolerated (Attridge & Berscheid, 1994; Clark & Grote, 2003; Fiske, 1992). Given that chimpanzees that grew up together do not respond to these instances of inequity, while those who have less long-term relationships do, it has been posited that relationship quality is a major factor in determining chimpanzee responses. Further primate data may in turn inform students of human behavior about how such variations in relationship quality are linked to differences in response.

There are several outstanding issues in primatology research on inequity. In contrast to human research, the cognitive mechanisms underlying the inequity response in primates are currently unknown (Tyler & Smith, 1998). A contrast between what the individual expected and what they received could explain some of it (Reynolds, 1961; Roma, Silberberg, Ruggiero, & Suomi, 2006; Tinklepaugh, 1928). However, when monkeys' frustration and inequity reactions are directly compared, the response to inequity is stronger than that for frustration (Brosnan & de Waal, 2006; van Wolkenten et al., 2007). Future research should determine whether the mechanisms that cause inequity

aversion in primates are the same as that in humans (e.g., relative deprivation, frustration).

Another limitation of the primate research is that it is difficult to compare motivations between human and nonhuman subjects. Often human subjects are asked why they behaved in the way that they did (although there are no guarantees that humans have accurate insights into the true causes of their behavior; see Nisbett & Wilson, 1977). This type of methodology is of course not available to nonhuman primate researchers. However, careful experimentation can address some of these issues. For instance, if capuchin monkeys refuse to cooperate for inequitable rewards with only some partners, but not others, then we know that there is something about those individuals or relationships that is affecting behavior (Brosnan, Freeman, & de Waal, 2006). If, as we found, capuchin monkeys are more likely to cooperate with partners who do not dominate the better rewards, then we can reasonably assume that it is the behavior of those partners during the experiment that is the critical feature. As discussed above, in some cases the lack of debriefing may be a benefit, as researchers cannot be led astray, intentionally or unintentionally, by the reported motivations of their subjects.

While the social psychology literature has contributed immeasurably to developing a theory of inequity responses in nonhuman species, the primate data can help inform theories of human behavior through providing the comparative approach necessary for understanding the evolution of human behavior. At the most basic level, we recognize that we are not the only species that responds negatively to inequity. Eventually, such data may help us understand the conditions under which our responses

to inequity evolved, and will help us to predict which situations may cause a reaction and develop interventions prior to the incident.

Summary and implications. The study of equity represents one of the more fruitful interactions to date between social psychology and primatology. Thus far, primatological studies have primarily gained from the existing theory and framework developed by social psychology, but the comparative approach offers an opportunity to expand our understanding of humans' equity responses as well. Moreover, in this area primatologists and social psychologists are actively seeking one another out and intentionally incorporating each others' work, making this an unusual case. Future research to clarify important questions, such as whether psychological motivations are similar between the species, should continue to highlight the benefits of the interplay between these disciplines.

Case 3: Intergroup Relations

Intergroup relations represents a case in which extensive literatures have developed independently in behavioral primatology and social psychology (as well as political science). There is currently very little interaction between researchers of human and primate intergroup relations, and there is a clear need for comparison and integration of these literatures. Here we show how a better understanding of intergroup relations in humans and other primates can generate new knowledge about the antecedents and consequences of intergroup conflict.

There is a rich and diverse literature on intergroup behavior in both social psychology and primatology, including the use of the same definitions (Brewer & Brown, 1998; Fiske, 2002; Goodall, et al., 1979; Wilson & Wrangham, 2003). Intergroup

behavior is defined in both fields as a situation in which individuals as members of one group interact, individually or collectively, with members of another group. The study of intergroup relations has advanced at different rates and with different foci within each discipline. For instance, there is an extensive literature on intergroup conflict in humans, but the literature on primate intergroup conflict is still in its infancy. In contrast, primatologists have generated much data regarding other aspects of intergroup relations, for instance when and why individuals transfer to a different group and clashes at territorial boundaries, which deserve more emphasis in social psychology. One preliminary conclusion is that intergroup violence may be more common in humans than in other primates, but we need to know why.

Most of the primate data on intergroup aggression comes from chimpanzees and focuses on border patrols and the active hunting and killing of members from neighboring groups (Goodall, et al., 1979; Wilson & Wrangham, 2003). Understanding why chimpanzees engage in intergroup aggression might give us insights into some of the causes of human intergroup violence (Manson & Wrangham, 1991; Wrangham & Peterson, 1996). There are important convergences between the human and chimpanzee intergroup literature that shed light on this question. First, intergroup relations in primates are virtually always marked by conflict. Although it was once believed that early humans were essentially peaceful and that under the influence of wealth and progress they had degraded into a “warring” species (Rousseau’s noble savage hypothesis), this belief was shattered when researchers found evidence of intergroup killings in archaeological sites (Keeley, 1996). Moreover, social-psychological experiments, such as the minimum group paradigm, show that inter-group discrimination and aggression can be easily invoked in

humans. Similarly, among chimpanzees, there once was a mistaken belief that chimpanzee relations were peaceful. This belief was shattered when Goodall and colleagues (1979) reported incidents of systematic intergroup raiding and killing among neighboring chimpanzee communities in Gombe National Park, Tanzania, and other reports soon followed (Nishida, Haraiwa-Hasegawa, and Takahata, 1985; Watts, Muller, Amsler, Mbabazi, & Mitani, 2006). This might well indicate that intergroup aggression is a shared trait that is the result of homology (Manson & Wrangham, 1991; Wrangham & Peterson, 1996). Intergroup relationships in our other closest relative, the bonobo (*Pan paniscus*) remain intriguing in this regard (e.g., Hohmann, 2001).

A second commonality between the human and chimpanzee literatures are the causes of intergroup aggression, which in both species seem to derive from conflicts over scarce resources such as territories, food, and mates. Intergroup conflict in humans often begins with a dispute over a particular resource that one group possesses but other groups want to have. Donald Campbell's realistic group conflict theory (1965) proposed that intergroup conflicts emerge over valuable but scarce resources, and this theory can easily apply to primates. For instance, one functional outcome of intergroup aggression in chimpanzees is to increase access to reproductively relevant resources such as territory or mates (Wilson & Wrangham, 2003). The imbalance-of-power hypothesis (Wrangham, 1996) posits that chimpanzees use coalitional aggression to weaken rival groups so that their numbers decline and they can more easily dominate and exploit them. This theory has much in common with social dominance theory, a social psychological theory about the emergence of dominance hierarchies between human groups (Sidanius & Pratto, 1999). The imbalance of power hypothesis might also account for the tense relations

between majority and minority groups within society (Tropp & Pettigrew, 2005). Yet, as far as we are aware, the imbalance-of-power hypothesis is unknown to most social psychologists studying intergroup conflicts. It is clear that humans also engage in symbolic forms of intergroup competition. Unlike other primates, humans have the ability to think of themselves as members of symbolic groups (such as Yankees or Manchester United fans) and treat other groups disadvantageously not because they form a direct resource threat but because they threaten their symbolic group identity (Kinder & Sears, 1981). It is less likely that other primates engage in symbolic intergroup competition because this requires advanced cognitive abilities, such as theory of mind and language, which are not as developed in other primates.

A third convergent finding is that intergroup aggression in both humans and chimpanzees is primarily a male business. Intergroup violence in chimpanzees is conducted mostly by coalitions of males attacking outgroup males, which makes them appear, at least superficially, similar to all-male human fighting groups such as combat units, street gangs, and hooligans (Goldstein, 2003). Interestingly, although these sex differences are well documented in the chimpanzee literature (e.g., Goodall, 1986) it has only recently been given attention in the social psychological literature. Paralleling the chimpanzee data, men have a stronger intergroup dominance drive, they identify themselves more with tribal in-groups (Baumeister & Sommer, 1997), and respond more aggressively to intergroup threats – for instance, by forming cooperative alliances to attack members of out-groups (the male warrior hypothesis; Van Vugt, De Cremer, & Janssen, 2007). This is an excellent example of a social psychological research program inspired by primate research and theory.

In turn, primate intergroup studies could benefit from social psychological expertise in studying intergroup relations experimentally. In the minimal group paradigm (Tajfel & Turner, 1976) individuals allocate a valuable resource, such as money, between an in-group versus out-group member. It would be interesting to conduct equivalent experiments, say with food or useful tools, among primates. Further, primate researchers could benefit from social psychological expertise in studying the cognitive mechanisms underlying intergroup conflict (e.g., prejudice, out-group homogeneity). Although intergroup reactions may not be as subtle in primates, it would be interesting to see how perceptions and emotions change when primates encounter members of out-groups that vary in proximity, strength, and sex. Finally, social psychologists study various markers that humans use such as ethnicity, culture and language to classify someone as member of in-groups or out-groups (Van Vugt & Park, 2009). Given that primates apparently use vocalizations to identify group membership (Cheney & Seyfarth, 1982; Crockford, Herbinger, Vigilant & Boesch, 2004), the hypothesis that nonhuman primates also routinely utilize such markers warrants further investigation.

Summary and implications. Intergroup conflict has been extensively studied by social psychologists and primatologists, yet these fields have hardly influenced each other. Primate theories of intergroup conflict, such as the imbalance-of-power hypothesis, might generate novel insights into the causes of intergroup conflict in humans. A phylogenetic perspective in general may help uncover the causes of human intergroup violence. In turn, primatologists could benefit from social psychological expertise in designing experiments to study the cognitive mechanisms underlying intergroup relations.

Case 4: Sexual Behavior in Intimate Relationships

In this section, we focus on an area where integration of human and nonhuman studies is embryonic: sexual coercion. In humans, a substantial proportion of women suffer from violence and aggression in intimate relationships (Bradley et al., 2000; Browne & Williams, 1993; DeGroat, 1997; Straus & Gelles, 1986). Such violence can lead to various health problems including stress, infections, physical injuries and sometimes death (e.g., Berrios & Grady, 1991; Jurik & Winn, 1990). While this might seem a particular human problem, a glance at other primates reveals that male aggression towards females is widespread across primates as well as in other animals (Clutton-Brock & Parker, 1995; Hammerstein & Parker, 1987; Smuts & Smuts, 1993). As with humans, this aggression includes both threats and physical assault, and females suffer consequences that mirror those experienced by humans (Campbell et al., 2002; Dunbar, 1996; Goodall, 1986; Packer et al., 1995; Pereira, 1983; Rajpurohit & Sommer, 1991; Sapolsky, 1996; Schapiro et al., 1998; Smuts & Smuts, 1993).

Why do males engage in such behavior, and can studies of nonhuman species cast new light on this form of aggression in humans? Smuts and Smuts (1993) provide a useful cross-species definition of sexual coercion – the use of force, or the threat of force, by a male towards a female increasing the likelihood that she will mate with him rather than another, at some cost to her. Thus sexual coercion is viewed as a male reproductive strategy – males use aggression to increase the likelihood that they will successfully copulate with the targeted female(s), and so derive an evolutionary benefit from this behaviour while females suffer a cost. This definition is broader than that typically used in human studies, where ‘sexual coercion’ is distinguished from other forms of

relationship, or intimate partner, violence, relating only to coercive copulation (Goetz & Shackelford, 2002; Jaffe & Wolfe 2003). However, given that, in humans, relationship violence by men increases the likelihood of sexual behavior (Silverman et al., 2001) and fosters the acceptance of such behavior (Kearney, 2001), the more embracing definition seems to be useful (Goetz et al. 2008).

Clutton-Brock & Parker (1995) further distinguish three types of sexual coercion: forced copulation, harassment, and intimidation, the relative occurrence of which varies between species. *Forced copulation* (rape), for example, is relatively common in orangutans but comparatively rare in chimpanzees, where *harassment* is the typical form (Goodall, 1986; Mitani, 1985; Muller, 2002; Rijksen, 1978; Wrangham & Peterson, 1996). These comparative data suggest that, rather than types of coercion being points on a continuum determined by the level of some internal drive (e.g., Felson & Tedeschi, 1993), they may instead reflect different coercive strategies, or be facultative adjustments of the same strategy to differences in either current socio-ecological environments or developmental trajectories (cf. Goetz, 2008). The extent to which, across species, sexually coercive aggression is the outcome of the same processes, with shared ontogenetic or motivational components, is an empirical issue that needs to be addressed by looking for differences in apparently equivalent behaviors between close phylogenetic cousins, as well as exploring similarities in such behavior between distantly related species.

An important caution is warranted at this point. Not every form of male aggression towards females is necessarily sexually coercive. The perspective from primatology (Smuts & Smuts, 1993) is that male aggression that leads to mating benefits

for males may be the outcome of either a male strategy (coercion) or a female strategy related to inciting male competition or assessing male 'power' (mate selection). Thus instances of relationship violence, even at extreme levels, by men should not be assumed *a priori* to be sexual coercion, which has clear implications for psychological investigations of the proximate mechanisms that generate male aggression towards women; superficially similar behaviour may be functionally, ontogenetically and mechanistically distinct.

In human psychological studies, a distinction is drawn between the more common "situational couple violence" (violence that emerges from escalated argument) and "intimate terrorism" (violence concerned with dominance and control), with only the later showing a strong bias toward male perpetrators (Finkel, 2007, Johnson, 2008). This is based on the motivating factors for the aggression, and a different, but complementary, way of defining relationship violence to that emphasised above (Tinbergen, 1963). Considering both definitions together raises two interesting points that would be lost without the integrated approach we emphasize: first, the functional perspective from primatology suggests that some male-perpetuated elements of "situational couple violence" might in fact be sexual coercive; second, the level of such violence perpetrated by women, matching that by men, highlights the need to consider the importance of immediate social environments (of which socially monogamous pair-bonding is a rare case) as contexts that limit and shape the expression of both male and female coercive and counter-coercive strategies. The 'reproductive strategy' approach has provided novel insights into human sexual coercion, using the idea that men are sexually coercing women in order to retain them as mates (and thus mating access) they might otherwise

lose (Buss & Shackelford, 1997; Shackelford et al., 2005; Starratt et al., 2008; Wilson & Daly, 1992; Wilson et al., 1995). In this, it has built on longstanding interests in sexual coercion by social and other applied psychologists focusing on exploring men's attitudes and beliefs in an effort to understand the proximate causes (Holtzworth-Munroe & Stuart, 1994; McCollaum & Lester, 1997; Stets & Pirog-Good, 1987). In turn, investigations of sexual coercion in humans aid comparative studies in primates. For example, in humans, support from family and friends is important in limiting or ending domestic violence (Figueredo et al., 2001; O'Campo et al., 2002); leading to the idea that female chimpanzees are vulnerable to male aggression as they are often solitary (Wrangham & Peterson, 1996). Detailed testing of this hypothesis awaits, but where ecological conditions allow female chimpanzees to be more gregarious, they are able to respond collectively to male aggression and apparently limit its extent (Newton-Fisher, 2006).

Summary and implications.

Despite sexual coercion being widespread across species, a comparative perspective for humans has been slow to develop. This apparent reluctance may perhaps be due to overly simplistic parallels drawn between apes and human in the past, a fear of justifying of behavior in humans because its presence in other animals makes it 'natural,'² or to the same visceral reaction that greeted Darwin's conclusion that humans are, essentially, apes (Bowler, 2003). However, the very sensitivity of studying such behavior in humans should encourage investigations in other species to identify evolutionary function and underlying mechanism, as well as individual ontogenetic pathways. Such knowledge may offer opportunities for better understanding – and perhaps modifying – human behavior. For both psychologists and primatologists, this is an area of research

that needs to be studied ‘in the field.’ It also represents an interesting point of contact that should increasingly be synergistic between the two disciplines, with the findings for humans inspiring hypotheses to be investigated in primates, and the broader framework provided by the latter enabling the testing of ideas that might be more problematic to explore in humans in what is, inevitably, a highly charged subject to study (Wrangham, 2002).

Additional topics to pursue

Although these four cases show the diversity of opportunities for linking social psychology with primatology these are by no means the only examples. Recently, a number of psychologists and primatologists have taken up the call, investigating such themes as conflict resolution (Harcourt & de Waal, 1992), irrational decision-making (Brosnan et al, 2007, Chen, Lakshminarayanan, & Santos, 2006;), empathy (de Waal, 2006), helping (Barnes, Hill, Langer, Martinez, & Santos, 2008; Warneken & Tomasello, 2006;), prosocial behavior (Silk et al., 2005, Jensen, Hare, Call & Tomasello, 2006; de Waal, Leimgruber, & Greenberg, 2008), leadership (Van Vugt, 2006), social cognition (Jensen, Call, & Tomasello, 2007) and social networks (Dunbar, 2007) from an integrated perspective. Many of the research paradigms to study these phenomena in primates have been adopted from the human literature and sometimes they employ exactly the same designs for the purpose of replication (Brosnan et al, 2007 mirror their design from Knetsch, 1989; Tomasello et al, 1993 utilize the same paradigm for both humans and chimpanzee subjects).

Conclusions and Recommendations

There is great utility in comparing the social behavior of human and nonhuman primates to discover similarities and differences between closely related species. As demonstrated, collaborations between social psychology and primatology can be very rewarding. In addition, an integrated, comparative approach explicitly invokes an evolutionary perspective that provides powerful insights into the origins of many social psychological phenomena (Bering, McLeod, & Shackelford, 2005; Buss, 2005; de Waal, 2005; Van Vugt & Schaller, 2008). This approach could be thought of as a comparative social psychology that allows us to put our own behavior in perspective with fellow primates and other animals to see which of our traits are unique or shared. Of course, a comparative approach also broadens our understanding of nonhuman species.

The gains of interdisciplinary work

As discussed throughout this paper, there are numerous gains for those who engage in such interdisciplinary activities. First is the availability of new research ideas and methods. At the planning stage, when considering questions, researching the findings in another species can help clarify which questions are meaningful and interesting. The male warrior hypothesis (Van Vugt et al., 2007) emerged due to the observation that intergroup aggression across various mammal species is a male activity. Similarly, information on successful methods and paradigms used in other fields can improve data-gathering and help save time and resources. For instance, social psychologists might consider adopting methods from primatology, such as observation methods to develop paradigms that do not require language or technical understanding, and can therefore be used with young children, people with special needs, or people from different cultures.

Second, comparing results across primate species can shed light on unexpected or inconsistent data. For example, a study of reactions to inequity yielded quite different results among three groups of chimpanzees (Brosnan et al, 2005). An inspection of the social psychological literature revealed that this was likely the result of differences in levels of closeness between members within the different groups. A third benefit is the advancement of theory. Using insights from other disciplines can accelerate theory development (as in the case with the male warrior hypothesis) and avoid ‘reinventing the wheel’ in each discipline. Finally, a nonhuman perspective helps to illuminate the evolutionary underpinnings of particular social psychological phenomena. Careful analyses based on convergent evolution and homology can clarify when and under what conditions a particular behavior may have evolved and how it was initially useful.

Another benefit from taking a comparative primate approach is to help establish more conclusively which kinds of mental and behavioral processes are uniquely human. There is no doubt that the human capacities for language, theory of mind, and culture have created new opportunities for thinking about ourselves and others consciously and symbolically, in a way that other species may not (Povinelli & Giambrone, 2001). At a young age, human children are able to recognize themselves and appreciate that other people have mental states separate from theirs. Conscious thought plays an important role in human social judgment decision making. Most social psychological models of decision making (such as dual process models like ELM; Petty & Cacioppo, 1986) emphasize the role and utility of conscious thought processes in decision-making. Yet more recent research has found that many aspects of decision-making occur relatively automatically and that unconscious thought activity sometimes produces better judgments and decisions

(Dijksterhuis & Nordgren, 2006). A careful comparison of decision making between humans and other species could help to clarify which aspects of human social judgment and decision-making rely on language and conscious thought, and in what domains they produce better outcomes. For instance, it may well be that conscious problem-solving works particularly well for evolutionarily novel problems (such as solving math puzzles), whereas unconscious activity works better with problems that are phylogenetically ancient and therefore shared between humans and other species – such as finding a mate or rating the quality of food items or sleeping sites.

Practical implications

Although there are many potential gains from integration there are various obstacles that must be overcome. First, the data gathered from each field must be comparable. This does not necessarily mean that identical research protocols should be followed in each species, but that explicit effort must be made to link the data sets. There are several success stories in generating compatible data, such as in personality research (see Case 1) and research in to the endowment effect (Brosnan et al, 2007). More studies such as these need to be developed to compare individuals across several different species.

Second, researchers ought to avoid oversimplifying and over-interpreting findings obtained in other species. We already discussed the fallacy of assuming homology without justification. Particularly when comparing humans with other primate species, it is easy to draw anthropomorphic conclusions. Yet it is important to remember that similar-looking behaviors can arise due to quite different causes, and equally that

different environments can cause profound differences in behavior even in closely related species.

Third and related, human and primate researchers must make real effort to cross disciplinary boundaries, read each other's journals, attend each other's meetings, invite each other to talks, send relevant work to researchers in the other discipline, cite each other's papers, and invite each other to publish in the other's journals (see Appendix for concrete steps). A practical concern is the socialization of individuals into each other's fields. To expedite this, we must help each other to format papers appropriately and overlook initial gaffs on submissions if we are to truly encourage cross-disciplinary publication. With good journals already sporting quite high rejection rates, this may be difficult. Tenure and promotion committees will also need to develop expertise to reward applicants with an interdisciplinary focus appropriately.

Fourth, the fields must strive toward common operational definitions of key constructs. Different definitions of terms such as altruism, prosocial behavior, imitation, or Machiavellianism cause substantial problems in translating findings. There is also a tendency for disciplines to be rather imperialistic, assuming that their definitions are the correct ones. Finally, while recognizing the need to avoid unnecessary jargon in the interests of communication, researchers should try to avoid anthropomorphic and socially loaded constructs such as fairness, rape and warfare when describing the behavior of primates, or at least be very clear in their definitions, to avoid misunderstandings. This, at least, should ensure that when such terms are used, there is a commonality in the definition that applies across both nonhuman, and human, primates.

CODA

This article set out to examine what it takes to develop a comparative approach to study social psychology in humans and other animals, with a focus on the Family Primates. Looking to the future we envision a new conception of social psychology that takes an explicitly evolutionary focus and develops into something akin to a primate social psychology. This new discipline would address the same questions as are currently being investigated separately in social psychology and primatology, but examine them across all primates. Such an explicitly comparative approach will broaden our understanding of the origins, development and manifestation of human social psychology. At that point we may be in a better position to address many of the most intractable questions that vex social psychology today.

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FIGURE CAPTIONS

Figure 1: A basic taxonomic tree of nonhuman primates. MYA = million years ago, that is, the age of the most recent common ancestor. Note that while the arms are depicted evenly spaced, the divergence times vary (indicated at junctions; each number indicates how many million years ago the branch diverged). Humans are a member of the great apes, and are most closely related to the genus *Pan*, which includes chimpanzees and bonobos. Chimpanzees and bonobos separated approximately 1 MYA, *Homo* and *Pan* separated approximately 5 MYA, gorillas and *Homo/Pan* separated approximately 7 MYA, and orangutans and *Homo/Pan* separated approximately 12 MYA. Photograph of old world monkey by F. de Waal. All other photographs by S. Brosnan. Figure first appeared in Brosnan, 2009.

Figure 2: Traits which are shared can be due to homology or convergence, as depicted in the schematic phylogenetic tree below. In homologous situations, the trait is shared among species because a common ancestor, here indicated by the closed black circle, possessed Trait A (e.g., the 6 species possessing trait A on the right side of the tree). In convergent situations, species share a trait because similar ecological circumstances led to selection for a similar trait and their common ancestor does not possess the trait in question. In this case the open circle at the base of the tree indicates that the trait was not present in the last common ancestor to the left and right branches of the tree, yet the 6 abovementioned species and the species on the left share trait A. In divergence, a species develops a new trait (here, Trait B) that differs from other species to which is it closely evolutionarily related (e.g., the far right species possesses a new trait, trait B, which is not present in any of the species most closely related to it).

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Appendix 1:

This appendix provides a list of meetings and journals which social psychology practitioners may find useful to investigate when beginning an exploration of related primatology studies. By necessity this list is not comprehensive, but is designed to provide the reader with a starting point. Note that many works of animal behavior are published in more general biology journals (e.g., *Current Biology*), for which behavior is not the primary focus, so we here leave these out. We also recognize that there are a great many organizations that are specific to a region or a taxon (e.g., the International Primatological Society), or are overly broad (e.g., the APA or APS), which we here leave out for the sake of brevity.

We do not focus on nonhuman primate cognition and behavior in this case, as most of the ‘species specific’ or ‘taxon specific’ journals and meetings cover a broad range of topics related to a specific group of animals. Instead we here focus on journals and meetings which focus on cognition and behavior in nonhuman species, inclusive of primates.

Journals for nonhuman primate cognition and behavior

- Animal Behaviour
- Animal Cognition
- Behaviour
- Behavioral Ecology
- Behavioral Ecology and Sociobiology
- Ethology
- Journal of Comparative Psychology

- Journal of Experimental Psychology: Animal Behavior Processes

Annual or Biannual meetings for nonhuman primate cognition and behavior

- Animal Behavior Society
- International Behavioral Ecology Society
- International Society for Comparative Psychology

Endnotes

¹ Note that while in the US personality and social psychology are often treated as one field, in Europe these are distinct disciplines. Thus, in this review we choose to treat the two as highly similar (although not necessarily the same) and address personality psychology as an inter-related part of our quest to understand how nonhumans can inform social psychology.

² Note that it is critical that researchers do not commit the naturalistic fallacy when studying humans and other species, that is, confound the determination that a behavior is ‘natural’ (in the sense of an evolved strategy; part of the species’ biology) with a moralistic judgment. The identification of the biology behind behavior makes it difficult to dismiss it as some form of cultural or developmental oddity, but says nothing about the morality of such behavior, that is whether we choose to accept or repudiate the behavior. Thus, even if sexual coercion, up to and including rape, are identified as mechanisms used by males in many species to promote their genetic fitness – and the extent to which this is true requires empirical study of each species – this does not impact our moral judgments regarding the unacceptability of such behavior in our own societies.

³ The 2007 SPSP meeting in Memphis, TN.