Special Article

On the Importance of Comparative Research for the Understanding of Human Behavior and Development: A Reply to Gottlieb & Lickliter (2004)

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Abstract

Comparative behavioral research is important for a number of reasons and can contribute to the understanding of human behavior and development in many different ways. Research with animal models of human behavior and development can be a source not only of general principles and testable hypotheses but also of empirical information that may be extrapolated to humans.

Keywords: comparative behavioral research; evolution of behavior; homologies; animal models; nonhuman primates

In their article 'The various roles of animal models in understanding human development' Gottlieb and Lickliter (2004) provide a useful review and discussion of some empirical and conceptual issues emerging from comparative research on behavior and development. They first provide some reasons why comparative behavioral research is generally worthwhile and then focus the rest of the article on 'the animal model approach', which entails finding 'nonhuman species with behavioral and psychological repertoires that are similar to humans so that the results of experiments with the model may throw light on seemingly related behavior in human beings' (pp. 311–312). Although Gottlieb and Lickliter provide some examples of cases in which research with animal models has advanced our understanding of human behavior and development, they argue that the main contribution of this research to psychology is to provide food for thought, i.e. hypotheses and not data. They use various arguments in support of their position, including the notion that animal models of human development may be simplistic or the difficulty of demonstrating homologies between animal and human behavior.

One may argue that a logical corollary of Gottlieb and Lickliter's position is that there is no strong rationale for doing research with animal models of human behavior and development. Computer simulations can be a good source of testable

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hypotheses about human development and behavior. Studying human development can be an excellent source of testable hypotheses about human development. Why bother with animals? Given the economic costs, the logistic difficulties, and the ethical issues associated with animal research, such research would no longer be warranted if its contribution is only to provide hypotheses or food for thought. Even animal studies with highly invasive experimental procedures that are impossible in humans would be difficult to justify if their main contribution were only to provide hypotheses.

In this article, I argue that there are reasons why comparative behavioral research is important other than those discussed by Gottlieb and Lickliter, and that comparative approaches other than the animal model approach can enhance our understanding of human behavior and development. Furthermore, I argue that animal and human development include both simple and complex processes and that the interpretation and generalization of comparative behavioral data do not intrinsically require any more caution than the interpretation and generalization of any behavioral data. Finally, I conclude by giving examples of cases in which comparative behavioral research provides data that can be directly extrapolated to humans, and not just hypotheses or general principles.

On the Many Reasons for Doing Comparative Research and Their Relevance for Humans

Gottlieb and Lickliter maintain that, in addition to providing models of human behavior, comparative behavioral research has three purposes: comparing different species to identify broad trends in behavioral and cognitive evolution that transcend particular lineages, comparing closely related species to reconstruct the evolution of specific behaviors, and trying to understand how animals adapt to their natural environment. Gottlieb and Lickliter do not discuss how comparative research conducted with these three purposes can contribute to our understanding of human behavior and development. Therefore, these purposes may seem important to a zoologist interested in understanding the evolution of biological diversity but not necessarily to a social scientist interested in understanding human behavior and development. Gottlieb and Lickliter seem to suggest that comparative research can make a contribution to human research only or mostly through the animal model approach, and then proceed to discuss the advantages and the limitations of this approach.

In reality, one can think of many more reasons why comparative behavioral research is useful and important. Just to give two additional examples, behavioral characters may be used to reconstruct phylogenetic relationships among species, the way anatomical traits or genetic markers are used (e.g. Lusseau, 2003). Furthermore, studying behavior, and behavioral development in particular, can elucidate the role of phenotypic plasticity in evolution and how interactions between organisms and their environment can give rise to evolutionary change at the genetic level (e.g. Gottlieb, 1992). Therefore comparative behavioral research can shed light not only on broad trends in behavioral and cognitive evolution or the evolution of specific behaviors; it can also contribute to understanding the phylogenetic relationships among species and the mechanisms by which evolution by natural selection generates adaptation.

The contributions of comparative behavioral research to our understanding of human behavior and development are not limited to those deriving from the animal model approach. The three other approaches described by Gottlieb and Lickliter can

also be very relevant to humans. For example, phylogenetic analyses of human behavioral or cognitive traits that are also shared by other animals can shed light on the evolutionary history of these traits. Many aspects of human behavior and cognition and their developmental trajectories were likely inherited from our primate or mammalian ancestors. Gottlieb and Lickliter, however, 'do not think that homologies can be readily documented with even our most closely related relatives' behavior and psychological functioning' (p. 311). Their pessimism is not justified. Phylogenetic analyses of behavior are one of fastest growing and most successful areas of comparative research; they have been used in a wide range of animal species including nonhuman primates (e.g. Autumn, Ryan & Wake, 2002; Cleaveland, Jager, Rossner & Delius, 2003; Di Fiore & Rendall, 1994; Hale, Long, McHenry & Westneat, 2002; Martins, 1996; Preuschoft & van Hooff, 1995; Stratton, Suter & Miller, 2003; Thierry, Iwaniuk & Pellis, 2000) and nothing prevents them from being extended to humans as well. For example, homologies between some human facial expressions of emotion and those of Old World monkeys and apes can be readily identified (Darwin, 1872; Preuschoft & van Hooff, 1995; van Hooff, 1972). Similarly, the infant attachment system is clearly not a new product of the human brain or the modern human environment but has a history that can be tracked in the evolution of the primate order (Bowlby, 1969; Maestripieri, 2003a; Mason & Mendoza, 1998).

Phylogenetic analyses of behavior are typically pursued by evolutionary biologists and biological anthropologists whereas the animal model approach is what psychologists are most familiar with. Even psychologists who investigate human psychological and behavioral adaptations from a comparative and evolutionary perspective do not fully appreciate the importance of phylogenetic analyses (Andrews, Gangestad & Matthews, 2002; Tooby & Cosmides, 1989; see Roney & Maestripieri, 2002 for a critique). Understanding human behavior in its complexity and entirety, however, is an enterprise that can be successfully accomplished only with interdisciplinary research. Therefore, it is important that psychologists be aware of the benefits and limitations of the animal model approach but also of the potential contributions that other disciplines and approaches can make to their research.

Phylogenetic considerations are also important for the choice of animal models of human behavior and development. Discounting the role of phylogeny implies that whether an animal species is phylogenetically close or distant to humans is relatively unimportant in determining its potential value as an animal model of human behavior. In reality, animals that are phylogenetically closer to humans are more likely to share with humans not only homologies but also analogies in their behavioral and psychological functioning. This is because there are many constraints on the type of adaptations to the environment that organisms can evolve through natural selection. Therefore, similarities in genetic, anatomical, physiological, and cognitive constraints increase the probability that organisms will evolve similar adaptations to the environment. Thus, human behavior is generally more likely to be not only homologous but also analogous to the behavior of other primates than to the behavior of nonprimate species (Maestripieri, 2003b). For example, maternal behavior in humans and other primates probably depends on experience acquired during development to a greater extent than in other mammals with shorter life spans such as rats. Therefore, early interest in infants is likely to be a developmental adaptation that human females share with other female primates, but not necessarily with female rats (Maestripieri & Pelka, 2002).

Do Animal Models Provide Inaccurate or Simplistic Representations of Human Psychological, Behavioral, and Social Processes or Their Development?

Gottlieb and Lickliter argue that 'the certainty that animal models are faithfully mimicking their presumed human counterparts in the arena of psychological, social, and behavioral function is always open to even greater question' (p. 312). One may argue, however, that comparative research since Darwin has highlighted a growing number of similarities in psychological, social, and behavioral function between humans and other animals (e.g. Richards, 1987) and that, given the current success of disciplines such as biopsychology or evolutionary psychology, this trend is likely to continue. As Gottlieb and Lickliter recognize, animal models are not expected to reproduce identical aspects of human behavior or even to 'faithfully mimic' them. Animals can provide models, not duplicates or surrogates of human behavior. Humans are unique, just like any other animal species, and extrapolating hypotheses and data from one species to another requires a great deal of caution. The same degree of caution, however, is also required to extrapolate hypotheses and data from any subject population to another one, and more generally to interpret and generalize any behavioral data, whether animal or human. Caution in the interpretation and generalization of research findings is one of the things that distinguishes good science from bad science. Unless there is more bad science in comparative behavioral research than in other behavioral disciplines, there is no good reason to think that the former requires special scrutiny or caution.

Gottlieb and Lickliter maintain that 'animal models may not do justice to human development when they emphasize (or seem to implicate) single development pathways to psychological or behavioral outcomes' (p. 312). This is because human development, as well as animal development, involves equifinality (more than one developmental pathway to a given outcome) and multifinality (early experiences do not necessarily always result in the same outcome). Although the occurrence and importance of equifinality and multifinality in human development cannot be denied, there is no reason why simpler and more linear processes with highly predictable outcomes should be viewed as rare or unimportant. For example, many aspects of early social and cognitive development including the development of attachment to a caregiver and language development follow predictable trajectories, and specific early experiences within these trajectories have predictable outcomes. In fact, one may argue that the concepts of equifinality and multifinality are more applicable to psychopathological development (Cicchetti, 1993) than to normative psychological and behavioral development, in part because the clinical syndromes that show multiple developmental pathways such as child maltreatment or schizophrenia are still ill-defined and may represent heterogeneous categories including many distinct typologies, each with its own developmental trajectory. Therefore, animal and human development probably involve both simple and complex processes and there is no a priori reason to believe that animal models do not do justice to human development when they emphasize single developmental pathways to psychological or behavioral outcomes. The validity and usefulness of animal models of particular behavioral or psychological processes in humans must be assessed on a case-to-case basis and not on the basis of general criteria of simplicity or complexity (e.g. Maestripieri & Carroll, 1998; Maestripieri & Wallen, 2003).

Do Animal Models Provide Useful Data?

Gottlieb and Lickliter maintain that the main contribution of research with animal models of human development is to provide hypotheses and not data, or to discover general principles but not facts. This position is not new and has previously been advanced with regard to research with animal models of human behavior in general (e.g. Hinde, 1982). Clearly, not everyone shares this view. Animal models of human emotions and cognition, or the development of emotions and cognition, are widely used in psychopharmacological research, where the main goal is to obtain data on the behavioral effects of drugs (e.g. dose–response curves) and their mechanisms of actions, and not to develop new hypotheses or theories. If the animal data could not be directly extrapolated to humans, there would be very little use for animal models in psychopharmacology. Much research in behavioral endocrinology and behavioral neuroscience also rests on the assumption that many specific interactions between the endocrine system and behavior, or between brain and behavior, are very similar in humans and some other animals (e.g. Porges, 2003). For example, the endocrine regulation of pregnancy and lactation is very similar in humans and in other mammals. Early findings from studies of rats showing that a high estrogen-to-progesterone ratio in late pregnancy is associated with increased maternal responsiveness (e.g. Rosenblatt, Mayer & Giordano, 1988) have subsequently been replicated in nonhuman primates and in humans (Fleming, Ruble, Krieger & Wong, 1997; Maestripieri & Zehr, 1998). In these cases, the animal data have clear cross-species validity and applicability. Many examples may also be provided in the field of human development, e.g. with regard to early affective and cognitive development, developmental sex differences in behavior and cognition, or behavioral changes associated with puberty and adolescence. John Bowlby (1969) did not use information from nonhuman primate research only to develop the hypothesis there they might be an attachment system in humans or some general principles about its functioning. He showed that there were 'formal similarities' in the infant response to separation, the development of fear of strangers, and the use of the mother as a secure base in monkeys and in humans. Based on these and other similarities, he argued that the development, regulation, and adaptive function of the attachment system are very similar in humans and some other primates, and that this similarity is probably due to common descent. Thus, Bowlby provided a clear example of how data from nonhuman animals, and not just hypotheses or general principles, could be directly extrapolated to humans and how one can develop a theory of behavior that has a strong phylogenetic foundation and cross-species validity.

References

Andrews, P. W., Gangestad, S. W. & Matthews, D. (2002). How to carry out an exaptationist program. *Behavioral and Brain Sciences*, *25*, 489–553.

Autumn, K., Ryan, M. J. & Wake, D. B. (2002). Integrating historical and mechanistic biology enhances the study of adaptation. *Quarterly Review of Biology*, *77*, 383–408.

Bowlby, J. (1969). *Attachment and Loss. Vol. I: Attachment*. New York: Basic Books.

Cicchetti, D. (1993). Developmental psychopathology: Reactions, reflections, projections. *Developmental Review*, *13*, 471–502.

Cleaveland, J. M., Jager, R., Rossner, P. & Delius, J. D. (2003). Ontogeny has a phylogeny: Background to adjunctive behaviors in pigeons and budgerigars. *Behavioural Processes*, *61*, 143–158.

Darwin, C. (1872). *The expression of the emotions in man and animals*. London: Murray.

Di Fiore, A. & Rendall, D. (1994). Evolution of social organization: A reappraisal for primates

by using phylogenetic methods. *Proceedings of the National Academy of Science USA*, *91*, 9941–9945.
Fleming, A. S., Ruble, D., Krieger, H. & Wong, P. Y. (1997). Hormonal and experiential correlates of maternal responsiveness during pregnancy and the puerperium in human mothers. *Hormones and Behavior*, *31*, 145–158.
Gottlieb, G. (1992). *Individual development and evolution*. Oxford: Oxford University Press.
Gottlieb, G. & Lickliter, R. (2004). The various roles of animal models in understanding human development. *Social Development*, *13*, 311–325.
Hale, M. E., Long, J. H., McHenry, M. J. & Westneat, M. W. (2002). Evolution of behavior and neural control of the fast-start escape response. *Evolution*, *56*, 993–1007.
Hinde, R. A. (1982). The uses and limitations of studies of nonhuman primates for the understanding of human social development. In L. W. Hoffman, R. Gandelman & H. R. Schiffman (Eds.), *Parenting: Its causes and consequences* (pp. 5–17). Hillsdale, NJ: Erlbaum.
Lusseau, D. (2003). The emergence of cetaceans: Phylogenetic analysis of male social behaviour supports the Cetartiodactyla clade. *Journal of Evolutionary Biology*, *16*, 531–535.
Maestripieri, D. (2003a). Attachment. In D. Maestripieri (Ed.), *Primate Psychology* (pp. 108–143). Cambridge, MA: Harvard University Press.
Maestripieri, D. (2003b). The past, present, and future of primate psychology. In D. Maestripieri (Ed.), *Primate Psychology* (pp. 1–16). Cambridge, MA: Harvard University Press.
Maestripieri, D. & Carroll, K. A. (1998). Child abuse and neglect: Usefulness of the animal data. *Psychological Bulletin*, *123*, 211–223.
Maestripieri, D. & Pelka, S. (2002). Sex differences in interest in infants across the lifespan: A biological adaptation for parenting? *Human Nature*, *13*, 327–344.
Maestripieri, D. & Wallen, K. (2003). Nonhuman primate models of developmental psychopathology: Problems and prospects. In D. Cicchetti & E. Walker (Eds.), *Neurodevelopmental mechanisms in psychopathology* (pp. 187–214). Cambridge: Cambridge University Press.
Maestripieri, D. & Zehr, J. L. (1998). Maternal responsiveness increases during pregnancy and after estrogen treatment in macaques. *Hormones and Behavior*, *34*, 223–230.
Martins, E. P. (1996). *Phylogenies and the comparative method in animal behavior*. New York: Oxford University Press.
Mason, W. A. & Mendoza, S. P. (1998). Generic aspects of primate attachments: Parents, offspring, and mates. *Psychoneuroendocrinology*, *23*, 765–778.
Porges, S. W. (2003). Social engagement and attachment: A phylogenetic perspective. *Annals of the New York Academy of Sciences*, *1008*, 31–47.
Preuschoft, S. & van Hooff, J. A. R. A. M. (1995). Homologizing primate facial displays: A critical review of methods. *Folia Primatologica*, *65*, 121–137.
Richards, R. J. (1987). *Darwin and the emergence of evolutionary theories of mind and behavior*. Chicago, IL: University of Chicago Press.
Roney, J. R. & Maestripieri, D. (2002). The importance of comparative and phylogenetic analyses in the study of adaptation. *Behavioral and Brain Sciences*, *25*, 525.
Rosenblatt, J. S., Mayer, A. D. & Giordano, A. L. (1988). Hormonal basis during pregnancy for the onset of maternal behavior in the rat. *Psychoneuroendocrinology*, *13*, 29–46.
Stratton, G. E., Suter, R. B. & Miller, P. R. (2003). Evolution of water surface locomotion by spiders: A comparative approach. *Biological Journal of the Linnean Society*, *81*, 63–78.
Thierry, B., Iwaniuk, A. N. & Pellis, S. M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: *Cercopithecidae*, genus *Macaca*). *Ethology*, *106*, 713–728.
Tooby, J. & Cosmides, L. (1989). Adaptation versus phylogeny: The role of animal psychology in the study of human behavior. *International Journal of Comparative Psychology*, *2*, 175–188.
van Hooff, J. A. R. A. M. (1972). A comparative approach to the phylogeny of laughter and smile. In R. A. Hinde (Ed.), *Nonverbal communication* (pp. 209–241). Cambridge: Cambridge University Press.

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