

This is a section of [doi:10.7551/mitpress/1885.001.0001](https://doi.org/10.7551/mitpress/1885.001.0001)

The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

Edited by: Marc Bekoff, Colin Allen, Gordon M. Burghardt

Citation:

The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition

Edited by: Marc Bekoff, Colin Allen, Gordon M. Burghardt

DOI: 10.7551/mitpress/1885.001.0001

ISBN (electronic): 9780262268028

Publisher: The MIT Press

Published: 2002



The MIT Press

55 Eye Gaze Information-Processing Theory: A Case Study in Primate Cognitive Neuroethology

Brian L. Keeley

Cognitive Neuroethology

The eyes of others represent an important social cue for humans and other animals, a cue that is often used to support inferences about the mental states of those whose eyes we observe. Is she *paying attention* to what I'm saying? Does he *know* that I was just smiling at his predicament? Does this person *find me attractive*? One important clue for answering such questions can be found in paying attention to where eye gaze has been directed. In essence, we use eyes to read the minds of others.

This is not a new or startling observation; as the sixteenth-century proverb goes, "The eyes are the window of the soul." This commonplace observation generates a number of interesting questions in a variety of different areas of inquiry. *Philosophy*: What do we really learn from observing eyes? Can we ever be certain that our mental attributions are correct? *Neurobiology*: What brain mechanisms are at play when we perceive eyes and draw inferences about them? *Ethology*: What are the relevant eye gaze behaviors and how do they relate to the life of the organism? For example, what is the relationship between eye gaze behavior and social hierarchy? Or, how is it used to facilitate turn taking during conversation? *Evolutionary and comparative biology*: How did this capacity evolve? How do human skills with eyes relate to those of other animals? Do canids or nonhuman apes, say, draw inferences from eye gaze similar to those that we do? Finally, all of these questions are related to the concerns of *cognitive ethology*: How do animals use the eye gaze behavior of other organisms to reason about their unseen mental attitudes? For lack of a better term or acronym, I refer to our scientific understanding of the capacity to process information about mental states from the eye gaze behavior of other organisms as eye

gaze information-processing theory (EGIPT, for short).

Eye gaze phenomena come in a variety of forms (Argyle and Cook 1976). We *follow gaze* when we look at the eyes of another and then gaze in the direction they are looking, usually to see what they are looking at. *Mutual gaze* occurs when two individuals look each other in the eye; that is, they make "eye contact." There also seems to be an important difference between looking *at* another's eyes and looking *into* those eyes. (Consider the difference between a lover gazing into your eyes and your ophthalmologist doing the same thing.) *Gaze avoidance* is the behavior of avoiding eye contact with another. Some cultures single out certain eye gaze phenomena as socially significant, such as the phenomenon of the "evil eye." Finally, not all eye gaze reading requires making inferences about the mental states of others. It is possible to follow the gaze of another without also thinking about the other in mental terms; so we often need to be careful to rule out simpler, nonmental mechanisms when comparing the eye gaze perception of other animals with our own. Just because they seem to be doing the same thing that we are does not mean that they are in fact doing so.

My particular theoretical orientation is best described as cognitive neuroethology. I see cognitive neuroethology as the natural synthesis of the recent flowering of interest in the mental lives of animals represented by cognitive ethology with the traditional concerns of neuroethology. Neuroethology is the branch of biology that attempts to elucidate the evolutionary and neurobiological basis of naturally occurring animal behavior (Ewert 1980; Camhi 1984). In other words, neuroethologists first attempt to identify natural behaviors and perceptual capacities in organisms and then investigate (1) how the nervous systems

of those animals mediate those behaviors and capacities and (2) how both the behavior and the brain mechanisms have evolved. (“Natural” in this context is meant to distinguish those behaviors that animals *in fact* perform in their native environments from those an organism can be induced to perform under artificial, laboratory conditions.)

Just as neuroethology was a natural outgrowth and addition to the science of ethology, cognitive neuroethology seems to me to be a natural outgrowth and addition to cognitive ethology. Also, just as neuroethology is not intended as a more fundamental replacement of ethology, neither should cognitive neuroethology be construed as eliminating the need for cognitive ethology. However, if successful, one would expect that discoveries concerning the neural basis of behavior should affect how cognitive ethologists characterize and understand the mental capacities of animals. Certainly, an influence in the opposite direction is also to be expected.

For the past several years I have been arguing that there is scientific and philosophical profit in taking a more neuroethological approach to the questions of cognitive science. I began by noting that a then-novel theoretical orientation in neuroethology—computational neuroethology—was successfully addressing questions about the evolution and neural basis of animal behavior within a framework mirroring that of cognitive science (Keeley 1997). From the perspective of philosophy of science, the structure is not identical. The primary difference is that neuroethology, by its nature, is much more concerned with evolution and comparative biology than traditional cognitive science has ever been. I argued that computational neuroethology’s success suggests that cognitive science can be more comparative, and furthermore, that it should be (Keeley 2000a). [However, mentioning this in this volume is likely to be preaching to the choir; one of the features that separates cognitive ethology from cognitive science is the

former discipline’s explicit embracing of the comparative method (e.g., Allen and Bekoff 1997; see also Keeley 1999b).] Central to the aforementioned “profit” of taking a more neuroethological approach to the issues of cognitive science is that it offers novel ways of dealing with long-standing philosophical conundrums in the philosophy of cognitive science, including those related to the indeterminacy of content and function (Keeley 1999a) and the alleged theoretical autonomy of psychology owing to the multiple realization of psychological states (Keeley 2000b).

One potential drawback to all the work just described is that it is based on the computational neuroethology of weakly electric fish. However, I argue that we can use the success of neuroethology in understanding the behavior of electric fish—exemplified in the work of the late Walter Heiligenberg (1991a,b)—as a philosophical model for a slightly reconfigured but potentially more successful cognitive science. But because fish are not the most cognitively interesting of creatures, this argument is at best one of principle. Even if correct, I am still left with the question of what this all would mean in practice; what exactly would a cognitive neuroethology of human intelligent behavior look like anyway? The goal of the work described here is to begin to put some flesh on the bones of my largely philosophically motivated proposal.

The State of Play in EGIPT

If any phenomenon were a currently strong contender for yielding to a cognitive neuroethological perspective, EGIPT would seem to be it. During the past decade, significant progress has been made in the relevant areas of study, although on the whole these investigations have been carried out in relative isolation from one another. However, as work in each of these areas continues to mature, it should be fruitful to combine their insights in order to come to a

deeper and more general understanding of how human and nonhuman animals use eye gaze cues to read one another's minds. I am not alone in this assessment. In a recent, important review, N. J. Emery (2000) has brought together much of the research I describe here (although not the computational research; see the later discussion) in an attempt to sketch a series of interesting hypotheses about EGIPT. In the following sections I describe recent work in a number of areas brought together under the rubric of EGIPT: work on the developmental disorder of autism, the comparative biology and neurobiology of social cognition, and computational and robotic models of eye gaze-related phenomena.

Autism and Mindblindness

Autism is a pervasive developmental disorder of unknown etiology. In addition to some straightforward cognitive deficits affecting general intelligence, language skills, and attentional control, autistic subjects exhibit consistent and often severe problems with socialization. Compared with mental age-matched individuals, such as those with Down syndrome, autistic subjects have been shown to have difficulties reasoning about the mental states of others (Baron-Cohen et al. 1993). This difficulty in dealing with a theory of mind has led some theorists to propose that the core feature of autism is "mindblindness" (Baron-Cohen 1995; Frith and Happé 1999).

Autistic individuals also typically have an unusual relationship to eyes. Originally, gaze avoidance was considered a diagnostic feature of the disorder, although it is now thought that autistic individuals do not so much *avoid* gaze as restrict their sampling to quick glances at the eyes of others (O'Connor and Hermelin 1967; Volkmar and Mayes 1990). Some theorists, for example, Baron-Cohen (1995), interpret current data as showing that eye gaze detection in autism is unimpaired, meaning that the deficit is likely isolated in a putative theory of mind module,

which is receiving accurate information about eye gaze.

One intriguing possibility is that eye gaze stimuli adversely stimulate the autonomic nervous system in autism, perhaps inhibiting the normal development of a theory of mind. If so, any deficit in autism is likely to be much more low level and pervasive than a cortical theory of mind module. With this possibility in mind, I have been collaborating with William Hirstein and V. S. Ramachandran to encourage their exploration of this subject (Hirstein et al. in press).

The jury is still out with respect to the "autism as mindblindness" hypothesis. Nonetheless, it seems safe to say that there is something unusual about the autistic subject's perceptual relationship to eyes. This is an interesting observation in light of the current project for a historical reason. One of the final research projects of Niko Tinbergen—who shared a 1973 Nobel Prize for his role in creating the field of ethology—was the ethological study of autism (Tinbergen and Tinbergen 1983). In these studies, characterizing the behavior of autistic children in natural contexts was central, and chief among these behaviors were a variety of avoidance behaviors, including, not surprisingly, those related to gaze. The current project can be seen as a return to Tinbergen's final project, a promising subject that has been neglected since his passing.

The Comparative Perspective

The study of EGIPT in primates has been an explosive area of research in the past decade. It has long been known that the eyes of primate species vary; the color contrast between the sclera and pupil of the human eye is greater than that found in bonobos and chimpanzees, which in turn is greater than that found in other apes and monkeys. For this and other reasons, it seems reasonable to hypothesize that our eyes have evolved to be more easily read at a distance. What is more, the capacity to read gaze

information seems to have evolved with the most recent common ancestor of apes and monkeys. While most primates can follow the gaze of others (Tomasello et al. 1998), lemurs—prosimians (i.e., the next closest relatives of primates)—cannot (Anderson and Mitchell 1999). At what point in evolution primates began inferring the mental states of others from their eyes is currently under debate. Some argue that this is a uniquely human adaptation and that even chimpanzees lack this skill (Povinelli and Eddy 1996). However, traditionally, apes have been thought to make such inferences, although the new debate has brought about a new series of more careful studies of exactly what apes do and do not understand about the mental significance of gaze (Hare et al. 2000, 2001).

EGIPT may be of central importance to the social cognition of primates, but it is clearly not restricted to them. For prey species, the visual cue of two black or colored circles in a horizontal orientation may be indicative of predation in the near future. Therefore it should not be surprising that a wide range of species, from fish to birds to mouse lemurs, have developed aversive responses to such stimuli (see Emery 2000 for a review). Animals as diverse as plovers (Ristau 1991) and black iguanas (Burger et al. 1992) have been shown to respond differently to approaching human experimenters who are looking directly at them and those who approach while looking in other directions. Even hognose snakes, which feign death when harassed by predators, use eye gaze cues when deciding whether to continue feigning death or whether it is safe to beat a retreat (Burghardt 1991; Burghardt and Greene 1988).

As a final example, Agnetta et al. (2000) report the interesting finding that while domesticated dogs are capable of using human gaze as a cue to perform tasks, such as finding hidden food, they do not spontaneously follow human gaze. This suggests potentially interesting questions about the EGIPT mechanisms of dogs

(and, by extension, other animals). Prior to this work, it might have been natural to think that an ability to draw inferences from gaze cues was built on top of a prior existing gaze-following mechanism. However, the situation may be more complicated than previously surmised. So suffice it to say, EGIPT offers the opportunity to compare the social cognition of humans with non-human primates and other animals that have evolved related capacities.

Neurobiology

What neural structures underlie the processing of information about gaze? Research on that workhorse of visual neurophysiology, the macaque monkey, has found cells that are selectively responsive to the face in several visual subareas of the temporal cortex. These include the lateral and ventral surfaces of the inferior temporal cortex and the upper bank, lower bank, and fundus of the superior temporal sulcus. Perrett and colleagues have found cells in the upper bank of the superior temporal sulcus that are selective for the orientation of facial stimuli. One obvious functional interpretation of this is that these cells help detect where faces are looking (Perrett et al. 1991, 1992; see also Hasselmo et al. 1989).

In humans, functional magnetic resonance imaging (fMRI) studies have identified the extrastriate cortex as a center of activity in the processing of facial images (Kanwisher et al. 1996a,b). Using both intracranial electrodes and fMRI, Puce and colleagues have discovered that “Faces primarily activated the fusiform gyrus bilaterally, and also activated the right occipitotemporal and inferior occipital sulci and a region of lateral cortex centered in the middle temporal gyrus” (Puce et al. 1996, p. 5205; see also Allison et al. 1994).

Of the areas that are implicated in the processing of faces, which are responsible for our being able to extract gaze information from a face? Both the amygdala and extrastriate cortex

are suggested in separate studies. A study of D.R., a 51-year-old woman with a partial bilateral amygdalotomy, reported that she is impaired in verbally reporting gaze information (Young et al. 1996). (Since the amygdala is part of the limbic system, which in turn is intimately connected to the autonomic nervous system, findings such as these represent a potential bridge to current work on autism.) It has also been reported that results of evoked-response potential studies of the extrastriate cortex suggest the possible presence of an “eye detector” module (Allison et al. 1996; Bentin et al. 1996). So while we are far from a complete understanding of the neural basis of EGIPT, we have a firm and growing foundation of knowledge from which to test hypotheses generated from our understanding of autism and comparative studies.

Computational Work

In its early years, the field of artificial intelligence (AI) pointedly avoided building systems that were too close to the physical or biological nature of humans and other animals. All of this has changed in recent decades, as neural nets—based on a rough analogy to neurobiological systems—saw a resurgence of interest beginning in the 1980s. As we approached the millennium, a movement in AI started with the goal of exploring the possibility of “humanoid robots”; that is, robots with a roughly human form. This in turn has raised issues of EGIPT because these robots need to behave as humans do and understand human eye gaze behavior so that their human interlocutors can better understand the humanoid robots, and vice versa.

The vanguard of this new work is coming out of the Artificial Intelligence Laboratory at the Massachusetts Institute of Technology, particularly the work of Rod Brooks on “Cog” (Brooks et al. 1999) and Cynthia Breazeal on “Kismet” (Breazeal and Scassellati 1999, in press; Breazeal et al. 2000). While Cog is an attempt to build a

general and sophisticated humanoid robot, Kismet is focused more on eye gaze behavior and communication via facial expressions. Breazeal and colleagues describe Kismet as

[A]n active vision head augmented with expressive facial features. Kismet is designed to receive and send human-like social cues to a caregiver, who can regulate its environment and shape its experiences as a parent would for a child. Kismet has three degrees of freedom to control gaze direction, three degrees of freedom to control its neck, and fifteen degrees of freedom in other expressive components of the face (such as ears and eyelids). To perceive its caregiver Kismet uses a microphone, worn by the caregiver, and four color CCD cameras. The positions of the neck and eyes are important both for expressive postures and for directing the cameras towards behaviorally relevant stimuli. (Breazeal et al. 2000, p. 2)

Kismet and other humanoid robots (see, for example, Mousset et al. 2000) are important testbeds of theories of eye gaze behavior and perception. The computational and robotic models of AI allow us to put into physical reality our theories of how biological and psychological phenomena seem to work and behave. This then allows us to test these theories and to discover more general theoretical principles of EGIPT that apply across species.

Conclusion

This project of synthesizing the recent work on EGIPT from a variety of scientific perspectives is still in its early stages, and in the short space allowed here, I can only begin to sketch the wealth of new discoveries that continue to appear. Since it is still “early days yet” for cognitive neuroethology and EGIPT, let me conclude by pointing to a number of questions that call for interdisciplinary interaction between the scientific areas I have discussed here:

What is the role of the autonomic nervous system in the eye gaze and facial perception of

nonhuman animals? How does the emotional significance of eyes for humans compare with that of other animals who do (or do not) attend to eye gaze?

What differences in neural processing are there in humans between mere gaze following versus drawing mental inferences from gaze? If it is true that some animals follow gaze without attributing mental states to others, this raises the possibility that human mind reading is independent of gaze perception by itself. Is this indeed the case?

How do the deficits of autistic subjects compare with the natural capacities of nonhuman primates? If it is indeed the case that autism is mindblindness, what exactly is the relationship between EGIPT capacities in autistics and those of nonhuman animals that are similarly “mind blind”?

What general principles of EGIPT can be discovered in robotic and other computational models, and what does this tell us about the cognitive neuroethology of EGIPT in primates and other animals? Are there general principles that apply across phylogeny?

Finally, since my primary academic training is in philosophy, my hope is that in the end this work will shed light on that hoary chestnut of philosophical skepticism: the problem of other minds. If we can be said to mind read using the eyes of others, what are the epistemic limits of this process? How certain can we be of our mental attributions to others; to what illusions are we susceptible and under what conditions? There are many unanswered questions here, but there is also much promise of progress to be made and understanding to be had.

Acknowledgments

The work described here is supported by a grant to the author from the *McDonnell Project in Philosophy and the Neurosciences*. I thank my colleagues in that project for useful feedback, including Kathleen Akins, Tony Atkinson, Tori

McGeer, Evan Thompson, and Pete Mandik. Thanks also to Bill Hirstein and to Eric Courchesne (and the members of his Laboratory for Research on the Neuroscience of Autism, San Diego) for help in the earliest stages of this project.

References

- Agnetta, B., Hare, B., and Tomasello, M. (2000). Cues to food location that domestic dogs (*Canis familiaris*) of different ages do and do not use. *Animal Cognition* 3: 107–112.
- Allen, C. and Bekoff, M. (1997). *Species of Mind: The Philosophy and Biology of Cognitive Ethology*. Cambridge, Mass.: MIT Press.
- Allison, T., Ginter, H., McCarthy, G., Nobre, A. C., Puce, A., Luby, M., and Spencer, D. D. (1994). Face recognition in human extrastriate cortex. *Journal of Neurophysiology* 71: 821–825.
- Allison, T., Lieberman, D., and McCarthy, G. (1996). Here's not looking at you kid: An electrophysiological study of a region of human extrastriate cortex sensitive to head and eye aversion. *Society for Neuroscience Abstracts* 22: 400.
- Anderson, J. R. and Mitchell, R. W. (1999). Macaques but not lemurs co-orient visually with humans. *Folia Primatology* 70: 17–22.
- Argyle, M. and Cook, M. (1976). *Gaze and Mutual Gaze*. Cambridge: Cambridge University Press.
- Baron-Cohen, S. (1995). *Mindblindness: An essay on Autism and Theory of Mind*. Cambridge, Mass.: MIT Press.
- Baron-Cohen, S., Tager-Flusberg, H., and Cohen, D. J. (eds.) (1993). *Understanding Other Minds: Perspectives from Autism*. Oxford: Oxford University Press.
- Bentin, S., Allison, T., Puce, A., Perez, E., and McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience* 8: 551–565.
- Breazeal, C. and Scassellati, B. (1999), “How to build robots that make friends and influence people.” In *Proceedings of IEEE International Conference on Intelligent Robots and Systems (IROS99): Human and Environment Friendly Robots with High Intelligence*

- Quotients*, Oct 17–Oct 21, 1999, Kyongju, South Korea, IEEE, Piscataway, NJ, USA, pp. 858–863.
- Breazeal, C. and Scassellati, B. (2000). Infant-like social interactions between a robot and a human caretaker. *Adaptive Behavior* 8: 49–74.
- Breazeal, C., Edsinger, A., Fitzpatrick, P., and Scassellati, B. (2000). Social constraints on animate vision. In *IEEE Intelligent Systems and Their Applications*, v. 15. n. 4, Jul 2000, Piscataway, NJ, USA pp. 32–37.
- Brooks, R. A., Breazeal, C., Marjanovic, M., Scassellati, B., and Williamson, M. W. (1999). The Cog project: Building a humanoid robot. In *Computation for Metaphors, Analogy and Agents*. Vol. 1562, *Springer Lecture Notes in Artificial Intelligence*, C. L. Nehaniv, ed., pp. 52–87. New York: Springer-Verlag.
- Burger, J., Gochfield, M., and Murray, B. G. (1992). Risk discrimination of eye contact and directness of approach in black iguanas (*Ctenosaura similis*). *Journal of Comparative Psychology* 106: 97–101.
- Burghardt, G. M. (1991). Cognitive ethology and critical anthropomorphism: A snake with two heads and hog-nose snakes that play dead. In *Cognitive Ethology: the Minds of Other Animals*. C. A. Ristau, eds., pp. 55–90. Hillsdale, N.J.: Lawrence Erlbaum Associates.
- Burghardt, G. M. and Greene, H. W. (1988). Predator simulation and duration of death feigning in neonate hog-nose snakes. *Animal Behaviour* 36: 1842–1844.
- Camhi, J. M. (1984). *Neuroethology: Nerve Cells and the Natural Behavior of Animals*. Sunderland, Mass.: Sinauer Associates.
- Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews* 24: 581–604.
- Ewert, J.-P. (1980). *Neuroethology: An Introduction to the Neurophysiological Fundamentals of Behavior*. New York: Springer-Verlag.
- Frith, U. and Happé, F. (1999). Theory of mind and self-consciousness: What is it like to be autistic? *Mind and Language* 14: 1–22.
- Hare, B., Call, J., Agnetta, B., and Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour* 59: 771–785.
- Hare, B., Call, J., and Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour* 61: 139–151.
- Hasselmo, M. E., Rolls, E. T., Baylis, G. C., and Nalwa, V. (1989). Object-centered encoding by face-selective neurons in the cortex in the superior temporal sulcus of the monkey. *Experimental Brain Research* 75: 417–429.
- Heiligenberg, W. (1991a). *Neural Nets in Electric Fish*. Cambridge, Mass.: MIT Press.
- Heiligenberg, W. (1991b). The jamming avoidance response of the electric fish, *Eigenmannia*: Computational rules and neuronal implementation. *Seminars in the Neurosciences* 3: 3–18.
- Hirstein, W., Iversen, P., and Ramachandran, V. S. (in press). Autonomic responses of autistic children to people and objects. *Proceedings of the Royal Society of London, Series B*, vol. 268.
- Kanwisher, N., Chun, M. M., and McDermott, J. (1996a). FMRI in individual subjects reveals loci in extrastriate cortex differentially sensitive to faces and objects. *Investigative Ophthalmology and Visual Science* 37: S193.
- Kanwisher, N., Chun, M. M., McDermott, J., and Hamilton, R. (1996b). FMRI reveals distinct extrastriate loci sensitive for faces and objects. *Society for Neuroscience Abstracts*, 22: 1937.
- Keeley, B. L. (1997). Cognitive Science as the Computational Neuroethology of Intelligent Behavior: Why Biological Facts Are Important for Explaining Cognition. Unpublished Ph.D. thesis, University of California, San Diego.
- Keeley, B. L. (1999b). Review of C. Allen and M. Bekoff, *Species of Mind*. *Philosophical Psychology* 12: 543–546.
- Keeley, B. L. (2000a). Neuroethology and the philosophy of cognitive science. *Philosophy of Science* 67 (proceedings): S404–S417.
- Keeley, B. L. (2000b). Shocking lessons from electric fish: The theory and practice of multiple realization. *Philosophy of Science* 67: 444–465.
- Mousset, E., Jabri, M., Carlile, S., and Sejnowski, T. (2000). Gaze-shifting in humans and humanoids. *Humanoids 2000*.
- O'Connor, N. and Hermelin, B. (1967). The selective visual attention of autistic children. *Journal of Child Psychology and Psychiatry* 8: 167–179.
- Perrett, D. I., Oram, M. W., Harries, M. H., Bevan, R., Hietanen, J. K., Benson, P. J., and Thomas, S. (1991). Viewer-centred and object-centred coding of heads in the macaque temporal cortex. *Experimental Brain Research* 86: 159–173.

- Perrett, D. I., Hietanen, J. K., Oram, M. W., and Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society of London. B: Biological Sciences* 335: 23–30.
- Povinelli, D. J. and Eddy, T. J. (1996). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development* 61: 1–152.
- Puce, A., Allison, T., Asgari, M., Gore, J. C., and McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional magnetic resonance imaging study. *Journal of Neuroscience* 16: 5205–5215.
- Ristau, C. A. (1991). Before mindreading: Attention, purposes and deception in birds? In *Natural Theories of Mind*, A. Whiten, ed., pp. 209–222. Oxford: Blackwell.
- Tinbergen, Niko and Tinbergen, Elisabeth A. (1983). *“Autistic” Children: New Hope for a Cure*. London: George Allen and Unwin.
- Tomasello, M., Call, J., and Hare B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour* 55: 1063–1069.
- Volkmar, F. R. and Mayes, L. C. (1990). Gaze behavior in autism. *Development and Psychopathology* 2: 61–69.
- Young, A. W., Hellawell, D. J., Van De Wal, C., and Johnson, M. (1996). Facial expression processing after amygdalotomy. *Neuropsychologia* 34: 31–39.

©2002 Massachusetts Institute of Technology

All rights reserved. No part of this book may be reproduced in any form by any electronic or mechanical means (including photocopying, recording, or information storage and retrieval) without permission in writing from the publisher.

This book was set in Times New Roman on 3B2 by Asco Typesetters, Hong Kong. Printed and bound in the United States of America.

Library of Congress Cataloging-in-Publication Data

The cognitive animal: empirical and theoretical perspectives on animal cognition /
edited by Marc Bekoff, Colin Allen, and Gordon M. Burghardt.

p. cm.

“A Bradford book.”

Includes bibliographical references.

ISBN 0-262-02514-0 (hc. : alk. paper)—ISBN 0-262-52322-1 (pbk. : alk. paper)

I. Cognition in animals. I. Bekoff, Marc. II. Allen, Colin. III. Burghardt, Gordon M.,
1941—

QL785 .C485 2002

591.5'13—dc21

2001057965