

8. Jilkine, A., and Edelstein-Keshet, L. (2011). A comparison of mathematical models for polarization of single eukaryotic cells in response to guided cues. *PLoS Comput. Biol.* *7*, e1001121.
9. Narang, A. (2006). Spontaneous polarization in eukaryotic gradient sensing: A mathematical model based on mutual inhibition of frontness and backness pathways. *J. Theor. Biol.* *240*, 538–553.
10. Onsum, M., and Rao, C.V. (2007). A mathematical model for neutrophil gradient sensing and polarization. *PLoS Comput. Biol.* *3*, e36.
11. Verkhovskiy, A.B., Svitkina, T.M., and Borisy, G.G. (1999). Self-polarization and directional motility of cytoplasm. *Curr. Biol.* *9*, 11–20.
12. Kozlov, M.M., and Mogilner, A. (2007). Model of polarization and bistability of cell fragments. *Biophys. J.* *93*, 3811–3819.
13. Sheetz, M.P., and Dai, J. (1996). Modulation of membrane dynamics and cell motility by membrane tension. *Trends Cell Biol.* *6*, 85–89.
14. Ofer, N., Mogilner, A., and Keren, K. (2011). Actin disassembly clock determines shape and speed of lamellipodial fragments. *Proc. Natl. Acad. Sci. USA* *108*, 20394–20399.
15. Batchelder, E.L., Hollopeter, G., Campillo, C., Mezanges, X., Jorgensen, E.M., Nassoy, P., Sens, P., and Plastino, J. (2011). Membrane tension regulates motility by controlling lamellipodium organization. *Proc. Natl. Acad. Sci. USA* *108*, 11429–11434.
16. Gauthier, N.C., Fardin, M.A., Roca-Cusachs, P., and Sheetz, M.P. (2011). Temporary increase in plasma membrane tension coordinates the activation of exocytosis and contraction during cell spreading. *Proc. Natl. Acad. Sci. USA* *108*, 14467–14472.
17. Keren, K. (2011). Cell motility: the integrating role of the plasma membrane. *Eur. Biophys. J.* *40*, 1013–1027.
18. Bodin, S., and Welch, M. (2005). Plasma membrane organization is essential for balancing competing pseudopod- and uropod-promoting signals. *Mol. Biol. Cell* *16*, 5773–5783.
19. Niggli, V. (2003). Microtubule-disruption-induced and chemotactic-peptide-induced migration of human neutrophils: implications for differential sets of signalling pathways. *J. Cell Sci.* *116*, 813–822.

¹Department of Neurobiology, Physiology and Behavior and Department of Mathematics, University of California, Davis, CA 95616, USA.

*E-mail: mogilner@math.ucdavis.edu

DOI: 10.1016/j.cub.2011.12.013

Animal Cognition: Chimpanzee Alarm Calls Depend On What Others Know

After a wild chimpanzee encounters a model of a dangerous snake, whether or not he gives an alarm call depends on his perception of another individual's knowledge.

Robert M. Seyfarth
and Dorothy L. Cheney

Birds and mammals do not always give alarm calls when they see a predator. Instead, alarm call production is affected by the presence and composition of an audience. Animals are more likely to give alarm calls when they are near other conspecifics than when they are alone, and more likely to give alarm calls in the presence of kin and preferred companions than in the presence of non-kin or rivals. To date, however, there has been no evidence that calling also depends on the signaler's perception of whether recipients are ignorant or already informed about the presence of danger. Indeed, whether any animal is even capable of making this distinction — whether any animal has a 'theory of mind' — has been the subject of considerable debate. In this issue of *Current Biology*, Catherine Crockford, Roman Wittig, and colleagues [1] describe the results of a field experiment suggesting that chimpanzees recognize when others are ignorant about the presence of danger and adjust their alarm calls accordingly.

Many field experiments have shown that, when producing vocalizations,

non-human primates take into account subtle contingencies, including the context, the recipient's identity, the identity of others nearby, and the nature of their own recent interactions with their recipient and the recipient's kin [2–5]. Despite this broad sensitivity, monkeys and apes generally seem inattentive to the one feature that underlies much human communication: the perception of another individual's knowledge and beliefs [6]. The issue, however, is fraught with methodological complications [7].

Searching for a theory of mind in animals is difficult because intentions and beliefs are usually correlated with behavior, making it hard to determine whether one animal is attending to another's behavior or her mental state. Research on children, moreover, has shown that having a theory of mind is not an all-or-nothing phenomenon: before the age of two, children recognize that others have likes, dislikes, and motives, but the same children cannot distinguish between what they believe and what others believe. Like young children, animals may have a partially developed theory of mind. Several studies, for example, have shown that animals are sensitive to other individuals' direction of gaze

and behavioral intentions. However, there is little convincing evidence that any animals — including in particular chimpanzees — can attribute knowledge states to others.

Experiments that attempt to address this question in primates [8–10] are difficult to evaluate because of the artificial settings in which they are conducted, the involvement of humans, and repeated testing of the same individuals.

In the wild, chimpanzees form temporary parties that fluctuate in size and composition throughout the day [11,12]. This 'fission-fusion' society would seem to provide an ideal setting for the evolution of a theory of mind. Some individuals can acquire knowledge that others do not have and 'decide' whether to share it or not; others, meanwhile, must determine who knows what.

As they followed a lone chimpanzee in the Budongo Forest of Uganda, Crockford and colleagues [1] guessed where it was about to go and placed in its path a stuffed model of either a Gaboon viper or a rhinoceros viper, two highly poisonous snakes. They then waited until — with luck — the subject discovered the snake and then recorded its vocal behavior as — with more luck — other chimpanzees (termed 'receivers') approached the area.

Subjects were classified as having no prior knowledge about the snake or having some prior knowledge, either because they had already seen the snake or they had been within 50 m when an earlier discoverer had produced an 'alert hoo' in response

to the snake. Receivers' knowledge states were classified from the perspective of the subject as: ignorant (the subject did not see the receiver see the snake and did not hear a *hoo* when the receiver was within 50 m); partially knowledgeable (the subject did not see the receiver see the snake but heard a *hoo* when the receiver was within 50 m); or fully knowledgeable (the subject saw the receiver see the snake). This classification will make some readers uneasy, as it claims insight into the subject's mind. In justification, the authors point out that in the vast majority of cases both the subject and the receiver had some knowledge of the snake through shared experience. Under these conditions, it is perhaps not unreasonable for the authors to assume that subjects had some first-hand knowledge of receivers' prior interactions and hence receivers' knowledge.

As it turned out, the subject's and the receiver's information about the snake were positively correlated, though by no means always alike. Consequently, these two potential predictors of the subject's behavior could not be tested in the same statistical model. Crockford and colleagues [1] therefore tested them in separate models, with two measures of *hoo* production as responses. Both models yielded significant results, suggesting that one or more predictors could account for subjects' behavior. Further analysis was therefore conducted to disentangle the effects of subject and receiver information.

The authors focused on a subset of cases in which receivers either already had precise information about the snake's location (because they had seen it) or had only partial information (because they had heard a *hoo* but not yet seen the snake). To control for the subject's possible habituation to the stimulus, they included as a potential predictor the duration of time since the subject had seen the snake. The results showed that the primary factor affecting the subject's calling behavior was whether the receiver was fully or only partially knowledgeable about the snake's location, and not the subject's own risk or habituation to the stimulus. Subjects called more if the receiver had not seen the snake and least if the receiver had. In a final, intriguing twist, subjects were also more likely to call if they shared a close social bond with the receiver. Although this observation

supports previous findings that strong, enduring social bonds play a major role in the lives of chimpanzees [13], it also complicates matters, because it suggests that a chimpanzee who recognizes another's ignorance may nonetheless not choose to warn that individual. Failure to inform cannot, therefore, be taken as proof of a lack of a theory of mind.

This important paper [1] reminds us that, while experiments with captive animals can be criticized for their artificiality, field experiments have their liabilities, too. They are time-consuming (the study took 20 months to complete) and beset by ambiguity, relying on complicated statistics for their *denouement*. There is simply no way around this problem. The attribution of knowledge to another, if it exists at all in animals, has evolved in the context of a rich network of social interactions where many different behaviors and memories of past events are correlated with each other. Psychologists who study theory of mind in children can easily create situations that both preserve the richness of their subjects' social lives and isolate crucial experimental variables. For those who study animals in the wild the task is much more difficult.

References

1. Crockford, C., Wittig, R., Mundry, R., and Zuberbuhler, K. (2012). Wild chimpanzees

inform ignorant group members of danger. *Curr. Biol.* 22, 142–146.

2. Engh, A.L., Hoffmeier, R.R., Cheney, D.L., and Seyfarth, R.M. (2006). Who, me? Can baboons infer the target of vocalizations? *Anim. Behav.* 71, 381–387.
3. Wittig, R.M., Crockford, C., Seyfarth, R.M., and Cheney, D.L. (2007). Vocal alliances in chacma baboons, *Papio hamadryas ursinus*. *Behav. Ecol. and Sociobiol.* 61, 899–909.
4. Wittig, R.M., Crockford, C., Wikberg, E., Seyfarth, R.M., and Cheney, D.L. (2007). Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proc. Roy Soc. Lond. B* 274, 1109–1115.
5. Slocombe, K., and Zuberbuhler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proc. Nat. Acad. Sci. USA* 104, 17228–17233.
6. Rendall, D., Cheney, D.L., and Seyfarth, R.M. (2000). Proximate factors mediating "contact" calls in adult female baboons and their infants. *J. Comp. Psychol.* 114, 36–46.
7. Cheney, D.L., and Seyfarth, R.M. (2007). *Baboon Metaphysics* (Chicago: University of Chicago Press), chapter 8.
8. Hare, B., Call, J., and Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Anim. Behav.* 61, 139–151.
9. Kaminski, J., Call, J., and Tomasello, M. (2008). Chimpanzees know what others know, but not what they believe. *Cognition* 109, 224–234.
10. Flombaum, J.I., and Santos, L.R. (2005). Rhesus monkeys attribute perceptions to others. *Curr. Biol.* 15, 447–452.
11. Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior* (Cambridge, MA: Harvard University Press).
12. Boesch, C. (2009). *The Real Chimpanzee: Sex Strategies in the Forest* (London: Cambridge University Press).
13. Mitani, J.C. (2009). Male chimpanzees form enduring and equitable social bonds. *Anim. Behav.* 77, 633–640.

Departments of Psychology and Biology,
University of Pennsylvania, Philadelphia,
PA 19104, USA.

E-mail: Seyfarth@psych.upenn.edu

DOI: 10.1016/j.cub.2011.11.050

Motor Proteins: Kinesin Can Replace Myosin

Directional transport of specific cargos is tuned to specific molecular motors and specific cytoskeletal tracks. Myosin V transports its cargo on actin cables, whereas kinesin or dynein transport their cargo on microtubules. A recent study shows that an engineered kinesin can substitute for myosin V and its cargo-specific transport and subsequent cellular functions.

Kathleen Scheffler¹
and Phong T. Tran^{1,2,*}

Cell polarity and shape are defined by the cytoskeleton, which can serve as tracks for intracellular trafficking of organelles, vesicles and molecules. Distinct roles for the microtubule and actin cytoskeletons in the

establishment and maintenance of polarized growth have been described in diverse cell types [1,2]. Budding yeast relies on an actin-based delivery of secretory vesicles to the forming bud, whereas filamentous fungi appear to use microtubules as the major transport system to direct polarized cell growth [3]. Mammalian cells, such