Science

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The Perception of Rational, Goal-Directed Action in Nonhuman Primates

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Science **317**, 1402 (2007);
DOI: 10.1126/science.1144663

genome size, including *F. verticillioides*, *F. oxysporum*, and *F. solani*, have many more, ranging from 9 to >17. All closely related species in the *F. graminearum* species complex, as well as *F. culmorum*, also have four chromosomes, which indicates that if chromosome fusion occurred, it was not a recent event.

The regions of highest SNP density were significantly correlated with the regions of highest recombination (0.55, $P = 1.2 \times 10^{-13}$), similar to correlations of SNP distribution or nucleotide diversity with recombination frequency observed in humans and *Drosophila* (*13*, *14*). Additionally, regions of high SNP density have significantly lower G+C content than the rest of the genome (-0.43, $P = 1.1 \times 10^{-8}$). The low G+C content of internal regions further supports the idea that these regions may represent ancestral telomeres.

To determine whether high diversity SNP regions evolved recently, we examined the sequence divergence of genes in these regions. We compared *F. graminearum* coding regions to those resulting from a low coverage (4X) assembly of *F. verticillioides* (*7*). Comparing the best matches for *F. graminearum* proteins from high and low SNP density regions (top and bottom quartiles) to the *F. verticillioides* assembly revealed that proteins from the highest SNP density regions have fewer putative orthologs compared with the rest of the genome and that these orthologs share lower identity (*7*). Although variation in the local mutation rate is expected to produce a correlation between polymorphism and divergence, more polymorphisms were found in high SNP regions than predicted on the basis of divergence (table S13), and the ratio of synonymous to nonsynonymous polymorphisms is higher than that of less diverse regions (χ^2 value = 3.7 $\times 10^{-7}$) (table S14).

Blast analysis (*7*) identified 704 genes as specific to *F. graminearum*, and these show significant enrichment in the high-density SNP regions ($P = 4.5 \times 10^{-15}$). We also compared *F. graminearum* with the closely related *F. asiaticum*, *F. boothii*, *F. culmorum*, and *F. pseudograminearum* using genomic DNA hybridizations to a *F. graminearum* microarray (*15*) and identified 382 genes that are *F. graminearum* specific. These genes were overrepresented (by a factor of 2.7) in the high-density SNP regions ($P = 3.4 \times 10^{-34}$). These data further demonstrate that genomic regions exhibiting the highest intraspecific variability also exhibit the highest interspecific variability.

F. graminearum genes specifically expressed during plant infection—including predicted secreted proteins, major facilitator transporters, amino acid transporters, and cytochrome P450s—are all overrepresented in high SNP density regions (Fig. 2, table S14, and SOM text). Conversely, genes predicted to be highly conserved, such as nuclear encoded mitochondrial genes or genes involved in translation, are underrepresented in regions of high diversity (table S15 and SOM text).

Comparison of gene expression of *F. graminearum* infection on barley and under varied nutritional culture conditions (*7*, *15*) identified 408 genes as exclusively expressed during barley infection. These genes are highly enriched in the high-SNP-density regions ($P = 7.4 \times 10^{-15}$), and 31% are predicted to be secreted, representing enrichment by a factor of 3 over the genome as a whole (table S14 and SOM text). Four of these genes have similarity to known virulence factors, and another 32 genes are predicted plant cell-wall degrading enzymes (table S16). Among these enzymes are xylanases, which degrade xylan, the major hemicellulose portion of monocot cell walls, pectate lyases, which cleave pectin, another essential component of plant cell walls and cutinases, enzymes that hydrolyze cutin polyesters that coat all outer plant surfaces. Such enzymes may function in the penetration and maceration of plant tissues and for the acquisition of nutrients from plant polymers (*16*) and may be involved as effector molecules that trigger host-plant defense responses (*17*). The high genetic diversity of this group of genes suggests that the fungus has a great capacity for adaptability and genetic change during its interaction with even this single host species.

The completed genome of *F. graminearum* allowed us to identify distinct regions of high diversity. We found that these regions are enriched for infection-related genes, which may allow the fungus to adapt rapidly to changing environments or hosts. Recognition of these high-diversity areas of the genome focuses the direction of future work toward those regions that may have the greatest potential in elucidating the dynamics of host pathogen interactions.

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18. We thank the Genome Sequencing Platform at the Broad Institute; A. Rokas, M. Borowsky, and G. Fink for critical reading of the manuscript; D. Neafsey, M.-J. Daboussi, and P. Tiffin for helpful discussions; S. Gale, H. Khalili, L. Gaffney, and D. Park for technical assistance; and Syngenta for sharing their 0.5X sequence from *F. graminearum* and their 4X sequence from *F. verticillioides*. Supported by the National Research Initiative of the USDA Cooperative State Research, Education, and Extension Service. F.G.D.B. was supported by the Austrian genome program GEN-AU, the Impuls- und Vernetzungsfonds der Helmholtz-Gemeinschaft, and a grant from the German Federal Ministry of Education and Research. Sequences have been deposited in GenBank: *F. graminearum* assembly AACM00000000, Broad *F. graminearum* annotation (XM_380177-XM_391816), *F. verticillioides* assembly AAIM01000000, SNP sequences (ss# 73405725 to 73416217), and hygromycin Loss/gain clones DV998659 to DV998664.

The Perception of Rational, Goal-Directed Action in Nonhuman Primates

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Humans are capable of making inferences about other individuals' intentions and goals by evaluating their actions in relation to the constraints imposed by the environment. This capacity enables humans to go beyond the surface appearance of behavior to draw inferences about an individual's mental states. Presently unclear is whether this capacity is uniquely human or is shared with other animals. We show that cotton-top tamarins, rhesus macaques, and chimpanzees all make spontaneous inferences about a human experimenter's goal by attending to the environmental constraints that guide rational action. These findings rule out simple associative accounts of action perception and show that our capacity to infer rational, goal-directed action likely arose at least as far back as the New World monkeys, some 40 million years ago.

A central characteristic of human action perception is the capacity to read beneath the surface appearance of behavior. When someone acts, we make inferences about their goals and intentions by referencing each action against a backdrop of environmental constraints. In humans, this capacity appears around the first year of life. For instance, Gergely

and colleagues (*1*) showed that when 14-month-old infants watched an experimenter use her head to illuminate a box, infants imitated this precise action only if the experimenter's hands were free to move and could have been used to illuminate the box; if the experimenter's hands were occupied, and could not be used, then the infants used their hands. Infants most likely inferred that since the experimenter could have used her hands, but used her head instead, the head must confer some advantage for illuminating the box. These results, and others (*2, 3*), suggest that human infants assess whether an agent's actions are rational by evaluating how the intervening environmental circumstances constrain the achievement of a target goal; as such, they infer properties of mental life that are not transparent from the surface appearance of behavior. Presently unclear, however, is whether this capacity is the product of human evolution or uniquely human pedagogy, or rather is shared with other animals.

Behavioral and neurophysiological studies show that nonhuman primates attend to subtle details of the surface properties of actions, including differences in the gestures used to achieve a goal (*4–6*). Further, there is suggestive evidence that animals go beyond the mere consequences of actions, distinguishing intentional from accidental consequences (*6–7*). For example, captive chimpanzees show more heightened signs of frustration when an experimenter appears to tease intentionally by offering and then taking away food as opposed to offering and then clumsily dropping food—two events with the same consequences, that is, the failure to obtain food (*6*). In addition, cotton-top tamarins are more likely to cooperate with a partner who gives food altruistically than with a partner who gives food as an accidental by-product of otherwise selfish behavior (*7*). Moreover, Hare and Tomasello (*5*) found that chimpanzees can use information about an agent's apparent intentions to find hidden food; in other contexts, however, chimpanzees have considerable difficulty understanding intentional cues by humans (*8–11*). Thus, these results leave three questions unanswered: (i) To what extent can animals spontaneously use information about an agent's apparent intentions to make inferences about their goals? (ii) Are their inferences based solely on the surface appearance of behavior, as opposed to information about whether actions are rational with regard to current environmental constraints? (iii) What is the phylogenetic distribution of these capacities, especially among our closest living relatives, the monkeys and apes?

To begin addressing these questions, we adopted a broad comparative perspective, conducting experiments on three nonhuman primate species (cotton-top tamarins, rhesus macaques, and chimpanzees), representing the three major groups (New World monkeys, Old World monkeys, and apes). We tested all three species in largely the same way, but due to housing conditions and sample sizes, there were some differences (*12*).

In experiment 1, we asked whether members of these species perceive actions as intentional and accidental, and critically, use this information when making inferences about the apparent goal of a human agent. We used a forced-choice method designed to measure subjects' spontaneous foraging behavior in response to actions performed by a human experimenter. During each trial, an experimenter presented subjects with two potential food containers, performed an action on one, and then allowed the subject to select one of the containers. In the intentional condition, the experimenter reached directly for

and grasped the container. In the accidental condition, the experimenter flopped his hand onto the container with palm facing upwards in a manner that appeared, from a human perspective, accidental and non–goal-directed (*13*). If nonhuman primates fail to distinguish between intentional and accidental actions when making inferences about others' goals, attending to the mere association of the hand and container, then they should show the same pattern of searching in both conditions—that is, approach the experimenter-contacted container. However, if they distinguish between intentional and accidental actions, then they should selectively inspect the container targeted by the experimenter's intentional action but not that targeted by accidental action.

Based on the statistical methodology used in our other studies of rhesus behavior, we elected to use one-tailed tests in this work, too. All three species inspected the intentionally targeted container a greater proportion of time than the accidentally targeted container: tamarins [$F(1,9) =$
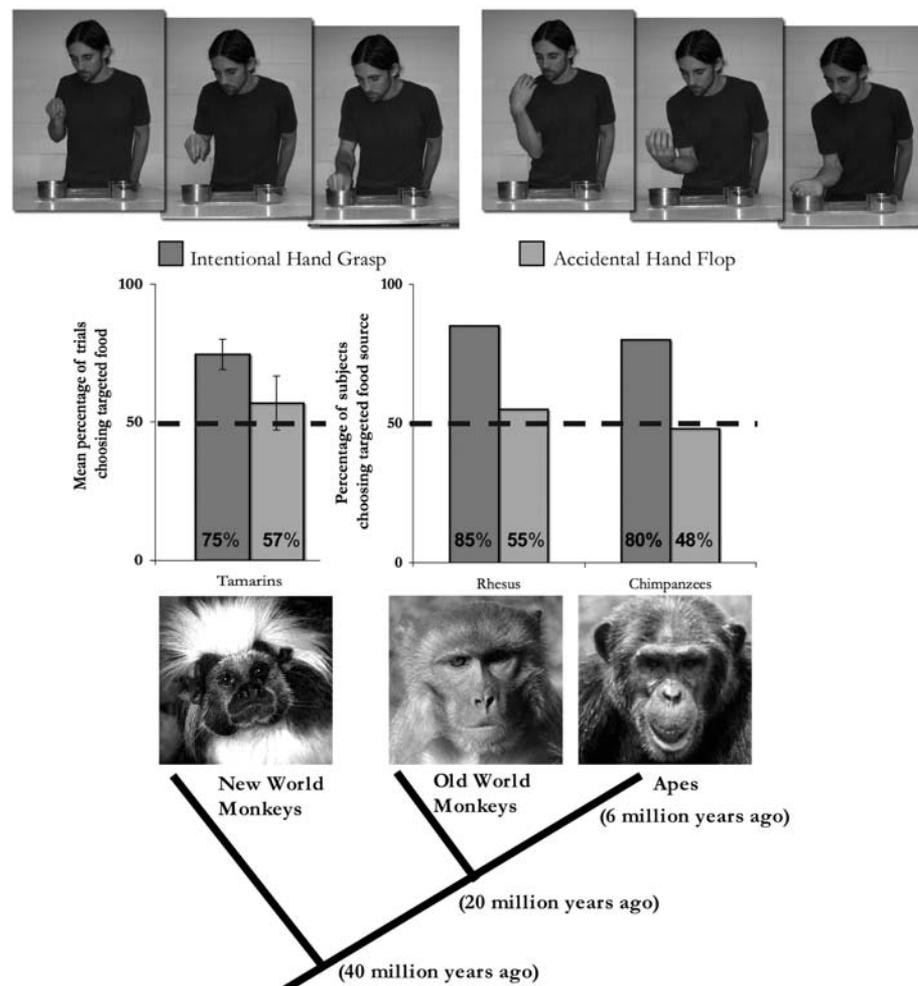

Fig. 1. Performance for choosing the container targeted by the intentional (dark gray) versus accidental (light gray) actions by tamarins, rhesus, and chimpanzees. The tamarin data illustrate the mean percentage of trials (±SEM). See fig. S1 for the mean percentage of trials as measured by both looking and grasping behaviors. The rhesus and chimpanzee data illustrate the percentage of subjects choosing the container targeted by each action type. The dashed line indicates chance performance.

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3.57, $P = 0.05$]; rhesus [$\chi^2(1, N = 40) = 4.29$, $P = 0.02$]; chimpanzees (Wilcoxon signed ranks test: $z = -2.02$, $P = 0.02$). All species selectively inspected the targeted container after observing the intentional action (Fig. 1): tamarins [$t(9) = 4.45$, $P = 0.001$]; rhesus (17 out of 20 subjects; binomial probability: $P = 0.001$); chimpanzees (20 out of 25 subjects; binomial probability: $P = 0.002$). In contrast, none of the species selectively inspected the targeted container after the accidental action: tamarins [$t(9) = 0.70$, $P = 0.25$]; rhesus (11 out of 20 subjects; binomial probability: $P = 0.41$); chimpanzees (12 out of 25 subjects; binomial probability: $P = 0.50$). Thus, tamarins, rhesus monkeys, and chimpanzees spontaneously distinguish between intentional and accidental actions and use this information to make inferences about others' goals. These results provide further support for studies of chimpanzees (*5, 6*) and extend the pattern to tamarins and rhesus. In addition, they suggest that these three species go beyond the mere association of contact or the attention drawn to one container to correctly infer the agent's target goal.

How do these species distinguish between intentional and accidental actions: Do they do so solely on the basis of the surface appearance of behavior, or, like humans, do they interpret actions in relation to the broader environment in which they occur? That is, did the subjects tested in experiment 1 judge the hand grasp as goal-directed and the hand flop as accidental because grasping and flopping actions are automatically interpreted as intentional and accidental, respectively? Alternatively, did they evaluate the hand flop as accidental because, in this particular situation, the experimenter could have used the more rational grasping action?

In experiment 2, we asked whether these three species integrate information about the surface properties of an action with the environmental constraints facing the agent in order to make inferences about rational, goal-directed action. We presented subjects with an experimenter performing very similar actions under two contrasting environmental circumstances. In the first condition, the experimenter touched one of the containers with his elbow while the associated hand was occupied ("hand-occupied"); in the second contrasting condition, the experimenter performed the same elbow touch action while the associated hand was free ("hand-empty"). One-half of both the chimpanzee and rhesus subjects observed the experimenter perform the hand-occupied elbow touch while holding an object in his acting hand only; the other hand was placed behind his back. The other half of the subjects observed the experimenter perform the action while holding an object in both hands. If nonhuman primates evaluate actions merely on the basis of surface appearance (e.g., the association between the elbow and the container), then they should show the same pattern of searching in both the hand-occupied and hand-empty conditions because the surface

properties of the actions are very similar, including, especially, the structure of the final point of contact. However, if these species take into account the environmental constraints facing the experimenter, then only the hand-occupied condition should be perceived as a rational, goal-directed action; given that the experimenter's acting hand was occupied at the moment of gesturing, his elbow provides an alternative means to both indicate and contact the target goal. Accordingly, the hand-empty condition would not be perceived as a rational, goal-directed action because at the time, the experimenter could have used his unoccupied acting hand to grasp and indicate the target container (as in the intentional condition of experiment 1), leaving the subject uncertain as to the target goal. Therefore, subjects should not infer that the experimenter's goal was to contact the box with the potentially concealed food.

We note that our target species do not naturally use their elbows to indicate or draw attention to objects or events in their environment, and nor have they been trained to either use their elbows in an indicative manner, or respond to this action. This condition therefore also explores their capacity to use an indicative, but unfamiliar gesture, to make inferences about goal-directed action under specific environmental constraints.

All species inspected the targeted container a greater proportion of the time after observing the hand-occupied versus the hand-empty action: tamarins [$F(1,24) = 2.60$, $P = 0.06$]; rhesus [$\chi^2(1, N = 64) = 10.47$, $P < 0.001$]; chimpanzees (Wilcoxon signed ranks test: $z = -1.87$, $P = 0.03$). All species selectively inspected the targeted

container in the hand-occupied condition (Fig. 2): tamarins [$t(9) = 4.31$, $P = 0.001$]; rhesus (28 out of 32 subjects; binomial probability: $P < 0.001$); chimpanzees (19 out of 25 subjects; binomial probability: $P = 0.007$). In contrast, none of the species selectively inspected the targeted container in the hand-empty condition: tamarins [$t(14) = 0.29$, $P = 0.39$]; rhesus (16 out of 32 subjects; binomial probability: $P = 0.57$); chimpanzees (11 out of 25 subjects; binomial probability: $P = 0.35$). Thus, subjects used the elbow action as a cue to find hidden food only when the experimenter's acting hand was occupied, and thus unavailable for gesture and action. One possibility is that in the hand-empty condition, subjects attended primarily to the experimenter's hand in expectation of rational, goal-directed action; when this did not occur, the elbow cue could have gone unnoticed or been dismissed as irrational and accidental. In contrast, when the experimenter's hands were occupied, subjects may have been particularly attentive to other body parts because they became viable alternatives for rational, goal-directed action. These results [along with other evidence recently presented (*14, 15*)] suggest that all these primate species—and possibly other animals as well—go beyond the surface appearance of behavior as well as their own experiences acting on or indicating objects when making inferences about others' goals. Like humans, they evaluate others' actions with respect to environmental constraints imposed on the agent.

It is interesting that these species perceived the hand-occupied elbow touch as goal-directed given that it is impossible to pick up an object with one's elbow. The most likely explanation for
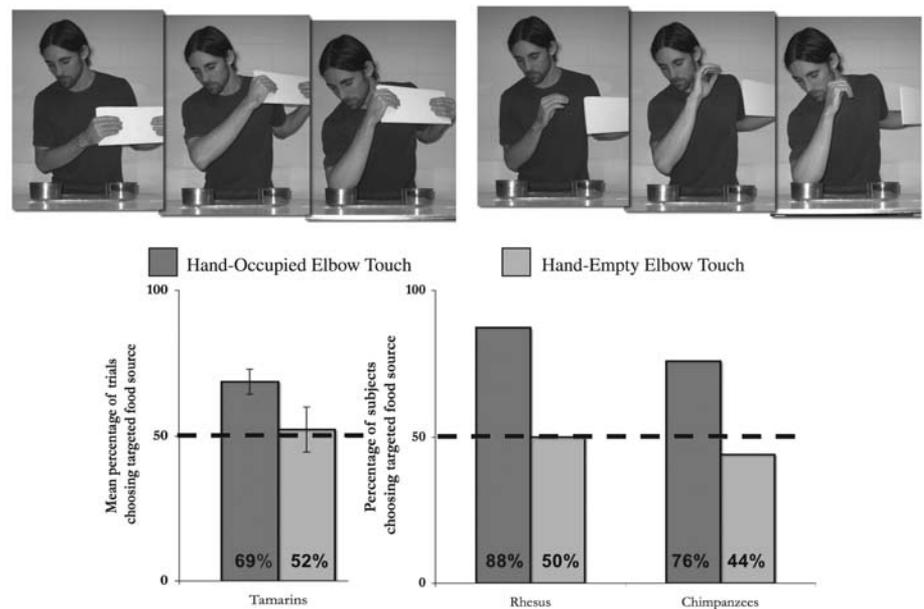

Fig. 2. Performance for choosing the container targeted by the hand-occupied (dark gray) versus hand-empty (light gray) elbow actions by tamarins, rhesus, and chimpanzees. The tamarin data illustrate the mean percentage of trials (±SEM). See fig. S1 for the mean percentage of trials as measured by both looking and grasping behaviors. The rhesus and chimpanzee data illustrate the percentage of subjects choosing the container targeted by each action type. The dashed line indicates chance performance.

this pattern is that subjects inferred that the experimenter's goal was to contact or indicate the presence of food, rather than to grasp the food.

Given enough time and leisure, human adults are free to consider almost any action as irrational. For instance, the subjects in our study, and the human infants in previous studies (*1*), perceived uncharacteristic elbow and head actions as rational and goal-directed provided that the experimenter's hands were occupied; this response obtained even though the experimenter could have dropped the object and then performed the more efficient hand action. Similarly, our subjects showed the same pattern of searching regardless of whether the hand-occupied elbow touch was performed with both hands occupied or with one hand behind the back; the latter condition is of interest because the experimenter could have performed the grasping action with the hand that was behind his back. We suggest that at the initial stage of action analysis, rational actions are defined in terms of current and immediate constraints on the agent. Thus, at the moment the experimenter indicates the target object with his elbow while one hand is occupied and the other rests behind his back, the subject's initial interpretation is that both of the experimenter's hands are unavailable. This amendment to current theoretical models of action perception makes sense of both human (*1*) and nonhuman animal results.

The present results appear to contrast with previous studies indicating that chimpanzees have difficulty using human pointing, looking, or many other communicative gestures to find a hidden reward. In particular, in an object choice task, in which an experimenter conceals a piece of food in one of two or more hiding locations, several studies reveal that captive chimpanzees (*8–11*), as well as other primates (*16*, *17*), generally fail to use a human agent's pointing gesture and direction of eye gaze to correctly infer the location of hidden food. We cannot precisely pinpoint the exact nature of the differences between these studies and the present one. However, support for the chimpanzee results is aided by the converging evidence from tamarins and rhesus based on similar methods.

Our results support three primary conclusions that bear on the origins and nature of action perception, restricted to these three primate species, but potentially generalizable to other closely and distantly related species. First, the species tested are highly sensitive to the surface properties of observed actions. All three species selectively inspected a potential food source targeted by the experimenter's action after observing the hand grasp action, but not after observing the hand flop action. A low-level explanation in terms of attention via eye gaze, body position, or other social cues cannot explain these results given that in both experiments, contact with the target container and the experimenter's visual attention were held constant, but subjects' patterns of search differed.

Second, results show that tamarins, rhesus, and chimpanzees distinguish between goal-directed and accidental behavior based on the relation between actions and environmental constraints. This finding has notable implications for cognitive and neurobiological models of action understanding. Physiological studies of macaque mirror neurons in area F5 of the premotor cortex indicate that these cells activate both when the subject acts and when this same subject observes another acting in the same way (*4*). On the basis of these activation patterns, theorists have suggested that the mirror neuron system plays a critical role in action perception, where organisms interpret the actions of others by appealing to their own actions (*4*, *18*). Current neurobiological models of the mirror neuron system often state that action understanding consists of mapping the surface properties of observed actions onto the observer's motor system. Our results show, however, that action perception cannot be based solely on a mechanism that analyzes the surface properties of actions. In experiment 2, subjects distinguished between hand-occupied and hand-empty elbow touches, even though these actions have similar surface properties and are not within the repertoire of actions performed by these species. Thus, action perception must also consist of a mechanism that evaluates action means in relation to goals, and places this analysis into a broader context that entails constraints imposed by the current environmental situation. As a result, some system must supplement the mirror neuron circuitry to provide a fuller account of action perception in primates.

Third, the psychological mechanisms underlying the socio-cognitive abilities of animals have been widely debated, often acting as a proxy for larger debates between supporters of associative as opposed to more mentalistic accounts of animal learning and behavior. Associative models classically explain behavior as a result of direct reinforcement history—for example, the capacity to understand actions as goal-directed may be the product of learning, acquired by forming associations between observed actions and the objects that they target. Such models cannot explain the present findings without modification. In experiment 2, all three species perceived an elbow touch as goal-directed, despite presumably having little or no experience witnessing other agents manipulate objects with their elbow when their hands were occupied, and certainly no experience with other conspecifics indicating objects with their elbows; consequently, there was no opportunity to form an association between this action and object-directed outcomes. Thus, we suggest that nonhuman primates' ability to perceive actions as goal-directed extends beyond these associative mechanisms, drawing upon inferences about an agent's goals in the context of particular environmental constraints.

In sum, our results show that both closely and distantly related primate species distinguish between goal-directed and accidental actions when making inferences about another individual's apparent goals. Furthermore, they do so by evaluating the rationality of the action in relation to the constraints of the situation. The fact that these results hold across three different primate species, and that the methods entail spontaneous, nontrained responses, adds substantially to the robustness of our findings and their implications for thinking about the evolution of action perception. We conclude that our capacity to perceive rational, goal-directed actions is not uniquely human, having evolved at least as far back as the New World monkeys, some 40 million years ago.

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19. We are grateful to L. Pharoah, R. Atencia, K. Brown, and the Jane Goodall Institute USA and staff to Tchimpounga Sanctuary for their help and ethusiasm with our research. In particular, we appreciate the hard work of the animal caregivers: J. Maboto, B. Moumbaka, A. Sitou, M. Makaya, B. Bissafi, C. Ngoma, W. Bouity, J. Tchikaya, L. Bibimbou, A. Makosso, C. Boukindi, G. Nzaba, B. Ngoma. We also appreciate permission from the Congolese Ministere de la Recherche Scientifique et de l'Innovation Technique for allowing us to conduct our research in their country. This publication was made possible by grant CM-5-P40RR003640-13 from the National Center for Research Resources (NCRR), a component of NIH. Its contents are solely the responsibility of the authors and do not necessarily represent the official views of NCCR or NIH. Further support comes from an NIH National Research Service Award (NRSA) to J.N.W. (grant F31MH075298), a National Science Foundation: Human and Social Dynamics (NSF-HSD) grant, a Guggenheim Fellowship, and gift from J. Epstein to M.D.H. We thank M. Gerald for facilitating our work on Cayo Santiago, and F. Cushman, B. Hare, N. Kanwisher, J. Rubin, L. Santos, and R. Saxe for comments on the data and earlier drafts of this paper.