

Short report

Image scoring in great apes[☆]

Yvan I. Russell^{a,*}, Josep Call^b, Robin I.M. Dunbar^{a,2}

^a British Academy Centenary Research Project, School of Biological Sciences, University of Liverpool,
Crown Street, Liverpool L69 7ZB, UK

^b Department of Developmental and Comparative Psychology, Max-Planck-Institute for Evolutionary Anthropology,
Deutscher Platz 6, Leipzig D-04103, Germany

Received 31 August 2007; accepted 16 October 2007

Abstract

'Image scoring' occurs when person A monitors the giving behaviour of person B towards person C. We tested for 'image scoring' in chimpanzees, bonobos, gorillas, and orangutans. Subjects passively observed two types of incident: (i) a 'nice' person gave grapes to a human beggar, and (ii) a 'nasty' person refused to give. The subject witnessed both incidents in succession (but was unable to obtain the grapes). Shortly after, the ape had an opportunity to approach one or both human actors (nice/nasty), both of whom were now sitting side-by-side holding grapes. However, neither human offered their grapes if approached. The subject's expectation of which human was more likely to offer food was measured by comparing the proportion of time that subjects spent near each person. Chimpanzees ($n = 17$) spent significantly more time at the 'nice' window compared to 'nasty'. Also, preference for 'nasty' declined as trials progressed. Results for other apes were not significant.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Reputation; Image scoring; Chimpanzees; Orangutans; Bonobos; Gorillas

1. Introduction

'Reputation' refers to *knowledge about an individual's typical behaviour based on knowledge of that individual's past behaviour* (Russell, 2007). Animals learn about the typical behaviour of others in three ways (Smith and Harper, 2004): *direct* reputation (personal encounters), *indirect* reputation (observing events as uninvolved bystander), and *reported* reputation ('gossip'). Animals respond deftly to immediate signals of intention from other animals (Krebs and Dawkins, 1984), but reputation is relevant only if knowledge about a particular individual's past behaviour is remembered and influences current behaviour towards that individual. Reputation has been of interest to scientists investigating the evolu-

tion of cooperative behaviour (see Hammerstein, 2003; Fehr, 2004).

Nowak and Sigmund (1998) operationalised reputation as an 'image score': a numerical measure of how generous (or not) a person has been. Their agent-based computer simulations explored conditions where 'image scoring' donors (who preferentially reward those with sufficiently high image scores) would dominate a population. Subsequently, real-life human experiments showed that people spontaneously consider 'image score' when deciding whom to reward (Wedekind and Milinski, 2000). Possibly, such pro-social behaviour is not purely altruistic. It may be a by-product of the observer's desire to initiate interaction with someone known to be cooperative (Tullberg, 2004). Do animals use 'indirect reputation' as an information source? Our pilot study was designed to test for 'image scoring' in great apes.

2. Methods

2.1. Participants

Chimpanzees (*Pan troglodytes verus*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla gorilla*), and orangutans (*Pongo pygmaeus abelii*) were tested in 2004. They included 5 male, 12 female chimpanzees (age 3–29 years, mean 15.6), 3 male, 2

[☆] Research was carried out at the Wolfgang Köhler Primate Research Centre, Leipzig Zoo, Pfaffendorfer Straße 29, Leipzig D-04105, Germany (part of the Max-Planck-Institute for Evolutionary Anthropology in Leipzig).

* Corresponding author.

E-mail address: yvanrussell@gmail.com (Y.I. Russell).

¹ Present address: Department of Psychology, School of Social Sciences, Brunel University, Uxbridge, Middlesex UB8 3PH, UK.

² Present address: Institute of Cognitive & Evolutionary Anthropology, University of Oxford, 51 Banbury Road, Oxford OX2 6PE, UK.

female bonobos (age 7–22, mean 11.4), 1 male, 3 female gorillas (age 7–27, mean 20.8), and 1 male, 4 female orangutans (age 7–31, mean 18.6). All were housed at the Wolfgang Köhler Primate Research Centre (Leipzig Zoo, Germany).

Four human actors participated in every trial: a ‘beggar’ (begged for food), a ‘nice’ person (always gave food to beggar), and a ‘nasty’ person (always refused to give). Identities of human actors were alternated between (but not within) participants. Human actors were all female, except for the male beggar (Y.I.R.). The fourth person was the animal keeper, whose job was to move the apes into the appropriate places for the procedure. All actors (except keeper) were unfamiliar to subjects before the experiment.

2.2. Apparatus

Fig. 1 depicts the testing room. Apes and humans could see each other at all times. Dimensions varied slightly between species (mean area: apes 13.0 m², humans 7.9 m²). Apes used *compartment 1* (observing area) and *compartment 2* (testing area)—separated by a human-operated upward-sliding door. In *compartment 2*, there were two adjacent plexiglas windows (69 cm × 49 cm) where humans sat during the latter part of the trial. The two windows were conspicuously partitioned (separated by a steel beam). Along the bottom of each window were three unobstructed round holes (3.5 cm diameter; 7.0 cm for some gorillas) which normally functioned as feeding sites. For three chimpanzees and one gorilla, only a metal grid was available (spaces: 4.5 cm × 4.5 cm). Short plastic stools for humans were at positions A and B (Fig. 1).

Green grapes were the sole food source (separate grapes were used for humans but looked identical). Human grapes were separated from their branches and shown to apes inside the transparent plastic containers they were sold in (18 cm × 12 cm × 6 cm, lid removed). Everything was videotaped using one camera.

2.3. Procedure

Apes received no pre-training. Each was allowed to passively witness two types of food sharing incident that occurred between

human actors: a ‘nice’ incident and a ‘nasty’ incident (approx. 50 s long). In every trial, the subject witnessed both incidents in succession (presented in counterbalanced order between trials). Every subject was tested four times (but one gorilla managed only three; and one gorilla and one bonobo were tested extra times after failing to approach windows). The reason to test four times was to allow the subject time to realise a possible connection between the observed incident and the window choice.

Each trial began with the subject in *compartment 1* (isolated from conspecifics; all exit doors closed). The keeper fed the subject three grapes. Then, two human actors entered. In the ‘nice’ incident, the beggar and nice person (eater) kneeled down at a conspicuous location (see Fig. 1). The nice person was holding a transparent container of grapes and began eating them. Then, the beggar extended his hand in a silent begging gesture. The nice person deposited a grape into the beggar’s hand and the beggar ate it. This occurred three times per trial. The subject was unable to interfere or obtain grapes. In the ‘nasty’ incident, the procedure was identical except that the nasty person ignored the begging and continued eating. The beggar then attempted to reach into the nasty person’s container of grapes. In response, the nasty person slapped the beggar on the hand; the beggar uttered a pain vocalisation and withdrew his hand. This occurred three times per trial.

After witnessing both incidents, the ape was allowed into *compartment 2* where both human actors were now sitting side-by-side on stools in front of contiguous plexiglas windows (positions A and B). Each person was holding her transparent container of grapes above and near the open holes. Positions of ‘nice’ and ‘nasty’ persons (left/right) were counterbalanced between trials. If the subject approached any window (nice/nasty), neither person offered grapes. The subject’s expectation of which human was more likely to offer food was measured by calculating the percentage of seconds that subjects spent at each window. Accordingly, the experimenter activated his stopwatch when the ape approached either window. After 20 s had passed, the humans retreated and the trial was over. Percentage of time spent at each window was calculated as total time out of 20 s. Percentage ‘away from window’ was included in analysis.

When the ape entered *compartment 2*, the experimenter waited up to 5 min for the subject to approach. An ‘approach’ was operationally defined as the subject positioning its body (or part thereof, e.g. outstretched hand) within about 50 cm of the window. If no approach occurred, it was counted as zero for both windows. In most cases, it was easy to determine which ‘side’ the ape had chosen, but in 6% of trials, the choice was ambiguous (e.g. sitting directly in middle, sitting on one side but extending hand to other window, etc.). In such cases, it was counted as ‘approach to both’ (and hence total time might sum over 20 s). Scores for individual apes were derived from the mean of all of their trials. Scores were calculated separately for ‘nice’ and ‘nasty’ windows.

After the trial ended, the keeper fed the subject three grapes (away from where test occurred). All data were coded from videotape. Numbers of seconds at each window were counted

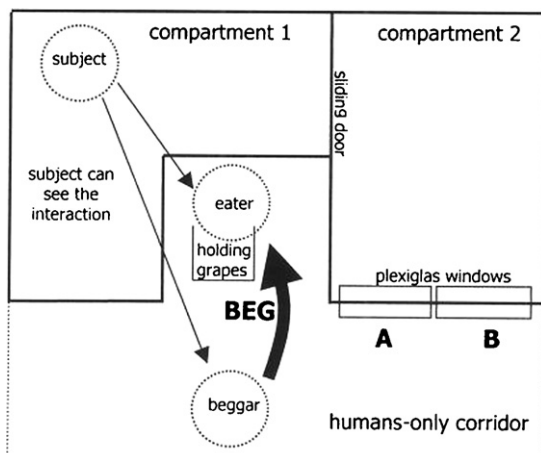


Fig. 1. Testing room and procedures.

Table 1
Average time (percentage of seconds) per species spent at ‘nice’ and ‘nasty’ windows, and mean attentiveness per species

Species	Chimpanzee* ($n = 17$)	Bonobo ($n = 5$)	Gorilla ($n = 4$)	Orangutan ($n = 5$)
Mean—‘Nice’ window (% of 20 s period)	28.48	41.5	28.02	45.75
Standard deviation	13.97	30.44	13.27	10.25
Mean—‘Nasty’ window (% of 20 s period)	20.46	27.75	27.36	45.25
Standard deviation	9.59	21.29	30.53	16.94
Mean ‘attentiveness’ (% of incident subjects were within 1 m of window)	46.06	NA	56.94	95.09

* Significant difference between ‘nice’ and ‘nasty’.

with a millisecond stopwatch two to three times and then rounded to the nearest second. A naïve volunteer re-coded 20% of trials. The inter-observer agreement score (Pearson) was 0.987.

3. Results

Throughout the procedure, subjects could see the food that humans displayed. Begging behaviour was routinely observed when the ape was near food. Table 1 displays results. Paired-samples t -tests were used to compare how subjects might differentially respond to ‘nice’ and ‘nasty’ windows. The difference was significant for chimpanzees, $t(16) = 3.092$, $p = 0.007$, but not for bonobos, $t(4) = 0.799$, $p = 0.469$, gorillas $t(3) = 0.089$, $p = 0.935$, or orangutans $t(4) = 0.294$, $p = 0.783$. Species results were not pooled together due to the unequal sample sizes (results heavily weighted by chimpanzee sample). No significant age/sex differences were found. Position preference (when subjects prefer one side habitually) was mitigated by window position counterbalancing. When we incorporated side preference into the analysis, it made no difference (see analysis in Russell, 2007).

Some chimpanzees were inattentive during the incidents, possibly hampering results. Therefore, we calculated ‘attentiveness’ for each individual: as mean percentage of time spent within 1 m of window(s) facing the nice/nasty incident. The eight most attentive chimpanzees paid attention during 54–80% of incident time (mean scores per subject over all trials). Our main result remained intact for the top eight subjects, $t(7) = 4.057$, $p = 0.005$, but not for the bottom eight (13–50% attention), $t(7) = 1.588$, $p = 0.156$. Attention measurements were also available for gorillas and orangutans (see Table 1). Interestingly, orangutans were the most attentive yet showed the least tendency to differentiate the windows.

Fig. 2 shows how chimpanzees responded individually. Bars represent percentage ‘nice’ minus ‘nasty’ (per individual). Positive scores represent a preference for ‘nice’; negative scores for ‘nasty’. As shown, 13/17 individuals spent more time at the ‘nice’ window. Of the six individuals who scored 9% or higher, five were rated as highly attentive. Another way to analyse individual results is to look at how chimpanzee responses varied over time. Every chimpanzee did four trials. Fig. 3 shows how each individual responded in every trial. Using Page’s test (Siegel and Castellan, 1988), we confirm that there was a declining interest in the ‘nasty’ window ($Z_L = 1.638$, $p < 0.05$) but no decline for ‘nice’ ($Z_L = 0.252$, $p > 0.05$).

4. Discussion

In our pilot study, we show that chimpanzees do ‘image score’, based on indirect reputation, which caused them to spend more time near the ‘nice’ than the ‘nasty’ person. The behaviour was untrained, and it was especially strong among those who paid close attention to the incidents. Fig. 2 shows that three-quarters of chimpanzees followed this pattern. The weaker results (5% or under) may be due to inattention or youth (in the bottom five, there were four juveniles and one subadult). The most encouraging data come from the top scorers, who tended to be older and more attentive.

An alternative explanation is that chimpanzees were simply avoiding the ‘nasty’ person due to fear. Fig. 3 provides evidence against this interpretation. In trial 1, there was no difference between ‘nice’ and ‘nasty’. If fear were important, then the difference would have been apparent immediately. As shown, the disparity actually increased over time, as the subjects apparently realised the possible connection between the incident and the window choice.

Species differences did not emerge clearly because the sample sizes of non-chimpanzees were small. However, chimpanzee and bonobo results appear similar. Chimpanzees and bonobos spent 28% and 33% more time near the ‘nice’ than the ‘nasty’ person, respectively. In contrast, gorillas and orangutans spent a mere 2% and 1%, respectively. Whether this represents a real cognitive divide between *Pan* and non-*Pan* needs more investigation.

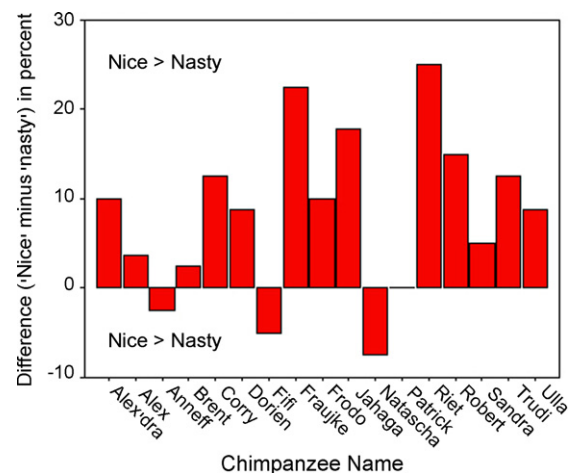


Fig. 2. Individual results for chimpanzees.

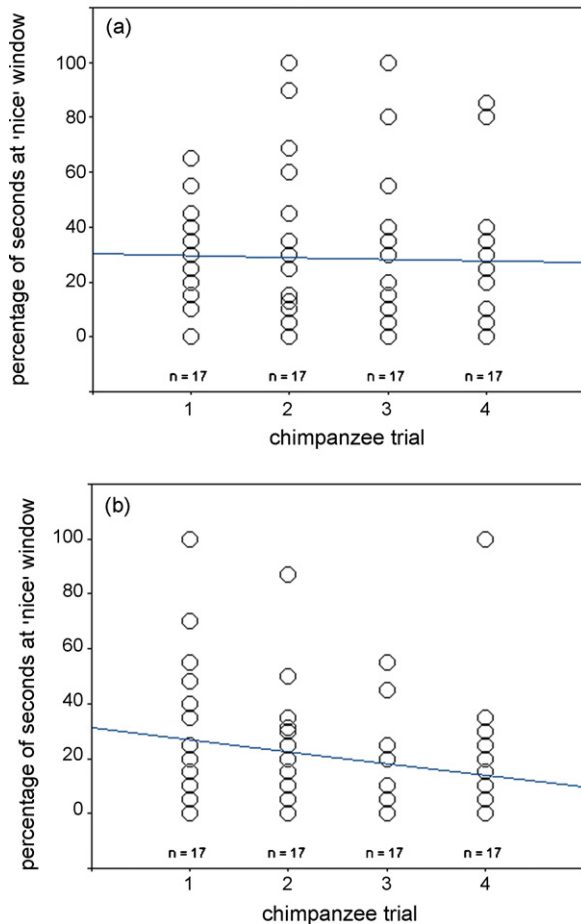


Fig. 3. Trial-by-trial chimpanzee behaviour. Circles represent time an individual spent at window during that trial (percentage of seconds). (a) 'Nice' window. (b) 'Nasty' window.

Image scoring likely occurs in many animal species. It would be helpful to determine the underlying cognitive abilities that enable animals to use 'indirect reputation' as an information source. In the case of great apes, skills such as social eavesdropping (McGregor, 2005), understanding intention (Call et al., 2004), and analogical reasoning ('if A fed B, then A will

feed me') might play a role (see theoretical discussion in Russell, 2007). Further tests using an eavesdropping paradigm (cf. Ophir and Galef, 2003) can clarify these issues.

Acknowledgements

Many thanks to staff (especially D. Hanus and C. Tennie), primate keepers and volunteer actors (especially K. Greve) at the Wolfgang Köhler Research Centre; staff and students at the Max-Planck-Institute for Evolutionary Anthropology; D. Danel and M. Juda for assistance; J. Lycett for a pivotal suggestion; J. Dolinsky for support (Y.I.R.). R.D. was supported by a British Academy Research Professorship. Also thanks to Prof. F.B.M. de Waal and two anonymous reviewers for comments on an earlier version of the manuscript.

References

- Call, J., Hare, B., Carpenter, M., Tomasello, M., 2004. 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action. *Dev. Sci.* 7, 488–498.
- Fehr, E., 2004. Don't lose your reputation. *Nature* 432, 449–450.
- Hammerstein, P. (Ed.), 2003. *Genetic and Cultural Evolution of Cooperation*. The MIT Press, Berlin.
- Krebs, J.R., Dawkins, R., 1984. Animal signals: mindreading and manipulation. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology: An Evolutionary Approach*. Blackwell, Oxford, pp. 380–402.
- McGregor, P.K. (Ed.), 2005. *Animal Communication Networks*. Cambridge University Press, Cambridge.
- Nowak, M.A., Sigmund, K., 1998. Evolution of indirect reciprocity by image scoring. *Nature* 393, 573–577.
- Ophir, A.G., Galef Jr., B.G., 2003. Female Japanese quail that 'eavesdrop' on fighting males prefer losers to winners. *Anim. Behav.* 66, 399–407.
- Russell, Y.I., 2007. *Reputations and Polyadic Interactions Among Great Apes*. Ph.D. thesis. University of Liverpool.
- Siegel, S., Castellan, N.R., 1988. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.
- Smith Maynard, Harper, D., 2004. *Animal Signals*. Oxford University Press, Oxford.
- Tullberg, J., 2004. The distinction between reciprocity and altruism, and a comment on suicide terrorism. *Am. J. Econ. Sociol.* 63, 1193–1212.
- Wedekind, C., Milinski, M., 2000. Cooperation through image scoring in humans. *Science* 288, 850–852.