

Chimpanzees and bonobos distinguish between risk and ambiguity

Alexandra G. Rosati* and Brian Hare

Department of Evolutionary Anthropology, Center for Cognitive Neuroscience, Duke University, Durham, NC 27708, USA
*Author for correspondence (alexandra.rosati@duke.edu).

Although recent research has investigated animal decision-making under risk, little is known about how animals choose under conditions of ambiguity when they lack information about the available alternatives. Many models of choice behaviour assume that ambiguity does not impact decision-makers, but studies of humans suggest that people tend to be more averse to choosing ambiguous options than risky options with known probabilities. To illuminate the evolutionary roots of human economic behaviour, we examined whether our closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), share this bias against ambiguity. Apes chose between a certain option that reliably provided an intermediately preferred food type, and a variable option that could vary in the probability that it provided a highly preferred food type. To examine the impact of ambiguity on ape decision-making, we interspersed trials in which chimpanzees and bonobos had no knowledge about the probabilities. Both species avoided the ambiguous option compared with their choices for a risky option, indicating that ambiguity aversion is shared by humans, bonobos and chimpanzees.

Keywords: decision-making; primates; uncertainty; metacognition

1. INTRODUCTION

Studies of decision-making in both primates and a variety of other taxa suggest that many of the biases that shape human economic decision-making are shared with other species. Taxa ranging from insects and birds to primates exhibit some human-like biases, including framing effects, or preferences that depend on whether options are presented as potential gains or losses [1,2], the endowment effect or individuals overvaluing items when they possess them [3,4], violation of rational choice principles [5–7], and aversion to risk or variability in outcomes [8,9]. Two hypotheses can explain these comparative data. One is that the economic biases observed in humans are evolutionarily ancient and widely shared [1,4]. Alternatively, the observed similarities may be owing to evolutionary convergence on a decision-making strategy in a particular taxa [2,10]. Importantly, examining a few distantly related species, as many previous studies

have done, cannot distinguish between these two hypotheses. That is, humans, capuchins and starlings may show similar choice strategies either because biases are widely shared or because of convergence. Thus, a critical initial step in distinguishing between these two hypotheses is assessing whether our closest phylogenetic relatives share the same bias.

In the current study, we examined whether chimpanzees and bonobos share human-like aversion to ambiguity. Theoretical models suggest that decision-makers should choose between different options based on the value they expect to receive. However, in the real-world decision-makers often lack complete information about different available resources: individuals might be quite certain about what some options will provide, but have less confidence in their judgements about other alternatives. Although risk and ambiguity are typically confounded in normal contexts, studies that disentangle these two factors suggest that aversion to uncertainty tends to be greater than aversion to risk [11]: people do not like choosing the unknown. From an evolutionary perspective, decision-making with incomplete knowledge better reflects the situation animals face in the wild when foraging [12]. From a psychological perspective, studies of ambiguity can illuminate the cognitive roots of metacognitive skills, or knowledge about one's own knowledge state. Studies of animal metacognition typically test whether animals recognize their own lack of knowledge [13]. The current study, by contrast, examines how uncertainty affects the decision strategies that animals exhibit, or the *functional impact* of lack of knowledge on behaviour. Although ambiguity aversion therefore does not require that animals think about what they know, the ability to respond differently based on degrees of knowledge may be a necessary cognitive prerequisite for more complex metacognitive skills.

To examine the response of chimpanzees and bonobos to ambiguity, apes participated in a decision-making task where we manipulated (i) the probability of receiving a good outcome from a variable option and (ii) the apes' knowledge about probabilities. We predicted that both species, like humans, would choose the variable option less on ambiguity trials where they did not know the probabilities, than on risk trials where they did. As bonobos show greater aversion to risk [8,14], and respond with greater hesitation to novel contexts where they lack information [15], we further predicted that bonobos would show greater ambiguity-aversion than would chimpanzees.

2. MATERIAL AND METHODS

We tested 30 semi-free ranging apes: 16 chimpanzees from Tchimpounga Chimpanzee Sanctuary in Pointe Noire, Republic of Congo and 14 bonobos from Lola ya Bonobo Sanctuary in Kinshasa, Republic of Congo (see the electronic supplementary material for details). All apes were socially housed, had ad libitum access to water and were not food-restricted for testing. Subjects were tested only once per day, and all tests were voluntary: if subjects stopped choosing for more than three trials, the session was halted and repeated the next day.

We used a variation of a decision-making task previously used to assess risk preferences ([16]; see the electronic supplementary material). Apes chose between a certain option that always provided an intermediately preferred food type, and a variable option in which the probability of receiving a good outcome could vary. For three trial types, apes saw the two potential outcomes that the variable

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2010.0927> or via <http://rsbl.royalsocietypublishing.org>.

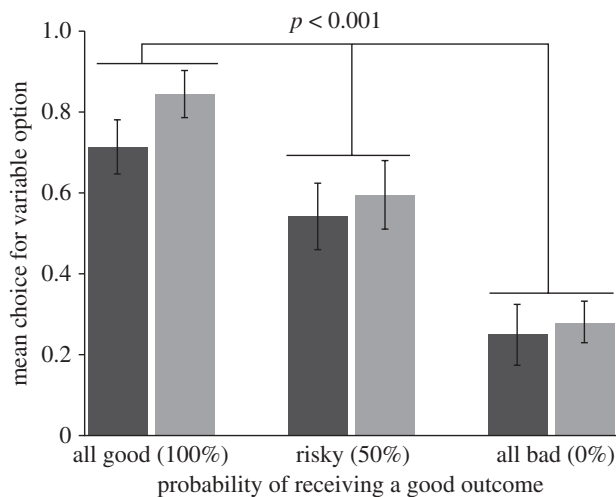


Figure 1. Choices for the variable option by chimpanzees ($n = 16$; black bars) and bonobos ($n = 14$; grey bars) on trials where they knew the probability of receiving different outcomes (all-good, risk, and all-bad trials). Error bars indicate standard error of mean choices.

option could provide (of which they then ultimately received only one): two pieces of preferred food on *all-good* trials (100%), two pieces of non-preferred food on *all-bad* trials (0%) or a preferred food and a non-preferred food on *risk* trials (50%). Interspersed with these trials were *ambiguity* trials, where apes could not see the possible outcomes (see electronic supplementary material, figures S1 and S2). On average, the outcomes from the ambiguous option were equivalent to those from the risky option. As chimpanzees and bonobos previously showed divergent risk preferences in this paradigm, for greater sensitivity we equalized their preferences for risk by altering the value of the certain option: it was always three pieces of intermediately preferred food for chimpanzees, but only two pieces for bonobos.

Subjects completed five sessions. First, they completed a *food preference pretest* to determine the food outcomes. Apes next completed a *risk introduction session* with three types of control trial to assess their comprehension of the basic risk task (following [14]), and then an *ambiguity introductory session* with three additional types of control trials to confirm that subjects were willing to choose the ambiguous option when it paid to do so. Finally, subjects completed two *test sessions*, each with six trials of each type (all-good, all-bad, risk and ambiguity) in quasi-randomized order, with not more than two trials of the same type in a row within a session. Our main comparison was thus between responses on risk trials—where apes did not know the outcome they would receive but did know the probability associated with those outcomes—and ambiguity trials where apes did not even know the probability of the two potential outcomes.

3. RESULTS

Both species showed clear patterns of food preference with no species differences (see the electronic supplementary material). Moreover, both species were above chance on all six types of controls ($p < 0.001$ in all cases), again with no differences in performance (see the electronic supplementary material). Importantly, the three ambiguity control trial types demonstrate that while both species prefer a known good outcome to the ambiguous option (*ambiguity versus good* trials), they also overwhelmingly preferred to choose the ambiguous option when the alternative provided no food (*ambiguity inhibition* trials) or provided low-quality food (*ambiguity versus bad* trials). Thus, our main results cannot stem from a general unwillingness of the apes to choose the ambiguous

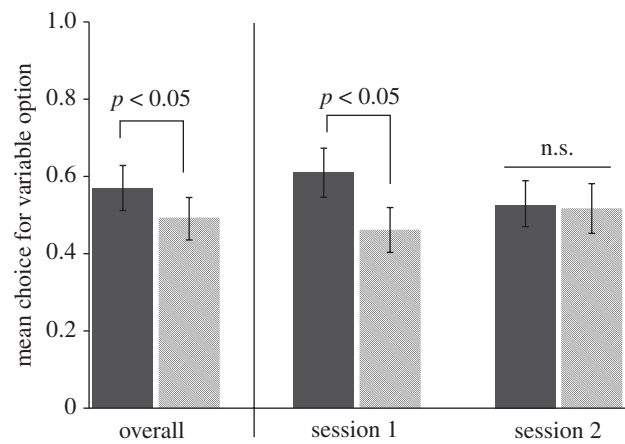


Figure 2. Apes' choices for the variable option on risk trials (solid black bars) and ambiguity trials (striped grey bars) overall, and split by session. Error bars indicate standard error of mean choices.

option because they did not see the potential outcomes beforehand, as in the other trial types.

Examining performance in test sessions, we first assessed the species' choices when they knew the probability of receiving a good outcome. Overall, apes chose the variable option $77.5 \pm 4.6\%$ on all-good trials, $56.7 \pm 5.9\%$ on risk trials and $26.5 \pm 4.6\%$ on all-bad trials (figure 1). A repeated-measures analysis of variance (ANOVA) revealed a main effect of trial type ($F_{2,56} = 62.164$, $p < 0.001$), no effect of species ($F_{1,28} = 0.927$, $p = 0.34$, n.s.) and no significant interactions. Post hoc tests indicated that apes chose differently between all three trial types (Tukey test: $p < 0.001$ for all comparisons), indicating that the apes attended to the potential outcomes on a trial-by-trial basis and modulated their choices according to the specific trial type they faced. Furthermore, our manipulation of the certain option's value was successful: the two species did not differ in their risk preferences.

We next compared how the two species chose on ambiguity versus risk trials. Overall, apes chose the variable option on $48.9 \pm 5.6\%$ of ambiguity trials (figure 2). A repeated-measures ANOVA revealed a main effect of trial type ($F_{1,28} = 4.528$, $p < 0.05$), but no main effect of session ($F_{1,28} = 0.004$, $p = 0.95$, n.s.) or species ($F_{1,28} = 0.153$, $p = 0.70$, n.s.), or significant interactions with species. That is, apes chose the variable option significantly more on risk trials than on ambiguous trials, and the two species did not differ in their level of ambiguity-aversion. However, there was a significant interaction between trial type and session ($F_{1,28} = 4.305$, $p < 0.05$); post hoc tests indeed revealed that, while apes chose the variable option significantly more on risk trials than on ambiguity trials in session one (on $60.6 \pm 6.3\%$ of risk trials versus $46.1 \pm 5.8\%$ of ambiguity trials; Tukey test: $p < 0.05$), they showed no difference in session two.

Finally, we conducted an analysis to assess how the outcome of the previous trial (e.g. good outcome, bad outcome or picked the certain option) drove the apes' choices on the subsequent trial (following [16]). An initial analysis collapsing across all trial

types indicated that previous outcome did not influence the apes' choice overall ($F_{2,56} = 0.731$, $p = 0.485$, n.s.). A second analysis further revealed that there was no effect of previous outcome on risk and ambiguity trials specifically ($F_{2,34} = 1.408$, $p = 0.26$, n.s.; see the electronic supplementary material for details). Together, this suggests that trial type was the main factor influencing apes' choices, and not the previous outcome.

4. DISCUSSION

Our results demonstrate that chimpanzees and bonobos exhibit ambiguity-aversion. The control trials confirmed that the apes preferred the ambiguous option when the alternative was no food or non-preferred food. Nonetheless, they were less willing to choose the ambiguous option than the risky option in the main task. Moreover, the previous trial's outcome did not impact their choice, suggesting that apes' different preferences for risk versus ambiguity did not stem from a simple win-stay lose-shift rule. Overall, these comparative data suggest that ambiguity-aversion has an evolutionary origin in the last common ancestor of humans and other apes. Studies of other more distantly related species could therefore assess whether this bias is more widely shared across other taxa.

Importantly, apes' divergent preferences for risk and ambiguity diminished with time: although apes chose the risky option more frequently than the ambiguous option in the first session; by session two they showed no difference. One possibility is thus that the apes are able to rapidly incorporate new information about previously ambiguous options into their decision strategies: after choosing the ambiguity option and receiving some feedback about what it provided, they may have treated the ambiguity and risk option as equivalent because the functional outcome was the same. Future studies can thus assess how much information or feedback apes need to assess the potential outcomes of an ambiguous option like this.

In comparative studies of metacognition, animals typically make judgements of certainty or can opt-out on uncertain trials. These paradigms may involve extensive training, raising the possibility that the animals are actually responding to differences in reward history [17]. In the current study, we examined how apes' spontaneous reactions to uncertainty impacted their choices, and apes received identical rewards from the risky and ambiguous options. Our results demonstrate that apes are sensitive to the differences in their own knowledge, and use this information when making foraging decisions. Future studies could therefore assess whether apes *knew* they had less knowledge about the ambiguous option by examining whether apes would actively seek out new knowledge about this option if it is available (as in [18,19]).

Our hypothesis that bonobos would show greater ambiguity-aversion than chimpanzees was not supported: although these species show divergent preferences for risk [8,14], they responded similarly to ambiguity. Notably, recent neuroimaging studies suggest that decisions about risk and ambiguity

recruit different brain regions [20,21]. In other domains, species may show divergent patterns of decision-making when different choices depend on distinct neural mechanisms. For example, temporal and effort-based discounting depend on different neural substrates [22], and cotton-top tamarins and common marmosets show a double dissociation in their preferences [23,24], a pattern that maps onto differences in their feeding ecology. Thus, one possibility is that chimpanzee and bonobo preferences for these different types of uncertainty—risk and ambiguity—have been differentially shaped both at the ultimate and proximate levels.

All behavioural tests had IACUC approval from Duke University and were in accordance with the local laws.

We thank Kerri Rodriguez with assistance on coding. At Tchimpounga, we thank Rebeca Atencia, Lisa Pharoh, Keith Brown and the Jane Goodall Institute USA in collaboration with the Congolese Ministère de la Recherche Scientifique et de l'Innovation Technique for hosting our research. At Lola ya Bonobo we thank Claudine Andre, Dominique Morel, Pierrot Mbonzo and Fanny Mehl for their support in collaboration with the Ministry of Research and the Ministry of Environment in the Democratic Republic of Congo (research permit: #MIN.RS/SG/004/2009). We appreciate the assistance of all the animal caretakers. This work was supported in part by a grant to B.H. from the European Research Commission Advanced Grant Agreement 233297 and the National Science Foundation NSF-BCS-08-27552-02 and NSF-BCS-10-25172.

- 1 Chen, M. K., Lakshminarayanan, V. & Santos, L. R. 2006 How basic are behavioral biases? Evidence from capuchin monkey trading behavior. *J. Polit. Econ.* **114**, (doi:10.1086/503550)
- 2 Marsh, B. & Kacelnik, A. 2002 Framing effects and risky decisions in starlings. *Proc. Natl Acad. Sci. USA* **99**, 3352–3355. (doi:10.1073/pnas.042491999)
- 3 Brosnan, S. F., Jones, O. D., Lambeth, S. P., Mareno, M. C., Richardson, A. S. & Schapiro, S. J. 2007 Endowment effects in chimpanzees. *Curr. Biol.* **17**, 1704–1707. (doi:10.1016/j.cub.2007.08.059)
- 4 Lakshminarayanan, V., Chen, M. K. & Santos, L. R. 2008 Endowment effect in capuchin monkeys. *Phil. Trans. R. Soc. B* **363**, 3837–3844. (doi:10.1098/rstb.2008.0149)
- 5 Shafir, S., Waite, T. A. & Smith, B. H. 2002 Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). *Behav. Ecol. Sociobiol.* **51**, 180–187. (doi:10.1007/s00265-001-0420-8)
- 6 Waite, T. A. 2001 Background context and decision making in hoarding gray jays. *Behav. Ecol.* **12**, 318–324. (doi:10.1093/beheco/12.3.318)
- 7 Waite, T. A. 2001 Intransitive preferences in hoarding gray jays (*Perisoreus canadensis*). *Behav. Ecol. Sociobiol.* **50**, 116–121. (doi:10.1007/s002650100346)
- 8 Heilbronner, S. H., Rosati, A. G., Hare, B. & Hauser, M. D. 2008 A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biol. Lett.* **4**, 246–249. (doi:10.1098/rsbl.2008.0081)
- 9 Kacelnik, A. & Bateson, M. 1996 Risky theories: the effects of variance on foraging decisions. *Am. Zool.* **36**, 402–434.
- 10 Pompilio, L., Kacelnik, A. & Behmer, S. T. 2006 State-dependent learned valuation drives choice in an invertebrate. *Science* **311**, 1613–1615. (doi:10.1126/science.1123924)

- 11 Camerer, C. & Weber, M. 1992 Recent developments in modeling preferences: uncertainty and ambiguity. *J. Risk Uncertain.* **5**, 325–370. (doi:10.1007/BF00122575)
- 12 Dall, S. R. X., Ghaldeau, L. A., Olsson, O., McNamara, J. M. & Steohens, D. W. 2005 Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 183–187. (doi:10.1016/j.tree.2005.01.010)
- 13 Terrace, H. S. & Son, L. K. 2009 Comparative metacognition. *Curr. Opin. Neurobiol.* **19**, 74–76. (doi:10.1016/j.conb.2009.06.004)
- 14 Rosati, A. G. & Hare, B. Submitted. Emotion, motivation, and decision-making in chimpanzees and bonobos.
- 15 Herrmann, E., Hare, B., Cissewski, J. & Tomasello, M. Submitted. A comparison of great apes' and human childrens' temperament.
- 16 Beran, M. J., Evans, T. A. & Harris, E. H. 2009 When in doubt, chimpanzees rely on estimates of part reward amounts. *Proc. R. Soc. B* **276**, 309–314. (doi:10.1098/rspb.2008.1027)
- 17 Smith, J. D., Beran, M. J., Cosuchman, J. J. & Coutinho, V. C. 2008 The comparative study of metacognition: sharper paradigms, safer inferences. *Psychon. Bull. Rev.* **15**, 679–691. (doi:10.3758/PBR.15.4.679)
- 18 Call, J. 2010 Do apes know that they could be wrong? *Anim. Cogn.* **13**, 689–700.
- 19 Hampton, R. R., Zivin, A. & Murray, E. A. 2004 Rhesus monkeys (*Macaca mulatta*) discriminate between knowing and not knowing and collect information as needed before acting. *Anim. Cogn.* **7**, 239–246. (doi:10.1007/s10071-004-0215-1)
- 20 Hsu, M., Bhatt, M., Adolphs, R., Tranel, D. & Camerer, C. 2005 Neural systems responding to degrees of uncertainty in human decision-making. *Science* **310**, 1680–1683. (doi:10.1126/science.1115327)
- 21 Huettel, S. A., Stowe, J. C., Gordon, E. M., Warner, B. T. & Platt, M. L. 2006 Neural signatures of economic preferences for risk and ambiguity. *Neuron* **49**, 765–775. (doi:10.1016/j.neuron.2006.01.024)
- 22 Rudebeck, P. H., Walton, M. E., Smyth, A. N., Bannerman, D. M. & Rushworth, M. S. F. 2006 Separate neural pathways process different decision costs. *Nat. Neurosci.* **9**, 1161–1168. (doi:10.1038/nn1756)
- 23 Stevens, J. R., Hallinan, E. V. & Hauser, M. D. 2005 The ecology and evolution of patience in two New World monkeys. *Biol. Lett.* **1**, 223–226. (doi:10.1098/rsbl.2004.0285)
- 24 Stevens, J. R., Rosati, A. G., Ross, K. & Hauser, M. D. 2005 Will travel for food: spatial discounting in two New World monkeys. *Curr. Biol.* **15**, 1855–1860. (doi:10.1016/j.cub.2005.09.016)