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Intuitive statistical inferences in chimpanzees and humans follow Weber's law

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ABSTRACT

Humans and nonhuman great apes share a sense for intuitive statistical reasoning, making intuitive probability judgments based on proportional information. This ability is of fundamental importance, in particular for inferring general regularities from finite numbers of observations and, vice versa, for predicting the outcome of single events using prior information. To date it remains unclear which cognitive mechanism underlies and enables this capacity. The aim of the present study was to gain deeper insights into the cognitive structure of intuitive statistics by probing its signatures in chimpanzees and humans. We tested 24 sanctuary-living chimpanzees in a previously established paradigm which required them to reason from populations of food items with different ratios of preferred (peanuts) and non-preferred items (carrot pieces) to randomly drawn samples. In a series of eight test conditions, the ratio between the two ratios to be discriminated (ROR) was systematically varied ranging from 1 (same proportions in both populations) to 16 (high magnitude of difference between populations). One hundred and forty-four human adults were tested in a computerized version of the same task. The main result was that both chimpanzee and human performance varied as a function of the log(ROR) and thus followed Weber's law. This suggests that intuitive statistical reasoning relies on the same cognitive mechanism that is used for comparing absolute quantities, namely the analogue magnitude system.

1. Introduction

Statistical reasoning is of fundamental importance in human life and one of the hallmarks of human thinking: we continually generalize from sample observations and use these generalizations to predict the outcome of events and to make rational decisions under uncertainty. Nevertheless, over many decades statistical reasoning was deemed to be dependent on language and mathematical training and to remain difficult and error-prone throughout an individual's lifespan (e.g. Piaget & Inhelder, 1975; Tversky & Kahneman, 1974, 1981). More recently, however, developmental research produced evidence that even preverbal infants are capable of basic forms of intuitive statistics: For example, when confronted with two jars containing mixtures of attractive and neutral candy in different proportions, infants were able to infer which of the two was more likely to lead to a preferred candy as randomly drawn sample (Denison & Xu, 2010a, 2014). This also works in the other direction: When confronted with samples, infants could draw conclusions about the proportional composition of the associated populations (Denison, Reed, & Xu, 2013; Xu & Garcia, 2008). Even more impressively, such statistical information is integrated with knowledge from other cognitive domains from very early on: Infants seem to understand that a sample does not necessarily reflect the population's distribution, for instance when the experimenter has the intention to draw a certain type of object as well as visual access to the population (Xu & Denison, 2009), or when a mechanical constraint prevents her from drawing some of the objects (Denison, Trikutam, & Xu, 2014; Denison & Xu, 2010b). Similarly, infants can integrate complex spatio-temporal information into their statistical inferences to judge single event probabilities: When a population of objects bounced randomly in a container with one opening, infants formed expectations as to which object was most likely to exit, based on the proportional composition of the population (majority objects are more likely to exit) and each objects' spatial distance from the opening (the closer objects are, the more likely they are to exit; Teglas et al., 2011).

These findings demonstrated that neither language nor mathematical education are prerequisites for basic statistical reasoning. Instead,

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infants seem to be equipped with an efficient and powerful statistical inference mechanism from very early on, which presumably helps them to rapidly learn about rules and regularities of the world. From a comparative point of view, these findings raise the question of whether intuitive statistics may be part of our evolutionary heritage and therefore not necessarily uniquely human.

To shed light on this question, comparative research adapted Denison and Xu's (2010) paradigm and tested nonhuman great apes for their statistical reasoning capacities: Rakoczy et al. (2014) presented chimpanzees, gorillas, orangutans and bonobos with two transparent buckets containing mixtures of preferred and non-preferred food items (banana pellets and carrot pieces) in specific ratios. Subsequently, the experimenter drew one sample each and the subject was allowed to choose between the two covered samples. Apes were able to infer which of the two populations was more likely to lead to a pellet as a sample. Moreover, they chose systematically even when absolute and relative frequencies were disentangled, i.e. when the population with the more favorable ratio of pellets to carrots contained absolutely fewer pellets than the other one. A very recent study (Eckert, Rakoczy, Call, Herrmann, & Hanus, 2018) showed that these statistical inferences are not an isolated and automatic process; instead, just like human infants, apes did consider additional information about the experimenter (her preferences and visual access) when predicting the outcome of her draw. Hence, some great ape intuitive statistical abilities seem to be on a par with those of human infants, suggesting that they constitute an evolutionary ancient ability.

However, when great apes were presented with the reverse task, requiring inferences from sample to population, they exhibited some limitations: Eckert, Rakoczy, and Call (2017) presented apes with covered containers holding populations of preferred and non-preferred food-items. After observing multi-item samples being drawn from these populations, apes could choose between the two covered containers. Subjects were able to correctly reason from sample to population, but only in conditions, in which the proportionally favorable sample also contained absolutely more preferred food items than the other (4:1 vs. 1:4 preferred to non-preferred food items). In experiments contrasting absolute and relative frequencies of preferred food items (e.g. 2:1 vs. 4:8 preferred to non-preferred food items), apes tended to choose the population from which the sample with absolutely more preferred items was drawn (4:8), despite its unfavorable ratio.

There are at least two possible interpretations of these findings: First, they may indicate that apes relied on absolute quantity heuristics to reason from sample to population. In fact, even in the human literature there is a great deal of research suggesting that most probabilistic inferences are actually just the result of different heuristics (e.g. Davidson, 1995; De Neys & Vanderputte, 2011; Jacobs & Potenza, 1991; Kahneman & Tversky, 1972, 1973; Tversky & Kahneman, 1974, 1981). Hence, controlling for absolute number heuristics is of substantial importance in the field of intuitive statistics. Nevertheless, many studies (both on human and nonhuman species) have unfortunately failed to sufficiently control for such strategies. The previously described studies on great apes, for instance, included control conditions for heuristics dealing with the absolute quantity of preferred items (which apes passed in Rakoczy et al. (2014), but failed in Eckert et al. (2017)). None of them, however, tested for the reverse strategy: a heuristic based on avoiding the population or sample containing more non-preferred food items. Hence, to be able to draw conclusions about apes' intuitive statistical abilities, there is an urgent need for studies controlling for all types of absolute quantity heuristics.

A second interpretation for Eckert et al.'s (2017) negative findings is that they merely reflect performance, rather than competence limitations. The critical conditions in that study may have been especially difficult because the magnitude of difference between samples (i.e. the ratio of the two ratios, ROR) was relatively small, and perhaps beyond the signature limits of apes' capacity: While the ROR was 16 in the successful confounded conditions (and also in all conditions of Rakoczy and colleagues' population to sample study), it was as low as 4 in the critical condition in which absolute and relative frequencies of preferred food items were disentangled.

This, in turn, raises a much more fundamental question: What are the cognitive foundations of intuitive statistics that explain both the scope and limits of this capacity? And are these the same in humans and our closest living relatives, the chimpanzees?

Nonhuman primates (and other animals) share with humans a cognitive mechanism for basic quantitative cognition. This mechanism, the analogue magnitude system, is used for dealing with absolute numerical information: It represents number (and also other magnitudes like duration or space) by a mental magnitude that is roughly proportional to and thus a direct *analogue* of the number of individuals in the set being enumerated (see, e.g. Carey, 2009; Dehaene, 2011).[1] It thus enables subjects to estimate and compare arbitrarily large quantities, but only in an approximate way (e.g. Nieder & Dehaene, 2009). Its accuracy follows Weber's Law: Discriminability of two sets varies as a function of the ratio of the set sizes to be compared, independent of their absolute numerosity (e.g. Cantlon & Brannon, 2006, 2007). For example, if a subject can discriminate 2 from 4 objects, it is also able to discriminate 10 from 20 or 500 from 1000. This fundamental characteristic yields specific signatures that can be used to identify the involvement of this system in cognitive tasks. Numerous comparative studies have shown that many species across the animal kingdom exhibit the same signatures in accordance with Weber's law when confronted with quantity comparison tasks. For example, fish (Buckingham, Wong, & Rosenthal, 2007), birds (Ain, Giret, Grand, Kreutzer, & Bovet, 2009; Rugani, Cavazzana, Vallortigara, & Regolin, 2013), monkeys (Barnard et al., 2013; Cantlon & Brannon, 2007), and great apes (Beran, 2004; Call, 2000; Hanus & Call, 2007) all showed a ratio-dependent performance when discriminating absolute quantities, suggesting that the analogue magnitude system is an evolutionary ancient mechanism (see Beran, 2017 for a review).

Are the limits reported by Eckert et al. (2017) a first hint that apes employed their analogue magnitude system in a statistical reasoning task as well? Is the ability to reason probabilistically from population to sample and vice versa dependent on the ratio between the two proportions to be discriminated, i.e. on the ratio of ratios (ROR)? To our knowledge, no study has directly tested for this hypothesis in nonhuman primates yet; indeed, even in human adults the evidence is ambiguous. One study (O'Grady, Griffiths, & Xu, 2016) tested human adults in a computer based task that required them to reason statistically from population to sample. The authors varied the magnitude of difference between the two populations' ratios and included both trials in which absolute and relative frequencies of target stimuli were confounded and trials in which they were disentangled. Statistical analysis revealed that the effect of the ROR on humans' performance was dependent on the trial type, with much stronger effects in the confounded condition. In this condition, participants could simply compare the two (absolute) amounts of target stimuli, a capacity known to be enabled by the analogue magnitude system. Unfortunately, it remained unclear whether there was any significant ROR impact in the crucial trials controlling for absolute quantity heuristics.[2] Hence, this study is yet

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[1] We prefer to refer to the more general "analogue magnitude system" rather than the more specific "approximate number system" since this leaves open the possibility that the system in question is not restricted to discrete numerical information in the more narrow sense, but potentially also represents continuous magnitudes such as length, duration, etc. Whether or not there is a separate cognitive system processing numerical information only is still highly debated (see e.g. Lourenco, 2015 for a review).

[2] In fact, the authors found a significant three-way-interaction between ROR, condition and age. Hence, the effect of the ROR was not only dependent on the trial type, but also on the age of participants (yet this age effect was not discussed in the paper). It is generally not meaningful or reasonable to interpret the individual effects of the components of a significant interaction (Bortz,

another example of the problematic confound of absolute and relative frequencies in intuitive statistical reasoning tasks.

The only two studies investigating signatures in a statistical reasoning task in human infants used looking-time patterns and produced mixed results. On the one hand, Téglás, Ibanez-Lillo, Costa and Bonatti (2015) found that, after watching a scene containing moving objects of two ensembles, infants looked longer at an unlikely than at a likely single-case outcome when the scene depicted a 3:1 ratio. However, they did not do so with a 12:4 ratio, suggesting that absolute set sizes, rather than ratios, influenced performance in this intuitive statistical reasoning task. On the other hand, Kayhan, Gredebäck and Lindskog (2017) measured infants' looking patterns at two multi-item-samples drawn from one population. In order to vary the magnitude of difference in likelihoods between samples, they manipulated both the ratios within samples and within the population. Here, results showed that infants' looking patterns varied as a function of the magnitude of difference in likelihood, suggesting that ROR does modulate infants' probability estimations. Hence, to date it remains unclear whether or not the analogue magnitude system is the primary cognitive mechanism enabling intuitive statistics in humans.

Despite this controversy, there is some indirect evidence supporting the idea of the analogue magnitude system as foundation of statistical reasoning: Both developmental and comparative research have shown that one important prerequisite capacity for statistical reasoning – tracking relative frequencies – is subject to the same signatures as tracking absolute frequencies. McCrink and Wynn (2007) presented human infants with a ratio discrimination task: After habituating them with multiple examples of a single ratio, infants were able to discriminate between new examples of this ratio and novel ratios. Infants' accuracy was highly dependent on the ratio between ratios, in accordance with Weber's law. Similar results were found for a nonhuman primate species (Drucker, Rossa, & Brannon, 2015): two rhesus macaques were trained to choose arrays that contained the greater ratio of positive to negative stimuli. Subjects' performance was modulated by the ratio between ratios: they responded more quickly and accurately the higher the ratio between ratios was, regardless of the absolute number of stimuli within the arrays. Results of these two studies (Drucker et al., 2015; McCrink and Wynn, 2007) suggest that the ability to discriminate ratios is a function of the ratio between the ratios to be discriminated, similarly as the ability to discriminate absolute quantities is a function of the ratio of the absolute set sizes. This raises the question whether the analogue magnitude system not only enables an individual to *track* relative frequencies, but also to *use* relative frequency information to draw statistical inferences from population to sample and vice versa.

One recent study did find some such evidence for an involvement of the analogue magnitude system in decision making under uncertainty in nonhuman great apes: Hanus and Call (2014) gave chimpanzees the choice between two trays on which food items were hidden under cups. The trays differed with respect to the ratio of food items to cups and thus in chances of finding food. Results showed that chimpanzees' performance varied as a function of the ratio between the two ratios, even in conditions where one tray constituted a 100% likelihood of finding food. This suggests that the ratio between ratios, more than the magnitude of difference within the single ratios, is decisive for apes' ability to discriminate probabilities. However, chimpanzees' success in this study could be explained with an absolute quantity heuristic, not regarding the amount of food items available, but regarding the number of cups on each tray. In particular, the tray depicting the more favorable food/cup ratio always held the smaller number of cups. The authors added a control condition in which they excluded simple associative learning explanations (subjects did not preferentially choose the tray with fewer cups when the food was visibly removed from all cups). Nevertheless, it cannot be excluded that, as soon as there was any food to be found, chimpanzees at least partially relied on a mental shortcut such as "fewer cups = higher likelihood of finding food".

In sum, nonhuman great apes share with humans the fundamental ability to draw statistical inferences from population to sample and (to a certain extent) vice versa. Yet, it still remains an open question what the cognitive foundations of intuitive statistics are and whether they are the same in humans and their closest living relatives. To date, two main reasons suggest that the analogue magnitude system is the most plausible candidate for a basic statistical inference mechanism. First, the prerequisite capacity for this kind of inferences, tracking ratios, shows the same signatures as absolute quantity discrimination, both in human and nonhuman primates. Second, decision making under uncertainty seems to be ratio dependent in chimpanzees. What is missing is a comparative study testing great apes and humans in an intuitive statistical reasoning task that systematically varies the ROR and, crucially, controls for the use of absolute quantity heuristics.

The rationale of the present study, therefore, was threefold. First, we wanted to elucidate the cognitive and evolutionary underpinnings of intuitive statistics in chimpanzees and humans by testing its signatures. If intuitive statistics are based on the same analogue magnitude system, we would expect the characteristic performance patterns and signatures in both species. Much like the discrimination of absolute set sizes varies as a function of the ratio of the set sizes, we expected that the accuracy of intuitive statistics would vary as a function of the ROR between sets. We were particularly interested in determining the ROR lower threshold where performance breaks down in each species. A comparison of these signature limits with those found in simple quantity discrimination tasks helped us determine whether the inclusion of the statistical operation adds error to the representation in comparison to basic quantity discrimination. As described earlier, quantities are represented in an analogue, approximate way. We assumed that discriminating ratios of quantities *and* forming probabilistic expectations on their basis adds considerable noise relative to absolute quantity discrimination, since it requires representing and operating on quantities over multiple accounts (see, e.g. Barth et al., 2006 for an example of how subtraction operations add error to the quantity representation in comparison to simple quantity discrimination tasks). Accordingly, we expected the ROR threshold to be higher (i.e. less sensitive) than the threshold for discriminating absolute quantities. To address these questions, we presented chimpanzees with a previously established paradigm (Rakoczy et al., 2014) that required them to reason from populations of food items with different ratios of preferred and non-preferred food items to randomly drawn samples. We systematically varied the ratio between the two ratios (of preferred to non-preferred food items; ROR) ranging from 1 (equal proportions in both populations) to 16 (high magnitude of difference between populations). We tested human adults in a computerized version of the same task.

Our second goal was to replicate and validate previous findings on intuitive statistics in great apes. So far, only one experimentally highly experienced population of chimpanzees (and other apes) has been tested for their statistical abilities (Rakoczy et al. 2014). Therefore, it remains an open question whether findings of this particular population are generalizable to chimpanzees as a species. To investigate whether intuitive statistics is in fact a common, natural capacity in chimpanzees, we used the same task setup to test completely naïve individuals who were raised and housed in a different environment. This allowed us to directly compare between the previously tested, captive born and zoo housed chimpanzees, and the wild born, sanctuary housed chimpanzees tested in the present study.

Lastly, our study rules out alternative explanations based on absolute quantity heuristics. Most importantly, we included a crucial

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(*footnote continued*)
1999; Underwood, 1997; Zar, 1999). The only legitimate statement this study can draw regarding ROR effects is, therefore, that the effect was only visible in certain age groups depending on whether or not absolute and relative frequencies were confounded.

experiment to control for the possibility that apes used a strategy based on avoiding the population with the largest number of non-preferred items. The to date only study on nonhuman primates addressing such an avoidance heuristic has produced negative results: Capuchin monkeys failed to choose the sample from the proportion wise favorable population when they could not rely on the absolute amount of non-preferred items (Tecwyn, Denison, Messer, & Buchsbaum, 2016). It is, therefore, crucial to explore the possibility that apes' success in the present and previous studies was due to this simple quantity heuristic. Moreover, our study design ensured that apes could not succeed by choosing based on the absolute quantity of preferred food items. While previous studies (Eckert et al., 2017; Rakoczy et al., 2014) addressed this issue in separate control conditions, we designed our study in a way that apes were prevented from using such a strategy in *all* test conditions. Lastly, we also controlled for heuristics dealing with the total amount of food in each population. Hence, this is the first study on intuitive statistics in great apes comprehensively controlling for absolute number heuristics both regarding preferred and non-preferred items as well as their absolute total amount.

2. Methods

2.1. Chimpanzees

2.1.1. Subjects

We tested 24 chimpanzees (12 females) aged between 9 and 32 years at Ngamba Island Chimpanzee Sanctuary, Uganda. All individuals were born in the wild and orphaned at young age before they were transferred to the sanctuary. Research strictly adhered to the legal requirements of Uganda and was approved and reviewed by the Ugandan Wildlife Authorities and the Ugandan National Council for Science and Technology. The study was approved by the ethics committees of the Max Planck Institute for Evolutionary Anthropology and the Chimpanzee Sanctuary & Wildlife Conservation Trust.

2.1.2. Design and procedure

Subjects were tested in eight ROR conditions and one condition controlling for the usage of a non-preferred food avoidance heuristic (hereafter: carrot avoidance control; see Fig. 2). All conditions consisted of 12 trials, presented in a single session. The sequence of conditions was randomized for each subject, with the exception of the carrot avoidance control, which was the fifth condition for all subjects (see SI for more details).

We presented subjects with two transparent buckets filled with mixed populations of peanuts and carrot pieces of roughly equal size and shape. In all but one condition (ROR 1), one of the buckets contained a population that was more favorable in terms of its proportion of peanuts to carrots compared to the other. The experimenter showed both buckets to the subject, directed her gaze towards the ceiling and drew one item (always of the majority type) out of each of the buckets in a way that the chimpanzee could not see what was drawn. The experimenter kept the items hidden in her fists and the subject was allowed to indicate a choice to receive the chosen sample. In half of the trials, the experimenter crossed her arms when moving the fists towards the mesh to ensure that subjects made a choice between samples and not just chose the side where the favorable population was still visible. Trials with and without crossing were alternated (see Fig. 1 for an illustration).

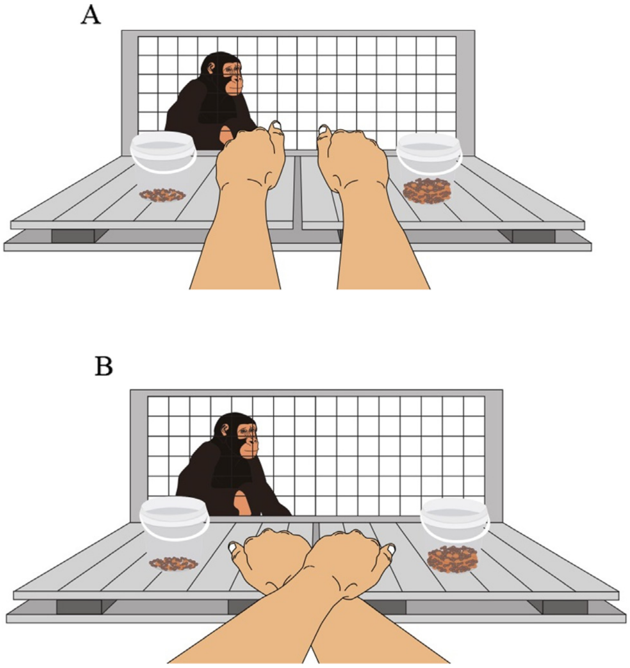


Fig. 1. Experimental setup. The experimenter simultaneously drew one sample from each of two populations in a way that kept the object hidden from the chimpanzee. The experimenter then gave the subject a choice between the two hidden samples (A). In half of the trials the experimenter crossed her arms before the subject was given a choice (B).

2.1.2.1. ROR conditions. To find the signatures of intuitive statistics, we systematically varied the ratio between populations ratios (ROR) ranging from 1 (equal ratio in both populations) to 16 (high magnitude of difference between ratios). In all ROR conditions we disentangled absolute and relative frequencies of peanuts: the bucket containing the less favorable ratio of peanuts to carrots contained twice as many peanuts as the bucket containing the more favorable ratio (see Fig. 2). This ensured that subjects truly reasoned about proportional information, rather than about absolute numbers of peanuts. RORs were calculated in the following way (following Drucker, Rossa, & Brannon, 2016; for more details see SI):

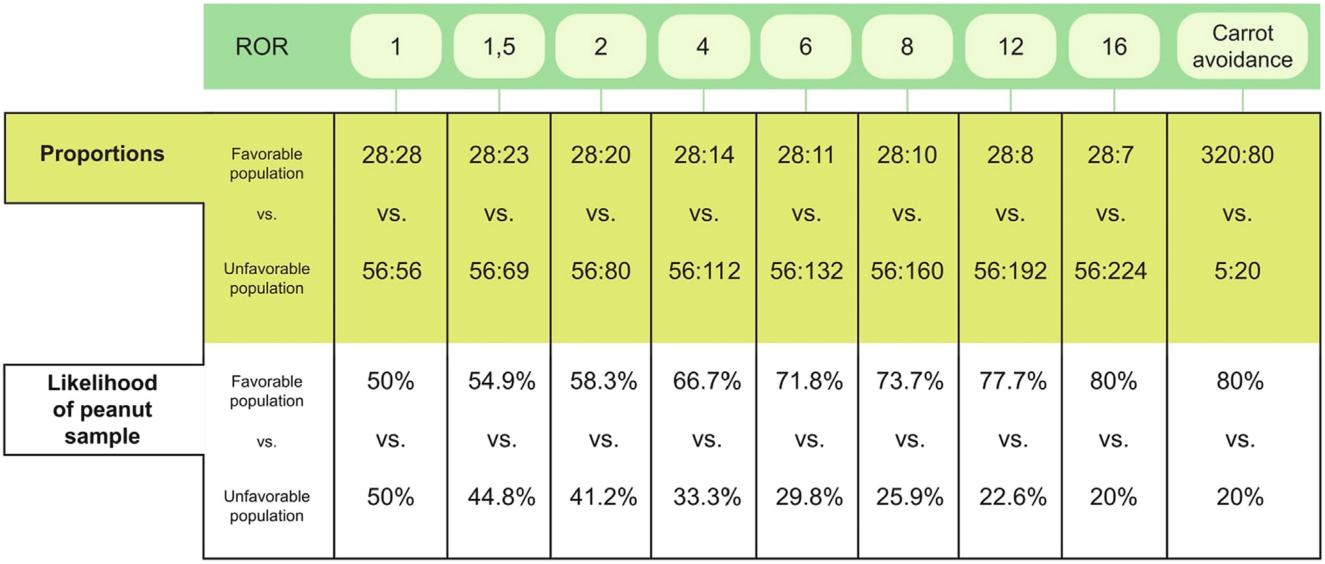
$$\frac{\text{Ratio of peanuts to carrots in the more favorable population}}{\text{Ratio of peanuts to carrots in the less favorable population}}$$

One consequence of this was that the favorable population always contained a smaller total amount of food items across ROR conditions (see Fig. 2). Hence, it is theoretically possible that subjects learned over the course of sessions to always pick the sample from the bucket with fewer items. Although this seems unlikely considering that chimpanzees have proven to be poor in learning arbitrary associations (e.g., Call, 2004), we included a ROR 1 condition in which both populations contained the same proportion of peanuts to carrots (i.e. both of them were equally likely to lead to a peanut as randomly drawn sample), while one contained double the amount of food items in absolute terms. If they still preferred the sample of one of the two populations, this would suggest that chimpanzees used other information than intended to solve the task. The reward pattern in this condition was adjusted accordingly: In randomized order, the experimenter drew a peanut from both buckets in half of the trials; in the other half she drew a carrot.

2.1.2.2. Carrot avoidance control. To test whether subjects solved the task using a non-preferred food avoidance strategy focusing on the absolute number of carrots, here the favorable population contained four times more carrot pieces than the unfavorable population, while the ROR was 16 (see Fig. 2). If chimpanzees used a carrot avoidance strategy, we expected them to perform worse than in the ROR 16 condition.

2.1.3. Coding and data analysis

The apes' choice was coded live by the experimenter. A second blind observer coded 25% of the trials from video. Both raters were in



ROR		1	1,5	2	4	6	8	12	16	Carrot avoidance
Proportions	Favorable population	28:28	28:23	28:20	28:14	28:11	28:10	28:8	28:7	320:80
	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.
	Unfavorable population	56:56	56:69	56:80	56:112	56:132	56:160	56:192	56:224	5:20
Likelihood of peanut sample	Favorable population	50%	54.9%	58.3%	66.7%	71.8%	73.7%	77.7%	80%	80%
	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.
	Unfavorable population	50%	44.8%	41.2%	33.3%	29.8%	25.9%	22.6%	20%	20%

Fig. 2. List of conditions (eight ROR conditions and carrot avoidance control) and the respective proportions within the populations as well as the likelihood of drawing a peanut as a sample. Numerals in front of the colon depict numbers of preferred items, numerals after the colon depict numbers of non-preferred items. The first line always displays the favorable population except in ROR 1 in which both proportions were identical.

excellent agreement (K = 0.95, N = 576). To investigate whether there was an effect of the ROR on chimpanzees' performance across ROR conditions, we ran a Generalized Linear Mixed Model (GLMM; Baayen, 2008). "Correct choice" (choice of sample from population with higher peanut proportion) was the dependent variable. Note that data for the ROR 1 condition was not included in the model, since there was no "correct choice" in this condition (both populations were equally likely to lead to a preferred food item as a reward). As fixed effects we included logROR (since we expected the effect to be logarithmic), session and trial number (to test for potential learning effects) as well as all second and third order interactions among logROR, session number and trial number. To control for the effect of age and age^2 (in case of a nonlinear age-effect) they were included as further fixed effects. Subject ID and session ID were included as random effects. To keep type I error rate at the nominal level of 5% (Schielzeth & Forstmeier 2009; Barr 2013) we included all possible random slopes components (logROR, session number, trial number within subject ID and trial number within session ID) and also the respective correlations between random slopes and intercepts (see SI for more details on the statistical analysis). In order to determine the ROR lower threshold where performance breaks down, we inspected the confidence interval limits of the model: The model predicts performance to be above chance level in conditions for which the confidence interval limits lie above 0.5.

To investigate whether chimpanzees' performance in the carrot avoidance control was different from the ROR 16 condition, we ran a second GLMM. Again, "correct choice" was the response variable. As fixed effects we included condition (carrot avoidance control vs. ROR 16), session number and trial number as well as the two-way interactions between condition and trial number and between session number and trial number. Again, we included age and age^2 as further fixed effects, subject ID and session ID as random effects, and all random slopes components (condition, session number and trial number within subject ID and trial within session ID) as well as the respective correlations between random slopes and intercepts (see SI for more details).

2.2. Humans

2.2.1. Subjects

We tested 144 adult humans (80 women) aged between 18 and 34 years at the University of Göttingen, Germany. Participants were tested in a computerized version of the same task as the chimpanzees. On a test computer, they were invited to imagine collecting as many red balls as possible from pairs of transparent urns filled with red and blue balls. They were asked to envision drawing from one urn of each pair with eyes closed and to indicate their choice by pressing one of two keys as quickly as possible.

2.2.2. Design and procedure

Similar to the apes, humans were tested in eight ROR conditions ranging from 1 to 16, with proportions resembling those for chimpanzees (see Fig. 2). To prevent participants from learning to always pick the urn with the smaller absolute quantity (since humans were tested in a single session the likelihood for learning such a rule was high), we also tested seven additional conditions (RORs between 1.5 and 16) in which absolute and relative frequencies were confounded. Since we expected getting a ceiling effect for confounded conditions (and their interpretation would not have been meaningful in terms of statistical reasoning), we did not plan to focus on these conditions in the analysis (but see SI for results). To prevent participants from counting the balls, images were only displayed for a maximum of 4 s (see SI for an example stimulus). Participants saw six trials per condition and trials of all conditions were randomized for each subject in one single test session.

2.2.3. Coding and data analysis

Participants' choice and response time were recorded automatically by EPrime (mean response times are depicted in SI Fig. 2). We used the same analysis as for chimpanzees, with the following exceptions: We ran two separate models, one for disentangled RORs and one for confounded RORs. Since humans were tested in a single session, we did not include session number as fixed effect, nor did we include session ID as random effect. Further, we only included age, but not age^2 as fixed effect, since we tested a small age range and did therefore not expect a nonlinear effect. Due to a significant effect of trial number, we ran the model for disentangled RORs again with only trial 1 performance considered (see SI for further details and results of the trial 1 model).

3. Results

3.1. Chimpanzees

3.1.1. ROR conditions

Chimpanzees performance was significantly influenced by the

Table 1
Influence of logROR, session, trial, age and age^2 on chimpanzees' proportion of correct choices.

Term	Estimate	SE	X^2	Df	P
Intercept	0.60	0.11	(1)	(1)	(1)
logROR(2)	0.21	0.05	15.44	1	$p < 0.001$
Session(2)	0.12	0.07	2.65	1	0.104
Trial(2)	−0.02	0.05	0.19	1	0.667
Age(2)	0.03	0.09	0.10	1	0.750
(Age)^2(2)	−0.08	0.06	2.06	1	0.151

Note: (1) not shown because lacking a meaningful interpretation; (2) these predictors were z-transformed.

logROR (GLMM, estimate ± SE = 0.21 ± 0.05, $X^2 = 15.44$, df = 1, $P < 0.001$; see Table 1 and SI for details), i.e. performance increased as a function of the ROR (see Fig. 3A) from a mean of 56.9% correct trials in ROR 1.5 to 69.8% in ROR 16 (see Table 2). The mean number of correct trials in ROR 1 was 51.4%. The model predicted the limit of chimpanzees' abilities to be between ROR 2 and 4 (see Fig. 3A). There was no effect of session or trial number, suggesting that chimpanzees' performance did not change with increasing experience within a session or over the course of sessions (see Table 1 and SI for more detailed information).

3.1.2. Carrot avoidance control

We found that subjects performed significantly better in the carrot avoidance control compared to the ROR 16 condition (GLMM, estimate ± SE = 0.78 ± 0.25, $X^2 = 9.44$, df = 1, P = 0.0016; see Fig. 3A and SI for details), which suggests that they did not use a strategy based on avoiding the population with more non-preferred food items.

3.2. Humans

Humans' performance was significantly influenced by the logROR (GLMM, estimate ± SE = 1.36 ± 0.08, $X^2 = 163.53$, df = 1, $P < 0.001$; see Table 3 and SI for details): Performance increased logarithmically as a function of the ROR (see Fig. 3B) from a mean of 43.4% correct trials in ROR 1.5 to 80.0% in ROR 16 (see Table 2 and Fig. 3B). The model predicted the same limit as for chimpanzees. We found an effect of trial number ($X^2 = 4.58$, df = 1, P = 0.029) indicating that participants' performance slightly increased with increasing experience. However, significance of the overall results did not change when considering trial 1 performance only (see SI for more information).

4. Discussion

We found that chimpanzee and human performance in a task requiring inferences from population to sample varied systematically as a function of the ROR, i.e., the magnitude of difference between the ratios of two populations. In accordance with Weber's law, performance increased logarithmically as a function of the ROR. This is the first piece of evidence to suggest that the analogue magnitude system is involved in intuitive statistical reasoning in both species. Intriguingly, and although methods for both species were somewhat different (e.g. live demonstration for chimpanzees vs. computer setup for humans) chimpanzees and humans displayed the same approximate limit: While the model predicted above chance level performance for ratios that differed by a factor of 4, it predicted failure for those that differed by a factor ≤ 2. Given that this is the first study addressing this topic and considering the small sample size, these results should be treated with caution. Nonetheless, the rather high threshold may suggest that, in comparison to simple quantity discrimination tasks, the statistical operation adds some error to the representation. Human adults, for instance, are able to discriminate absolute set sizes that differ by a factor of 1.15 (e.g. Barth, Kanwisher, and Spelke, 2003; Pica, Lemer, Izard, & Dehaene, 2004) compared to 6-month old infants who can discriminate ratios > 1.5 (Lipton & Spelke, 2003; Xu & Spelke, 2000). Not many studies documented the threshold for absolute quantity discrimination in nonhuman primates. Reported limits range from values as low as 0.9 for great apes (Hanus and Call, 2007) to 1.25 for rhesus macaques (Brannon & Terrace, 2000). The finding of a higher threshold for ratio discrimination within the realms of statistical inferences relative to basic quantity discrimination is consistent with the idea that additive error is to be expected when an organism represents and operates over multiple amounts (see, e.g. Barth et al., 2006; McCrink & Wynn, 2007

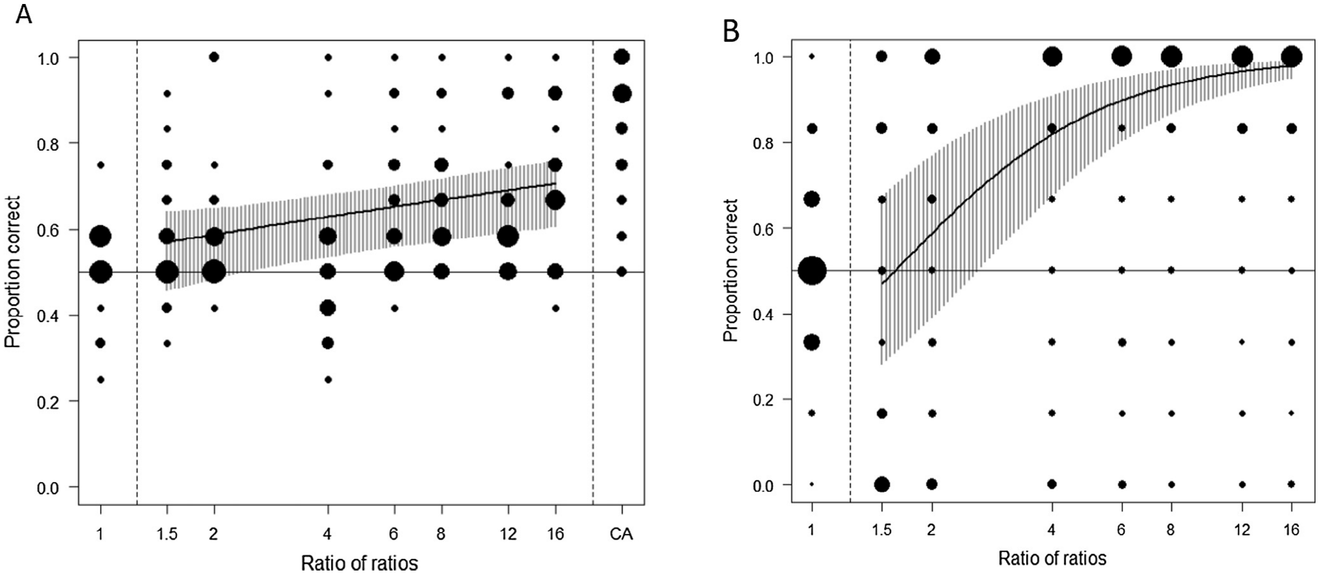


Fig. 3. Chimpanzee (A) and human (B) performance across conditions. Shown is the proportion of trials in which subjects chose the sample from the favourable population for all (disentangled) ROR conditions (in ROR 1 proportion of trials in which subjects chose sample from smaller population) and, for chimpanzees the carrot avoidance control (CA). The dot size indicates the number of subjects performing at the same level (for readability purposes we used a different scale for the number of subjects in humans and chimpanzees). The horizontal line depicts chance level. The solid diagonal and vertical lines indicate the fitted model and its confidence limits. The model predicts performance to be above chance level in conditions for which the confidence interval limits lie above 0.5.

Table 2

Mean percentage of correct choices for each condition. *In ROR1 was no correct answer; here the percentage depicts the mean proportion of trials in which subjects chose the sample drawn from the population with the smaller absolute number of items.

Species		ROR1	ROR1.5	ROR2	ROR4	ROR6	ROR8	ROR12	ROR16	Carrot Avoidance
Chimpanzees	Mean proportion correct choices	51.4%*	56.9%	59.0%	53.1%	63.4%	66.2%	64.2%	69.8%	81.9%
Humans	Mean proportion correct choices	51.9%*	43.4%	59.8%	69.3%	72.1%	78.6%	79.5%	80.0%	/

Table 3

Influence of logROR, trial number and age and on humans' proportion of correct choices.

Term	Estimate	SE	X^2	df	P
intercept	1.96	0.27	(1)	(1)	(1)
logROR$^{(2)}$	1.36	0.08	163.53	1	$p < 0.001$
Trial$^{(2)}$	0.16	0.07	4.59	1	0.029
Age$^{(2)}$	−0.32	0.27	1.36	1	0.239

Note: $^{(1)}$ not shown because lacking a meaningful interpretation; $^{(2)}$ these predictors were z-transformed.

for discussion of this hypothesis). Future studies with other populations of chimpanzees and humans, as well as different absolute quantities will have to examine whether we are truly dealing with a universal signature limit of statistical reasoning abilities. While chimpanzee performance was still far from ceiling even at the highest tested RORs, human performance rapidly increased and reached a plateau at ROR 8. This resembles findings on absolute quantity discrimination, where humans showed higher accuracy compared to other primates (e.g. Cantlon & Brannon, 2007), therefore suggesting that the same cognitive mechanism is utilized in both types of tasks. Future studies should test chimpanzees with a wider range of RORs to investigate whether (and when) they, like humans, also reach a maximum performance plateau.

One question that the present findings raise is whether intuitive statistics is based on an analogue magnitude system that is potentially not restricted to numerosity, but extends to all kinds of magnitudes, or alternatively on an approximate number system (ANS) in the more narrow sense, restricted to numerosity alone. This is related to the broader debate of whether numerical cognition is a quintessential cognitive domain with a specialized cognitive mechanism or whether the ANS is part of a broad domain in which all quantitative dimensions share computational mechanisms (see, e.g. Cantlon, Platt, & Brannon, 2009; Lourenco, 2015 for reviews). One way to inform this debate is to develop an intuitive statistical inference task disentangling discrete from continuous quantity information.

Another important question is whether the signatures of intuitive statistics and their limits extend to differences across life-stages known to apply in the case of the ANS with regard to absolute set sizes. More specifically, do we find better accuracy in older compared to younger individuals (analogous to findings by Halberda & Feigenson, 2008)? And are early inter-individual differences in accuracy predictive of later explicit statistical reasoning, as it is the case regarding the ANS with respect to absolute set sizes and later mathematical achievement (for a review see, e.g. Feigenson, Libertus, & Halberda, 2013)?

Our study not only gives insights into the cognitive foundation of intuitive statistics, the results also replicate those from our previous study (Rakoczy et al. 2014) in which we tested chimpanzees (and other nonhuman great apes) with substantial experience with cognitive testing. In that study, we had included a critical condition in which absolute and relative frequencies of preferred items were disentangled while keeping the ROR at a value of 16 – similar as in the present ROR 16 condition. While chimpanzees in Rakoczy et al. (2014) chose the sample from the favourable population in 66% of trials, chimpanzees in our present study performed correct in 69.8% of trials, even slightly exceeding the previously tested individuals' performance. Therefore, our ROR 16 condition replicated previous findings with a new population of chimpanzees that was completely naïve to this kind of task and was raised and housed in a different environment (wild born and sanctuary housed vs. captive born and zoo housed). This suggests that intuitive statistical reasoning is a natural capacity in chimpanzees and not restricted to a single population with extensive experimental experience. Recent studies with two different monkey species (capuchin monkeys: Tecwyn et al., 2016; long-tailed-macaques: Plací, Eckert, Rakoczy, and Fischer, unpublished) using the same test paradigm failed to find unambiguous evidence for the presence of intuitive statistical abilities in levels comparable to apes.[3] Although much more research is needed, this might indicate that statistical reasoning has emerged late in primate evolution, perhaps only in the ape lineage. It would be of great interest to investigate the ecological pressures that could have led to the evolution from quantity discrimination abilities to probabilistic reasoning capacities.

Importantly, and in contrast to previous studies, our test design comprehensively controlled for the usage of simple heuristics based on absolute numbers of food items. In all ROR conditions we disentangled absolute and relative frequencies of peanuts, excluding the possibility that chimpanzees succeeded by simply picking the sample from the population with absolutely more preferred items. Crucially, the carrot avoidance control, which had not been tested in previous studies with apes, revealed that chimpanzees did not simply avoid the population containing more non-preferred food items (by contrast, capuchin monkeys did not perform significantly above chance level in a comparable condition in Tecwyn et al., 2016). Moreover, our ROR 1 condition provided evidence that chimpanzees truly used proportional information to solve the task, rather than, e.g. a "choose the sample from the bucket with less food"-strategy. Lastly, we did not detect any effect of session or trial number on chimpanzees' performance, making it unlikely that subjects used strategies learned over trials.

In sum, this study revealed that the signatures of intuitive statistics in chimpanzees and humans closely resemble those found in quantity discrimination tasks, thus strongly suggesting that these two abilities share the same basic and evolutionary ancient cognitive foundation, the analogue magnitude system. Moreover, we replicated previous findings on statistical reasoning in great apes with a new population of chimpanzees with a different housing and rearing background, suggesting that intuitive statistics is in fact a common capacity in chimpanzees. Lastly, this is the first study on intuitive statistics in great apes controlling for absolute number heuristics both regarding preferred and non-preferred items as well as absolute total amount, providing further evidence for true intuitive statistical reasoning in chimpanzees.

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[3] On the group level, long-tailed macaques were only successful in conditions in which they could rely on a quantity heuristic dealing with the absolute number of preferred food items (e.g. 64:16 vs. 16:64). They failed in conditions, in which absolute and relative frequencies were disentangled (e.g. 48:12 vs. 12:192; Placi et al., unpublished). Capuchin monkeys, by contrast, succeeded even in conditions disentangling absolute and relative frequencies of preferred food items. Their performance in a non-preferred food avoidance control, however, only reached marginal significance after individuals, who exhibited a side-bias in this condition were removed from the analysis (Tecwyn et al., 2016).

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Conflict of interest

The authors declare that they have no conflict of interest.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.cognition.2018.07.004.

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