Anim Cogn (2014) 17:983–995
DOI 10.1007/s10071-014-0730-7

ORIGINAL PAPER

Gambling primates: reactions to a modified Iowa Gambling Task in humans, chimpanzees and capuchin monkeys

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Received: 18 April 2013 / Revised: 17 January 2014 / Accepted: 29 January 2014 / Published online: 7 February 2014

Abstract Humans will, at times, act against their own economic self-interest, for example, in gambling situations. To explore the evolutionary roots of this behavior, we modified a traditional human gambling task, the Iowa Gambling Task (IGT), for use with chimpanzees, capuchin monkeys and humans. We expanded the traditional task to include two additional payoff structures to fully elucidate the ways in which these primate species respond to differing reward distributions versus overall quantities of rewards, a component often missing in the existing literature. We found that while all three species respond as typical humans do in the standard IGT payoff structure, species and individual differences emerge in our new payoff structures. Specifically, when variance avoidance and reward maximization conflicted, roughly equivalent numbers of apes maximized their rewards and avoided variance, indicating that the traditional payoff structure of the IGT is insufficient to disentangle these competing strategies. Capuchin monkeys showed little consistency in their choices. To determine whether this was a true species difference or an effect of task presentation, we replicated the experiment but increased the intertrial interval. In this case, several capuchin monkeys followed a reward maximization strategy, while chimpanzees retained the same strategy they had used previously. This suggests that individual differences in strategies for interacting with variance and reward maximization are present in apes, but not in capuchin monkeys. The primate gambling task presented here is a useful methodology for disentangling strategies of variance avoidance and reward maximization.

Keywords Primate · Gambling · Risk · Iowa Gambling Task · Behavioral economics

Introduction

Despite the fact that most humans are risk-averse (Kahneman and Tversky 1979), in Macau, Philippines, the largest gaming zone in the world, casino revenue was over $33 billion in 2011 (O'Keeffe 2012). Gambling is an activity in which a risk or chance dictates whether a valued resource is gained or lost (Ladouceur et al. 2000) and often leads to long-term economic losses. Rogers (1998) reports that decisions to gamble are often based on feelings, irrational thoughts and a misunderstanding of odds rather than on probabilities of earning a net profit. As evidenced by the above-mentioned casino revenue, humans do not always act optimally when presented with a conflict between the chance of an immediate payout from a bet and the long-term economic consequences (losses) of gambling behavior.

Electronic supplementary material The online version of this article (doi:10.1007/s10071-014-0730-7) contains supplementary material, which is available to authorized users.

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One frequently used method to examine choices when immediate and long-term outcomes conflict is the Iowa Gambling Task (IGT; Bechara et al. 1997). Bechara and colleagues developed the IGT to assess deficient executive processes among VMPFC-lesioned patients who were otherwise neurologically intact, but it has since been used to explore gambling in both typical and clinical populations. In their task, participants were given four decks of cards and $2,000 in facsimile money and instructed to earn as much as possible. Participants drew a card that contained either wins or losses. The decks differed in payoff structure such that two decks resulted in net losses, but included some cards that gave high (and presumably tempting) payouts, while the other two decks included no cards that led to large payouts, but over the long term consistently resulted in net gains. Most typical participants formed a preference for the less variable decks (e.g., Bechara 2005; Bowman and Turnbull 2003; Kerr and Zelazo 2004; Sevy et al. 2007; Turnbull et al. 2005; Wood et al. 2005). However, a substantial subset of individuals fail to develop a preference for the decks that will net them the greatest rewards (Glicksohn and Zilberman 2010; Glicksohn et al. 2007). Thus, while the IGT was originally used to explore the relative poor performance in lesioned as compared to intact participants, it can be a useful tool for examining patterns of choices in a variety of contexts.

A critical question is why some humans make seemingly irrational decisions in these contexts. Humans, as well as other animals, are faced with weighing costs, benefits and risk in a variety of contexts, such as finding food and mates, and often do make accurate assessments of risk and probabilities (e.g., Bechara et al. 1997; Clutton-Brock et al. 1979; Clutton-Brock and Albon 1979; Cosmides and Tooby 1996). Why, then, does the ability to accurately assess payouts sometimes fail in gambling scenarios, such as the IGT? The first goal of the current study was to take a first step toward understanding the evolutionary trajectory of suboptimal decision-making in gambling contexts by examining how other primate species respond to an IGT style task.

As a second goal, we sought to disentangle the potential strategies of reward maximization and variance avoidance, which are confounded in the IGT. That is, there are two potential motivations for people in the IGT to select the advantageous decks. They could either be motivated to earn the most overall rewards or they could be motivated to avoid too much variation in how rewards are distributed over time. For example, in the Soochow Gambling Task, a variation in the IGT, gain–loss frequency rather than overall rewards influenced deck preferences (Chiu et al. 2008). Therefore, the IGT payout structure alone is insufficient to determine *why* a participant selected the advantageous deck.

As an analogue to the IGT, we developed the Primate Gambling Task (PGT). Based on a simplified IGT designed for human children (Kerr and Zelazo 2004), the PGT is a methodology that can be used across multiple species, including humans, and is comparable to the existing human literature. As in the IGT, the primates made a choice between options with variable reward structures. We kept the methodology as similar as possible to the IGT, including having individuals interact with physical objects when making choices. One difference was that we simplified the structure to a pair of decks, rather than four, to avoid the possibility that the nonhuman species would be unable to discriminate between the larger number of options (Bunch et al. 2007). Second, we eliminated negative payoffs, as they are impossible to enact with nonhuman subjects being given food rewards on a trial-by-trial basis. The other option, having food deposited and withdrawn from cups outside of their reach, risked not being sufficiently salient to generate the emotional reactions seen in human participants. Instead, we incorporated zero payoffs, which are sufficiently aversive for these subjects to discriminate between the options (Sutton and Barto 1998). Third, to explore our second goal, we included two additional payoff structures, in addition to the original one from the IGT, to dissociate an aversion to low overall payoffs from an aversion to variability. These factors are confounded in both the traditional IGT payout structure and other studies examining choice behavior with variable payout structures (e.g., Heilbronner et al. 2008; Bechara et al. 1997; Yen et al. 2012). As a result, we were able to independently assess subjects' reactions to both variability in the payout structure and overall payoffs.

Our study consisted of three experiments. In Experiment 1, we determined how chimpanzees (*Pan troglodytes*), capuchin monkeys (*Cebus apella*) and humans (*Homo sapiens*) responded to an IGT style task and verified that humans performed similarly in our task as compared to traditional IGT tasks. Additionally, this allowed us to disentangle reactions to reward variability from those to overall payoffs. In some cases, individuals did not form a preference for one deck over the other. Because delays to rewards can influence performance on cognitive tasks (Hayden and Platt 2007; Beran et al. 2009; Wright 1999; Roche et al. 1997), for Experiment 2 we reran Experiment 1 with a longer intertrial interval to explore whether this influenced capuchins' and chimpanzees' responses. Finally, we ran a standard IGT with humans from the same population (but a different sample) as Experiment 1 to validate that this population of humans performed as expected in a traditional IGT task (Experiment 3). This step is essential as demographic factors affect performance on this task (Cauffman et al. 2010; Hooper et al. 2008; Davis et al. 2007; Evans et al. 2004).

Experiment 1

The goal of Experiment 1 was to directly compare humans and other primates using a procedure that both enabled comparisons between species and parsed the potentially competing strategies of variance aversion and reward maximization. To fully disentangle whether choices were made to maximize rewards or to seek/avoid variance in the reward distribution required three conditions. First, we used the standard payoff structure from the human IGT literature in which the low variability deck had a higher average payoff than the high variability deck, although it could pay out less on individual trials (PGT condition). In the equitable PGT condition (EPGT), we used a standard payout model from the animal literature (cf. Kacelnik and Bateson 1996; Shafir 2000; Heilbronner et al. 2008), in which average payouts of the low and high variability decks were the equivalent, so that the only factor that differed between decks was the distribution of payoffs. Finally, in the reverse PGT (RPGT) condition, the high variability deck had a higher overall payout than the low variability deck. This latter condition allowed us to fully disentangle tolerance for a varied distribution of rewards from overall reward maximization by making a variance aversion strategy conflict with a reward maximization strategy.

We hypothesized that in all three species, participants' behavior would differ across conditions. Specifically, we predicted that all three species would develop preferences for the low variability/high reward option in the PGT condition, as that option *both* minimized variability and maximized overall rewards. This is also the preferred option for humans in the typical IGT (Bechara et al. 1997). In the EPGT condition, we predicted that none of the three species would form preferences for one option over the other because, although the options differed in the way rewards were distributed (high or low variability), the mean payouts of both options were equivalent and many species appear indifferent when payouts are equivalent (Kacelnik and Bateson 1996; Shafir 2000; Steelandt et al. 2011). Finally, in the RPGT condition, in which reward maximization and risk aversion were in conflict, we did not have a directional prediction, as there are no previous studies using this payout structure.

Subjects

Humans

We tested 30 undergraduate students ($N = 21$ females, 9 males, age range 18–26 years, mean age 19.8 years) in the Learning and Development Laboratory at Georgia State University. Participants were recruited through an online recruitment system and received course credit in introductory psychology courses for participation. Participants could choose to withdraw at any time with no penalty and were debriefed after the experiment. Each participant was tested in only one condition, resulting in a between-subject design. Ten participants were tested in each condition. The Institutional Review Board at Georgia State University approved all testing procedures.

Nonhuman primates

We tested nine chimpanzees from two research centers (Yerkes National Primate Research Center Field Station (YFS): $N = 6$ females, age range = 19–39 years, mean age = 29.00 years; Language Research Center (LRC): $N = 3$, 1 female, 2 males, age range = 25–41 years, mean age = 35.00 years) and eight capuchin monkeys from the LRC ($N = 3$ females, 5 males, age range = 7–22 years, mean age = 12.75 years). All primates were socially housed and received chow, fresh fruits and vegetables several times per day. All primates had ad libitum access to water and were never food deprived. At the YFS, the chimpanzees had access to large (over 500 m^2) outdoor enclosures with climbing structures and enrichment devices as well as an indoor area with multiple rooms. These chimpanzees lived in social groups of 12 individuals. Chimpanzees at the LRC also had access to large outdoor areas (288 m^2) with multiple story climbing towers and enrichment devices as well as an indoor area with multiple rooms. Similarly, capuchin monkeys lived in indoor and outdoor enclosures with six individuals in each of two groups (Group 1: 38.79 m^2, Group 2: 39.29 m^2).

Chimpanzees were tested alone either in their home enclosure (LRC) or in a testing facility adjacent to their home enclosure (YFS). Capuchin monkeys had previously been trained to voluntarily enter individual testing chambers adjacent to their home enclosure (Evans et al. 2008). All testing was voluntary as subjects could choose whether or not to enter the testing area and participate in the study. Every individual was tested in each condition, and the condition order was counterbalanced (but limited by our number of individuals) across subjects, resulting in a within-subject design (note that this differed from the human design). All procedures complied with the American Psychological Association's Guidelines for Ethical Conduct in the Care and Use of Nonhuman Animals in Research (2012) and were approved by the Institutional Animal Care and Use Committee of each facility.

Methods

Each species was tested with the same procedure, except when species-appropriate adjustments had to be made (see

Fig. 1 Arrangement and presentation of decks. A capuchin monkey reaches for a deck of containers using specially designed doors. When the monkey opened one door, the other one closed. This prevented the monkeys from trying to select both decks simultaneously. Decks were presented to the subjects in five stacks of ten containers. Note that there were ten more containers in each deck than was necessary to complete 40 trials. This was so it never appeared to the subjects that they were nearing the end of the task or running out of containers, even if they preferentially selected from one deck. The presentation of the decks was identical across species, including humans. The monkeys were trained to voluntarily enter their test enclosures. After testing, they were returned to their social group

Table 1 Sample reward distribution by condition

Trial	PGT		EPGT		RPGT	
	LV	HV	LV	HV	LV	HV
1	3	3	3	1	2	0
2	3	0	3	6	2	6
3	2	1	2	0	1	0
4	3	6	3	3	2	0
5	2	0	2	2	1	6
6	3	0	3	1	2	6
7	2	1	2	1	1	0
8	3	0	3	6	2	6
9	2	1	2	3	1	0
10	2	1	2	2	1	6
Average payout	2.5	1.3	2.5	2.5	1.5	3
Net payout	25	13	25	25	15	30
Chance of zero	0 %	40 %	0 %	10 %	0 %	50 %

We tested three conditions with varying payout schedules. In all conditions, there was a low variability (LV) and a high variability (HV) option. In the PGT condition, the LV option led to the most overall rewards. In the EPGT, the overall rewards were equivalent. In the RPGT, the HV option led to the most overall rewards. Testing these conditions allowed us to disentangle the issues of risk and reward maximization. Randomized versions of these distributions were used for each block of ten trials. NHP was given two sessions of 40 trials each, with different randomization orders in each session. Humans received one session of 40 trials

Table 2 Individual Results for NHPs in Experiment 1

Species	Subject	PGT	EPGT	RPGT	Strategy
Chimpanzee	Barbie	I	–	I	Avoid
	Ericka	I	I	D	Max
	Georgia	I	I	I	Avoid
	Katie	I	–	–	–
	Lana	I	I	D	Max
	Mercury	I	I	D	Max
	Missy	I	–	I	Avoid
	Rita	I	I	I	Avoid
	Sherman	I	–	D	Max
Capuchin	Drella	–	–	–	–
	Gabe	–	D	–	–
	Liam	–	I	–	–
	Lily	I	–	I	Avoid
	Logan	–	–	–	–
	Nala	–	–	–	–
	Wren	–	–	D	–

In each condition, each individual was classified as having (1) an increasing monotonic function (I) indicative of learning to prefer the low variability deck, (2) a decreasing monotonic function (D) indicative of learning to prefer the high variability deck or (3) not having shown evidence of learning (-). We were also able to classify individuals as having an overall strategy of reward maximization (Max) or variance avoidance (Avoid)

below). In lieu of decks of cards, subjects of all species chose between two "decks" of small (118 ml) stackable containers (Gladware Mini Rounds©). Each deck consisted of fifty opaque containers with the same color and pattern. The decks were presented in five stacks of ten containers that were grouped together as a "deck" (see Fig. 1). Note that there were more containers in each deck than was necessary to complete the required number of trials. This was so that it never appeared to the subjects that they were nearing the end of the task or running out of containers, even if they preferentially selected from one deck. Each stack of containers was topped with an opaque lid, so that rewards inside were hidden from view. The decks differed in their payoff structure depending on the condition (see Tables 1, 2). We did not train individuals on the payout structure of each deck prior to the task, and thus, we expected learning over time.

Rewards were loaded in the containers out of view of the participant prior to the start of the session. When a participant indicated their choice of a deck, the top container was removed and the contents were immediately given to the participant. This resulted in immediate rewards, which are typically used in animal, but not human, studies (for other studies in which humans received immediate rewards, see Brosnan et al. 2011, 2012).

The decks of containers were randomized for presentation side as well as meaning. That is, for half of the participants of each species, one color/pattern was the low variability deck, while that same deck was the high variability deck for other participants. Each deck was unique to one condition (i.e., pairs of differently colored/patterned decks were used in each condition; see Online Resource Table S1 for the specific colors and patterns). The next trial began as soon as the participants finished processing the rewards. Choices were recorded during the experiment and video recorded for verification.

Human methods

Humans indicated their choice by either pointing to or verbally indicating the deck. They were rewarded with facsimile money, as in Bechara et al. (1997). Even though humans were not tested with a valuable reward, previous work demonstrated that facsimile and real money yielded similar results on the IGT (Bowman and Turnbull 2003). After the subject made a selection, the researcher poured the rewards on the table in front of the participant, who then collected the coins and stored them in a bag. It is important to note that we did not give the humans explicit instructions to maximize their rewards. We instead relied on them having a preference for more rewards over fewer, as was assumed with monkeys and chimpanzees. Humans were tested in only one session (40 trials) and one condition (i.e., a between-subject design) to avoid biasing their decisions by running longer sessions (the other primates received two sessions of 40 trials of each condition) or by running all three conditions in a row (they were only given one session per day). We were not able to bring human subjects back to the laboratory on subsequent days.

Nonhuman primate methods

Prior to being included in the study, nonhuman primates had to pass quantity preference tests to ensure they preferred larger to smaller quantities. This was essential to compare the current study to the typical human IGT, in which participants are told to maximize their rewards (Bechara et al. 1997). As we could not give verbal instructions, we had to assume this was driving their behavior based on their quantity preferences. In our task, potential reward quantities were 6, 3, 2, 1 and 0. To test their preferences, subjects were presented with a choice of two quantities with the lowest ratio difference between them, as lower ratio differences are more challenging to discriminate (Hanus and Call 2007). Two sessions of ten trials for each of the following quantities were given: 6/3, 3/2 and 2/1 (a total of 6 sessions). If the nonhuman primates could discriminate between the quantities with the lowest ratio difference (e.g., 2/1), we assumed they could discriminate quantities with a higher ratio difference (e.g., 6/1). They had to demonstrate a significant preference for the larger quantity in at least 15 out of 20 trials (Binomial test, $p < 0.05$) to be included in the study. All animals successfully discriminated these quantities.

During testing, chimpanzees and capuchin monkeys were given two sessions of 40 trials (80 total trials) of each condition. The order of conditions was counterbalanced (within the limits of our sample size) to eliminate order effects (i.e., a within-subject design). No subject was given more than one session per day.

Chimpanzees Chimpanzees touched the tray in front of the stacks of containers to indicate a choice. If a chimpanzee touched the tray in front of both stacks simultaneously or touched a space that was not directly in front of a deck, the tray was removed and the trial was restarted. After a choice, the selected container was emptied into the chimpanzee's enclosure. Rewards were 1 cm^3 dried, non-sweetened pieces of coconut.

Capuchin monkeys Each test chamber was fitted with doors that allowed capuchin monkeys to reach for one deck, but blocked them from reaching toward both decks simultaneously (see Fig. 1). The monkeys all had prior experience making a dichotomous choice using this mechanism (Salwiczek et al. 2012). After the monkey made a choice, the container was presented to the monkey, and it was able to take the rewards (Bio-Serv® 45-mg, grain-based, banana-flavored, dustless precision pellets) directly from the container.

Results

Individual differences

As individual differences are well documented in human IGT performance, we follow previous work (Glicksohn and Zilberman 2010; Glicksohn et al. 2007; Davis et al. 2007) and first assess whether or not each individual showed performance indicative of learning in each condition. Online Resource Figure S1 includes individual graphs for the nonhuman primates. Unfortunately, due to the restrictions of the IRB, which followed the typical IRB standards, our consent form signed by human subjects stated that findings would be "summarized and presented in group form"; hence, we cannot present the individual human graphs. We discuss humans' results and present graphs of group means by each learning type in each condition for humans.

To assess learning over time, we divided the trials into four equal blocks of trials. For nonhuman primates, trial

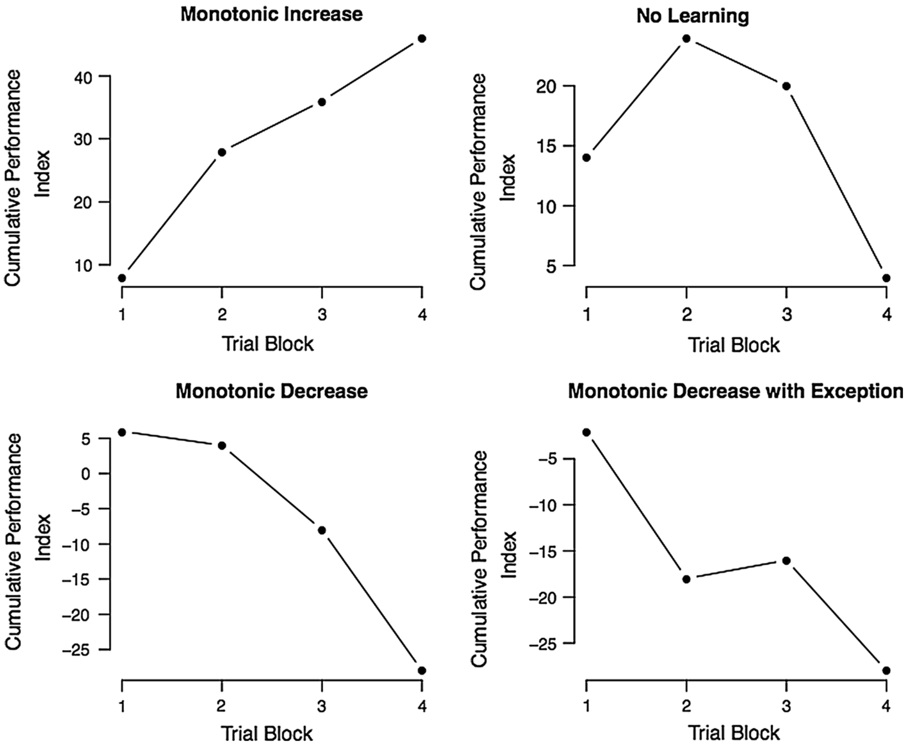

Fig. 2 Examples of monotonic curves. We classified each individual as having an increasing or decreasing monotonic function or as not having learned. Here we show examples of each category. Increasing monotonic functions are indicative of having learned to prefer the less variable reward distribution, while decreasing monotonic functions are indicative of having learned to prefer the more variable reward distribution. Note that we allowed one violation of monotonicity for nonhuman primates, as there was a temporal break and side counterbalancing between sessions (i.e., between trial blocks 2 and 3). See Online Resource Figure S1 for the graphs for each individual in each condition

blocks consisted of 20 trials with blocks 1 and 2 run successively in session 1 and blocks 3 and 4 run successively in session 2. For humans, trial blocks consisted of 10 trials and occurred within one session. For an individual to be classified as having learned, their cumulative number of low variability choices minus the number of low variability choices across trial blocks had to result in a monotonic function (Glicksohn and Zilberman 2010; Glicksohn et al. 2007). A monotonic function is either nonincreasing or nondecreasing. Monotonically increasing functions were indicative of learning to preferentially select the low variability deck, while monotonically decreasing functions were indicative of learning to preferentially select the high variability deck. Although previous work assumes that only monotonically increasing functions are a valid strategy (Glicksohn and Zilberman 2010; Glicksohn et al. 2007), we counted both monotonically increasing and decreasing functions as evidence of learning, because a decreasing monotonic function was a valid strategy in the RPGT condition that indicated reward maximization. If an individual's cumulative performance did not result in a monotonically increasing or decreasing function, they were classified as not having learned. Note that our definition of monotonicity likely excluded some individuals who showed weaker evidence of learning. That is, an animal that experimented with both options during trial blocks 1 and 2 but settled on a strategy in blocks 3 and 4 may not have been classified as having learned. However, in order to avoid inappropriately assigning animals a preference, we used the most conservative definition. See Fig. 2 for example of monotonic functions.

However, we allowed two exceptions to monotonicity. First, because there was both a temporal delay and deck location counterbalancing between sessions for the chimpanzees and monkeys, we a priori expected some experimentation during the beginning of the second session (i.e., between trial blocks 2 and 3). Therefore, we allowed for one violation of monotonicity if, and only if, that violation occurred between the second and third trial blocks (see Fig. 2). Second, we made a *post hoc* exception for five humans who chose equally from both decks over the last three trial blocks, indicating performance at chance, but due to their experimentation in the first trial block, their cumulative performance measure resulted in a monotonic function. These humans were classified as not having learned. Using these exceptions resulted in one additional chimpanzee being classified as having learned in the RPGT condition and five humans being classified as not having learned (these were evenly distributed across conditions; two in the PGT condition, two in the EPGT condition, and one in the RPGT condition). We also excluded one capuchin monkey from the study because he chose the deck on the left side in over 95 % of trials across all three conditions, indicating a strong side bias.

Finally, we computed a low to high variability choice ratio (LH ratio), which was the number of low variability choices divided by the number of high variability choices, to compare the ratio of choices between individuals that learned and those that did not (Glicksohn et al. 2007; Glicksohn and Zilberman 2010).

PGT Condition In the PGT condition, which most closely resembled the IGT payoff structure, 40 % of humans, 100 % of chimpanzees and 14.3 % of capuchin monkeys had monotonically increasing functions, indicative of learning to prefer the low variability, high reward deck (humans: $N = 4$, mean LH ratio = 4.25, SE = 1.59, range 1.35–7.00; chimpanzees: $N = 9$, mean LH ratio = 4.30, SE = 0.95, range 1.35–10.43; capuchin monkeys: $N = 1$, LH ratio = 3.00). The remaining individuals did not show evidence of learning. See Online Resource Table S2 for mean choices for the low variability option for each learning type by trial block.

We did not have sufficient numbers of individuals within each species to statistically examine differences between learners and nonlearners within each species. We do note that the LH ratio of all learners and those who failed to show evidence of learning were significantly different (Mann–Whitney U = 7.00, $p < 0.001$; learners: $N = 14$, mean = 4.19, SE = 0.73, range 1.35–10.43; nonlearners: $N = 12$, mean = 1.13, SE = 0.09, range 0.60–1.67); however, due to the fact that this measure lumps all species together, this result may be masking important differences between the species.

EPGT condition In the EPGT condition, in which overall payoffs were equivalent but variability differed, 20 % of humans, 55.6 % of chimpanzees and 14.3 % of capuchin monkeys had monotonically increasing functions, indicative of learning to prefer the low variability deck (humans: $N = 2$, mean LH ratio = 1.29, SE = 0.07, range 1.22–1.35; chimpanzees: $N = 5$, mean LH ratio = 11.53, SE = 7.15, range 1.67–39.00; capuchin monkeys: $N = 1$, LH ratio = 2.48). One capuchin monkey had a monotonically decreasing function, indicating learning to prefer the high variability deck (LH ratio = 0.01). The remaining individuals failed to show evidence of learning. See Online Resource Table S2 for mean choices for the low variability option for each learning type by trial block.

Again, monotonically increasing learners and nonlearners had significantly different LH ratios (Mann–Whitney U = 13.00, $p < 0.001$; learners: $N = 8$, mean LH ratio = 7.84, SE = 4.64, range 1.22–39.00; nonlearners: $N = 17$, mean LH ratio = 1.24, SE = 0.11, range 0.67–2.33). There was only a single capuchin monkey who showed evidence of learning to prefer the high variability option (LH ratio = 0.01).

RPGT condition In the RPGT condition, reward maximization and variance avoidance were in conflict. That is, the low variability deck led to fewer overall rewards than the high variability deck. In all species, subjects were roughly equally likely to prefer the variance avoiding (low payoff) strategy and the high variability (high payoff) strategy. The former included 20 % of humans, 44.4 % of chimpanzees and 14.3 % of capuchin monkeys who learned to prefer the low variability, low payoff deck, suggesting a variance avoidance strategy (humans: $N = 2$, mean LH ratio = 0.75, SE = 0.75, range 0.00–1.50; chimpanzees: $N = 4$, mean LH ratio = 2.81, SE = 0.34, range 1.86–3.35; capuchin monkeys: $N = 1$, LH ratio = 79.00). The latter included 40 % of humans, 44.4 % of chimpanzees and 14.3 % of capuchin monkeys who learned to prefer the high variability, high payoff deck, suggesting a reward maximizing strategy (humans: $N = 4$, mean LH ratio = 0.39, SE = 0.08, range 0.18–0.54; chimpanzees: $N = 4$, mean LH ratio = 0.60, SE = 0.10, range 0.48–0.90; capuchin monkeys: $N = 1$, LH ratio = 0.36). The remaining individuals did not show evidence of learning. See Online Resource Table S2 for mean choices for the low variability option for each learning type by trial block.

In the RPGT there were sufficient individuals within each type of learning (monotonically increasing and decreasing) as well as nonlearners to compare all three groups, which were significantly different from each other (Kruskal–Wallis $H(2) = 14.18$, $p < 0.001$; monotonically increasing: $N = 7$, mean LH ratio = 13.10, SE = 10.99, range 0–79; monotonically decreasing: $N = 9$, mean LH ratio = 0.48, SE = 0.07, range 0.18–0.90; nonlearners: $N = 10$, mean LH ratio = 0.97, SE = 0.04, range 0.74–1.22).

Consistency within individuals Because the chimpanzees and capuchin monkeys were tested in a within-subject design, we were able to look at individual strategies across conditions. In this task, there are two strategy dimensions, one based on the amount of variability in each deck and one based on the overall payout of each deck. We classified individuals as reward maximizing, variance avoidant or not having a strategy. Reward maximizing individuals were those that learned to select the low variance, high payout deck in the PGT condition and the high variance, high payout deck in the RPGT condition. In the EPGT there was no reward maximizing option, so we did not require any specific choice pattern in this condition to classify individuals as reward maximizing.

Variance avoidant individuals preferred the low variance, high payout deck in the PGT condition, the low variance deck in the EPGT condition and the low variance, low reward option in the RPGT. We also classified individuals as variance avoidant if they preferred the low variance, high payout deck in the PGT condition, had no preference in the EPGT condition and preferred the low variance, low reward option in the RPGT, as they appeared variance avoidant, in the conditions with the most variance (see Table 2).

Using this classification system, four chimpanzees were reward maximizers and four chimpanzees and one capuchin monkey were variance avoidant. The remaining individuals did not show a consistent strategy across conditions.

Discussion

Our results suggest that the PGT is appropriate for exploring decision-making in nonhuman primates and that deck preferences in our PGT condition, and by analogy, the IGT, are largely due to the conflation of reward maximization and variance reduction; most individuals showed strong preferences on one of these dimensions or the other, but individuals vary on which of these dimensions drives their choice behavior. While most individuals were either indifferent or variance avoidant when the overall rewards were equivalent (EPGT condition), there was a great deal of individual variation when reward maximization and variance avoidance conflicted (RPGT condition). When these dimensions conflicted, 50 % of both the chimpanzees and the humans who showed evidence of learning preferred each option. This suggests that there is substantial individual variation in preferences for reward maximization or variance avoidance in both humans and chimpanzees that, again, likely drives the strong consistency seen in the typical IGT. Only one of our capuchin monkey subjects showed evidence of learning to prefer a deck in multiple conditions. Whether this represents a species difference or a difference in approach to the task is not clear and is the question that we address in Experiment 2.

Experiment 2

Comparative cognitive tests are particularly susceptible to influence due to features of the test design that may imply species differences where none exist, so before concluding that capuchin monkeys did indeed behave differently than the apes, we followed up with a variation on our procedure. One common feature that influences responses to cognitive tasks is the time period between trials within the test session (e.g., the intertrial interval, or ITI; Beran et al. 2009; Wright 1999; Roche et al. 1997). Capuchin monkeys in particular appear to be sensitive to changes in ITI (at least as compared to another frequently tested primate species, rhesus macaques; Wright 1999). Some studies suggest that subjects' choices are less consistent with shorter ITIs (Prétôt, Salwiczek, Bshary & Brosnan, unpublished data; Salwiczek et al. 2012), possibly because the costs of a less rewarding choice are lower when the ITI is shorter, reducing learning. To determine whether more capuchin monkeys would show evidence of learning with a longer ITI, we replicated Experiment 1 with a 10-second ITI between all trials. The inclusion of chimpanzees allowed us to determine the degree to which the ITI length influenced capuchin monkeys as compared to chimpanzees in our study.

Subjects

We tested the three chimpanzees and seven capuchin monkeys housed at the LRC of Georgia State University that were used in Experiment 1. We were unable to test chimpanzee from the YFS as the chimpanzees there were undergoing social group restructuring for management purposes and were not available for research.

Methods

The methods were identical to those of Experiment 1 except for the inclusion of a 10-s ITI that began as soon as they acquired their rewards. For capuchin monkeys, the choice doors were held closed during this time to prevent them from grabbing the decks. For chimpanzees, the tray on which the decks were presented was pulled away from them during this time. All new colors and patterns were used for the decks to minimize carryover learning from Experiment 1. All subjects were tested on this version of the task subsequent to completing Experiment 1.

Results

Individual differences

As in Experiment 1, we allowed one exception to strict monotonicity between trial blocks 2 and 3 due to the temporal distance between sessions 1 and 2 and the deck counterbalancing (because humans were not tested, we did not allow the second exception). This resulted in seven monotonic exceptions (one chimpanzee and one capuchin in the PGT condition, one chimpanzee in the EPGT condition and four capuchin monkeys in the RPGT condition). Although we can make only a qualitative assessment, it appears that in our study, temporal spacing and/or counterbalancing may have a greater influence on capuchin monkeys relative to chimpanzees. See Online Resource 1 for graphs of each individual's cumulative performance measure in each condition.

PGT condition Chimpanzees' behavior was similar between Experiments 1 and 2, but capuchin monkeys

Table 3 Individual Results in Experiment 2

Species	Subject	PGT	EPGT	RPGT	Strategy
Chimpanzee	Lana	I	I	D	Max
	Mercury	I	I	D	Max
	Sherman	I	I	D	Max
Capuchin	Drella	I	–	D	Max
	Gabe	I	–	D	Max
	Liam	I	–	D	Max
	Lily	–	–	D	–
	Logan	I	–	D	Max
	Nala	–	–	D	–
	Wren	I	D	D	Max

In each condition, each individual was classified as having (1) an increasing monotonic function (I) indicative of learning to prefer the low variability deck, (2) a decreasing monotonic function (D) indicative of learning to prefer the high variability deck or (3) not having shown evidence of learning (-). We were also able to classify individuals as having an overall strategy of reward maximization (Max) or variance avoidance (Avoid)

showed increased learning with the increased ITI length in Experiment 2. As in Experiment 1, 100 % of chimpanzees showed evidence of learning to prefer the low variability, high payoff option ($N = 3$, mean LH ratio = 3.36, SE = 0.81, range 1.76–4.33). In contrast, capuchin monkeys' behavior differed substantially between the two experiments. In Experiment 2, 71.4 % showed evidence of learning to prefer the low variability, high payoff option ($N = 5$, mean LH ration = 2.11, SE = 0.21, range: 1.50–2.64), while only 28.6 % ($N = 2$) showed evidence of learning in Experiment 1. See Table 3 for individual strategies and online Resource Table S2 for mean choices for the low variability option for each learning type by trial block.

EPGT condition Neither chimpanzees nor capuchins showed a change in behavior with the increase in ITI. In the EPGT condition, where payouts were the same and the decks only differed in the variance of rewards, chimpanzees and capuchins both showed similar behavior in Experiments 1 and 2. In this experiment, 100 % of chimpanzees showed evidence of learning to prefer the low variability deck (N = 3, mean LH ratio = 5.70, SE = 3.34, range: 1.76–12.33). In Experiment 1, two of these three chimpanzees showed the same strategy and the remaining chimpanzee did not show evidence of learning. Among capuchins in Experiment 2, one monkey (LH ratio = 0.82) showed evidence of learning to prefer the high variability option and six capuchin monkeys did not show evidence of learning (mean LH ratio = 1.08, SE = 0.08, range: 0.82–1.42). In Experiment 1, two monkeys showed evidence of learning: one for the low variability deck and one for the high variability deck. See Table 3 for individual strategies and online Resource Table S2 for mean choices for the low variability option for each learning type by trial block.

RPGT condition In this condition, as in the PGT, the chimpanzees' behavior was the same between the experiments, but more capuchin monkeys showed evidence of learning with the longer ITI. In the RPGT condition of Experiment 2, where variance avoidance and reward maximization conflicted, 100 % of both chimpanzees and capuchin monkeys showed evidence of learning to prefer the high variability deck that led to the most overall rewards (chimpanzees: $N = 3$, mean LH ratio = 0.20, SE = 0.13, range: 0.01–0.45 $N = 7$, mean; capuchin monkey: LH ratio = 0.39, SE = 0.06, range: 0.13–0.57). For chimpanzees, this is the same pattern they showed in Experiment 1, but only two capuchin monkeys had shown evidence of learning with the shorter ITI in Experiment 1 (one for the low variability deck and one for the high variability deck). See Table 3 for individual strategies and online Resource Table S2 for mean choices for the low variability option for each learning type by trial block.

Consistency within individuals in Experiment 2

Using the same classification system as in Experiment 1, we classified all three chimpanzees and five capuchin monkeys as reward maximizers. The remaining two monkeys did not show consistency across conditions. Thus, more capuchin monkeys showed evidence of consistent behavior (reward maximization) with the longer ITI, although the chimpanzees' behavior was not affected (see Table 3).

Consistency within individuals between Experiments 1 and 2

All three of the chimpanzees tested in Experiment 1 were classified the same way, as reward maximizers, in Experiment 2. In contrast, there was no consistency between capuchin strategies in Experiments 1 and 2. The single monkey who was classified as variance avoidant in Experiment 1 did not exhibit a strategy in Experiment 2. Five monkeys who failed to develop a strategy in Experiment 1 were reward maximizers in Experiment 2. The remaining monkey failed to exhibit a strategy in both Experiments (see Tables 2 and 3).

Discussion

The inclusion of an ITI affected capuchin monkey performance in the PGT and RPGT conditions, with subjects overwhelmingly preferring options that maximized rewards, but not the EPGT condition, in which the average rewards were the same in both conditions. In contrast, all three chimpanzees showed the same pattern of choices in the PGT and RPGT conditions, and a single chimpanzee avoided variance in the EPGT where he had not before. We hypothesize that the inclusion of an ITI likely made the costs for choosing options that did not lead to the greater average payout relatively higher by increasing the time until the next opportunity to be rewarded (Roche et al. 1997). However, the inclusion of an ITI may have affected chimpanzees and capuchin monkeys differently. The one chimpanzee who showed any change in behavior appeared to become more sensitive to variance, while capuchin monkey seemed to make choices solely on the basis of reward maximization.

We cannot rule out the possibility that the behavioral change between Experiments 1 and 2 was due to the fact that the subjects had more exposure to the task and so may have better learned the game parameters. However, as both species completed Experiment 1 prior to Experiment 2, but only the capuchins showed a change in behavior, the results nonetheless indicate that a longer ITI influenced the capuchin monkeys more so than the chimpanzees. Additionally, while the subjects had previous experience with the procedure and payoff contingencies, they had experienced relatively few trials in Experiment 1 (80 per condition) and we used all new color/pattern combinations for each deck in Experiment 2. The use of novel decks meant that they still had to explore the game space and develop a strategy within each condition. Additionally, we note that the important result is that the capuchins do, in some circumstances, develop consistent patterns of choice behavior that are similar to those seen in chimpanzees (Brosnan et al. 2011). This indicates that while there may be a species difference in how they are influenced by the test procedure, both species still show a preference for reward maximization in the three conditions of our PGT.

Experiment 3

Human performance on the IGT is fairly consistent (see, e.g., Bechara 2005; Bowman and Turnbull 2003; Kerr and Zelazo 2004; Sevy et al. 2007; Turnbull et al. 2005; Wood et al. 2005), but some population differences have been noted related to age (Cauffman et al. 2010), personality (Hooper et al. 2008; Davis et al. 2007), education level (Evans et al. 2004) and culture (Bakos et al. 2010). Thus, to verify that subjects from our human population respond similarly to the IGT as compared to subjects from other populations, we ran a traditional IGT on a separate sample of human participants from the same pool of subjects. This allowed us to verify that the similarity in responses between the PGT and the typical IGT was due to similarity in how humans and other primates interpreted the procedure and was not influenced by differences in our human population.

Methods

We tested 110 undergraduate students ($N = 94$ females, 16 males, age range 18–48 years, mean age 20.26 years) in the Individual Differences and Developmental Psychopathology Laboratory at Georgia State University. Participants were recruited through an online recruitment system and received partial course credit for participation. The Institutional Review Board at Georgia State University approved all testing procedures. Participants completed the standard administrations of the computerized version of the IGT that consists of 100 trials (i.e., 100 card selections; Bechara 2007). As described earlier, in this task participants are instructed to select a card from among four decks of cards labeled A', B', C' and D'. In two decks (A' and B'), immediate gains are large, but at unpredictable times, the gains are followed by a high penalty. In the long run, these decks are disadvantageous. In the other two decks (C' and D'), immediate gains are smaller, but eventual losses are also smaller. In the long run, these decks are advantageous.

Results

Results were consistent with findings among human participants on the PGT (see Experiment 1 above), as well as previous research on the traditional IGT (e.g., Bechara et al. 1997). Specifically, the mean IGT Total Net Score (a typical human measure of IGT performance), an index of the difference between the total number of cards selected from advantageous decks and the total number of cards selected from disadvantageous decks, was positive, indicating a preference for the advantageous decks ($M = 10.76$, $SD = 29.01$).

Discussion

Subjects from the same subject pool made choices in the IGT that were expected based on results of other typical IGT tests in other populations. This confirms that the human results in the PGT in Experiment 1 are derived from a population that shows anticipated results on a traditional computerized IGT (Bechara 2007). This provides further support for the PGT as an IGT analogue.

General discussion

Our goal was to begin to explore the evolutionary trajectory of human decision-making as evidenced in the IGT as well as to disentangle reward maximization and variance avoidance in both humans and other primates. We accomplished this by modifying the IGT to include three conditions (the original condition plus two that disentangled reward maximization from variance avoidance) and made it appropriate for nonhuman species. When reward maximization and variance avoidance coincided (our PGT condition), all three species chose the option that maximized reward and minimized variance, as in traditional IGTs with human subjects (e.g., Bechara et al. 1997). We additionally found that, as with humans in the IGT, not all individuals developed a strategy, suggesting that some individuals are relatively less influenced by these factors (Davis et al. 2007; Glicksohn and Zilberman 2010; Glicksohn et al. 2007). Thus, we find evidence for consistency in responses across the primates in an IGT style task.

Moreover, we were able to disentangle the strategies of reward maximization and variance avoidance by the inclusion of two additional payoff structures that disentangle these confounded goals (Chiu et al. 2008). In all species, we found that subjects were more likely to maximize rewards when these goals conflicted (e.g., in our RPGT; in particular see the chimpanzees' and monkeys' responses in Experiment 2), although a subset preferred to minimize variance at the expense of reward when the ITI was short (e.g., Experiment 1). Because of the within-subject design used with the nonhuman primates, we were also able to compare the capuchins' and chimpanzees' responses across all three conditions. Chimpanzees were equally likely to be reward maximizing or variance avoidant, which is in line with data from humans (Zaleskiewicz 2001; Trimpop 1994; Bromiley and Curley 1992; Horvath and Zuckerman 1993; Wong and Carducci 1991; Zuckerman 1994). In contrast, capuchin monkeys predominantly chose to maximize rewards (only in Experiment 2, with the longer ITI; in Experiment 1 only one subject showed a consistent strategy across conditions). This may indicate that there is less overall individual variation in capuchin monkeys as compared to chimpanzees, something that has been seen in other situations in which they respond to rewards in an experimental setting (e.g., Brosnan and de Waal 2003; Brosnan et al. 2005).

Risk is used in many different ways in the animal literature, but here we compare our results to others that vary the probability of a given outcome. Most of the work on risk preferences in primates has used a payoff structure where the "risky" and constant options had equivalent overall rewards and only varied in the way those rewards were distributed, as in our EPGT condition (Rosati and Hare 2012; Heilbronner et al. 2008). Typically, the "risky" option involves a 50 % probability of getting the highest value reward and a 50 % chance of getting the lowest value reward; the average payoff was the same between this and the "safe" option. In another capuchin study, capuchins in this payoff structure varied in whether they were risk avoidant or seeking and no species wide patterns emerged (Steelandt et al. 2011), much as we found in our EPGT. Chimpanzees present a more complex picture. In the "risky" payoff structure described above, chimpanzees have been classified as risk-prone, preferentially selecting the more variable option with this payout structure (Heilbronner et al. 2008; Rosati and Hare 2012). In contrast, in our EPGT condition, where both options also had the same average payoff, chimpanzees were either variance avoidant or indifferent.

We suspect that this difference in behavior is due to the salience of the frequency of gains, or jackpots, in the previous work. That is, when the probability of winning a jackpot is 50 % and both options lead to equivalent overall rewards, primates may attend preferentially to gains (Hayden et al. 2008; Chiu et al. 2008). In our EPGT condition, the probability of getting a jackpot was 20 %, and we included five different potential payouts rather than two. Supporting this, Haun et al. (2011) also found that chimpanzees were risk-prone, but noted that they decreased their preference for risk as the probability of getting a jackpot decreased. Additionally, humans preferentially select options with higher gain frequencies even when that leads to fewer overall rewards (Chiu et al. 2008). Thus, the way variability is constructed in the experimental design may be influencing these choices rather than risk preferences, *per se*. Even within our task, factors such as different numbers of potential outcomes may play a role. By altering the number of potential payouts, we also manipulated the amount of uncertainty within each condition. Thus, a possible explanation for individuals selecting the more variable option in the RPGT condition, where there are two potential outcomes, but not in the PGT condition, where there are five potential outcomes, could be due to the lower amount of uncertainty in the RPGT condition. This suggests that future work should incorporate a measure of relative risk, such as the coefficient of variability, which takes into account all of the potential outcomes (Weber et al. 2004).

Clearly, additional work is needed to explore both the degree to which there are continuities between humans and other species and individual differences between individuals within a species, as well as to determine the differing influences of reward maximization and variance reduction (and, possibly, other factors) on decision-making. In particular, the nonhuman primates studied to date show convergences in both social structure and feeding ecology, both of which may influence decision-making in the context of risk; more studies are needed that explore the influences of these features on the above-mentioned questions, both in primates and in nonprimate species. Additionally, emerging work on nonhuman primate personalities (e.g., Freeman et al. 2013; Morton et al. 2013) may shed light on the individual variation seen here, as is the case in humans (Davis et al. 2007; Glicksohn and Zilberman 2010; Bechara and Damasio 2002). We encourage the use of the PGT or other tasks that disentangle competing goals and are comparable to existing studies to better develop comparative literature on decision-making in the context of risk.

Acknowledgments We thank the animal care and veterinary staff at the Yerkes National Primate Research Center and the Language Research Center for maintaining the health and well-being of the chimpanzees. DP was supported by an American Psychological Association Dissertation Research Award (2011), NIH/NIGMS IRACDA grant K12 GM000680 awarded to Emory University and NSF SES 0847351 awarded to SFB. SFB was funded by NSF CAREER Award SES 0847351, NSF HSD grant SES 0729244 and NSF SES 1123897. At Yerkes, this work was supported by the Living Links Center, Emory's College of Arts and Sciences and the base grant of the National Center for Research Resources P51RR165 to the YNPRC, currently supported by the Office of Research Infrastructure Programs/OD P51OD11132. The YNPRC is fully accredited by the American Association for Accreditation for Laboratory Animal Care. This research complied with all laws of the United States of America.

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