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Capuchin Monkeys Exercise Self-control by Choosing Token Exchange Over an Immediate Reward

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Self-control is a prerequisite for complex cognitive processes such as cooperation and planning. As such, comparative studies of self-control may help elucidate the evolutionary origin of these capacities. A variety of methods have been developed to test for self-control in non-human primates that include some variation of foregoing an immediate reward in order to gain a more favorable reward. We used a token exchange paradigm to test for self-control in capuchin monkeys (*Cebus apella*). Animals were trained that particular tokens could be exchanged for food items worth different values. To test for self-control, a monkey was provided with a token that was associated with a lower-value food. When the monkey exchanged the token, the experimenter provided the monkey with a choice between the lower-value food item associated with the token or another token that was associated with a higher-value food. If the monkey chose the token, they could then exchange it for the higher-value food. Of seven monkeys trained to exchange tokens, five demonstrated that they attributed value to the tokens by differentially selecting tokens for higher-value foods over tokens for lower-value foods. When provided with a choice between a food item or a token for a higher-value food, two monkeys selected the token significantly more than expected by chance. The ability of capuchin monkeys to forego an immediate food reward and select a token that could then be traded for a more preferred food demonstrated some degree of self-control. Thus, results suggest a token exchange paradigm could be a successful technique for assessing self-control in this New World species.

Comparative cognitive ethology, or the study of the evolution of cognitive functioning, involves investigation of the presence or absence of cognitive capacities across species (Shettleworth, 2010). Of interest are nonhuman primates because knowledge of their abilities may inform the evolution of cognitive abilities in humans (*Homo sapiens*). Complex cognitive processes localized to some extent within the prefrontal cortex are of particular interest because these so-called executive functions govern response inhibition, planning, decision-making, and other processes (Fuster, 2008). Experimental investigations of prefrontal structure and function using animal models indicate a great degree of homology with humans in many of these executive functions (Chudasama, 2011). The study of response inhibition, or self-control, is a particularly rich area because some degree of self-control or lack of impulsivity is thought to be a prerequisite for adaptive decision-making, future planning, and cooperative behavior (Kacelnik, 2003; Rachlin, 2002; Rosati, Stevens, Hare, & Hauser, 2007).

Self-control can be defined as seeking to obtain a larger reward in the future over a smaller reward in the present (Rachlin, 1974). A wide variety of exchange and choice tasks have shown that nonhuman primates will forego an immediate reward to obtain a larger or more valued reward. For example, brown capuchin monkeys (*Cebus apella*) will exchange low-value foods for high-value foods (Drapier, Chauvin, Dufour, Uhlrich, & Thierry, 2005; Ramseyer, Pelé, Dufour, Chauvin, & Thierry, 2006). Chimpanzees (*Pan troglodytes*) and brown capuchins will exchange small quantities of food for larger quantities (Dufour, Pelé, Sterck, & Thierry 2007; Drapier et al., 2005). Brown capuchins will also choose not to eat a piece of food so that the food can be used as a tool to obtain a more valued food (Evans & Westergaard, 2006). Brown capuchins, cotton-top

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tamarins (*Saguinus oedipus*), common marmosets (*Callithrix jacchus*), rhesus macaques (*Macaca mulatta*), long-tailed macaques (*Macaca fascicularis*), Tonkean macaques (*Macaca tonkeana*), chimpanzees and bonobos (*Pan paniscus*) will choose a larger delayed reward over a smaller more immediate reward (Addessi, Paglieri, & Focaroli, 2011; Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999; Pelé, Micheletta, Uhlrich, Thierry, & Dufour, 2011; Rosati, Stevens, & Hauser, 2006; Stevens, Hallinan, & Hauser, 2005; Stevens, Rosati, Ross, & Hauser, 2005; Szalda-Petree, Craft, Martin, & Deditius-Island, 2004; Tobin, Logue, Chelonis, Ackerman, & May, 1996). Similarly, many primate species (capuchin monkeys, squirrel monkeys, *Saimiri sciureus*, rhesus macaques, long-tailed macaques, Tonkean macaques, chimpanzees, and orangutans, *Pongo pygmaeus*) will forego consuming a small quantity of rewards to allow them to accumulate up to a larger quantity (Anderson, Kuroshima, & Fujita, 2010; Beran, 2002; Beran & Evans, 2006, 2009; Evans & Beran, 2007; Pelé, Dufour, Micheletta, & Thierry, 2009; Pelé et al., 2011). Cotton-top tamarins and common marmosets will also choose to travel greater distances to obtain large rewards rather than shorter distances for smaller rewards (Stevens et al., 2005). The studies show general success across a wide range of primate species in foregoing an immediate reward to optimize yield. Evidence also exists for self-control in non-primate species (sea lions, *Zalophus californianus*, Genty & Roeder, 2006; cleaner wrasse, *Labroides dimidiatus*, Danisman, Bshary, & Bergmüller, 2009).

A recent study by Beran and Evans (2012) has experimented with using a symbol for a reinforcer rather than the reinforcer itself in the study of self-control. Animals can learn to attribute value to particular objects after they are associated with particular foods (Addessi, Crescimbene, & Visalberghi, 2007; Addessi, Mancini, Crescimbene, Padoa-Schioppa, & Visalberghi, 2008; Brosnan & de Waal, 2004). The objects become symbols or tokens for the food items and animals then selectively choose to exchange the token associated with the higher-value food with an experimenter to obtain the food item. In the Beran and Evans (2012) study, chimpanzees given a choice between a food item and a token that could be exchanged for a higher-quality food item displayed self-control in that they tended to select the token for later exchange rather than the immediately available food. Symbols as reinforcers have been incorporated into other self-control studies and have been shown to improve performance. For example, Boysen and Berntson (1995) trained two chimpanzees on a reversed-reward contingency task in which the animals were given a choice between a large and small quantity of food. In the reversed-reward task, the animals needed to select the smaller amount of food to obtain the larger amount. Neither animal could learn the task, but when the food arrays were changed to Arabic numeric symbols, both chimpanzees successfully selected the smaller numeral to obtain the larger reward. Similar improvement was found in brown capuchins undergoing a reverse-reward contingency task with tokens as symbols for the real foods (Addessi & Rossi, 2011). The same pattern was found in human children (*Homo sapiens*) undergoing a reverse-reward contingency task in which selecting a smaller amount of candy over a larger amount yielded the larger amount (Carlson, Davis, & Leach, 2005). Children's performance improved when the actual candies were replaced with symbols for the candy.

As in the Beran and Evans (2012) study of chimpanzees, we tested whether brown capuchin monkeys would select a token symbol for a food reward over an immediately available food of lesser value. If animals exercised self-control, we expected that they would forego the immediate food reward and instead select the token that could then be exchanged for the more preferred food. We designed some of the tests so that both foods were highly preferred (e.g., apple versus raisin), so if monkeys elected to forego the immediate reward, it was not because they did not desire the food item being offered. We expected capuchins to show some degree of self-control because they have performed successfully in other self-control tasks (Addessi et al., in press; Addessi, et al., 2011; Addessi & Rossi, 2011; Anderson, Hattori, & Fujita, 2008; Anderson et al., 2010; Bramlett, Perdue, Evans, & Beran, 2012; Drapier et al., 2005; Evans &Westergaard, 2006; Ramseyer et al., 2006). Animals might be more successful at this task than similar self-control tests in which capuchin monkeys exchanged low-value foods for higher-value foods or small quantities of food for larger quantities (Drapier et al., 2005; Ramseyer et al., 2006) because, in our task, they would not have to wait with or relinquish food that was already in their possession. On the other hand, our task might be more challenging because monkeys would have to forego taking a valued food and select a non-food object instead. In most other self-control studies involving an exchange task, on every trial, the monkey either chooses an option that allows it to retain a piece of food already in its possession or exchanges food directly for food. Further, only two out of three chimpanzees in the Beran and Evans (2012) study selected the high-value token over a lower-value piece of food significantly more often than chance. Since apes sometimes outperform monkeys on tests of self-control (Evans & Beran, 2007; Evans, Beran, Paglieri, & Addessi, 2012), perhaps capuchins might not exhibit self-control in this situation. Or, if capuchins could perform the task, we expected to see similar individual differences in performance.

Method

Subjects and Housing

Seven animals from a captive colony of 14 capuchins participated. The colony was established in 2000 from six individuals and all new members were born and raised in the group. The seven individuals used were one adult male and six adult females. The colony was housed in three interconnecting rooms located at the Bucknell University Animal Behavior Laboratory. The enclosure consisted of a series of seven compartments made of caging wire, which were interconnected by doorways or overhead tunnels made of caging wire. Interconnecting doorways could be closed and/or metal barriers could be inserted into the tunnels to seal off individual compartments. The compartments were furnished with perches, swings, platforms, and poles to allow naturalistic climbing and movement. Food, water and enrichment items were available *ad libitum*. All procedures were approved by the Bucknell University Institutional Animal Care and Use Committee and adhered to guidelines in the Guide for the Care and Use of Laboratory Animals (Committee for the Update of the Guide for the Care and Use of Laboratory Animals, 2011).

Procedures

Training. Animals were isolated into subcompartments of their enclosure for training and testing. Animals were trained to token exchange by handing them a small metal object (a token) through the caging and then proffering a cupped hand to them. If the animal returned the token through the caging and placed it in the experimenter’s hand, they received a preferred piece of food. The food (mealworms) and token (a wing nut) that were used during initial training were not used for later training or testing. After animals learned the token exchange procedure, they learned to associate two food items with particular tokens. Foods used were preferred items that were part of their normal diet. The food items selected for each monkey were two preferred foods for which they were willing to exchange tokens and for which there was a clear preference of one over the other. Food preferences were determined by providing the monkeys with a pair of foods and recording which ones were selected over others. While standing directly in front of the monkey in its cage, the experimenter presented the monkey with an item in each hand. A preference was considered clear if a monkey selected one food over another potential food in ten out of ten paired choices conducted in a single session. Using these criteria, we were able to use a raisin as the preferred food and a piece of apple as the less preferred, but highly desirable, food for most monkeys (N = 6). Dried banana chips served as the preferred food for the seventh monkey. We determined that animals desired the less preferred food by providing them with ten pieces in succession. All animals ate each piece.

Once a food pair was established for each monkey, animals then learned to associate a particular food with a particular token. The two tokens used were a 3 cm long carriage bolt and a 3.5 cm diameter metal washer. The washers were crimped along their diameter so they would not lay flat and could easily be picked up. Before association training, we acclimated and desensitized the animals to these novel objects by placing ten or more of each in their enclosure for several days. We assumed that the tokens would become assimilated into the abundant assortment of enrichment devices in their enclosure, which were continually available. We then conducted paired testing sessions to determine if animals had a predetermined preference for either of the objects. The experimenter held one of the objects in each hand, simultaneously offering both to a monkey, and allowed the monkey to select one. At first, the monkeys would select both objects seemingly randomly but quickly lost interest in these sessions and would not select either object. Thus, we did not accumulate enough trials to statistically evaluate a predetermined object preference. We concluded that no interest in both objects was evidence for no predetermined preference or aversion for either one of them.

As in Brosnan and de Waal (2004), we taught the monkeys to associate each of the tokens with a particular food by placing five of each token in a 25 x 12 x 5 cm stainless steel tray in a random arrangement and attaching the tray to the caging inside an animal's testing compartment. As animals gave the tokens to the experimenter, they received the food associated with that token. If animals associated the tokens with the foods, we assumed that they would first hand out the five tokens associated with the preferred food followed by the five tokens associated with the less preferred food. We considered association training complete if nine out of ten of an animal's first five exchanges in two consecutive 10-trial training sessions were with the token associated with the preferred food. The washer was assigned as the token paired with the preferred food and the bolt was assigned to the less preferred food.

In the token association training described above, animals picked tokens out of a tray and handed them to the experimenter for the associated food reward, however, for the token exchange test trials, animals would need to select between a token and a food item held in the experimenter's hands. Animals were accustomed to handing tokens to the experimenter, but they were not accustomed to selecting a token held by the experimenter in order to exchange the token. To accustom the animals to this procedure, we conducted training sessions in which the monkeys were provided with a choice between the two tokens held in front of the caging by the experimenter. The animals could select one token and then use it to exchange for the corresponding food item. During these training trials, both food items were visible in plastic containers on a cart next to the experimenter. If an animal selected the token for the more preferred food on nine out of ten of these trials, they were provided with five test trials. If animals selected the token associated with the less preferred food item more than once in ten trials, their test session was postponed until the next day of testing.

Test phase 1: High- and medium-value foods. In a trial during the first condition of testing, the token for the less preferred food (the bolt) was handed to a monkey by the experimenter. Once the monkey gave the token back, the experimenter held both hands up to the caging, one holding a piece of the less preferred food and the other holding the token for the more preferred food (the washer). The items were held out of a monkey's reach approximately 15 cm away from the wire caging and approximately 30 cm apart so that a monkey would need to unambiguously reach through the 1 x 2 in (2.54 x 5.08 cm) caging wire for one item. A choice was recorded when a monkey put its hand through the hole in the caging wire in front of an item and reached out for the item. The experimenter would then place the item in the animal's hand. If the animal selected the token, they could then immediately exchange it for the preferred food item. Again, both food items were visible in plastic containers on a cart next to the experimenter. Animals were provided with five such trials per testing session and the hand in which the token was held was alternated from left to right on successive trials. The starting hand of the alternating sequence also alternated between successive testing sessions. Animals participated in four such testing sessions, accumulating 20 test trials.

Test phase 2: High- and low-value foods. In a second condition of the study, we used a less preferred food (green pepper) as one of the food items and paired it with the animals' most preferred food. In the previous testing sessions, animals exchanged for two highly preferred food items, one of which was just slightly less preferred than the other. Foregoing an immediately available valued food to select a token for exchange for a slightly better one may have tested the limits of the animals' self-control. We assumed that if the immediate reward was not as favored, animals might be more likely to select the token to obtain the higher-value food. Green pepper was chosen because animals will work for this food item, but it is only a moderately preferred food among the diversity of food items in their diet. We determined that animals would willingly eat the bell pepper by providing them with ten pieces in a row. Every animal ate all ten pieces. We established that the green pepper was a less preferred food by offering the monkeys a choice between the green pepper and one of the more preferred foods. The green pepper was not selected in any of ten paired choices offered. Training and testing with the bell pepper versus a preferred food were conducted identically to the previously described procedures with animals receiving association training, paired token choice training, and then the token versus food tests. The token associated with the bell pepper was an oval shaped 3.5 x 1.75 cm stainless steel quick link.

Test phase 3: High- and medium-value foods retest. In a third condition in the study, we retested the animals using the high-value and medium-value items to determine if experience selecting between a high-value token and a low-value piece of food in Phase 2 influenced performance with two fairly highly preferred foods.

Test phase 4: Control. If animals performed flawlessly on the test trials and always chose the token for the more preferred food over a piece of the less-preferred food, the result might be because they learned the simple rule "always choose the token" as this would allow them to obtain the more preferred food. To test for this possibility, in a fourth condition, we allowed the monkeys to select between a medium-value food and the token for the low-value food. In these token exchange test trials, monkeys were handed the token for the medium-value food (apple). Once they gave the token back, they were given a choice between a piece of the medium-value food and the token for the low-value food (green pepper), which they could then exchange for the low-value food. The control test trials were conducted identically to the original procedures with animals receiving association training, paired token choice tests and then the token versus food choice tests. We assumed that if animals had learned an "always choose the token" rule, they would choose the token for the lower-value food and consequently obtain the lower-value food on many trials.

Data Analysis

According to a binomial distribution, the two-tailed probability of selecting 15 or more out of 20 (or five or fewer out of 20) would be $p = 0.041$, so we considered these upper and lower cutoffs as statistically significant at alpha = 0.05.

Results

Two monkeys were not tested because, although they learned to exchange a token for food, they never progressed through association training in which they were required, when presented with a tray containing five tokens associated with a high-value food and five tokens associated with a lower-value food, to first hand to the experimenter the tokens for the high-value food. The two monkeys showed no inclination to exchange the higher-value tokens first after up to 17 sessions of training.

Test Phase 1: High- and medium-value foods. During token association training with high- and medium-value foods, three of the five remaining subjects learned to exchange the five tokens for the high-value food first and then exchange the five tokens for the medium-value food, indicating that they had learned to associate particular tokens with particular foods. These animals always exchanged all ten tokens, which means they continued to work to obtain the medium-value food after obtaining the five high-value foods. Animals ranged from six to eight sessions of training in order to reach the criterion of two consecutive sessions of first exchanging the tokens for the high-value food. The other two subjects did not show any indication of exchanging first with the tokens associated with the high-value food after twelve sessions of training and were not used in this test phase.

For the three animals that advanced to the next phase of training, the experimenter provided the animals with a choice between the token for the high-value food and the token for the medium-value food. They were then tested to determine whether they would choose the token for the high-value food. All three monkeys passed this phase of training and would select the token for the more preferred food at least nine times out of ten. On days when these animals reached the nine out of ten criterion, they were given a session of five test trials with a high-value token paired with a medium-value food until they accumulated 20 test trials across four sessions. None of the three monkeys (Schroeder, Newton, and Scocrates) selected the token for the high-value food over the piece of medium-value food significantly more often than chance (Figure 1: High token-medium food). In fact, one monkey (Socrates) selected the token significantly less than chance (binomial test, $p < 0.05$). The monkey that selected the token over the food most often (Schroeder) seemed to learn she could optimize her reward midway through her twenty trials. In her first five test trials, she did not choose the token once. In her second five trials, she chose the token over food once on the last trial. In her third and fourth five-trial sessions, she selected the token over food every time.

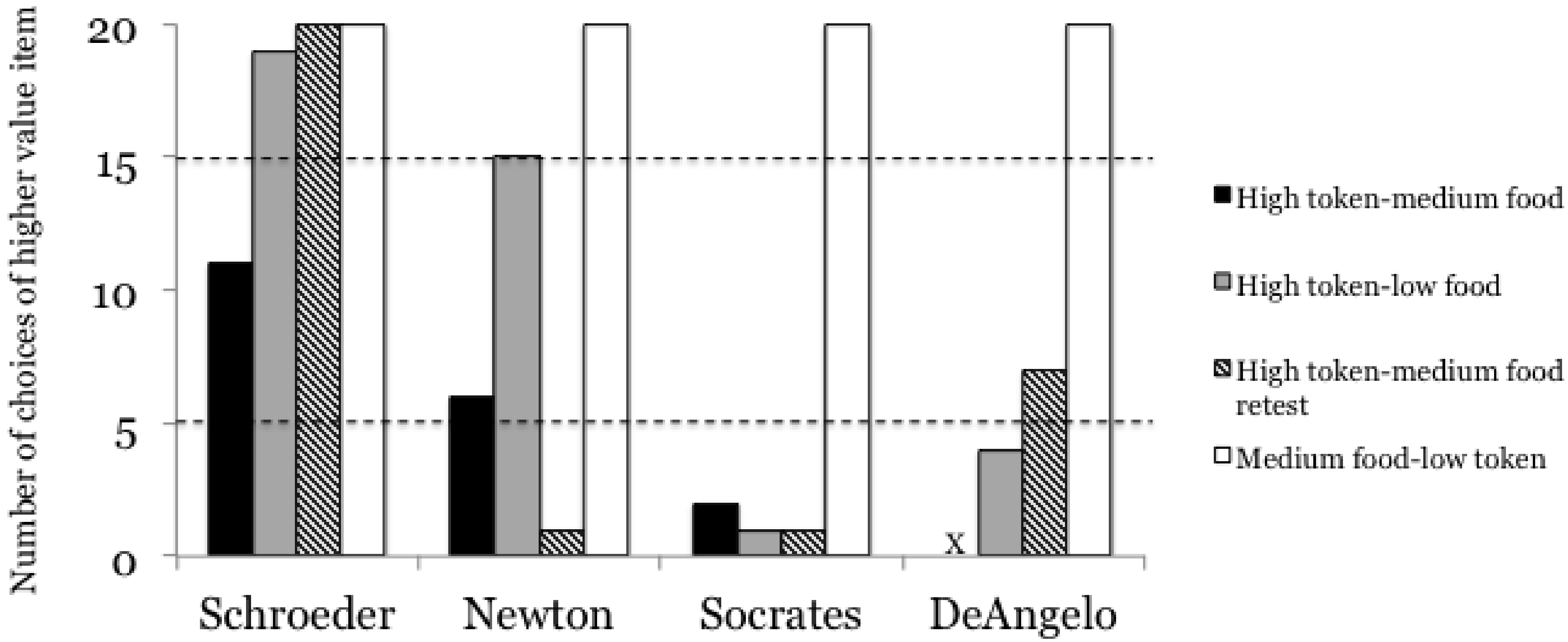

Figure 1. The number of choices (out of 20) in which the four monkeys chose the item (token or food) that resulted in obtaining the higher value food reward. For the black bar for each monkey, the high-value token was paired with a medium-value food. For the grey bar, a high-value token was paired with a low-value food. For the hatched bar in the third position for each monkey, the high-value token was again paired with a medium-value food. For the white bar, a medium-value food was paired with a low-value token. The dashed lines indicate choices significantly different from chance that were either above expected ($N \geq 15$) or below expected ($N \leq 5$; $p < 0.05$). The "X" indicates that DeAngelo was not tested in the first condition because she did not advance through training.

Test Phase 2: High- and low-value foods. In this condition, we retrained all of the animals using two foods that had a larger preference disparity (e.g., raisin versus green pepper) to determine if a larger disparity would enhance association training and possibly result in more selections of the high-value token over the lower-value piece of food. All five of the remaining animals learned to exchange the five tokens for the high-value food before exchanging the five tokens for the low-value food. Four out of five of these animals also learned to select the token for the more preferred food nine out of ten trials when given a choice between the token for the high-value food and the token for the low-value food. The fifth monkey (the adult male) succeeded at association training in this phase, but he developed an acute left side preference when selecting between two choices held by the experimenter and was excluded as a subject. On days when the remaining four animals selected the token for the more preferred food nine out of ten times, they were given a session of five test trials with a choice between a high-value token or a low-value food until they accumulated 20 test trials in four sessions. Two of the four animals (Schroeder and Newton) selected the token over food 15 or more times in 20 trials, attaining our criterion for statistical significance, binomial test, $p < 0.05$, while two others' selections (Socrates and DeAngelo) were significantly below chance, binomial test, $p < 0.05$ (Figure 1: High token-low food). One of the two successful monkeys was Schroeder, the animal that began to consistently select the token for the high-value food over the piece of medium-value food in her second ten trials of the first testing condition.

Test Phase 3: High- and medium-value foods retest. One monkey (DeAngelo) advanced through association training when a low-value food (green pepper) was paired with a high-value food (raisin), but not when a high-value food (raisin) was paired with a medium-value food (apple). As we were most interested in whether monkeys would select the token over the food when both foods were highly preferred, we re-conducted association training with this monkey using two highly valued foods (raisin and apple) and she now progressed through association training. We then tested her with a choice between a high-value token and medium-value piece of food. We also retested the other three monkeys (Schroeder, Newton, and Socrates) in this condition to determine if experience selecting between a high-value token and a low-value piece of food influenced subsequent performance with two fairly highly preferred foods. One monkey (Schroeder) selected the token for the high-value food significantly more often than the medium-value piece of food, binomial test, $p < 0.05$, while the other three monkeys tended to select the medium-value food over the high-value token (Figure 1: High token-medium food retest) with two of these animals (Newton and Socrates) selecting the token significantly less than chance, binomial test, $p < 0.05$.

Test Phase 4: Control. On the 20 control trials on which we allowed these four monkeys to select between a medium-value piece of food (apple) and the token for the low-value food (bell pepper), no monkey ever selected the token for the low-value food. All monkeys selected the apple piece on each trial (Figure 1: Medium food-low token).

Discussion

Five of seven monkeys completed training by selectively choosing to exchange tokens associated with more preferred foods. The result indicated that the monkeys attributed value to the tokens and was a replication of earlier work (Addessi et al., 2007, 2008; Brosnan & de Waal, 2004). Two monkeys selected a token significantly more often than chance when provided a choice between a piece of food or a token that could be exchanged for a more preferred food. Foregoing an immediate food reward and instead selecting a token that could be exchanged for a more preferred food item demonstrated some degree of self-control. One of these two monkeys (Schroeder) selected the token over food when both foods were highly preferred indicating that the animal refrained from taking a desirable food (apple) and selected a token to obtain an even more desirable food (raisin). The other monkey (Newton) would take the token over the food when the food was of low value and she could obtain a high-value food by selecting the token, however, she would not select the high-value token over the food when the food offered was also of fairly high value.

As in similar self-control studies involving exchange in capuchins (e.g., Drapier et al., 2005), there were marked individual differences in performance. One monkey (Schroeder) learned to select the token for the higher-value reward on every opportunity. However, she did not do so spontaneously and appeared to grasp the process midway through her first twenty trials of testing with two highly preferred foods. Once she selected the token over food for the first time on her tenth trial, she continued to do so on every trial except one throughout the remainder of the study, both when the two foods were each high in value and when one of the foods was fairly low value. She did not simply learn a "select a token over food" rule, because, when given an opportunity to select a token that would result in obtaining a food of lesser value, she always selected the food rather than the token. In contrast, another monkey (Socrates) almost always chose the immediately available food rather than a higher-value token, demonstrating no self-control and/or a lack of understanding that an opportunity was present to obtain a more preferred food item.

One might question whether selecting the token over food is a case of self-control. If the token became a secondary reinforcer after repeated pairings of the token with the food item, selection of the token over food might be explained as simple association learning. If the token for the higher-value food became a substitute for the food, they may have simply selected it in place of the food it represented. We cannot rule out this explanation but several factors lead us to suggest that the behavior observed is more complex than simple association learning. First, Schroeder was the most successful monkey at optimizing her rewards by selecting the token for the higher-value food. If simple association of the token with the food were the explanation for her behavior, we would expect her to begin selecting the token on her initial trials. Instead she began by selecting the food over the token, but once she tried the token option and learned that she could receive the preferred reward by forgoing the food, she began to select the token on almost every trial. Further, if simple association learning were responsible for performance, we would expect some of the other animals (e.g., Socrates and DeAngelo) to select the token for the higher-value food. Most often animals chose the food rather than the token associated with the more preferred reward even though all animals selected the token at least once and experienced a trial in which the token was exchanged for the higher-value food. Also, Newton would select the token to obtain a high-preference food over a low-preference food, but she did not tend to select the token for a higher-preference food when both foods were fairly high value. If simple association learning were influencing her behavior, we would expect her to select the token for the higher-value food over the piece of medium-value food. Instead, she was unable to refrain from taking the food when that offered (apple) was fairly high in value. The lure of an immediately available food item did not overcome the association between the higher-value food and the token, even when the token offered was for a highly preferred food (raisin). We suggest, then, that animals were demonstrating some form of response inhibition when they selected the token over food.

One advantage of incorporating token exchange into a self-control task is that an animal's choice produces an unambiguous result. In similar self-control studies involving qualitative exchange with capuchins, animals exchanged a less preferred food item for a more preferred food item, (e.g., Drapier et al., 2005) and did so with increasing waiting periods before the exchange (Ramseyer et al., 2006). However, the monkeys would frequently eat some of the reward before making the exchange, which might not be considered a case of self-control. In fact, some animals would no longer exchange less preferred items for more preferred items, or delay the exchange, if they were required to return the food item intact (Drapier et al., 2005; Ramseyer et al., 2006). Using tokens precludes a partial exchange and might enhance such "delay tolerance" studies. Using a symbol for a reinforcer rather than the reinforcer itself has been shown to improve self-control during a reversed-reward contingency task in chimpanzees, capuchins and humans (Addessi & Rossi, 2011; Boysen & Berntson, 1995; Carlson et al., 2005). For example, a delay could be included from the time an animal selected a token until it was able to exchange the token for the higher-value reward. We would predict that waiting for an exchange with a token might produce more and longer tolerance than waiting while holding a food item. Tolerance could be assessed if, at longer delays, the animal reached an indifference point and began selecting the available food over the token.

From a comparative perspective, two out of three chimpanzees optimized their rewards by selecting the token for the higher-value food over the piece of lower-value food in the Beran and Evans (2012) study. In our study, two out of the four monkeys that underwent testing selected higher-value tokens over lower-value food. One could argue that these proportions are similar and that capuchins performed comparably to chimpanzees on this task. The studies had some notable differences, however. The one chimpanzee that did not select a token significantly more often than chance still selected the token over half of the time (66%). In contrast, three capuchins selected the token associated with the high-value food significantly less than expected at some point in their testing and one of these (Socrates) always selected the token significantly less than expected, meaning she almost always took the food. For them, there was no indication of impulse control. Further, in the chimpanzee study, there was an approximately 15 s delay between the time the animal selected a token rather than food and then walked over to exchange the token for a reward, while, in our study, there was no appreciable delay. Nevertheless, some capuchins did forego an immediately available food item to select a token that could be exchanged for a more preferred food. Results provide another example of self-control in capuchin monkeys suggesting that this executive capacity could have early roots among nonhuman primates, however, more research needs to be conducted with this paradigm in capuchins and a broader selection of nonhuman primates for solid conclusions to be drawn.

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