



Learning to inhibit prepotent responses: successful performance by rhesus macaques, *Macaca mulatta*, on the reversed-contingency task

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To reinvestigate whether macaque monkeys could learn the reversed-contingency task, we trained six rhesus monkeys on the problem. On each trial, the monkeys chose between one and four pieces of the same food item. If a monkey selected four pieces of food, it received one instead; choice of one piece of food led to the receipt of four. All of the monkeys initially tended to select the larger quantity of food, but eventually learned to choose the smaller amount. The results confirmed a previous report that macaque monkeys quickly reached a performance level of roughly 50% 'correct', defined as choosing the smaller amount of food, and some individuals continued to perform at that level for a protracted period of testing. Contrary to that report, however, the present findings show that macaque monkeys can master the reversed-contingency task.

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Inhibitory control processes play a central role in mammalian behaviour. For example, it is often advantageous to withhold actions, and a once advantageous behaviour can become otherwise over time. Inhibitory control mechanisms help animals select among actions that have had positive outcomes previously or that are innately prepotent.

Inhibitory control processes guide response selection at several levels, many of which involve parts of the frontal cortex (Fuster 1998; Hauser 1999). Aspects of response inhibition include countermanding programmed movements (Schall 2001) and suppressing responses based on their affective consequences (affective inhibition), stimulus features (attentional inhibition), or other aspects of information processing. For example, ventromedial and orbital portions of human prefrontal cortex mediate affective inhibition, but dorsolateral prefrontal cortex apparently does not (Milner 1963; Bechara et al. 1994; Damasio 1996; Fuster 1998; Rogers et al. 2000). Similarly, in marmoset monkeys (*Callithrix jacchus*), orbital and lateral portions of prefrontal cortex mediate affective and attentional inhibition, respectively (Dias et al. 1996).

Affective inhibition has typically been assessed with variations of reversal learning, object retrieval and laboratory-based gambling tasks (e.g. Iversen & Mishkin 1970; Diamond 1990; Bechara et al. 1994; Dias et al. 1996; Fuster 1998; Wallis et al. 2001). Although a wide diversity of species can learn such tasks, the same is not true for one task that probes inhibitory control processes, the reversed reward contingency task, or simply, the reversed-contingency task. In what we will call the standard version of this task, subjects choose between a small and a large quantity of food. If they choose the smaller quantity, they receive the larger amount and vice versa. To receive the most food, the subject must learn to choose the smaller quantity consistently. Previous work has reported that one species of ape (chimpanzee, *Pan troglodytes*), one species of Old World monkey (Japanese macaques, *Macaca fuscata*), two species of New World monkeys (squirrel monkeys, *Saimiri sciureus*; cottontop tamarins, *Saguinus oedipus*), and two species of lemurs (brown, *Eulemur fulvus*; black lemurs, *Eulemur macaco*) could not learn the standard version of the reversed-contingency task, at least when experimenters presented that task to relatively naïve animals.

In the original experiments, Boysen and her colleagues gave chimpanzees a choice between two amounts of food, for instance, one versus four pieces of candy (Boysen & Berntson 1995; Boysen et al. 1996, 1999, 2001). The

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chimpanzees never learned to perform this version of the reversed-contingency task; they tended to select the larger quantity throughout testing. However, because the experimenters trained these individuals to associate food quantities with Arabic numerals in prior experiments, such that the number '1' was associated with one piece of food and the number '4' with four pieces of food, Boysen and her colleagues studied a second condition in which the chimpanzees viewed Arabic numerals instead of food items. The experimenters marked the numbers on plaques and placed them in the food dishes, then, after the animals' choices, they took the food rewards from a different location and gave them to the chimpanzees. If the chimpanzees selected the number '1', they received four pieces of candy and vice versa. From the onset of testing, the animals performed this task successfully, regularly selecting the number '1'. This finding suggests that the chimpanzees had learned the reversed reward contingency in the originally presented, standard version of the task, but could not override a prepotent response tendency to select the larger of two food rewards.

Silberberg & Fujita (1996) tested Japanese macaques on the reversed-contingency task using one versus four pieces of food. They reported that their monkeys could not learn the standard version of the task, and chose one piece of food at the same rate as four pieces. The same monkeys could, however, learn a different version of the task, in which choice of the larger quantity of food led to the receipt of no food (the no-reward version). Their task also had correction trials: after an error, the experimenter repeatedly presented the food items in the same configuration until the monkeys made the correct choice.

In another experiment, Anderson et al. (2000) found that squirrel monkeys could perform the standard version of the task, but only after training on a no-reward version and using a correction procedure like that used by Silberberg & Fujita. Similarly, another New World species, cottontop tamarins, also failed in the standard version of the task. The tamarins could perform the task only when they chose colour cues that they had learned to associate with the two quantities of food, and then only in a no-reward version that included a correction procedure (Kralik et al. 2002). The data from lemurs (Genty et al. 2004) closely resemble the results from squirrel monkeys, in that these species could not perform the standard version of the task until they first received a no-reward condition and, for some of the subjects, also a correction procedure.

On the other hand, Shumaker et al. (2001) reported that two orang-utans, *Pongo pygmaeus*, learned to point to a smaller quantity of grapes to receive the larger quantity, a task successfully performed by humans over the age of 4 years (Russel et al. 1991). We find the former results difficult to interpret, however, because both orang-utans initially selected the quantity to their right regardless of magnitude and thus appeared to be poorly motivated to choose the larger amount of food.

In summary, no nonhuman species has unambiguously shown the ability to learn to override the tendency to select the preferred, larger quantity over the smaller quantity in the standard version of the reversed-contingency task.

Such learning has depended on prior experience with a no-reward version of the task and a correction procedure. The present study reassessed the ability of macaque monkeys to learn the standard reversed-contingency task.

METHODS

Subjects

We studied six adult, male rhesus monkeys, *Macaca mulatta*, designated monkey 1 to monkey 6, weighing between 8.2 and 14.1 kg at the beginning of the study. All monkeys had experience with object discrimination learning and other, related tasks. Our facility housed the animals individually in rooms with automatically regulated lighting (12:12 h light:dark cycle, lights on at 0700 hours). The monkeys' diet consisted of primate chow (no. 5038, PMI Feeds Inc., St Louis, Missouri, U.S.A.), supplemented with fresh fruit. This controlled diet ensured sufficient motivation to respond in the test apparatus and maintained each monkey at a healthy body weight. The monkeys always had water available in their home cage.

Apparatus

The experimenter brought each monkey from its housing room to an isolated testing room in a wheeled transport cage. She then conducted the testing in a modified Wisconsin General Test Apparatus (WGTA), which consisted of a large monkey compartment that held the transport cage plus the monkey, together with a smaller test compartment, which contained the test tray. Two 60-W light bulbs illuminated the test compartment, whereas the monkey's compartment remained unlit. During test sessions, the experimenter turned off the room lights as well. An opaque screen separated the monkey compartment from the test compartment during intertrial intervals. The test tray, measuring 19.2 cm (width) by 72.7 cm (length) by 1.9 cm (height), contained two food wells located 29 cm apart, centre to centre, on the midline of the tray. The wells had dimensions of 38 mm in diameter and 6 mm in depth.

Testing Procedure

A trial began when the experimenter raised the opaque screen separating her from the monkey. On each trial, she gave the monkeys a choice between one and four pieces of food. Each food item consisted of one-half of a peanut, which we will simply call a 'peanut' for convenience. The experimenter placed the peanuts in the palms of her gloved hands, as she sat on the opposite side of the test tray from the monkey. The experimenter held her hands over the two food wells, palms up, so that the monkey could see both choices. Use of blue vinyl gloves yielded excellent visual contrast of the peanuts against the hand. During each trial, the experimenter projected a neutral expression and looked straight ahead.

When the monkey made a choice by reaching for and touching one hand, the experimenter immediately closed the fingers of both hands over the food, turned her hands upside down, and dropped the appropriate amount of food into the underlying food well. In practice, the experimenter counted reaches as responses, rather than requiring the monkeys to touch her hand. If the monkey chose four peanuts, it received the one-peanut reward; if it chose one peanut, it received the four-peanut reward. In each case, the experimenter deposited the reward into the food well on the side opposite the choice. After the monkey had retrieved the food from the food well, the experimenter lowered the opaque screen, thereby terminating the trial. After an intertrial interval of approximately 20 s, she ran the next trial, and so on, until the monkey had completed the 20 trials comprising the daily test session. The location (left or right) of the larger food amount followed a pseudorandom order, with the constraint that its side of presentation occurred equally often within each set of 10 trials. Every choice of the smaller amount of food counted as a 'correct' response, and we set

criterion at a mean of 90% correct responses over five consecutive days (i.e. 90 correct responses or more in 100 trials). The experimenter tested the monkeys at the rate of one session per day, 5 days per week.

To help determine whether the monkeys used any inadvertent cues provided by the first experimenter, after the monkeys attained criterion a second experimenter retested the monkeys with the same procedures.

RESULTS

Initially, all six monkeys tended to select the larger quantity of peanuts. As a result, all monkeys performed significantly (t test: $t_5 = 12.5$, $P < 0.0001$) below a chance level of performance (50%) for at least the first session ($\bar{X} \pm \text{SE} = 11 \pm 3\%$ correct responses in 20 trials). With additional testing, however, all six monkeys eventually learned to select the smaller quantity of peanuts instead of the larger quantity. As a group, they required a mean of 1087 trials (54.4 sessions) and 498 errors to attain criterion, with large individual differences (Fig. 1). At the

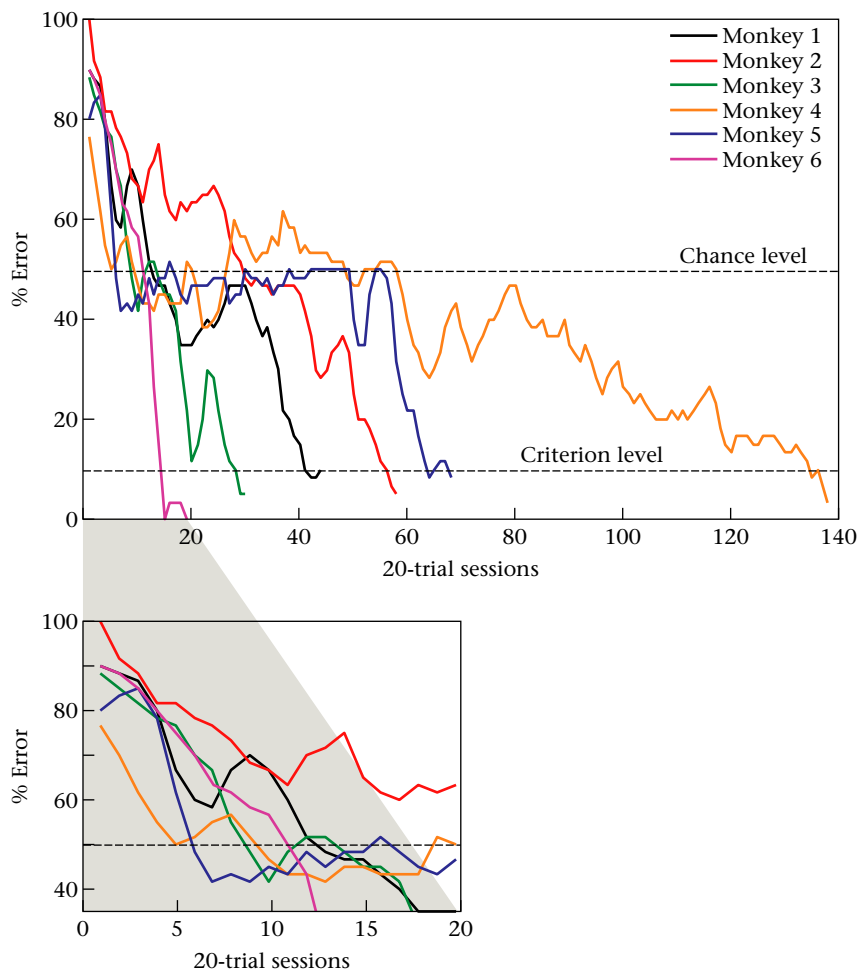


Figure 1. Learning curves for the six monkeys tested on the reversed-contingency task, with percentage error (percentage choice of the larger quantity of peanuts) plotted as a function of 20-trial sessions. We smoothed the curves using a three-point moving average. The dashed line at 50% shows the level of chance performance; the dashed line at 10% shows the criterion level of performance. For ease in viewing the individual learning curves, the shaded area shows an expanded plot of the first 20 sessions of training. Monkeys 1–6: the six rhesus monkeys studied in the present experiment.

extremes, monkey 6 reached criterion in ~ 340 trials; monkey 4 took over 2700 trials to do so.

Figure 1 shows the learning curve for each individual monkey, and Fig. 2 documents the group mean. The shaded area in Fig. 1 shows that within the first 20 sessions of training, all monkeys showed a dramatic reduction in percentage of error. For the group mean (Fig. 2), as for most of the individuals (Fig. 1), the learning curve appeared to comprise three distinct phases: an initial phase in which error rates fell rapidly from $\sim 90\%$ to approximately chance level (50%); a second phase of highly variable duration in which performance remained roughly stable at approximately chance level; and a final phase in which error rates fell to $\sim 10\%$.

The duration of the stable, chance-level performance varied considerably among individuals. The monkeys continued to perform between 40 and 60% correct for a mean of 25 sessions (500 trials), but this value ranged from six sessions (120 trials, for monkeys 1 and 6) to 58 sessions (1160 trials, for monkey 4). Thus, in the initial and final phases of learning, the percentage of error decreased exponentially (Fig. 2), whereas in the middle phase no consistent change in performance occurred. We compared the learning rate for each monkey against all other monkeys with the Kolmogorov-Smirnov two-sample test (two-tailed $\alpha = 0.05$). Monkeys 4 and 5 differed from each of the other monkeys, and, in addition, monkey 1 differed from monkey 2.

Figure 3 shows a comparison of the initial learning rates for the six rhesus macaques studied here (open circles) and

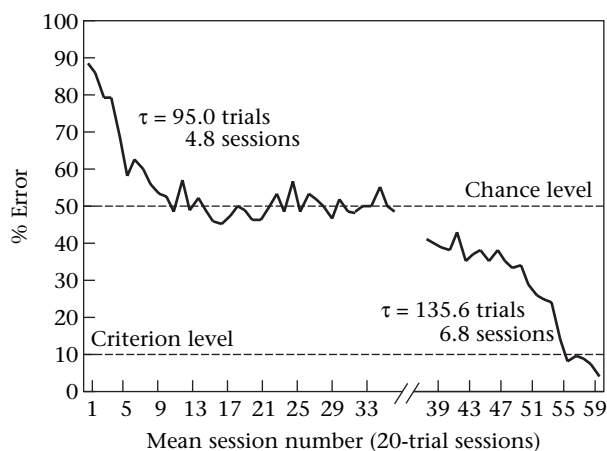


Figure 2. The group mean learning curve from the data plotted in Fig. 1. For the left side of the figure, which is constructed in the usual manner, the mean session number is identical for each monkey. For the right side, the curve is constructed in reverse, starting from the session in which each monkey attained criterion. Consequently, for the right side of the figure, the actual session numbers differ from individual to individual depending on their learning rate. The time constants (τ) result from three-parameter fits to an exponential curve. The time constants provide a measure of the learning rate (decrease in errors) in the first and final phases of learning. For instance, in the first phase of learning, in which the error rates dropped to $\sim 50\%$, 63% of this change occurred, on average, in 95 trials. The dashed line at 50% shows the level of chance performance; the dashed line at 10% shows the criterion level of performance.

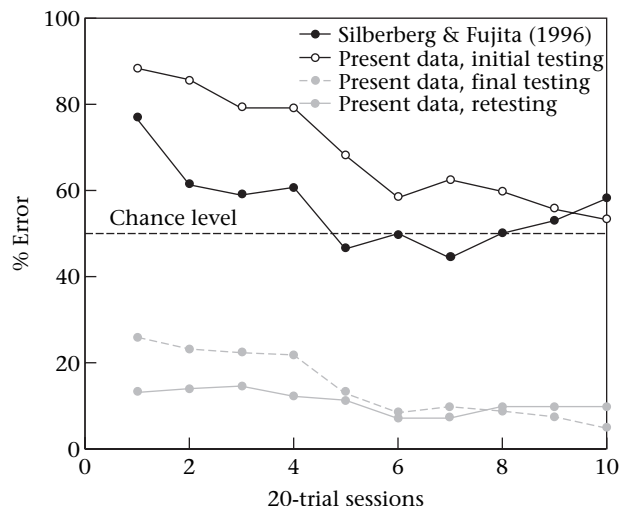


Figure 3. The group mean learning curve from initial testing in the present study (\circ) and the data of Silberberg & Fujita (1996) from Japanese macaques (\bullet). The dashed line at 50% shows the level of chance performance. Below the dashed line are group means from the final test sessions conducted by the first experimenter (\bullet) and the additional sessions given by the second experimenter (\circ).

the three Japanese macaques studied by Silberberg & Fujita (1996) (solid circles). Even though the Japanese macaques had the benefit of correction trials, an ANOVA with repeated measures on percentage of error scored over the first 10 sessions indicated that the learning rates of the two groups did not differ ($F_{1,7} = 4.63$, $P = 0.07$).

When tested by the second experimenter (see Methods), five of the six monkeys reattained criterion in a mean of 50 trials and eight errors, with four of the five showing either perfect retention or near perfect retention. We discontinued retesting of the remaining monkey (monkey 4), the last monkey to complete the experiment, after seven sessions because, although the monkey failed to regain criterion performance within this period of time, it scored well above chance levels. This monkey performed at 83% correct over the seven sessions and, perhaps more importantly, scored 18 correct responses in 20 trials on the first session with the second experimenter. Therefore, in summary, although the monkeys did not display perfect transfer, all the monkeys continued to perform at a high level of accuracy when tested by the second experimenter. Figure 3 (grey circles, solid line) shows these retesting scores in comparison with the group's mean score in initial testing (open circles) and final testing (grey circles, dashed line) by the first experimenter.

DISCUSSION

As expected, when challenged with the reversed-contingency task, all six monkeys initially selected the larger of two quantities of food. Choice of a larger amount of food thus appears to be a reliable prepotent response. With experience, however, all of the monkeys overcame this prepotent tendency and learned to select the smaller quantity in order to obtain the larger reward.

Species Comparisons

The nonhuman primates that showed an initial preference for a larger quantity of food, chimpanzees, Japanese macaques, squirrel monkeys, tamarins and lemurs, all failed to learn the standard version of the reversed-contingency task when first confronted with it. Successful performance instead depended on the animals obtaining some prior experience with a no-reward version of the task, on a requirement for remedial training (correction trials), or on symbolic mediation, as in the use of Arabic numerals for chimpanzees (see Introduction). The present results show that rhesus macaques require none of these aids to solve the problem posed by the reversed-contingency task; they can learn to solve the problem without any prior experience on related versions of the task, and without correction after errors.

Although the differences in performance could conceivably reflect species variation, we believe that differences in the number of trials administered in the various experiments may account for the discrepancy in results, especially for macaque monkeys.

In their study of Japanese macaques, Silberberg & Fujita (1996) gave monkeys 20 trials per test session, as in the present experiment, but this sum included correction trials, which they eliminated from their analysis. Thus, their three monkeys had 49, 91 and 85 noncorrection trials, respectively, which Silberberg & Fujita scored. In the final session, the monkeys averaged 43% correct on those trials. Over the final five test sessions (100 trials), their monkeys averaged 49% correct. Including both correction and noncorrection trials, their monkeys accumulated only 200 trials of experience with the standard version of the reversed-contingency task. Figures 1 and 2 show that our monkeys had yet to attain chance levels at a comparable stage of training. Figure 3 shows that the group mean performances of the monkeys in the two studies differed very little over the first 10 sessions and, as already indicated, statistical analysis revealed no group difference in learning rates.

In their study of squirrel monkeys, Anderson et al. (2000) terminated testing on the standard reversed-contingency task after 200 trials (including both correction and noncorrection trials). Only one of eight monkeys reached chance level of performance. After another 200 trials, in this case with the larger quantity reduced from four to two, three of four monkeys reached chance levels. The experimenters then began using the no-reward version of the task. Similarly, in the study of lemurs, Genty et al. (2004) first tested their animals on the standard version of the task, for a total of 200 trials, then tested them on the no-reward version.

As for chimpanzees, in the first study (Boysen & Berntson 1995), one individual reached chance level at some point within 300 trials, whereas the other reached chance level in just over 300 trials. However, in a subsequent study (Boysen et al. 1996), all five chimpanzees continued to select the larger quantity after 400 trials, and thus never reached chance level. They also maintained poorer-than-chance performance for an additional 200 trials, intermixed with sessions that involved other manipulations.

By comparison, in the present study only one monkey reached criterion performance (90% correct) within 400 trials and only one of the five others performed substantially above chance levels (50% correct) after that amount of testing. Thus, our results suggest that other primate species might also be able to learn the standard version of the reversed-contingency task, even without prior, related experience or remedial training, given a substantially increased number of trials in which to do so.

Stimulus Valuation and Suppression of Prepotent Responses

Although it is difficult to account for the three phases of learning observed for most of our monkeys, we can offer some speculative hypotheses, along with some suggestions about the apparent species differences. The following discussion of the rhesus monkey data emphasizes the concept of value assignment, whereas the discussion of the chimpanzee data emphasizes response suppression. Note, however, that both concepts apply to both sets of data.

We propose that, initially, the higher value of the larger amount of food guided monkeys' choices, by virtue of the larger quantity being a prepotent stimulus. During the first phase of learning, whenever the monkeys selected the larger quantity and received the smaller amount, the value of the larger quantity decreased, resulting in the weakening of the prepotent response. Similarly, whenever the monkeys selected the smaller quantity and received the larger amount, the value of the smaller quantity increased. At some point, the value of the larger and smaller quantities of food may have equalized and led to performance at chance level. Our monkeys reached this phase relatively quickly, as illustrated in Figs 1–3.

The consequence of the initial stage of learning, when performance reaches chance levels, might have produced something akin to a 'credit-assignment' problem. The assignment of value to a given number of peanuts is particularly difficult in the reversed-contingency task because the number of peanuts serves as both the discriminative choice stimulus and the reinforcer. When the monkeys selected one peanut and received four, we speculate that the representation of one peanut, as a stimulus, became more highly valued. But because the monkeys saw and reached for a stimulus consisting of four peanuts prior to consuming them, the representation of four peanuts also increased in value. Conversely, when the monkeys chose four peanuts and received only one, we posit that the value of both what they chose and what they received decreased. If both representations changed in concert, in this or in some other way, the monkeys would have difficulty assigning an appropriately enhanced value to the single peanut relative to the group of four peanuts. Such a 'locked up' learning mechanism would account for the persistence of the error rate near 50% correct, which occurred in several of the monkeys tested here.

Finally, to pull the learning system out of this 'locked up' state, we speculate that a higher-level system eventually

became sufficiently engaged to enable the monkeys to learn the correct response. A relevant idea is that regions of frontal cortex, such as the anterior cingulate cortex and other medial frontal areas, monitor responses and detect errors (e.g. Botvinick et al. 1999; Bush et al. 2000; Gehring & Knight 2000; Stuphorn & Schall 2002; Ito et al. 2003; Schultz et al. 2003). The persistence of detected errors might contribute to solving the problem. For example, having recorded the occurrence of erroneous responses at a 50% rate, and having received only one peanut as a result on half of the trials, the monkeys may have adopted a different problem-solving strategy. For instance, they may have begun to view the array of choices (one versus four pieces of food) as a single, conjunctive or configural stimulus and solved the problem by learning conditional associations between those configural stimuli, the potential responses to those stimuli, and their outcomes (Passingham 1993). According to this potential strategy, when four peanuts appeared to the left and one to the right, the monkeys eventually learned to make the right-most choice and vice versa. This strategy would solve the credit-assignment problem by introducing additional stimulus and response representations to which the monkeys could assign values. Of course, other high-level solutions are also possible. We note, however, that rhesus monkeys are adept at solving such conditional associations, and the time course of learning observed here resembles their initial learning rates on such problems (Passingham 1993; Wise & Murray 1999; Murray et al. 2002).

The proposal concerning a credit-assignment problem is consistent with findings from the earlier investigations using variations of the reversed-contingency task. For example, replacement of a small quantity of food with no food (i.e. the no-reward version of the task), as carried out by Silberberg & Fujita (1996) in Japanese macaques, by Anderson et al. (2000) and Kralik et al. (2002) in different species of New World monkeys, and by Genty et al. (2004) in lemurs, would allow individuals to resolve the credit-assignment problem. This is because if the selection by these primates of four peanuts resulted in their receiving none, the value of the representation of four peanuts (as a stimulus) would decrease without any change in the representation of one peanut. Similar procedures that provide the animal with experience in selecting the smaller quantity might also contribute to their ability to solve the standard version of the reversed-contingency task once they have obtained such prior experience (Kralik, in press).

A different, but related set of ideas might account for some of the findings in chimpanzees. Even as the chimpanzees continued to select the larger quantity of food in the standard version of the task, they nevertheless learned something about the reversed reward contingency (Boysen & Berntson 1995; Boysen et al. 1996). This learning revealed itself when the experimenters changed the choice items from visible food to plaques marked with Arabic numerals (see Introduction). When presented with a choice between symbols (the numerals) that had been previously associated with a given quantity of food, the chimpanzees immediately began selecting the number associated with the smaller food quantity (and thus

received the larger reward). According to one hypothesis, although the animals had learned the lower value of the larger quantity of food, they could not sufficiently suppress the prepotent response of reaching for the larger amount when they could see the food. Because nonfood items such as numerals do not act as prepotent stimuli, when the chimpanzees could not see the food, the use of numerals in place of food revealed their learning. In those experiments, erroneous performance only occurred when the animals had to choose between two amounts of food. When the experimenters gave the chimpanzees the choice between a numeral and a quantity of food, they performed correctly, just as when they chose between two numerals.

This latter aspect of the chimpanzee results resembles those reviewed by Baxter & Murray (2002) for rhesus monkeys that were either intact or had sustained damage to the amygdala-orbital frontal cortex network. Monkeys with lesions, like intact monkeys, chose nonpreferred foods when preferred ones had been devalued through selective satiation. The lesion group could not, however, use arbitrary symbolic stimuli (objects), which had been previously associated with those foods, to make the same choices. When choosing between objects, they did so based on their long-standing food preference rather than the associated food's current value. Thus, the brain mechanisms for making choices among food items seem to differ from those involved in selecting among nonfood items associated with foods, and it is likely that the chimpanzees studied by Boysen and her colleagues made use of those alternative mechanisms when numerals were used as discriminative stimuli.

Interpretational Limitations

Although the present experiment has demonstrated that rhesus macaques can learn to select the smaller quantity, one, over the larger quantity, four, it did not test whether the monkeys could generalize this performance to other quantities of food. Given that other studies have shown that rhesus macaques appear capable of forming number concepts in other contexts (Hauser et al. 1996; Tomasello & Call 1997; Brannon & Terrace 1998; Orlov et al. 2000; Sulkowski & Hauser 2001), and that the two species of lemur appeared to generalize to new quantities (Genty et al. 2004), we expect that macaques will be capable of performing the reversed-contingency task by selecting the smaller quantity when presented with different quantity combinations. Further studies will be needed to explore this issue.

An alternative explanation of the results, that all the monkeys discerned and then employed a cue unwittingly provided by the experimenter, seems unlikely given the good performance when tested by the second experimenter (Fig. 3). We cannot, however, completely rule out this alternative account. Future studies should consider the use of a computer-controlled apparatus, which will eliminate the possibility of the monkeys picking up inadvertent, experimenter-provided cues.

Individual Variation and Relevance to Natural Environments

Although the present experiment demonstrated that rhesus macaques can learn to solve the problem posed by the reversed-contingency task, it took our monkeys more than 1000 trials on average to reach criterion performance. Even the fastest-learning monkey still performed at an error rate of 60% after ~200 trials. We can only speculate about what utility this kind of laboratory behaviour might have to macaques in the wild. Foraging sites or specific locations within a site that have more food may, none the less, result in individuals receiving less. This could happen if competitors, including higher-ranking conspecifics, have also chosen the same site or location. Thus, under certain circumstances, individuals may learn that they can obtain more food if they select an apparently sparser food source. Our results further suggest that such learning might proceed in stages. Macaques could learn that richer food sources do not necessarily yield larger amounts with fewer than 100 experiences (see Fig. 2), but take longer to learn that an apparently sparser food source will yield a larger amount. Furthermore, the laboratory version of the reversed-contingency problem might make it more difficult to solve than in a natural foraging context, in which more distinctive contextual cues aid learning and larger differences could exist between vision-based choices and the underlying food cache.

It is also possible that the reversed-contingency task draws, however imperfectly, on more general inhibitory control processes that endow these monkeys with important advantages. As noted in the Introduction, withholding potential actions, including those that have proven valuable in the past, can become beneficial in the face of changing circumstances. Inhibitory control mechanisms can provide crucial delays in decision making that help animals select among diverse and conflicting estimations about future outcomes.

Conclusion

The present results suggest the possibility, denied by the literature in its present state, that catarrhine primates (Old World monkeys, apes and humans) conserve the abilities required to master the standard version of the reversed-contingency task, when presented to them without any prior, related training. Whether anthropoid primates (catarrhines and New World monkeys) also conserve that ability, or primates in general do, remains an open question.

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