

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.

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