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Position Learning of Degus (*Octodon degus*) in a Semi-natural “Counting” Task

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Abstract

Following recent interest in the cognitive abilities of degus, a relatively uncommon rodent species in behavioral research, we assessed the performance of 4 degus using a semi-natural “counting” task. The degus were rewarded when they visited the fourth box in an array of six boxes along a wall. Contrary to our expectations, our subjects had difficulties in learning the task. Although special training resulted in mastery of the task in 3 out of the 4 degus, there were striking individual differences in performance. Furthermore, test performance suggested some degree of contribution of distance cues to success. Accordingly, the apparently ordinal position learning shown by our subjects might rather be ascribed to absolute position learning.

Key words: counting, number, position learning, degus

The degu (*Octodon degus*) is a moderate-sized hystricomorph rodent from central Chile with a brush-like tail (Najecki & Tate, 1999; Woods & Boraker, 1975). The use of degus in physiological research on circadian rhythms has become popular in recent years due to their diurnal nature (e.g., Lee, 2004). In contrast, the cognitive abilities of the degu have only recently started to attract the attention of scientists. According to Tokimoto and Okanoya (2004a), degus vocally

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communicate with mates using at least 17 different calls with specific meanings, such as contact, alarm, grooming, courtship, and post-copulation. They have good visual, auditory, and olfactory senses (Tokimoto, Tokin, & Okanoya, 2005) and can be trained to use a rake to collect sunflower seeds (Okanoya, Tokimoto, Kumazawa, Hihara, & Iriki, 2008). There is also observational evidence of their impressive cognitive skills: they have been documented to engage in the spontaneous construction of a Chinese nested box with a set of three cups of graduated size by fitting one inside the other (Tokimoto & Okanoya, 2004b). Furthermore, a study by Uekita and Okanoya (2011) explored social and spatial recognition in this species. Yet, despite these studies, the degu's cognitive abilities are still relatively unknown. The present study attempts to explore position learning in this species by using a semi-natural paradigm devised by Davis and Bradford (1986) for laboratory rats, subsequently modified by Suzuki and Kobayashi (2000).

Davis and Bradford (1986) reported that 12 male hooded rats quickly learned to enter the third, fourth, or fifth tunnel (the target ordinal number depended on the individuals) in an array of six wooden square tunnels to obtain food. The absolute positions of the tunnels were set up to widely vary in order to minimize the use of distance cues (i.e., physical features of the arena and/or proprioceptive feedback from running), while the olfactory cues were rendered useless by baiting all tunnels (all doors of the tunnels except the target one were locked). Suzuki and Kobayashi (2000, Experiment 1) replicated their results with 3 female albino rats and a modified apparatus (an array of boxes rather than tunnels): the rats easily learned to enter the fourth of six boxes. Furthermore, when the number of boxes was increased to 12 in Experiment 2, the rats correctly chose the fourth box, suggesting that they were not using the ratio cue but a numerical one.

Because degus, as well as rats, live in burrows in the wild (Fulk, 1976; Woods & Boraker, 1975), we employed the semi-natural "counting" task of these studies (Davis & Bradford, 1986; Suzuki & Kobayashi, 2000) in order to assess the cognitive ability of 4 degus.

Experiment 1

Method

Subjects

Four male degus (Ichiro, Jiro, Saburo, and Shiro) were obtained from a local pet-shop. Three of them (Jiro, Saburo, and Shiro) were from the same litter. When they arrived at the laboratory, Ichiro was 3 weeks old and the remaining three were 4 weeks old. The animals were kept in pairs in wire cages with free food (pellets and timothy hay) and water for 20 days. Hand-taming and food restriction procedures followed this initial acclimation period: The hand-taming was

conducted for 15 min per animal for 10 days, during which time the animals' bodyweights were reduced to 90–95% of their free-feeding body weights (133–174 g) by restricting their food intake. The body weights were maintained within this range throughout the study. Water was freely available except during the training and testing sessions that occurred in the experimental apparatus. Each cage had an activity wheel, a piece of biting wood, and a food dish, and its floor was covered with wood-chip bedding. The vivarium was on a 12:12 h light-dark cycle (lights on at 0800 h) at 23 °C and had a humidity level of 55%.

Apparatus

The apparatus used in this study (Fig. 1) differed slightly from that of Suzuki and Kobayashi (2000, Experiment 1). First, the dimensions of the apparatus in this study were smaller due to the smaller size of degus. Second, the apparatus was constructed of acrylic plastic rather than wood to facilitate cleaning. Six identical black boxes (20 cm long, 10 cm wide, and 10 cm high) were set inside a long and perpendicular wall to the left of a white enclosure (110 cm long, 60 cm wide, and 30 cm high). The front panel (10×10 cm) of each box was hinged at the top edge to make it an in-swinging door, but the door opening was restricted when a wooden stopper was inserted in the box. A white start chamber (25 cm long, 15 cm wide, and 15 cm high) was abutted to the center of the short wall of the enclosure. The animals entered from the start chamber to the enclosure through a guillotine door (15×15 cm) manually operated by the experimenter, who stood 1 m away from the start chamber. A video camera located above the enclosure recorded the animals' behavior. The experimental room was illuminated by fluorescent lamps on the ceiling and maintained at 22 °C. An FM radio delivered inter-band noise at 65.5 dB (re Scale C) in order to mask the external noise.

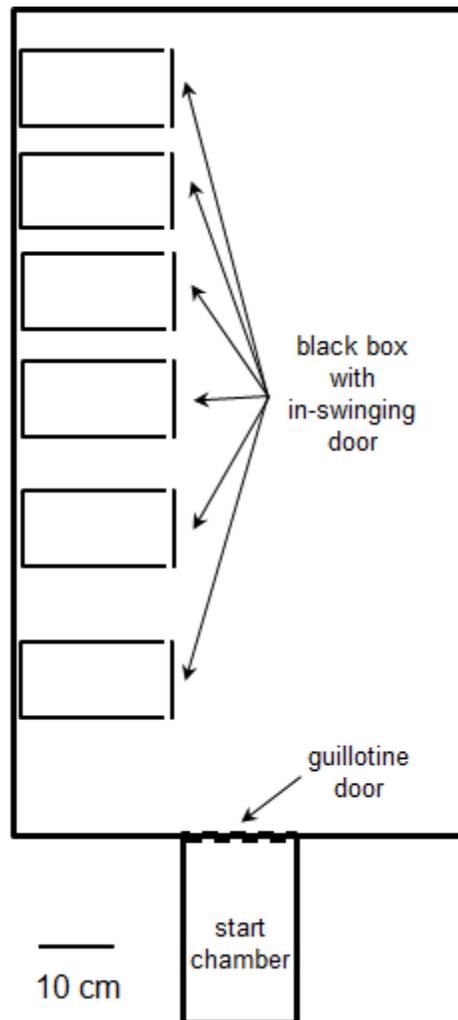


Fig. 1. Floor plan of the apparatus employed in Experiment 1. The length of the enclosure and the number of boxes were doubled in Experiment 2.

Procedures of Part I

All experimental sessions were administered during the light phase of the light-dark vivarium cycle. Initially, the animals were individually acclimated to the white enclosure by keeping them there without the black boxes for 30 minutes per day for 3 days. Following this acclimation period the animals received training for 7 days.

All boxes except the fourth from the start wall had locked doors. Each trial started when the experimenter opened the guillotine door of the start chamber for each animal. Touching any boxes with the mouth or forepaws was coded as a response. The first touch in the given trial was recoded on site by the experimenter

as the choice of that trial. A post-session check of the videotapes verified the experimenter’s record. All trials of this and following experiments ended when the animal entered the target box and ate a 130-mg food pellet located 2.5 cm inside the door. The excreta were wiped away with alcohol wet tissues after the trial. In addition, the floor of the enclosure and the doors were cleaned with wet tissues after each animal completed the daily training session.

On the first and second training days, six boxes were located an equal distance (7 cm) apart. Each daily session consisted of five trials with an inter-trial interval (ITI) of 40 s. On Day 3, the number of trials was increased to 10 with an ITI of 90 s, and the absolute positions of the six boxes were randomly varied trial by trial with a minimum edge-to-edge inter-box distance of 2 cm. On Days 1–3, the fourth box had no door and was the only one baited with the pellet.

From Day 4 on, all boxes were baited with pellets (one pellet per box). The absolute box positions were randomly changed trial by trial, as on Day 3. Each session consisted of 10 trials with an ITI of 90 s. On Day 4, the fourth box had no door as in the first five trials of the session, but the unlocked door was attached to it in the remaining five trials. When the animal failed to open this door to enter the fourth box, the experimenter pushed the door for the animal (cf. Davis & Bradford, 1986; Suzuki & Kobayashi, 2000). Because this guidance technique was not too helpful for our subjects, we administered 3 more training days. On Day 5, the fourth box had no door in the first 2 of 10 trials. Experimenter guidance was in effect during the remaining eight trials. On Days 6 and 7, the fourth box had an unlocked door in all trials, and no guidance was given.

Testing consisted of 10 trials that were administered over the following 2 days (Days 8 and 9). As before, all boxes were baited, and the absolute box positions were randomly changed trial by trial. In order to exclude the use of olfactory, visual, or tactile box cues by which the animals might have found the fourth box, we swapped the boxes trial by trial. In addition, the box-stopper combinations and the box-pellet combinations were also changed each time to prevent the use of specific olfactory cues from the individual stoppers and pellets (cf. Suzuki & Kobayashi, 2000). The ITI was doubled to 180 s in the test, because the experimenter had to clean up the enclosure floor and the doors with alcohol wet tissues after each trial in order to remove odor trails.

Procedures of Part II

As the results of Part I suggested that the procedures developed for rats were not suitable for our degus (see below), we modified the training regimen and continued training until the animals showed good performance prior to testing. Six days after the end of Part I, the following procedure was administered to the same degus with the same apparatus. Three training stages were designed, and the

animals had to make 6 or more correct choices out of 10 trials in each of 2 successive days to pass each stage. Although the experiment was normally conducted 7 days a week, there were occasionally skipped days. If a degu reached the criterion on a day just before a break, a review session was conducted afterwards to confirm good performance prior to the next stage.

Stage 1. Six boxes were located 7 cm apart. The fourth box had no door, while the remaining five boxes had locked doors. The daily session consisted of 10 trials with an ITI of 20 s.

Stage 2. The fourth box had an unlocked door. Other details were the same as in Stage 1.

Stage 3. The absolute box positions were changed trial by trial. The ITI was 90 s. The other details were the same as in Stage 2. The procedure of this stage was identical to that of the last 2 training days (Days 6 and 7) of Part I.

Testing. Testing occurred over 2 days as in Part I. Specifically, we swapped the boxes and changed the box-stopper and box-pellet combinations for each trial. The apparatus was cleaned with alcohol wet tissues after each trial. Each test session consisted of 10 trials with an ITI of 120 s.

Results and Discussion

Part I

Table 1 shows the distribution of the choices in 20 test trials of Part I (Days 8 and 9). In order to assess the correct choice of the fourth box, we set two values of chance against which we applied a one-tailed binominal test. The first was 1/6, because there was one correct box (the fourth box) out of six. The second, more conservative, value was 1/4, because the first and the sixth boxes were unique (i.e., they were end points) and the animals could easily discriminate them from the other four boxes. The alpha level was set at $p < .05$ throughout the study.

Table 1

Frequency of choices (i.e., the first visit) per 20 test trials in Part I of Experiment 1

Degu	Ordinal number of boxes					
	1	2	3	4*	5	6
Ichiro	2	11	6	1	0	0
Jiro	2	9	7	2	0	0
Saburo	0	0	4	8	6	2
Shiro	1	4	12	2	1	0

Note. The correct target box was the fourth of six boxes.

The binomial tests revealed that Saburo was significantly above the generous chance value of $1/6$ ($p = .011$). The above-chance performance of Saburo, however, should be taken with caution, because it did not pass the conservative chance value of $1/4$. More importantly, the number of correct choices in the preceding 2 training days (Days 6 and 7) were only 2 out of 20 trials for this animal. The corresponding numbers for the remaining animals were 4 for Ichiro, 8 for Jiro, and 7 for Shiro. Thus, the poor test performance of our subjects was not surprising, because even in training they had not shown good performance.

Part II

Due to large individual differences in training, we describe the results for each degu in order of effectiveness of performance.

Shiro completed each training stage with the minimum number of sessions (i.e., two). Its test performance is shown in the first data line of Table 2. Binominal tests revealed that its 14 correct choices out of 20 trials were significantly above chance by both the generous and conservative criteria ($ps < .001$).

Jiro demonstrated proficiency within three training sessions in each training stage. The second data line of Table 2 shows its choices in the test. Its 13 correct choices out of 20 trials were above chance by both criteria ($ps < .001$). Saburo completed Stages 1–3 with five, four, and three sessions, respectively. The test performance of this degu was not as high as the other 3 subjects, as shown in the third data line of Table 2. This animal tended to make a primary touch to the incorrect third box. The 7 correct choices of the fourth box out of 20 trials were significantly above chance by the generous criterion ($1/6$, $p = .037$), but not by the conservative one ($1/4$, $p = .214$). The retest of this animal after four sessions of review training at Stage 3 yielded a poorer performance, as shown in the fourth

Table 2

Frequency of choices (i.e., the first visit) per 20 test trials in Part II of Experiment 1

Degu	Ordinal number of boxes					
	1	2	3	4*	5	6
Shiro	1	0	5	13	1	0
Jiro	0	0	5	13	2	0
Saburo1	0	2	11	7	0	0
Saburo2	0	3	13	4	0	0
Saburo3	0	0	2	14	4	0

Note. The correct target box was the fourth of six boxes. Saburo was tested 3 times.

data line of Table 2. The bias of the third box seemed to be amplified. The 4 correct choices out of 20 trials were above chance by neither criterion ($ps > .433$). After this testing, a fading technique (i.e., a gradual shift from the procedure of Stage 3 to the test procedure with respect to swapping boxes, changing box-stopper and box-pellet combinations, and increasing the ITI) was employed for 35 sessions to see whether this animal could be trained to show good performance in the test condition. The final performance of this animal is shown in the fifth data line of Table 2. The 14 correct choices of the fourth box out of 20 trials were significantly above chance by both criteria ($ps < .001$).

Ichiro completed Stages 1 and 2 within 5 and 2 days, respectively. However, it did not attain the criterion of Stage 3 even with 34 training sessions. Amazingly, the removal of the door of the fourth box did not improve its performance for 10 sessions. It visited the third box before entering the fourth box in 61 out of 100 trials of this phase.

In summary, 3 out of 4 degus were successfully trained to choose the fourth box and showed above-chance performance in testing, although one of them required repeated training including a fading technique to show good test performance. It might be noteworthy that these successful subjects chose the fourth box on 5 out of the 6 *initial* trials of the test days (3 degus by 2 test days equals 6 opportunities), suggesting long-term memory of the correct position. The remaining animal (Ichiro) was unsuccessful in learning to choose the fourth box and had a strong bias toward visiting the third box.

Experiment 2

In their study with laboratory rats, Suzuki and Kobayashi (2000, Experiment 2) excluded the possibility that their subjects had used a relative position (roughly middle of the array) as a cue to choose the target box by doubling the length of the enclosure and the number of boxes. The rationale and general procedures of the present experiment were identical to those of their experiment.

Method

This experiment consisted of 2 successive test days administered with Shiro, Jiro, and Saburo 1–3 months after the end of each animal's treatment in Experiment 1. Refresher training, which was identical to the Stage 3 training in Part II of Experiment 1, was conducted once per day for 3 days during the interval days between the end of Experiment 1 and the beginning of this experiment. In addition, the animals had to pass the 2-day learning criterion of that stage again immediately preceding the testing of this experiment.

The test was carried out in a new enclosure that was double the length of the previous one (220×60×30 cm) and the number of boxes was also doubled to 12. The absolute box positions of the boxes were randomly changed trial by trial with a minimum edge-to-edge inter-box distance of 2 cm. Entering an unlocked door of the fourth box was rewarded with a pellet. Each of the other 11 boxes also contained a single pellet, but their doors were locked. The physical identities of the 12 boxes were varied trial by trial. Also varied in each trial were the box-stopper and box-pellet combinations. The apparatus was cleaned with alcohol wet tissues after each trial. Each subject participated in two test sessions consisting of 10 trials each with an ITI of 120 s.

Although there were 12 boxes in this experiment, we assessed the test performance against the 1/6 and 1/4 levels employed in the preceding experiment, because the animals were anticipated to respond in the same way (cf. Suzuki & Kobayashi, 2000).

Results and Discussion

As in Part II of Experiment 1, the results of the animals are described individually. The test performance of Shiro is shown in the first data line of Table 3. Although 9 correct choices out of 20 trials was above chance by either criterion (1/6, $p = .003$; 1/4, $p = .041$), this did not merit any claim to superb performance, because the animal also made the same number of incorrect visits to the third box. Closer inspections of the data revealed that it made only 3 correct choices out of 10 trials on the first test day; the majority of the incorrect choices (6 choices) were distributed to the third box.

The second and third data lines of Table 3 show the results of Jiro and Saburo. Jiro visited the fourth box 13 times out of the 20 test trials, a performance that is above chance by either criterion ($ps < .001$). On the other hand, Saburo chose the fourth box only 6 times out of the 20 test trials, a performance which is not above

Table 3

Frequency of choices (i.e., the first visit) per 20 test trials of Experiment 2

Degu	Ordinal number of boxes											
	1	2	3	4*	5	6	7	8	9	10	11	12
Shiro	0	1	9	9	1	0	0	0	0	0	0	0
Jiro	0	0	5	13	2	0	0	0	0	0	0	0
Saburo	0	0	2	6	9	3	0	0	0	0	0	0

Note. The correct target box was the fourth of 12 boxes.

chance by either criterion ($1/6$, $p = .102$; $1/4$, $p = .383$).

To summarize, only 1 out of 3 degus showed excellent performance in the lengthened enclosure with 12 boxes. However, this does not mean that the remaining 2 subjects used a relative position (roughly middle of the array) as a cue to choose the target box. If that were the case, their choices should have been concentrated on the eighth box, because the length of the enclosure and the number of boxes were doubled in this experiment. However, their incorrect responses were mainly to the boxes near the target one (i.e., erroneous entries to the third or fifth boxes).

General Discussion

This study was planned to explore the cognitive ability of the degu, a relatively uncommon species in comparative cognition research. Because of its excellent perceptual systems (Tokimoto et al., 2005), complexity of vocal communications (Tokimoto & Okanoya, 2004a), and good abilities of tool use (Okanoya et al., 2008), Chinese-box construction (Tokimoto & Okanoya, 2004b), and social and spatial recognition (Uekita & Okanoya, 2011), it seemed reasonable to speculate that this species might be competent in solving other kinds of cognitive tasks. Accordingly, we expected that the degu would easily learn to enter the fourth box in an array of boxes, a semi-natural “counting” task that laboratory rats can master without difficulty (Davis & Bradford, 1986; Suzuki & Kobayashi, 2000). Surprisingly, our subjects failed to learn the task in Part I of Experiment 1 when we employed the standard procedure used by Suzuki & Kobayashi (2000, Experiment 1).

Although special training resulted in mastery of the task in 3 out of 4 degus in Part II of Experiment 1, the individual variability among these successful animals was striking. Furthermore, the fourth degu did not learn to enter the fourth box, even when its door was open. One of the possible reasons for individual differences is that of genetic variation. Our subjects were not genetically similar compared with laboratory rats, because the degus had not been bred as laboratory animals. It might be worth noting that the 3 successful subjects, but not the dropout, were from the same litter.

It is important here to discuss the cues that our subjects used in the present study. As all boxes were baited, they could not use olfactory cues of the food to locate the correct box. It is also unlikely that they followed the odor trails, because we wiped the box doors and the enclosure floor with alcohol wet tissues after each test trial. Furthermore, they could not rely on the unique olfactory, visual, or tactile property of the target box because the boxes were swapped trial by trial in the testing. The relative position in the array of boxes could not have served as a

cue, because doubling the length of the enclosure and the number of boxes did not shift the degus’ choice from the fourth box to the eighth box in Experiment 2.

Although a straightforward account of the mastery of the task is that our subjects learned the ordinal position of the target box (“the fourthness”) by nonverbally counting the boxes or taking a protocounting strategy (Davis & Pérusse, 1988), another possibility is that they used distance cues to locate the target box (i.e., absolute position learning). Although we varied the absolute box positions trial by trial, the ranges were narrower in our study (Figs. 2 and 3) than those of the previous studies with rats. For example, the fourth box in Experiment 1 varied only from 44 to 72 cm: the corresponding values in Davis and Bradford (1986) and Suzuki and Kobayashi (2000) were 45.7–117 cm and 49–140 cm, respectively. More importantly, the position range of the fourth box overlapped only with that of the adjacent boxes in Experiment 1. Accordingly, our subjects could have been able to show above-chance performance by using distance cues only.

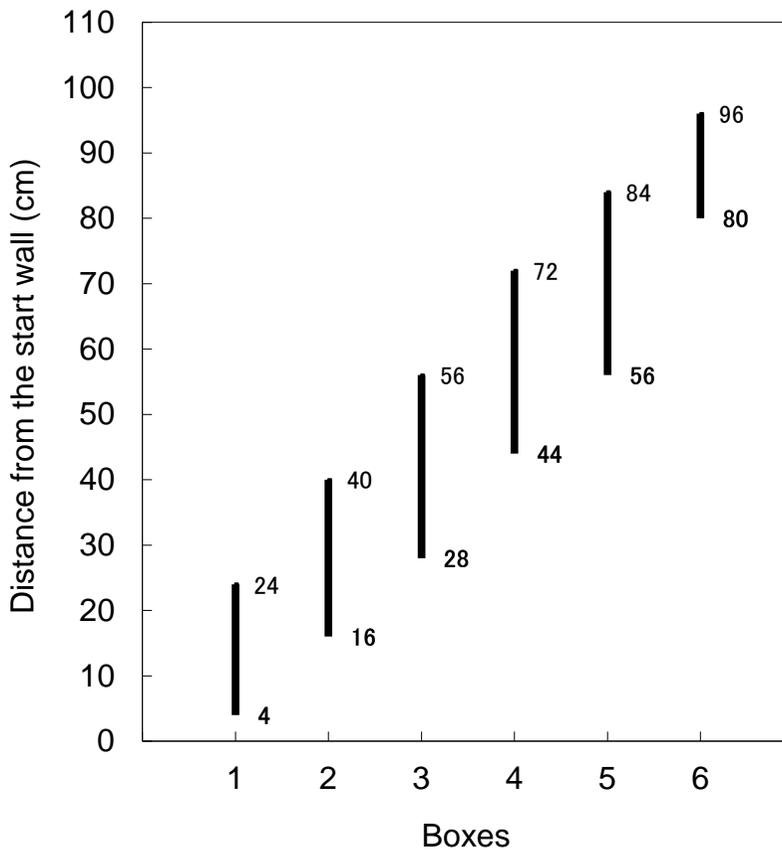


Fig. 2. The absolute positions of the boxes in Experiment 1.

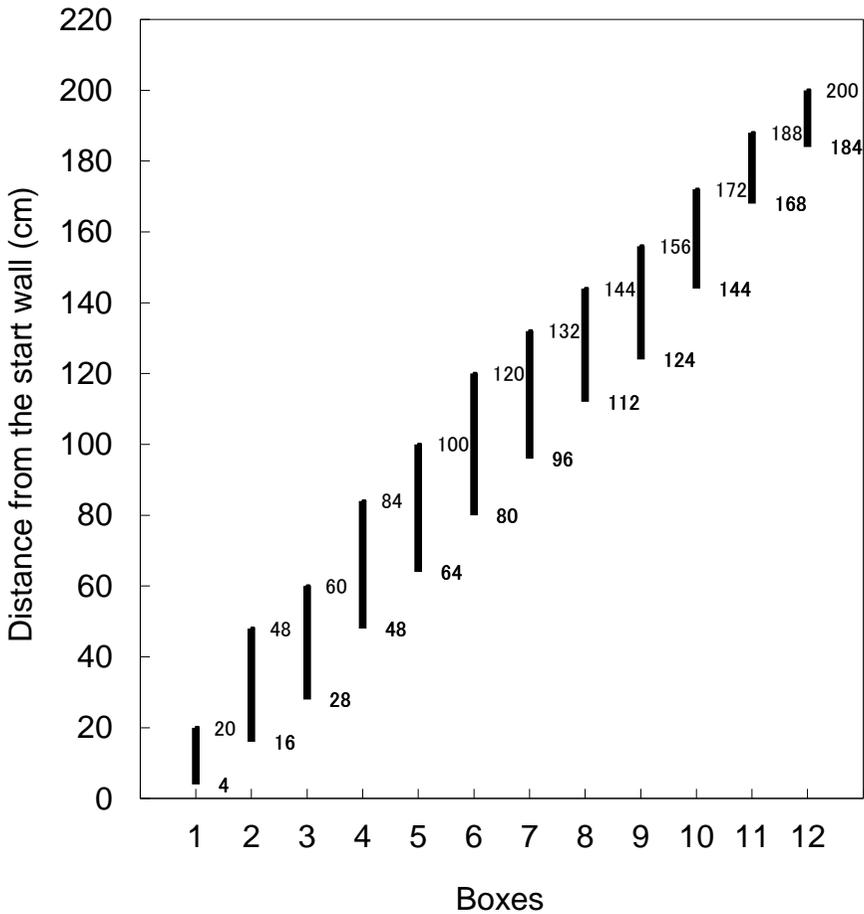


Fig. 3. The absolute positions of the boxes in Experiment 2.

Unfortunately, due to time constraints, we could not directly test this possibility by widely varying absolute box positions after the experiments reported here. However, as a test of this possibility, we examined the test results on the trials when the third box was in the possible absolute position range of the fourth box (Type A trials) and compared them with those of the other test trials (Type B trials). If the subjects were using distance cues, then they should have chosen the third box more often in the Type A trials than the Type B trials. The test data of Part II of Experiment 1 seem to support the distance-cue hypothesis for Shiro and Jiro, but not for Saburo, as shown in Table 4. The same kind of analysis for the test data of Experiment 2 yielded similar patterns for Shiro and Jiro. Furthermore, in that experiment, Saburo made incorrect initial choices for the fifth box on 9 out of 20 trials (Table 3); and these erroneous entries took place much more easily when

Table 4
Reanalysis of the test data in Part II of Experiment 1

		Ordinal number of boxes					
		1	2	3	4*	5	6
Shiro	Type A	1	0	5	2	0	0
	Type B	0	0	0	11	1	0
Jiro	Type A	0	0	7	4	0	0
	Type B	0	0	1	8	0	0
Saburo	Type A	0	0	2	7	1	0
	Type B	0	0	0	7	3	0

Note. The correct target box was the fourth of six boxes. Type A was the trial in which the third box was in the possible absolute position range of the fourth box; and Type B was the trial in which the third box was out of that range (see Fig. 2 for the position ranges of the boxes).

the fifth box was in the possible absolute position range of the fourth box (7 out of 12 trials) relative to the other cases (2 out of 8 trials). Because of these results, we can conclude that the distance cues contributed at least partly, or perhaps largely, to the successful performance of our degus.

We employed the narrow ranges of the absolute box positions because of concern over the failure of our subjects to learn the task. However, the performance of the degus was a disappointment to us. In short, their performance was not satisfactory, even though they had been trained under conditions in which they could have used both numerical and distance cues to solve the task. It seems implausible to ascribe their failures to a low level of motivation (90–95 % of free-feeding weights), because they immediately ate the food when they found it in the target box. In addition, the same weak level of deprivation was employed for rats in Suzuki and Kobayashi (2000). Although we could not determine the reasons for the subjects’ relatively poor task performance observed in this research, the present article provides new behavioral data regarding degus. Further investigation of this species with other tasks would give us a better understanding of their cognitive abilities.

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