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メタデータ	言語: eng 出版者: 公開日: 2017-10-02 キーワード (Ja): キーワード (En): 作成者: メールアドレス: 所属:
URL	http://hdl.handle.net/2297/44940

Abstract Numerical Discrimination Learning in Rats ¹

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¹ Author's note

This paper is based on experiments conducted by the second and third authors for their graduate theses at Kanazawa University, under supervision of the first author. Correspondence may be sent to T. Taniuchi (tohruta@staff.kanazawa-u.ac.jp). This work was partly supported by JSPS KAKENHI Grant Number 24530913.

Abstract

This study examines rats' discrimination learning of the numerical ordering position of objects. In Experiments 1 and 2, five out of seven rats successfully learned to respond to the third of six identical objects in a row and showed reliable transfer of this discrimination to novel stimuli after being trained with three different training stimuli. In Experiment 3, the three rats from Experiment 2 continued to be trained to respond to the third object in an object array, which included an odd object that needed to be excluded in identifying the target third object. All three rats acquired this selective counting task of specific stimuli, and two rats showed reliable transfer of this selective counting performance to a test set of novel stimuli. In Experiment 4, the three rats from Experiment 3 quickly learned to respond to the third stimulus in object rows consisting of six identical objects or six different objects. These results offer strong evidence for abstract numerical discrimination learning in rats.

Keywords: rat, selective counting, absolute ordering, numerical processing, discrimination

A long-standing topic in comparative psychology is whether nonhuman animals can learn an abstract numerical concept. Numerical competence allows animals to comprehend the numerical aspects of a variety of aggregations that differ in specific physical features. Using the abstract numerical concept, we can apply common calculation rules to a wide variety of stimuli.

The abstract concept of number has been divided into two components, concepts of abstract numerosity and order of the numerosities (Brannon & Roitman, 2003; Gelman & Gallistel, 1978; Neider, 2005). Abstract numerosity is suggested by responding to numerosities of stimuli regardless their physical properties, such as size, color, shape, and so on. The concept of ordering relationships among these abstract numerosities enables animals to recognize, for example, that “fourness is greater than threeness and less than fiveness”.

Various animal species have proven their ability to learn an abstract numerosity. For example, a chimpanzee (Matsuzawa, 1985) or pigeons (Xia, Emmerton, Siemann, & Delius, 2001; Xia, Siemann, & Delius, 2000) have showed that they could respond correctly to the number of visual stimuli using arbitrary symbols. Rhesus monkeys (Brannon & Terrace, 1998, 2000) and capuchin monkeys (Judge, Evans, & Vyas, 2005) can respond to the ordinal relationship of a number of different figures on a computer monitor correctly. A male African gray parrot could give a vocal answer to the number of specific objects or the sum of two cardinal numbers (Pepperberg, 1994, 2012). More recently, precise discrimination of small numerosities or rough discrimination of large numerosities has been reported for various species, e.g., elephants (Perdue, Talbot, Stone, & Beran, 2012), infant chicks (Rugani & Vallortigara, 2008), and guppies (Miletto Petrazzini, Agrillo, Izard, & Bisazza, 2015).

A number of studies have also been conducted on numerical competence in rats. For example, it has been reported that rats can discriminate the number of reinforced runs in a straight runway (Capaldi & Miller, 1988), the number of touches to their body (Davis, Mackenzie, & Morrison, 1989), the number of auditory tones (Breukelaar & Dalrymple-Alford, 1998; Davis & Albert, 1986), and the number of lined tunnels in an open field (Davis & Bradford,

1986; Suzuki & Kobayashi, 2000). However, excluding an exceptional study, which tested the transfer of numerical discrimination of auditory stimuli to visual stimuli and showed no sign of transfer of learning (Davis & Albert, 1987), abstractness of numerical concepts in rats has not been elucidated because the clear transfer of counting behavior to novel stimuli has not yet been documented in rats.

Recently, Kamijo and Taniuchi (2015) found that rats could successfully learn to respond to the third stimulus in an object row consisting of identical objects (see Figures 1 and 2). Four to six identical objects were placed in front of ten goal boxes and the spatial position of the target stimulus was changed trial-by-trial to prevent it from serving as an effective discriminative cue. However, despite their successful acquisition of this task, they failed to show clear transfer of discrimination to novel test stimuli, even after acquisition with six different training stimuli. The simplest explanation of the results is the absence of abstract numerical competence in rats. That is, rats might learn a certain kind of stimulus-specific cue for each object. Nonhuman animals frequently learn and use a stimulus-specific cue, e.g., the specific configuration of multiple stimuli, to solve a relational concept learning task, particularly when a small number of training stimuli are used (e.g., Wright & Katz, 2006).

However, we need to examine several other possibilities before concluding that rats lack an abstract numerical competence. First, it is known that novelty of test stimuli in a matching-to-sample task interferes with test performance, provoking exploration of the novel stimuli in monkeys (D'Amato, Salmon, & Colombo, 1985). It has also been shown that rats exhibit not only an exploration tendency (e.g., Ennaceur, Michalikova, & Chazot, 2009), but also neophobia, an avoidance tendency (Wallace & Barnett, 1990), toward novel test objects. In Kamijo and Taniuchi (2015), rats showed a significant avoidance tendency toward novel test stimuli and frequently responded to a goal box with no test object in front of it. Therefore, in Kamijo and Taniuchi, test performance could have been affected by neophobia toward the novel test stimuli. In the present study, rats were habituated to test stimuli before they were used in test phases,

increasing familiarity with test stimuli and reducing a possible exploration tendency or neophobia toward test stimuli, which might interfere with test performance.

A second possible problem in Kamijo and Taniuchi (2015) is related to the procedure by which food rewards were placed in all goal boxes in order to control for a possible olfactory cue, while the small one-way doors immediately in front of the food cups in incorrect goal boxes were locked so that rats could only access food rewards in correct goal boxes. It was informally observed by experimenters that rats sometimes persisted in trying to open the small one-way door in incorrect goal boxes to get at the food reward behind it, possibly due to an olfactory cue from the food reward. Although this procedure may have been an appropriate way to control for a possible odor cue from food rewards, a persistent, irrelevant behavior in an incorrect goal box might interfere with acquisition of numerical discrimination learning. That is, when rats experience a reinforcement event (permitting or denying access to food rewards), they need to associate the reinforcement event with the stimulus they responded to. Given that it was impossible for a rat inside a goal box to perceive the object outside the box, rats need to associate the reinforcement event in short-term memory with information about the discriminative stimulus. Thus, persistent emission of irrelevant responses possibly interfered with forming associations between discriminative responses and reward events in short-term memory. To avoid interfering with association formation, food rewards were only put in the correct goal box during the later training phases. The influence of an olfactory cue from the food reward was controlled on test trials by non-differential reinforcement, placing food rewards in incorrect goal boxes as well as in the correct goal box.

The goal of the present study is to reexamine whether rats can learn an absolute ordering position of stimuli in an object row at an abstract level with some methodological modifications of Kamijo & Taniuchi (2015). Rats were trained to respond to the third object in an object row consisting of identical objects. After acquisition of this discrimination, several tests were conducted to assess whether rats could learn to transfer this discrimination to novel objects and

varying numbers of objects, in order to elucidate whether they could learn an abstract numerical property of discriminative stimuli.

Experiment 1

Experiment 1 examined whether rats could learn a specific ordering position in an object row and transfer this discriminative behavior to novel stimuli. Four rats were trained to respond to the third of six identical objects arranged in a row. Spatial position of the correct stimulus was varied trial-by-trial to prevent spatial location from being an effective discriminative stimulus.

Unlike Kamijo & Taniuchi (2015), which placed food rewards in all goal boxes, food rewards were put only in the correct goal boxes behind the correct stimulus during training to avoid the possibly disruptive behavior of trying to get food rewards in an incorrect box. Thus, the odor cue might be available as an effective discriminative cue during acquisition training. After learning to respond reliably with three different training stimuli, probe test trials with novel objects were inserted into training trials. On a probe test trial, food rewards were put in goal boxes behind the second, third, and fourth stimuli in an object row to evaluate the possible effect of an olfactory cue. This selective non-differential reinforcement probe test is a variant of a non-differential reinforcement probe test in which any choice of response is reinforced (e.g., Castro, Lazareva, Vecera, & Wasserman, 2010). We reinforced only the second, third, and fourth objects, not all objects, because our preliminary investigation showed that complete non-differential reinforcement or extinction treatment to test stimuli disrupted rats' baseline performance completely. If rats learned to respond to the odor cue from food rewards, response rates should be equal across the second, third, and fourth objects because these objects were reinforced equally. By contrast, if a rat transferred its discriminative response to the third stimulus to novel test stimuli, we would expect response rates to the third object to be significantly better

than chance, even on probe test trials.

Method

Subjects

The subjects were four experimentally naive, male Long-Evans rats, approximately 60 days old at the beginning of the experiment. Rats were given 14 g food daily except for experimental rewards. These rats were acquired from Kiwa Laboratory Animals Co., Ltd. and were cared for and used according to guidelines approved by Kanazawa University Animal Experimentation Regulations.

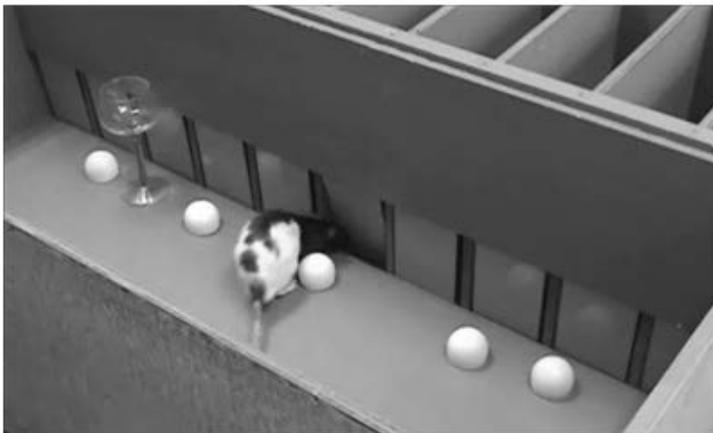
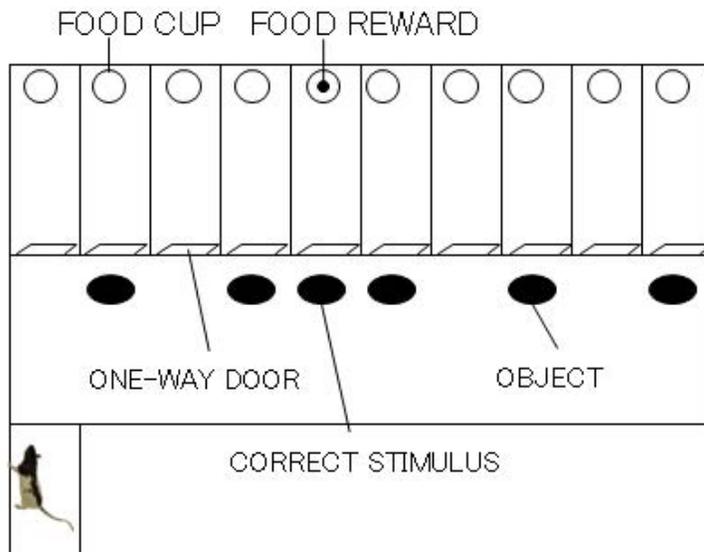


Figure 1. Diagram of the apparatus (top) and photos of performance during acquisition task of Experiment 1 (middle) and selective counting task of Experiment 3 (bottom).

Apparatus

Figure 1 shows a schema of the apparatus and photos of performance in Experiments 1 and 3. Ten goal boxes, 30 cm long, 10 cm wide, and 40 cm high, were lined up next to each other in the apparatus. Each goal box had a one-way swing door at its entrance. A food cup was placed at the end of the goal box, and two 0.045 g food pellets were placed in the cups as a food reward. The apparatus was painted flat gray, and the one-way doors were made of gray PVC board. Objects used in the initial training and transfer tests were glass bottles, metallic 350 ml cans, hemispherical capsules, and rhinoceros beetle models. The assignment of these objects to items A, B, C, and D was counterbalanced among subjects. A glass fish tank, 60 cm long, 30cm wide, and 36 cm high, was used for exploration of test objects in advance of testing.

Procedure

During the first 7 days, rats were handled for three minutes and ten food pellets were placed in their home cages for familiarization. Exploration of the apparatus was allowed on days 8 and 9 for 20 min. individually. All doors were open and rats could eat the food pellets scattered over the apparatus floor and food cups. From day 10, rats were shaped to open the one-way doors. A rat was put in the start box and then the guillotine door was opened about 3 s later. Nine of the 10 doors were blocked and rats could only enter the single open goal box. Rats were eventually trained to enter a completely closed door.

After completion of shaping, Phase 1 of acquisition training with stimulus A commenced. Figure 2 shows how objects were placed for a trial. Six objects were arranged in random order in front of the 10 goal boxes, and the rats were trained to choose the goal box fronted by any object A. Correct responses were rewarded by two food pellets. For an incorrect response, rats were confined in the goal box with no reward for 10 s. The intertrial interval was 4-8 min. When rats attained the learning criterion of 70% correct in a daily 24-trial session, Phase 2 training was started. In Phase 2, responses to the second, third, and fourth objects, counting from the left in

the object row, were reinforced. Other aspects of the procedure and learning criterion were identical to Phase 1. In Phase 3, the correct response was restricted to the third object. Possible correct (third) goal boxes for the arrangement of the six objects were the third, fourth, fifth, sixth or seventh in the row of 10 boxes. The frequency of each of the five goal boxes, as the correct box, was made equal and counterbalanced over five trials. Learning criterion for Phase 3 was 70% correct in a daily 24-trial session or 50% correct for four successive sessions. In Phase 4, object B was added to the training, and objects A and B were each used for 12 daily trials, in a daily 24-trial session. Order of trials with objects A or B was randomized for every two trials. Learning criterion was 50% correct for both of A and B and 80% correct in total in a session or 70% correct for three successive sessions. In Phase 5, object C was added to the training and eight trials were given for each object. Learning criterion was 50% correct for each of the three objects and 80% correct in total for four successive sessions. Order of trials with these three objects was randomized every three trials. On the day a rat attained the learning criterion for Phase 5, exploration of test stimuli was provided after training, to habituate the rats to the new stimuli. Four identical test objects D were placed in a glass fish tank, set in an identical experimental room, and each rat was individually allowed to explore them freely for 20 min.

After completion of Phase 5, probe tests were conducted for six days. 21 training trials with objects A, B, or C and three probe trials with novel object D were conducted in a daily 24-trial session. The procedure for the probe test was identical to that of Phase 5, except for following two points. A probe trial with D was inserted after every seventh training trial. Responses to the second, third, and fourth objects from the left in the object row were reinforced non-differentially for test stimulus D. The reason for reinforcing these three objects is as follows: by reinforcing the second, third, and fourth objects, we could evaluate two possible non-transfer effects, i.e., utilization of an olfactory cue from food rewards and training effects during the test period. That is, if rats responded to olfactory cues from food rewards, they should respond to the second, third and fourth test objects equally. Similarly, if rats learned how to respond to novel

test stimulus D based on reinforced experience on the test trials, rats should also respond to these three objects equally. Conversely, if a rat responded to the third object more frequently than the second or fourth object, it could be attributed to a transfer effect from acquisition training.

Following the probe test, rats were trained with objects A, B, C, and D in Training Phase 6 until they attained the learning criterion of 50% correct for each of the three objects and 70% correct in total in four successive sessions. After acquisition with four different objects, the total number of objects presented in a trial varied randomly among four, five, or six objects across trials to evaluate the possibility that rats count objects from the right end of an object row or use a relative position in an object row to identify a target object. That is, if rats count objects from the far right end of the row, it was expected that their performance would deteriorate when the total number of objects was changed from six into four or five because the ordinal position of the target object from the right end varied, depending on the total number of objects in a row. By contrast, if rats count objects from the left end, the total number of objects would not influence rats' performance because ordinal position of the target object remained the third place regardless of the total number of objects. Similarly, if the total number of objects were six, the correct third stimulus was always located just to the left of the point dividing the row of six objects in half. However, the correct stimulus was placed just to the right of the halfway mark for a four-object row or on center of the five-object row. Therefore, if rats learned the relative position of the correct stimulus in the object row, their performance would deteriorate when the total number of objects was changed from six to four or five. Only responses to the third object were reinforced. For the four- and five-object conditions, we maintained the same possible positions for the correct goal box as in the six-object condition, thereby excluding the first, second, eighth, ninth, and tenth boxes as correct goal boxes. Order of these three different conditions was randomized for every three trials, and this test was conducted for two sessions.

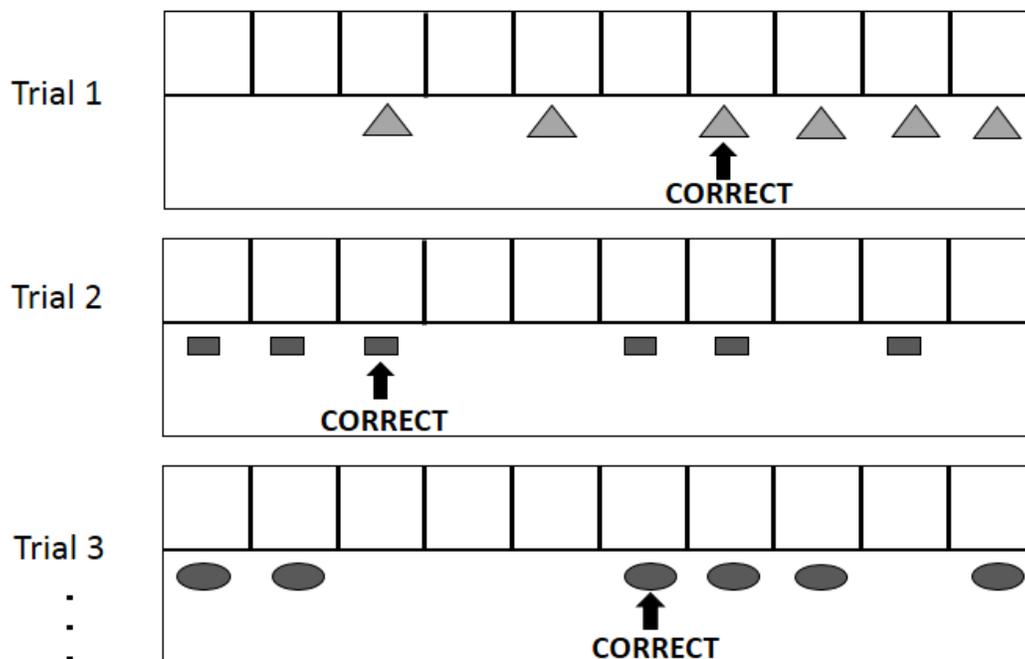


Figure 2. An example of object arrangement for Phase 5 trials, where three types of objects, A, B, and C, were used for training. Only a single type of object was used per trial. Object types were changed every three trials.

Results

Figure 3 shows the percentage of correct responses during acquisition training. Solid lines in the figure represent shifts of training phase. Rats 1 and 2 were excluded from training in Phase 3 because their performance did not improve and remained at a low level. In contrast, Rats 3 and 4 attained the learning criterion of Phase 5 acquisition training with three different stimuli, A, B, and C.

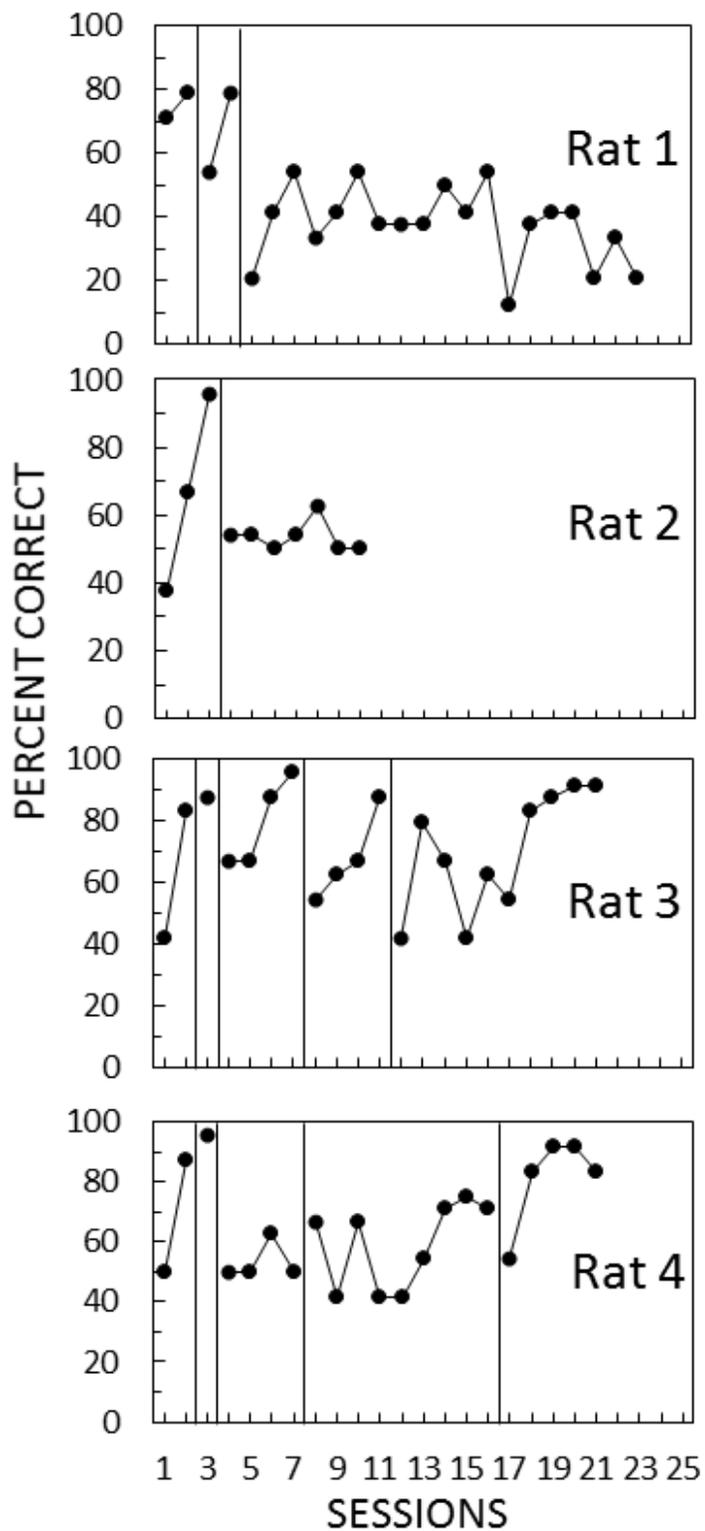


Figure 3. Percentage of correct responses during acquisition training for Experiment 1. The solid vertical lines represent the beginning of a new training phase.

We can assume several different chance levels for the acquisition-training phase. The first is the “objects” model, a chance level of 16.67%, which is the expected value when rats respond randomly to six presented objects. The second is the “possible goals” model, set at 20%, which would be expected if rats respond randomly to five possible goal boxes, that is, the third to the seventh box, because the target third object could not be placed in front of the first, second, eighth, ninth, or tenth goal box in a row of six objects. The third chance level is the “objects and goals” model, which could be set at 35.93% of correct responses, when rats respond randomly to objects in front of the five possible goal boxes. That is, there are 35 patterns of object arrangements in which the target third object is set in front of Goal 3. In these 35 arrangements, 95 objects in total may be set in front of possible Goals 3-7. Therefore, in the case of the third box being correct, the chance level is 36.84% (35/95), where rats respond to objects in front of the possible goals randomly. Similarly, the chance level is 31.58% (60/190), 34.45% (60/174), 33.90% (40/118), and 42.85%(15/35) in each case where the target third object is set in front of Goals 4, 5, 6, and 7, respectively. Since we used these possible goals with equal frequency, the total chance level of the “objects and goals” model could be set at 35.93%, an average of the chance levels for Goals 3-7. Thus, we assume that 35.93% would be the most conservative chance level to evaluate a rat’s performance in acquisition training. Performance of Rats 3 and 4 on the last four sessions of Phase 5 was significantly higher than the most conservative chance level (one-tailed binomial test; $p < .01$).

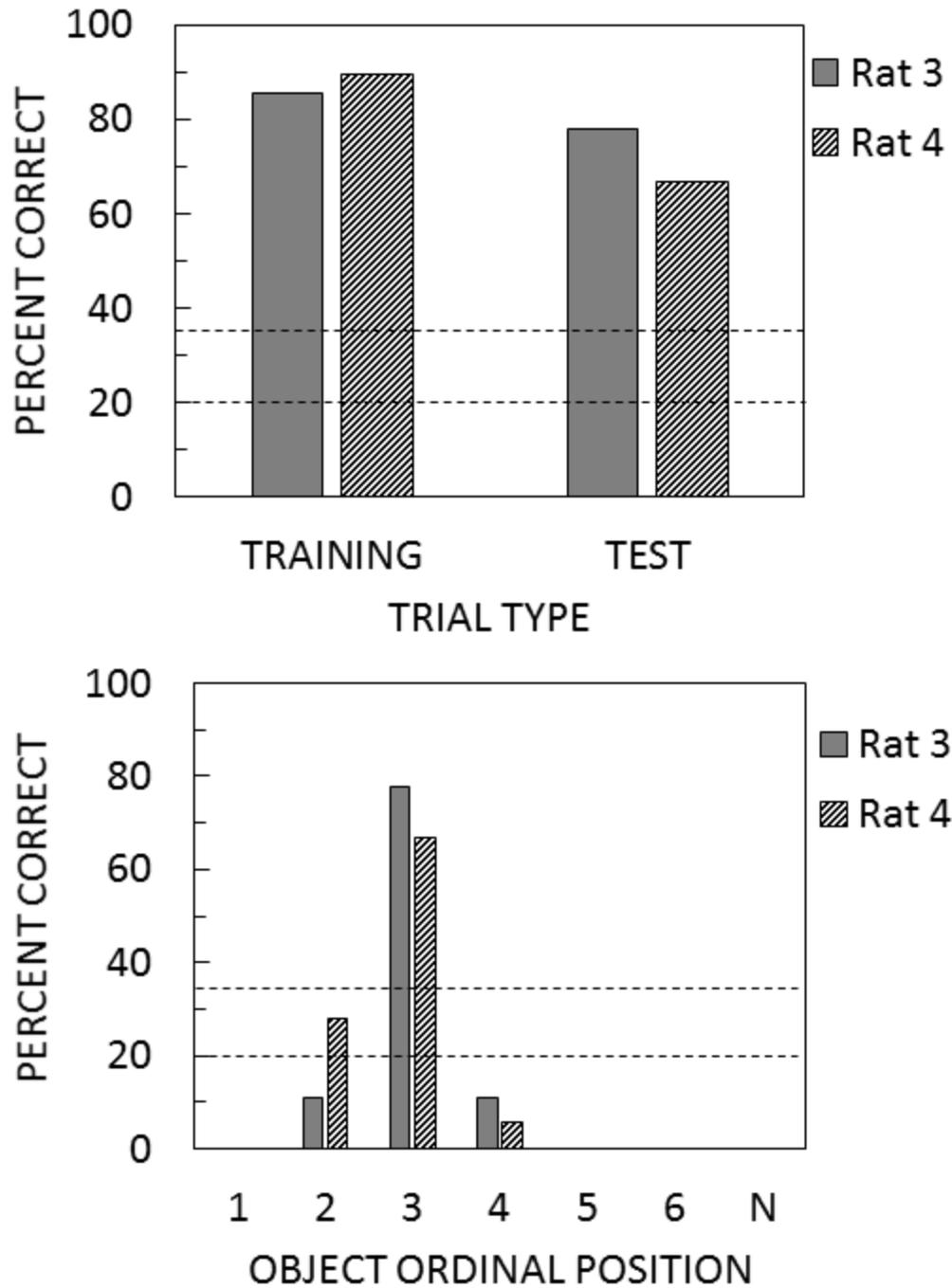


Figure 4. Percentage of correct responses for training and test objects (top panel) and percentage of responses to objects in each ordinal position in Experiment 1 Probe Test (bottom panel). “N” represents goal boxes with no object in front of them. The broken horizontal lines represent the chance levels. Details about chance levels are in the text.

Figure 4 shows the results of the probe test with novel stimulus D. Rats made some errors by choosing the second and fourth objects, but they never responded to objects in more remote ordinal positions or goals with no object. We reinforced responses to the second, third, and fourth objects in an object row to control for olfactory cues from food rewards or learning effects during test trials. Thus, the chance level was $1/3 = 33.33\%$ for these two possible non-numerical choices on test trials (models of “olfactory cue” and “reinforced experience”). Rats 3 and 4 both made correct responses at a significantly higher than chance level when compared to the 33.33% chance level for olfactory cues from food rewards or from learning effects (one-tailed binomial test; $ps < .01$), but also to the more conservative “objects and goals” model of chance level of 35.95% (one-tailed binomial test; $ps < .01$).

However, if rats combined olfactory cues during test trials with possibly correct goal boxes, that is, if rats responded randomly to a goal box from boxes 3-7 with an olfactory cue from a food reward, the chance level for correct response would be 43.00% (“olfactory cues and possible goals” model). That is, there are 35 patterns of object arrangement in which the target third object is set in front of the possible Goal 3. In these 35 patterns, the second object was never placed in front of possible Goals 3-7 and the fourth object could be set in front of these possible goals in 34 patterns of object arrangement. Therefore, if rats responded to the olfactory cue presented in the possible Goals 3-7, the chance level would be 50.72% (35/69). There are 60 patterns of object arrangement in which the target stimulus is set in front of the Goal 4. In these 60 patterns, the second, third, and fourth object could be set in front of the possible goals in 40, 60, and 57 patterns, respectively. Therefore, the chance level of “olfactory cues and possible goals” model would be 38.22% (60/157) when the third object was placed in front of Goal 4. Similarly, the chance level of “olfactory and possible goals” model would be 36.59% (60/164), 37.74% (40/106), and 51.72% (15/29) when the third object was set in front of possible Goals 5, 6, and 7, respectively. Since we used Goals 3-7 in equal frequency, the chance level of the “olfactory cues

and possible goals” model could be set at 43.00%, an average of the chance levels for Goals 3-7.

Using this most conservative chance level of the “olfactory cues and possible goals” model to evaluate the significance of transfer performance to test stimuli, the percentage of correct responses was significant for both rats (one-tailed binomial test; Rat 3; $p=.003$, Rat 4; $p=.037$).

The results of changing the total number of objects are shown in Figure 5. The effect of the total number of objects was very slight and performance was significantly better than the “objects and goals” model of chance level of 35.93% in all conditions for both rats (one-tailed binomial test; $ps<.01$).

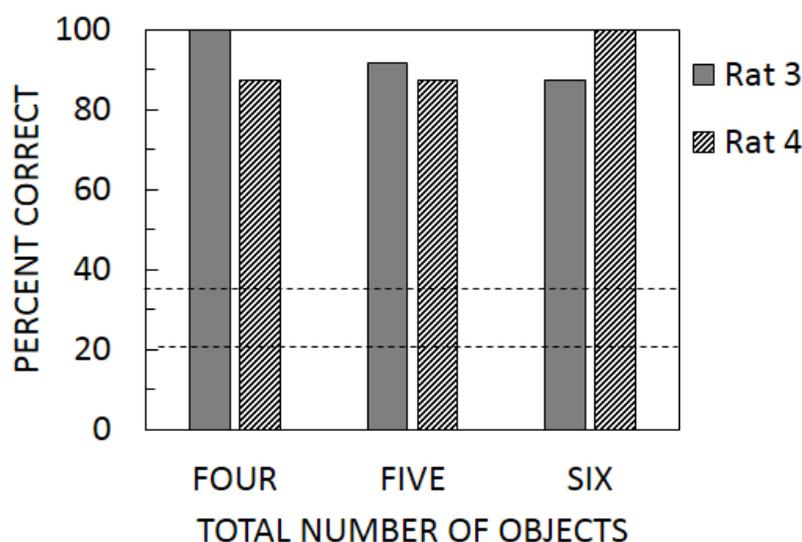


Figure 5. Percentage of correct responses for conditions with varying numbers of objects in Experiment 1. Details about chance levels are in the text.

Discussion

Two out of four rats successfully learned numerical discrimination of the third object in an object row consisting of six objects. As the spatial location of objects was changed trial-by-trial, any specific spatial position of the target object or correct goal box could not serve as an effective discriminative cue. Moreover, rats’ performance was not affected by changing the total number

of objects. The possibility of counting from the far right end of the row was also excluded because the ordinal position of the target object from right end varied depending on the total number of stimuli. This result also eliminates the possibility that rats used relative position in a row of objects. For example, if the total number of objects were six, the correct third stimulus was always located just to the left of the point dividing the row of six objects in half. However, the correct stimulus was placed just to the right of the halfway mark for a four-object row or on center of the five-object row. Therefore the relative position of the correct stimulus in the object row could be eliminated from possible accounts for rats' successful acquisition of the task.

Two rats also showed reliable transfer of discrimination to novel object D after acquisition training with three different stimuli, A, B, and C. We reinforced responses to the second, third, and fourth stimuli in a row of test object D to control for olfactory cues and learning effects during test trials. If rats responded to the smell of food pellets in the goal box or if rats learned how to respond to the novel test object through reinforced experience during the test period, rats should have responded equally to the second, third, and fourth objects. Given that the test performance of Rats 3 and 4 was reliably better than chance, an olfactory cue or reinforced experience can be eliminated as a reasonable explanation for the results of the probe test. Moreover, the transfer performance of Rats 3 and 4 was significantly higher than the most conservative "olfactory cues and possible goals" model of chance, 43.00%, that might be expected if rats could combine the conditions for possible correct goal boxes and olfactory cues from food rewards or reinforcement experience during test trials. Therefore, results of Experiment 1 strongly suggest learning of abstract numerical discrimination in rats.

Experiment 2

In Experiment 1, two rats learned numerical discrimination of the third object in a row successfully. However, successful acquisition and presumed transfer of the third ordinal position

was only confirmed with two subjects. Although the assignment of four different objects to training and test stimuli was counterbalanced across subjects, it might be possible that test object D for Rats 3 and 4 had, by chance, some specific similarity of physical features with training stimuli, and such similarity contributed to their good transfer performance through a simple stimulus generalization process. Experiment 2 was designed to replicate Experiment 1 and to confirm a further inter-subject generality of transfer of numerical discrimination to novel stimuli. If successful acquisition and transfer of discrimination to novel test stimuli were confirmed in additional subjects, the possibility that specific physical similarities mediated the transfer effect would decrease.

Method

Subjects

The subjects were three experimentally naive, male Long-Evans rats, approximately 70 days old at the beginning of the experiment. Other aspects of the animals and their treatment were identical to those of Experiment 1.

Apparatus

Objects used in the initial training and probe tests were chosen from metallic 150 ml cans, glass bottles, ceramic dolls, metallic 350 ml cans, hemispherical capsules, artificial sunflowers, and transparent wine glasses. The assignment of these objects to items A, B, C, and D was counterbalanced among subjects. Other aspects of the apparatus were identical to those of Experiment 1.

Procedure

The procedure for pre-training was identical to that of Experiment 1, except that exploration of the apparatus was conducted for four days. After completion of pre-training, training was initiated. The procedure for this training was identical to that of Experiment 1, except for following points. Learning criteria were 70% correct for two successive sessions and 50% correct for each training stimulus. During the Probe test, 20 training trials with object A, B,

or C and four probe test trials with novel object D were conducted in a daily 24-trial session. A probe test with D was inserted after every fifth training trial. Test sessions were conducted for four days (16 test trials in total).

Following the probe test, rats were trained with objects A, B, C, and D until they attained a learning criterion of 50% correct for each of the three objects and 70% correct in total for two successive sessions. Then they were tested with a varying total number of objects A, B, C, or D, that is, four, five, or six objects, for two days.

Results

Figure 6 shows the percentage of correct responses during acquisition training. All three rats learned the acquisition task with three different stimuli, A, B, and C. Performance on the last two sessions of Phase 5 was significantly higher than the “objects and goals” model of chance level of 35.93% (one-tailed binomial test; $ps < .01$).

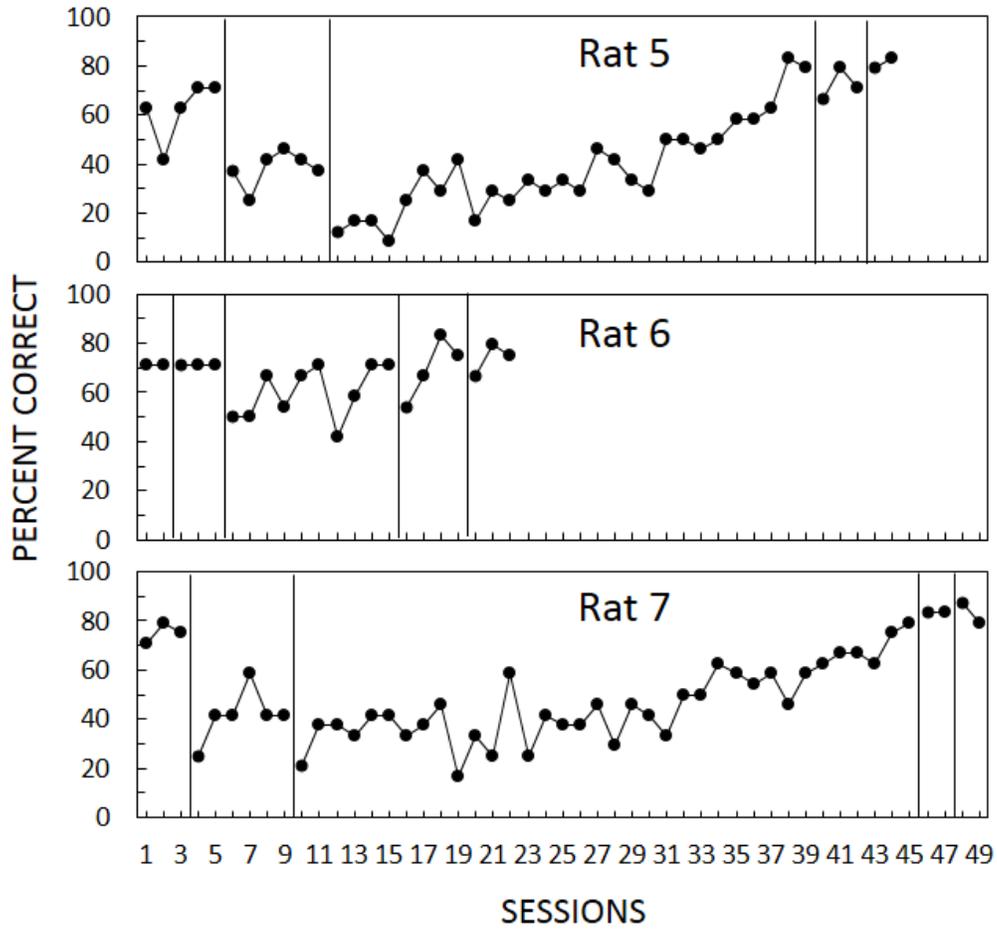


Figure 6. Percentage of correct responses during acquisition training in Experiment 2. The solid vertical lines represent the beginning of a new training phase.

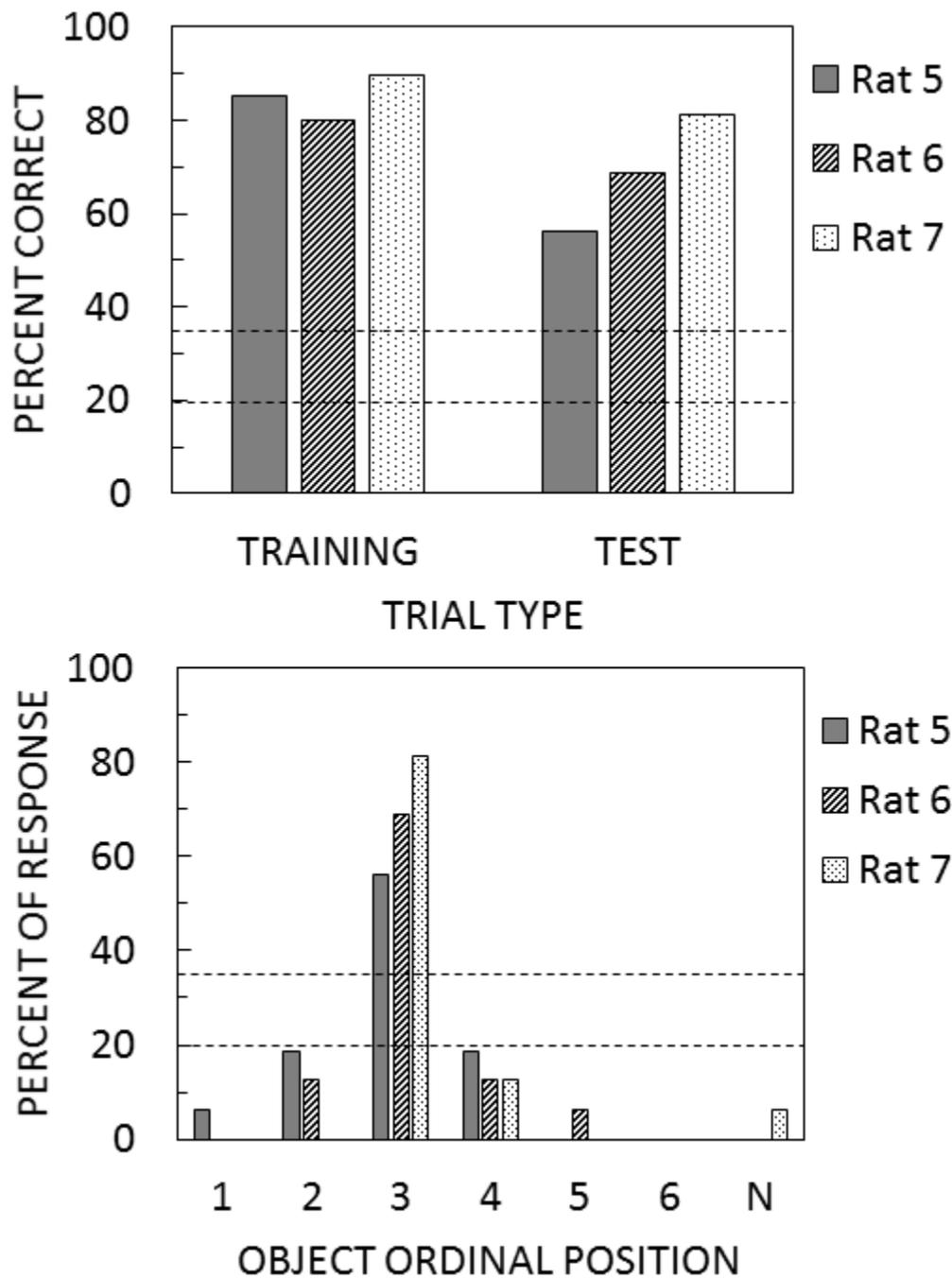


Figure 7. Percentage of correct responses on training and test object (top panel) and percentage of responses to objects in each ordinal position in Experiment 2 Probe Test (bottom panel. “N” represents goal boxes with no object in front of it). The broken horizontal lines represent the chance levels. Details of these chance levels are in the text.

Figure 7 shows the results of the probe test with novel stimulus D. Rats made most of their errors on the second and fourth objects, and very few errors were made with objects in more remote ordinal positions or goals with no objects. Rats' performance was significant for test trials (one-tailed binomial test; $ps < .01$), as well as for training trials (one-tailed binomial test; $ps < .01$), even when compared to a chance level calculated from the combination of five possible boxes and the presence of objects ("objects and goals" model; 35.90%). Compared to the most conservative chance level of 43.00%, which was derived from a possible combination of olfactory cues from food rewards and/or reinforced experience during test trials with the possible correct goal boxes ("olfactory cues and possible goals" model), performance on test trials was not significant for Rat 5 (one-tailed binomial test; $p = .205$), but Rats 6 and 7 showed significant transfer performance compared with the most conservative chance level (one-tailed binomial test; Rat 6; $p = .034$, Rat 7; $p = .002$).

The data from the transfer tests in Experiments 1 and 2 were also combined to compare training and test performance statistically. Combined mean percentage of correct response of the five rats was 86.12% and 70.14%, for training and test stimuli respectively. A Trial type * Subjects analysis of variance revealed significant main effects of Trial type ($F(1, 4) = 13.91, p = 0.020$), showing significantly better performance for training stimuli than for test stimuli.

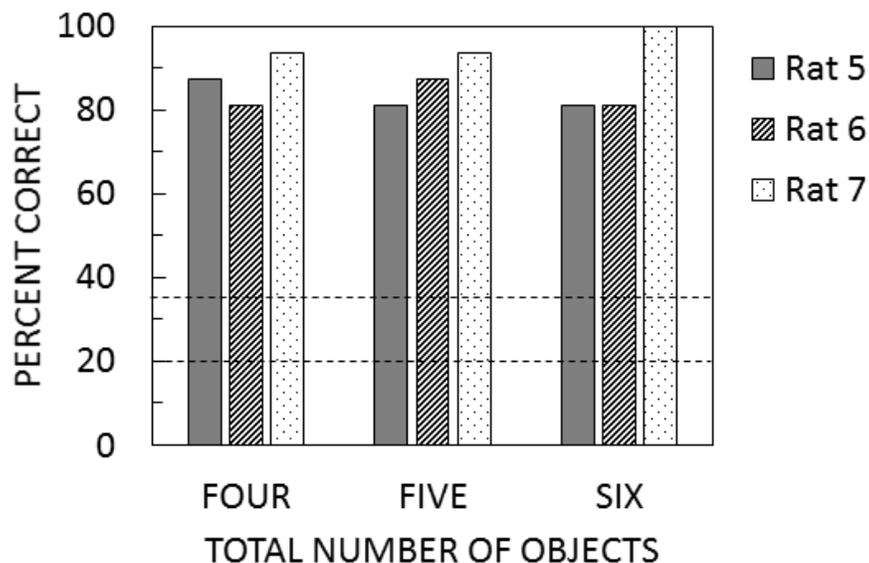


Figure 8. Percentage of correct responses for conditions with varying numbers of objects in Experiment 2. Details about these chance levels are in the text.

Figure 8 shows the results of a test with Rats 5-7, where the total number of objects varied among four, five, or six. The total number of objects in a row had almost no influence on the performance of each rat, and their performance was significantly better than the chance level of the “objects and goals” model (35.93%) in all conditions (one-tailed binomial test; $p < .01$). Again, the data from Experiment 1 (Rats 3 and 4) were combined with those from Experiment 2 to evaluate the effect of the total number of objects. The combined mean percentage of correct responses for the five rats was 90.00%, 88.33%, and 90.00% for the four-, five-, and six-object conditions respectively. Main effects of Number of objects ($F(2, 8) = 0.151, p = 0.867$) was not significant in a Number of objects * Subjects analysis of variance.

Discussion

All three rats in Experiment 2 successfully learned to discriminate the third object in an object row. Importantly, Rats 6 and 7 showed significant transfer performance compared with the most conservative chance level of 43.00%, derived if rats could combine an olfactory cue of

food reward and/or reinforced experience during test trials with the possibly correct goal boxes. These results strongly suggest that possible non-numerical explanations may be eliminated.

Successful acquisition and transfer of learning to novel test stimuli was shown for two rats in Experiment 1 and it was also replicated for three rats in Experiment 2. Such replication helps to confirm inter-subject generality of numerical discrimination learning of objects and its transfer to novel stimuli in rats. Given that the assignment of objects to training and test stimuli was counterbalanced across subjects, an explanation of the transfer effect in terms of any specific physical similarities shared between training and test stimuli could be eliminated. Therefore, the transfer effect shown by these five rats strongly suggests that the rats learned an abstract numerical property during acquisition training and applied it to novel stimuli in the transfer test.

Experiment 3

A total of five out of seven rats successfully learned to respond to the third object in an object row in Experiments 1 and 2. Moreover, four out of these five rats showed reliable transfer of learning to the novel test stimuli after training with three different training stimuli. However, there is still a possible alternative explanation of the transfer that does not assume abstract numerical competence in rats. That is, if rats ignored or were insensitive to differences among training and test objects, good transfer performance to novel test stimuli would be expected. In this case, good transfer of learning would represent ignorance of specific differences in physical features of different objects used for training and testing, but it would not signify a rat's abstract numerical discrimination that could be applicable to dissimilar stimuli in common.

Experiment 3 was designed to elucidate this problem. The three rats from Experiment 2 continued to be trained with stimuli A, B, C and D as in Experiment 2. However, in Experiment 3, an odd stimulus was inserted among five identical stimuli in a row and rats were trained to

respond to the third object in a row by ignoring the odd object. For example, in a row of AAABAA object, where capital letters and their order represent type and position of each object in the row, the third object A from the left was a positive stimulus as in Experiment 2. By contrast, in a row of ABAAAA objects, the fourth object, an A (the third A object), not the third object, was a positive stimulus because the odd object, B, was excluded from the count. Since all stimuli of A, B, C, and D were assigned to both the identical and the odd stimuli, rats had to not only count objects based on a numerical rule, but also to discriminate the objects from each other to exclude the odd stimulus from the count. Following acquisition training, transfer of learning to novel test stimulus sets, consisting of novel objects E and F, was examined. If rats could learn numerical discrimination of specific stimuli and transfer that learning to test sets of novel stimuli, rats' numerical competence in learning an abstract ordering position would be strongly supported.

Method

Subjects

The three rats from Experiment 2 were also used for Experiment 3, which began two days after Experiment 2 ended. During the inter-experiment period, food deprivation was continued. The treatment of the animals was identical to that of Experiments 1 and 2.

Apparatus

The assignment of objects, from the pool of seven types of items, to training stimuli A, B, C, and D for each rat, was identical to that of Experiment 2 and counterbalanced across subjects. The two test objects, E and F, were selected from among the remaining three types of items, as listed in Experiment 2. Other aspects of the apparatus were identical to those of Experiments 1 and 2.

Procedure

Rats were presented with stimulus sets consisting of five identical objects and an odd object in a trial (thus, six objects in total) and were required to respond to the third object from the left

belonging to the set of identical objects, omitting the odd object from the count. The 12 stimulus sets were derived from possible combinations of A, B, C, and D. These 12 sets were presented randomly in a 12-trial block and repeated twice daily for 24 trials per session. There were two types of trials, differing in whether the odd object was located prior to the fourth object or whether the odd object was the fourth, fifth, or sixth object in the row. In the former case, rats had to exclude the odd object from counting and respond to the fourth object in the row. By contrast, in the latter case, because the odd object was not included in the first three objects, rats did not have to exclude the odd object from counting and had to respond to the third object in the row. These two patterns of stimulus sets were presented randomly in every two-trial block. Therefore the probability of whether rats had to exclude the odd object from counting or not on a trial was equally 50%. The learning criterion for acquisition training was 70% correct for two successive sessions. On the same day that each rat attained the learning criterion, they were allowed to explore new test stimuli. Four test objects, two each of E and F, were placed in a glass fish tank, and each rat was individually allowed to explore them freely for 20 min.

After completion of acquisition training, probe tests were conducted for six days. A total of 24 training trials and three probe trials were given in a daily session. Two novel probe sets, consisting of novel objects E and F, were inserted in every ninth trial. Whether E or F was used as an identical or an odd stimulus was determined randomly for each two probe-trial block. For the test trial, the total number of objects varied between five and six, using four or five identical objects along with an odd object. For probe sets, an odd stimulus was placed as the first, second, or third stimulus in an object row and responses to the third and fourth objects were reinforced non-differentially. That is, responses to the fourth object, based on selective counting, and to the third object, based on non-selective counting of the identical stimuli, were equally reinforced with food rewards on the test trials. This enabled us to distinguish the transfer effects of selective counting on the probe test sets during the test trials from olfactory cues from food rewards or training effects.

Results

All three rats learned the acquisition task of selective counting very quickly. The number of sessions required to attain the learning criterion of the acquisition task was three for Rats 5 and 6, and four for Rat 7. Figure 9 shows the proportion of each response type of selective counting (responses to the fourth object by excluding the odd object from counting) and non-selective counting (responses to the third object by including the odd object in counting) of the identical stimuli, and other errors (responses to the other objects or goals with no objects) during 18 test trials. When the proportion of selective and non-selective counting was compared to evaluate the learning transfer effect, the proportion of selective counting responses was significantly higher than that of non-selective counting responses for Rat 6 (one-tailed binomial test; $p=.006$) and Rat 7 (one-tailed binomial test; $p=.025$), but not for Rat 5 (one-tailed binomial test; $p=.315$).

The proportion of selective counting responses was analyzed separately for each total number of objects in a row, i.e., five or six. For Rats 6 and 7, the proportion of selective counting responses was relatively high in both the five-object condition (6/9=66.7% and 7/9=77.8%, respectively) and six-object condition (6/9=66.7% and 6/9=66.7%, respectively). In contrast for Rat 5, the proportion of selective counting performance was poor in the five-object condition (3/9=33.33%), although it was good in the six-object condition (7/9=77.8%), resulting in an overall non-significant selective counting performance.

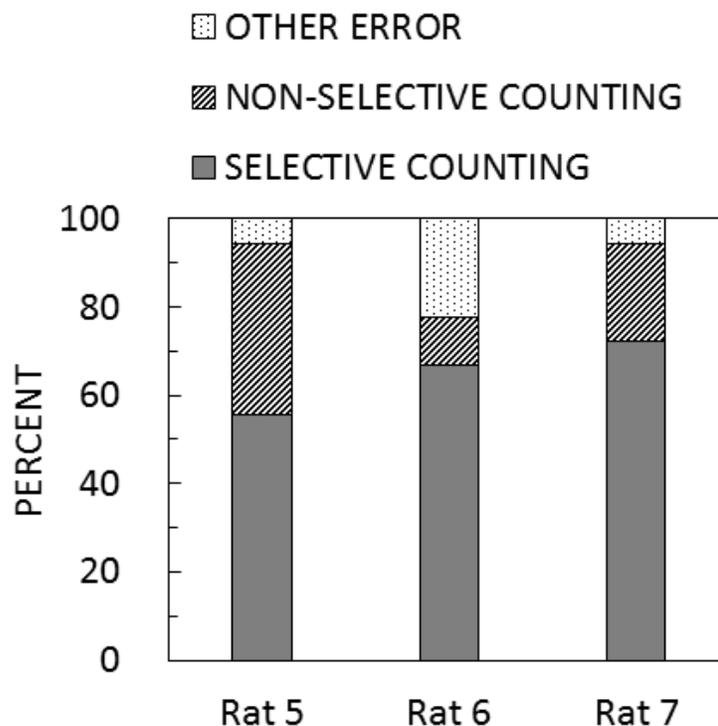


Figure 9. Percentage of each rat's response type in Experiment 3 Probe Test.

Discussion

All three rats learned the selective counting task of identical stimuli within four sessions. Considering 22-49 sessions were needed for acquisition of the original counting task in Experiment 2, the selective counting task in Experiment 3 was learned very quickly. These results suggest that rats had a tendency to exclude the odd stimulus from counting at the initial stage of selective counting training, rather than learning to exclude it by trial-and-error through the acquisition training of Experiment 3. Even when rats were trained with the acquisition task in Experiment 2, in which only identical objects were used, there were extraneous stimuli around the target objects, e.g., goal doors with no object in front of them. Rats might learn to exclude such extraneous stimuli from counting during Experiment 2, and this tendency to exclude extraneous stimuli might transfer to the selective counting task in Experiment 3. Additionally, it is known that rats discriminate an odd stimulus among identical stimuli

spontaneously without explicit oddity discrimination training (Forwood, Bartko, Saksida, & Bussey, 2007). Therefore, an odd stimulus in the present setting might also be naturally salient and processed differently from identical stimuli. An interesting experiment would be to investigate whether rats can be trained explicitly to switch between excluding and including an odd stimulus in counting by explicit stimulus control training.

Rats 6 and 7 showed reliable transfer of selective counting to novel test stimuli. As described in the introduction to Experiment 3, transfer of learning in a task consisting of only identical stimuli, as in Experiments 1 and 2, could be explained by mere ignorance or insensitivity to a specific difference existing among training and test objects. But the selective counting task of identical stimuli in Experiment 3 required rats to discriminate various objects from each other. Therefore, successful acquisition of the selective counting task and its transfer to novel stimuli by the two rats strongly suggests that rats can learn abstract ordering position of objects.

Although Rat 5 acquired the selective counting task, it only performed well in the six-object condition, but not five-object condition in the transfer test. Since acquisition training of selective counting was given only as six-object condition in Experiment 3, counting the identical stimuli from either the left end or the right end could have been an effective strategy. That is, the third identical object both from left and right ends was always the correct stimulus, although both of these response strategies require strict discrimination of the identical stimuli from the odd one. The results of the test of the total number of the objects in Experiment 2 suggest that Rat 5 responded to the target object by counting from the left end in the object row. We cannot find any plausible reason for such a possible shift in response strategy, but it could reasonably explain good performance in six-object trials (77.8%), but not in five-object trials (33.3%), because counting from the right end produced erroneous results only in the five-object trials. That acquisition training was only conducted in the six-object condition might affect Rat 5's

performance. Obviously, reexamination of training by varying the total number of objects in a row is needed to show clearer evidence of abstract selective counting of specific stimuli in rats.

Experiment 4

In Experiment 3, rats could successfully learn to respond to the third object, excluding an odd object in a row. Experiment 4 was conducted to examine whether rats could be insensitive to or ignore physical differences among objects. Rats from Experiment 3 continued to be trained with two kinds of trials, object rows consisting of six identical objects on half of the trials and six different objects on the remaining trials. If rats could switch their response strategy between ignoring and not ignoring differences in objects, rats would learn to respond correctly in both conditions.

Method

Subjects

The three rats from Experiment 3 continued as subjects. Experiment 4 began three days after Experiment 3 ended. During the inter-experiment period, food deprivation was continued. Treatment of animals was identical to that of Experiments 1-3.

Apparatus

Assignment of objects to training stimuli A, B, C, D, E, and F for each rat was identical to that of Experiment 3. Other aspects of the apparatus were identical to those of Experiments 1-3.

Procedure

Rats were trained to respond to the third object in a six-object row. There were two types of trials. For half of the trials, object rows consisted of six identical objects, AAAAAA,BBBBBB, CCCCCC, DDDDDD, EEEEEEE, or FFFFFFFF. For the remaining trials, object rows consisted of different arrangements of A, B, C, D, E, and F (CABFED, FDCBEA, and so on). These two types of trials were presented randomly in two-trial blocks in a daily session of 24 trials. Training was

conducted for two sessions. Other aspects of the procedure were identical to acquisition training in Experiments 1 and 2.

Results

Figure 10 shows performance for the identical objects trials and the different objects trials separately. Performance did not differ markedly between trial types and reached a high level on the second session for both conditions. A Trial Type * Session * Subjects analysis of variance showed no reliable main effects of Trial Type ($F(1, 2) = 0.00$) and Session ($F(1, 2) = 1.73, p=.319$) or interaction of Trial Type and Session ($F(1, 2) = 0.00$).

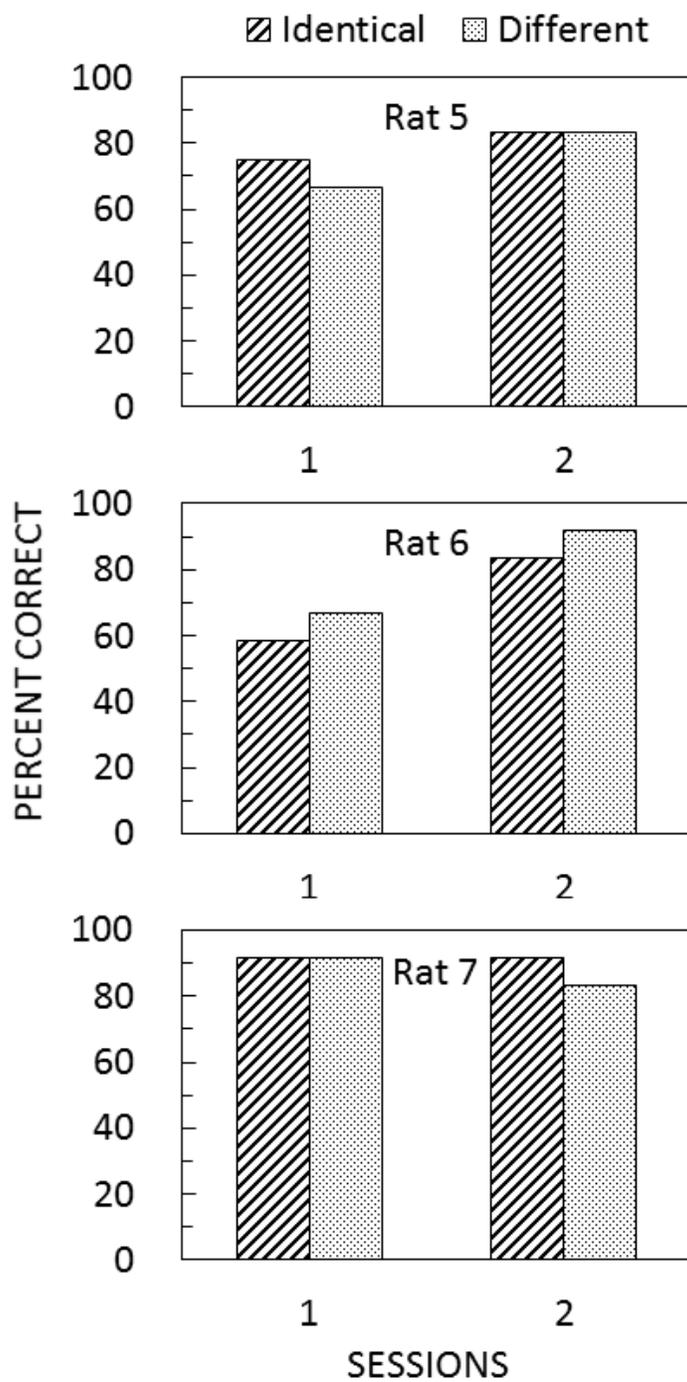


Figure 10. Percentage of correct responses by each rat for the Identical and Different Object conditions. Object rows consisted of six identical objects in the Identical Object condition and six different objects in the Different Object condition.

Discussion

Experiment 3 suggested that rats could learn to respond to specific identical stimuli and exclude an odd stimulus mixed into an object row. In Experiment 4, the same rats from Experiment 3 quickly learned to respond to the third stimulus of a different-objects row as well as an identical-objects row. These results suggest that rats can switch the stimulus property to be counted, depending on task demands.

A similar phenomenon is known as categorical flexibility in humans. For example, we can count two apples and three oranges separately but also in combination as “five pieces of fruit”. In runway experiments, it was reported that rats showed categorical flexibility to a certain extent. For example, Burns, Goettl, and Burt (1995) showed that rats trained with the R'RRN series showed positive transfer of learning to both the RRN and the RRRN series, compared with appropriate control conditions (R, R', and N refer to qualitatively different food rewards and non-rewards respectively). These results suggest that rats can count two different rewards, R and R', not only separately, but also in combination. In the present study, the same rats that learned to respond only to identical objects by excluding an odd stimulus in Experiment 3, also learned very quickly to respond to different objects nonspecifically. These results suggest that categorical flexibility in rats may also be demonstrated in an object counting task.

However, the reason why rats could switch their strategies so quickly from excluding (Experiment 3) to including (Experiment 4) different stimuli in counting is still unclear. Specifically, Rat 7 showed asymptotic performance from the first session. There were no explicit cues that informed the shift from the selective counting task in Experiment 3 to the task of counting different objects in Experiment 4. One possible account might be that rats have a spontaneous tendency to exclude different stimuli from counting when a very small number of different stimuli (e.g., one in Experiment 3) are mixed in with a large number of identical stimuli, because the different stimuli provide perceptual oddity (Forwood et al., 2007) and are

processed differently from identical stimuli. Rats may include different stimuli in counting spontaneously when there are no identical stimuli, as in Experiment 4, because the different stimuli do not offer perceptual oddity, given the of lack of identical stimuli. Obviously, additional examination of these possibilities, by manipulating the number of identical and different stimuli in a row, is needed in addition to an examination of explicit training in stimulus control of shift in learning strategies, including or excluding different stimuli in counting as mentioned in the discussion of Experiment 3. A promising future study with rats would be an examination of explicit training of categorical flexibility in the object counting task.

General discussion

Five out of seven rats learned to respond to the third object in an object row. In this discrimination task, the spatial position of a target stimulus could not act as an effective discriminative cue because it was changed trial-by-trial. The relative position of a target stimulus in an object row also could not serve an effective discriminative cue because a change in the total number of objects in a row did not affect the rats' performance. More importantly, four out of the five rats also attained significant performance when their individual data were compared to the strictest chance level of 43.00%. These results strongly suggest that rats can learn abstract ordering position of the target stimulus and that possible non-numerical artifacts can be controlled.

Unlike Kamiyo and Taniuchi (2015), which reported a failure to transfer learning to novel test stimuli despite successful acquisition of discrimination of the third object in a row, a significant transfer of discrimination was observed in the present study. There were two major methodological differences between the present study and Kamiyo and Taniuchi (2015). The first is the inclusion of habituation treatment for test stimuli. Kamiyo and Taniuchi presented test objects as completely novel stimuli, whereas in this study, we allowed rats to explore test

stimuli in advance of testing. Kamijo and Taniuchi (2015) reported that rats responded to goal boxes with no object in front more frequently on test trials than on training trials. This result might possibly reflect stronger neophobia toward the novel test stimuli (e.g., Wallace & Barnett, 1990) than the familiar training stimuli, and this possible neophobia might interfere with test performance in Kamijo and Taniuchi (2015). Although we cannot evaluate the possible effects of habituation treatment for test stimuli because there was no relevant control condition in the present study, considering the mean percentage of responses to goals with no object on test trials was 1.25% in the present study and 17.83% on average in Kamijo and Taniuchi (2015), familiarization of test stimuli by habituation treatment might contribute to a significant transfer effect by suppressing a possible exploration tendency or any neophobia toward the test stimuli.

A second major difference between Kamijo and Taniuchi (2015) and this study is the control of the odor of food rewards. Kamijo and Taniuchi placed food rewards in all the goal boxes, in order to control for any possible olfactory cue from the food rewards, and locked the small one-way door, blocking access to the food cup, in the incorrect goal boxes to prevent rats from getting those rewards. Although this procedure is a strict means of control for any possible odor cue from food rewards, it was observed that rats sometimes persisted in trying to open the small one-way door in the incorrect goal boxes (Kamijo & Taniuchi, 2015). When rats encounter correct or incorrect feedback by reinforcement outcomes, they need to associate the reinforcement outcome with their immediate discriminative response in order to learn the task. In this situation, persistent emission of irrelevant responses in an incorrect goal box possibly interfered with forming an association between reinforcement outcomes and discriminative responses. Considering this possible interferential effect, we placed the food reward only in the correct goal box during training trials in this study. Rats encountered empty food cups in incorrect goal boxes and any persistent irrelevant behavior trying to get food rewards was not observed. Although we cannot compare acquisition speed in these two studies directly because

there are several differences in experimental procedure, it took about 2,000-3,000 trials in Kamijo and Taniuchi (2015) and about 500-1,200 trials in the present study to acquire the discrimination task with three different objects. Suppressing persistent irrelevant behaviors by not setting food rewards in incorrect goal boxes might have contributed to faster learning of the task in the present study.

One may be concerned that an odor cue from food rewards might guide rats' discriminative responses because a food reward was only placed in the correct goal box during training. However, four rats showed significant performance at even the most conservative chance level, which took a possible odor cue into account when evaluating test performance. That is, if rats could combine the information of possible goal boxes with an odor cue from food rewards placed in the goal box behind the second, third, or fourth test object on the test trial, the strictest chance level would be 43.00%. Four out of the five rats who mastered acquisition training with objects A, B, and C, showed significant performance. Although we cannot completely exclude the possible effects of an olfactory cue from the food reward on rats' performance, these statistical results show that an odor cue from a food reward alone cannot adequately explain the transfer performance.

Another possible explanation might be that rats searched for the general location of food rewards based on an odor cue. In that case, they might respond more strongly to middle of three food rewards on the test trials because it possibly received indirect odor from both of first (behind of the second object) and third food rewards (behind of fourth object) as well as the direct odor of the second food reward (behind of the third object). The second object must have received a relatively weaker indirect odor cue than the third object because it could only receive indirect odor from one proximate food reward (behind of the third object) and one distant food reward (behind of the fourth object), and the same might be true for the fourth object. However, this view cannot explain the significant transfer of the selective counting performance in Experiment 3. On the test trial of the selective counting task, food rewards were always set

behind both the third and fourth objects, regardless of the position of an odd object. In this situation, possible strength of direct and indirect odor cues must have been equal for the third and fourth objects. Therefore, a general search for a food reward, based on direct and indirect odor cues, cannot explain the significant transfer performance of selective counting in Experiment 3. However, reexamination with a stricter control of possible odor cues by a test with an extinction procedure might be needed to rule out the influence of odor cues on rats' performance.

Therefore, we conclude that rats in the present study did learn abstract ordering position applicable to various objects. Experiment 3 shows that rats could learn to count only the specific identical stimuli, excluding the odd stimulus added to the object row. Moreover, two out of three rats showed significant transfer of the selective counting behavior to test sets consisting of novel stimuli. As mentioned earlier, transfer of learning of a non-selective counting task, as in Experiments 1 and 2, can be explained by simple insensitivity to or ignorance of differences among various objects. However, the selective counting task in Experiment 3 could never be learned without discrimination between the identical stimuli and an odd stimulus. Therefore, reliable learning and transfer of the selective counting behavior in Experiment 3 strongly suggests rats' capacity to learn an abstract numerical property of objects.

Similar selective counting has been reported in runway experiments. For example, Capaldi and Miller (1988) showed that rats could learn to anticipate a final non-reward trial in four different reward series of RRN, R'R'N, R'RRN, and RR'R'N concurrently (R, R', and N refer to qualitatively different food rewards and non-reward respectively). To identify the final non-reward in the series, rats had to count just two identical reward events, ignoring any odd reward. Moreover, as mentioned earlier, Burns, Goettl, and Burt (1995) showed that rats trained with a R'RRN series showed positive transfer of learning to both RRN and RRRN series compared with appropriate control conditions. Their results suggest that rats can count R and R' not only separately but also in combination. In the present study, the same rats that learned to

count only identical objects in Experiment 3, also learned very quickly to count different objects nonspecifically in Experiment 4. These results strongly suggest that categorical flexibility in counting might be found in an object-counting task, as well as in runway experiments. It would be interesting to examine explicit training of categorical flexibility in object counting tasks in rats.

As explained in Experiment 2, although rats' performance to test stimuli was reliably better than chance in Experiments 1 and 2, it was also reliably poorer than with training stimuli. Katz and Wright (2006) describe different levels of transfer to novel stimuli in terms of full or partial transfer. It is said that partial transfer represents partial concept learning, that is, discriminative behavior is controlled not only by the abstract concept but also by certain stimulus-specific cues that involve learning specific physical features of training stimuli. Therefore, although reliable transfer to novel test stimuli in the present study ensures that rats learned, at least partially, a type of abstract numerical concept, it should be possible to enhance numerical concept learning in rats. In relational same/different concept learning studies, we know that increasing the number of exemplars used in acquisition training leads to better transfer performance, perhaps because animals abandon stimulus-specific learning given a large number of stimuli (Katz & Wright, 2006; Wright & Katz, 2006). We might expect similar effects in numerical concept learning in rats. In this study, we trained rats with just three or four kinds of training stimuli before the transfer test. To explore additional possibilities of abstract numerical concept learning in rats, it would be worthwhile to examine numerical discrimination learning of objects with a greater variety of training stimuli.

In this series of experiments, we examined rats' ability to identify the third object in a row. A simple question might arise: how many objects can a rat enumerate? This matter is related to the important topic of subitizing, which is a rapid and effortless perceptual apprehension of a small number of items, generally up to four through pre-attentive mechanisms (Kaufman, Lord, Reese, & Volkman, 1949; Neider, 2005). In contrast, counting refers to a slow, effortful mental

enumeration process applied to relatively larger numbers of items, generally greater than four in human adults (Oyama, Kikuchi, & Ichihara, 1981). Because the experimental setup of our study might have allowed rats to perceive multiple objects simultaneously and as the target aggregation, three objects, was less than four, rats might respond to the target object not only by counting, but also by subitizing the target aggregation. Therefore, additional assessments are needed to distinguish a true counting process from subitizing. There are at least two ways to accomplish this goal. First, we can examine acquisition of discrimination learning of a larger number of item stimuli. Since subitizing can be applied to only a relatively small number of item stimuli, generally four or less, if rats could learn a numerical task where discrimination of more than four stimulus items is required, true counting, rather than subitizing in rats, would be the most likely form of processing. Second, since subitizing is mainly used with stimuli presented simultaneously or those presented sequentially within very short intervals (Beran & Beran, 2004), if rats could learn to count objects presented serially with sufficiently long intervals, it would be strongly suggestive of counting, rather than subitizing. We may be able to accomplish this goal by modifying the apparatus to ensure that the rats encounter each object serially, e.g., by separating the row of objects with one-way doors.

Examining discrimination of a larger number of objects is also important in exploring the influence of another counting process. It has been reported that nonhuman animals, as well as humans, estimate set size of stimuli based on the analog magnitude system or approximate number system (e.g., Neider, 2005). Unlike subitizing, there is no upper limit of the number of the stimuli to estimate in the analog magnitude system, but estimation becomes less precise as the number of stimuli increases. For example, when rats were trained to make some specific number of responses to targets, variance of the number of responses made by rats increased as the target number increased (Mechner, 1958; Platt & Johnson, 1971). It has also been reported that rats (Meck & Church, 1983) and monkeys (Jordan & Brannon, 2006) judge similarity between two and four items to be as similar as that between four and eight items. Thus, it is

known that estimation by the analog magnitude system follows Weber's law, that is, the ratio between numerosities is critical for discriminability. If the analog magnitude system is responsible for rats' numerical discrimination in the present experiments, it is predicted that errors to incorrect stimuli would increase in proportion to the magnitude of the ordinal position of the target stimuli in a row.

It would be constructive to examine discrimination of a larger number of objects in a serial presentation apparatus in order to more fully ascertain abstract numerical discrimination learning in rats. Additionally, in the present study, absolute ordinal position of the target stimulus was always the third. Training identical rats to respond to different target ordinal positions, depending on different conditional cues, would be interesting to examine to add to our knowledge of flexibility of numerical competence in rats.

Primate studies have revealed that numerical cues are salient for rhesus monkeys because they use numerical cues even when other stimulus dimensions also available (Cantlon & Brannon, 2007). Rhesus monkeys also showed cross-modal matching of the number of sounds and the number of visual stimuli, suggesting their number representations, like that of humans, are not fettered to a specific stimulus modality (Jordan, MacLean, & Brannon, 2008). Rhesus monkeys (Brannon & Terrace, 1998, 2000) and capuchin monkeys (Judge, Evans, & Vyas, 2005) responded to the ordinal relationship of a number of different figures on a computer monitor correctly. A chimpanzee responded correctly to the number of visual stimuli using arbitrary symbols (Matsuzawa, 1985). Chimpanzees could estimate the total number of food items shown to them sequentially and they also could estimate the remainder when one food item was subtracted (Beran, 2004). All these topics involving salience of numerical cues, cross-modal abstractness of numerical representation, ordinal judgment, symbolic matching of number of items and arbitrary symbols, and addition or subtraction have not yet been demonstrated in rodents. In this study, we succeeded in demonstrating rats' ability to count objects in a flexible and somewhat abstract way. These findings also suggest promising new

experiments to probe rats' responses to greater complexity in numerical processing.

References

Beran, M. J. (2004). Chimpanzees (*Pan troglodytes*) respond to nonvisible sets after one-by-one addition and removal of items. *Journal of Comparative Psychology, 118*, 25-36. DOI: 10.1037/0735-7036.118.1.25

Beran, M. J., & Beran, M. M. (2004). Chimpanzees remember the results of one-by-one addition of food items to sets over extended time periods. *Psychological Science, 15*, 94-99. DOI: 10.1111/j.0963-7214.2004.01502004.x

Brannon, E. M., & Roitman, J. D. (2003). Nonverbal representations of time and number in animals and human infants. In W. H. Meck (Ed.), *Functional and Neural Mechanisms of Interval Timing. Methods and New Frontiers in Neuroscience*, pp. 143-182. Boca Raton, FL: CRC Press. DOI: 10.1201/9780203009574

Brannon, E. M., & Terrace, H. S. (1998). Ordering of the numerosities 1 to 9 by monkeys. *Science, 282*, 746-749.

Brannon, E. M., & Terrace, H. S. (2000). Representation of the numerosities 1-9 by rhesus macaques (*Macaca mulatta*). *Journal of Experimental Psychology: Animal Behavior Processes, 26*, 31-49.

Breukelaar, J. W. C., & Dalrymple-Alford, J. C. (1998). Timing ability and numerical competence in rats. *Journal of Experimental Psychology: Animal Behavior Processes, 24*, 84-97.

Burns, R. A., Goettl, M. E., & Burt, S. T. (1995). Numerical discrimination with arrhythmic serial presentations. *The Psychological Record, 45*, 95-104.

Cantlon, J. F., & Brannon, E. M. (2007). How much does number matter to a monkey (*Macaca mulatta*)? *Journal of Experimental Psychology: Animal Behavior Processes, 33*, 32-41. DOI: 10.1037/0097-7403.33.1.32

Capaldi, E. J., & Miller, D. J. (1988). Counting in rats: Its functional significance and the independent cognitive processes that constitute it. *Journal of Experimental Psychology: Animal Behavior Processes*, *14*, 3-17.

Castro, L., Lazareva, O. F., Vecera, S. P., & Wasserman, E. A. (2010). Changes in area affect figure-ground assignment in pigeons. *Vision Research*, *50*, 497-508. DOI: 10.1016/j.visres.2009.12.016

D'Amato, M. R., Salmon, D. P., & Colombo, M. (1985). Extent and limits of the matching concept in monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes*, *11*, 35-51.

Davis, H., & Albert, M. (1986). Numerical discrimination by rats using sequential auditory stimuli. *Animal Learning & Behavior*, *14*, 57-59.

Davis, H., & Albert, M. (1987). Failure to transfer or train a numerical discrimination using sequential visual stimuli in rats. *Bulletin of the Psychonomic Society*, *25*, 472-474.

Davis, H., & Bradford, S. A. (1986). Counting behavior by rats in a simulated natural environment. *Ethology*, *73*, 265-280.

Davis, H., Mackenzie, K. A., & Morrison, S. (1989). Numerical discrimination by rats (*Rattus norvegicus*) using body and vibrissal touch. *Journal of Comparative Psychology*, *103*, 45-53.

Ennaceur, A., Michalikova, S., Chazot, P. L. (2009). Do rats really express neophobia towards novel objects? : Experimental evidence from exposure to novelty and to an object recognition task in an open space and an enclosed space. *Behavioural Brain Research*, *197*, 417-434. DOI: 10.1016/j.bbr.2008.10.007

Forwood, S. E., Bartko, S. J., Saksida, L. M., & Bussey, T. J. (2007). Rats spontaneously discriminate purely visual, two-dimensional stimuli in tests of recognition memory and perceptual oddity. *Behavioral Neuroscience*, *121*, 1032-1042. DOI:10.1037/0735-7044.121.5.1032

Gelman, R. & Gallistel, C. R. (1978). *The Child's Understanding of Number*. Cambridge, MA: Harvard University Press.

Jordan, K. E., MacLean, E. L., & Brannon, E. M. (2008) Monkeys match and tally quantities across senses. *Cognition*, *108*, 617-625. DOI:10.1016/j.cognition.2008.05.006

Judge, P. G., Evans, T. A., & Vyas, D. K. (2005) Ordinal representation of numeric quantities by brown capuchin monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes*, *31*, 79-94.

Kamijo, M. & Taniuchi, T. (2015) Acquisition and limited transfer of numerical discrimination of object stimuli in rats. *The Psychological Record*, *65*, 289-300. DOI: 10.1007/s40732-014-0105-0

Katz, J. S., & Wright, A. A. (2006). *Same/different* abstract-concept learning by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, 80-86.

Kaufman, E. L., Lord, M. W., Reese, T. W., Volkman, J. (1949). The discrimination of visual number. *American Journal of Psychology*, *62*, 498-525. DOI: 10.2307/1418556

Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature*, *315*, 57-59.

Mechner, F. (1958). Probability relations within response sequences under ratio reinforcement. *Journal of the Experimental Analysis of Behavior*, *1*, 109-121.

Miletto Petrazzini, M. E., Agrillo, C., Izard, V., Bisazza, A. (2015). Relative versus absolute numerical representation in fish: Can guppies represent "fourness"? *Animal Cognition*, *18*, 1007-1017. DOI 10.1007/s10071-015-0868-y

Neider, A. (2005). Counting on neurons: The neurobiology of numerical competence. *Nature Reviews*, *6*, 177-190. DOI: 10.1038/nrn1626

Oyama, T., Kikuchi, T., & Ichihara, S. (1981). Span of attention, backward masking, and reaction time. *Perception and Psychophysics*, *29*, 106-112.

Pepperberg, I. M. (1994). Evidence for numerical competence in an African Grey parrot (*Psittacus erithacus*). *Journal of Comparative Psychology*, *108*, 36-44.

Pepperberg, I. M. (2012). Further evidence for addition and numerical competence by a Grey parrot (*Psittacus erithacus*). *Animal Cognition*, *15*, 711-717.

Perdue, B. M., Talbot, C. F., Stone, A. M., & Beran, M. J. (2012). Putting the elephant back in the herd: Elephant relative quantity judgments match those of other species. *Animal Cognition*, *15*, 955-961. DOI 10.1007/s10071-012-0521-y

Platt, J. R., & Johnson, D. M. (1971). Localization of position within a homogeneous behavior chain: Effects of error contingencies. *Learning and Motivation*, *2*, 386-414.

Rugani, R., Regolin, L., & Vallortigara, G. (2008). Discrimination of small numerosities in young chicks. *Journal of Experimental Psychology: Animal Behavior Processes*, *34*, 388-399. DOI: 10.1037/0097-7403.34.3.388

Suzuki, K., & Kobayashi, T. (2000). Numerical competence in rats (*Rattus norvegicus*): Davis and Bradford (1986) extended. *Journal of Comparative Psychology*, *114*, 73-85.

Wallace, R. J., & Barnett, S. A. (1990). Avoidance of new objects by the black rat (*Rattus rattus*) in relation to object presentation and object change. *International Journal of Comparative Psychology*, *3*, 253-265.

Wright, A. A., & Katz, J. S. (2006). Mechanisms of *same/different* concept learning in primates and avians. *Behavioural Processes*, *72*, 234-254.

Xia, L., Emmerton, J., Siemann, M., & Delius, J. D. (2001). Pigeons (*Columba livia*) learn to link numerosities with symbols. *Journal of Comparative Psychology*, *115*, 83-91.

Xia, L., Siemann, M., & Delius, J. D. (2000). Matching of numerical symbols with number of responses by pigeons. *Animal Cognition*, *3*, 35-43.