



# Distance and direction, but not light cues, support response reversal learning

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## Abstract

Across three experiments, we examined the cuing properties of metric (distance and direction) and nonmetric (lighting) cues in different tasks. In Experiment 1, rats were trained on a response problem in a T-maze, followed by four reversals. Rats that experienced a change in maze orientation (Direction group) or a change in the length of the start arm (Distance group) across reversals showed facilitation of reversal learning relative to a group that experienced changes in room lighting across reversals. In Experiment 2, rats learned a discrimination task more readily when distance or direction cues were used than when light cues were used as the discriminative stimuli. In Experiment 3, performance on a go/no-go task was equivalent using both direction and lighting cues. The successful use of both metric and nonmetric cues in the go/no-go task indicates that rats are sensitive to both types of cues and that the usefulness of different cues is dependent on the nature of the task.

**Keywords** Discrimination · Orientation · Spatial learning · Rat

The context in which learning occurs is very important for subsequent successful retrieval (Bouton & Brooks, 1993; Bouton & Moody, 2004). An early report showed that a change in context reduces the interference that can occur between two learned and competing responses (Chiszar & Spear, 1969). Subsequent work showed that successive discrimination reversal learning was more successful when contextual cues were changed between discrimination reversals than when the context was unchanged (Cheng, 2005; Cheng & Wignall, 2006; Pagani, Brown, & Stanton, 2005; Thomas, McKelvie, & Mah, 1985; Walsh, Skinner, & Martin, 2007; Wright, Williams, Evans, Skinner, & Martin, 2009). Bees (Cheng, 2005; Cheng & Wignall, 2006; Chittka, 1998; Colborn, Ahmad-Annuar, Fauria, & Collett, 1999), rats (Chiszar & Spear, 1969; McDonald, King, & Hong, 2001; Pagani et al., 2005), pigeons (Thomas et al., 1985), and seals

(Walsh et al., 2007) have all learned successive reversals more quickly when context changes have been part of the reversal.

The changes in context, including location changes, that have been shown to facilitate reversal learning are also correlated with activity in the hippocampus (see Jeffery, 2007, and O’Keefe, 2007, for reviews). Hippocampal place cells generate internal representations of the external environment based on both spatial (e.g., Colgin et al., 2010; O’Keefe & Nadel, 1978; Leutgeb et al., 2005) and nonspatial (e.g., Bahar, Shirvalkar, & Shapiro, 2011; Eschenko & Mizumori, 2007; Ferbinteanu, Shirvalkar, & Shapiro, 2011; Frank, Brown, & Wilson, 2000; Griffin, Eichenbaum, & Hasselmo, 2007; Markus et al., 1995; Moita, Rosis, Zhou, LeDoux, & Blair, 2004; Muller & Kubie, 1987; Wood, Dudchenko, Robitsek, & Eichenbaum, 2000) information. It has been suggested that these hippocampal “maps” provide protection from interference when different behaviors are required in similar contexts (Smith & Mizumori, 2006). However, we showed that not all contextual changes that are correlated with hippocampal activity facilitate response reversal learning (Skinner et al., 2014).

Skinner et al. (2014) examined response reversal learning and spatial map separation by training rats to criterion on a response problem (i.e., turn right in a T-maze) and then subjecting them to a series of reversals under changing environmental conditions. Spatial map separation was assessed by using cellular compartment analysis of temporal activity by

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fluorescent in situ hybridization (catFISH) with *Arc* mRNA (Guzowski, McNaughton, Barnes, & Worley, 1999; Schmidt, Satvat, Argraves, Markus, & Marrone, 2012). We showed that room changes facilitated response reversal learning and produced remapping of the hippocampal representation. Changes to visual cues within the same room (the color and shape of a curtain surrounding the maze) caused remapping of the hippocampal representation to the same extent as room changes but, surprisingly, did not facilitate response reversal learning, though there was some evidence for a decrease in interference on the first reversal.

On the basis of these findings, Skinner et al. (2014) speculated that key to the facilitating effects of room changes on response reversal learning were changes in heading direction (or maze orientation) within the two rooms. The rooms used across reversals had very different distal cues and were located on different floors, with the consequence that rats were carried along different paths to the different rooms. These differences in cues would have supported distinct headings at the two maze positions. In the distinct-curtain condition the room and, consequently, the path to the room were identical across reversals. In addition, a subset of cues and the maze orientation were identical across reversals. Thus, few, if any, cues supported a change in directional heading across reversals.

Earlier work had shown that changes in maze orientation, even in the same room, facilitated response reversal learning to a degree similar to room changes (Wright et al., 2009). The importance of direction (or orientation) has been revealed by its contribution to apparent place learning (Hamilton, Akers, Weisand, & Sutherland, 2007; Peckford, McRae, Thorpe, Martin, & Skinner, 2013; Skinner et al., 2003) and its impact on place cell activity (Knierim, Kudrimoti, & McNaughton, 1995), although the impact of lesions to the head direction circuit on place cell firing are often mild (e.g., Calton et al., 2003). The formation of spatial memories in humans has also been shown to be orientation-dependent (McNamara, 2003). Participants showed impaired recall of object locations when there was a change in orientation between training and test.

The purpose of the present study was to assess whether direction has a privileged role in response reversal learning or whether another metric cue, distance, also facilitates response reversal learning. The entorhinal cortex, the major input to the hippocampus, contains cells that are sensitive to both distance and direction (Hafting, Fyhn, Molden, Moser, & Moser, 2005; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006), suggesting that these features may play similar roles in guiding spatial choices. In the first experiment, we trained rats on a response task, followed by four reversals. For rats in the Distance condition, the length of the start arm (the stem of the T-maze) changed from long (300 cm) to short (100 cm) across reversals. The rats in this group were compared to those in a Direction group, in which the orientation of the maze was changed across reversals, and a Light/Dark

group, in which the room lights were turned on or off across reversals. On the basis of our previous findings (Wright et al., 2009), we expected facilitation of response reversal learning in the Direction group but not in the Light/Dark group. Experiment 1 demonstrated that both metric cues facilitated response reversal learning, as compared to nonmetric cues. Experiments 2 (discrimination task) and 3 (go/no-go task) were conducted to further assess the cueing properties of our nonmetric in comparison to metric cues.

## Experiment 1: Response reversal task

In this first experiment, we examined rats' performance on a response task followed by four reversals when distance, direction, or lighting cues acted as discriminative stimuli to indicate a change in the response-reward contingency. The response requirement (right or left turn) and the cue (direction, distance, or light) were counterbalanced within each group.

## Method

**Subjects** Twenty-four naïve male Long-Evans rats obtained from Charles River (St. Constant, Quebec Canada) were group-housed for ten days and fed a standard lab chow (Lab Diet) ad libitum. Subsequently, the rats were individually housed and placed on a food restriction schedule for four days prior to training. The rats weighed between 205 and 250 g at the beginning of food restriction and were subsequently maintained at 85% of their free-feeding weight. Water was provided ad libitum. The housing room was maintained on a reverse 12:12 light:dark schedule with lights off at 0900. The rats were handled for 5 min a day for three days prior to training. Animal care and all procedures were approved by Memorial University's Institutional Committee on Animal Care and followed the Canadian Council on Animal Care guidelines for all experiments.

**Apparatus** Behavioral training took place on a black, wooden T-maze that was elevated 53.3 cm from the ground. The T-maze had a square center (15.24 cm × 15.24 cm), with three arms radiating out from the center at 90° angles. At the end of the two choice arms (101.6 cm × 15.24 cm), a circular depression in the wood formed a food cup (2.54-cm diameter). The stem of the maze was either 101.6 cm (short) or 304.8 cm (long) in length. The training room measured 4.26 m (length) × 3.66 m (width), with doors on the south and west walls. There were cupboards on the south, east, and north walls, and a chalkboard extended across the west wall. Two counters extended across the north and south walls, and a filing cabinet and three desktop computer terminals lay adjacent to the east wall. In the light condition, the overhead lights were on. In the dark condition, the overhead lights were off

and a red floodlight was located on the west side of the room, pointed away from the maze. A radio was on for all trials.

**Procedure** The rats were given Kellogg's Froot Loops in their home cage for three days prior to the start of training. During this time, they were also trained to eat the Froot Loop pieces on a white laminate table in a room located next to the colony room. All rats received four 1-min trials daily until they consumed the Froot Loops on each trial. The lights remained on during these trials. The rats were not habituated to the T-maze prior to training.

After pretraining, the rats were randomly assigned to one of three groups: Distance ( $n = 8$ ), Direction ( $n = 8$ ), and Light/Dark ( $n = 8$ ). The rats were trained to make either a left or a right turn in one of the two cue conditions (Distance group: short or long start arm; Direction group: start arm faced south or west; Light/Dark group: lights on or off), followed by four reversals.

The rats were transported in their home cages to the testing room on a cart. Rats were brought into the testing room in squads of four or five, depending on the training condition, and remained in the testing room until all rats in the squad had received five trials. In turn, each rat was removed from its home cage and placed on the start arm facing the experimenter. A rat was considered to have made a choice when its body, minus the tail, was in either the left or right choice arm. Rats were trained using a noncorrection method; if they made a correct choice, they were allowed to eat the Froot Loop, but they were removed from the maze once they had made an incorrect choice. For the initial acquisition and all subsequent reversals, the rats received five trials/day, with an intertrial interval of approximately 60 s, until they reached a criterion of 9/10 correct trials. The maze was wiped with alcohol between trials.

On the initial response task, half the rats in each group were trained to make a right turn, and the other half were trained to make a left turn. Once the rats in the Distance group had reached criterion, the length of the start arm was changed (e.g., from short to long), but the lighting and maze orientation remained the same. In the Direction group, the orientation of the maze was changed (e.g., from facing south to facing west) when the response contingency changed, but the lighting and length of the start arm remained the same. In the Light/Dark group, the lighting was changed (e.g., from lights on to off), but the length of the start arm and the orientation of the maze remained the same. The rats in the Distance and Direction groups were always trained with the lights on. The length of the start arm and maze orientation were counterbalanced in all groups (e.g., half the rats in the Direction and Light/Dark groups were trained with the long start arm, and the other half were trained with the short start arm). The second and fourth reversals mirrored acquisition, and the third reversal mirrored the first reversal.

## Results

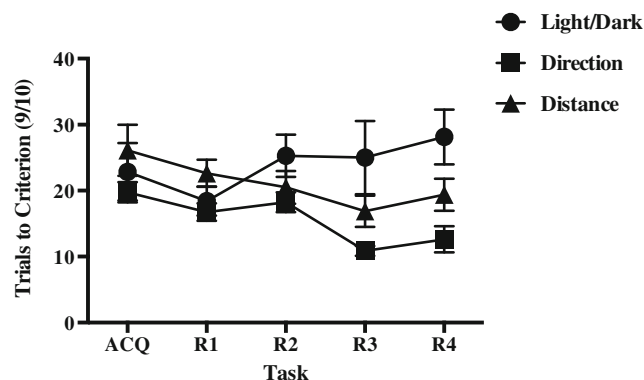
One rat was dropped from the Light/Dark group because it failed to respond during the initial task. A  $3 \times 5$  (Group  $\times$  Task) ANOVA revealed a significant Group  $\times$  Task linear interaction,  $F(2, 20) = 6.23$ ,  $p < .008$ , confirming that the groups' performance differed over acquisition and the four reversals. A linear trend analysis on each group revealed that the Direction,  $F(1, 7)_{\text{linear}} = 9.892$ ,  $p = .016$ , and Distance,  $F(1, 7)_{\text{linear}} = 6.051$ ,  $p = .043$ , groups improved across reversals, whereas the Light/Dark group,  $F(1, 6)_{\text{linear}} = 2.429$ ,  $p = .163$ , did not improve (see Fig. 1).

## Experiment 2: Discrimination task

The findings from Experiment 1 supported our earlier results showing that direction cues, but not lighting manipulations, facilitated response reversal learning (Wright et al., 2009). The novel finding from Experiment 1 was that distance, another metric cue, also facilitated response reversal learning. Do metric cues have a privileged role in guiding spatial choices, or can other cues work outside of the response reversal paradigm? In the second experiment, we examined whether rats could use light cues as discriminative stimuli when a discrimination task was used in which rats were exposed to the different cues across training trials within a day.

## Method

**Subjects** Twenty-four naïve male Long-Evans rats, weighing between 225 and 280 g at the beginning of training, were obtained from Charles River Company (St. Constant, Quebec Canada). The rats were maintained as in Experiment 1.



**Fig. 1** Mean ( $\pm$  SEM) trials to criterion on the initial response task (ACQ) and the four subsequent reversals (R1–R4) by the Light/Dark, Direction, and Distance groups in Experiment 1.

**Apparatus** The T-maze, testing room, and cues were identical to those used in Experiment 1. A radio was on for all trials.

**Procedure** The pretraining phase was identical to that of Experiment 1. After pretraining, the rats were randomly assigned to one of three groups: Distance ( $n = 8$ ), Direction ( $n = 8$ ), or Light/Dark ( $n = 8$ ). The rats in the Direction group were rewarded for turning right when the maze faced one direction (south or west) and left when the maze faced the alternate direction. The short start arm was always used, and the overhead lights were always on. The rats in the Distance group were rewarded for turning right when the start arm was short and left when the start arm was long. The maze always faced south, and the overhead lights were always on. Finally, the rats in the Light/Dark group were rewarded for turning right when the lights were off and left when the lights were on. The maze always faced south, and the short start arm was always used.

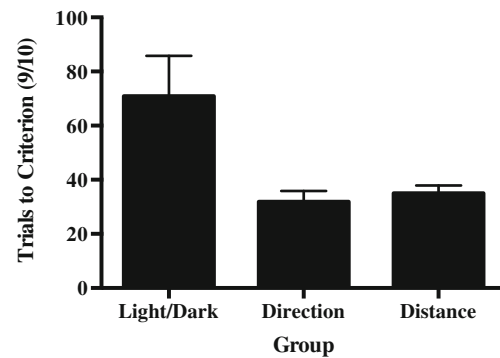
As in Experiment 1, the rats were transported in their home cages to the testing room on a cart. The rats remained in the testing room until all rats in the squad had received four trials. In turn, each rat was placed on the start arm facing the experimenter. The first 12 trials (i.e., the first three days of training) were correction trials, in which rats were allowed to explore the maze until they had found the Froot Loop reward in one of the food wells. After Trial 12, a noncorrection procedure was used. The rats received four trials/day, and the discriminative cue changed at least once per day (e.g., the rats in the Distance group never had four trials in a row with the short start arm) until they had reached a criterion of 9/10 correct trials.

## Results

One rat from the Light/Dark group was removed due to illness. A one-way analysis of variance (ANOVA) revealed a significant difference in trials to criterion across the three groups,  $F(2, 19) = 6.02$ ,  $p < .01$ . Comparison of the groups using a Bonferroni adjustment showed that the Light/Dark group took significantly more trials to reach criterion than did either the Distance or the Direction group ( $ps < .01$ ). The latter two groups did not differ (see Fig. 2).

## Experiment 3: Go/no-go task

The pattern of findings from Experiment 2 replicated that from the first experiment and suggested that metric cues (i.e., distance and direction) have better cuing properties than do nonmetric cues (e.g., lighting manipulations). The poor performance of rats on both the response reversal (Exp. 1) and discrimination (Exp. 2) tasks when light cues were used may indicate that light cues are not adequate discriminative stimuli or that light cues are not as readily



**Fig. 2** Mean (+ SEM) trials to criterion on the discrimination task by the Light/Dark, Direction, and Distance groups in Experiment 2.

used in spatial tasks. Evidence to suggest the latter as a possibility comes from research on daily time–place learning (TPL). In daily TPL tasks, rats are trained that food is available in one location at one time of day and in another location at a different time of day. For example, Means, Arolfo, Ginn, Pence, and Watson (2000) trained rats that in morning sessions food was available in the left arm of a T-maze, whereas in afternoon sessions food was available in the right arm. Only 63% of the rats learned the time-of-day discrimination in 96 trials. Similarly, Thorpe, Bates, and Wilkie (2003) found that rats did not use time of day as a discriminative stimulus in radial arm maze and water maze versions of the TPL task. In contrast, both Thorpe et al. and Means et al. (2000) found that rats quickly learned a go/no-go task in which time of day was the discriminative stimulus. In this task, rats are trained that food is available in both arms of a T-maze at one time of day and that no food is available in either arm at a different time of day. In both cases, the latency of rats to leave the start arm was significantly shorter on rewarded trials. This suggests that time of day is used as a cue to tell when food is available, but not necessarily as a cue to where it will be found. It is possible that light cues may also function in the same way. That is, light cues might function as discriminative stimuli in a nonspatial go/no-go task, but not in the previously tested spatial tasks. This possibility was tested in Experiment 3.

## Method

**Subjects** Sixteen naïve male Long-Evans rats, weighing between 155 and 193 g, were obtained from Charles River, QC, Canada. The rats were housed in pairs for one week with free access to food and water. Subsequently, the rats were housed individually and placed on a food restriction schedule in which they were allowed to gain 5% of their previous week’s weight per week. The rats were maintained on a reverse 12:12 light:dark cycle with lights off at 0700. In all other respects, they were maintained as in Experiments 1 and 2.

**Apparatus** Training took place on a straight wooden runway (15 cm wide  $\times$  150 cm long). The training room (455 cm  $\times$  330 cm) had a door on the south wall, a sink on the north wall, and posters on the walls. In the dark condition, a red floodlight directed away from the maze was situated on the east side of the room and the overhead light was turned off. In the light condition, the red light was turned off and the normal room lighting was turned on. On rewarded trials, the Froot Loop was placed in a food well at the end of the alley. A radio was on during all trials.

**Procedure** The rats were pretrained to eat Froot Loops as in Experiments 1 and 2. After pretraining, training took place on a runway in a different room. The rats were transported to the training room in their home cages on a cart and left outside the room until needed. The rats were randomly assigned to one of two conditions: Direction ( $n = 8$ ) or Light/Dark ( $n = 8$ ). In the Direction group, the alley was positioned in the North–South orientation for half the trials and in the East–West orientation for the other half. The rats received food when the maze faced one direction, but not when it faced the other (counterbalanced across rats). Unlike in the previous two experiments, the lighting manipulation for the Direction rats was counterbalanced, such that the light was always on for half the rats and always off for the other half. The Light/Dark group was trained such that the lights were on for half the trials and off for the other half. The rats received food in one lighting condition but not the other (counterbalanced across rats). For each rat, the maze orientation was always either North–South or East–West. Each rat was given four trials/day: two reinforced trials and two nonreinforced trials. The reinforced and nonreinforced trials were carried out in separate sessions. Rats were brought into the room in squads of eight for two trials with the room light either on or off. Each rat was given 60 s to run to the end of the maze to obtain food. The second trial for each rat did not begin until all eight rats in the room had had their first trial. Rats were removed from the room after two trials and were returned to the room for the next session after the other squad had been given two trials. The order of reinforced and nonreinforced sessions was changed each day, in an attempt to prevent the rats from learning the order on the basis of a sequence of reinforced and nonreinforced trials. Learning based on time of day was also unlikely, since the reinforced trials were sometimes before and sometimes after the nonreinforced trials, and the order in which the squads of rats were trained varied. The initial training phase lasted 30 days. Ten days after training ended, the rats were given a retention test using the same procedure described above. Because changing the distance to the goal across trials would impact the latency to reach the goal, distance cues were not used in the go/no-go task.

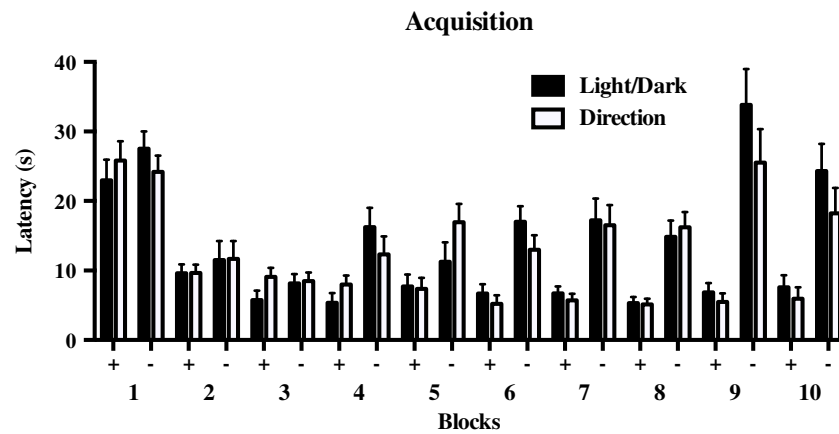
## Results

One rat from the Light/Dark condition froze on every trial and was removed from the experiment after 80 trials. The acquisition data revealed that both groups learned the discrimination equally well (see Fig. 3). The 30 days of acquisition (60 sessions) were divided into ten blocks, with three days in each block, and were analyzed with a  $2 \times 10 \times 2 \times 2$  (Groups [Light/Dark or Direction]  $\times$  Blocks  $\times$  Sessions [reinforced or not reinforced]  $\times$  Trials [Trial 1 or 2]) mixed ANOVA. The significant Blocks  $\times$  Sessions interaction,  $F(9, 117) = 13.53$ ,  $p < .05$ , reflected acquisition of the go/no-go discrimination by both groups. The absence of a Group  $\times$  Blocks  $\times$  Sessions interaction,  $F(9, 117) = 1.25$ ,  $p = .272$ , confirmed that both groups solved the discrimination equally well. We also observed a significant trials effect,  $F(1, 13) = 27.87$ ,  $p = .0011$ , which, as can be seen in Fig. 4, reflected shorter latencies on the second trial of each session, regardless of the cue or of whether the first trial was reinforced. This indicates that the outcome from the previous trial did not determine the rats' performance and suggests that they were not using a win–stay/lose–shift strategy. An additional analysis on latencies, carried out using difference scores (no/go-go), revealed similar results.

The retention test revealed that the discrimination was maintained in both the Light/Dark and Direction groups ten days after the end of training. A  $2 \times 2 \times 2$  (Groups [Light/Dark vs. Direction]  $\times$  Sessions [reinforced vs. not reinforced]  $\times$  Trials [first vs. second trial of session]) ANOVA revealed a significant effect of sessions,  $F(1, 13) = 47.47$ ,  $p = .0011$ , reflecting retention of the discrimination in both groups (see Fig. 5). There was a significant trials effect,  $F(1, 13) = 4.92$ ,  $p = .045$ , which again reflected a lower latency on the second ( $M = 13.19$ ), relative to the first ( $M = 17.22$ ), trial, regardless of whether the first trial had been reinforced.

## Discussion

Animals use contextual cues to determine which response or stimulus is correct, even though contextual cues are not part of the reinforcement contingency. The findings from the present experiments suggest that animals' use of these contextual cues depends on the task. As in our earlier study (Wright et al., 2009), we showed that direction/orientation cues, but not visual cues, facilitated response reversal learning in Experiment 1. We also showed, for the first time, that distance cues facilitate response reversal learning. These findings suggest that metric cues might have a privileged role in guiding spatial choices. The results from Experiment 2 seem to support this claim, in that rats did not use light/dark cues as discriminative stimuli as readily as metric cues, even when trained on a discrimination task in which they were exposed to the cue



**Fig. 3** Mean (+SEM) latencies (in seconds) on reinforced (+) and nonreinforced (–) trials by the Light/Dark and Direction groups over ten blocks of training on the go/no-go task in Experiment 3.

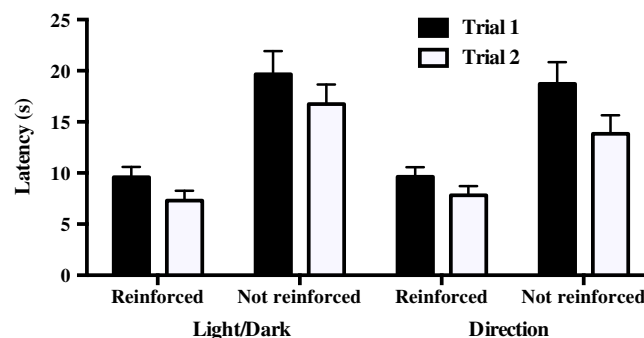
changes within a day. However, Experiment 3 showed that rats could use both metric (i.e., direction) and light/dark cues equally well in a go/no-go discrimination task.

The findings from Experiment 3 suggest that the difficulty rats had in using light/dark cues relative to metric cues in the response reversal task (Exp. 1; see also Wright et al., 2009) and the discrimination task (Exp. 2) cannot be attributed to differences in salience of the two types of cues. In fact, we found evidence that rats detected the difference in light cues on the first day of training, since they ran more slowly on light than on dark trials. The rats also remembered the discrimination after ten days, regardless of whether direction or light/dark cues had been used during training. Rather, the type of cue used depended on the task. Metric cues were readily used in spatial tasks, when rats had to choose “where” to go. Nonmetric cues were used just as readily on a nonspatial task in which the animals chose “when” to respond rather than where to go. The use of light/dark cues in spatial and discrimination tasks appears akin to the use of time of day in similar tasks. Rats readily use time of day to determine when to respond, but they struggle to use the same cues to determine where to go (Means et al., 2000; Thorpe et al., 2003).

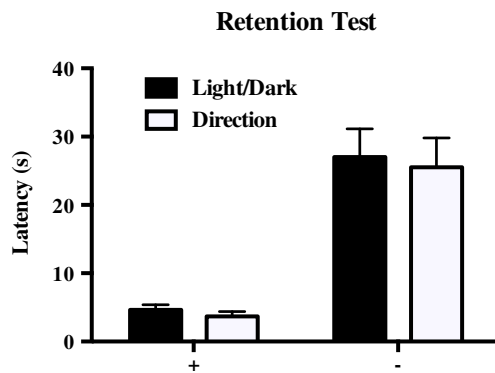
It is possible that spatial (where to go) tasks are inherently more difficult than nonspatial (go/no-go) tasks, and that any

differences in salience between metric and nonmetric cues are highlighted only in these more difficult tasks. Although it is difficult to say which task might be more difficult, the observation that discriminative performance emerged in similar numbers of trials suggests that the tasks are not dramatically different. For example, the rats in the Direction group reached criterion on the discrimination task in Experiment 2 in approximately 30 trials and showed a difference in latencies between reinforced and nonreinforced trials on the go/no-go task in Experiment 3 by the fourth block of training (48 trials). These findings, combined with the lack of any difference between the Direction and Light/Dark groups in Experiment 3, lead us to favor the argument that cue use is task-dependent.

One interesting result from Experiment 3 is that the rats had shorter latencies on the second trial of each session, regardless of cue or whether the first trial was reinforced. This difference in latencies was evident in both acquisition and the retention test, and may reflect an initial disruption in rats’ performance due to the novelty of the situation or some anxiety on first being removed from the home cage. To our knowledge, this has not been reported before. Because the decrease in latencies from the first to the second trial was also evident on nonreinforced sessions, this indicates that the outcome from the previous trial did not determine the rats’ performance and



**Fig. 4** Mean (+SEM) latencies (in seconds) of rats in the Light/Dark and Direction groups on Trial 1 versus Trial 2 of both reinforced and nonreinforced sessions of the go/no-go task in Experiment 3.



**Fig. 5** Mean (+ SEM) latencies (in seconds) on reinforced (+) and nonreinforced (–) trials by the Light/Dark and Direction groups during the retention test in Experiment 3.

suggests that they were not using a win–stay/lose–shift strategy. Such a strategy could be used on reversal tasks in which there are no cues to indicate a shift in reinforcement contingencies; the animals eventually learn to use the outcome of one trial as a cue to control their choice on the next trial (Restle, 1958). If the rats in Experiment 3 had used a win–stay/lose–shift strategy on the go/no-go discrimination task, we would have predicted a decrease in latencies on the second trial of reinforced sessions, but an increase in latencies on the second trial of nonreinforced sessions.

In recent years, our lab has focused on the role of direction in spatial tasks. The facilitation of response reversal learning seen in rats that received changes in starting orientation between reversals (present results; Wright et al., 2009) is not as well-known as the effects of context changes (e.g., room changes) but is not surprising, given the ability of rats and mice to use starting orientation as a conditional cue in a variety of spatial problems (Cahill, Fifield, Thorpe, Martin, & Skinner, 2015; Peckford et al., 2013; Skinner et al., 2003; Whyte, Martin, & Skinner, 2009). The role for orientation in the choosing of a correct response is mirrored in findings with humans, in which the formation of spatial memories is orientation-dependent. Humans who have been studied in virtual-reality tests of spatial memory have been shown to use their sense of orientation independently of local views when locating objects (Hartley, Trinkler, & Burgess, 2004; Spetch, Cheng, & MacDonald, 1996). Humans also show impaired recall of the locations of objects when there is a change of orientation between the times of training and test (McNamara, 2003).

Until the present study, we had not examined the effects of distance on spatial tasks. That rats are sensitive to distance information has been shown in a variety of tasks. Using an object recognition task in an open field, Goodrich-Hunsaker, Hunsaker, and Kesner (2008) showed that rats were sensitive to the distance between two objects. In spatial tasks, rats have been shown to be sensitive to the distance between the platform and the pool wall in water maze tasks (Hamilton et al.,

2007), and to the distance between the current location and refuge in food-foraging tasks (Whishaw & Gorny, 1999). In these spatial tasks, distance and directional information are often used together, as animals also learn the direction of the platform relative to the room cues or the direction of the refuge from the current location. Indeed, it may be difficult to completely separate distance from directional information in spatial tasks. For example, in the T-maze used in the present study, the angle or direction to the goal changed as the length of the start arm changed.

Although we argue that the distance task in Experiments 1 and 2 involved the use of a metric cue, it is possible that the rats were using a nonmetric timing strategy, since a change in the length of the start arm would change the amount of time it took a rat to reach the choice point. Animals are capable of using the duration of signals as a discriminative stimulus in operant tasks (e.g., Church & Deluty, 1977; Stubbs, 1968) and can use the length of time they are restrained at the start arm as a cue to guide choices on a T-maze (Cowles & Finan, 1941). It would have been difficult for the rats in the present task to use time as a reliable discriminative stimulus, since the time required to leave the start arm and the time spent at the choice point were variable across trials and would have masked any differences between traveling times on the short versus the long start arms. However, future research will be needed to adequately dissociate these two types of information.

The successful use of metric and nonmetric cues in the go/no-go task indicates that rats are sensitive to both types of cues, even though nonmetric cues may not be used to guide choices in spatial tasks. These findings are consistent with our recent report that hippocampal cells represent changes in nonmetric cues, despite the failure of those cues to facilitate response reversal learning (Skinner et al., 2014). It appears, then, that the usefulness of cues is to some extent dependent on the nature of the task. The use of time of day (Means et al., 2000; Thorpe et al., 2003) and light cues (present results) to predict the occurrence of food but not where it can be found is reminiscent of the literature on learning constraints, in which animals were sensitive to stimuli but were unable to use them in all tasks (Foree & LoLordo, 1973; Garcia, McGowan, Ervin, & Koelling, 1968; Garcia & Koelling, 1966; Gillette, Martin, & Bellingham, 1980). These constraints on learning are typically reported as reflecting which stimuli are relevant to each other or belong together (Capretta, 1961; Seligman, 1970). The nature of this relationship was recently captured by Sadtler et al. (2014), who looked at the network properties of neurons in the primary motor cortex of rhesus monkeys that could support the movement of a cursor in a brain–computer interface task. They first observed the characteristic activity of a population of neurons that was presumably determined by underlying circuitry. They subsequently showed that animals could use these activity patterns to control a cursor, whereas animals were less able to use activity patterns that were

outside the normal ones (Sadler et al., 2014). Their findings suggest that learning constraints may be the result of characteristic population activity, in that difficulties in learning reflect the absence of shared population activity. The characteristic neuronal population activity for location is based on direction and distance, and this may facilitate the use of these cues in spatial problems like the ones used in our experiments.

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