



Effects of string length on the organization of rat string-pulling behavior

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Abstract

The string-pulling paradigm has been adapted to investigate many psychological phenomena across a range of animal species. Although varying string length has been shown to influence performance, the nature of the representation remains to be determined. Across three experiments, rats were shaped to pull string to receive food reinforcement. Either string length or reinforcement rate was manipulated to examine the influence on string-pulling behavior. Experiment 1 demonstrated that varied string length was sufficient to elicit an odor discrimination. Subsequent experiments provided evidence that varying string length (Experiment 2) and reinforcement rate (Experiment 3) produced qualitatively distinct patterns of string-pulling behavior. In Experiment 2 rats that received a long string were more likely to pull in the probe string to the end, yet no differences were observed in approach time between short and long groups. However, in Experiment 3 rats that received low reinforcement were less likely to pull in the probe string to the end and were slower to approach the string to begin pulling. These results are consistent with rats using temporal and motivational characteristics to guide responding during string-pulling behavior.

Keywords Time · Reinforcement rate · Odor · Discrimination · Probe trials · Movement kinematic

Introduction

String-pulling is a highly conserved, spontaneously occurring behavior that has been adapted to investigate multiple psychological phenomena (for a review see Jacobs and Osvath 2015). As such, multiple representational systems have been posited to support the organization of string-pulling behavior. Early work demonstrated that varying task demands during training influenced performance observed during non-reinforced probe trials (Crutchfield 1939). For example, exposure to longer string lengths during training increased rats' persistence to pull a string during non-reinforced probe trials. The effect of manipulating string length and other task demands on string-pulling behavior was attributed to rats using a representation of energy expenditure encoded during training to guide performance during probe trials. More recently, motion capture analysis of rat hand movements during string-pulling has supported a role

for direction and distance estimates guiding manipulatory-scale behavior, or movement by the hands (Blackwell et al. 2018a). Therefore, it is possible the nature of the representation that mediates the effects of varying string length may vary, reflecting multiple dimensions of the task.

String-pulling behavior unfolds in the seconds to minutes range and likely depends on information processing and neural systems that support interval timing (Buhusi and Meck 2005). Early work investigating interval timing showed that varying temporal and reinforcement characteristics of fixed interval schedules of reinforcement produced qualitatively distinct patterns of responding (Roberts 1981). Specifically, increases in the fixed interval schedule (FI20 vs. FI40) were associated with longer peak response times during non-reinforced probe trials; however, peak response rates did not differ between schedules. In contrast, increasing the number of non-reinforced probe trials reduced the peak response rates without influencing peak response times. This dissociation was critical in providing evidence that temporal and motivational factors differentially contribute to performance. Subsequently, researchers have used the peak procedure extensively to investigate the neurobiology of interval timing (Meck and Church 1987; Meck et al. 1987; Meck

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1996; Lake and Meck 2013). Similar temporal processes and neural systems have been posited to organize spontaneously occurring behaviors like grooming (Matell et al. 2006) and food protection (Whishaw and Gorny 1994; Wallace et al. 2006a, b; Martin et al. 2008; Blankenship et al. 2017). One limitation of these spontaneously occurring behaviors is their inability to allow for the investigation into the effects of independently manipulating temporal and reinforcement factors on performance.

String-pulling behavior occurs spontaneously and several aspects of the task can be independently manipulated. This series of experiments investigated the effects of varying both string length and reinforcement frequency on the organization of string-pulling behavior. Experiment 1 investigated whether short (1.5 m) and long (3.0 m) string lengths were sufficient to elicit an odor discrimination. The subsequent experiments either used these same string lengths (Experiment 2) or varied reinforcement frequency (Experiment 3) to characterize the effects on the organization of string-pulling behavior. The results provide evidence that string-pulling can be adapted to investigate individual contributions of temporal and reinforcement factors to organizing spontaneous behaviors.

Experiment 1

The goal of Experiment 1 was to determine whether varying string lengths would be sufficient to elicit an odor discrimination. Rats received either consistent (predictable group) or inconsistent (unpredictable group) length (1.5 m vs 3.0 m)-odor (lemon vs. vanilla) pairings during reinforced standard trials. If string length is salient enough to influence the organization of string-pulling behavior, then a predictable length/odor pairing should elicit an odor discrimination. Standard reinforced trials had a piece of cashew tied to the end of the string. Each odor was presented once per day with a longer (5.0 m) non-reinforced probe string. Non-reinforced trials did not have a piece of cashew tied to the end of the string. It was anticipated that the results would provide evidence as to whether string lengths were sufficient to elicit an odor discrimination.

Methods

Subjects

Twelve adult male Long-Evans rats (*Rattus norvegicus*) were obtained from the Northern Illinois University vivarium with temperature (20°–21°), humidity (40–60%), and light/dark cycle (12-h) remaining consistent throughout behavioral testing. Rats were food deprived at 85% of their free-feeding body weight and provided water

ad libitum. Rats were pair-housed in opaque plastic cages (46 cm × 26 cm × 26 cm) with a wire mesh top; however, if the combined weight of cage mates exceeded 1,000 grams then the rats were single housed in clear plastic cages with a wire mesh top. All experimental protocols were approved by the NIU Animal Care and Use Committee.

Apparatus

The string-pulling apparatus was a clear plastic cage (46 cm × 26 cm × 26 cm) with a wire mesh top. The apparatus was placed on a table in a room with many visual cues. A video camera was positioned at the front of the short side of the apparatus to record string-pulling behavior. The resulting videos were saved to DVDs. Strings were twisted 100% cotton of varied lengths. During testing, strings were 5.0 m long with a piece of cashew secured at 1.5 m (short) or 3.0 m (long; see Fig. 1a). The probe string was 5.0 m long with a bundle of string attached to the end to simulate the weight of the cashew piece (see Fig. 1b).

Strings were scented with either lemon or vanilla extract (McCormick, MD, USA). String scenting involved submerging the string in the extract for 5 min, removing

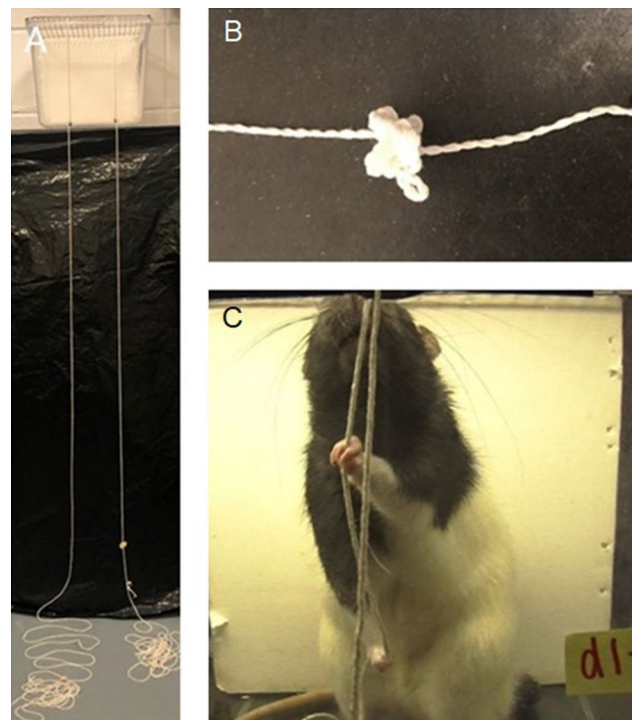


Fig. 1 A photograph of the string presentation during odor discrimination in Experiment 1 is displayed (a). A bundle of string was tied to the end of the 5 m probe string to simulate the weight of the cashew (b). A close-up of a rat pulling in a single string in the testing apparatus during shaping is displayed (c)

the string from the extract, and letting the string dry on paper towels overnight.

Procedure

Habituation started once rats were food deprived to 85% of their free feeding weight and involved housing rats overnight singly with access to strings. Specifically, twenty strings of varying lengths were draped over each wall of the cage. Half of the strings were baited with a piece of cashew as partial reinforcement yields the highest response rate.

Pre-training with a single string began the following day (see Fig. 1c). Rats were placed in the apparatus and given eight trials to retrieve a piece of cashew from the end of a 1.0 m string. The string was draped vertically and hung outside the front of the testing apparatus for each trial. Between trials, rats were transferred to an opaque cage in the same room while the apparatus was cleaned and strings were baited again. After rats successfully retrieved a piece of cashew on all eight trials with a 1.0 m string, rats were trained with a 2.0 m string. Rats continued pre-training with the 2.0 m string until successfully retrieving a piece of cashew on all eight trials for 2 days in a row.

Once rats completed pre-training, they were randomly assigned to predictable ($n=6$) and unpredictable ($n=6$) groups. The predictable group received consistent length/odor pairings (e.g. short–lemon vs. long–vanilla or short–vanilla vs. long–lemon). In contrast, the unpredictable group did not receive consistent length/odor pairings. Instead, rats always received lemon and vanilla scented strings; however, odor was not consistently paired with string length.

Rats were tested for 15 days total. During the first 10 days of training, rats received eight trials per day in which both scented strings were presented side-by-side simultaneously. String presentation was pseudo-randomized and counterbalanced across testing to prevent position-based responding. The cashew piece was attached either to a short or a long distance from the beginning of the string. On the last 5 days of testing, two additional trials were included to assess responding to a lemon- and a vanilla-scented probe string. Rats pulled in both scented strings during standard and probe trials. Recall that during testing, string weight was controlled for by lengthening all strings to 5.0 m and attaching the cashew piece at 1.5 m (short) or 3.0 m (long). During a probe trial, groups' length–odor pairings remained the same as it was on training trials except one reinforced standard string was presented with a non-reinforced probe string. If the probe string was pulled in first, then rats continued the trail and pulled in the baited string. The odor of the non-reinforced probe string varied across trials.

Behavioral analysis

Several measures were used to quantify string-pulling behavior during standard and probe trials. Approach time was defined as the latency to initiate string-pulling after placement in the apparatus. Pull time was the latency to reach the cashew after string-pulling was initiated. These measures were averaged across all trials within a day and collapsed into 2-day blocks.

Several additional measures were used to quantify behavior during probe trials. Percent complete was calculated as the number of probe trials in which the probe string was pulled until reaching the end (approximately 5.0 m) divided by 10 (i.e., total number of probe trials across testing) and multiplied by 100. All rats did not pull in the probe string completely; therefore, motion capture software was used to digitize hand movements during bouts of string-pulling behavior. The Peak Modus system captured string-pulling videos, and hand position was manually digitized at 30 Hz. Peak speed (cm/s) was recorded for both hands during a bout of string-pulling. The failure to observe a significant difference between hands prompted averaging across hands and collapsing into 2-day blocks.

Repeated-measures ANOVAs were conducted on approach and pull time with group and block as main effects. The Greenhouse–Geisser correction was used in analyses in which the Mauchly's test indicated significant departure from the assumption of sphericity. Partial eta squared (η_p^2) was used as a measure of effect size for each main effect and interaction. Linear trend analysis and HSD post hoc analyses were used to further investigate main effects and interactions.

The design of probe trials for the current experiment precluded direct statistical comparison of groups. Specifically, counterbalancing of length–odor pairings in the predictable group did not provide a common odor comparison for the unpredictable group. Therefore, paired samples *T* tests were used to evaluate within-group differences in performance on probe trials. Cohen's *d* was used as a measure of effect size.

Results

Although groups did not differ in approach time, a significant change was observed across blocks (see upper left panel of Fig. 2; see Table 1). The Greenhouse–Geisser correction ($\epsilon=0.523$) was used to adjust the degrees of freedom associated with the lack of sphericity in approach time. The repeated-measures ANOVA conducted on approach time revealed a significant effect of block; however, neither the main effect of group nor the Group

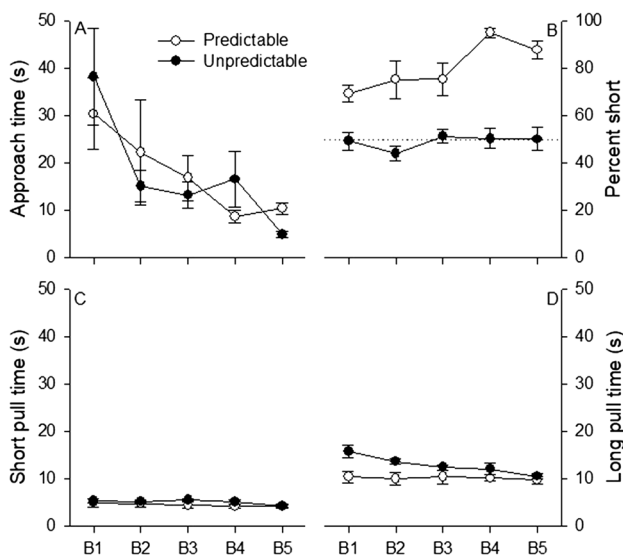


Fig. 2 Average group approach time is plotted for each 2-day block (a). The average percent of trials the short string was chosen first is plotted for both groups across blocks (b). The dotted lines represent chance. Average group pull time for the short (c) and long (d) strings are plotted across blocks. Standard error was used for all error bars

Table 1 Experiment 1

	<i>df</i>	<i>F</i>	<i>p</i>	<i>n</i> _p ²
Approach time				
Block	2.092, 20.916	7.512	0.003	0.429
Block × Group	2.092, 20.916	0.991	0.391	0.090
Group	1, 10	<0.001	0.988	<0.001
Short string first				
Block	4, 40	3.202	0.023	0.243
Block × Group	4, 40	2.313	0.074	0.188
Group	1, 10	101.492	<0.001	0.910
Short pull time				
Block	1.893, 18.926	3.449	0.055	0.256
Block × Group	1.893, 18.926	1.349	0.282	0.119
Group	1, 10	0.724	0.415	0.068
Long pull time				
Block	4, 40	6.171	0.001	0.382
Block × Group	4, 40	4.162	0.007	0.294
Group	1, 5	0.390	0.053	0.326

Results from repeated-measures ANOVA are displayed for each measure from standard trials in Experiment 1. Degrees of freedom were adjusted using Greenhouse–Geisser

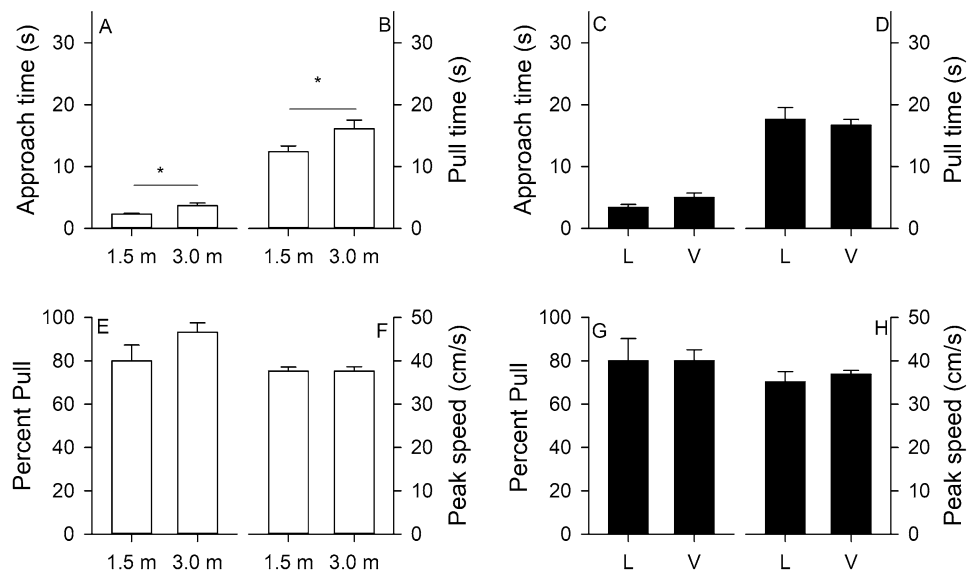
× Block interaction was significant. Post hoc analysis revealed a significant linear trend for both groups across blocks. Approach time decreased across blocks for both groups.

Groups significantly differed in the percent of trials when the short string was chosen first (see top right panel of Fig. 2) across blocks. The repeated-measures ANOVA conducted on the percent of trials when the short string was chosen first revealed a significant effect of group and block; however, the Group × Block interaction was not significant. Post hoc analysis revealed a significant linear trend [$F(1,10) = 7.663, p = 0.020, \eta_p^2 = 0.434$] for both groups across blocks. The predictable group exhibited a high percent of trials when the short string was selected first relative to the unpredictable group. In addition, the percent of trials when the short string was chosen first increased across blocks.

The time required to pull the short string (bottom left panel of Fig. 2) did not vary as a function of block or group; however, pull times for the long string (bottom right panel of Fig. 2) were observed to differ between groups and depended on the training block. The Greenhouse–Geisser correction ($\epsilon = 0.473$) was used to adjust the degrees of freedom associated with the lack of sphericity in pull time for the short string. The repeated-measures ANOVA conducted on short string pull time failed to reveal a significant effect of group, block, and Group × Block interaction. Both groups exhibited similar times to pull the short string across blocks. The repeated-measures ANOVA conducted on long string pull time revealed a significant effect of block and Group × Block interaction; however, the main effect of group was not significant. Post hoc analysis revealed a significant linear trend across blocks for the unpredictable group [$F(1,5) = 16.848, p = 0.009, \eta_p^2 = 0.771$] but not the predictable group [$F(1,5) = 0.390, p = 0.560, \eta_p^2 = 0.072$]. The unpredictable group exhibited longer pull times that decreased across blocks when responding to the long string.

Despite identical string lengths during probe trials, differences in performance were observed in the predictable group (see Fig. 3). The paired samples *T* tests revealed that the predictable group exhibited significant differences in approach [$T(5) = -3.977, p = 0.011, d = 1.818$] and pull time [$T(5) = -3.098, p = 0.027, d = 1.274$] when presented with strings of consistent length/odor pairings. In contrast, no differences in approach [$T(5) = -2.448, p = 0.058, d = 1.081$] and pull [$T(5) = 0.713, p = 0.507, d = 0.251$] time were observed in the unpredictable group during probe trials. The predictable group did not differ in the percent of trials the string was pulled to the end [$T(5) = -1.348, p = 0.235, d = 0.913$] or peak speed [$T(5) = -0.014, p = 0.990, d = 0.008$] across string lengths. Similarly, the unpredictable group exhibited a similar average percent of trials that the string was pulled to the end [$T(5) = 0.000, p = 1.000, d < 0.001$] and average peak speed [$T(5) = -0.978, p = 0.373, d = 0.410$]. The predictable group took longer to approach and pulled the string

Fig. 3 Average predictable group approach (a) and pull (b) times are plotted for short (1.5 m) and long (3.0 m) strings during the non-reinforced probe trials. Average unpredictable group approach (c) and pull (d) times are plotted for the lemon (l) and vanilla (v) scented strings during non-reinforced probe trials. Average percent pulled (e) and peak speed (f) are plotted for the predictable group during non-reinforced probe trials. Average percent pulled (g) and peak speed (h) are plotted for the unpredictable group during non-reinforced probe trials. Standard error was used for all error bars. (* $p < 0.05$)



with the odor paired with the longer length relative to the string with the odor paired with the shorter length.

Discussion

The results of this study demonstrate that string length was sufficient to elicit an odor discrimination. Rats in the predictable group exhibited an early preference for the odor paired with the short string. In addition, the predictable group's preference for the odor paired with the short length was also observed during probe trials with faster approach and pull times; however, odor did not elicit a differential tendency to pull the probe string to the end when odors were consistently paired with specific string lengths. This may be related to rats experiencing reinforcement at both string lengths; therefore, more training may be needed. Operant work provides rats with extensive training during standard and non-reinforced probe trials. It is possible this experience is critical for differential performance. Further, the length of the probe string (5.0 m) might not have been long enough to elicit differential responses after training with two different string lengths. This seems unlikely considering that previous operant work has demonstrated that doubling the length of training trials was sufficient to elicit performance differences on non-reinforced probe trials (Roberts 1981). These results establish that string length is salient enough to elicit an odor discrimination and provides a foundation to further evaluate how temporal or motivational factors influence performance. Subsequent experiments were designed with a between-subjects factor, thereby minimizing the interference associated with subjects experiencing multiple string lengths or reinforcement conditions.

Experiment 2

This experiment investigated the effects of varying string length on string-pulling performance. Specifically, groups received either a short (1.5 m) or a long (3.0 m) string during standard reinforced trials. String length (short vs long) was predicted to differentially influence the organization of string-pulling behavior with a short string eliciting less engagement during probe trials. Recall that standard reinforced trials have a piece of cashew at the end of the string. During non-reinforced probe trials, both groups had access to all 5.0 m of the string. The pattern of results was expected to establish whether varying string length is sufficient to differentially organize string-pulling behavior.

Methods

Subjects

Fourteen adult male Long–Evans rats (*Rattus norvegicus*) obtained from the same source were maintained under the same conditions as described in the previous experiment.

Apparatus

The apparatus was the same as described in the previous experiment with the exception that strings were not scented.

Procedure

Habituation and pre-training procedures were identical to that described in the previous experiment.

Once pre-training concluded, rats were randomly assigned to short string ($n = 7$) and long string ($n = 7$) groups.

During training, rats received seven standard reinforced trials with one non-reinforced probe trial. Only one string was presented during standard and probe trials. The probe trial occurred randomly with the exception that it was never the first or last trial of the day. Training continued for 10 days. All strings were replaced with new strings every 2 days.

Behavioral analysis

The behavioral analyses and measures were the same as described in the previous experiment, with the exception that independent sample *T* tests were used to compare group performance during probe trials.

Results

Both groups displayed a progressive decrease in approach time during reinforced trials across training blocks (see left panel of Fig. 4; see Table 2). The Greenhouse–Geisser correction ($\epsilon=0.321$) was used to adjust the degrees of freedom associated with the lack of sphericity in approach time. The repeated-measures ANOVA conducted on approach time revealed a significant effect of block; however, neither the effect of group nor Group \times Block interaction was significant. Post hoc analysis revealed a significant linear trend across blocks. Rats took less time to approach the reinforced string across training blocks.

Pull time during reinforced trials significantly differed between groups and changed across training blocks (see right panel of Fig. 4). The Greenhouse–Geisser correction ($\epsilon=0.605$) was used to adjust the degrees of freedom associated with the lack of sphericity in pull time. The repeated-measures ANOVA conducted on pull time revealed a significant effect of group, block, and Group \times Block interaction. Post hoc analysis revealed a significant linear trend across blocks for the long group; however, the short group did not exhibit a significant linear trend

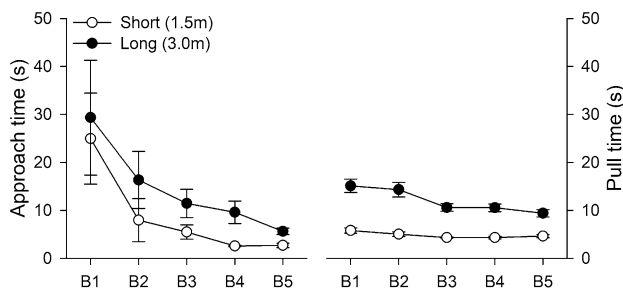


Fig. 4 Short and long groups’ approach (left panel) and pull (right panel) times are plotted across blocks. Standard error was used for all error bars

Table 2 Experiment 2

	<i>df</i>	<i>F</i>	<i>p</i>	η_p^2
Approach time				
Block	1,284, 15,407	7.540	0.011	0.386
Block \times Group	1,284, 15,407	0.103	0.813	0.009
Group	1, 12	1.306	0.275	0.089
Pull time				
Block	2,419, 29,034	12.051	<0.001	0.501
Block \times Group	2,419, 29,034	5.216	0.008	0.303
Group	1, 12	70.888	<0.001	0.855

Results from repeated-measures AONVA are displayed for each measure from standard trials in Experiment 2. Degrees of freedom were adjusted using Greenhouse–Geisser

[$F(1,6) = 3.619, p = 0.106, \eta_p^2 = 0.379$]. The short group took less time to reach the end of the string relative to the long group.

In general, performance during probe trials was similar between groups (see Fig. 5). Both groups exhibited similar approach times [$T(12) = 0.328, p = 0.748, d = 0.176$], pull times [$T(12) = -1.895, p = 0.082, d = 1.013$], and peak speeds [$T(12) = -1.085, p = 0.299, d = 0.580$]. However, groups significantly differed in the percent of strings completely pulled until the end [$T(12) = -4.341, p = 0.001, d = 2.320$]. The long group exhibited a higher percent of pulling relative to the short group.

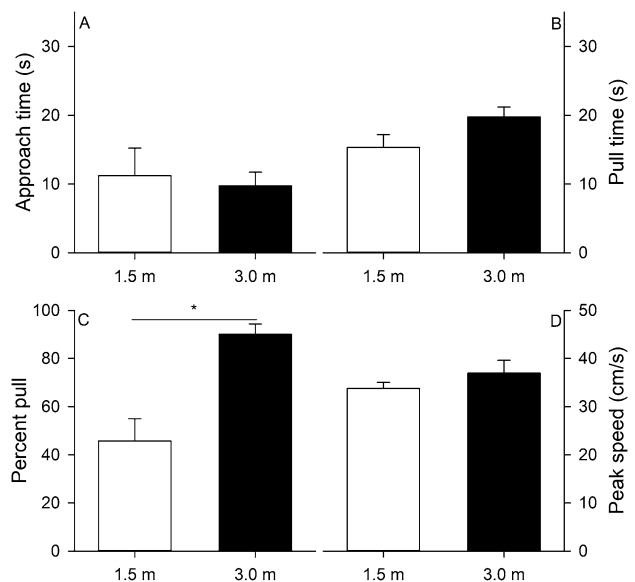


Fig. 5 Average approach (a) and pull (b) times are plotted for both groups during non-reinforced probe trials. Average percent pulled (c) and peak speed (d) are plotted for both groups during non-reinforced probe trials. Standard error was used for all error bars (* $p < 0.05$)

Discussion

This pattern of results is consistent with a stimulus dimension associated with string length eliciting group differences in performance. During reinforced trials, group differences were restricted to pull time. This difference likely reflected the short group encountering and consuming the cashew piece prior to the long group. Both groups experienced the same string length (5.0 m) during non-reinforced probe trials and exhibited similar approach time, pull time, and peak speeds. However, the long group exhibited a significantly higher probability of pulling the probe string to the end. One explanation for this pattern of results is that rats encoded the distance pulled or time elapsed prior to encountering the food item on reinforced trials. It may also be possible that rats are using a combination, or an average, of both time and distance (Cheng et al. 1996). This representation was used to guide engagement in string-pulling during the probe trial. For example, rats in the short group stopped string-pulling earlier on the probe string, because the match between the representation and perceived distance traveled or time elapsed occurred earlier, relative to the long group. Another possible explanation for these group differences may be related to the effects that partial reinforcement has on responding during extinction. Specifically, more robust responding is observed during extinction when preceded by a period of partial reinforcement relative to a period of continuous reinforcement (Weinstock 1954). These effects have been attributed to developing a tolerance for frustration (Amsel 1958) or encoding reinforcement sequences (Capaldi 1966). In either case, experience with different motivational factors (e.g., frustration, reinforcement) is posited to mediate varied levels of performance observed during extinction. In the current experiment, rats exposed to the long string may be viewed as experiencing a reinforcement sequence more similar to the probe string. Therefore, the long group was more likely to continue pulling during the probe string relative to rats exposed to the short string. The next experiment investigated these competing explanations for the effects of string length on string-pulling performance.

Experiment 3

Experiment 3 examined the effect of varying reinforcement frequency on performance. All rats pulled short (1.5 m) strings to obtain food; however, groups received either high (seven standard trials; one probe trial) or low (four standard trials; four probe trials) reinforcement frequency during daily sessions. It was anticipated that the results would aid in establishing whether varying reinforcement frequency produces a change in string-pulling behavior distinct from varying string length. Varying reinforcement rate (low vs

high) was hypothesized to differentially influence string-pulling performance.

Methods

Subjects

Sixteen adult male Long–Evans rats (*Rattus norvegicus*) were obtained from the same source and maintained under the same conditions as described in Experiment 1.

Apparatus

The apparatus was the same as described in previous experiments, with the exception that cashews were attached at 1.5 m along a 5.0 m string for all reinforced standard trials.

Procedure

Habituation and pre-training procedures were identical to that described in the previous experiments.

Once pre-training concluded, rats were randomly assigned to low ($n=8$) and high ($n=8$) reinforcement groups receiving eight trials a day for 10 days. The high group received seven trials with a cashew piece attached at 1.5 m along a 5.0 m string and one non-reinforced probe trial (5.0 m). The low group received four trials with a cashew piece attached at 1.5 m along a 5.0 m string and four non-reinforced trials (5.0 m). Only one string was presented during standard and probe trials. Probes could occur on any trial with the following exceptions: first trial, last trial, and more than two trials in a row. All strings were replaced with new strings every 2 days.

Behavioral analysis

The behavioral analyses and measures were the same as described in the previous experiments.

Results

Groups differed in approach time during reinforced trials, and they displayed a change across training blocks (see left panel of Fig. 6; see Table 3). The Greenhouse–Geisser correction ($\epsilon=0.631$) was used to adjust the degrees of freedom associated with the lack of sphericity in approach time. The repeated-measures ANOVA conducted on approach time revealed a significant effect of group and block; however, the Group \times Block interaction was not significant. Post hoc analysis revealed a significant trend across blocks. Rats in the high group exhibited shorter latencies to approach the string.

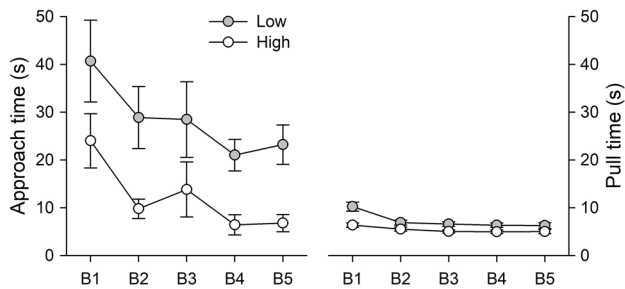


Fig. 6 High and low groups' approach (left panel) and pull (right panel) times are plotted across blocks. Standard error was used for all error bars

Table 3 Experiment 3

	<i>df</i>	<i>F</i>	<i>p</i>	η_p^2
Approach time				
Block	2.525, 35.346	6.107	0.003	0.304
Block \times Group	2.525, 35.346	0.095	0.943	0.007
Group	1, 14	9.481	0.008	0.404
Pull time				
Block	1.597, 22.359	14.408	<0.001	0.507
Block \times Group	1.597, 22.359	3.541	0.055	0.202
Group	1, 14	13.040	0.003	0.482

Results from repeated-measures AONVA are displayed for each measure from standard trials in Experiment 3. Degrees of freedom were adjusted using Greenhouse–Geisser

Reinforced trial pull time significantly differed between groups and changed across training blocks (see right panel of Fig. 6). The Greenhouse–Geisser correction ($\epsilon = 0.399$) was used to adjust the degrees of freedom associated with the lack of sphericity in pull time. The repeated-measures ANOVA conducted on pull time revealed a significant effect of group and block; however, the Block \times Group interaction was not significant. Post hoc analysis revealed a significant linear trend for both groups across blocks [$F(1,14) = 30.271$, $p < 0.001$, $\eta_p^2 = 0.684$]. Pull time was shorter for rats in the high group, and decreases in pull time were observed across blocks.

Group differences were observed during probe trials (see Fig. 7). Groups differed in time to approach the string [$T(14) = 3.427$, $p = 0.004$, $d = 1.714$]; however, no group differences were observed in time to pull the string [$T(14) = -1.442$, $p = 0.171$, $d = 0.721$]. Groups differed in the percent of strings pulled to the end [$T(9.040) = -2.880$, $p = 0.018$, $d = 1.440$]. No group differences were observed in peak speed [$T(14) = -0.601$, $p = 0.558$, $d = 0.300$]. The low group took longer to approach the string and was less likely to pull it to the end.

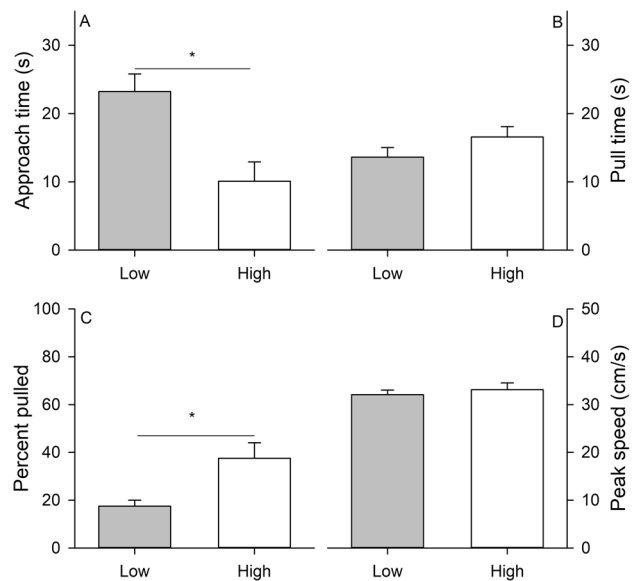


Fig. 7 Average approach (a) and pull (b) times are plotted for both groups during non-reinforced probe trials. Average percent pulled (c) and peak speed (d) are plotted for both groups during non-reinforced probe trials. Standard error was used for all error bars. (* $p < 0.05$)

Discussion

The results of this experiment demonstrate that modifying reinforcement frequency influences string-pulling performance. In general, low frequency of reinforcement elicited longer approach and pull times during reinforced standard trials. During non-reinforced probe trials, low frequency of reinforcement elicited longer approach times and in only a lower percent of trials the string was pulled to the end. However, varying reinforcement frequency did not impact pull time or peak speed during probe trials. This pattern of results is qualitatively distinct from Experiment 2. Recall, the short group in Experiment 2 experienced identical training and probe conditions as the high group in the current experiment. Increasing string length (long group in Experiment 2) did not impact approach time; however, the percent of probe trials the string was pulled to the end increased. In contrast, decreasing reinforcement frequency (low group in the current experiment) increased approach time and decreased the percent of probe trials in which the string was pulled to the end. The direction of these effects is consistent with string length and reinforcement frequency influencing performance by different mechanisms. The varying reinforcement frequency may have engaged cognitive processes related to motivational factors described by the matching law (Davison and McCarthy 1988). In contrast, manipulating string length may have recruited cognitive processes involved in estimating distance or time.

General discussion

Rats in the current series of experiments spontaneously engaged in string-pulling behavior and this behavior was maintained by providing reinforcement at the end of the string. Several aspects of the string-pulling task were manipulated to evaluate their impact on performance. In the first experiment, only rats exposed to the consistent length/odor pairing exhibited a preference for the short-odor string during training trials and differential approach time during probe trials. In the second experiment, groups did not differ in approach time. However, the group trained with the longer string exhibited a significantly higher likelihood of pulling the string to the end during probe trials. In the third experiment, rats exposed to lower reinforcement frequency were slower to approach the string and less likely to pull the string to the end during probe trials. These qualitative differences in performance associated with manipulating string length and reinforcement frequency are consistent with independent information processing systems contributing to the organization of string-pulling behavior.

There are several sources of information that may have contributed to the representation used to guide performance in string-pulling when varying string length. First, it is possible that rats are encoding distance until the reinforcement is encountered. Previous work has demonstrated that rats use distance to organize spontaneous behaviors at multiple scales of movement. For example, rodents exploring a novel environment organize their movements into a sequence of progressions and stops that are focused around a home base (Eilam and Golani 1989; Golani et al. 1993). Progressions towards the home base are faster (Tchernichovski and Golani 1995) and exhibits a consistent temporal pacing of moment-to-moment speed (Wallace et al. 2006a, b) relative to progressions away from the home base. Specifically, the peak speed typically occurs at the midpoint of the path and increases in magnitude with increase in the Euclidian distance of the progression. Similar movement kinematics have been observed at the manipulatory scale in rats engaged in string-pulling behavior (Blackwell et al. 2018a). Rats scale the reach and withdraw peak speeds to the Euclidian distance of each movement component. It is possible that concatenation of manipulatory-scale distance estimates support encoding distance information at the ambulatory scale; therefore, both scales may contribute to encoding string length in the current study. Different neural systems have been posited to contribute to ambulatory (Whishaw and Vanderwolf 1973; Kjelstrup et al. 2008; Winter et al. 2013; Blankenship et al. 2015) and manipulatory (Georgopoulos et al. 1982; Blackwell et al. 2018b) distance estimation. Demonstrating that

the effects of varying string length depend on either of these neural systems will provide converging evidence to support a role for distance estimation in organizing string-pulling behavior. However, deriving distance estimated from movement is computationally demanding. Rate of movement must be continuously monitored relative to the time engaged in the task; therefore, it is possible that more parsimonious accounts of the effects of string length on string-pulling behavior should be considered.

Several lines of evidence are consistent with rats using temporal information to organize string-pulling behavior. At a computational level, time to reach the food item would be sufficient to guide performance provided that the rate of string-pulling did not significantly vary. In the current set of studies, string-pulling peak speeds did not significantly differ between groups across each experiment, and consistent string-pulling peak speeds (approximately 35 cm/s) were observed independent of task manipulation. This consistency in string-pulling peak speed provides a basis to use interval timing processes to guide performance. At a behavioral level, early work demonstrated that varying temporal and reinforcement components of a fixed interval schedule of reinforcement had qualitatively distinct effects on operant responding (Roberts 1981). For example, increasing the fixed interval schedule from 20 to 40 s was associated with an increase in peak response time without changing the magnitude of peak response rate. In contrast, increasing the number of non-reinforced probe trials was associated with decreasing peak response rate, without changes in the peak response time. Similar dissociations in performance variables were observed in the current study. Increasing string length (1.5 m vs. 3.0 m) significantly increased the probability of pulling the probe string to the end during probe trials without significantly influencing time to approach the string during standard or probe trials (Experiment 2). In contrast, increasing the number of non-reinforced probe trials (1 vs. 4) significantly increased approach time during standard and probe trials (Experiment 3). In addition, increase in the number of non-reinforced probe trials decreased the probability of pulling to the end of the string, which is in the opposite direction observed with an increase in string length. This pattern of results is consistent with at least two factors influencing the organization of string-pulling behavior. One of these factors may have involved encoding the time to encounter the food item. Further work investigating the contribution of interval timing neural systems to string-pulling may provide evidence critical to evaluating this claim.

Another source of information is related to the magnitude of reinforcement associated with engaging in string-pulling behavior. Recent work has provided evidence that engaging in species-specific behaviors (e.g., tool use) is intrinsically motivating, or induces positive emotions (McCoy et al. 2019). Rats and mice spontaneously engage in string-pulling

behavior possibly because it may be related to species-specific behaviors like nest building or retrieving food from a branch or blade of grass. Therefore, both the string-pulling behavior and the attached food item may influence magnitude or reinforcement, thereby influencing performance. Experiment 1 demonstrated that the odor associated with the short string quickly (within the first 2 days) elicited a string preference and led to shorter approach times during probe trials relative to the odor associated with the long string. These results show parallels to work investigating the effects of varying reinforcement rate (Herrnstein 1961; Norman and McSweeney 1978) or delayed reinforcement (Chung and Herrnstein 1967) on choice behavior. Specifically, schedules with higher rates or shorter delays of reinforcement elicit higher rates of responding. These similarities establish a foundation for the use of string-pulling behavior to investigate factors and neural systems that contribute to choice behavior.

This work provides evidence that rats may use a multidimensional representation to guide string-pulling behavior. The first experiment demonstrated that varying string length was sufficient to elicit a preference for an odor consistently paired with a short string. The following experiments demonstrated that varying string length (Experiment 2) and reinforcement frequency (Experiment 3) had qualitatively distinct effects on the organization of string-pulling behavior. These results are consistent with rats using temporal and reinforcement rate information to guide string-pulling behavior and establish a foundation for studies to investigate the neural basis of processing this information.

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