Does bumblebee preference of continuous over interrupted strings in string-pulling tasks indicate means-end comprehension?

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Abstract: Bumblebees (*Bombus terrestris*) have been shown to engage in string-pulling behavior to access rewards. The objective of this study was to elucidate whether bumblebees display a means-end comprehension in string-pulling task. We presented bumblebees with tasks involving choosing between two options: one where a string is connected to an artificial flower containing a reward and the other involving interrupted strings. Surprisingly, bumblebees displayed a consistent preference for pulling connected strings over interrupted ones after training with a stepwise pulling technique. Intriguingly, when exposed to novel string colors, bees continued to exhibit a bias towards pulling the connected string. This suggests that bumblebees engage in featural generalization of the visual display of the string connected to the flower in this task. When the bumblebees were confronted with coiled connected strings during the testing phase, they failed to identify and reject interrupted strings. This finding underscores the significance of visual consistency in enabling the bumblebees to perform the task successfully. Our results suggest that

bumblebees to distinguish between continuous strings and interrupted strings relies on a combination of image matching and associative learning, rather than means-end understanding. These insights contribute to a deeper understanding of the cognitive processes employed by bumblebees when tackling complex spatial tasks.

Keywords: associative learning, featural generalisation, image matching, means-end understanding

Introduction

String pulling is one of the most extensively used approach in comparative psychology to evaluate the understanding of causal relationships (*Jacobs & Osvath, 2015*), and has been found mainly in mammals and birds, where a food item is visible to the animal but accessible only by pulling on a string attached to the reward (*Taylor, 2010; Range et al., 2012; Jacobs & Osvath, 2015; Wakonig et al., 2021*). A fundamental challenge revolves around unraveling the strategies that animals employ when confronted with specific tasks for animal cognition research (*Chittka et al., 2012*). The complexity of the string-pulling paradigm can be altered by manipulating the number and mutual positions of the strings and reward, allowing the investigation of different aspects of cognition (*Jacobs & Osvath, 2015; Wang et al., 2019*).

Means-end understanding is expressed as goal-directed behavior, which involves the deliberate and planned execution of a sequence of steps to achieve a goal (*Ortiz et al., 2019*). String-pulling studies have directly tested means-end comprehension in various species (*Riemer et al., 2013; Jacobs & Osvath, 2015*). In these studies, organisms are presented with two or more strings, where one is interrupted and the other one is connected to a reward; pulling the connected string indicates that animals comprehend that a continuous string is a mean to the end of obtaining the reward (*Piaget 1953; Wasserman et al., 2013; Jacobs & Osvath, 2015; Hofmann et al., 2016; Wang et al., 2019*). Most animals fail in such string-pulling tasks when they have to spontaneously solve them, but they can be trained to recognize that an interrupted string is useless through trial and error learning (*Mayer et al., 2014; Ortiz et al., 2019; Wang et al., 2019*).

To our knowledge, bumblebees are the only reported invertebrates that have been

trained to learn to pull a string to obtain rewards. However, the performance of bumblebees in this study could be explained by simple associative learning (*Alem et al., 2016*). It remains unknown whether the bumblebees understand the connectivity of the string. The present study aims to explore the question of means-end comprehension in bumblebees when tackling string-pulling tasks. We conducted eight horizontal string-pulling experiments. These experiments were meticulously designed to manipulate factors such as string color and spatial arrangement during both the training and testing phases. Firstly, bumblebees without string-pulling experience were tested to discriminate between strings connected to a target containing the reward and disconnected strings. In another set of experiments, we examined whether bumblebees with string-pulling experience would discriminate between connected and disconnected strings. Furthermore, we changed the color of strings in training to determine whether bees generalize features learned to solve tasks with different colored strings. In another experiment, a black tape was covered between the strings and the reward, to exclude that bees could see the familiar image during string-pulling progress. Finally, to further verify whether bumblebees choose strings through image learning, the straight strings were changed to coiled so that the image of the strings is distinct from those in training.

Results

In Experiment 1, we evaluated whether uninformed bumblebees with no string-pulling experience could discriminate between connected and disconnected strings. Bees were trained to retrieve a yellow flower (without a string) containing sugar water from under a transparent table (***Movie supplement 1***). In the test, bees had two different flowers to choose from, one with a connected string and the other with a disconnected string. Bumblebees showed no preference for either string during the test [n = 21, generalized linear model (GLM): 95% CI = -0.09 (-0.48 to 0.29), Z = -0.48, P = 0.629; ***Figure 1***], suggesting that there is no spontaneous comprehension of the significance of the gap, and that any preference for connected strings would have to be acquired through training.

We next examined whether bumblebees with string-pulling experience would

discriminate between connected and disconnected strings. In Experiment 2, bees were first trained to retrieve yellow flowers from under a transparent table by pulling an attached white string (***Movie supplement 2***). After training, bees were presented with two different flowers: one was a connected to a string and the other had a disconnected string. We found that 13 of 18 bumblebees chose the connected string as their first choice in the test (***Table 1***). Bees selected the connected strings (76 ± 4%) significantly more than the disconnected strings [n = 18, GLM: 95% CI = 1.06 (0.78 to 1.33), Z = 7.56, P < 0.001; ***Figure 1***]. In addition, bees spent much more time attempting to pull the connected strings (94.67 ± 13.19 s) than the disconnected strings (13.61 ± 4.59 s) [n = 18, generalized linear mixed model (GLMM): 95% CI = 0.06 (0.02 to 0.10), t = 3.08, P = 0.002; ***Figure 2***].

In Experiment 3, we trained another group of bees with the same procedure as in Experiment 2, but the disconnected string pointed to the flower in the test (there was no lateral displacement between the disconnected string and flower in the test; Figure 2). Again, we found that, most bees (17/18) choose the connected string as their first choice (Table 1). The percentage of the bees pulling connected strings (79 ± 4%) was significantly above chance level [n = 18, GLM: 95% CI = 1.21 (0.88 to 1.55), Z = 7.08, P < 0.001], and bees spent longer times manipulating connected strings (79.59 ± 10.15 s)[GLMM: 95% CI = 0.08 (0.04 to 0.13), t = 3.48, P < 0.001; ***Figure 2***].

To explore whether bees simply memorized the visual display of the “lollipop shape” of a string connected to a flower during training with a given color combination, we then asked whether bees can generalize from the string color used during training. Bumblebees were trained with green strings (***Movie supplement 3***) or blue strings (***Movie supplement 4***) connected to flowers. If the bees had the ability to generalize the function of strings, this color change should not affect their ability to discriminate connected and disconnected strings. Overall, changing the color of the string in training reduced the accuracy of the choice, but the bees still maintained the basic discrimination at well above chance levels when bees trained with green strings (61 ± 5%) [n = 10, GLM: 95% CI = 0.54 (0.28 to 0.80), Z = 4.11, P < 0.001], and 7/10 bees selected the connected string in the first choice (Table 1). In addition, the duration of pulling connected strings (47.79 ± 9.91 s) was significantly longer than

disconnected ones (24.78 ± 6.05 s) [n = 10, GLMM: 95% CI = 0.10 (0.02 to 0.18), t = 2.44, $P < 0.05$; ***Figure 2***]. In this sense, bees might possess the ability to generalize string color from the originally learned stimulus. A similar result was found in bees trained with blue strings. The percentage of bees pulling connected strings was significantly higher than the chance level [n=16, GLMM: 95% CI = 0.60 (0.30 to 0.90), Z = 3.90, $P < 0.001$; ***Figure 1***], and the duration data also indicate that the bees prefer pulling connected strings [n=16, linear mixed-effects model (LMM): 95% CI = 0.03 (0.01 to 0.05), t = -66.91, $P < 0.001$; ***Figure 2***].

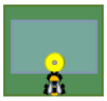
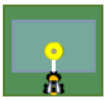
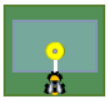
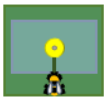
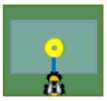
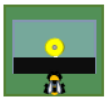
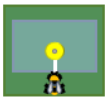
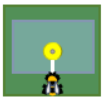
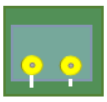
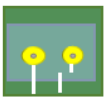
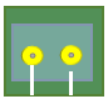
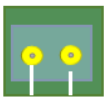
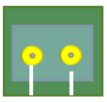
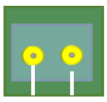
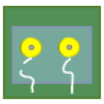
The question of whether animals rely on perceptual feedback during string pulling has been tested with occluders between the string and the reward in a variety of other species (Taylor *et al*., 2010; Gaycken *et al*., 2019; Molina *et al*., 2019; Wakonig *et al*., 2021). We trained the bees with transparent tables and strings covered by black tape (***Movie supplement 5***), hypothesizing that bees were not able see the image when they were pulling the strings. Interestingly, ten out of fifteen bees pulled the connected string in their first choice (***Table 1***). The percentage of the bees pulling connected strings (82 ± 3%) was significantly higher than chance level [n=15, GLM: 95% CI = 1.31(1.00 to 1.62), Z = 8.23, $P < 0.001$; ***Figure 1***], and the duration data also indicate that the bees preferred pulling connected strings [n=15, GLMM: 95% CI = 0.10 (0.03 to 0.16), t = 2.88, P = 0.004; ***Figure 2***]. It makes sense because the bees could see the “lollipop shape” once they pulled it out from the table.

So far, our results show that bumblebees could have been using image matching to discriminate connected from disconnected strings in the test. We therefore performed further experiments to test this hypothesis. Bumblebees were trained with the same procedure, but the connected strings were coiled in the test. Bees failed to choose the connected strings when strings were coiled. We observed no difference in the percentage of pulling connected strings compared with chance level [n=20, GLM: 95% CI = 0.05 (-0.14 to 0.24), Z = 0.49, P = 0.60; ***Figure 1***]. There was also no significant difference between the duration of bees pulling the connected strings and disconnected strings [n=20, likelihood ratio test: P = 0.52; ***Figure 2***], suggesting that bumblebees did not recognize the continuity of coiled strings. Another group of bees were trained with straight strings, while both connected and disconnected strings were

coiled in the test. Similarly, no differences were found in percentage [n=19, GLM: 95% CI = -0.06 (-0.71 to 0.59), Z = -0.64, *P* = 0.87] and duration [n=19, likelihood ratio test: *P* = 0.86; ***Figure 2***] of pulling each string.

Latency to the first choice was defined as the latency to initiate pulling the string after the bee entered the set-up. The latency of the bees that were trained with blue strings (684.33 ± 105.45 s) was substantially longer than that of bees which were trained with white strings and tested with straight strings (***Figure 3***). The reason might be attributable to bees' searching time for the familiar string color or neophobic response (Muller *et al*., 2010), because the blue strings during training were changed to white strings in test, which the bees had not encountered before.

Table 1. The number of total choices and bees that chose connected strings at first choice.

Training program								
Test								
Number of choices (mean ± SE)	5.10 ± 0.54	15.00 ± 1.53	15.56 ± 2.16	12.10 ± 2.19	11.63 ± 1.66	15.87 ± 2.05	20.60 ± 1.80	14.37± 2.82
Number of bees choosing continuous strings at first choice/N	10/21	13/18	17/18	7/10	14/16	10/15	11 /20	10/19

Note: The numbers before the slash are the numbers of bumblebees pulling connected strings on the first choice, and the numbers after the slash are the total number of tested bumblebees. N is the total number of the bees.

Discussion

Our results show that: (i) bumblebees require experience with string pulling to distinguish between connected and disconnected strings; (ii) bumblebees are able to generalize features learned during string-pulling training to solve a task with different colored strings; (iii) bumblebees solve string-pulling tasks through image matching.

The results suggest that bumblebees require experience to recognize interrupted strings and acquire a preference for connected ones. This corroborates previous

findings that most bees failed to solve single string-pulling tasks without previous training (Alem *et al*., 2016). Since the vast majority of animals, including dogs (Osthaus *et al*., 2005), cats (Whitt *et al*., 2009), western scrub-jays (Hofmann *et al*., 2016) and azure-winged magpies (Wang *et al*., 2019) are fail in such tasks spontaneously. A complete comprehension of the functionality of strings is rare in the animal kingdom, and has so far only been found in parrots, ravens and primates (Heinrich, 1995; Schuck-Paim *et al*., 2009; Krasheninnikova *et al*., 2013; Mayer *et al*., 2014).

Our findings suggest that bumblebees acquire their preferences for flowers with connected strings at least in part by learning the visual appearance of the "lollipop shape" present during training. Trained bees may have memorized this image as a predictor of reward and applied it to solve novel string-pulling tasks. Bees often need to match memorized images of flowers to currently visible flowers while foraging in the wild (Chittka *et al*. 1999; Giurfa, 2003). In addition, bumblebees are able to generalize features learned to solve tasks with different colored strings. Color generalized learning has also been observed in bumblebees solving other non-natural tasks (Ings *et al*., 2012). For example, bumblebees learned to roll a ball that matched the color of a goal, and the performance in the generalization task depended on the colors used in the training (Chow *et al*., 2022).

Rather than relying on means-end comprehension, most animals likely use simpler associative strategies to solve string-pulling tasks, as observed in the bumblebees in the present study (Jacobs & Osvath, 2015; Wakonig *et al*., 2021). Empirical evidence from several vertebrates has shown that success in object use does not necessarily imply causal understanding; rather, it involves abstracting simple rules based on observable features of the physical task at hand (Seed *et al*., 2006; Schuck-Paim *et al*., 2009; Herrmann *et al*., 2008; Gagne *et al*., 2012). In several vertebrate string-pulling studies, animals relied on a "proximity rule" in most cases, choosing to pull the strings closest to the reward, regardless of their connectivity (Whitt *et al*., 2009; Wang *et al*., 2021).

In conclusion, our results suggest that even though bumblebees may not initially understand the causality of string-pulling, they can match the image of the strings

connected to flowers, and rely on associative mechanisms to remember the previously visited stimuli. Bumblebees, whether with or without string-pulling experience, do not appear to understand the value of strings to target objects. This negative result does not necessarily mean that bumblebees are entirely unable to comprehend the link between a means and an end, but our results suggest that for the paradigms tested here, such comprehension is not required.

Materials and methods

Animals and experimental arena

The experiments were conducted from May 2021 to February 2023. Seventeen colonies of bumblebees (*Bombus terrestris*) each containing a queen were obtained from commercially available stocks provided by a distributor in China (Biobest, Belgium N.V.; Shouguang Biotechnology Co., Ltd; Biobest Shouguang Biotechnology Co., Ltd). Bees were housed in a plastic nest box (29 × 22.5 × 13.3 cm [L × W × H]) that was connected to a flight arena (100 × 75 × 30 cm [L × W × H]) by an acrylic corridor (25 × 3.5 × 3.5 cm [L × W × H]; ***Figure 4A***). The flight arena was covered with an acrylic lid. Three sliding doors were placed along the corridor, allowing the experimenter to control bees' access to the arena. The floor of the flight arena was painted green, which provided a smooth surface and high-contrast pattern visual panorama between the strings and background. Outside of experiments, the colonies were provided with 20% (w/w) sucrose solution from a gravity feeder placed in the center of the arena, and with ~5g commercially obtained pollen (Changge Yafei Beekeeping Professional Cooperative, China) every other day. All the training programs and tests were conducted in the flight arena between 9 am and 7 pm under light (12 : 12 h) at room temperature (23 ± 4℃). Illumination was provided by fluorescent lighting (YZ36RR, 36W, T8/765, FSL, China) fitted with high-frequency ballasts (T8, YZ-36 W, 50 Hz, FSL, China) to generate lighting above the bee flicker fusion frequency (Skorupski & Chittka, 2010).

Before each experiment, bees were first pretrained to find sucrose solution (50%, w/w) in yellow artificial flowers (3 cm diameter yellow discs with an inverted Eppendorf cap at the center; henceforth "flowers"), which were randomly located in

the arena with sucrose solution (50%, w/w) in the Eppendorf cap (***Figure 4B***). Bees that seemed to forage with regularity were number-tagged for individual identification. In detail, one forager bee was transferred to a cylindrical cage (diameter=3.8 cm, length=7.7 cm) with a sponge plunger, and a numbered tag (Bienen-Voigt & Warnholz GmbH & Co. KG, Germany) was glued to bee's thorax for individual recognition (***Figure 4B***).

General Methods: For each experiment, bumblebees were trained to retrieve a flower containing, in the central well, 25 microliters of 50% sucrose solution from underneath a transparent acrylic table [0.6 cm above the ground, 15 × 10 × 0.4 cm (L × W × H); henceforth "table"]. For Experiment 1, bees were trained in a stepwise manner – Step 1, 50% of the flower covered by the transparent acrylic table, Step 2, 75% of the flower was covered; Step 3, 100% of the flower was covered (***Figure 4B***). For Experiment 2-8, the first three steps are similar to Experiment 1, but the flowers were connected to strings (length = 4.5 cm, diameter = 0.3 cm), and bees were trained with the fourth step: 2 cm strings were attached to the flower and accessible from outside the table. The bees received rewards five times in each of the steps, except for the last step. The training phase was completed when a bee pulled the strings and drank from the flowers twenty times after the first occurrence of string pulling during the last step (***Figure 4B***). For each test, bees were individually tested in the arena and presented with four transparent tables. Two options were placed under each table, parallel to each other, and perpendicular to the long side of the table. To avoid developing a side bias, the position and direction of the strings varied randomly from left to right for each table. During tests, both strings were glued to the floor of the arena from prevent the air flow generated by flying bumblebees' wings from changing the position of the string. Each forager bee was used only once, and the tested bees were removed from the nest and then placed in the freezer to be euthanized. The strings and flowers used were discarded after each test, to prevent the use of chemosensory cues. All the experiments were videotaped with an iPhone 12 (Apple, Cupertino, CA, USA) placed above the arena. The choice and duration of the bees pulling the connected or disconnected strings were recorded. A choice was recorded when a bee used her legs or mandibles to pull the connected or disconnected strings.

The test was terminated when the bee stopped engaging with the tables, flowers and strings for more than one minute, and a testing session lasted a maximum of 30 min.

Experiment 1: Do bumblebees without string-pulling experience discriminate between connected and disconnected strings?

Bumblebees (n=21) were trained with artificial flowers under a transparent table. Initially, half of the flower was placed under the table, and the central Eppendorf cap (containing the sucrose solution reward) at the edge of the table so that the bees could access sugar water directly without moving the flower (***Figure 4B***). In the final step, the edge of the flower was aligned with the table, and bees had to pull the edge of the flower to obtain the reward (***Figure 4B***). In the test, four transparent tables were placed on the arena floor, and two artificial flowers were placed 3 cm apart under each table, with one connected to a string (length=2.5 cm, including 1 cm accessible from outside the table, diameter=0.3 cm), while another flower was presented with a 1.5 cm string with a cm gap between the string segment and the flower (***Figure 5***). If the bees prefer to pull the connected strings, this would indicate that bees naturally recognize the connectivity of strings in this task.

Experiments 2-3: Do bumblebees with string-pulling experience discriminate between connected and disconnected strings?

In Experiment 2, bumblebees (n=18) were trained to pull a white string (length = 4.5 cm, diameter = 0.3 cm) attached to the yellow artificial flower that was placed under a transparent table, following the stepwise string-pulling training protocol used by Alem *et al*. (2016) with some modifications. Briefly, selected bees were trained to pull the string when the flowers were gradually positioned further under the table, finally, the strings protruded 2 cm outside the table edge (***Figure 4B***). In the test, four tables were placed on the arena floor, two artificial flowers were placed 3 cm apart under each table, with one flower connected to a long string (length=4.5 cm), whereas another flower was attached to a short string (length=1 cm), and a 3.5 cm string segment (2 cm accessible from outside the table) was positioned with a lateral displacement. The short string and string segment were placed along parallel lines and

1.5 cm apart from each other (***Figure 5***). The position of the string segment was randomly assigned on the left or right side of the short string.

In Experiment 3, a further 18 bumblebees were trained with the same procedure as Experiment 2. In the test, four tables were placed on the arena floor, two artificial flowers were placed 3 cm apart under each table, with one connected to a long string (length=4.5 cm), a 3.5 cm string segment was placed along with another flower, and a 1 cm gap was created between the string segment and flower (***Figure 5***). If the bees show a preference for the strings connected to flowers, this would indicate that bees with string-pulling experience can recognize connected and disconnected strings.

Experiments 4-5: Do bumblebees generalize when string colors differ between training and testing?

In Experiment 4, to further verify whether bees can generalize from the string color used during training, bees (n=21) were trained with yellow flowers connected to green strings (length=4.5 cm), such that strings were visually different from the white strings in the test (***Figure 5***). The training method was the same as Experiment 2 and the test protocol was the same as for Experiment 3. If the bees prefer to pull the connected strings, indicating that bees generalize the color of the strings in the training. In Experiment 5, bumblebees (n=16) were trained with yellow flowers connected to blue strings (length=4.5 cm) (***Figure 5***). The training method was the same as for Experiment 2. The test protocol was the same as for Experiment 3. If the bees prefer to pull the connected strings, this indicated the bees can generalize from the string color used during training.

Experiment 6-8: Do bumblebees use image matching to discriminate connected versus disconnected strings?

In Experiment 6, bumblebees (n=15) were trained with a transparent Perspex table where the edge on which the strings protruded was covered with opaque black tape (15 × 2.5 cm [L × W]) **(*Figure 5*)**. This was to ensure that the bees could not see the familiar “lollipop shape” while pulling strings. The test protocol was the same as

for Experiment 3. If the bees prefer to pull the connected strings, this would indicate that bees memorize the arrangement of strings-connected flowers in this task.

In Experiment 7, bumblebees (n=20) were trained with the same protocol as for Experiment 2. In the test, two artificial flowers were placed 3 cm apart under each table, with one flower connected to a coiled string (length=20 cm, four turns), this pattern was visually different from a straight string during training. Another flower was attached to a short string (length=1 cm), a 2.5 cm straight string segment was placed along the short string (***Figure 5***), and a 1 cm gap between the short string and the 3.5 cm string segment was presented. If the bees show a preference for the straight strings (same arrangement in training) over the coiled string or show no preference for either of the two strings, this would indicate that they use image matching to solve this task.

In Experiment 8, bumblebees (n=19) were trained with the same protocol as for Experiment 2. In the test, two artificial flowers were placed under each table, with one flower connected to a coiled string (length=8 cm, one turn). The other flower was attached to a short string (1 cm), a coiled string segment (length=6 cm, one turn) was placed along the short string, and there was a 1 cm gap between the flower and the 6.5 cm coiled string segment (***Figure 5***). The two coiled strings in the test were visually different from a straight string in training. If bumblebees use image matching to discriminate connected and disconnected strings, they will exhibit no preference for either of the two strings.

Statistical Analyses

All statistical analyses were conducted with R version 4.2.0. Bees identity and colony were analyzed with likelihood ratio tests. The percentage of bees choosing connected strings was analyzed with generalized linear models (GLM) [R Development Core Team, lme4 package] with binomial distribution and logit function and the number of total choices as weights (Bates *et al*., 2015). The number of bees choosing connected string as the first choice was analyzed with the binomial test. The duration of pulling different kinds of strings were compared with generalized linear mixed models (GLMM) or linear mixed-effects models (LMM). The significance of

the fixed effect was analyzed using likelihood ratio tests and models were constructed as follows: the duration of the bee pulling the strings (string type as a fixed effect). Latency to the first choice of each bee was recorded. Latency across experiments was compared with GLM in which experiment was set as fixed effect with Gamma distribution and linked with log function. The significance of fixed effect was also tested with likelihood ratio test. Multiple comparisons among experiments were conducted with emmeans package (Lenth *et al*., 2024).

Acknowledgments

We thank Jian Chen (Usda-Ars, Biological Control of Pests Research Unit, Stoneville, Mississippi) for valuable comments and suggestions on the early version of the manuscript.This work was supported by the National Natural Science Foundation of China (32301292) and National Natural Science Foundation of China (32271888). Cwyn Solvi was supported by a Templeton World Charity Foundation project grant (TWCF-2020-0539).

Authors' contributions

Chao Wen, Conceptualization, Resources, Data curation, Formal analysis, Supervision, Funding acquisition, Investigation, Writing-original draft, Project administration, Writing-review and editing; Yuyi Lu, Resources, Data curation, Formal analysis, Investigation, Methodology, Writing-review and editing; Cwyn Solvi, Writing-review and editing, Methodology, Writing-review and editing; Cai Wang, Xiujun Wen, Shikui Dong, Junbao Wen Resources, Writing-review and editing; Fei Peng, Lars Chittka, Methodology, Funding acquisition, Validation, Visualization, Project administration;

Competing interests

We declare we have no competing interests.

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Figure legend

Figure 1. Bumblebee's preferences for continuous strings in different string-pulling experiments. Percentage of pulling connected strings compared with chance level (50%). Median, interquartile range and range are given. Boxes show the 25th percentile, 50th percentile (median), 75th percentile. The dashed line represent chance level (50%) and the circles indicate individual bees' data points. *** indicates $P<0.001$.

Figure 2. Duration of bumblebees attempting to pull the strings across experiments. Median, interquartile range and range are given. Boxes show the 25th percentile, 50th percentile (median), 75th percentile. Circles indicate individual bees' data points. *** - $P<0.001$; ** - $P<0.01$; * - $P<0.05$.

Figure 3. Latency to the first choice in different experiments. Median, interquartile range and range are given. Boxes show the 25th percentile, 50th percentile (median), 75th percentile. Circles indicate individual bees' data points. Different letters indicate significant differences ($P<0.05$).

Figure 4. Experimental apparatus and summary of training in different experiments. (A) The experimental setup consisted of a flight arena connected to a hive via a Perspex corridor. (B) Foraging bumblebees were number-tagged, and the marked bees were trained in a stepwise manner.

Figure 5. Schemes of eight string-pulling experiments. Bumblebees were trained and tested in different situations. Two flowers were placed under each transparent table in the test, with one string connected to a flower and another was detached. For further details and descriptions of each experiment, see the text.

Supporting Information

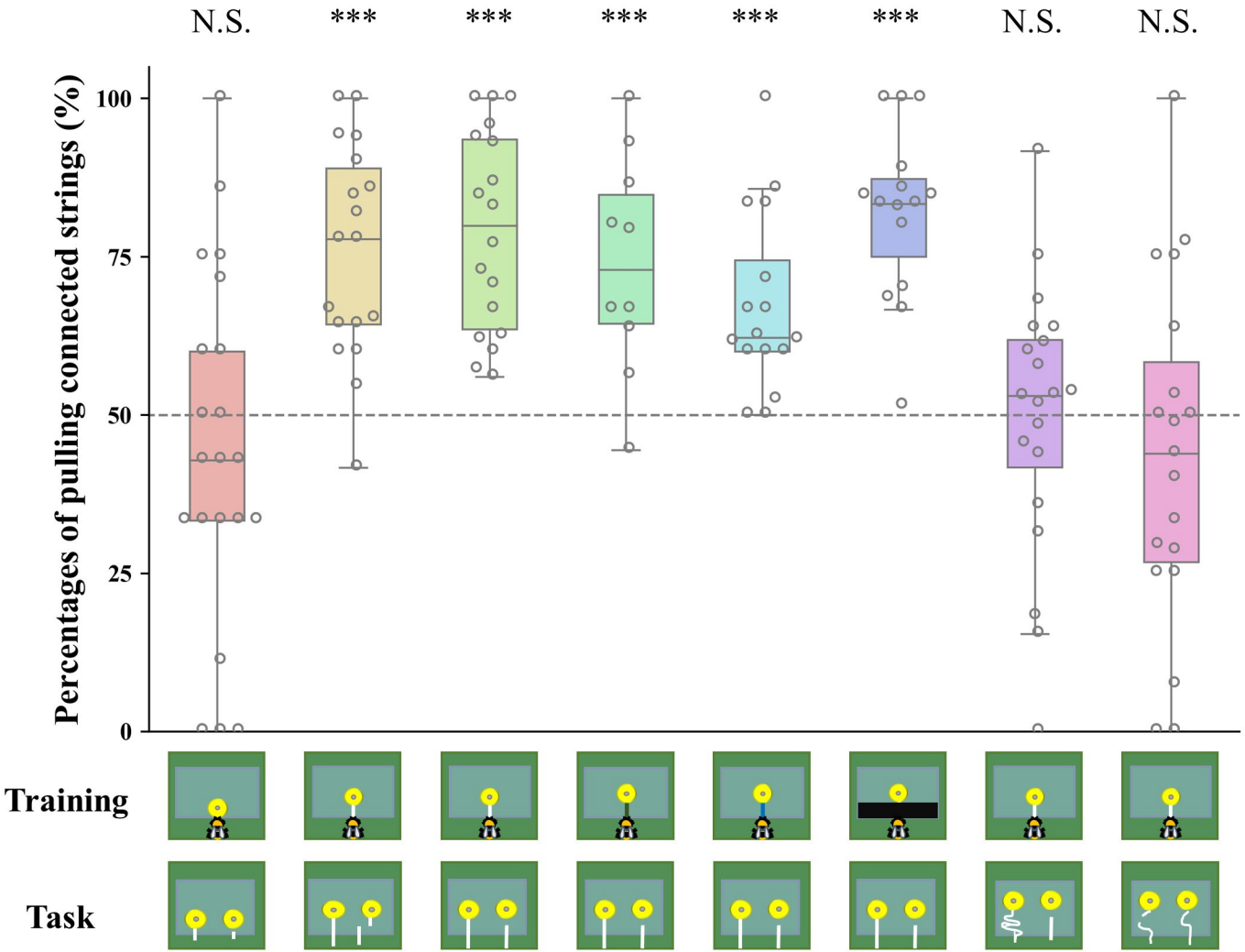
S1 Video. String pulling without string. Bumblebees were trained to retrieve a yellow flower (without a string) containing sugar water from under a transparent table.

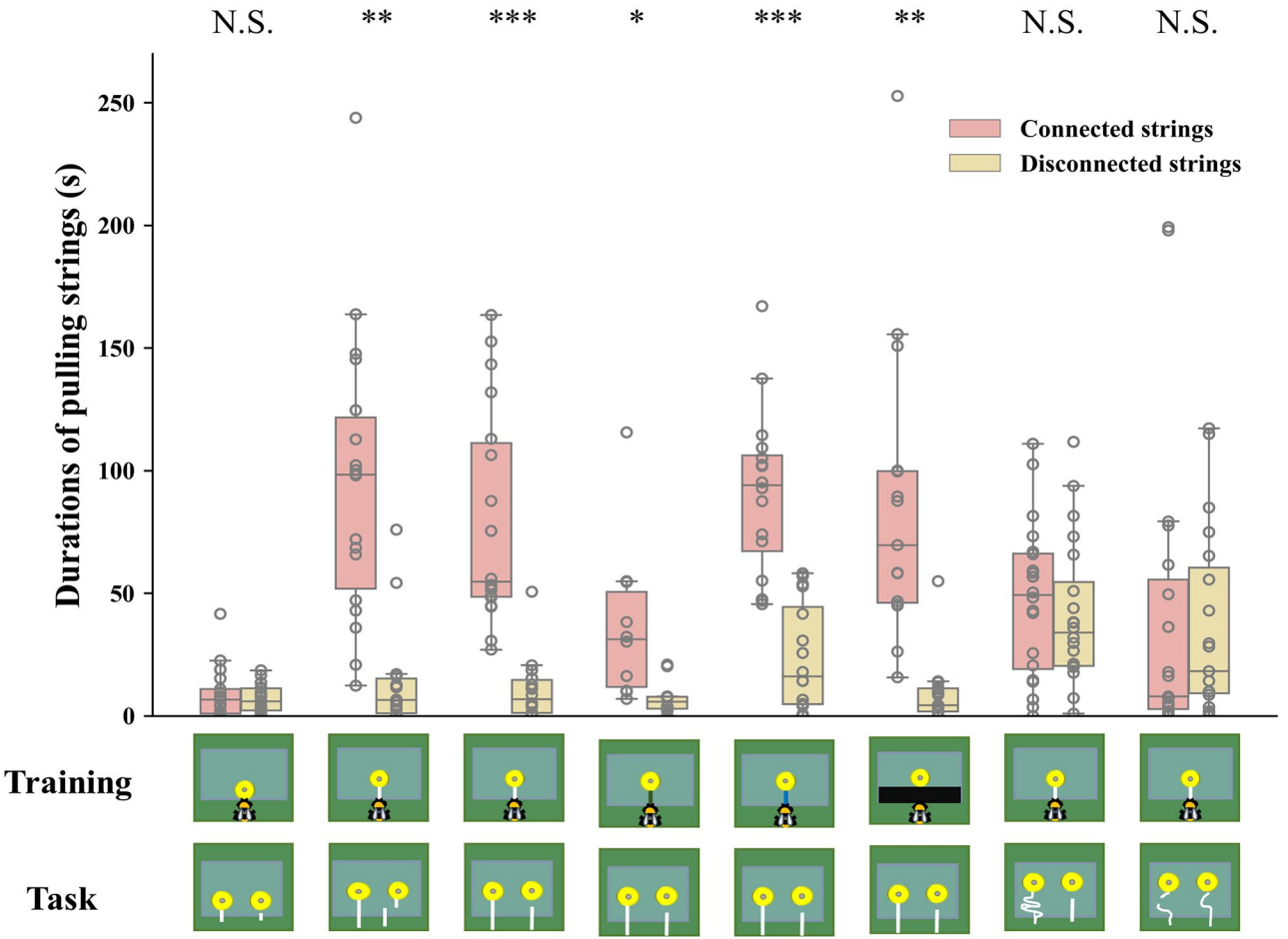
S2 Video. String pulling with white string. Bumblebees were trained to retrieve yellow flowers from under a transparent table by pulling an attached white string.

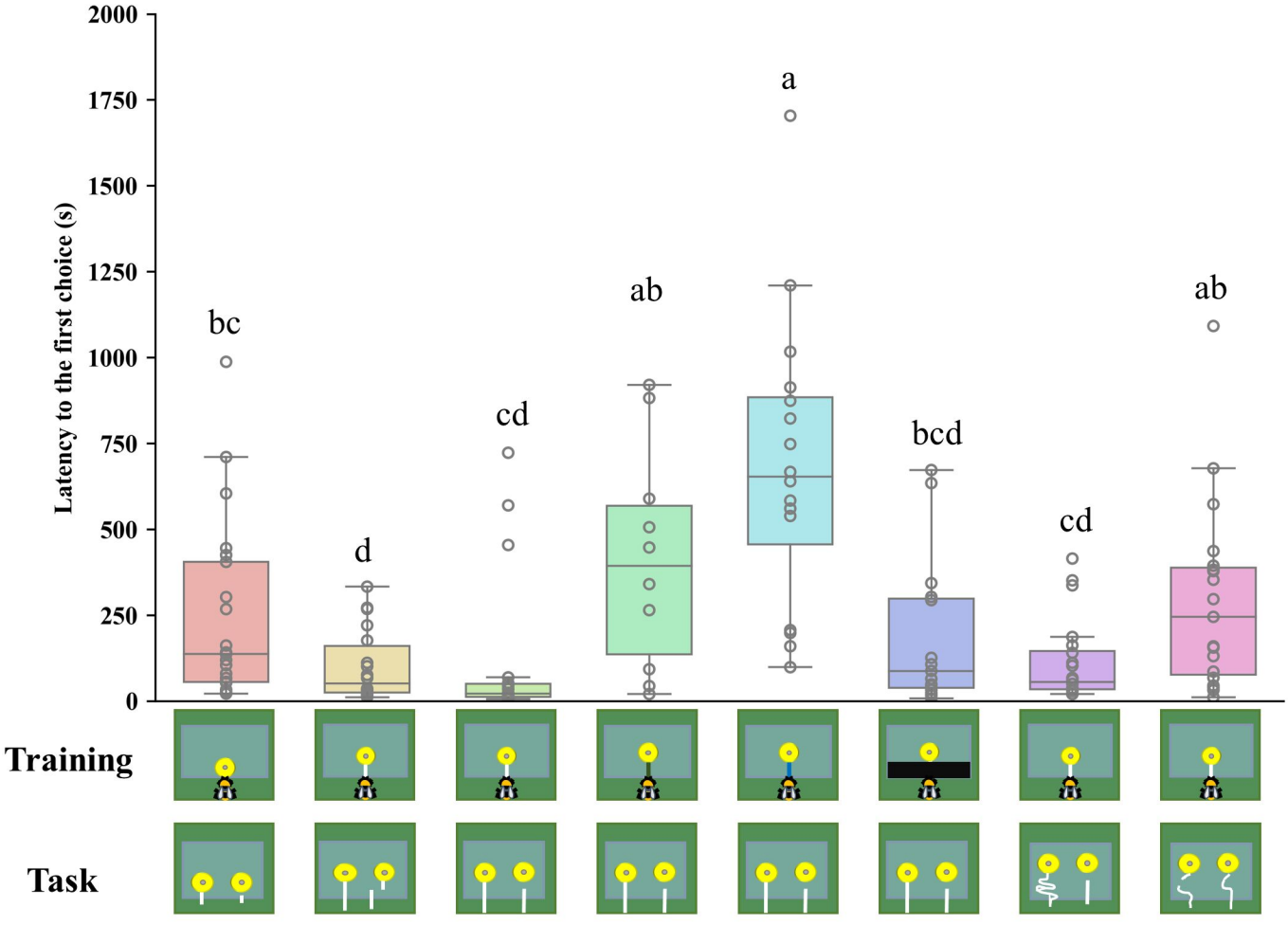
S3 Video. String pulling with a green string. Bumblebees were trained to retrieve yellow flowers from under a transparent table by pulling an attached green string. To test whether bees can generalize from the string color used during training.

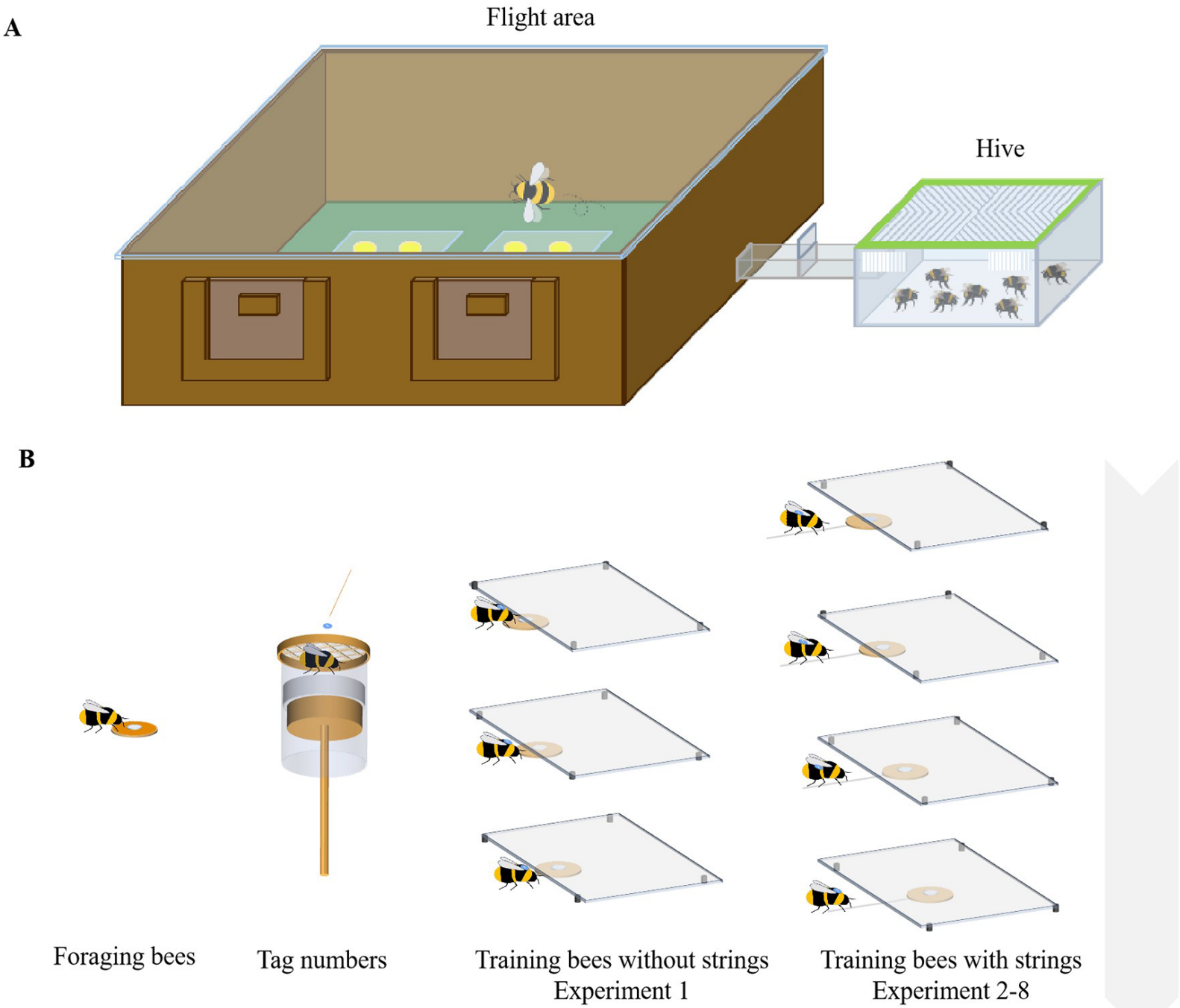
S4 Video. String pulling with a blue string. Bumblebees were trained to retrieve yellow flowers from under a transparent table by pulling an attached blue string. To test whether bees can generalize from the string color used during training.

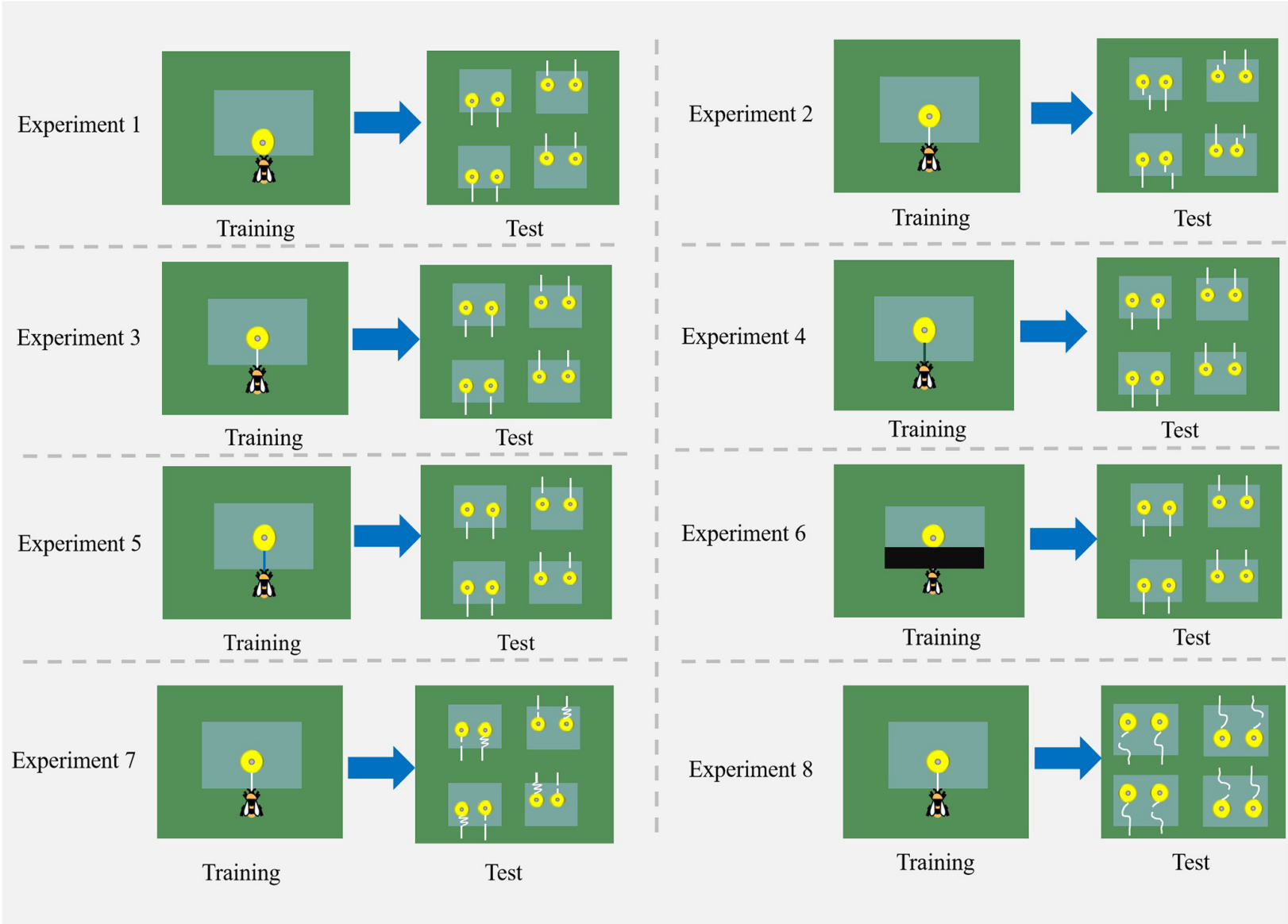
S5 Video. String pulling with a occluder between the string and the reward. Bumblebees were trained to retrieve yellow flowers from under a transparent table covered by black tape, hypothesizing that bees were not able see the image when they were pulling the strings.


N.S.
***
***
***
***
***
N.S.
N.S.
Percentages of pulling connected strings (%)
100
75
50
25
0
Training
Task


N.S.
**
***
*
***
**
N.S.
N.S.
Durations of pulling strings (s)
250
200
150
100
50
0
Connected strings
Disconnected strings
Training
Task


Latency to the first choice (s)
2000
1750
1500
1250
1000
750
500
250
0
bc
d
cd
ab
a
bcd
cd
ab
Training
Task


A
Flight area
Hive
B
Foraging bees
Tag numbers
Training bees without strings
Experiment 1
Training bees with strings
Experiment 2-8


Experiment 1
Training
Test
Experiment 2
Training
Test
Experiment 3
Training
Test
Experiment 4
Training
Test
Experiment 5
Training
Test
Experiment 6
Training
Test
Experiment 7
Training
Test
Experiment 8
Training
Test