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Incidental memory in dogs (*Canis familiaris*): adaptive behavioral solution at an unexpected memory test.

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Abstract

Memory processing in nonhuman animals has been typically tested in situations where the animals are repeatedly trained to retrieve their memory trace, such as delayed matching to sample, serial probe recognition, etc. In contrast, how they utilize incidentally formed memory traces is not well investigated except in rodents. We examined whether domestic dogs could solve an unexpected test based on a single past experience. In Experiment 1, leashed dogs were led to 4 open, baited containers and allowed to eat from 2 of them (Exposure phase). After a walk outside for more than 10 min, during which time the containers were replaced with new identical ones, the dogs were unexpectedly returned to the site and unleashed for free exploration (Test phase). Eleven out of 12 dogs first visited one of the containers from which they had not eaten. In Experiment 2, two containers had food in them, one had a nonedible object, and the last one was empty. Dogs visited all 4 containers and were allowed to eat one of the food rewards in the Exposure phase. In the Test phase, unleashed dogs first visited the previously baited container from which they had not eaten significantly more often than chance. These results demonstrate that in an unexpected test dogs may retrieve “what” and “where” information about seen (now invisible) items from incidental memory formed during a single past experience.

Keywords: incidental memory, dogs, memory retrieval, episodic memory

Introduction

Memory has been one focus of comparative cognitive research and large amount of data have accumulated. Topics of behavioral studies include short-term retention, list memory and serial position effect, prospective and retrospective coding, directed forgetting, and memory capacity, mostly in rats, pigeons, and nonhuman primates (see Shettleworth, 2010, for review). More recent developments include episodic memory in food-caching birds (e.g., Clayton & Dickinson, 1998) and rodents (e.g., Babb & Crystal, 2005; Eacott, Easton, Zinkivskay, 2005) and metamemory in nonhuman primates (e.g., Fujita, 2009; Hampton, 2001). These studies have shown that multiple functions of memory systems are shared between humans and nonhuman animals.

To test functions of memory systems we need subjects to utilize their memory trace in tests. We can easily verbally instruct humans to do this. But with nonhumans, we typically train them repeatedly to base their responses on their memory trace. Thus the animals are "told" to encode study items for subsequent use through repeated training.

However, humans not only use memory traces of actively encoded study items, they also rely on memory traces formed without active encoding. One such instance is implicit memory, often identified using a priming paradigm in which, for an example, a very brief, even subliminal, presentation of a stimulus leads to better recognition of an item that is phonetically or semantically related (e.g., Schacter, 1987 for review). In this case, the particular memory-based behavior is not a consequence of active retrieval of previous information but of a rather automatic and uncontrollable function inherent to the memory system.

Another example is retrieval of previous episodes by various methods. For instance, we often try to recall the directions to a specific destination when we have a vague memory that we have visited a place before. Ultimately we might recall all of the events we experienced there previously.

In both cases above, there is no active attempt to encode what happens at a given time and place. This incidental nature is one of the key properties of the human episodic memory system. The other key property of episodic memory is that it contains the “what, where, and when” of the event in an integrated fashion (Tulving, 2002; 2005).

The nature of the memory system that handles incidental memory is important, when comparing humans and nonhumans, in particular for elucidating to what extent memory functions depend on language and are unique to the human brain. Unfortunately, however, how nonhumans utilize incidentally formed memory traces has not received much attention except in rodents tested in the classic “object-in-place” paradigm (Ennaceur & Delacour, 1988).

In this paradigm, after being exposed to several objects in the enclosure, animals are tested in a novel situation where they find novel objects or familiar objects in novel locations. Rodents would more often explore novel objects or moved objects than familiar ones. Various application of this procedure has been conducted for the effects of brain lesion (e.g., Eacott & Norman, 2004; Easton, Zinkivskay & Eacott, 2009; Li & Chao, 2008), drug administration (e.g., Kart-Teke, et al., 2006), and genetic modification (e.g., Good, Hale, & Staal, 2007) on this memory performance. Because no active encoding is forcibly required in the exposure phase, this procedure may be viewed as testing incidental memory. However, as the exploration in the test phase is induced by stimulus change, this procedure could be also viewed as testing detection of such change in stimulation, not as active retrieval of the incidentally formed memory of previous episodes.

Eacott, Easton, and Zinkivskay (2005) nicely eliminated this possibility. Rats explored objects placed in an E-shaped maze. The middle arm of E was the start arm and two distinctive objects (A and B) were placed at the end of side arms. The placement of the objects A and B was reversed depending on the color and the texture of the floor of the maze. After exploration in both conditions, the rats were exposed to one of the objects, A or B, in their home cage. Then the rats explored the maze again. They tended to go into the arm where they could find the relatively more novel object that they had not seen in the home cage. Because the animals were unable to see the object at the end of side arms from the position where they made their first turn, the rodents had to retrieve their memory trace formed at the first exploration.

Investigation into such incidental memory process in other groups of animals has been scarce. Among the few relevant literatures, Zentall, Clement, Bhatt, & Allen (2001) trained pigeons to choose color A after pecking at stripe A and to choose color B after no pecking at stripe B. Next they learned to peck at a novel color C and not to peck at color D. In the test that followed, the pigeons were suddenly asked to choose color A or B after being exposed to either color C or D. They tended to choose color A after pecking at color C and to choose color B after not pecking at color D. This suggests that the pigeons recalled their pecking episodes, at least for memory traces within working memory formed in the immediate past.

Using an artificial sign system, Mercado, III, Murray, Uyeyama, Pack, & Herman (1998) tested whether bottlenosed dolphins could repeat a previously performed action sequence such as “swim-circle-with_mouth_open.” Dolphins had been taught two special commands: “repeat” and “creative.” To be creative, they had to perform a sequence of actions not previously performed in the last several trials. When “repeat” followed “creative,” the dolphins had to recall the action sequence that they had just ”created” in order to be correct. One dolphin, Elele, was correct in 3 out of 4 test trials. Elele may have episodically recalled her own experience. However, it is also possible that Elele had learned to memorize her performance through intensive past training of "repeat" sign.

More species, particularly non-rodents, should be tested for their ability to retrieve incidentally formed memory trace in order to answer such questions as how widespread this ability is in the animal kingdom, how it has evolved, whether it is limited to exploration of environments, what is the nature of this ability in nonhumans, and how it is related to human episodic memory. In this report, we present a new and simpler method to test incidental memory in nonhuman animals and provide first data on this capacity in domestic dogs. Dogs have been trained and tested for various memory tasks involving spatial memory and word learning (e.g., Fiset 2007; Fiset et al. 2003; 2007; MacPherson & Roberts 2010; Pilley & Reid, 2011). Here we test retrieval of the memory incidentally formed in a single past experience, without change in external stimulation; that is, we test behavior by dogs supposedly driven by their internal memory.

Experiment 1

Participants

Twelve domestic dogs (*Canis familiaris*) (3 males and 9 females) and their owners participated voluntarily. Participant dogs were of various breeds and ranged in age from 8 months to 7 years (see Table 1). All of the dogs and owners were unfamiliar with the test room and were naive to this memory test.

Table 1 about here

Apparatus

For each dog, 2 identical sets of 4 open containers, different in various dimensions such as shape, size, color, etc., were prepared. The apperance of each container varied but all were about 25 - 30 cm in diameter, width and length. The depth was between about 10 - 15 cm. The bottom shape was either round or rectangular and the color was either white, pink, red, blue, brown, or yellow. The material was either plastic or cardboard. Four small pieces of each dog's favorite food such as dog biscuits, jerky, and chicken meat were used as rewards. The rewards were small enough for the dogs to consume instantly just by one pick. The test room was a ca. 6 x 7 m office space in a building located in the city of Kyoto.

Procedure

Exposure Phase: The 4 containers were arranged so that they made a fan shape with a radius of ca. 1.5 m (Fig. 1a) from a mark on the floor (X in Fig. 1a). The experimenter (E) placed one piece of food in each container. Then E asked the owner (O) to take the dog by the leash to the mark. Once the dog was there and stationary, E asked O to lead the dog to each container one by one in clockwise or counterclockwise order and to allow the dog to eat two rewards specified in advance (Fig. 1b). E also asked O to prohibit the dog from eating the remaining rewards. Thus the dog checked (and often tried to collect) all the rewards but was allowed to eat only two of them. The containers the dog was allowed to eat from will be hereafter referred to as "baited-eaten" containers and those not allowed to eat from will be referred to as "baited-uneaten" containers. The combinations of the location of permitted food (6: 2 combinations out of 4) and the visiting order (2: clockwise or counterclockwise) made for 12 types of exposure trials. Each participant received one trial type without repetition.

Delay Phase: Immediately after the Exposure Phase, E asked O to take the dog out of the room for a walk of at least 10 min on the street. E also asked O to take all of his/her personal belongings as if going back home; E also said "Bye-bye" to the dog (Fig. 1c). This procedure was followed to minimize the possibility that the dogs would expect to come back to the test site. During this delay period, E replaced the containers with the identical set in exactly the same layout, but no food was placed in any container, to control for olfactory clues. The actual delay ranged from 12 to 18 min, which is thought to be beyond the human working memory capacity for retaining such an episode.

Test Phase: Immediately after being brought back to the room, the dog was unleashed at the mark on the floor and encouraged by O to go (Fig. 1d). The dog was thus free to visit the containers, which were now replaced and empty, in any order. E asked the owner not to look at the dog or the containers during the test but to look at the wall ahead or else to turn around and face away. The trial ended when the dog either a) visited all of the containers, b) spent at least 3 sec 2 meters or more from the test area, or c) returned to O.

Fig. 1 about here

Each dog's behavior was recorded using a portable digital camcorder (Victor GZ-MG40 or GZ-MG275) for later analyses by a second experimenter. The order of visits by each dog was recorded. A visit was defined as looking into a container, which was apparent by the dog's poking its muzzle toward the container. This behavior was obvious; two coders analyzed all the videos and the reliability was 100%.

Predictions

Two different predictions about the dogs' behavior in the Test Phase may be made. First, if the dogs' search behavior is determined through operant learning in the Exposure Phase, they should visit the containers where they obtained rewards (i.e., baited-eaten containers) before those where they did not (i.e., baited-uneaten containers). Second, conversely, if the dogs retrieve and adaptively utilize specific experiences in the Exposure Phase, they should first visit the containers where they received no reward (i.e., baited-uneaten containers), because this is the only way to collect more rewards.

Results and discussion

Eleven out of 12 dogs visited one of the baited-uneaten containers as their first choice in the Test Phase. This was well above chance, which was 0.5 ($p = 0.006$, binomial test, two-tailed). Among the 9 dogs that visited more than one container, 4 dogs visited 2 baited-uneaten containers in sequence. This was also above chance, which was 0.167 ($p = 0.048$) by a one-tailed test, which is validated by the significant visit to baited-uneaten containers in their 1st visit). Second-visit performances were slightly worse than the first probably due to extinction of their first visit of the container, meaning their first visit in anticipation of food resulted in no reward.

Thus the dogs' behavior in the Test Phase was consistent with our second prediction, supporting the view that dogs can spontaneously retrieve and utilize specific past experiences to succeed in this simple food-searching task. Operant learning in the Exposure Phase does not account for the results; that is, the dogs' Test Phase selections were not determined by simple association learning. Note also that they solved this unexpected challenge without change in external stimulation; that is, the dogs' exploration appears to have been driven purely by their memory retrieval.

The behavior of our dogs may look like radial-arm maze performances by rats (e.g., Olton & Samuelson, 1976). However, there are two important differences. First, rats in the radial-arm maze are typically familiarized with the maze in the absence of food prior to being trained on the maze. This gives a good opportunity for latent learning (Tolman & Honzik, 1930) and the rats may establish a strategy for navigating in this space. In our experiment, dogs were tested with a completely novel setup in a completely novel place. Thus, latent learning appears unlikely. Second, rats learn to collect most of the food available without revisiting arms after repeated training trials. This enables use of semantic memory (or a memorized set of visited places) rather than retrieving a previously experienced single episode. As our dogs, being naïve to this memory test, performed almost perfectly on the very first occasion, their performances are different from those of rats in the radial-arm maze, though the difference in the number of options might have to be considered.

One potential cue that might have guided the dogs' behavior is odors. However, the odors left on the containers, which the dogs had interacted with in the Exposure Phase, were completely eliminated because in the Test Phase the containers were replaced with identical counterparts but with no food present. It might be possible that the dogs utilized the odors left on the floor instead. We admit that failure to clean up the floor was our fault, though we did not notice that the dogs dropped their saliva either on the floor or the containers (note that the food was very small), nor actively marked the floor with odors. However, we suppose that the dogs had not relied on this cue because their typical response in the Test Phase was to go straight to one of the containers (see the Supplementary Video) without observable sniffing behavior. Further even if they used this olfactory clue, it does not necessarily lead to a specific prediction that the dogs would visit baited-uneaten containers first.

A second potential cue might come from how the owners controlled their dogs. However, physical control was impossible because the dogs were unleashed in the Test Phase, and no specific verbal commands were given other than "Go".

A third possibility might be that inadvertent cueing by the owner occurred, such as by eye gaze or postures might be possible, despite our request to the owners not to look at the dogs. Dogs may readily choose items indicated by human-given cues including variations of pointing gestures and head orientation (e.g., Hare et al. 1998; Lakatos et al. 2007; Miklósi & Sopron i 2006; Soproni et al. 2002. See Miklósi 2007, for a review), though they may not use very subtle cues such as eye-gaze without repeated training (Hare et al. 1998; Miklósi et al. 1998). In fact, as noted above however, our dogs typically went straight to the containers either after being unleashed or hearing the command “Go”, without obviously checking the owners’ behavior.

As the owners were not informed of the purpose of the study beforehand, it seems unlikely that they had clear-cut expectations about their dogs’ behavior in the Test Phase. There are at least two possible predictions, as indicated above. In informal conversation with owners after the test it was clear that their expectations varied; some predicted visits to baited-uneaten containers, whereas others predicted returning to baited-eaten containers, and others had no specific expectations. Another possible objection might be on the grounds of a Clever-Hans effect, with the dogs responding to inadvertent cues from the experimenter. We suppose that this is also unlikely because when the dogs were tested for the very first time there was no opportunity to learn to identify possible cues. However, we eliminated this potential cue in the following Experiment.

Yet others might argue that the dogs showed a simple win-shift strategy. For such a strategy to work, however, dogs would have to remember where they visited (and ate) in the past anyway, because there was no change in the object arrangement. Thus this does not negate retrieval of the memory of a specific past experience. Finally, it might be argued that the dogs’ behavior reflects simple novelty-seeking. However, this can be also discounted because there was no physical change in the visual layout from the Exposure Phase to the Test Phase.

Therefore, it seems reasonable to conclude that the dogs solved the unexpected problem by spontaneously retrieving their prior experience. Note that this behavior was an untrained, adaptive performance in a novel situation that the dogs encountered for the first time.

Experiment 2

Experiment 1 demonstrated that dogs are able to retrieve and utilize memories for a single past experience or episode, in an unexpected situation where such memory retrieval is advantageous. A question that arises is what aspects of memory they are able to retrieve as a unitary episode.

Experiment 1 showed that, at least, the “where” of an item can be retrieved. It is possible that the dogs might have also retrieved “what” of the item, but this may not be warranted because the contents of the containers were homogeneous in the Exposure Phase.

In primates including humans, visual information processing goes through “where” and “what” pathways in the central nervous system (Ungerleider & Mishkin, 1982). “Where,” that is the location or motion of objects, is typically processed through the dorsal stream from primary visual cortex (V1) to parietal cortex through middle temporal cortex (MT), whereas “what,” that is identification of shape and object, goes through the ventral stream, from primary visual cortex (V1) to temporal extreme cortex (TE). Thus the two types of information may be fundamentally different from the early stage of information processing (Milner & Goodale, 1995).

Although dogs are generally considered to be more dependent upon olfaction and audition rather than vision, recent studies have shown that they are capable of visual concept formation (Range, Aust, Steurer, & Huber, 2008), recognizing human attentional states (Call, Bräuer, Kaminski, & Tomasello, 2003), understanding pointing (Hare, Brown, Williamson, & Tomasello, 2002; Szetei, Miklósi, Topál, & Csányi, 2003), and possible understanding of human perspective (Kaminski, Bräuer, Call, & Tomasello, 2009). Thus it is evident that dogs recognize both what and where of items of interest using vision. It may thus be asked whether these two types of information in the same sensory modality are somehow integrated. Integration of information from two separate modalities is within dogs' capacity; they may recall their owners' faces upon hearing their voices (Adachi, Kuwahata, & Fujita, 2007). The question whether and how "what" and "where" information are integrated in canids is worthy of investigation.

Method

Participants

Thirty-nine new domestic dogs (18 males and 21 females) and their owners participated voluntarily. Participant dogs were of various breeds and ranged in age from 8 months to 10 years old (see Table 2). Some of the dogs and owners were familiar with the test room but all were naive to this memory test. Eighteen dogs were recruited and tested in Kyoto, Japan, and the remaining 21 in Berlin, Germany.

Table 2 about here

Apparatus

As in Experiment 1, 2 identical sets of 4 open containers, different in shape, size, color, etc., were prepared for each dog. Two pieces of each dog's favorite food suggested by the owner were used as rewards. Another object that would not capture special attention or interest by dogs such as a natural stone or a small plastic anchor was also used. The test in Kyoto was conducted in the same room used in Experiment 1, and the test in Berlin was conducted in a ca. 5 x 6 m office space in the Free University of Berlin.

Procedure

Exposure Phase: This phase was run in almost exactly the same way as in Experiment 1 but with two important modifications. First, E deposited two (not four) pieces of food in two containers and the neutral object in another container; the fourth container remained empty. Second, E asked O to allow the dog to eat one of the two food rewards. The combination of the location of allowed and prohibited pieces of food, object, empty container (24) and visiting order (2: clockwise or counterclockwise) made for 48 types of exposure trials. Each participant received one randomly chosen type without repetition.

Test Phase: This phase was conducted in exactly the same way as in Experiment 1 with one improvement; that is, to avoid possible inadvertent cues from E, each dog's behavior was filmed by an assistant who did not witness the Exposure Phase, while E faced away from or left the test area until the trial ended.

Predictions

Based on the results of Experiment 1, two different predictions about the dogs' behavior in the Test Phase may be made. First, if the dogs are able to retrieve only "where" information, they should simply avoid visiting the sole baited-eaten container; that is they should visit the three remaining containers (baited-uneaten, neutral, and empty) randomly. Second, if they retrieve and adaptively utilize "what" and "where" information in integrated fashion, they should visit the baited-uneaten container more often than chance to collect food.

Results and discussion

The left panel of Fig. 2 shows the proportion of dogs that visited each container, on their first visit. Twenty dogs out of 39 visited the baited-uneaten container first; this was well above chance on a binomial test with the chance level .25 (p=0.001, two-tailed). The overall proportion of dogs visiting the baited-uneaten container was also above chance if we take a more conservative chance level of .333 (p=0.03, two-tailed), assuming that the dogs would never return to the empty container, which they might have simply ignored in the Exposure Phase.

Fig. 2 about here

Interestingly, separate analyses of Japanese and German dogs revealed an unpredicted difference; 10 out of 18 Japanese dogs visited the baited-uneaten container in the test, which was significantly above chance (p=0.011, two-tailed), whereas only 1 dog visited the baited-eaten container, which was significantly below chance (p=0.039, two-tailed). In other words, among 11 Japanese dogs who returned to the container where they had seen food inside, 10 went to the container from which they had not eaten. This suggests that Japanese dogs were not simply attracted to the containers previously associated with food but showed a clearly differentiated behavior toward the two containers depending upon their previous experience (p=0.012, two-tailed, chance 0.5). In contrast, whereas a comparable proportion of German dogs (10 out of 21) visited the baited-uneaten container, which was also statistically above chance (p=0.041, two-tailed), 9 out of 21 German dogs visited the baited-eaten container though this did not reach a statistical significance (p=0.112, ns, two-tailed). Thus it is possible that German dogs might have been simply returned to the containers associated with food. In fact, the difference in the proportion of the dogs visiting the baited-eaten containers between the two countries (1 out of 18 vs. 9 out of 21) was statistically significant (Fisher exact test, p=0.011). This might be due to subtle differences such as the breeds used, the test room, or, possibly, how people train dogs in Japan and Germany. This difference should be revisited in the future.

The right panel of Fig. 2 shows the dogs' second visit. Two of the dogs did not make a second visit and were not analyzed. Among the 17 dogs who failed to visit the baited-uneaten container in their first visit, 11 now did so. This proportion was also well above chance level of .33 (p=0.016, two-tailed). Separate analyses of Japanese and German dogs revealed a significant effect in the latter (p=0.039, two-tailed)

These results support our second prediction: dogs, particularly those kept in Japan, appear to have retrieved and utilized "what" and "where" information from their past experience in this novel test situation. The results suggest that dogs possess an ability to store and integrate the "what" and "where" of experienced episodes.

As in Experiment 1, potential explanations of the dogs' behavior other than retrieved memory appear unlikely, though the odor left on the floor might have affected their choice. However, we controlled inadvertent cuing by having the experimenter leave the test area. Therefore this experiment provided even stronger evidence for dogs' spontaneous retrieval of their memory of previous episodes.

General discussion

In Experiment 1 we showed that dogs can spontaneously retrieve and utilize memories of a previous experience. Specifically, considerably later after eating two of four pieces of food in separate containers, dogs preferentially visited the containers they had not been allowed to eat from in a novel, unexpected test. This shows that dogs are at least able to retrieve incidentally encoded "where" information. This exploration by dogs appears to have been driven by their internal processes rather than the change in external stimulation. Such behavior seems impossible without active attempt to retrieve their incidentally formed memory trace. In a recent report, MacPherson & Roberts (2010) demonstrated a similar win-shift strategy by dogs in a radial-arm maze after training. Our result shows that, at an unexpected situation where retrieval of their episodic experience could provide a sole clue to finding more food, dogs can readily go to collect food left uneaten in their preceding exploration without training.

In Experiment 2 we showed that dogs' utilization of incidental memory involves "what" as well as "where" information about previous episodes. In other words, dogs selectively visited the "uneaten" containers according to what they had seen their previous contents to be. Containers that should hold food were preferred over those that should have a neutral item in them. This suggests that dogs are able to retrieve and utilize incidentally encoded "what" and "where" information in an integrated fashion.

Potentially contaminating factors such as physical control and odor left on the containers were carefully excluded in the procedure, and the possibility of inadvertent cuing either by the owner or by the experimenter were eliminated. The only uncontrolled cue might have been odor left on the floor but, as discussed above, this does not necessarily predict that the dogs would visit baited-uneaten containers first. Therefore, our results demonstrate that dogs may possess an exercising incidental memory system similar to that of humans.

A methodological merit of the present procedure is that it requires no training. A wide variety of species may be tested in the same way, with slight modifications to suit particular species; this would be a valuable extension to comparative memory studies. One outcome of such comparative studies would be a better picture of how widespread such voluntary retrieval of incidentally-encoded memory is in the animal kingdom.

One question for future study is how long the incidental memory system can maintain information about a particular experience. The delay in the present study was less than 20 minutes. Although long-term memory capacity by dogs has not been well documented, this species is believed to remember familiar people for years, and, they are able to learn ca. 1000 labels for individual items (Pilley & Reid, 2011). Whether dogs are able to retrieve information about specific experiences days later remains an interesting question.

Another question may be related to the incidental finding of the difference in the behavior of Japanese and German dogs in Experiment 2; Japanese dogs more reliably returned to the baited-uneaten container than German dogs. We suspect that this difference may be most likely to be due to a difference in how people train dogs; our casual impression is that German owners tend to train their dogs to follow their command more strictly than Japanese owners do. A consequence could be that German dogs may have learned that taking food from the baited-uneaten container is prohibited in the Exposure Phase. This possibility may be investigated further.

A final question is whether dogs integrate "when" information in their retrieval of incidental memory of previous experiences. As briefly described in the Introduction, integration of "what," "where," and "when" is a key property of episodic memory system in humans. Although such integration has been demonstrated in food-caching birds, apes, and rodents (e.g., Babb & Crystal 2005; Clayton & Dickinson 1998; Martin-Ordas et al. 2010), many of these performances may result from training on how to retrieve the information; i.e., the performance could rely at least in part on the semantic memory system. This procedure, if combined with "when" information, could be a perfect easy test of episodic memory in nonhuman animals. For instance, it may be tested in the future how dogs and other animals respond to two types of food different in degradation as time.

In conclusion, we have demonstrated that dogs may retrieve and utilize "what" and "where" of specific past experiences encoded incidentally. How widespread this ability is in the animal kingdom and whether "when" information may be also retrieved are questions that remain to be answered.

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Tables

Table 1. Dogs used in Experiment 1.

Breed	Sex	Age (yy:mm)
Border Collie	F	5:00
Cavalier King Charles Spaniel	M	4:06
Chihuahua	F	2:10
Miniature Dachshund	F	7:07
Miniature Dachshund	F	6:02
Mongrel	F	5:00
Mongrel	F	3:01
Mongrel	M	3:00
Pomeranian	F	2:09
Shetland Sheepdog	F	0:09
Toy Poodle	F	3:00
Toy Poodle	M	4:09

Table 2. Dogs used in Experiment 2.

Breed	Sex	Age (yy:mm)	Location
Japanese dogs			
American Pit Bull Terrier	M	1:10	Kyoto
Border Collie	M	2:01	Kyoto
Chuhuhua	F	5:04	Kyoto
Chuhuhua	F	7:01	Kyoto
Chuhuhua	F	9:02	Kyoto
Golden Retriever X Labrador Retriever	F	4:10	Kyoto
Labrador Retriever	M	1:09	Kyoto
Labrador Retriever	M	3:09	Kyoto
Lakeland Terrier	F	6:09	Kyoto
Miniature Dachshund	F	7:10	Kyoto
Miniature Dachshund	F	7:10	Kyoto
Miniature Dachshund	M	7:10	Kyoto
Mongrel	F	2:02	Kyoto
Mongrel	M	10:04	Kyoto
Shepherd	M	0:11	Kyoto
Shiba	M	2:05	Kyoto
Toy Poodle	F	1:00	Kyoto
Toy Poodle	F	4:04	Kyoto

German dogs

American Pit Bull Terrier	M	5:03	Berlin
Baset Hound	M	2:01	Berlin
Border Terrier	F	2:04	Berlin
English Cocker Spaniel	M	1:40	Berlin
Golden Retriever	F	7:08	Berlin
Hungarian Vizsla	F	2:00	Berlin
Hungarian Vizsla	F	7:03	Berlin
Huski X unidentified	M	>4:00	Berlin
Jack Russel Terrier	F	4:06	Berlin
Labrador Retriever	M	4:00	Berlin
Labrador Retriever	M	8:11	Berlin
Miniature Pinscher X Jack Russel Terrier	M	4:06	Berlin
Mongrel	F	0:08	Berlin
Mongrel	F	4:11	Berlin
Mongrel	F	1:08	Berlin
Mongrel	M	>6:00	Berlin
Pomeranian X unidentified	F	7:01	Berlin
Saluki	M	9:05	Berlin
Scottish Deer Hound	M	>7:00	Berlin
Whippet	F	3:06	Berlin
Whippet	F	9:02	Berlin

Figure legends

Figure 1. a: A schematic top view of the arrangements of the apparatus. b-d: A schematic drawing of the testing procedure.

Figure 2. The results of Experiment 2. a: The first choice by the dogs in the Test Phase. b: The second choice by the dogs in the Test Phase that failed to visit the baited-uneaten container in their first attempt.

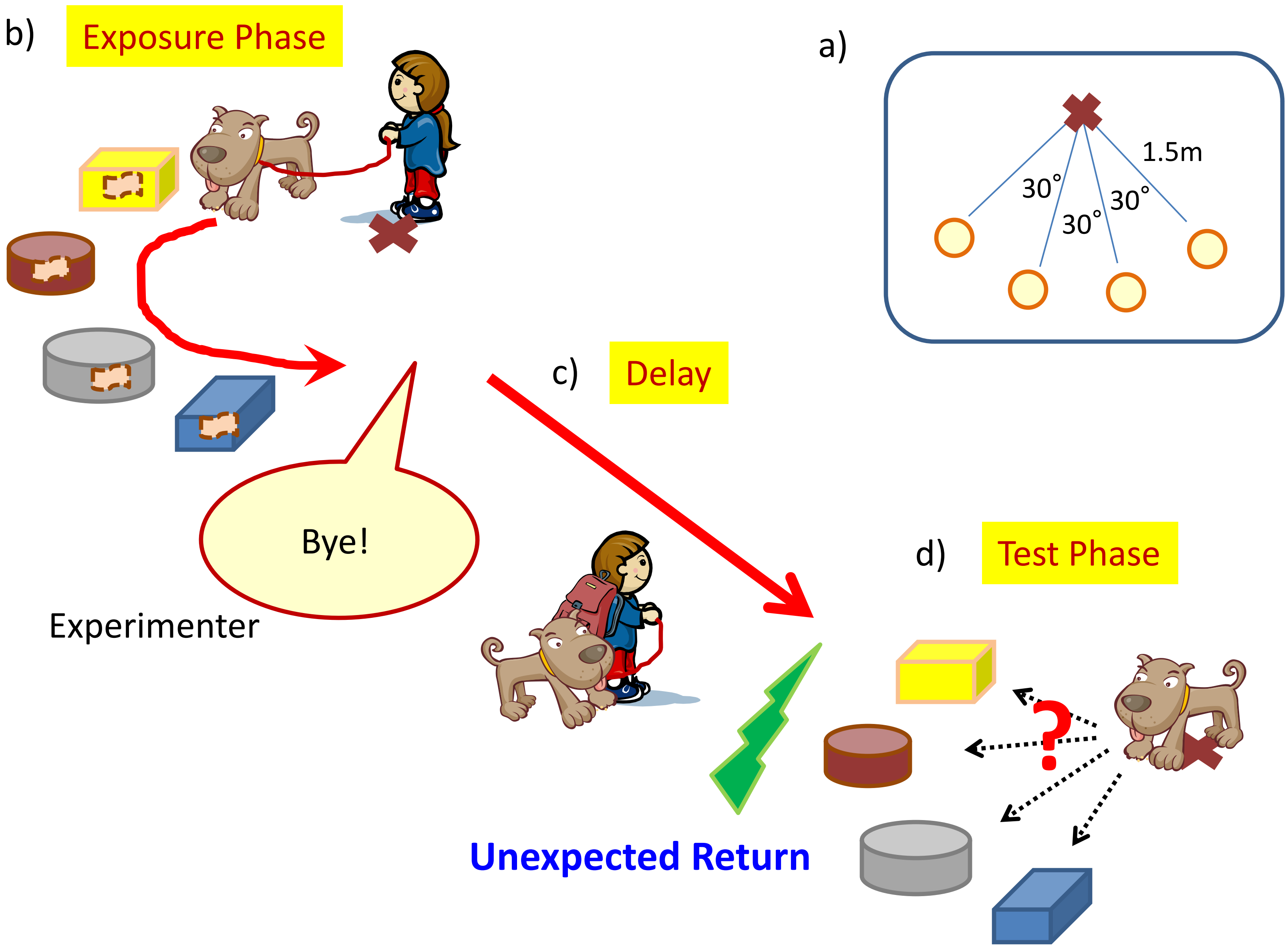
b)
Exposure Phase
a)
1.5m
30°
30°
30°
c)
Delay
Bye!
Experimenter
d)
Test Phase
?
Unexpected Return

Figure 1

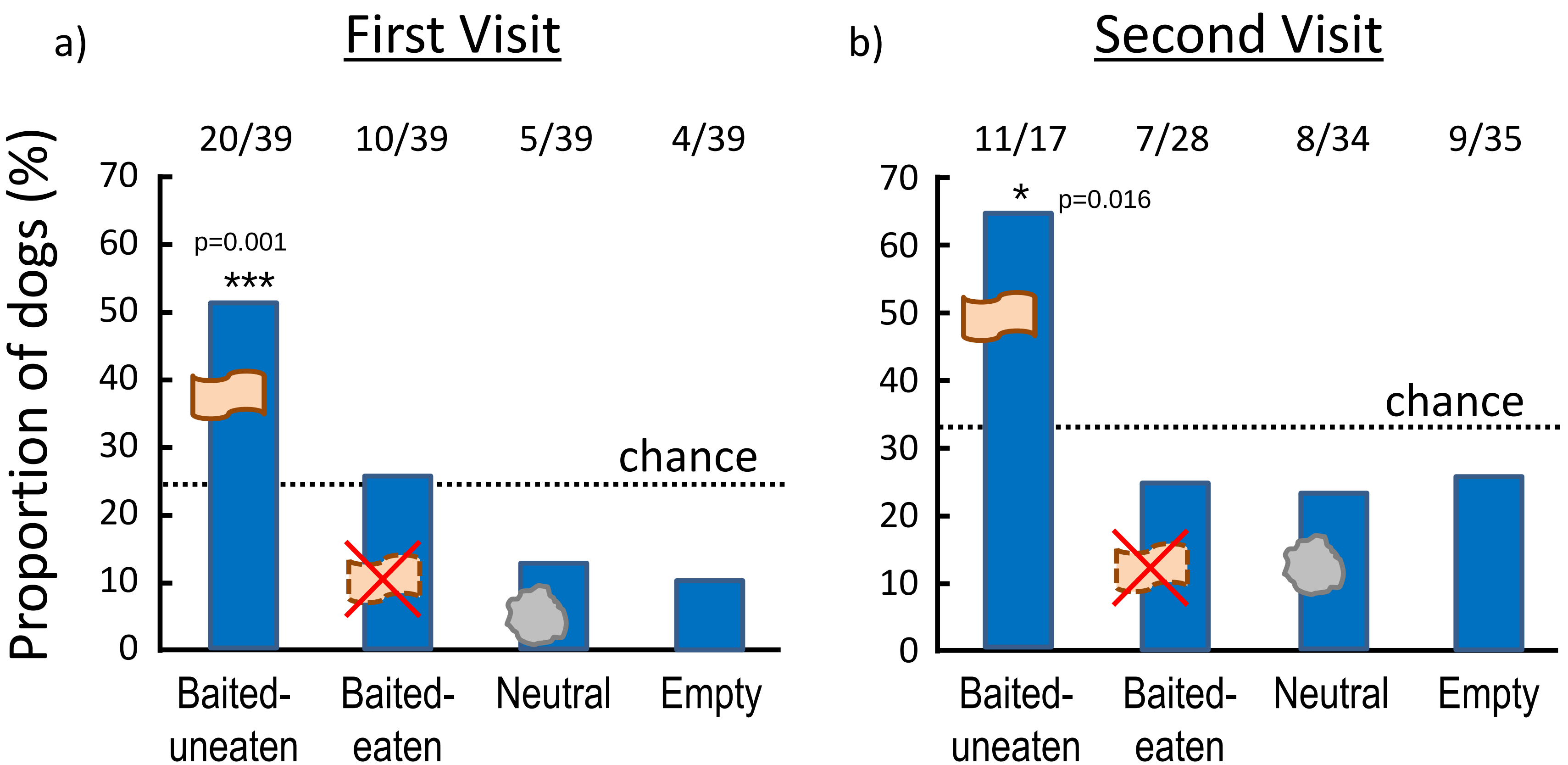
a)
First Visit
b)
Second Visit
Proportion of dogs (%)
20/39
10/39
5/39
4/39
11/17
7/28
8/34
9/35
70
60
50
40
30
20
10
0
p=0.001
***
*
p=0.016
chance
Baited-uneaten
Baited-eaten
Neutral
Empty

Figure 2