Incidental spatial memory in the domestic dog (*Canis familiaris*)

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Abstract

We built upon previous work by Fujita et al. (2012, *Animal Cognition*, 15(6), 1055–1063) to create an experiment that investigated the presence of incidental memory for the spatial location of uneaten food in the domestic dog. Here, we dissociated potentially incidental spatial memory from the incidental memory for the characteristics of objects, in this case, food bowls. Eighteen household domestic dogs of various breeds and age were presented with four bowls. Each bowl contained either a novel object, treats the dog could consume, treats it could not consume, or it was left empty. Following a delay, the dogs returned to the laboratory and were presented with empty bowls in the same spatial orientation as the initial exposure and could move freely between bowls. This experiment required no previous training outside of basic obedience and so avoids the possibility that performance on the test was a conditioned response. We hypothesized that domestic dogs would be able to remember the location of uneaten food when presented with an unexpected memory test. We found that dogs in this study showed no evidence that they encoded spatial location in the absence of other cues that could be used to distinguish food bowls at specific locations. This suggests that dogs in previous experiments were more dependent on incidentally encoding the “what” and “in what” of this task than the “where,” in the absence of features making each location distinct.

Keywords memory · episodic memory · spatial learning · dog

As of 2016, domestic dogs were companions to about 60.2 million households in the United States, over 10 million more households than those with cats (Springer, 2017, p. 10). Despite dogs being such a fixture in human society, the scientific study of canine cognition is a relatively recent phenomenon, and there is still much to learn about humanity’s oldest companion animal.

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This new field has given rise to studies that show dogs may be comparable with humans in tasks involving learning and memory, especially complex memory types such as episodic memory (Fugazza, Pogány, & Miklósi, 2016). It is even suggested that dogs may be an ideal animal model for the study of human age-related diseases affecting memory, such as Alzheimer’s and dementia (Cummings, Head, Ruehl, Milgram, & Cotman, 1996). However, questions remain about the accuracy of short-term canine spatial memory, prompted by the observation that domestic dogs appear to perform worse than other species, including wolves and nonhuman primates, on certain memory tasks (Frank & Frank, 1982; Macpherson & Roberts, 2010).

Incidental encoding occurs when a memory of past events or details of the environment formed without the knowledge that this information will be needed later. For example, the memory of police suspects is often provided by witnesses who, at the time, may not have been aware that said person was of interest and that they should remember qualities of their clothes or face (Thompson, Herrmann, Read, Bruce, & Payne, 2014). Therefore, incidental memory is that which is perceived but not necessarily attended to, and which is nevertheless committed to memory. This is the same type of memory that allows you to tell someone what you ate for breakfast

without having specifically committed it to memory that morning with the intent of telling another person about it. It also plays into the type of memory known in humans as episodic memory. This is the memory of past personal events in relation to the what, where, and when aspects of the event (Tulving, 1985). Incidental memory plays an important role in episodic memory as episodic memories are, notably, not encoded purposefully. This means that episodic memory is inherently incidental, and a species that lacks the ability to encode information incidentally may not be capable of episodic memory as psychologists currently define it. While it is relatively easy to attribute episodic memory to humans because we can discuss our memories and experiences with each other, it is much harder to assume or attribute episodic memory in animals.

Since the idea's conception by Tulving in the 1970s and 1980s, the search for episodic memory in animals has been ongoing. Studies in pigeons have found that they can demonstrate incidental memory of past actions as shown by Singer and Zentall (2007), which may suggest episodic-like memory. Further, work by Zhou, Hohman, and Crystal (2012) demonstrated a similar ability in rats, where they could report on the incidental memory of the previous presence or absence of food. Then, after incidental memory in rats was established, Panoz-Brown et al. (2016) provided evidence that rats can remember multiple unique events in context. This study provided strong evidence that rats may exhibit a memory system that is strikingly episodic-like.

These advancements in the study of episodic-like memory in animals brings us to approach other species in search of evidence for this type of memory. The domestic dog remains a species in which there is high interest. Dogs are the most popular pet in the United States and Europe, as well as an integral part of human culture. Dogs have been important to human survival since at least 26,000 years ago, as shown by zooarchaeological remains, but genetic analysis indicates that dogs could have emerged as a distinct breeding group as much as 100,000 years ago (Serpell, 2016). For these reasons, dogs are of great interest to both the public and the memory and cognition community. Over the past few years, studies on canine cognition and memory have produced many interesting comparisons between humans and dogs. For example, dogs show similar effects of aging on learning and memory to that seen in humans (Overall, 2011), and the expression of mutations in brain tissues are comparable between humans and dogs (Saetre et al., 2004). It has also been shown that dogs mirror humans in the development of social cognition and are similar to 2-year-old children in that they can understand communicative gestures like gaze and pointing, are capable of social learning, and exhibit basic theory of mind (Maclean, Herrmann, Suchindran, & Hare, 2017). However, despite high performance in social cognition, dogs are shown to have relatively

low performance in spatial cognition when compared with apes such as chimpanzees (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006).

The goal of this study is to add to our understanding of incidental spatial memory in the domestic dog. Fujita, Morisaki, Takaoka, Maeda, and Hori (2012) tested the ability of dogs to recall which of several bowls, to which they had been given a single prior exposure, contained an uneaten food reward. They used a combination of fixed spatial location and distinctive bowl characteristics as cues. Here, we slightly modified the procedure of Fujita et al. (2012) to separate spatial cues from other cues, such as bowl characteristics, that could be used to clearly mark a location. Unlike Fujita et al. (2012), we used identical bowls, forcing the dogs, if successful, to rely on memory for location alone to locate a specific bowl. During the test phase, we expected that dogs would attend to the location of food that they had previously been prevented from eating. We also surmised that behavioral tendencies that were specific to individual dogs might predict behavior on the task, and thus we had owners complete the online Canine Behavioral Assessment and Research Questionnaire (C-BARQ). Details of the C-BARQ and its reliability are discussed in Hsu and Serpell (2003) and Duffy and Serpell (2012). C-BARQ assesses certain behavioral traits, such as trainability, which may be important to this task, as especially trainable dogs may refuse to eat from a container from which they had previously been restrained because they are especially obedient. We also conducted a simple motivational assessment prior to the formal experiment to better assess the attachment and food motivation of the dog, which may have affected its performance on a food-based test such as ours.

Method

Subjects

The 18 dogs participating in this study were voluntarily brought to the Canine Cognition Laboratory at Indiana University by their owners. Owners were recruited by flyers and word of mouth. The dogs were of various breeds, including mixed breed, and comprised eight females and 10 males. Dogs were admitted to the study on the condition that they were at least 1 year of age, had a current rabies vaccination, and could follow basic commands such as “sit” and “stay.” Owners were also instructed to bring a bag of their dog's preferred treats (Table S1 in the Supplemental Materials provides information on the sex, breed, and age of each dog). All protocols were reviewed and approved by the Institutional Animal Care and Use Committee at Indiana University, Bloomington.

Experimental rooms

All studies were conducted in the laboratory's two adjoining rooms and were run by two experimenters, the primary and secondary. Dogs were staged and observed in the 37.6 m² observation room (O room) and exposed to the test conditions in the 17.5 m² test room (T room). Both rooms lacked windows. They were connected by an interior door, and each had a door to the hallway outside the lab. All movements and responses were recorded by one tripod-mounted video camera in each room. Video was coded by two independent researchers who had been trained by the first author.

Procedure

Dogs were brought into the laboratory at varying times throughout a period of 6 months for an average duration of 30 minutes. Each experimental session consisted of five phases: introduction, observation, exposure, delay, and test. Prior to the scheduled laboratory session, owners were asked to complete the C-BARQ behavioral assessment online.

Introduction phase

The introduction phase included meeting the owner and dog outside the building and escorting them into the building via less than two meters of hallway to the O room. The dog was then allowed off leash to familiarize itself with both the O and T rooms. The dog was encouraged to greet all experimenters and investigate both rooms through the open adjoining door to habituate to the new space and people. This phase lasted until the dog explored all regions of both rooms and did not show any signs of stress or fear, such as tail-tucking or cowering, in typically about 5 minutes.

Observation phase

The observation phase consisted of a simple motivation test. After the dog had become familiar with the rooms and experimenters, the primary experimenter presented the dog with one of the treats brought to the laboratory by the owner. Once the dog had accepted the treat, some of the treats were given to the secondary experimenter to begin the setup for the next phase while the primary experimenter placed the rest of the treats on a high shelf in direct sight of the dog. The joining door was then closed to isolate the secondary experimenter in the T room. During this time, the secondary experimenter set up four bowls in the T room in the arrangement seen in Fig. 1 and further described later. The primary experimenter then stood with the owner at one end of the O room while the dog roamed freely. At this time the primary experimenter explained the rest of the study while the O room camera recorded the dog's behavior. This phase was intended to measure the

Fig. 1. Schematic depicting the relative bowl arrangement and an example of bowl contents for the exposure phase. A check indicates treats to be eaten, an *x* indicates treats to be left uneaten. In the test phase, the arrangement was the same, except all bowls were empty

dog's food motivation in comparison with their attachment to their owner. This phase lasted about 5 minutes.¹

Exposure phase

After the 5-minute observation, the dog and owner were moved into the T room. Here, the secondary experimenter had arranged four bowls in an arc around a central *X* on the floor, as illustrated in Fig. 1. The bowls were 1 m from the central *X* and spaced 1.22 m apart. Each bowl was identical, being the same shape, size, and color. The bowls were positioned upside down as the owner and dog entered to limit observation of the bowl contents and to prevent the dog from “accidentally” eating from the bowls as they entered before they were positioned correctly. Additionally, this mirrors the setup used for the test phase, as described later, and so maintains consistency. Each bowl had already been scent controlled with a piece of the owner-provided treat taped inside the inner edge of a deep groove on the bottom of the bowl, so as to not be directly visible to the dog. The contents of each bowl were one of the following: one to three pieces of treat to be eaten, one to three pieces of treat to be left uneaten, a rock, or empty. The number of treats presented to each dog varied, based on the size of the treats provided by the owner, to present each dog with approximately the same amount of treat, regardless of the treat size. The position of the different contents had been randomized for each dog.

Once the owner and dog had entered the room, the dog was positioned on the central *X*. The primary experimenter then went to each bowl, flipped it over, showed the dog the contents, and repositioned it right-side up, with the

¹ Due to issues with equipment and data loss, data from the observation phase was analyzed for only a portion of the original sample and therefore is not reported in the [Results](#) section below. This phase is described here to give an accurate description of the experiment.

associated items placed inside. Next, moving clockwise, the owner led the dog to each bowl, allowing the dog to touch and smell the empty bowl and the novel object bowl (i.e., rock bowl), allowing them to eat from one of the treat bowls (as previously directed by the primary experimenter) and allowing the dog to see and smell but not eat from the treat bowl designated the one to be left uneaten. The owner could use any means necessary to restrain their dog from the uneaten bowl, including voice commands and physical restraint with a leash and/or harness. After the dog was exposed to all the bowls, the owner and dog immediately moved back into the O room.

Delay

Before the test phase, the dog was taken out of the building for a 10–15 minute walk. During this time, the two experimenters removed the bowls used in the exposure phase and replaced them with clean, identical, empty bowls. The new bowls were rebaited with treats to control for scent cues and placed upside down in the same manner as the exposure phase. None of the bowls in the test phase contained any treats or objects. Placing the bowls upside down both maintained consistency with the exposure phase and eliminated the chance that dogs could observe that the bowls were empty as they entered the room for the test phase, an observation that could have reduced the chance that they would attend to the bowls at all once released.

Test phase

After the delay, the dog and owner immediately returned to the T room and positioned themselves on the *X*, facing away from the upside-down bowls. The primary experimenter then flipped the four empty bowls over and moved away from the setup. Both experimenters then faced away from the setup and instructed the owner to release the dog accompanied by a word of encouragement, such as “Go!,” if necessary. The dog’s response was then recorded by the video camera for approximately 2 minutes. During this time, both experimenters and the owner stayed facing away from the dog and the bowls to avoid giving any unintentional cues to the dog. After 2 minutes, the camera was stopped, and the owner was thanked and was free to leave. This phase took approximately 5 minutes.

After the owner and dog had left, the bowls and laboratory floors were sanitized with a bleach and water solution, according to the Institutional Animal Care and Use Committee of Bloomington’s stipulations, both to prevent the spread of canine disease and to neutralize any odors left on the bowls and floors that may have distracted the next subject.

Coding

After all data collection was complete, two laboratory members were trained to code video data. Coders were blind to the contents of the bowls visible in the test-phase videos and were not shown the exposure-phase videos prior to coding. Bowls were labeled from A to D. Coders were trained to identify in what order dogs visited the bowls, up to five bowls. Dogs were said to have visited a bowl when any part of their muzzle contacted the bowl or when the dog’s muzzle was within 5 cm of the bowl. Agreement across coders of the order in which each dog visited the bowls was 100%.

Results

The first and second bowls visited by each dog in the test phase are shown in Table 1. Of the 18 tested dogs, six first returned to the uneaten bowl; three first returned to the bowl from which they had eaten; four returned to the empty bowl first; and five returned to the bowl that contained the novel object (a rock) first in the test phase. On average, dogs visited at least four bowls out of a maximum of five recorded in the test phase, and so did not exhibit any decrease in motivation to visit other bowls once they encountered the first empty bowl. Complete data for all dogs, including first and second choice condition, and five C-BARQ scores, are provided in Supplementary Material Table S1.

The first choice of these dogs does not appear to deviate significantly from that which would have occurred by chance (see Table 1). Because the chi-squared test becomes unreliable at small sample sizes (i.e., when expected values are below 5), its appropriateness here may be questioned. Thus, while we can report a chi-squared *p* value of .77 to describe these data with an expected value for selecting the uneaten bowl on the first choice as 4.5 (18/4), we also performed Fisher’s exact test on the data as organized in Table 2. Failure to approach the “uneaten” bowl first did not significantly increase the chance that they would approach this bowl second (Fisher’s exact test, two-tailed *p* value: .0537). Here and in the following results, the null hypothesis used for the Fisher’s calculations was based on chance, with the number of dogs answering correctly being one quarter of the sample size (i.e., 4.5 dogs) and the number answering incorrectly being three quarters (13.5 dogs).

The fact that some dogs were pure bred, and others mixed breed, also did not predict their performance in this task, according to a Fisher’s exact test (two-tailed *p* value: .6199) (Table 3).

Additionally, while five out of six dogs that chose the uneaten bowl first were male, this result is not significant according to a Fisher’s exact test (two-tailed *p* value: .1516) (Table 4).

Table 1 First choices by category, and number of dogs that chose each bowl by category on their first visit

Category	Dogs
Uneaten	6
Eaten	3
Empty	4
Object	5

Through indications given by the C-BARQ, we found that dogs varied with respect to behavioral tendencies and also whether they had any behavioral characteristics that deviated significantly from their breed average. In our analysis, we defined dogs as having “of concern” behavioral issues if their score for any category was deemed as serious or severe (indicated by a red bar on the dog’s behavioral report) by the C-BARQ system. For example, a dog with a particularly low score in the “trainability” category compared with their breed average would have a bar on their report graph colored red, indicating a potentially severe behavioral issue. A dog marked as “normal” was defined as one that showed no serious or severe scores in their C-BARQ report. Based on these questionnaire results, we found that having one or more traits that are “of concern” versus “normal” did not significantly predict which bowl would be visited first (Fisher’s exact test, two-tailed p value: .0987) (Table 5).

Through C-BARQ records, we also recorded the approximate age of each participating dog. Then, based on the average longevity of any breed (11.5 years; Michell, 1999), we divided the participants into “old” and “young” dogs. Old dogs were those older than half of the average longevity, and young dogs were those less than half the average age. However, based on a two-tailed Fisher’s exact test, there was no significant relationship between age and selecting the correct answer on the first try ($p = .600$) (Table 6).

Figure 2 shows the average C-BARQ scores for each of the five C-BARQ categories we selected across first choice. These five categories were selected from the 14 factors analyzed by the online questionnaire prior to any testing. They were selected to represent a variety of major canine behaviors that appeared most relevant to our test. The other nine factors provided by the C-BARQ were not analyzed for their

Table 2 Order of correct and incorrect choices, and dogs that selected the correct or incorrect choice on the first and second visits

Second	First	
	Correct	Incorrect
Correct	0	6
Incorrect	6	6

Table 3 First-choice condition of mixed and pure breeds. Number of mixed or pure-bred dogs that selected the *uneaten* bowl, which was defined as correct, and those that selected any other category, which were defined as *incorrect*

Breed	First Choice	
	Correct	Incorrect
Mixed	2	7
Pure	4	5

association with any of our other results. These C-BARQ results also do not appear to predict first choice in the test phase.

Discussion

Fujita et al. (2012) concluded that dogs may encode the “what” and “where” of information given a single chance to learn about the location of uneaten food. They reported that 10/18 Japanese dogs visited the baited-uneaten bowl first during the test phase, and a similar proportion of the remaining dogs who did not choose baited-uneaten first visited the baited-uneaten bowl second.

Our experiment failed to produce a similar pattern of results. Here, we contend that dogs cannot remember the location of uneaten food based solely on location. Because the dogs in our experiment were confronted with bowls that could be distinguished only based on their location, whereas the containers used by Fujita et al. (2012) varied in shape, size, and color, the task confronting the dogs in our experiment was different and likely more difficult than the one in Fujita’s study. While Fujita et al. (2012) suggest that dogs may encode “what” and “where” information, we think that because they did not dissociate location from other cues related to the features of the containers (e.g., by rearranging the bowls between exposure and test), it would be more accurate to say that they showed the majority of dogs in their experiment encoded “what” and “in what.” This still shows that some information was incidentally encoded by most of the dogs, but not necessarily the “where” or location of an item of interest.

Table 4 First-choice category of males and females. Number of males and females that selected the *uneaten* bowl, which was defined as *correct*, and those that selected any other category, which were defined as *incorrect*

Sex	First Choice	
	Correct	Incorrect
Male	5	5
Female	1	7

Table 5 Behavioral status and first-choice category. Number of animals with an *of concern* or *normal* marker in their C-BARQ results that selected the *uneaten* bowl (correct) versus the other categories (incorrect)

Status	First Choice	
	Correct	Incorrect
“Of Concern”	3	1
“Normal”	3	10

Note: One dog was excluded from this table because of the lack of C-BARQ data

An alternative explanation for our negative finding is that there is a potential national difference between U.S. and Japanese dogs. Fujita et al. (2012) reported differences between Japanese and German dogs in their study, which was conducted in laboratories in Kyoto and Berlin. During testing, 10 out of 21 German dogs and 10 of the 18 Japanese dogs went to the baited-uneaten container first, both significantly above chance, according to their analysis. However, nine out of 21 German dogs went to the baited-eaten container first versus (n.s.) only one out of the 18 of the Japanese dogs (significantly below chance). Fujita et al. (2012) speculated that these differences might reflect different training methods in Japan and Germany and suggested that further research is necessary. It is possible that the dogs in our sample represent a third kind of training background which does not support the kind of performance observed in Japanese and German dogs. However, in a more recent study, it was found that, given large enough sample sizes, basic cognitive tests, including that done by Fujita et al. (2012), are reproducible across different countries, breeds, and sexes (Szabó, Mills, Range, Virányi, & Miklósi, 2017). This study supported the original claim by Fujita et al. (2012) that a slight majority of dogs chose the bowl that they had left food in. However, they suggest that further investigation is needed before the claim about regional differences can be accepted. Therefore, we believe it is more likely that bowl location alone was insufficient for our dogs to remember the location of uneaten food rather than having found a regional difference between American and Japanese dogs.

Table 6 First-choice category of young and old dogs. Correct and incorrect first choice as shown by those characterized as *old* or *young* dogs. Old dogs were between 7 years 6 months and 14 years 6 months old. Young dogs were between 1 year and 5 years 3 months old

Age	First Choice	
	Correct	Incorrect
Young	5	7
Old	1	5

Another alternative is that because the bowls were arranged in an arc, with only a distance of 1.22 m between them, the dogs failed to distinguish them as individual locations. Due to space constraints, our distance between bowls of 1.22 m was slightly smaller than the 1.5 m used by Fujita et al., and this small difference could account for the results obtained. However, it seems unlikely that such a small change would greatly affect the dogs' ability to remember location. Rather, this would suggest that dogs do not have a very fine spatial paradigm and rely on other cues, such as characteristics, landmarks, or scent, to hone in on an object in a search. Perhaps if the bowls had been placed at other locations in the room, such as in corners or along certain walls, orientation within the room using structural or other cues as landmarks would have been sufficient for the dogs to locate specific bowls. However, as to whether dogs would have been more accurate in this alternative setup, it remains more likely that the positional arrangement used by Fujita et al. (2012) did not prove sufficient to support “where” memory in the present study. Additionally, the arc arrangement used in Fujita et al. (2012) and the experiment presented here could have led some dogs to revisit the bowls in the same pattern in which they were exposed to them (i.e., in a clockwise order). In our study, only one dog repeated the clockwise pattern that she had been led through in the exposure phase, and we learned from the owner that she had previously received odor-detection training, which often uses the same arc setup used here. Therefore, since no other dog repeated the clockwise pattern in the test phase, we do not believe that this method of exposure affected the dogs' behavior in the test.

Finally, domestic household dogs have varying kinds of experience with observing food on the ground and not being able to eat it. For example, when someone drops food and the owner prevents the dog from eating it, or when on a walk and the owner prevents the dog from consuming trash. Therefore, it is possible that some dogs may have learned that food they are not allowed to eat will likely be gone the next time they are in the vicinity. For example, dropped food is removed from the floor, and trash on a sidewalk may be picked up or blown away (or eaten by less-disciplined dogs). This would cause dogs who are regularly prevented from eating food at ground level to learn that it is never worthwhile to remember the location of this food because it will almost always be gone when they come back to it. This means that dogs with this experience would fail in our study, as they are not inclined to remember the location of previously observed food. In contrast, some household dogs may regularly be allowed to eat dropped food, and if they see food left but are not allowed to eat it immediately, they regularly find it in the same spot later, ready to be eaten. This would cause these dogs to expect uneaten food to be left on the floor and available for consumption later, thus training the dog to remember the location of dropped food. These dogs then would perform better than the previous dog because of differences in experience. However, it is important

Fig. 2. Average C-BARQ score across first-choice category. Average C-BARQ score (0–4) of the group of dogs that selected each category first. *Note.* One dog was excluded from this figure because of the lack of C-BARQ data. Error bars indicate the standard error of the mean

to note that for such dogs this experiment would not be a sufficiently unexpected test to warrant description as incidental memory. Additionally, while dogs likely have previous experience with food left on the ground, they also likely have experience with food left in a dog bowl, which is more applicable to this study. This previous experience may have led them to generalize our dog bowls as like those with which they have had experience. This generalization may also remove the aspect of “unexpectedness” from our test, as all dogs may selectively remember the location of a bowl containing leftover food, regardless of how unexpected the situation is. Without further investigation, these hypotheses remain untested.

Although interest in the cognitive abilities of dogs is currently high, it has not yet been agreed on whether dogs are capable of episodic-like memory. Many experiments with dogs and other animals rely on a period of training to get an individual to respond or to “tell us” something about what it knows or remembers. As discussed by Zentall and colleagues, when an animal is trained, it learns to expect the test or question following its exposure to information, and so can learn to remember what will be tested, and nothing else (Singer & Zentall, 2007; Zentall, Singer, & Stagner, 2008). The learned rules that allow subjects to perform well on such tests are part of semantic memory and do not require the memory of a specific event in a specific time and place that is characteristic of episodic memory. The study of incidental memory in dogs is the first step to eliminating this confounding factor of expectations of the test. Therefore, our study included no

training prior to the exposure and test, and attempted to demonstrate what dogs incidentally encode (the spatial location or quality of a food source?). The failure of these dogs to remember the location of food based simply on location suggests that they did not or do not generally encode information about location incidentally and, as shown by well-trained dogs, can only do so after extensive training (e.g., teaching a dog “go to your bed” or “go home” in relation to lying down in a specific place, i.e., their bed, requires training).

Our finding is interesting on an evolutionary level as well. Multiple comparative studies between domestic dogs and gray wolves showed that wolf pups outperform domestic puppies of the same age in spatial tasks, such as finding their way through a series of barriers to reach a reward (e.g., Frank & Frank, 1982). Additionally, a modern dog’s brain is approximately 30% smaller than that of a gray wolf (Kruska, 2005). This difference may be even more exaggerated with respect to the hippocampus, the portion of the brain thought to play the largest role in forming and retrieving memories. Kruska (2005) reported that a poodle’s hippocampus was approximately 42% smaller than that of a gray wolf of similar body size, while a laboratory rat’s hippocampus is only about 12% smaller than a wild rat’s hippocampus. This suggests that the process of domestication has reduced brain size in multiple species, but especially so in domestic dogs, possibly because of a longer domestication history. This would explain the poor performance seen in domestic dogs in radial maze experiments when directly compared with laboratory rats. In

Macpherson and Roberts's (2010) study, they found that on three common maze experiments done with rats, dogs had similar performance patterns to rats, but, overall, their accuracy was significantly lower, while still above chance. While this may have been because the maze is better suited to a tunneling scavenger species (Small, 1901, p. 208), it is still implied that dogs are somewhat less endowed with spatial and incidental memory capabilities. This may be because dogs have relied on humans for their entire evolutionary history and simply did not need such an extensive hippocampus to remember the location of food stores or of a previously killed carcass when they can simply follow humans to food. It is possible that extensive spatial and incidental memory may have been replaced with the ability to "read" human faces and gestures to get information about the location of food as opposed to remembering it themselves, as suggested by Rossi et al. (2014). This was seen observationally in many of the dogs that participated in our study. Some dogs would investigate the bowls for a moment then look to their owner for direction. When they received none, many either explored the rest of the room or stood still with no apparent purpose or attention to specific items in the context.

Conclusion

We demonstrated that the dogs in our study did not utilize information about the specific location of uneaten food when given the opportunity to encode that information incidentally. Further experiments should test whether dogs will approach a container associated with uneaten food based on features of the container, regardless of its position in a spatial array. Additionally, more comparative studies between wolves and domestic dogs and the wolf's capacity for encoding the location of uneaten food incidentally should be pursued to corroborate the theory that domestic dogs lost this ability with domestication.

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