

Current Biology

Episodic-like memory in common bottlenose dolphins

Highlights

- Common bottlenose dolphins demonstrate evidence for episodic-like memory
- Dolphins incidentally encoded spatial (“where”) and social (“who”) information
- Dolphins were able to use this information to solve an unexpected memory task
- A complex socioecological background may have selected for this ability in dolphins

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In brief

Davies et al. provide evidence of episodic-like memory in dolphins. Dolphins were able to use incidentally encoded spatial (“where”) and social (“who”) information to solve an unexpected memory task. This suggests that dolphins can recall and access information within remembered events, which is an ability indicative of episodic memory in humans.

Report

Episodic-like memory in common bottlenose dolphins

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SUMMARY

Episodic memory involves the conscious recollection of personally experienced events, which has often been argued to be a uniquely human ability.^{1–5} However, evidence for conscious episodic recall in humans is centered around language-based reports. With no agreed upon non-linguistic behavioral makers of consciousness,⁶ episodic-like memory⁷ therefore represents the behavioral characteristics of human episodic memory, in the absence of evidence for subjective experience during recall. Here, we provide compelling evidence for episodic-like memory in common bottlenose dolphins (*Tursiops truncatus*), based on the incidental encoding and unexpected question paradigm.⁸ This methodology aims to capture the incidental encoding characteristic of human episodic memory, in that when we recall an experience, we remember information that was trivial at the time of encoding, but was encoded automatically.⁹ We show that dolphins are able to use incidentally encoded spatial (“where”) and social (“who”) information to solve an unexpected memory task, using only a single test trial per test type, which ensured that the dolphins did not have the opportunity to semantically learn “rules” to pass the test. All participating dolphins made correct choices in both the “where” and “who” tests. These results suggest that dolphins are capable of encoding, recalling, and accessing incidental information within remembered events, which is an ability indicative of episodic memory in humans. We argue that the complex socio-ecological background of dolphins may have selected for the ability to recall both spatial and social information in an episodic-like manner.

RESULTS AND DISCUSSION

Mental time travel is the ability to internally travel through one’s own subjective time, re-living past experiences as well as imagining possible future events. Episodic memory, the structural foundation of mental time travel, is the memory system that involves the consciously experienced recollection of personally experienced events. Within the declarative memory system, it is considered distinct from semantic memory, which concerns factual information and does not involve a subjective experience during recall.¹⁰ Episodic memory is thought by many psychologists to be uniquely human.^{1–5} For example, Tulving and Markowitsch² argue that while animals have a sophisticated and sensitive semantic knowledge of their environment, they cannot consciously recall and relive specific past experiences as we can. However, as evidence for conscious episodic recall in humans is centered around language-based reports, and with there being no agreed upon non-linguistic behavioral makers of consciousness,⁶ it is potentially impossible to establish if non-human animals have true episodic memory accompanied by its phenomenological components. However, Tulving’s original definition¹¹ states that episodic memory “receives and stores information about temporally dated episodes or events and temporal-spatial relations among these events” (p. 385). Therefore, Clayton and her colleagues^{7,12} argue that the

simultaneous retrieval and integration of information about the “what” and “when” of unique experiences (“temporally dated experiences”), and “where” they occurred (“temporal-spatial relations”), can be experimentally demonstrated in animals through their behavior. Episodic-like memory⁷ thus represents the purely behavioral characteristics of human episodic memory, in the absence of evidence for subjective conscious experience during recall.

Dolphins and other cetaceans are often noted as being among the most cognitively complex taxa, rivaling the abilities of non-human primates.^{13–20} Despite this, research investigating memory and mental time travel in dolphins is scarce. Nevertheless, the limited literature sometimes cited in this context^{8,21–24} suggests that bottlenose dolphins are able to recall and repeat their own novel behaviors.^{25–27} However, these studies use small sample sizes of two²⁵ and one²⁶ and test recall immediately after the dolphin performs the action, thus testing for short-term working memory and not for episodic-like recall.

We tested eight common bottlenose dolphins on their ability to recall information encoded within episodic-like memories, using the incidental encoding and unexpected question paradigm.⁸ This paradigm aims to capture the incidental encoding characteristic of human episodic memory, in that when we episodically recall an experience, we remember information that was trivial at the time of encoding, but was nevertheless encoded

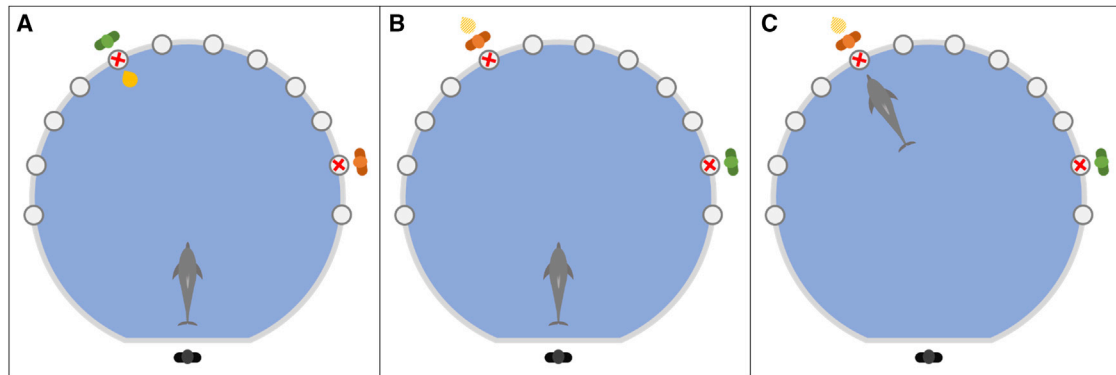


Figure 1. Schematic representation of the incidental encoding of “where” trials

(A) The dolphin was instructed by the commanding experimenter (black figure) to retrieve a visible object (gold ball) in front of one of two location cues (red X), each with a person behind (green and orange figures), using a specific previously taught command: two consecutive hand motions pointing with a closed fist (index finger facing upward) toward the middle point between the two location cues. The dolphin then approached the object to request it (a request/choice was considered as the dolphin raising their head above the water with their ventral side facing the location cue and pausing their movement), which it was subsequently given by the person behind the appropriate location cue (in this case the green figure). The dolphin then brought the object back to the commander. (B) After a 10-min rest period, in which the dolphin was free to swim around the test tank (with the experimenters out of sight), the dolphin was instructed to retrieve the object again, but this time the object is not visible. The location cues remained in the same place, but the person by each location had swapped, meaning the only available information to solve the task was the location cue where the object was previously given. (C) The dolphin then approached one of the locations and made a choice. In between the encoding phase and the memory phase of the test trial, the location cues were left in place (observable by the dolphins), in order to ensure that the dolphin was not using relative familiarity with either cue to solve the task.

automatically.⁹ For example, we may remember the facial characteristics of a waiter that served us the day before, or the location of the table within the restaurant. In this paradigm, subjects are “unexpectedly” asked to recall a unique event and thus do not learn the need to encode specific information in order to use it in the future. When subjects are trained repeatedly on memory tasks, they may learn that specific information is needed in the future, and so learn to actively encode this information. Some authors argue that this results in subjects passing these memory tasks based on semantic knowledge alone, without the use of episodic-like memory.^{8,28–31} Designing experiments with test trials that unexpectedly ask subjects to recall information that at the time of encoding was irrelevant to solving the task ensures that any information used to solve the test was encoded incidentally, thus forcing the use of an episodic-like memory system for the recall of these episodes. As dolphins may have evolved to have the ability to recall both spatial and social information in an episodic-like manner, due to selection pressures resulting from their foraging niche and complex social systems (discussed below), we tested them for the incidental encoding of either “where” or “who” information. These tests were extremely stringent, with only a single trial per test type (who or where). Using a single test trial ensures that subjects do not have the opportunity to semantically learn “rules” to pass the test and reduces the risk of a type I error, as studies with fewer trials will be less likely to detect effects (potentially falsely) than those with more trials, due to the error rates typical within animal cognition research.³²

After completing a training procedure in which the dolphins were trained to retrieve an object visibly held outside of the water by an experimenter (by approaching the object and “asking” the experimenter for it) we conducted a single test trial of each test type (where and who). The test trials required the dolphins to use information that was incidental at the time of encoding

(i.e., the location [where] or the experimenter [who]), and thus tested them on their ability to recall the encoding events in an episodic-like manner. These tests involved a trial-unique encoding phase (the same procedure as the training task) as well as an untrained memory phase 10 min later. This memory phase involved the dolphin being commanded to retrieve the object again, but this time the object was completely out of sight. Therefore, the only way the dolphin could solve this task and find the hidden object was to recall the previous retrieval episode along with any incidental information that was encoded automatically. As the dolphin had never been instructed to retrieve the object when it was not visible, the memory test was unexpected and thus any information used to solve the task cannot have been encoded actively with the expectation that it would be relevant in the future. Even if the test was to some degree expected, as the dolphins had received repeated training trials with a similar procedure in the same pool, the information required for the test trials could not have been anticipated to be required, and so was likely encoded incidentally. In the incidental encoding of “where,” dolphins had to remember the location of the object previously given (Figure 1). In the incidental encoding of “who” trials, the dolphin had to remember the experimenter that previously gave the object (Figure 2). To ensure that the information encoded during the unique test encoding event was in fact incidental, both the location and the experimenter giving the object were irrelevant to solve the training tasks, and thus actively encoding these cues was not reinforced. The only relevant information in training trials was the stimulus of the visible object, as the location and the person giving the object differed with each trial. Therefore, using actively encoded information regarding the location or the experimenter giving the object during training trials would result in incorrect choices. While it cannot be said that the second test was completely unexpected, as they had been instructed to retrieve a non-visible object in the previous test,

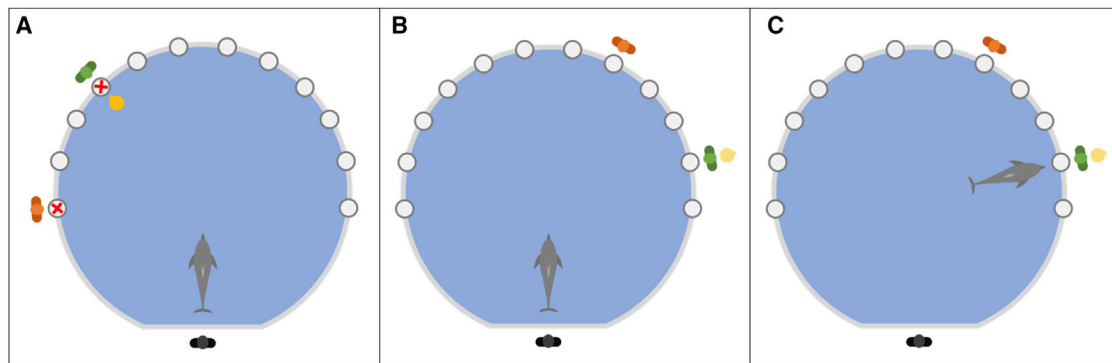


Figure 2. Schematic representation of the incidental encoding of “who” trials

(A) The dolphin was instructed by the commanding experimenter (black figure) to retrieve a visible object (gold ball) in front of one of two location cues (red X), each with a person behind (green and orange figures), using a specific previously taught command: two consecutive hand motions pointing with a closed fist (index finger facing upward) toward the middle point between the two location cues. The dolphin then approached the object to request it (a request/choice was considered as the dolphin raising their head above the water with their ventral side facing the location cue and pausing their movement), which it was subsequently given by the person behind the appropriate location cue (in this case the green figure). The dolphin then brought the object back to the commander. (B) After a 10-min rest period, in which the dolphin was free to swim around the test tank (with the experimenters out of sight), the dolphin was instructed to retrieve the object again, but this time the object is not visible. The location cues were removed after the encoding phase and the people moved to different locations on the opposite side of the pool, meaning the only available information to solve the task is the identity of who previously gave the toy. The combinations of locations used in the encoding phase and the test phase were pseudorandomized to ensure that the “correct” choice in the memory phase was not the closest location to the location rewarded in the encoding phase, more than other conditions. (C) The dolphin then approached one of the people and made a choice. In between the encoding phase and the memory phase, the person who did not give the object conducted a familiarity control in which they threw a different object in the water in order for the dolphin to retrieve, thus ensuring that the dolphin was not using relative familiarity with the person giving the object to solve the task.

the information used to solve each test type was entirely distinct. Indeed, actively encoding the information relevant from the previous test to use in the second test would also result in an incorrect choice (during “where” trials the experimenter giving the object was swapped between the memory and encoding phase, and in the “who” trials, saliently different locations were used in the memory phase than in the encoding phase). Test trials were separated by at least 48 h to maximize the “unexpectedness” of the second test. To control for an effect of experience, we counterbalanced which dolphins received which test type (where or who) first.

All eight dolphins made correct choices in the “where” test trials (Table S1), and seven dolphins made correct choices in the “who” test trials (one dolphin [Indi] did not make any choices after repeated commands, so the trial had to be terminated) (Table S2). As the information used to solve these tests cannot have been actively encoded, the dolphins must have been recalling an episodic-like memory of the previous retrieval episode. Furthermore, due to familiarity controls, the test could also not be passed using relative familiarity, a psychological process distinct to episodic(-like) recall.³³ We have therefore found evidence for episodic-like memory in bottlenose dolphins, and the first experimental evidence of mental time travel abilities in cetaceans.

Coining the term episodic-like memory, Clayton and her colleagues^{7,34–37} conducted a series of influential experiments demonstrating that scrub-jays fulfil the criteria for episodic-like memory. Many researchers have since used this “what-where-when” paradigm in order to test episodic-like memory in other non-human animals, including rats,³⁸ corvids and other species of birds,^{39,40} great apes,⁴¹ and cuttlefish.⁴² Due to the repeated training procedure essential for employing the what-where-when paradigm, however, it has been argued that some animals can

pass these experiments without recalling the encoding event in an episodic(-like) manner.^{8,28–31} For example, if an animal is presented with an event and, during encoding, expects an upcoming memory test reliant on specific information within the event, then it could maintain and carry forward a memory trace of this information to use later in the test, without recalling back in time to the event upon presentation of the memory test (as is the case for an episodic-like memory account).⁴³ Therefore, other studies investigating episodic-like memory in non-human animals use the unexpected question and incidental encoding paradigm,^{8,23,24,28–31,44} as we have adopted here. Despite the criticisms of the what-where-when paradigm, Holland and Smulders⁴⁵ show that humans do use episodic memory during a what-where-when caching task, even when instructed to actively remember the information (and thus closely resembling the animal studies). Furthermore, performance on the what-where-when test was significantly predicted by performance on an incidental encoding task, in which subjects were unexpectedly asked questions about the context of the caches that were unrelated to solving the task. This suggests that both paradigms are valid to test episodic-like memory, and in the future the use of both to corroborate each other would lead to more conclusive evidence.

While episodic-like memory was originally argued to have evolved in corvids as a result of selection pressures associated with food caching,⁴⁶ many of the other species that have shown evidence for episodic-like memory do not habitually cache food, e.g., apes⁴¹ and cuttlefish.⁴² This raises the possibility that other socio-ecological factors may drive the evolution of episodic-like memory, such as those experienced by dolphins in their evolutionary history. For example, intriguing observational evidence suggests that wild Risso’s dolphins (*Grampus griseus*), a relative

of bottlenose dolphins, appear to plan foraging dives based off memories of previously experienced prey distributions.⁴⁷ It is argued that as these air-breathing predators forage at deep depths, they may plan their diving activities in response to past experiences in order to maximize their foraging efficiency before returning to the surface. While bottlenose dolphins primarily feed within surface layers, they forage in the entire water column and do frequently dive to depths close to the seabed, and often forage on benthic prey.⁴⁸ Furthermore, the persistent constraint on foraging resulting from the requirement to consistently surface to breathe, even when diving at shallow depths, may mean that remembering and planning diving conditions and behavior, respectively, could be an adaptive advantage. As cetaceans, including dolphins, have very large day and home ranges and seek food that is distributed in mobile patches of schooling or benthic prey,⁴⁹ an episodic-like memory system would allow for the recall of briefly experienced spatial foraging conditions and enable flexible planning for future foraging dives. As all dolphins tested were able to recall spatial information in an episodic-like manner, based off a single experience, we show that this capability may be available to them when foraging and diving. Interestingly, while irrelevant in “where” test trials, “who” information was still utilizable. However, we did not observe this with any of our dolphins. This may be because the spatial cues were more salient to the dolphins compared to the social cues, but alternatively, they may prioritize the encoding of spatial information over other types of information, as has been demonstrated in dogs⁵⁰ and infants.⁵¹

Aside from foraging decisions, however, episodic-like memory would be considerably advantageous for facilitating the recall of social information.⁵² Bottlenose dolphins are highly social, living in pods with complex fission-fusion social dynamics⁵³ ranging in size from pairs to around 100 individuals, but can occasionally combine to over 1,000 individuals for a short time.⁵⁴ Within these pods there is individual recognition,⁵⁵ life-long social memory,⁵⁶ and possibly the most complex alliance system documented outside of humans.⁵⁷ Living in an “open” fission-fusion society, individual dolphins associate in groups ranging in size that change their composition often many times in a day.⁵³ In order to sequester and consort females for mating, male dolphins cooperate and form long-term, but often dynamic, bonds with other males to create nested, multi-tiered alliance systems. Groups of two to three males band together to form first-order alliances, often showing long-term stability, and these first-order alliances frequently combine to form second-order alliances that occasionally may combine again to produce third-order alliances.⁵⁷ The highly dynamic social milieu characteristic of complex fission-fusion dolphin societies may be highly cognitively demanding on an individual, as each dolphin’s relationships are managed and maintained within a constantly changing social environment,⁵⁸ involving complex (and often unobservable) third party interactions. As dolphins live in variably overlapping home ranges, these interactions may occur out of site for an individual, increasing the uncertainty about changes in third party relationships,⁵⁹ and thus adding further cognitive demands to an already demanding system. While individuals within first-order alliances tend to remain consistent, the composition and hierarchy of these groups may shift, with individuals even being

expelled on occasions. Furthermore, within higher-order alliances, transient relationships may bridge alliance levels,⁶⁰ and males may form temporary “consortship” partners with multiple different individuals from different first-order alliance groups, with individuals showing strong partner preferences and avoidances, suggesting that these high-order alliances may have complex internal structures.⁶¹ The cumulative social bond strength a male has within his second-order alliance has been demonstrated to significantly correlate with his reproductive output,⁶² showing that these affiliations, as well as the relative strength of different relationships, have direct fitness implications on the individual.

These relationships are formed and maintained through a number of affiliative behaviors, including signature whistles, “petting,” “gentle touching,” movement synchrony, and “contact swimming,” occurring both within and between alliances that are members of the same second-order alliances, and even between members of different but associating second-order alliances.⁵⁹ This complex structure of affiliative interactions therefore occurs at both the inter- and intra-group level, creating a more complex system than documented in other non-human animals, even in primates.⁵⁹ In theory, individuals can gain fitness benefits by developing or shifting alliances strategically, but these formed bonds are always at risk due to the potential decisions of others. A cognitively skilled social animal, such as a dolphin, must not only model the complexities of their current environment but may also mentally simulate the long-term outcomes of potential social scenarios (e.g., attack individual A, “pet” individual B, ignore individual C).⁶³ Recognizing and keeping track of complex third-party relationships in a huge and dynamic social network, with varying degrees of third-party uncertainty, and using this information to dictate strategic decisions would benefit hugely from a memory system that can encode events after only a single occurrence, with this information being available to be used in a flexible manner at a later time. When making a decision regarding a potential alliance, episodic-like recall of the interactions with this other individual, positive or negative, would allow the dolphin to assess the value of this alliance based on the value of previous interactions with this individual (e.g., if as a result of an interaction, the dolphin gained or lost an estrus female).⁵⁹ As all participating dolphins made correct choices in the “who” trials, we provide evidence suggesting that dolphins would be able to recall these interactions and thus could possibly use this information to dictate decision-making, although this requires further testing. While we tested them on their ability to recall social information regarding humans, we assume that they most likely can do this with conspecifics, especially if using visual information in combination with individual auditory signature cues made by allies.⁶⁴

In this study, we provide convincing evidence that bottlenose dolphins are capable of encoding, recalling, and accessing incidental information within remembered events, which is indicative of episodic memory in humans. The faultless performance of our sample of dolphins in both our incidental encoding tests suggests that they were able to access these episodic-like memories and use automatically encoded information within them to solve an unexpected task. The complex ecological and social characteristics of the lives of dolphins

may have selected for the evolution of this episodic-like memory system. This is the first evidence of episodic-like memory in cetaceans, despite the fact that they are often thought of as possessing cognitive abilities close to that of non-human primates.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2022.06.032>.

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AUTHOR CONTRIBUTIONS

Conceptualization, J.R.D., E.G.-P., and N.S.C.; methodology, J.R.D., E.G.-P., L.B., and N.S.C.; investigation, J.R.D., E.G.-P., L.B., and C.P.; writing – original draft, J.R.D.; writing – review & editing, E.G.-P., L.B., L.F., C.P., and N.S.C.; project administration, C.P. and L.F.; supervision, N.S.C.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Cognitive testing data	This paper	Tables S1 and S2
Experimental models: Organisms/strains		
Common bottlenose dolphins	ZooMarine Italia	<i>Tursiops truncatus</i>

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, James Davies (jd940@cam.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data reported in this paper will be shared by the [lead contact](#) upon request.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The experiments were reviewed and approved by the University of Cambridge AWERB (Animal Welfare Ethical Review Body) and were conducted under a university non-regulated license (OS2022/01). Eight dolphins (5 males and 3 females) were used in this study, with ages ranging from 6–29 years old (Tables S1 and S2). Individuals were identified using unique physical characteristics, such as facial variations and tooth rake patterns. The dolphins were housed in three groups in three adjacent pools (pool 1 = 2581 m³; pool 2 = 1840 m³; pool 3 = 1840 m³) at Zoomarine Italia (Torvaianica, Italy). The pools were all connected by gates, which also connected to another two veterinarian pools, one that was used for this experiment (1020 m³). This pool was not usually used for training purposes. The pools together totaled to 7667 m³. The organization of the groups was in line with social and breeding requirements and was already in place before this study began. Dolphins were tested individually in the dedicated pool where possible, but if not (e.g., when testing a dolphin with a calf), the other dolphin was kept distracted at the edge of the pool by a trainer. All dolphins used in this study were born and raised under human care and have been involved in different studies before this project, for example, on vocal communication, play behavior,⁶⁵ preferences tests and anticipatory behavior.⁶⁶ The dolphins under Zoomarine care are all trained to perform various behaviors for multiple reasons, e.g., medical or zoo performances, through operant conditioning with positive (and variable) reinforcement and social learning.

METHOD DETAILS

Dolphins were tested on two unexpected question tasks, one testing the incidental encoding of ‘where’ information and the other testing the incidental encoding of ‘who’ information. Both these tasks involved the dolphin being commanded to retrieve an object by an experimenter. The dolphin could choose between two possible options during training and test trials. Before the start of this experiment, the dolphins were trained by Zoomarine staff to retrieve an object in the water, using a specific command: two consecutive hand motions pointing with a closed fist (index finger facing upwards) in the direction of the object. Before the command was given, in general training and for this experiment, the dolphin was encouraged to face the experimenter and focus their attention on the forthcoming command (with the use of other trained commands: a flat palm either facing up or down, used to bring the dolphin closer and to cue the dolphin that they are about to be given a command, respectively). These commands were trained through operant conditioning with positive reinforcement, starting when the dolphins were young. They were then trained by the experimenters to retrieve an object that was outside of the water (using the same ‘retrieve’ command), by approaching a human experimenter (by one of the possible choices) and requesting them to lower it into the water. A request/choice was considered as the dolphin raising their head above the water with their ventral side facing the location cue and pausing their movement. All commands were given from

the same platform across the pool from the location cues, and the commanding experimenter focused their body position and direction of the retrieve command directly between the two possible choices, ensuring that the dolphin made a choice for which one to approach (rather than being directly cued). If on test trials the behavior of the dolphin did not result in a clear choice, the dolphin was recalled (with no object given) and instructed again. Only when a clear choice was made the object was lowered into the water (to avoid accidentally cueing the choice). During training, the two choice locations were randomized between 12 possible locations around the pool for each trial, meaning no location was more reinforced than any other. The choice locations were also randomized for each test trial, ensuring that the encoded event was trial-unique, an important characteristic for testing episodic(-like) memory. To ensure that the information encoded during the unique test encoding event was in fact incidental, both the location cue and the person giving the object was irrelevant to solve the training tasks. The only relevant information was the stimulus of the visible object; the location cue and the person giving the object differed with each training trial. Therefore, actively encoding information regarding the location cue and the person giving the object during training trials would result in incorrect choices. This meant that these behaviors were not trained and so not actively encoded. Therefore, when instructed to retrieve a non-visible object during the unexpected question test trial, any information about the location cue or person giving the object was necessarily encoded incidentally, and thus recalled in an episodic-like manner. Dolphins passed the training phase by completing 8/10 correct trials in a session and were subsequently tested.

Each dolphin received only a single test trial in order to ensure that these trials were unexpected and thus any information that was used was encoded incidentally. Although it cannot be excluded that the second test was somewhat expected, as they had been instructed to retrieve a non-visible object in the previous test, the information used to solve each test type was inherently different. Before each test trial, up to 5 refresher trials were conducted in which the training procedure was used. After completing 4/5 correct trials, a test trial was conducted. A test trial consisted of a unique encoding phase in which the object was visible, and after 10 minutes, a memory phase in which the dolphin was instructed to retrieve an object with no object in sight. Test trials were separated by at least 48 hours to maximize the 'unexpectedness' of the second test. We counterbalanced which dolphins received which test type (where or who) first, to control for an effect of experience.

Incidental encoding of 'where' (Table S1): The dolphin was instructed by the commanding experimenter to retrieve a visible object in front of one of two location cues, each with a person behind (Figure 1A). The dolphin then approached the object in order to 'ask' for it, which it was subsequently given by the person behind the appropriate location cue. The dolphin then brought the object back to the commander and was rewarded. After a 10-minute rest period, in which the dolphin was free to swim around the test tank (with the experimenters out of sight), the dolphin was instructed to retrieve the object again, but this time the object was not visible (Figure 1B). The location cues remained in the same place, but the person by each location had swapped, meaning the only available information to solve the task was the location cue *where* the toy was previously given. The dolphin then approached one of the locations and made a choice (Figure 1C). In between the encoding phase and the memory phase of the test trial, the location cues were left in place (observable by the dolphins), in order to ensure that the dolphin was not using relative familiarity with either cue to solve the task.

Incidental encoding of 'who' (Table S2): The dolphin was instructed by the commanding experimenter to retrieve a visible object in front of one of two location cues, each with a person behind (Figure 2A). The dolphin then approached the object in order to 'ask' for it, which it was subsequently given by the person behind the appropriate location cue. The dolphin then brought the object back to the commander and was rewarded. After a 10-minute rest period, in which the dolphin was free to swim around the test tank (with the experimenters out of sight), the dolphin was instructed to retrieve the object again, but this time the object was not visible (Figure 2B). The location cues were removed after the encoding phase and the people moved to different locations on the other side of the pool, meaning the only available information to solve the task is the identity of *who* previously gave the toy. The combinations of locations used in the encoding phase and the test phase were pseudorandomized to ensure that the 'correct' choice in the memory phase was not the closest location to the location rewarded in the encoding phase, more than other conditions (Table S2). The dolphin then approached one of the people and made a choice (Figure 2C). In between the encoding phase and the memory phase, the person who did not give the object conducted a familiarity control in which they threw a different object in the water in order for the dolphin to retrieve, thus ensuring that the dolphin was not using relative familiarity with the person giving the object to solve the task.

QUANTIFICATION AND STATISTICAL ANALYSIS

As all the participating dolphins made every choice correct in both trial types, statistical analysis was not necessary. 25% of the videos were coded by a second rater to confirm the robustness of the dolphins' 'choice' assignments, with an inter-rater reliability *kappa* score of 1.