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RESEARCH ARTICLE

Unruly octopuses are the rule: *Octopus vulgaris* use multiple and individually variable strategies in an episodic-like memory task

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ABSTRACT

Episodic-like memory has mainly been studied through experimental tasks in which subjects have to remember what they ate, where and when or in which context. Seemingly quite common in mammals and corvids, episodic-like memory ability has also been demonstrated in the common cuttlefish, a cephalopod mollusc. To explore whether this ability is common to all cephalopods or whether it has emerged to face specific ecological constraints, we conducted an episodic-like memory task with seven *Octopus vulgaris*. Only one individual learnt the replenishing rates during training and subsequently showed episodic-like memory ability, whereas the other individuals favoured simpler foraging strategies, such as avoidance of familiarity and alternation, use of a win–stay strategy and risk sensitivity. A high variability in the use of these strategies was observed between and within individuals throughout training. As octopuses seem to live under lighter environmental pressure than cuttlefish, they may not need to rely on episodic-like memory ability to optimize foraging as cuttlefish do. These results highlight the differences in the use of complex cognitive abilities between cuttlefish and octopuses, which might be linked to different environmental and predatory constraints.

KEY WORDS: Cephalopod, Cognitive ability, Foraging strategies, Individual variability

INTRODUCTION

Episodic-like memory is the ability of an animal to remember the content ('what'), the spatiotemporal context ('where' and 'when' or 'which') and the source (contextual details such as the sensory modality of the content, the emotional valence, etc.) of a single event (Clayton et al., 2003). The ability to remember, in an integrated manner, the what, where and when (how long ago) of an event has been shown in several taxa, including corvids (Clayton and Dickinson, 1998; Zinkivskay et al., 2009), rodents (Babb and Crystal, 2006) and apes (Ban et al., 2014; Martin-Ordas et al., 2010). Amongst invertebrates, common cuttlefish also show episodic-like memory ability (Jozet-Alves et al., 2013). In this experiment, the cuttlefish's ability to remember what they ate (shrimp or crab), where (position of the target) and how long ago (1 or 3 h) was tested. Identical targets at distinct locations (unique locations on each day) were associated with each prey type. Whereas the less-preferred crab supply was replenished after any delay, the preferred shrimp supply was replenished only after a long delay

(3 h). Cuttlefish quickly learnt to go to the target delivering the preferred shrimp after a long but not after a short delay. Cuttlefish showed great capacity for the task, understanding the rules of the task in about 20 trials (Jozet-Alves et al., 2013). A subsequent study confirmed the impressive memory abilities of cuttlefish, showing that their episodic-like memory does not fade, even in old age (Schnell et al., 2021a). Another recent study showed that cuttlefish possess the ability to retrieve the sensory modality (seeing or smelling a prey) of a past event (Billard et al., 2020b), indicating that cuttlefish can bind the source of a memory in addition to remembering the content and the spatiotemporal context of their memory.

We can question why cuttlefish possess episodic-like memory ability. The first hypothesis is that this ability is shared with other large-brained cephalopod species as the result of their shared phylogeny. The second hypothesis is that episodic-like memory has emerged in cuttlefish to cope with specific ecological challenges such as explained in the ecological intelligence hypothesis (Byrne, 1997; Milton, 1981) and in the predator–prey interaction hypothesis (van der Bijl and Kolm, 2016). Indeed, cuttlefish have to be constantly aware of predators while hunting, which requires time and energy and thus impacts fitness. Their prey are often spatiotemporally dispersed in patches which often do not offer shelters. Thus, when cuttlefish cannot minimize their risks by hunting from a hide, they may have to use an array of cognitive skills to find preys at the right place and time, such as spatial memory (Jozet-Alves et al., 2014), value-based decision making (Kuo and Chiao, 2020) or overcoming immediate gratification in order to obtain better prey (Schnell et al., 2021b). However, rather than being a coping ability to ecological challenges, we can also hypothesize that episodic-like memory in cuttlefish could be a mere by-product of the evolution of its complex cognition. It would have emerged from other abilities required by the cuttlefish to hunt and avoid predators, without any particular need for episodic-like memory itself.

Octopuses appear to be worthwhile species in which to explore the evolution of episodic-like memory ability in cephalopods. Indeed, some species, such as *Octopus vulgaris*, live in a similar environment to that of cuttlefish, as they are both shallow-depth bottom dwellers (Hanlon and Messenger, 2018), but possess different means to handle their environmental constraints. Indeed, because of their lack of an internal shell and their highly prehensile arms, octopuses possess a wider range of defensive strategies. While cuttlefish mainly use crypsis for defence, octopuses can also hide in crevices, arrange a shelter, cover themselves in rocks and shells in order to avoid attacks, or defend themselves aggressively against predators (Hanlon and Messenger, 2018). Consequently, octopuses may wander more easily in the open instead of relying on strategies minimizing the time spent out of safety as cuttlefish do. Moreover, thanks to their complex arms, the octopus diet is broader than that of cuttlefish as octopuses can consume bivalves and gastropods, in

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addition to decapods, fishes and other cephalopods (Anderson et al., 2008; Mather et al., 2012). Thus, while cuttlefish hunt moving prey living in patches, which may come back to suitable patches quickly, octopus forage partly on sessile prey such as bivalves, which replenish over very long time scales. Whereas remembering what was eaten where and when might be useful for cuttlefish, it might be unnecessary for octopuses. Instead, octopuses might rely on simpler foraging strategies based on rules of thumb to optimize foraging efficiency (Levine, 1959), such as: (a) familiarity, a memory process which uses a signal-detection function whereby elements exceeding a fixed criterion are recognized as having been perceived before (Yonelinas, 2001) – while foraging, individuals relying on this strategy will favour places they have already visited rather than exploring new ones; (b) risk sensitivity, the forager's response to variance in food reward rate when choosing what to eat (Young et al., 1990) – risk-averse individuals will favour food rewards that are always available but of less quality, while risk-prone individuals will look for food rewards of higher quality but random availability; (c) spontaneous alternation, the tendency to explore places that have been least recently explored (Ramey et al., 2009); and (d) win–stay/win–shift strategies, used when subjects either repeat (stay) or avoid (shift) their last choice, depending on whether the choice was previously rewarded (win) or not (Kamil, 1983).

In order to assess whether octopuses keep track of time when different food sources vary in space and time or whether they favour simpler foraging strategies, we first evaluated their ability to learn replenishing rates of preferred versus less-preferred food items (procedure adapted from Jozet-Alves et al., 2013). Octopuses succeeding this task were subsequently tested to assess their episodic-like memory ability (what–when–where experiment, adapted from Jozet-Alves et al., 2013). Given octopuses' ecology, we expected them to favour simpler foraging strategies rather than relying on time-tracking strategies as cuttlefish do, which could indicate that cuttlefish complex memory abilities might have arisen from their ecological and predator–prey interaction specificities.

MATERIALS AND METHODS
Ethical statement
Experiments were conducted in accordance with the directive 2010/63/EU (European Parliament) and with the French regulation applied to the protection and use of animals in research experiments. Procedures were approved (#22429 2019101417389263 v2) by the ethical committee of Normandy region (Comité d'Ethique de Normandie en Matière d'Expérimentation Animale, CENOMEXA; agreement number 54).

Subjects
The subjects used in the experiments were sub-adult common octopuses (Octopus vulgaris Cuvier). Octopuses were collected in the Mediterranean Sea by specialized fishermen (Carrodano, Poissons vivants, La Ciotat, France) in September 2020 (batch 1, $n=3$) and January 2021 (batch 2, $n=4$) (see Table 1 for names and sex). They

were transported to the marine station of the University of Caen (Centre de Recherche en Environnement Côtier, Luc-sur-Mer, France). Their size (dorsal mantle length) ranged from 5–10 cm at the beginning of the experiment to 15–20 cm at the end. They were individually housed firstly in glass tanks of 50×50×50 cm and transferred to glass tanks of 100×50×50 cm or 120×40×50 cm as they grew. Octopuses were maintained in circulated semi-artificial seawater (salinity: 37 g l^{-1}, Instant Ocean Salt – Aquarium systems; 17±1°C, 7.8<pH<8.2; [NH$_3$+NH$_4^+$]<0.25 mg l^{-2}, [NO$_2$]<0.2 mg l^{-2}; [NO$_3$]<50 mg l^{-2}), with artificial lighting following the natural light cycle. A sand bed, pebbles, shells and a shelter in the form of a terracotta pot or a PVC tube were provided in each tank. Octopuses were fed daily outside the experimental trials with live crabs (Hemigrapsus sanguineus or Carcinus maenas), thawed or live shrimps (Crangon crangon), pieces of thawed fish (mackerel Scomber scombrus, pollock Theragra chalcogramma, herring Clupea harengus and whiting Merlangius merlangus). Mussels (Mytilus edulis) were always available in the home tanks.

Procedure
Experiments were conducted in the home tank of each animal. Octopuses were pre-trained and tested for food preference (Fig. S1), before starting the replenishing rate training (see Supplementary Materials and Methods for details).

Replenishing rate training
Octopuses were trained to learn that two different prey types (preferred versus less-preferred prey types; determined for each individual during the food preference test) were available at specific locations and after specific delays (1 or 3 h delay; Fig. 1). Octopuses were tested 5 days a week, one trial per day, with each trial consisting of two presentations separated by either a short (1 h) or a long (3 h) delay. During each presentation, octopuses were simultaneously presented with two closed opaque pots. Each pot contained a different prey item. The position and the content of the two pots were kept the same throughout the trials ('where' and 'what' components were fixed for an individual for all the replenishing rate training).

During the first presentation of a trial, the octopus could open and consume the contents of each pot, and the pots were removed after 30 min. At the end of this delay, if octopuses did not open or consume the contents of both pots (a partial consumption of the less-preferred food item was tolerated), the experiment was postponed to the next day. The second presentation was conducted after either a short delay (1 h) or a long delay (3 h). Delays (either short or long) were pseudorandomized, so the same delay could not be repeated more than 3 days in a row. Pots were replenished according to the elapsed time since the first presentation. Following a short delay (1 h), only the pot containing the less-preferred food item was replenished. Following a long delay (3 h), both pots were replenished. The octopus could only consume the contents of one pot, the second pot being removed with a small net immediately after the

Table 1. Food preference of each octopus

	Suricate	Abe	Pipoune	Coquille	Rosy	Tickle	Teddy
Batch	1	1	1	2	2	2	2
Sex	Male	Female	Female	Female	Female	Female	Female
Preferred prey	Crab (10)*	Crab (10)*	Crab (11)**	Crab (10)*	Crab (11)**	Crab (10)*	Crab (11)**
Less-preferred prey	Whiting (2)	Shelled mussel (2)	Mackerel (1)	Shrimp (2)	Shrimp (1)	Pollock (2)	Shrimp (1)

Food preference was assessed by presenting two different prey types to octopuses during 12 consecutive trials. Octopuses chose a prey item by grabbing it and eating it. Numbers within parentheses correspond to the number of times a prey item was chosen during the test. Asterisks indicate a significant preference for crabs [binomial test, *P=0.039 (<0.05), **P=0.006 (<0.01)].
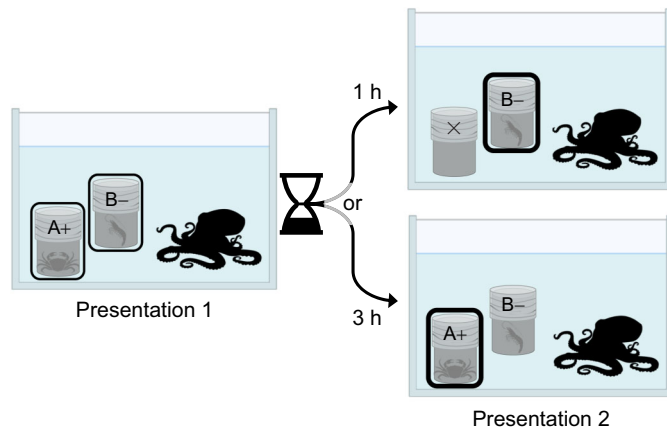
Fig. 1. Organization of a training trial. During presentation 1 of each trial, octopuses opened both opaque pots to consume their preferred food (A$^+$) and their less-preferred food (B$^-$). After either a short (1 h) or a long (3 h) delay, both pots were presented a second time. After a 1 h delay, the pot previously containing A$^+$ was empty (X), and thus octopuses had to go to the pot containing B$^-$ to realize a successful choice. After a 3 h delay, food was available in both pots, and choosing the pot containing A$^+$ was considered a successful choice. The position of the pots remained unchanged within trials. The position was altered between trials for the episodic-like memory task, but not for the replenishing rate task.

choice. A choice was considered correct when an individual chose the pot containing the less-preferred food after a short delay, and the pot containing the preferred food after a long delay.

The acquisition criterion was fixed at eight correct choices out of 10 consecutive trials, as per Jozet-Alves et al. (2013). The maximum number of training trials was set to 40, corresponding to double the number of trials cuttlefish needed to reach the acquisition criterion during previously published experiments (Jozet-Alves et al., 2013; cuttlefish learnt the replenishing rate in 21±4 trials). However, as the first batch of octopuses (n=3) did not reach the criterion in 40 trials, a second batch of octopuses (n=4) was subsequently created and the maximum number of training trials was set at 80. In the case of an octopus reaching seven correct responses out of 10 consecutive trials at its 40th (first batch) or 80th (second batch) trial, three supplementary trials were conducted to test whether the octopus would reach the learning criterion within this extended period of training.

Episodic-like memory task
Individuals which reached the acquisition criterion of the replenishing rate training within the pre-set number of trials were tested in the episodic-like memory task. This task was similar to the replenishing rate training task, except that the pots were randomly placed in any location in the tank and this location changed between each trial, while staying the same across the two presentations of a trial. During each trial, octopuses had to remember what prey was in each pot (what–where) and how much time had elapsed since the first presentation: the spatiotemporal information was thus unique. We considered that octopuses showed episodic-like memory ability when they realized 10 correct choices out of 12 consecutive trials (binomial test, P=0.039), with the maximum number of trials set to 40 trials.

Analysis
Data were analysed using R software (v. 3.5.1), using binomial tests for food preference tests and choices of octopuses. To investigate

the favoured strategies, we analysed choices in the second presentation for both batches as well as individual choices of octopuses during the replenishing rate training. Only the first 40 training trials were considered and analysed as we wanted to compare all octopuses, whether they were from the first batch (i.e. trained for 40 trials) or from the second batch (i.e. trained for 80 trials). Two-tailed Fisher exact tests were used to compare the use of one strategy between the first and the last 20 trials of training. It should be noted that for alternation and win–shift/win–stay strategies, the choice on the first trial was excluded from the analyses, as there was no previous reference trial. Therefore, we analysed 39 trials and compared the first 20 trials with the last 19 trials of training for these strategies. To simplify understanding of the following sections, we will use the expressions '40 trials' and 'first and last 20 trials' for all strategies.

In addition to replenishing rate learning, four strategies were explored in the second presentation of all trials: (a) familiarity, (b) risk sensitivity, (c) spontaneous alternation and (d) win–stay/win–shift. They can be split into two subcategories: within-trial strategies, where choices in the second presentation depend on the outcome of the first presentation, such as familiarity and risk sensitivity; and between-trials strategies, where choices in the second presentation of a trial depend on the outcome of the second presentation of the previous trial, such as spontaneous alternation and win–stay/win–shift. More precisely, each strategy was defined as the following: (a) familiarity (Fig. 2A) was observed when subjects chose the most familiar pot during the second presentation, which was the last opened (i.e. second opened) pot during the first presentation; (b) risk sensitivity (Fig. 2B) was observed when subjects preferentially chose one prey over the other during the second presentation of a trial – during this presentation, the less-preferred prey was always available no matter the delay, and hence was less risky, whereas the preferred prey was available half of the time (absent after a delay of 1 h, and present after a delay of 3 h), and was hence riskier; (c) spontaneous alternation (Fig. 2C) was observed when subjects alternated their choice between pots during the second presentation of each trial; and (d) win–shift/win–stay (Fig. 2D) was observed when subjects which won (obtained food in a given pot) during the second presentation of a first trial shifted their choice for the other pot (win–shift) or maintained their choice for the same pot (win–stay) during the second presentation of the next trial. The lose–shift/lose–stay counterpart of this strategy was not studied as instances of 'lose' were statistically scarce (1/4 of the trials if subjects chose by chance).

RESULTS
Food preference
All octopuses presented a significant preference for crabs (binomial test, P<0.039; Table 1). Less-preferred prey varied between individuals, with some octopuses tested with thawed fishes (whiting, mackerel or pollock), others with fresh shrimp or shelled mussels.

Replenishing rate training and episodic-like memory task
In the first batch (maximum number of training trials set at 40), none of the three octopuses reached the established learning criterion (i.e. eight correct choices out of 10 consecutive trials). In the second batch (maximum number of training trials sets at 80), only one individual (Teddy) out of four reached the learning criterion in 43 trials (Fig. S2). One individual (Tickle) reached seven correct responses out of 10 successive trials at its last trial (80th), but its performance did not improve in the three supplementary trials.
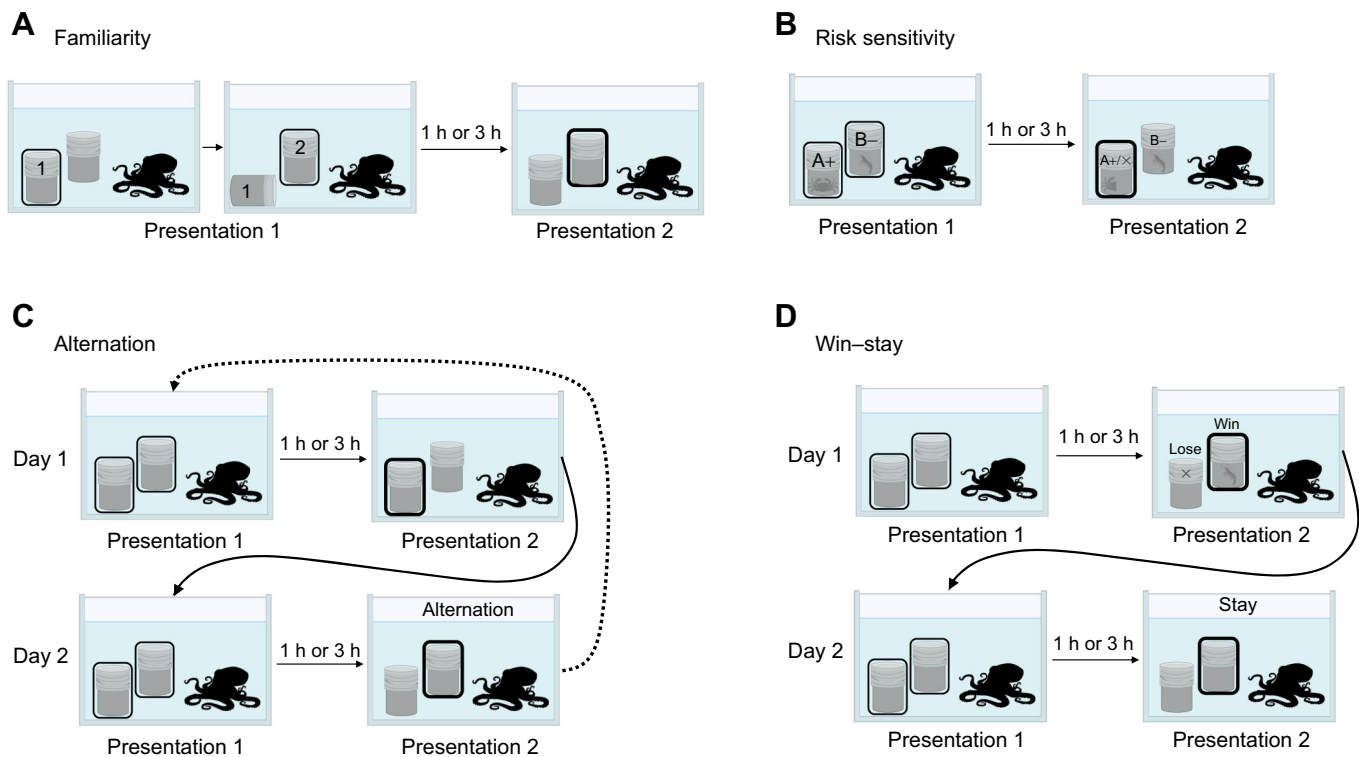
Fig. 2. Representation of strategies used by octopuses during the replenishing rate training. (A) Familiarity. During presentation 1, octopuses choose a first pot, then a second one. On presentation 2, they choose the pot last visited. (B) Alternation. Octopuses choose one pot on presentation 2 of a trial (1), and then choose the opposite pot on presentation 2 of the following trial (2). (C) Risk sensitivity. During presentation 2, the pot containing the less-preferred food is less risky (B−) than the pot containing the preferred food (A$^+$/X), as the less-preferred food is always available whereas the preferred food is available randomly if delays cannot be discriminated. The representation shows the choice of a risk-prone individual. (D) Win–stay strategy. On presentation 2, pots can either be a 'win', when replenished, or a 'lose', when empty. When octopuses open a pot with food inside on the second presentation during a trial (1; 'win'), then on the second presentation of the following trial (2) they choose the same pot as in the previous trial ('stay'), they use a win–stay strategy. '×' indicates empty pot.

Only Teddy was subsequently tested in the episodic-like memory task. She reached the acquisition criterion and thus succeeded in the task in 21 trials.

Strategies
If we consider the first 40 trials of training of all individuals (Fig. 3A), octopuses showed a significant avoidance of familiarity (109 familiarity choices out of 280 presentations, binomial test, $P<0.001$); they showed significant constancy rather than alternation (114 alternations out of 272 presentations, binomial test, $P=0.009$); and they significantly favoured a win–stay over a win–shift strategy (118 choices consistent with win–stay strategy out of 198 'win' presentations; binomial test, $P=0.008$). However, no significant preference could be observed for the less or more risky option (154 choices of the risky option out of 280 presentations; binomial test, $P=0.107$). Nevertheless, when distinguishing the first and the last 20 trials of training (Fig. 3B), octopuses were significantly more risk prone during the first 20 trials than during the last 20 (87/140 versus 67/140, two-tailed Fisher exact test, $P=0.022$). We note here that the preference for one prey over the other was not significant for the first pot opened during the first presentation (149/280, binomial test, $P=0.310$).

At the individual level, high variability in the strategies used was observed (Table 2, Fig. 4).

Suricate showed no significant use of familiarity (23/40, binomial test, $P=0.430$) but he presented a significant risk aversion (10/40, binomial test, $P=0.002$); he showed constancy by choosing the same pot for nine consecutive trials out of the last 10 training trials

(binomial test, $P=0.004$); and he significantly used a win–stay strategy during training (24/35, binomial test, $P=0.041$).

Abe showed significative avoidance of familiarity (12/40, binomial test, $P=0.017$); she presented a strong risk proneness (31/40, binomial test, $P<0.001$), combined with a clear preference for her preferred prey even when choosing the first pot to open during the first presentation (29/40, binomial test, $P=0.006$); she showed constancy by choosing the same pot for 10 consecutive trials in the second half of training (binomial test, $P=0.002$); but she did not significantly use a win–stay or win–shift strategy during training (13/25, binomial test, $P=1$).

Pipoune showed a significative avoidance of familiarity (13/40, binomial test, $P=0.039$) which was delay dependent: she avoided the familiar pot after a long delay but not after a short one (3/20 versus 10/20, two-tailed Fisher exact test, $P=0.041$); she presented risk sensitivity, with this sensitivity reversed between the first 20 and the last 20 training trials (16/20 versus 5/20, two-tailed Fisher exact test, $P<0.001$, Fig. S3): she was risk prone during the first 20 trials (16/20, binomial test, $P=0.012$), then risk averse for the following 20 trials (5/20; binomial test, $P=0.041$); she showed constancy by choosing the same pot nine times out of 10 consecutive trials in the second third of training (binomial test, $P=0.021$); but she did not significantly use a win–stay or win–shift strategy during training (20/29, binomial test, $P=0.061$).

Coquille showed avoidance of familiarity, by choosing the unfamiliar pot nine times out of 10 consecutive trials in the last 10 trials of training (binomial test, $P=0.021$); she presented a significant risk proneness in the first 20 training trials
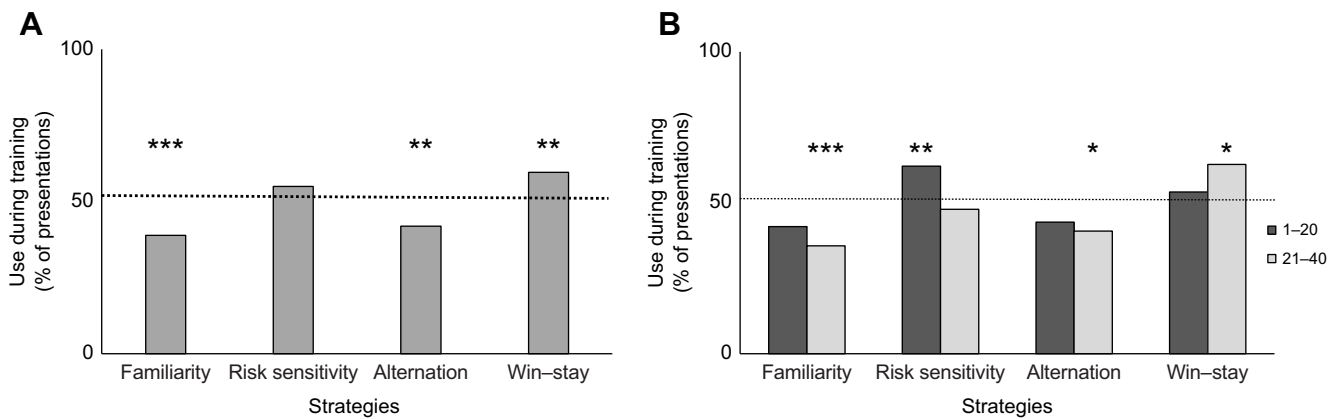
Fig. 3. Percentage of octopuses (*n*=7) using each strategy during replenishing rate training. See Materials and Methods and Fig. 2 for a description of these strategies. (A) Use of each strategy throughout the 40 training trials. (B) Use of each strategy throughout the training divided between the first and the last 20 trials. Risk sensitivity is expressed in the number of risky choices. Over their training, octopuses significantly avoided the use of familiarity, favoured constancy rather than alternation, and favoured a win–stay rather than a win–shift strategy. Individuals did not seem to show risk sensitivity when taking the 40 training trials together, but risk proneness was observed in the first 20 training trials (1–20) then disappeared in the following 20 trials (21–40). The other strategies were not observed in the first 20 training trials, but they were employed in the following 20 trials. Asterisks represent a significant difference from chance (i.e. dotted line; binomial test, *$P<0.05$, **$P<0.01$, ***$P<0.001$).

(15/20, binomial test, $P=0.042$), but this seemed to disappear in the following 20 trials (15/20 versus 8/20, two-tailed Fisher exact test, $P=0.054$; Fig. S3), with no significant risk sensitivity displayed anymore (8/20, binomial test, $P=0.503$); she showed alternation by choosing a different pot during 10 consecutive trials in the second 20 trials of training (binomial test, $P=0.002$); but did not significantly use a win–stay or win–shift strategy during training (10/26, binomial test, $P=0.327$).

Rosy showed no significant use of familiarity (19/40, binomial test, $P=0.875$); neither did she present risk sensitivity (25/40, binomial test, $P=0.154$); she showed constancy by choosing the same pot nine times out of 10 consecutive trials in the second 20 trials of training (binomial test, $P=0.021$); but she did not significantly use a win–stay or win–shift strategy during training (13/27, binomial test, $P=1$).

Tickle showed significative avoidance of familiarity (13/40, binomial test, $P=0.038$); she presented risk aversion, by choosing the 'safe' pot with her less-preferred food for 16 out of 20 consecutive trials between her 10th and 30th training trial (binomial test, $P=0.012$); but she did not significantly use constancy or alternation (19/39, binomial test, $P=1$); not did she use a win–stay or win–shift strategy during training (16/30, binomial test, $P=0.856$).

Teddy showed no significant use of familiarity (22/40, binomial test, $P=0.636$); but she presented risk proneness (27/40, binomial test, $P=0.038$); she presented constancy by choosing the same pot 15 times out of 20 consecutive trials in the second 20 trials of

training (binomial test, $P=0.041$); and she significantly used a win–stay strategy during training (19/26, binomial test, $P=0.029$).

DISCUSSION

In our study, seven common octopus (*O. vulgaris*) were tested in a task requiring them to keep track of time with different food sources varying in space and time. Most octopuses (six out of seven) relied on less-cognitively demanding strategies than keeping track of time during the replenishing rate learning task. Only one octopus learnt the replenishing rates of different prey types and was able to use these rules to solve an episodic-like memory task. When analysing the strategies used by tested octopuses during the replenishing rate training, such as familiarity, risk proneness, spontaneous alternation and win–stay, we observed above all a high interindividual variability.

We conducted this experiment to determine whether episodic-like memory is an ability shared by modern cephalopods, and thus present in both cuttlefish and octopuses, or whether it is instead a distinctive ability of cuttlefish to cope with specific ecological constraints. One individual (Teddy) learnt the replenishing rate of the different food items and subsequently succeeded in the episodic-like memory task. This may indicate that *O. vulgaris* possesses the neural prerequisites for episodic-like memory. Both cuttlefish and octopuses possess a central nervous system with similar brain shape and structures (Wang and Ragsdale, 2019). The vertical lobe is notably thought to be the place of higher cognitive functions (Shigeno et al., 2018), and it could be the basis of episodic-like memory ability for both species. If this is the case, we could

Table 2. Strategies used by each individual

Strategy	Suricate	Abe	Pipoune	Coquille	Rosy	Tickle	Teddy
Familiarity		Familiarity avoidance	Familiarity avoidance (3 h)	Familiarity avoidance		Familiarity avoidance	
Risk sensitivity	Averse	Prone	Prone (2–21) Averse (22–40)	Prone (2–21)		Averse	Prone
Alternation	Alternation	Constancy	Constancy	Alternation	Constancy		Constancy
Win–stay	Win–stay						Win–stay

The use of four different foraging strategies was analysed during the 40 training trials of each octopus: familiarity ('3 h' indicates a significant use of the strategy only after the 3 h delay), risk sensitivity (numbers in parentheses indicate use of the strategy during the first 20 or last 19 training trials), alternation and win–stay strategies. See Materials and Methods and Fig. 2 for a description of these strategies.
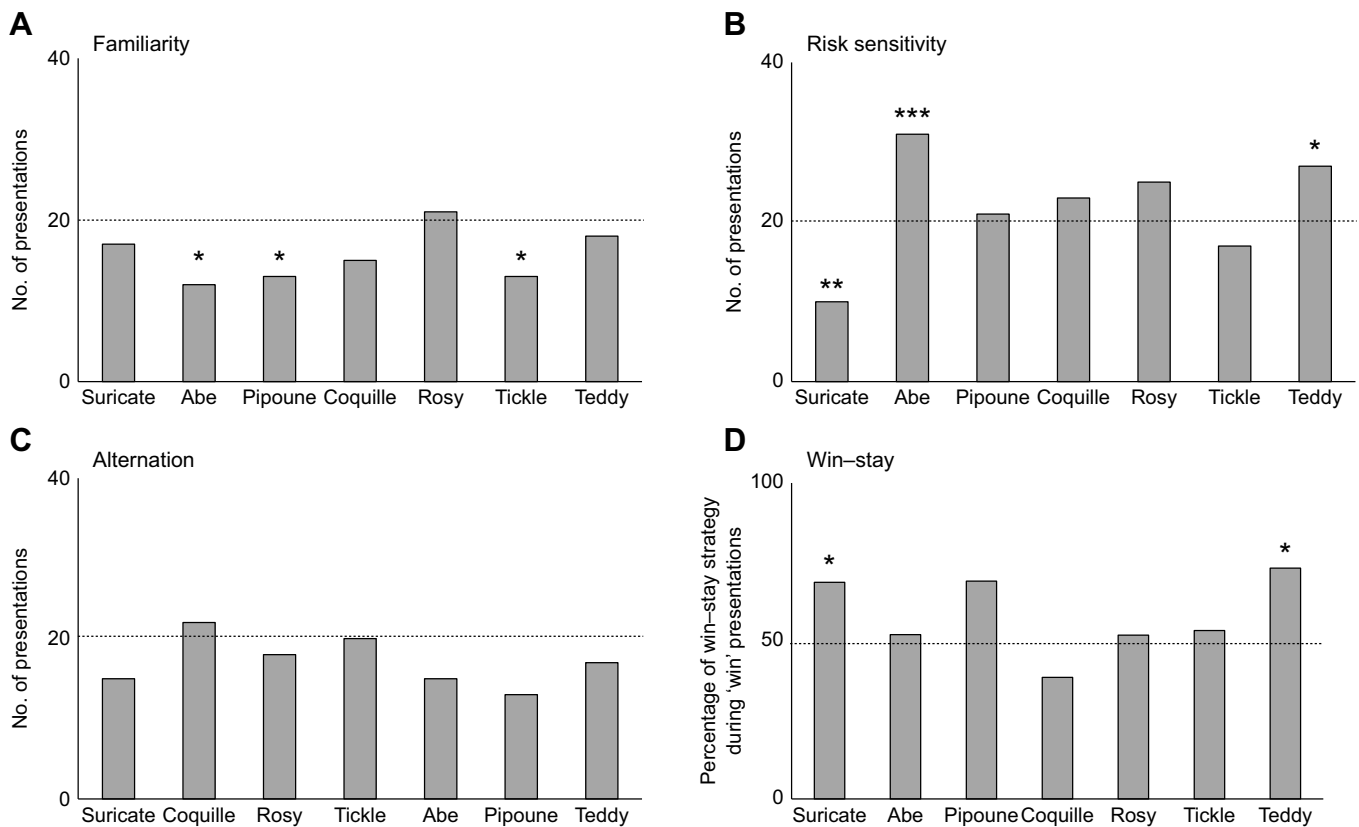
Fig. 4. Individual use of each strategy during replenishing rate training. See Materials and Methods and Fig. 2 for a description of these strategies. (A) Familiarity. (B) Risk sensitivity (number of risky choices). (C) Alternation. (D) Win–stay. During the 40 training trials, each individual favoured different strategies, with a high interindividual variability. Asterisks represent a significant difference from chance (dashed line indicates chance level; binomial test, *$P<0.05$, **$P<0.01$, ***$P<0.001$).

hypothesize that episodic-like memory may be an ability shared by cephalopods in general. As stated in the ecological intelligence hypothesis (Byrne, 1997; Milton, 1981) and in the predator–prey interaction hypothesis (van der Bijl and Kolm, 2016), such cognitive skill might be necessary to cope with the ecological constraints shared by cephalopods. Indeed, as they all evolve under high predatory pressure without a shell to protect themselves, they need to sustain their exponential growth by finding substantial amounts of food. However, other complex cognitive skills might allow them to efficiently find prey and avoid predators, and we cannot rule out the possibility that episodic-like memory might not be necessary and might rather be a simple by-product of the evolution of other cognitive abilities.

Nevertheless, we have to note that only one individual relied on episodic-like memory ability whereas most octopuses relied on other simple foraging strategies. We can only speculate why most tested octopuses did not learn the replenishing rate task successfully. Firstly, we consider the inability of most octopuses to learn the replenishing rates was not due to an insufficient number of training trials. Indeed, with the first batch of octopuses, we conducted two times more trials (i.e. 40) than needed by cuttlefish to learn the replenishing rates in previous studies (i.e. 20 trials on average in Jozet-Alves et al., 2013, and Schnell et al., 2021b), and doubled this number of trials (i.e. 80) with the second batch. In this second batch, one octopus reached the learning criterion in 43 trials, but the three other octopuses which were given twice this number of trials did not show any signs of replenishing rate learning. Secondly, the fact that mussels were available at all times in the tank

may have hindered the motivation to learn the replenishing rates. It might have lowered the pressure to find food, thus favouring random and simpler foraging strategies. However, this hypothesis is unlikely, as we observed that during the first months of the experiment, octopuses almost never consumed mussels, and while the quantity of consumed mussels slowly rose over the months, it remained quite a rare occurrence. Moreover, we observed that crabs always keenly drew octopuses' attention during our experiment, even when they had been fed shortly before. Indeed, cephalopods seem to possess strong hedonic motivation for their preferred food, like cuttlefish refraining from eating a less-preferred food available at all times when they know that their preferred food will be ensured at the end of the day (Billard et al., 2020a).

Thirdly, octopuses may not spontaneously encode the temporal component of their episodic-like memories in terms of 'how long ago' or may, but with a low accuracy: they might not, or hardly, detect the difference in elapsed delays of 1 or 3 h. 'How long ago', known as temporal distance, is often used to study the temporal feature of episodic-like memory (e.g. Babb and Crystal, 2006; Clayton and Dickinson, 1998; Feeney et al., 2009), but it is not the only way to encode time. Indeed, time can be perceived in terms of temporal distance ('how long ago'), by evaluating the elapsed time between the encoding of an event and its retrieval; but also in terms of temporal location ('when'), by relying on information linked with the encoding time; or in terms of temporal order (or relative times), by retrieving the succession of events (Friedman, 1993, 2007). While humans thrive in all these temporal perceptions, animals may favour one over the other. For example, black-capped chickadees

rely more on temporal locations than distances (Feeney et al., 2011), rats seem to have difficulty in using temporal locations (Roberts et al., 2008; Zhou and Crystal, 2009), but easily remember the temporal order of events (Fortin et al., 2002), and rhesus monkeys cannot perceive temporal distances (Hampton et al., 2005), but can recall the temporal order of events (Templer and Hampton, 2013). The possible absence of temporal distance perception in octopuses would not rule out their potential to use episodic-like memory, as it can be observed through other temporal modalities as well: indeed, episodic-like memory ability was tested in rodents using temporal distance (Babb and Crystal, 2006), temporal location (Zhou and Crystal, 2009) and temporal order (Dere et al., 2005). These different experimental approaches could be tested with octopuses to explore their episodic-like memory ability. They would offer an insight into time perception in octopuses, to observe whether octopuses really do not keep track of elapsed time, or whether our experiment could not bring to light this ability.

Finally, our last supposition is that octopuses, instead of relying on episodic-like memory ability, rather favour simpler foraging strategies that do not require a heavy cognitive load. When exploring these foraging strategies in our two batches of octopuses, we observed a group-level avoidance of familiarity, with octopuses favouring the least familiar pot (i.e. choosing the same pot first during both presentations of a trial); a general risk proneness at the beginning of training, with octopuses favouring the pot containing the more preferred prey which was available half of the time; a general constancy, with octopuses favouring the same pot in the second presentation over trials; and a general win–stay strategy, with octopuses favouring the pot which provided them with a reward in the previous trial. Nevertheless, analysing the use of different strategies at the group level might not be ideal, as we observed a remarkable interindividual variability, with each octopus using and combining strategies in a different way from others. Coquille, for example, was the only individual using spontaneous alternation rather than constancy when choosing; Suricate and Teddy were the only ones significantly using a win–stay strategy; Rosy relied mostly on random choices; and Teddy was the only one to learn the replenishing rates. Pipoune showed even more distinctive traits: firstly, she used familiarity only after long delays, maybe because she favoured other strategies when the memory trace was stronger (i.e. after a short delay). Indeed, she used constancy, but also risk sensitivity. Secondly, she shifted from risk proneness to risk aversion. Empirical studies on risk sensitivity in vertebrates indicate that when risk comes from the variability in the amount or presence of a reward, animals are most frequently risk averse or risk indifferent (Kacelnik and Bateson, 1996). We can thus consider that Pipoune may have required 10–20 trials to learn that her preferred food was riskier than her less-preferred food, then she shifted to risk aversion. To sum up, instead of using episodic-like memory ability to optimize their food intake and succeed in the task, octopuses rather relied on individually variable strategies which seemed equally relevant to satisfy their food needs.

In the wild, foraging strategies are a complex trade-off between predatory and starvation risk: risk-prone individuals may enhance their chances of finding more or better food but may also enhance the risk of finding no food at all, while risk-averse individuals may more easily find food but of a lesser quantity and quality; individuals which use familiarity, constancy or win–stay strategies may enhance their chances of finding food but may also enhance the chances of a predator predicting their arrival (Stephens and Krebs, 1986). Field studies show that common octopuses use different foraging strategies, with some being opportunistic and others

selective, and interindividual variability is also observed among selective individuals as they are specialized in different types of prey (Anderson et al., 2008; Mather et al., 2012). Interindividual variability in foraging strategies is in fact a common trait of various predatory species [e.g. seabirds (Ceia and Ramos, 2015), seals (Cherel et al., 2009), fishes (Szopa-Comley et al., 2020), squids (Lorrain et al., 2011)]. The use of one strategy over the other is often considered to be linked to the physiological status of an individual and its prior experiences (Kacelnik and Bateson, 1996). However, the foraging specialization of wild octopuses did not seem to be explained by environment or the status of the individual alone (Mather et al., 2012). This also seems to be the case in our experiment, as the observed differences were not explained by any physiological or behavioural parameters such as sex, size, batch or food preference. Differences in strategies may rather come from intrinsic parameters such as personality traits, as hypothesized by Mather and colleagues (2012).

High individual variability, even outside foraging, seems to be common in, if not characteristic of, octopuses. Octopuses show clearly distinguishable personality traits, through differences in activity level, reactivity, boldness and aggressivity (Mather and Anderson, 1993; Pronk et al., 2010; Sinn et al., 2001). When looking at playful behaviour, octopuses demonstrate various interactions with objects, with some individuals showing possessiveness and playful interactions, and others simply ignoring them (Kuba et al., 2003, 2006). The personality profile of each individual might affect its cognitive performance (Carere and Locurto, 2011), and thus individual differences are striking in cognitive tasks, such as in the number of trials octopuses need to reach a learning criterion in a discrimination task (e.g. 224–1463, n=4; Bublitz et al., 2017); in the number of successful reversals in reversal experiments (e.g. 4–13; Bublitz et al., 2021); or in the number of days to work out problem-solving tasks, such as retrieving through a hole and opening a container (e.g. in 3–24 days, n=7; Richter et al., 2016).

Interindividual variability can be an advantage as it provides unpredictability, which is a major, although often overlooked, modulator of predator–prey interactions (Chang et al., 2017; Pettorelli et al., 2015). Indeed, variability in the foraging behaviour of octopuses may prevent prey from predicting their attacks, and also prevent predators from anticipating the arrival of their cephalopod prey. Individual variability seems to enhance the persistence of a species in an environment under predatory pressure (Morozov et al., 2013), but also seems to favour the dispersal and colonization of new environments (Nanninga and Berumen, 2014), which might thus have promoted the development of O. vulgaris in diverse and world-distributed environments (De Luca et al., 2014). In the common cuttlefish, variability in foraging strategies has also been documented. However, this variability seems mainly driven by age and environmental predictability: in the wild, juveniles appear more selective than adults, which present generalist and opportunistic behaviours (Neves et al., 2009; Pinczon du Sel et al., 2000). A lab-conducted experiment showed that cuttlefish have a selective foraging behaviour when exposed to a predictable feeding schedule, and they switch to an opportunistic and less-risky strategy when the environment becomes unpredictable (Billard et al., 2020a). Unlike octopuses, cuttlefish seem to display a low level of interindividual variability in foraging strategies under the same physiological and environmental conditions.

The need to optimize the time spent exposed to predators while foraging might have been the main driver of the emergence of episodic-like memory in cuttlefish, while octopuses seem to cope

with their environmental constraints by displaying a wide range of foraging strategies varying both within and between individuals. Octopuses and cuttlefish have evolved different lifestyles and cognitive strategies to deal with the environmental challenges they are exposed to, while possessing the same fundamental brain architecture (Wang and Ragsdale, 2019). Comparative studies undertaken in cuttlefish and octopuses show how necessary it is to integrate ecological, cognitive and neurobiological data to understand how complex cognition has emerged.

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Supplementary Materials and Methods

Pre-training method

The pre-training (constituted of five consecutive steps,

Figure S1) consisted in training octopuses to open two pots within 30 minutes two times a day to obtain a food reward. Plastic pots (70mm x Ø35mm) opacified with grey tape (from step 2) and hermetically closed with Parafilm® (from step 3) were used during the experiment.

First step: Octopuses were presented with one open transparent pot containing a crab they should grab and eat. Two trials were conducted per day. When octopuses ate the content of at least one pot for three consecutive training days, they went to step 2.

Second step (no access to visual cues): Octopuses were presented with one open pot surrounded by opaque tape containing a crab they should grab and eat. Three trials were conducted per day. When octopuses ate the content of the three pots within a day, they went to step 3.

Third step (no access to visual and olfactory cues): Octopuses were presented with one pot surrounded by opaque tape and tightly covered with Parafilm®. Three trials were conducted per day. When octopuses opened the three closed opaque pots within a day, they went to step 4.

Fourth step (no access to visual cues): Two open opaque pots were simultaneously presented in the tank (random positions along trials). Each pot contained a different prey, from the two prey items used for the preference test. When octopuses retrieved food items from the two pots in less than 30 minutes, two times a day for at least four out of five consecutive training days, they went to step 5.

Fifth step (no access to visual and olfactory cues): The procedure used was the same than the one used during step 4, excepting that pots were closed with Parafilm®. The octopus had to consume the food of the two pots in less than 30 minutes, two times a day for at least four out of five consecutive training days to start the replenishing rate training.

Food preference test

Prey preferences of each individual subject was tested between the step 3 and 4 of pre-training. General avoidance of certain types of food was noted during pre-training. Only preys which were not avoided were randomly tested two by two during the food preference tests. Two different prey types were placed at the tip of two steel wires and simultaneously presented at equal distances to the octopus (about 10 cm), with the right/left position of each prey type randomized between trials. The octopus chose a prey item by grabbing it and eating it. Preference was assessed when octopuses choose one type of food over the other in at least 10 out of 12 consecutive trials (binomial test, p=0.039).
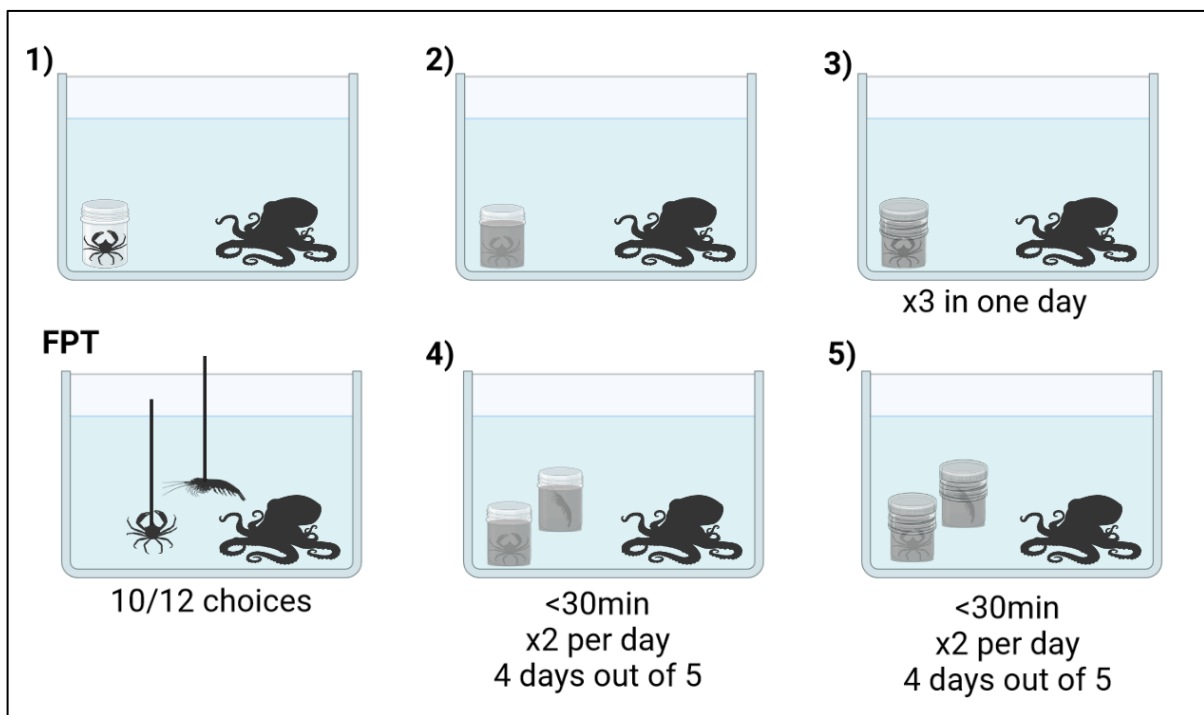

Fig. S1. Sequence of pretraining steps and the food preference test. 1) Step 1: Octopuse learn to grab a crab inside a transparent open pot; 2) Step 2: Octopuses learn to grab a crab inside an opaque pot; 3) Step 3: Octopuses learn to open a closed opaque pot to eat a crab; FPT: Food preference test during which octopuses are given 12 times a choice between two types of food to determine their preference; 4) Step 4: Octopuses learn to eat preys out of two open opaque pots in less than 30 minutes two times a day, at least four out of five consecutive training days; 5) Step 5: Octopuses learn to eat the preys out of two closed opaque pots in less than 30 minutes two times a day, at least four days out of five consecutive days.
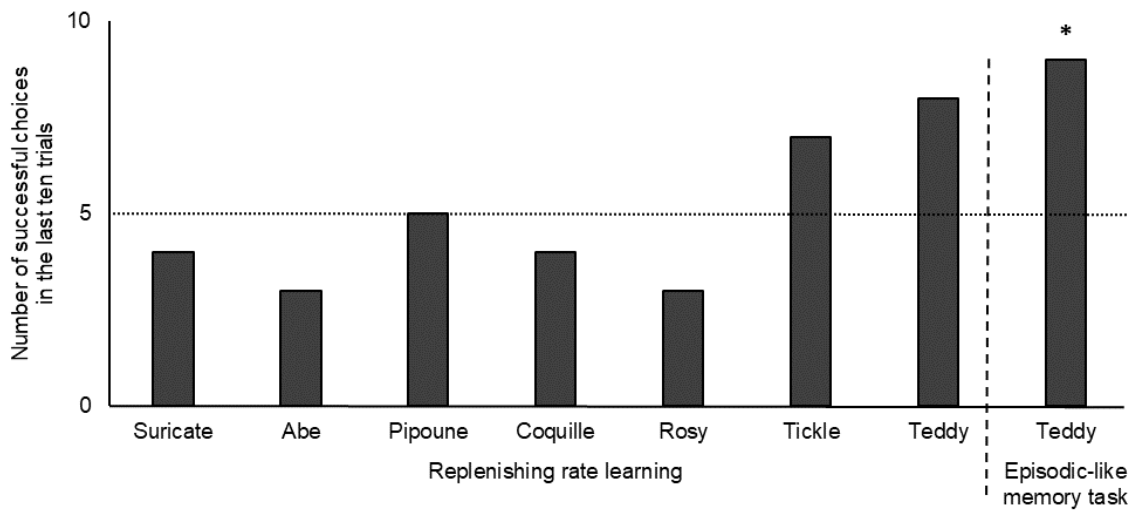
Fig. S2. Number of successful choices in the last ten trials of the replenishing rate training and the episodic-like memory task. None of the individuals, except Teddy, reached the learning criterion of eight successful responses out of ten consecutive trials during the replenishing rate training. Subsequently, only Teddy was tested in the episodic-like memory task, and reached the acquisition criterion of 10 out of 12 successive trials. The asterisk represents a number of success significantly different from chance (i.e. dotted line; binomial test, * p<0.05).
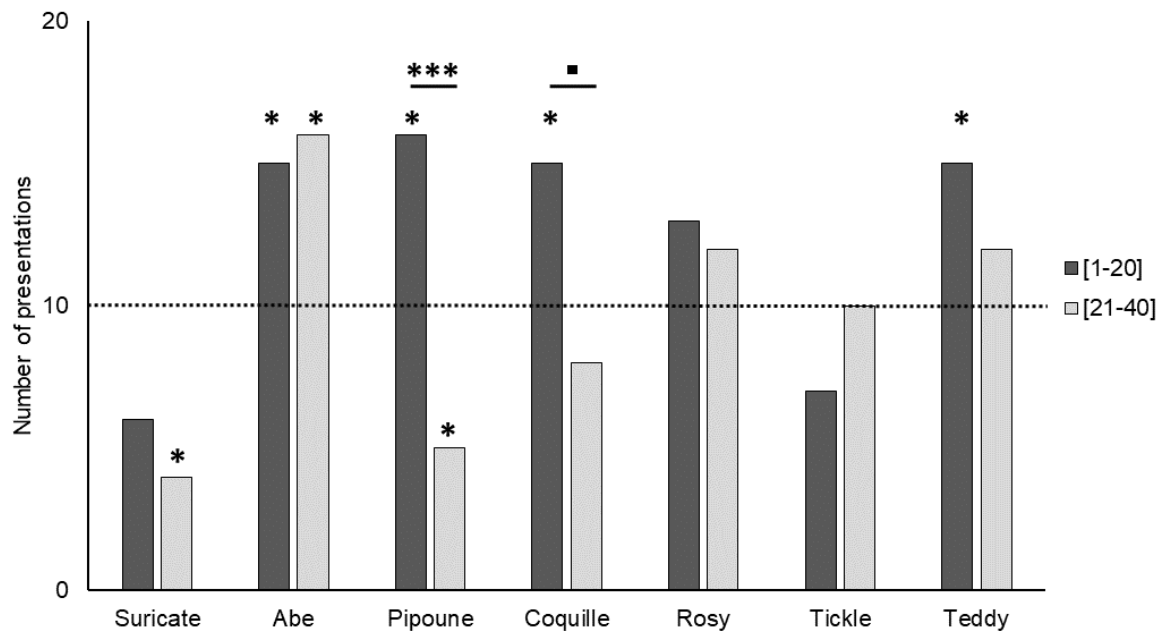
Fig. S3. Individual use of risk-sensitivity (in number of risky choices) during the first 20 and the last 20 trials of replenishing rate training (see methods and Fig.2 for description of risk-sensitivity). High inter-individual and intra-individual variability in risk-sensitivity was observed: some individuals did not show any risk-sensitivity throughout the training (Rosy, Tickle), while other showed a steady risk-proneness (Teddy) or risk-aversion (Suricate); and some others showed risk-proneness during the first 20 training trials and reversed to risk-aversion or risk-indifference during the last 20 training trials (Pipoune, Coquille). Asterisks represent significant difference from chance (*i.e.* dotted line; binomial test, ■ 0.06<p<0.05, * p<0.05, ** p<0.01, *** p<0.001).