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Cuttlefish exert self-control in a delay of gratification task

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The ability to exert self-control varies within and across taxa. Some species can exert self-control for several seconds whereas others, such as large-brained vertebrates, can tolerate delays of up to several minutes. Advanced self-control has been linked to better performance in cognitive tasks and has been hypothesized to evolve in response to specific socio-ecological pressures. These pressures are difficult to uncouple because previously studied species face similar socio-ecological challenges. Here, we investigate self-control and learning performance in cuttlefish, an invertebrate that is thought to have evolved under partially different pressures to previously studied vertebrates. To test self-control, cuttlefish were presented with a delay maintenance task, which measures an individual's ability to forgo immediate gratification and sustain a delay for a better but delayed reward. Cuttlefish maintained delay durations for up to 50–130 s. To test learning performance, we used a reversal-learning task, whereby cuttlefish were required to learn to associate the reward with one of two stimuli and then subsequently learn to associate the reward with the alternative stimulus. Cuttlefish that delayed gratification for longer had better learning performance. Our results demonstrate that cuttlefish can tolerate delays to obtain food of higher quality comparable to that of some large-brained vertebrates.

1. Introduction

Self-control, the ability to overcome immediate gratification in favour of a better but delayed reward, is a vital cognitive skill that underpins effective decision-making, goal-directed behaviours and future planning [1–5]. In humans, self-control has been linked to cognitive performance, whereby individuals who delay gratification for longer achieve higher scores in a range of academic tasks [6–10]. A recent study on chimpanzees has also demonstrated a link between self-control and cognitive performance, showing that their ability to delay gratification was correlated positively with performance across 13 cognitive tasks [11]. Yet, whether self-control is linked to cognitive performance in non-primate taxa remains to be tested.

The ability to delay gratification not only varies within but also across taxa. For example, relative degrees of self-control are typically higher in non-human great apes (henceforth apes), corvids and parrots [12–18]. By contrast, other taxa such as some monkey species, rodents, chickens and pigeons [19–24] find it difficult to inhibit the consumption of a desirable food item for a delayed gain and thus exhibit relatively lower degrees of self-control. Increased delayed gratification abilities have been attributed to a variety of factors including life-history characteristics, whereby larger species with lower metabolisms and longer life expectancies can potentially tolerate longer delays [25]. Specific socio-ecological factors might also influence self-control abilities across taxa. For example, social species that rely on cooperation to survive might exhibit advanced self-control because an individual must overcome immediate

gratification to help a conspecific in the present in order to receive a reciprocated favour in the future [26]. It has also been suggested that species that rely on variable food resources that are difficult to obtain or risky to retrieve possess advanced self-control because the ability to wait for the optimal moment to forage or hunt might increase their chances of success [27].

Currently, it is difficult to uncouple the factors that influence self-control because many of the previously studied species share similar life histories and face similar socio-ecological challenges. To illustrate this dilemma, consider the following example. Some species of apes and corvids are faced with the social challenge of sharing food with conspecifics [28–33]. To cooperate better with sharing affiliates, self-control may have evolved in these species to inhibit individuals from solely basing foraging decisions on their own needs. At the same time, both apes and corvids are faced with the ecological challenge of relying on variable and unpredictable food resources [34,35]. Consequently, self-control might have emerged in apes and corvids to inhibit eating food items immediately, dissociate current and future motivational needs, and to plan for future needs during periods of food scarcity. This type of future-oriented foraging could either be governed by cognitive abilities such as future planning [36–38] or through standard associative mechanisms such as incentive learning [39].

Here, we investigate self-control in the common cuttlefish (*Sepia officinalis*), a cephalopod mollusc related to octopus and squid, that has a fast metabolism, a short lifespan (i.e. typically shorter than 2 years) and lives in relatively simple social environments that do not require cooperation [40]. Cuttlefish, however, are faced with significant ecological challenges because they prey on transitory resources that demand substantial periods of exploration to locate and seize [41]. These demands are likely to have triggered advanced navigation [42,43], learning and memory abilities [44–46] in these large-brained molluscs. Indeed, several studies have demonstrated that cuttlefish are able to optimize their foraging behaviour through learned valuation (i.e. relative values of different prey items) [47] and by using sophisticated memory and future-oriented feeding strategies. For example, cuttlefish can remember *what*, *where* and *when* components of previous foraging encounters [48] and can quickly adjust their foraging behaviour in response to changing prey conditions by learning and remembering patterns of food availability [49,50]. Such dynamic feeding patterns are described as future-oriented behaviours because the decision-making processes involved are influenced by previous experiences and proximate-future expectations. However, it remains unclear whether future-oriented foraging in cuttlefish is also governed by the ability to exert self-control.

To investigate self-control, we use an inter-temporal delay maintenance task, which measures an individual's ability to choose a preferred outcome (i.e. choose between prey of different quality) as well as their ability to sustain the delay prior to that outcome. We also investigate learning performance using a reversal-learning task, whereby cuttlefish were required to first learn to associate a reward with one of two stimuli that differed in contrast (brightness-discrimination) and then subsequently learn to associate a reward with the alternative stimulus (discrimination-reversal). Performances in both tasks were analysed to determine whether self-control in cuttlefish is linked to learning performance.

2. Methods

(a) Subjects

Six sub-adult cuttlefish (nine months old) completed all training and testing. Subjects had not participated in any cognitive experiments prior to this study. The order in which the subjects experienced the experiments was pseudo-randomized across individuals (electronic supplementary material).

(b) Prey preference

We first conducted tests to determine individual prey preferences in which preferences for three commonly consumed prey types (i.e. live grass shrimp, live Asian shore crab and pieces of raw king prawn) were identified (electronic supplementary material).

(c) Self-control experiment

(i) Experimental apparatus

We used three-dimensional printing technology (<http://www.explorative.engineering>) to construct a movable two-chamber experimental apparatus consisting of two black plastic drawers 55 × 55 × 210 mm ($w \times l \times h$; dimensions of each chamber) with transparent sliding doors so that the content of each chamber was visible. Each chamber was fitted with a detachable white plastic visual symbol that differed in shape so that cuttlefish learnt to associate a specific shaped symbol with different types of accessibility. The chamber apparatus was inserted vertically at one end of a rectangular experimental aquarium 300 × 450 × 300 mm ($w \times l \times h$). The opposite side of the aquarium was fitted with two PVC barriers to create a triangular apex, forming a position for the cuttlefish to settle in a location that was equidistant from the two chambers (figure 1).

(ii) Training phase 1: visual symbol and chamber accessibility

Subjects were placed individually in the apex of the triangle in the experimental aquarium and left to settle with the posterior end of the mantle facing the point of the triangular apex (electronic supplementary material, figure S1a). In this training phase, subjects were presented with a single chamber that was vertically fixed to the centre of the tank wall. The single chamber was marked with a visual symbol and subjects were trained to learn to associate a specific shaped symbol with a different type of accessibility to the baited contents of the chamber (electronic supplementary material, figure S1a). There were three types of accessibility conditions: (i) immediate and accessible prey; (ii) delayed release with obtainable prey following the delay; and (iii) delayed release with unobtainable prey following the delay, whereby a second film of clear Perspex obstructed access to the prey once the sliding door was opened. In this training phase, four delays were used in the delay conditions including 3, 6, 9 and 12 s delays. The differently shaped symbols associated with each type of access were randomized across subjects.

Subjects received one session of 6 trials per day with each symbol presented 33% of the time. Specifically, each session consisted of 6 trials in blocks of 2 for each chamber type, i.e. 2 × immediate, 2 × delayed obtainable and 2 × delayed unobtainable (electronic supplementary material, table S1). This ensured that the level of reinforcement (i.e. number of prey items obtained) as well as the number of trials administered to learn the association was standardized across the training session. The order of the blocks was randomized across individuals.

Once subjects were settled in the triangular apex, the chamber was baited with a prey item fixed to a clear plastic dowel stick, which restrained the prey, but live prey were still able to move while fixed to the stick. Depending on the visual symbol, the transparent sliding door was either immediately

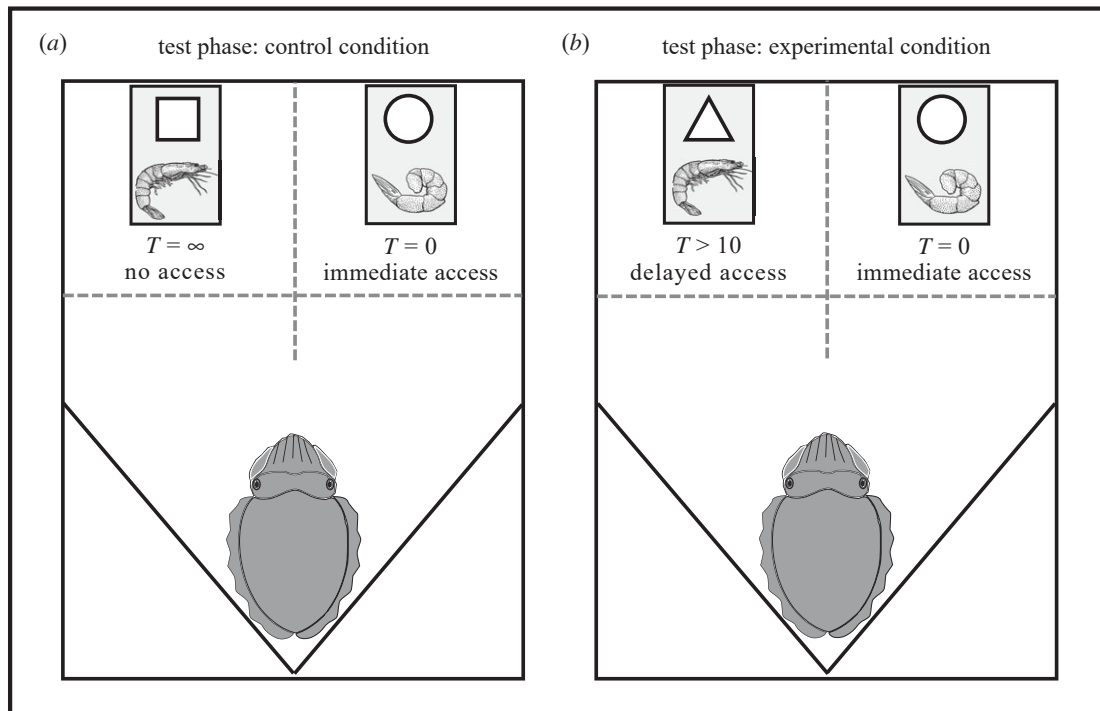


Figure 1. Schematic of the test conditions in the delay maintenance task: (a) control condition and (b) experimental condition. The different shaped visual symbols represent the time delays that were associated with each chamber. T represents the delay in seconds: $T = \infty$ represents a perpetual delay (a second film of clear Perspex obstructed access to the prey); $T = 0$ represents immediate access; and $T > 10$ represents delays ranging from 10–130 s. The immediate-release chamber ($T = 0$) was always baited with the less preferred prey whereas the delayed chambers ($T = \infty$ and $T > 10$) were always baited with the preferred prey. The dotted lines represent the decision point, where the cuttlefish makes a choice between the prey items on offer.

removed or removed after a delay. We measured the latency to approach the chamber following baiting. We also recorded the number of times the subjects attempted to obtain the prey item by striking the chamber with their two feeding tentacles. To gauge whether the cuttlefish were correctly associating the visual symbols with the different accessibility conditions, we monitored behavioural indicators that centred on latency to approach the chamber and latency to strike (electronic supplementary material).

(iii) Training phase 2: single-choice selection

In this training phase, subjects were presented with two unmarked chambers (i.e. no visual symbols attached) and both chambers were baited with the same type of prey (electronic supplementary material, figure S1b). Cuttlefish were trained to learn that once they approached a chamber, the prey in the alternative chamber was removed immediately. The subjects were able to learn this rule readily as they had already been trained to learn a single-choice selection rule during the prey preference trials. Since overtraining can result in habitual responses and lead to individuals developing a side bias [51], we minimized training in this phase. Specifically, we conducted two sessions of 6 trials to minimize any habitual responses and ensure that cuttlefish would respond using a goal-directed action (i.e. exert self-control or succumb to immediate rewards) in the test phase.

(iv) Pre-test phase: consecutive increase in delay duration

The pre-test phase was conducted so that subjects could learn that the delay durations were expected to consecutively increase in the test phase. Each delay chamber (i.e. obtainable or unobtainable) was presented alongside the immediate chamber in the pre-test phase at 10 increasing delay increments (i.e. 2, 4, 6, 8, 10, 12, 14, 16, 18, 20 s) so that each subject had to choose between an immediate and a delayed option. Providing the subjects with a choice between an immediate and a delayed option

allowed us to avoid training the cuttlefish to simply learn to delay consumption of all prey. Each session consisted of 5 trials in blocks of 2 for each delayed chamber type. The order of the blocks was randomized across individuals (electronic supplementary material).

(v) Testing phase: self-control

To test self-control, cuttlefish were presented with an inter-temporal delay maintenance task [10], which required them to choose between two prey items of different quality (i.e. preferred versus less preferred). Subjects were placed individually in the experimental aquarium, which contained two chambers. Cuttlefish experienced two testing conditions including a control and an experimental condition. In the control condition, subjects were required to choose between immediate prey and delayed but unobtainable prey (figure 1a). This condition allowed us to control for the possibility that the subjects were not trained to learn to delay consumption across all conditions. The control condition also allowed us to assess whether the subjects found the less preferred prey desirable when they had visual access to their preferred prey but no physical access. In the experimental condition, subjects were required to choose between immediate prey and delayed obtainable prey (figure 1b). This condition assessed whether the subjects were able to delay immediate gratification to obtain the food of higher quality. To determine the maximum amount of time that each subject was willing to wait for the preferred prey item, we tested a range of delay times, starting at 10 s and increasing by increments of 10 s.

Preliminary trials in the control condition showed that Asian shore crabs were not a sufficiently tempting immediate reward as latencies to approach the crab, which was baited in the immediate-release chamber, were excessive (greater than 3 min) and some subjects refused to eat the crab altogether. Consequently, the testing phase proceeded with only two prey items on offer: the live grass shrimp as the preferred prey item and a piece of raw king prawn as the less preferred prey item.

In both conditions, the immediate chamber was always baited with the less preferred prey item (i.e. piece of raw king prawn) and the delayed chamber was always baited with the preferred prey item (i.e. live grass shrimp). Subjects were able to discontinue waiting at any point and consume the less preferred prey item, which remained visible and accessible throughout each trial. This set-up allowed us to measure the cuttlefishes' ability to choose a preferred outcome (delay choice) as well as their ability to sustain the delay prior to that outcome (delay maintenance) [27]. Once subjects approached one chamber, the prey item in the alternative chamber was removed. For both conditions, we measured latency to consume the prey item. We expected cuttlefish to choose the immediate reward more often in the control condition and, by contrast, maintain the delay and wait for their preferred prey item in the experimental condition. We therefore predicted that latency to consume the prey item would be shorter in the control condition compared to the experimental condition.

Subjects received one session of 6 trials per day at a specific delay. This number of trials was chosen to minimize satiety and its effects on eating behaviour. With each delay, subjects experienced both conditions in blocks of three, the order of which (within a delay) was counter-balanced across subjects (e.g. EEECCC or CCCEEE, where C = control trial and E = experimental trial; electronic supplementary material). A subject moved onto the next delay increment if they waited for the preferred prey item in the experimental condition for all 3 trials within a session. If subjects did not fulfil this criterion, they were tested at the same delay time for three consecutive days. If the criterion was not fulfilled within this period, and the subject continued to consume the immediately available prey item, then the delay duration that the subject continued to succumb to immediate gratification (i.e. consumed the less preferred prey) was recorded as the subjects maximum wait time. To determine whether their maximum wait time was sustained at longer delay durations, all subjects continued to be tested at increasing delays and their abandon time was noted.

(d) Learning performance experiment

Learning performance was measured using a reversal-learning task. This experiment was divided into two phases, the brightness-discrimination phase and the discrimination-reversal phase. During brightness-discrimination, subjects received two sessions of 6 trials per day, one session in the morning and another in the afternoon, whereby cuttlefish were presented with two stimuli that differed in contrast, which were inserted into their home tanks. The positions of the two stimuli were chosen according to a pseudo-random pre-set scheme. The different stimuli associated with a reward were pseudo-randomized across subjects (e.g. for three subjects the white PVC square was rewarded and for the other three subjects, the dark grey PVC square was rewarded; electronic supplementary material).

The subjects were required to make a choice by approaching a single stimulus (within 10 cm). Once subjects approached one stimulus, the alternative stimulus was removed. Cuttlefish remained in this phase until they reached an acquisition criterion of 5 correct choices out of 6 consecutive trials. This weak learning criterion was selected to avoid overtraining in view of the discrimination-reversal phase. During discrimination-reversal, the procedure was the same except that the reward-related contingency was reversed between the two different stimuli. Cuttlefish remained in the discrimination-reversal phase until they reached an acquisition criterion of 5 correct choices out of 6 consecutive trials.

(e) Analysis

All data were HD recorded and coded *in situ*, cross-referenced with the videos and then assessed for inter-rater reliability

(electronic supplementary material). Statistical analyses were completed using JASP (v. 0.10.3, <http://jasp-stats.org>) and RStudio for Mac (v. 1.2.1335). To determine whether cuttlefish had preferences for different prey, we used binomial tests (against value: 0.5). To check parametric assumptions, we used normality tests (electronic supplementary material, table S2). To determine whether latency to consume prey was influenced by delay (ordinal factor) or condition (nominal factor: control versus experimental) we used a non-parametric permutation test (aovperm function, permuco package). To determine whether maintenance of delay was correlated with delay duration, we used a Spearman's rho test for correlations with an ordinal variable. We used a paired sample *t*-test to investigate the influence of the phase in the reversal-learning task on the subjects' learning performance. To determine whether the order in which the subjects were trained across experiments was correlated with self-control or learning performance, we used parametric Pearson's correlation coefficients. We also used Pearson's correlation coefficients to investigate whether delay maintenance was correlated with learning performance. The variables in the correlation analyses included mean abandon time for each subject and the number of trials taken to reach the learning criterions during brightness-discrimination and discrimination-reversal. The strength of the association between delay maintenance and learning performance was also examined by estimating a Bayes factor using Bayesian information criteria [52], comparing the fit of the data under the null and the alternative hypothesis ($BF_{10} = \text{alternative/null}$).

3. Results

(a) Prey preference

Cuttlefish showed a discrete preference order for the different prey items. For all subjects, the live grass shrimp was the most preferred prey, pieces of raw king prawn was second in the preference hierarchy and Asian shore crab was the least preferred prey (binomial tests: shrimp versus prawn $p < 0.001$; shrimp versus crab $p < 0.001$; prawn versus crab $p < 0.001$; electronic supplementary material, figure S2).

(b) Self-control

The latency to consume the different prey on offer differed significantly between the conditions ($p < 0.001$; effect size = 69.70; figure 2a). Cuttlefish modified their latency to consume the prey items in response to the increased delay, as demonstrated by the significant effect of delay duration ($p < 0.001$; effect size = 16.17). However, latency to consume prey was dependent on foraging context, as demonstrated by a significant interaction between delay duration and condition ($p < 0.001$; effect size = 15.89). In the experimental condition, delay maintenance was correlated significantly with delay duration. Specifically, cuttlefish showed a decrease in delay maintenance with increasing delay duration (Spearman's rho -0.723 ; $p < 0.001$; figure 2b). Maximum wait time differed across subjects ranging from 50 to 130 s (electronic supplementary material, table S3). Importantly, in subsequent trials with increasing delay durations, subjects typically abandoned waiting at their maximum wait time (electronic supplementary material, table S4).

(c) Learning performance

Brightness-discrimination was learnt by all subjects within 27 ± 4.58 trials (mean \pm s.e.) over 1–4 days and discrimination-reversal was learnt by all subjects within 46 ± 6.70

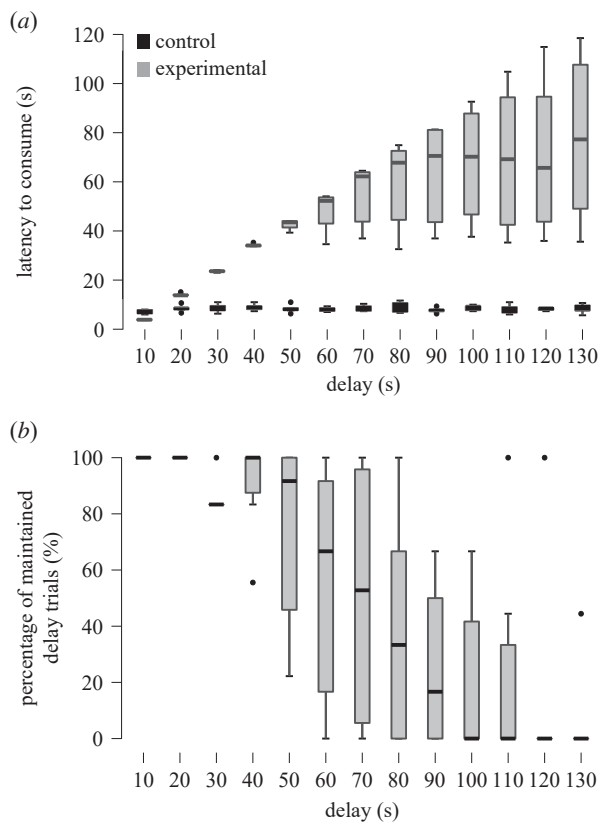


Figure 2. Delay maintenance in cuttlefish, *Sepia officinalis* ($n = 6$). (a) Mean latency to consume prey (s) (mean \pm s.e.) at different delay durations (10–130 s) in the control (immediate, less preferred prey versus delayed, unobtainable preferred prey) and experimental condition (immediate, less preferred prey versus delayed, obtainable preferred prey). (b) Mean proportion of trials where cuttlefish maintain delay (%) (mean \pm s.e.) at different delay durations (10–130 s).

trials (mean \pm s.e.) over 2–6 days. The mean number of trials to reach the learning criterion differed significantly between the two different phases ($t_5 = -5.92$, $p < 0.01$; electronic supplementary material, figure S4). Performance in the brightness-discrimination phase was correlated positively with performance in the discrimination-reversal phase (Pearson's $r = 0.861$, $p < 0.05$; figure 3).

(d) Self-control and learning performance

Cuttlefish that maintained delays for longer had better learning performance. Specifically, mean abandon time in the delay maintenance task was correlated significantly with both the number of trials taken to reach the learning criterion during brightness-discrimination (Pearson's $r = -0.854$, $p < 0.05$) and discrimination-reversal (Pearson's $r = -0.935$, $p < 0.01$; figure 4). The data were also analysed using a Bayesian correlation matrix, demonstrating that the strength of the evidence in favour of there being correlations is moderate (brightness-discrimination: $BF_{10} = 3.27$; discrimination-reversal: $BF_{10} = 8.83$). The estimated Bayes factors indicate that our data were 3.27 and 8.83 times more likely to be observed under the alternative hypothesis (i.e. significant correlation) than the null hypothesis (i.e. no correlation). Importantly, the order in which the subjects were trained across experiments was not correlated significantly with performance in the delay maintenance task (Pearson's $r = 0.050$, $p = 0.93$) or the reversal learning task (brightness-discrimination:

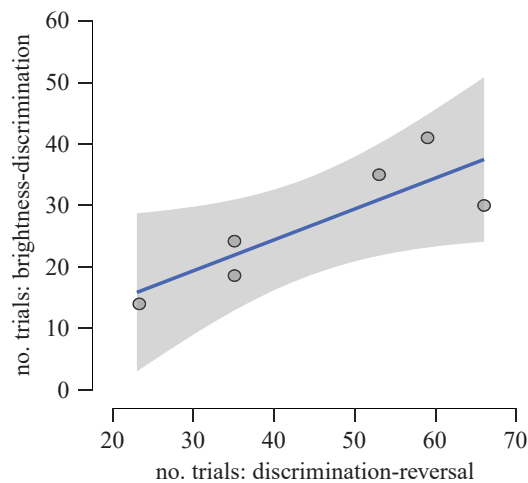


Figure 3. Learning performance in cuttlefish, *Sepia officinalis* ($n = 6$). Relationship between the number of trials to reach the learning criterion in the different learning phases: brightness-discrimination and discrimination-reversal. The relationship is indicated by a Pearson's correlation coefficient with 95% confidence intervals. (Online version in colour.)

Pearson's $r = -0.488$, $p = 0.33$; discrimination-reversal: Pearson's $r = -0.267$, $p = 0.61$).

4. Discussion

Cuttlefish delayed gratification when it led to a prey item of higher quality and they were able to maintain delays for periods of up to 50–130 s. The vital parameter determining the cuttlefishes' decisions was the duration of the delay. In line with other studies on self-control in mammals and birds, our results show that waiting appeared to be more difficult with increasing delay durations [27,53], and as delays increased, subjects were more likely to succumb to consuming immediately available but less preferred prey.

Some delayed gratification studies have been criticized for not reliably measuring *true* self-control due to methodological limitations. Specifically, many experiments test whether an individual can choose a better delayed outcome over a poorer immediately available option but fail to test whether the individual can *sustain* the inhibition required to acquire the better outcome [54]. For example, insects [55], birds [56,57] and mammals [57–59] have been tested using a delay choice task where individuals are presented with two choices, the choice to take a less preferred reward available sooner or the choice to wait for a more preferred reward that will be available later. The choice is irrevocable and thus once the choice is made it cannot be altered at any time during the trial. This type of set-up only tests the individual's willingness to attempt to delay gratification but fails to test their ability to sustain continuous inhibition of impulsive responses to the immediate option. In our study, cuttlefish were able to discontinue waiting at any point to consume the less preferred prey, which remained visible and accessible throughout the trial. Thus, our results indicate that the cuttlefishes' decisions to wait in the experimental condition reflects true self-control.

Chimpanzees (*Pan troglodytes*), dogs (*Canis lupus familiaris*) and grey parrots (*Psittacus erithacus*) have been shown to employ behavioural strategies such as looking away, closing their eyes or distracting themselves with other objects while waiting for a better reward [60–63]. Interestingly, in

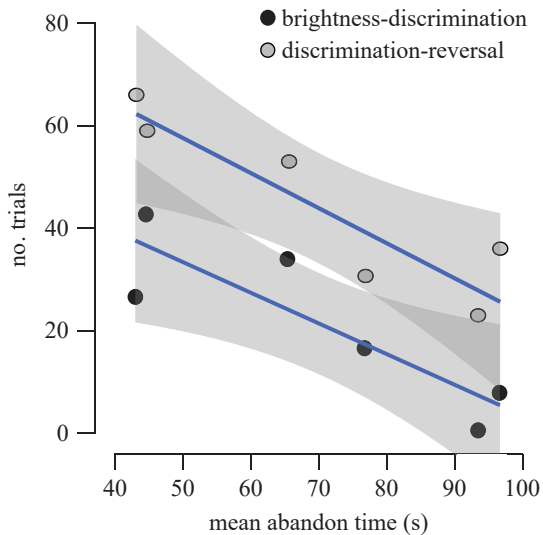


Figure 4. Delay maintenance and learning performance in cuttlefish, *Sepia officinalis* ($n = 6$). Relationships between the mean abandon time (s) in the delay maintenance task and the number of trials to reach the different learning phases during the reversal learning task. The relationships are indicated by Pearson's correlation coefficients with 95% confidence intervals. (Online version in colour.)

our study, cuttlefish were observed turning their body away from the immediately available prey item, as if to distract themselves when they needed to delay immediate gratification. However, this apparently self-distracting behaviour was not measured throughout the study because the top of the experimental aquarium was partially covered with an opaque roof, thus restricting our ability to visually monitor these behaviours across all trials. Further research is needed to determine whether cuttlefish consistently employ behavioural strategies, such as looking away, to cope with the temptation of immediate prey options.

Self-control is thought to be cognitively challenging because to gain future rewards individuals must not only resist temptation but also overcome temporal discounting (i.e. the tendency to discount rewards as they approach a temporal horizon) [64]. In apes, corvids and parrots, evolutionary drivers for self-control have been linked to socio-ecological factors [13,27,65] such as tool use [66], caching behaviour [18,27] and sociality that require individuals to coordinate and maintain multiple relationships, and recognize suitable cooperative partners [67,68]. These factors, however, are unlikely to have driven the capacity for self-control in cuttlefish because they are not habitual tool-users, they do not cache food and they exhibit 'simplified' sociality (i.e. sociality that does not require recognition or cooperation [69,70]).

In cuttlefish, the capacity to delay gratification might have evolved in response to different ecological pressures, such as the need to optimize foraging behaviour [47]. In the wild, cuttlefish have long rest periods where they remain stationary and camouflaged for the majority of the time [71]. Such periods are punctuated by brief foraging bouts in the open, which require effective foraging strategies [40]. The ability to exert self-control might increase their foraging success because ambush attacks are likely to be more successful when cuttlefish are within close proximity to their prey. Further research is required to determine whether other cephalopods are able to exert self-control. Octopuses are a particularly suitable candidate because they use saltatory

search patterns when they forage (i.e. they move forward, pause briefly, observe their surroundings, then typically change direction) [72,73]. The ability to exert self-control might enhance this type of searching behaviour.

The benefits of selecting delayed rewards over immediate rewards can change in different contexts. Thus, flexibly adjusting self-control behaviour in response to changing conditions is crucial for effective decision-making, goal-directed behaviours and future planning [3–5]. Flexible deployment of self-control allows individuals to trade-off between immediate and future benefits in response to changing environmental conditions such as conspecific competition, resource abundance and predation risk [27]. Like corvids, parrots and some primates [27,53], the cuttlefish in our study behaved like economic agents, flexibly adjusting their self-control behaviour in response to different conditions. In the control condition, where their preferred prey was visible but never obtainable, individuals readily abandoned waiting and consumed the less preferred prey item. By contrast, in the experimental condition, cuttlefish tended to wait for their preferred prey.

Note that abandon times in our subjects were relatively long compared to other species in previous studies [19–24,27]. The elevated self-control observed in cuttlefish might have emerged as a by-product of selection on unrelated phenotypic traits. For example, cuttlefish exhibit sophisticated camouflage abilities, which involve long periods where individuals remain motionless [74]. This 'sit-and-wait' behaviour might have altered the expression of cognitive abilities such as self-control. Alternatively, the advanced self-control in cuttlefish might be a result of our experimental design. To illustrate the reliability of self-control abilities within the same individuals [27,75], we used a repeated-measures design, whereby cuttlefish were exposed to the same delay duration consecutively before progressing to a longer delay. Repeated exposure to the same delay duration might result in improved self-control, a pattern that has been shown in various species of monkey [76,77]. However, no obvious learning effects across repeated trials were observed in our subjects. Nevertheless, it has been argued that some animals learn to wait if waiting is reinforced by the possibility of attaining a higher value reward at a later stage (e.g. predators learning to stalk prey) [78]. Furthermore, diverse taxa such as great tits (*Parus major*) [79], bluegill sunfish (*Lepomis macrochirus*) [80], shore crabs (*Carcinus maenas*) [81] and pharaoh cuttlefish (*Sepia pharaonis*) [47], can learn to reject low-value prey when high-value prey are abundant. Such patterns have been argued to reflect associative learning because theoretically behavioural patterns of self-control can develop through conditioned reinforcement learning [82]. Additional research will be needed to illustrate how learning mechanisms interact with patterns of self-control in diverse taxa including cuttlefish.

In humans and chimpanzees, self-control has been linked to general cognitive performance, whereby more intelligent individuals exhibit better self-control [6,8,11]. Here, for the first time, we provide evidence of a link between self-control and learning performance in a non-primate species. Specifically, cuttlefish that were faster at brightness-discrimination learning were able to delay gratification for longer. A similar pattern ensued for discrimination-reversal, individuals that were faster at learning the reverse reward-related contingency were also able to delay gratification for longer. Perhaps this latter correlation is only to be expected because reversal learning involves cognitive processes that are linked directly

to self-control such as attention, behavioural inhibition and thinking slow versus thinking fast [83]. Specifically, individuals must inhibit formerly learnt patterns towards previously rewarded stimuli, shift their attention and form a novel association with previously unrewarded stimuli [3,84]. By contrast, the significant correlation between brightness-discrimination and self-control cannot solely be attributed to the aforementioned cognitive processes (i.e. attention, behavioural inhibition and thinking slow versus thinking fast). Indeed, learning to discriminate between two different stimuli does not directly assess any form of behavioural inhibition. Rather, brightness-discrimination assesses perception and physical cognition, because an individual must visually distinguish between two unequal physical properties. Thus, in our study the positive correlation between brightness-discrimination and self-control suggests that better learning performance might improve effective decision-making when delaying gratification.

Nonetheless, potential limitations must be acknowledged. Note that both the delay maintenance task and the reversal-learning task in this study involve associative learning. A potential limitation of using associative learning in the training phases of both tasks is that it can be challenging to discern whether our results reflect a true relationship between the two cognitive traits, self-control and learning performance, or whether they simply reflect the strength of the learnt associations across both tasks. However, we feel confident that our results reflect the former for two reasons. First, to ensure that the subjects were not simply basing their decisions on learnt patterns in the delay maintenance task, we standardized the level of reinforcement across each training session. Moreover, during the pre-test and test phase, cuttlefish were presented with a novel scenario where they were given an option to choose between prey items of different quality at novel delay increments. The option to exert self-control or succumb to immediate rewards was thus spontaneous and had not previously been associated with punishment or reward.

Second, cuttlefish in the current study, like primates [85], corvids [67,86] and parrots [87], show a positive relationship between both learning phases of the reversal-learning task. This type of pattern suggests that the subjects are inhibiting previously learnt associations and applying a *win-stay-lose-shift* rule (i.e. choosing the response that was previously rewarded but shifting to the other response when original responses are no longer rewarded). When this occurs, it is thought that subjects use their previous experience to develop conditional rules that helps them rapidly switch between contingencies. Positive correlations between both learning phases thus demonstrates an ability to generalize information across reversal problems [88–90] and is indicative

of more cognitively demanding modes of learning that do not solely rely on associative processes [87,90].

Future research should focus on testing whether self-control is linked to other cognitive processes and abilities that do not directly assess behavioural inhibition, such as spatial memory, object permanence and causal reasoning. Moreover, it has been argued that self-control is an important cognitive prerequisite for more cognitively demanding abilities such as future planning [27]. Future studies on the capacity for planning in cuttlefish would provide important data on whether evolutionary pressures that selected for self-control had the collateral consequence of influencing the emergence of future planning. Taken together, our results demonstrate comparable cognitive capacities between cuttlefish and the more commonly studied mammals and birds with regard to self-control. Our results also provide the first evidence of a link between self-control and learning performance in a non-primate animal.

Ethics. Ethical approval was not required for the experiments as there are currently no ethical regulations in place for research on cephalopods in the USA. Nevertheless, this study was designed with the intention of minimizing potential stress to the animals and noxious stimuli were not used in any of the experiments.

Data accessibility. All data and analysis outputs are available as electronic supplementary material.

Authors' contributions. All authors contributed to the conceptualization of the study. A.K.S. and M.B. validated the methodology using corvid resources provided by N.S.C.; R.T.H. provided the cephalopod laboratory resources; A.K.S. and M.R. collected data. A.K.S. analysed the data. All authors participated in the interpretation of the data. A.K.S. drafted the manuscript with extensive discussions with N.S.C. and all authors edited and approved the final version. N.S.C. and R.T.H. provided critical input in their joint role as senior authors.

Competing interests. We have no competing interests to declare.

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References

- Mischel W. 1974 Processes in delay of gratification. *Adv. Exp. Soc. Psych.* **7**, 249–292.
- Kacelink A. 2003 The evolution of patience. In *Time and decision: economic and psychological perspectives on intertemporal choice* (eds G Loewenstein, D Read, R Baumeister), pp. 115–138. New York, NY: Russell Sage Foundation.
- Diamond A. 2013 Executive functions. *Annu. Rev. Psychol.* **64**, 135–168. (doi:10.1146/annurev-psych-113011-143750)
- McCormack T, Atance CM. 2011 Planning in young children: a review and synthesis. *Dev. Rev.* **31**, 1–31. (doi:10.1016/j.dr.2011.02.002)
- Santos LR, Rosati AG. 2015 The evolutionary roots of human decision making. *Annu. Rev. Psychol.* **66**, 321–347. (doi:10.1146/annurev-psych-010814-015310)
- Mischel W, Shoda Y, Peake PK. 1988 The nature of adolescent competencies predicted by preschool delay of gratification. *J. Pers. Soc. Psychol.* **54**, 687–696. (doi:10.1037/0022-3514.54.4.687)
- Mischel W, Shoda Y, Rodriguez ML. 1989 Delay of gratification in children. *Science*

- 244, 933–938. (doi:10.1126/science.2658056)
8. Boisvert D, Stadler W, Vaske J, Wright JP, Nelson M. 2012 The interconnection between intellectual achievement and self-control. *Crim. Justice Behav.* **40**, 80–94. (doi:10.1177/0093854812453129)
 9. Duckworth AL, Quinn PD, Tsukayama E. 2012 What no child left behind leaves behind: the roles of IQ and self-control in predicting standardized achievement test scores and report card grades. *J. Edu. Psychol.* **104**, 439–451. (doi:10.1037/a0026280)
 10. Mischel W. 2014 *The marshmallow test: mastering self-control*. New York, NY: Little, Brown and Company.
 11. Beran MJ, Hopkins WD. 2018 Self-control in chimpanzees relates to general intelligence. *Curr. Biol.* **28**, 574–579. (doi:10.1016/j.cub.2017.12.043)
 12. Beran MJ. 2002 Maintenance of self-imposed delay of gratification by four chimpanzees (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). *J. Gen. Psychol.* **129**, 49–66. (doi:10.1080/00221300209602032)
 13. Rosati AG, Stevens JR, Hare B, Hauser MD. 2007 The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Curr. Biol.* **17**, 1663–1668. (doi:10.1016/j.cub.2007.08.033)
 14. Dufour V, Pelé M, Sterck E, Thierry B. 2007 Chimpanzee (*Pan troglodytes*) anticipation of food return: coping with waiting time in an exchange task. *J. Comp. Psychol.* **121**, 145–155. (doi:10.1037/0735-7036.121.2.145)
 15. Dufour V, Wascher CAF, Braun A, Miller R, Bugnyar T. 2012 Corvids can decide if future exchange is worth waiting for. *Biol. Lett.* **8**, 201–204. (doi:10.1098/rsbl.2011.0726)
 16. Auersperg AMA, Laumer IB, Bugnyar T. 2013 Goffin cockatoos wait for qualitative and quantitative gains but prefer 'better' to 'more'. *Biol. Lett.* **9**, 20121092. (doi:10.1098/rsbl.2012.1092)
 17. Hillemann F, Bugnyar T, Kotrschal K, Wascher CAF. 2014 Waiting for better, not for more: corvids respond to quality in two delay maintenance tasks. *Anim. Behav.* **9**, 1–10. (doi:10.1016/j.anbehav.2014.01.007)
 18. Thom JM, Clayton NS. 2014 No evidence of temporal preferences in caching by Western scrub-jays (*Aphelocoma californica*). *Behav. Process.* **103**, 173–179. (doi:10.1016/j.beproc.2013.12.010)
 19. Ainslie GW. 1974 Impulse control in pigeons. *J. Exp. Anal. Behav.* **3**, 485–489. (doi:10.1901/jeab.1974.21-485)
 20. Richards JB, Mitchell SH, de Wit H, Seiden LS. 1997 Determination of discount functions in rats with an adjusting-amount procedure. *J. Exp. Anal. Behav.* **67**, 353–366. (doi:10.1901/jeab.1997.67-353)
 21. Abeyesinghe SM, Nicol CJ, Hartnell SJ, Wathes CM. 2005 Can domestic fowl, *Gallus gallus domesticus*, show self-control? *Anim. Behav.* **70**, 1–11. (doi:10.1016/j.anbehav.2004.10.011)
 22. Stevens JR, Hallinan EV, Hauser MD. 2005 The ecology and evolution of patience in two New World monkeys. *Biol. Lett.* **1**, 223–226. (doi:10.1098/rsbl.2004.0285)
 23. Ramseyer A, Pelé M, Dufour V, Chauvin C, Thierry B. 2006 Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. *Proc. R. Soc. B.* **273**, 179–184. (doi:10.1098/rspb.2005.3300)
 24. Hidetoshi A, Ai K, Toshiya M. 2010 Social influence of competition on impulsive choices in domestic chicks. *Biol. Lett.* **6**, 183–186. (doi:10.1098/rsbl.2009.0748)
 25. Stevens JR, Mühlhoff N. 2012 Intertemporal choice in lemurs. *Behav. Process.* **89**, 121–127. (doi:10.1016/j.beproc.2011.10.002)
 26. Stevens JR, Hauser MD. 2004 Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn. Sci.* **8**, 60–65.
 27. Miller R, Boeckle M, Jelbert SA, Frohnwieser A, Wascher CAF, Clayton NS. 2019 Self-control in crows, parrots, and nonhuman primates. *WIREs Cogn. Sci.* **e1504**, 1–17.
 28. De Kort SR, Emery NJ, Clayton NS. 2003 Food offering in jackdaws. *Naturwissenschaften* **90**, 238–240. (doi:10.1007/s00114-003-0419-2)
 29. De Kort SR, Emery NJ, Clayton NS. 2006 Food sharing in jackdaws, *Corvus monedula*: what, why and with whom? *Anim. Behav.* **72**, 297–304. (doi:10.1016/j.anbehav.2005.10.016)
 30. Gilby IC. 2006 Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Anim. Behav.* **71**, 953–963. (doi:10.1016/j.anbehav.2005.09.009)
 31. Scheid C, Schmidt J, Noë R. 2008 Distinct patterns of food offering and co-feeding in rooks. *Anim. Behav.* **76**, 1701–1707. (doi:10.1016/j.anbehav.2008.07.023)
 32. Ostojčić L, Shaw RC, Cheke LG, Clayton NS. 2013 Evidence suggesting that desire-state attribution may govern food sharing in Eurasian jays. *Proc. Natl Acad. Sci. USA* **110**, 4123–4128. (doi:10.1073/pnas.1209926110)
 33. Krupenya C, Tan J, Hare B. 2018 Bonobos voluntarily hand food to others but not toys or tools. *Proc. R. Soc. B* **285**, 20181536. (doi:10.1098/rspb.2018.1536)
 34. Seed AM, Emery NJ, Clayton NS. 2009 Intelligence in corvids and apes: a case of convergent evolution? *Ethology* **115**, 401–420. (doi:10.1111/j.1439-0310.2009.01644.x)
 35. Schnell AK, Clayton NS. In press. Evolutionary origins of complex cognition. In *Evolution of learning and memory mechanisms* (eds MA Krause, KL Hollis, MR Papini). Cambridge, UK: Cambridge University Press.
 36. Correia SPC, Dickinson A, Clayton NS. 2007 Western scrub-jays anticipate future needs independently of their current motivational state. *Curr. Biol.* **17**, 1–6.
 37. Raby CR, Alexis DM, Dickinson A, Clayton NS. 2007 Planning for the future by western scrub jays. *Nature* **445**, 919–921. (doi:10.1038/nature05575)
 38. Janmaat KRL, Polansky L, Dagui Ban S, Boesch C. 2014 Wild chimpanzees plan their breakfast time, type, and location. *Proc. Natl Acad. Sci. USA* **18**, 16 343–16 348. (doi:10.1073/pnas.1407524111)
 39. Clayton NS, Dickinson A. 1999 Motivational control of caching in the scrub jay, *Aphelocoma coerulescens*. *Anim. Behav.* **57**, 435–444. (doi:10.1006/anbe.1998.0989)
 40. Hanlon RT, Messenger JB. 2018 *Cephalopod behaviour*, 2nd edn. Cambridge, UK: Cambridge University Press.
 41. Amodio P, Boeckle M, Schnell AK, Ostojčić L, Fiorito G, Clayton NS. 2019 Grow smart and die young: why cephalopods evolved intelligence? *Trends Ecol. Evol.* **34**, 45–56. (doi:10.1016/j.tree.2018.10.010)
 42. Alves C, Boal JG, Dickel L. 2007 Short-distance navigation in cephalopods: a review and synthesis. *Cogn. Process.* **9**, 239–247. (doi:10.1007/s10339-007-0192-9)
 43. Scata G, Jozet-Alves C, Thomasse C, Josef N, Shashar N. 2016 Spatial learning in the cuttlefish *Sepia officinalis*: preference for vertical over horizontal information. *J. Exp. Biol.* **219**, 2928–2933. (doi:10.1242/jeb.129080)
 44. Borelli L, Fiorito G. 2008 Behavioural analysis of learning and memory in cephalopods. In *Learning theory and behavior* (ed. R Menzel), pp. 605–628. Amsterdam, the Netherlands: Elsevier.
 45. Darmaillacq AS, Dickel L, Mather J. 2014 *Cephalopod cognition*. Cambridge, UK: Cambridge University Press.
 46. Schnell AK, Amodio P, Boeckle M, Clayton NS. 2021 How intelligent is a cephalopod? Lessons from comparative cognition. *Biol. Rev.* **96**, 162–178. (doi:10.1111/brv.12651)
 47. Kuo T-H, Chiao C-C. 2020 Learned valuation during forage decision-making in cuttlefish. *R. Soc. Open Sci.* **7**, 201602. (doi:10.1098/rsos.201602)
 48. Jozet-Alves C, Bertin M, Clayton NS. 2013 Episodic-like memory in cuttlefish. *Curr. Biol.* **23**, R1033–R1035. (doi:10.1016/j.cub.2013.10.021)
 49. Billard P, Schnell AK, Clayton NS, Jozet-Alves C. 2020 Cuttlefish show flexible and future-dependent foraging cognition. *Biol. Lett.* **16**, 20190743. (doi:10.1098/rsbl.2019.0743)
 50. Billard P, Clayton NS, Jozet-Alves C. 2020 Cuttlefish retrieve whether they smelt or saw a previously encountered item. *Sci. Rep.* **10**, 5413. (doi:10.1038/s41598-020-62335-x)
 51. Dickinson A. 1985 Actions and habits: the development of behavioural autonomy. *Phil. Trans. R. Soc. B* **308**, 67–78. (doi:10.1098/rstb.1985.0010)
 52. Wagenmakers EJ. 2007 A practical solution to the pervasive problems of *p* values. *Psychon. Bull. Rev.* **14**, 779–804. (doi:10.3758/BF03194105)
 53. MacLean EV *et al.* 2014 The evolution of self-control. *Proc. Natl Acad. Sci. USA* **11**, e2140–e2148. (doi:10.1073/pnas.1323533111)
 54. Paglieri F, Focaroli V, Bramlett J, Tierno V, McIntyre JM, Addressi E, Evans TA, Beran MJ. 2013 The hybrid delay task: can capuchin monkeys (*Cebus apella*) sustain a delay after an initial choice to do so? *Behav. Process.* **94**, 45–54. (doi:10.1016/j.beproc.2012.12.002)
 55. Cheng K, Peña J, Porter M, Irwin J. 2002 Self-control in honeybees. *Psychon. Bull. Rev.* **9**, 259–263. (doi:10.3758/BF03196280)
 56. Cheloni J, King G, Logue AW, Tobin H. 1994 The effect of variable delays on self control. *J. Exp. Anal. Behav.* **62**, 33–43. (doi:10.1901/jeab.1994.62-33)

57. Mazur JE. 2007 Species differences between rats and pigeons in choices with probabilistic and delayed reinforcers. *Behav. Process.* **75**, 220–224. (doi:10.1016/j.beproc.2007.02.004)
58. Tobin H, Chelonis JJ, Logue AW. 1993 Choice in self control paradigms using rats. *Psychol. Rec.* **43**, 441–453.
59. Tobin H, Logue AW, Chelonis JJ, Ackerman KT, May JG. 1996 Self-control in the monkey *Macaca fascicularis*. *Anim. Learn. Behav.* **24**, 168–174. (doi:10.3758/BF03198964)
60. Evans TA, Beran MJ. 2007 Chimpanzees use self-distraction to cope with impulsivity. *Biol. Lett.* **3**, 599–602. (doi:10.1098/rsbl.2007.0399)
61. Leonardi RJ, Vick SJ, Dufour V. 2011 Waiting for more: the performance of domestic dogs (*Canis familiaris*) on exchange tasks. *Anim. Cogn.* **15**, 107–120. (doi:10.1007/s10071-011-0437-y)
62. Koepke AE, Gray SL, Pepperberg IM. 2015 Delayed gratification: a grey parrot (*Psittacus erithacus*) will wait for a better reward. *J. Comp. Psychol.* **129**, 339–346. (doi:10.1037/a0039553)
63. Brucks D, Soliani M, Range F, Marshall-Pescini S. 2017 Reward type and behavioural patterns predict dogs' success in a delay of gratification paradigm. *Sci. Rep.* **7**, 42459. (doi:10.1038/srep42459)
64. Loewenstein G, Read D, Baumeister R. 2003 *Time and decision: economic and psychological perspectives on intertemporal choice*. New York, NY: Russell Sage Foundation.
65. Addessi E, Paglieri F, Focaroli V. 2011 The ecological rationality of delay tolerance: insights from capuchin monkeys. *Cognition* **119**, 142–147. (doi:10.1016/j.cognition.2010.10.021)
66. Teschke I, Wascher CAF, Scriba MF, von Bayern AMP, Huml V, Siemers B, Tebbich S. 2013 Did tool-use evolve with enhanced physical cognitive abilities? *Phil. Trans. R. Soc. Lond. B* **386**, 20120418. (doi:10.1098/rstb.2012.0418)
67. Bond AB, Kamil AC, Balda RP. 2007 Serial reversal learning and the evolution of behavioural flexibility in three species of north American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *J. Comp. Psychol.* **121**, 372–379. (doi:10.1037/0735-7036.121.4.372)
68. Amici F, Aureli F, Call J. 2008 Fission-fusion dynamics, behavioural flexibility, and inhibitory control in primates. *Curr. Biol.* **18**, 1415–1419. (doi:10.1016/j.cub.2008.08.020)
69. Boal JG. 2006 Social recognition: a top down view of cephalopod behaviour. *Vie Milieu* **56**, 69–79.
70. Schnell AK, Clayton NS. 2019 Cephalopod cognition. *Curr. Biol.* **29**, R726–R732. (doi:10.1016/j.cub.2019.06.049)
71. Aitken JP, O'Dor RK, Jackson GD. 2005 The secret life of the giant Australian cuttlefish *Sepia apama* (Cephalopoda): behaviour and energetics in nature revealed through radio acoustic positioning and telemetry (RAPT). *J. Exp. Mar. Biol. Ecol.* **320**, 77–91. (doi:10.1016/j.jembe.2004.12.040)
72. O'Brien WJ, Browman HI, Evans BI. 1990 Search strategies of foraging animals. *Amer. Sci.* **78**, 152–160.
73. Forsythe JW, Hanlon RT. 1997 Foraging and associated behavior by *Octopus cyanea* Gray, 1849 on a coral atoll, French Polynesia. *J. Exp. Mar. Biol. Ecol.* **209**, 15–31. (doi:10.1016/S0022-0981(96)00057-3)
74. Hanlon RT. 2007 Cephalopod dynamic camouflage. *Curr. Biol.* **17**, R400–R404. (doi:10.1016/j.cub.2007.03.034)
75. Völter CJ, Tinklenberg B, Call J, Seed AM. 2018 Comparative psychometrics: establishing what differs is central to understanding what evolves. *Phil. Trans. R. Soc. B* **373**, 20170283. (doi:10.1098/rstb.2017.0283)
76. Anderson JR, Awazu S, Fujita K. 2000 Can squirrel monkeys (*Saimiri sciureus*) learn self-control? A study using array selection tests and reverse-reward contingency. *J. Exp. Psychol. Anim. Behav. Process.* **26**, 87–97. (doi:10.1037/0097-7403.26.1.87)
77. Beran MJ, Perdue BM, Rossettie MS, James BT, Whitham W, Walker B, Futch SE, Parrish AE. 2016 Self-control assessments of capuchin monkeys with the rotating tray task and the accumulation task. *Behav. Process.* **129**, 68–79. (doi:10.1016/j.beproc.2016.06.007)
78. Eaton RL. 1970 The predatory sequence, with emphasis on killing behaviour and its ontogeny, in the cheetah (*Acinonyx jubatus* Schreber). *Z. Tierpsychol.* **27**, 492–504. (doi:10.1111/j.1439-0310.1970.tb01883.x)
79. Krebs JR, Erichsen JT, Webber MI, Charnov EL. 1977 Optimal prey selection in the great tit (*Parus major*). *Anim. Behav.* **25**, 30–38. (doi:10.1016/0003-3472(77)90064-1)
80. Werner EE, Hall DJ. 1974 Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* **55**, 1042–1052. (doi:10.2307/1940354)
81. Elner RW, Hughes RN. 1978 Energy maximization in the diet of the shore crab *Carcinus maenas*. *J. Anim. Ecol.* **47**, 103–116. (doi:10.2307/3925)
82. Lind J. 2018 What can associative learning do for planning? *R. Soc. Open Sci.* **5**, 180778. (doi:10.1098/rsos.180778)
83. Dias R, Robbins TW, Roberts AC. 1996 Dissociation in prefrontal cortex of affective and attentional shifts. *Nature* **380**, 69–72. (doi:10.1038/380069a0)
84. Lucon-Xiccato T, Bisazza A. 2014 Discrimination reversal learning reveals greater female behavioural flexibility in guppies. *Biol. Lett.* **10**, 20140206. (doi:10.1098/rsbl.2014.0206)
85. Macphail E. 1982 *Brain and intelligence in vertebrates*. Oxford, UK: Clarendon Press.
86. Kamil ACJ, Pietrewicz ATB, Mauldin JE. 1977 Positive transfer from successive reversal training to learning set in blue jays (*Cyanocitta cristata*). *J. Comp. Physiol. Psychol.* **91**, 79–86. (doi:10.1037/h0077295)
87. van Horik JO, Emery NJ. 2018 Serial reversal learning and cognitive flexibility in two species of Neotropical parrots (*Diopsittaca nobilis* and *Pionites melanocephala*). *Behav. Process.* **157**, 664–672. (doi:10.1016/j.beproc.2018.04.002)
88. Day L, Crews D, Wilczynski W. 1999 Spatial and reversal learning in congeneric lizards with different foraging strategies. *Anim. Behav.* **57**, 393–407. (doi:10.1006/anbe.1998.1007)
89. Strang CG, Sherry DF. 2014 Serial reversal learning in bumblebees (*Bombus impatiens*). *Anim. Cogn.* **17**, 723–734. (doi:10.1007/s10071-013-0704-1)
90. Rumbaugh DM, Pate JL. 1984 Primates' learning by levels. In *Behavioural evolution and integrative levels* (eds G Greenberg, E Tobach), pp. 221–240. Hillsdale, NJ: Lawrence Erlbaum Associates.