Number sense and state-dependent valuation in cuttlefish

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Identifying the amount of prey available is an important part of an animal’s foraging behaviour. The risk-sensitive foraging theory predicts that an organism’s foraging decisions with regard to food rewards depending upon its satiation level. However, the precise interaction between optimal risk-tolerance and satiation level remains unclear. In this study, we examined, firstly, whether cuttlefish, with one of the most highly evolved nervous system among the invertebrates, have number sense, and secondly, whether their valuation of food reward is satiation state dependent. When food such as live shrimps is present, without training, cuttlefish turn toward the prey and initiate seizure behaviour. Using this visual attack behaviour as a measure, cuttlefish showed a preference for a larger quantity when faced with two-alternative forced choice tasks (1 versus 2, 2 versus 3, 3 versus 4 and 4 versus 5). However, cuttlefish preferred the small quantity when the choice was between one live and two dead shrimps. More importantly, when the choice was between one large live shrimp and two small live shrimps (a prey size and quantity trade-off), the cuttlefish chose the large single shrimp when they felt hunger, but chose the two smaller prey when they were satiated. These results demonstrate that cuttlefish are capable of number discrimination and that their choice of prey number depends on the quality of the prey and on their appetite state. The findings also suggest that cuttlefish integrate both internal and external information when making a foraging decision and that the cost of obtaining food is inversely correlated with their satiation level, a phenomenon similar to the observation that metabolic state alters economic decision making under risk among humans.

1. Introduction

Numerical ability in non-human animals has been known for decades (review [1,2]). There are many ecological situations in which a sense of number can be useful, such as when selecting the best mating strategy [3,4], counting landmarks during navigation [5–7], and discriminating group sizes during social interaction [8–10]. The benefit is probably most obvious when observing animal foraging behaviour, where ability to identify the quantity of prey present is important to the decision-making process [11–14]. However, choosing a larger number of prey is not always the best decision. Optimal foraging theory, a model commonly used to study how an animal behaves when searching for food, predicts that an animal gains the most benefit from food that has the lowest cost during foraging; this approach allows a maximization of its fitness. It follows that, when there is a risk-sensitive foraging choice to be made, an animal’s foraging decisions with regard to food rewards will depend on its satiation level [15]. This is akin to the observation that humans become more risk tolerant regarding their monetary decisions as they become more hungry [16]. Despite earlier studies targeting risk-sensitive foraging preferences, the precise interaction between optimal risk-tolerance and satiation level remains unclear.

Cephalopods (cuttlefish, octopuses and squids) have the most complex brains among invertebrates, and are known for their sophisticated cognitive
behaviours [17,18]. Although previous studies have shown that cuttlefish are able to discriminate prey based on differences in size [19,20], surprisingly there is no evidence to suggest that cuttlefish can distinguish prey groups based on differences in number. In nature, cuttlefish are constantly searching for food (shrimps, crabs and fishes). However, their prey are relatively scarce and often heterogeneously distributed, thus an effective foraging strategy is important to cuttlefish survival. According to the optimal foraging theory, when given a choice, cuttlefish will choose larger or smaller numbers of prey depending on the internal state of the animal and the potential risks associated with capturing the prey, the aim being to maximize the individual’s fitness.

There are two core systems for representing numbers in humans and other animal species. The first system involves precise representation of small numbers of individual objects, while the second system involves representing large but approximate numerical magnitudes (review [21]). The first system operates when there are a small number of items and works by keeping track of individual objects [22]. It is precise but, due to the limited capacity of an animal’s working memory, it only allows for the parallel representation of up to four elements. The second system is considered to be an analogue magnitude mechanism of numerical representations that obeys Weber’s Law [23]. The latter representation is imprecise and the discrimination involves determining the ratio between two numbers rather than the absolute difference.

In this study, we examined numerical representation by cuttlefish and showed that they were able to discriminate a small number of items, but their preference for prey numbers was not always for the larger one, but rather their preference depended on the quality of the prey and the satiation level of the predator.

2. Material and methods

(a) Subjects

Juvenile cuttlefish Sepia pharaonis (mantle length, 1–3 cm) were reared from eggs collected in Keelung and Nanliao, Taiwan. These cuttlefish eggs were transported to the National Tsing Hua University and maintained in the laboratory using two close-circulation aquarium systems (700 l each; water temperature, 23 ~ 25°C). The room was kept on a 12 L : 12 D cycle. After the eggs were allowed to hatch for one month, the young animals were housed individually in porous containers floating inside the aquarium. Depending on the size of the animal, different containers were used (ML < 2 cm, kept in a container 16 × 11 × 6 cm; ML > 2 cm, kept in a container 24 × 16 × 6 cm). They were fed live shrimps or fish at least twice a day; unless food restriction was required in certain experiments. When individual animals died during the experiment, a cuttlefish of the opposite side from the cuttlefish’s location. The experiment was initiated by allowing the cuttlefish to swim toward the two chambers and make a choice. Cuttlefish actively prey on shrimp; they capture them by shooting out their two tentacles making a strike. This behaviour is visually driven in cuttlefish [20]. Once the cuttlefish had passed an imaginary dotted line (figure 1), the apparatus was lifted to prevent passive avoidance learning, an inhibition of predatory behaviour observed during the ‘prawn-in-the-tube’ training procedure [24–29]. The time between the occurrence of convergent eye movement by the cuttlefish and when they cross the imaginary dotted line is the reaction latency. Each cuttlefish was tested six times during a trial, and each experiment contained three trials. Thus, there were 18 tests in total, unless stated otherwise. Within each trial, the two chambers were swapped left-and-right sequentially to minimize the cuttlefish’s visual lateralization effect [30]. Trials were conducted in the morning and/or the afternoon, but never exceeded two trials a day. Before each trial, the cuttlefish were forced to fast for at least 4 h, unless stated otherwise. Only when cuttlefish had completed six tests within a trial were they fed an adequate amount of food. To ensure that shrimps were vigorously active during experiment, the chambers were refreshed every 10–15 min. The tops of the chambers were marked clearly with the number of shrimp inside, and a digital video camera (Olympus STYLUS TG-3) was mounted above to record the responses of the cuttlefish. All experiments were conducted in the daytime (08.00–20.00) and in the home tank of the animals.

(b) Experimental apparatus and procedure

The experimental apparatus consisted of a movable two-chamber device made up of two small transparent plastic boxes (2.5 × 2.5 × 2.5 cm) separated by a protruding plastic sheet designed to force cuttlefish to make an irrevocable choice (two-alternative forced choice design, or 2AFC; figure 1). Depending on the experiment, different numbers of shrimps were placed in two chambers and the apparatus was lowered into the tank at the opposite side from the cuttlefish’s location. The experiment was conducted after

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(c) Experimental design

(i) Prey quantity preference

To investigate whether cuttlefish can discriminate numbers, a series of prey–quantity preference tests were carried out. Live shrimps of equal size, namely roughly 50% of the cuttlefish’s body length, were used in this experiment. The choice of 1 versus 5 shrimps was first examined (n = 12), and this was followed by the choices of 1 versus 2, 2 versus 3, 3 versus 4 and 4 versus 5 shrimps (n = 15, 10, 12 and 10, respectively). To control for non-numerical cues, two additional sets of experiments were conducted (n = 12). In the first one (density effect), prey density in two chambers was kept the same by using a thin glass slide to restrict shrimps in the chamber containing a smaller quantity to a reduced area. In the second one (motion effect), prey activity was eliminated by using freshly dead shrimps in two chambers. To ensure that cuttlefish can see individual motionless prey, dead shrimps were attached separately to a thin glass slide and placed it vertically in the chamber to avoid a clump of prey. Because cuttlefish prefer live food [18,31], the test was conducted after

Figure 1. Schematic representation of the top view of the experimental set-up. The two chambers containing shrimps are presented in front of the cuttlefish, and the animal is motivated to swim toward one of the two chambers. The imaginary dotted line indicates the decision point, where the cuttlefish determines the choice.

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starving animals for more than 20 h to increase their motivation. For the welfare of the animals, each cuttlefish only underwent one trial (six tests) in this experiment.

(ii) Prey quality preference
To examine whether cuttlefish prefer a small quantity of live prey or a large quantity of dead prey, one live shrimp and two freshly dead shrimps of equal size were presented together to the cuttlefish (n = 12).

(iii) Prey size and quantity trade-off
To elucidate how cuttlefish trade-off between a small number of large size prey and a large number of small size prey, one large shrimp and two small shrimps were presented to cuttlefish simultaneously. Note that the length of the small shrimp was less than 50% of the cuttlefish’s body length and the length of the large shrimp was more than 50% of the cuttlefish’s body length, such that the size of the shrimp was within their preferred prey size range and the sum of the body length of two small shrimps equals the body length of one large shrimp.

To control the appetite state, in the first experiment, cuttlefish (n = 10) in trials 1, 3 and 5 were tested in the morning after animals were fasted overnight (starved state), and cuttlefish in trials 2, 4 and 6 were tested in the afternoon after the animals had been fed less than 4 h previously (satiated state). In the second experiment, the appetite state was reversed. Cuttlefish (n = 12) in trials 1, 3 and 5 were tested in the late morning when cuttlefish had been fed less than 4 h ago (satiated state), and cuttlefish in trials 2, 4 and 6 were tested in the late afternoon after the animals had fasted for at least 10 h (starved state). No feeding took place between the morning and afternoon sessions during the second experiment. To control for cuttlefish’s prey size preference, two additional experiments were conducted (n = 12). In the first one, the choice of one small versus one large shrimp was examined at both the starved (morning) and satiated (afternoon) states. In the second one, the choices of 1 versus 2 small shrimps and 1 versus 2 large shrimps were tested at two different satiation levels.

(d) Data analysis
In both the prey quantity and the quality preference experiments, the numbers of choice during the 2AFC was compared using Wilcoxon’s signed rank test. The reaction latencies across the four number discrimination tasks (1 versus 2, 2 versus 3, 3 versus 4 and 4 versus 5) were compared using Kruskal–Wallis test with Bonferroni-correction post hoc comparisons of the Mann–Whitney test. To investigate the appetite state-dependent prey size and quantity trade-off, a preference index was devised. This was as follows: the difference between the number of time cuttlefish chose one large shrimp versus two small shrimps in a trial, i.e. [two – one]/[two + one]. Thus, positive values indicate that cuttlefish chose the side with two small shrimps more often, and negative values indicate that cuttlefish preferred one large shrimp. The univariate Wilcoxon signed rank test was used to assess whether indexes of the different trials were significantly different from zero. All statistics were conducted using SPSS.

3. Results
(a) Number discrimination in cuttlefish
It was first established whether cuttlefish are able to discriminate two numbers that have a large difference, namely the choice of 1 versus 5 shrimps; this was examined using a 2AFC task. The result showed that cuttlefish chose the side with five shrimps significantly more often than the side with one shrimp (Z = 3.129, p = 0.002; electronic supplementary material, figure S1), suggesting that cuttlefish are able to easily distinguish food numbers that are significantly different and they prefer prey with a large quantity.

Next, we examined whether cuttlefish are able to discriminate two numbers with a decreasing difference, and a series of prey quantity preference tests were carried out. Despite the fact that the difference in choice between the smaller and larger quantity was decreased from 1 versus 2 to 4 versus 5, the choice differences for the four experiments were all significant (1 versus 2, Z = 3.426, p = 0.001; 2 versus 3, Z = 2.814, p = 0.005; 3 versus 4, Z = 3.077, p = 0.002; 4 versus 5, Z = 2.414, p = 0.016; figure 2a). This suggests that cuttlefish have the ability to carry out number discrimination and they are able to distinguish number differences above the ratio of 1:2.5 that is 5:4.

To rule out the possibility of non-numerical cues in these prey quantity preference experiments, prey density was controlled in a series of 2AFC tasks (1 versus 2, 2 versus 3, 3 versus 4 and 4 versus 5). When prey density in two chambers was equalized, cuttlefish’s choice differences in the four experiments were still all significant (1 versus 2, Z = 3.081,
p = 0.002; 2 versus 3, Z = 2.969, p = 0.003; 3 versus 4, Z = 2.623, p = 0.009; 4 versus 5, Z = 2.536, p = 0.011; figure 2b). Similarly, when prey motion was eliminated in the same series of 2AFC tasks, the choice differences for the first three experiments were significant (1 versus 2, Z = 3.109, p = 0.002; 2 versus 3, Z = 3.115, p = 0.002; 3 versus 4, Z = 2.549, p = 0.011; 4 versus 5, Z = 1.702, p = 0.089; figure 2c). These results indicate that cuttlefish prefer a large quantity even when prey density and overall motion in each pair of comparisons were equalized. These findings also support that cuttlefish have a genuine number sense.

In order to determine whether cuttlefish’s number discrimination is a form of subitization, which is the process of glancing at a group consisting of a few objects and knowing how many there are without actually counting, the reaction latencies in each of four prey quantity preference tests (figure 2a) were measured. Across the four experiments (1 versus 2, 2 versus 3, 3 versus 4 and 4 versus 5), the mean reaction latencies were found to significantly increase during the four sets of number discrimination tasks as the numbers became closer (figure 3a). Furthermore, they were significantly different for two of pair-wise comparisons (1 versus 2 and 3 versus 4, Z = 2.781, p = 0.005; 1 versus 2 and 4 versus 5, Z = 3.550, p < 0.001). These findings suggest that cuttlefish number discrimination is probably not a form of subitization but rather an analogue magnitude mechanism of numerical representation.

To further exclude the possibility that the increased reaction latencies when the numbers to be discriminated are higher is the result of an increased number of prey moving at the same time and distracting the predator needing to choose one out of several shrimps located in the same chamber, we have done an experiment in which the reaction latencies of 0 versus 1 and 0 versus 5 were compared. Our result showed that the times needed for cuttlefish reaching the imaginary dotted line in both 0 versus 1 and 0 versus 5 were similar (Z = 1.334, p = 0.182; figure 3b). This supports that the longer time for cuttlefish to make a decision when the numbers are higher in the quantity preference test (figure 3a) reflects the increased difficulty of the task, evidence of counting not subitization.

(b) Quality over quantity in food choice
It is known that cuttlefish prefer live food if they have a choice [18,31]. To examine if cuttlefish value quality over quantity during food choice, one live and two dead shrimps were presented during a 2AFC task. Cuttlefish chose the side with one live shrimp significantly more often than the side with two dead shrimps (Z = 3.071, p = 0.002; figure 4). This confirms that cuttlefish, while having the capacity for number discrimination, also make the choice depending on the quality of the food, rather than the quantity of the food.

(c) Trade-off between prey size and quantity is satiation level dependent
The optimal foraging model predicts that foraging behaviour is a compromise between the benefits of nutrition and the cost of obtaining food [15,16]. To examine how cuttlefish trade-off prey size and quantity during food choice, the satiation level was manipulated. In one experiment, starved cuttlefish were given a choice of one large versus two small shrimps in the morning, and the satiated cuttlefish were tested again in the afternoon. It was clear that the satiated cuttlefish preferred the two small shrimps, while the starved cuttlefish preferred the one large shrimp (figure 5a). To ensure that this finding was not a result of a circadian rhythm effect on feeding preference, the satiation level was reversed in another experiment; thus satiated cuttlefish were tested in the morning and starved cuttlefish were tested in the afternoon. Regardless of the experimental time of day, satiated cuttlefish preferred the two small shrimps, while the starved cuttlefish preferred the one large shrimp (figure 5b). These findings strongly suggest that the trade-off between prey size and quantity in cuttlefish is satiation level dependent. As body length and body mass of shrimps are highly correlated (electronic supplementary material, figure S2), these results also imply that cuttlefish’s decision of foraging strategy depends on their metabolic state when overall body mass of prey is controlled.

To control for cuttlefish’s prey size preference at different satiation levels, the choice of one small versus one large shrimp was examined at both starved (morning) and satiated (afternoon) states. It is apparent that cuttlefish preferred larger prey regardless of their satiated states when the quantity on both sides was equal (AM, Z = 3.103, p = 0.002; PM,
Figure 5. The cuttlefish’s choice of one large versus two small shrimps depends on their satiation state. The preference index is the difference between the number of times the cuttlefish chose one large versus two small shrimps in a trial, that is [two – one]/(two + one). Thus, positive values indicate that cuttlefish chose the side with two small shrimps more often, and negative values indicate that cuttlefish preferred one large shrimp. (a) Trials 1, 3 and 5 were conducted in the morning before the cuttlefish were fed, while trials 2, 4 and 6 were conducted in the afternoon after the cuttlefish were fed. Cuttlefish chose two small shrimps when satiated, but preferred one large shrimp when starved. The preference index was significantly different from zero in four of six trials. n = 10. (b) Trials 1, 3, and 5 were conducted in the late morning after the cuttlefish were fed, while trials 2, 4, and 6 were conducted in the late afternoon before the cuttlefish were fed. A similar result was obtained to that outlined above, namely the cuttlefish chose two small shrimps when satiated, but preferred one large shrimp when starved; thus the choice was the same regardless of the time of day when the experiment was carried out. The preference index was significantly different from zero in five of six trials. n = 12. Error bars are s.e.m. *p < 0.05, **p < 0.01.

Z = 3.104, p = 0.002; figure 6a). To further examine cuttlefish’s prey quantity preference at different satiation levels, the choices of 1 versus 2 small shrimps and 1 versus 2 large shrimps were tested at two different satiated states. Notably, cuttlefish preferred a larger quantity regardless of the prey size and their satiation levels (small shrimps: AM, Z = 3.078, p = 0.002; PM, Z = 3.078, p = 0.002; large shrimps: AM, Z = 3.082, p = 0.002; PM, Z = 3.081, p = 0.002; figure 6b). These results suggest that despite cuttlefish’s foraging strategy to favour larger prey and larger quantity at various satiation levels, when there is a choice between a small number of large size prey and a large number of small size prey, cuttlefish’s decision is dependent on their satiation levels (figure 5).

4. Discussion

Effective foraging is an important aspect of cuttlefish life history in nature, thus distinguishing prey groups based on number differences is essential to their decision-making processes. This study demonstrates that cuttlefish are able to easily discriminate different food numbers and they preferred a large quantity of prey. Specifically, cuttlefish are able to distinguish number differences above the ratio of 1.25 (i.e. 5/4), and this implies an analogue magnitude mechanism of numerical representation. Furthermore, cuttlefish showed quality over quantity as part of their food choice, and the trade-off between prey size and quantity is satiation-level dependent. Thus, the integration of internal and external information is critical when cuttlefish are making foraging decisions.

(a) Number sense in cuttlefish

The numerical abilities of non-human animals have been studied for many years. However, some studies have required that animals learn to distinguish different numbers of items for rewards. Thus, number discrimination can in certain circumstances be considered to be a learned behaviour, rather than an innate behaviour based on these experiments. In this study, without training, cuttlefish turned toward the prey and initiated the visual attack behaviour, when food, namely live or dead shrimps, was present. Thus, the number sense demonstrated by cuttlefish is attributable to their innate cognitive ability.

There are two core systems for representing numbers in humans and other animal species: one regarding small values (the object file system) and one concerning large numerical magnitudes (the analogue magnitude system) (review [21]). The first system is commonly referred as a form of subitization, the process of glancing at a group of a few objects and knowing how many there are without actually counting them. It is an object-based attention mechanism, but due to the capacity of working memory, there is a limit to the quantity of object-files (up to four elements) that can be simultaneously tracked [22]. Our findings indicated that reaction latencies were significantly increased across the four sets of number discrimination.
tasks (figure 3a), which suggests that cuttlefish’s number discrimination is not a form of subitization. In human experiments of subitization, it has been shown that 12-month-old infants could distinguish 1 versus 2 and 2 versus 3 successfully, but failed when the tests involve 3 versus 4, 2 versus 4 and even 1 versus 4 [32]. In a similar experiment with rhesus macaques, it has been reported that the monkeys chose the greater number when the comparisons were 1 versus 2, 2 versus 3 and 3 versus 4, but failed when the comparisons were 4 versus 5 or larger [33]. However, recent studies with newborn chicks demonstrate that day-old domestic chicks could make a series of numerical discriminations, such as 2 versus 3, 2 versus 4 and 4 versus 6, suggesting that there is continuity in the representation of numbers [34,35]. Our finding that cuttlefish succeeded when the tests were 1 versus 5 and 4 versus 5 (electronic supplementary material, figures S1 and 2A,B, respectively) implies that cuttlefish are at least equivalent to infants and primates in terms of number sense, and their number discrimination is likely to be an analogue magnitude mechanism of numerical representation and perhaps a continuity of the number system.

(b) Food quality and satiation state-dependent valuation in cuttlefish

Cuttlefish are voracious carnivores, feeding on a wide variety of live prey (shrimps, crabs and fishes) that they detect mainly with their eyes [18,31]. Prey movement is an especially important visual cue that is able to elicit a visual attack by the cuttlefish [28,36]. Thus, while cuttlefish preferred a large quantity over a small quantity when making foraging decisions, they chose one live shrimp significantly more often than two dead ones during this study (figure 4). This finding suggests that cuttlefish’s food choice depends on their innate preference for live prey cues, and choosing the larger number of prey is not always the best decision during foraging.

Despite the wide interest in foraging among vertebrates and in the development of the optimal foraging theory [37], there have been few studies investigating this topic using cephalopods. Cuttlefish are predators that search for food and as a result are opportunistic feeders, attacking any edible prey that is available in the wild [18,31]. However, the prey are often heterogeneously distributed and prey species vary in their nutritional value; thus an effective foraging strategy is very important to cuttlefish. According to the optimal foraging model, one would predict that cuttlefish would gain the most benefit by having the lowest cost during foraging because this would maximize their fitness. It follows that, in a risk-sensitive foraging choice, cuttlefish’s foraging decisions with regard to food rewards may depend upon their satiation level. When given a choice of one large versus two small shrimps, a satiated cuttlefish preferred two small shrimps, but a starved cuttlefish chose one large shrimp (figure 5). As attacking one small prey in a group is less risky than capturing one large lone prey for the cuttlefish, it is likely that cuttlefish become more risk averse in terms of their decisions about food rewards when they are satiated, and become more risk tolerant when they are starved. This suggests that the trade-off between prey size and quantity in cuttlefish is satiation-level dependent. State-dependent valuation also occurs among desert locusts [38], and it is probably an ecologically rational solution to the widespread problem of choice. This finding is akin to the phenomenon of economic decision making whereby the risk attitudes of human subjects towards money, food and water rewards change as a function of their internal metabolic state [39]. For example, humans become more risk tolerant in their monetary decisions, as they get hungry [16]. Thus, our observation that the choice made by cuttlefish regarding food rewards is satiation-state dependent is in agreement with the hypothesis that metabolic state alters economic decision making under risk in humans.

Ethics. This work was carried out in 2015–2016 in accordance with the National Tsing Hua University guidelines and all procedures were approved by the institutional animal care and use committee.

Data accessibility. Data are available in the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.15981.

Authors’ contributions. T.-Y.C. conceived, designed, carried out the work and drafted the manuscript. C.-C.C. helped plan experiments, interpreted data and revised the manuscript.

Competing interests. We have no competing interests to declare.

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