Research Article

Arithmetic-Like Reasoning in Wild Vervet Monkeys: A Demonstration of Cost-Benefit Calculation in Foraging

Sayaka Tsutsumi,[1, 2] Tomokazu Ushitani,[3] and Kazuo Fujita[1]

[1] *Department of Psychology, Graduate School of Letters, Kyoto University, Sakyo, Kyoto 606-8501, Japan*
[2] *Japan Society for the Promotion of Science, Sumitomo-Ichibancho FS Building, 8 Ichibancho, Chiyoda-ku, Tokyo 102-8472, Japan*
[3] *Department of Cognitive and Information Sciences, Faculty of Letters, Chiba University, 1-33 Yayoi-cho, Inage, Chiba 263-8522, Japan*

Correspondence should be addressed to Sayaka Tsutsumi, sayaka.tsutsumi@gmail.com

Arithmetic-like reasoning has been demonstrated in various animals in captive and seminatural environments, but it is unclear whether such competence is practiced in the wild. Using a hypothetical foraging paradigm, we demonstrate that wild vervet monkeys spontaneously adjust their "foraging behavior" deploying arithmetic-like reasoning. Presented with arithmetic-like problems in artificially controlled feeding conditions, all the monkeys tested attempted to retrieve "artificial prey" according to the quantity of the remainder when the task involved one subtraction only (i.e., "2−1"), while one monkey out of four did so when it was sequentially subtracted twice (i.e., "2−1−1"). This monkey also adjusted his "foraging behavior" according to the quantity of the reminder for a task requiring stepwise mental manipulation (i.e., "(2−1)−1"), though the results became less evident. This suggests that vervet monkeys are capable of spontaneously deploying mental manipulations of numerosity for cost-benefit calculation of foraging but that the extent of such capacity varies among individuals. Different foraging strategies might be deployed according to different levels of mental manipulation capacity in each individual in a given population. In addition to providing empirical data, the current study provides an easily adaptable field technique that would allow comparison across taxa and habitat using a uniform method.

1. Introduction

Outstanding numerical competence characterizes human nature as much as language does. In search of the evolutionary origin of such ability, a broad range of nonhuman animals from both the laboratory and semiwild settings have been shown to possess the ability to attend to numerical attributes of the environment (see [1, 2] for review). For example, insects can attend to small number of landmarks that are passed en route (e.g., honeybees [3]), amphibians can discriminate between small number of objects (e.g., salamanders [4]), birds can count, discriminate numerosities, and attend to number (e.g., pigeons [5, 6], parrots [5, 7, 8], corvids [5, 9], and domestic chicks [9–12]). Mammals can count, discriminate numerosities, and attend to number

(e.g., dolphin [13], raccoon [14], lemurs [15, 16], monkeys [17–21], and apes [22, 23]).

Spontaneous application of such ability has also been seen in daily survival of wild animals, for example, avoiding brood parasitism in coots [24], assessing feasibility in intergroup contests in lionesses [25] and in chimpanzees [26]; thus, at least in those species there seems to be ecological validity [27] for the ability to represent numerical attributes.

Reasoning about those representations, for example arithmetic, requires more complex cognitive processes because it requires two levels of information processing: representation of numerical attributes and mental manipulation of those representations. There exist reports suggesting that birds and mammals might be capable of rudimental arithmetic (i.e., corvids [28], chicks [29], dogs [30], lemurs

[31], monkeys [32–36], and apes [37–42]), though chimpanzees [41] and orangutans [42] seem to have difficulties understanding subtraction (review in [1, 2]).

Given those evidences from the laboratory and seminatural settings, we would expect them to exploit such abilities in their daily interaction with the environment in the wild. How could such sophisticated competence have evolved had it not been put into practical use? Presumably, to be favoured by natural selection, a cognitive ability should confer adaptive value [43], given the costs of installing requisite neural processes in the brain. However we have not yet seen evidence of arithmetic-like manipulations of such representations in the wild. There even exists an anecdotal report of failed subtraction, in which a bird reacts as if it assumes "two persons minus one person = nobody there" when two birdwatchers go behind a blind screen and one then departs [44]. This behavior is generally known to birdwatchers and forms the basis of a birdwatching technique.

As a transitive attempt to bridge the gap between the documented competence of arithmetic-like reasoning in the captive and seminatural settings and yet-to-be-described application of such ability in the wild, the current study aimed to demonstrate a context in which practicing arithmetic-like reasoning may lead to increased fitness in wild animals. In such contexts, natural selection acts directly on the survival of animals, for example, foraging. Consider an insectivore that witnesses two insects go into a hollow up in a tree. One comes out and leaves. The ability to mentally subtract, glossed as "two insects minus one insect leaves one, not zero," before deciding whether to climb up the tree or not, would reduce wasteful costs of time and energy, thus leading to increased foraging efficiency. This presents an interesting situation where attention to numerical attributes of an object can guide cost-benefit calculation of a given behavior.

We asked a particular question: do animals spontaneously engage in arithmetic-like reasoning in a situation analogous to the above hypothetical foraging paradigm in their natural habitat? To answer this question, we experimentally set up an artificial foraging situation in the native habitat of a group of wild vervet monkeys (*Chlorocebus aethiops*) in Kenya, and opportunistically tested whether they would spontaneously change their behavior according to the quantity of the "artificial prey." This paradigm was developed by modifying Hauser et al.'s seminatural foraging paradigm [21, 36] in order to measure the response of wild monkeys to controlled feeding conditions in the normal and native home range of their troop.

The current paper deals with numerical and quantitative attributes of an object and not number per se (see [12] for discussion on strictly numerical attributes of a stimulus distinguished from the continuous physical variables of the stimulus that covary with number); thus, in this paper we refer to the term "subtraction" as "subtraction-like reasoning" rather than "strict arithmetic." We aimed to reveal a more compelling picture of how the ability has evolved by coupling approaches that examine how animals benefit from arithmetic-like reasoning (=ecological function) [27] with those that examine how numbers are represented by animals (=mechanism).

2. Methods

2.1. Field Experimental Site.

The field experiment took place in the backyard of the first author's residence, which happened to be inside the regular home range of a troop of wild vervet monkeys (Kibaki group) inhabiting areas adjacent to Mombasa Marine National Park, Kenya. Vervet monkeys are omnivorous and forage for a variety of food, including fruits, leaves, invertebrates, reptiles, birds, and mammals [45]. As vervets are not shy of humans by nature, they are known to forage in various habitats including human residential areas [46–49]; thus, in a sense those "artificial" habitats are "natural" in the very recent history of evolution (i.e., after farming started and early humans settled with food storage). The first author resided in the above location for two years prior to the commencement of the current study in March 2002, which provided an opportunity to collect general information regarding the troop, such as daily migration pattern, diet, population size, and individual identification. We set up a testing site on the veranda (4 m width × 50 cm depth × 90 cm height) of the first author's residence, which was regularly visited by the monkeys to forage for human food.

2.2. Subjects and Data Sampling Periods.

The subjects were adult members of the Kibaki group who spontaneously visited the field experimental site during the data sampling periods (experiment 1: March 2002 to May 2002, experiment 2-a: July 2004 to August 2004, experiment 2-b: February 2005). All the monkeys tested were identified by clear natural markings such as a torn-off limb, a bent tail, and skin spots. All of them were experimentally naïve.

2.3. Apparatus.

The apparatus consisted of a face-down opaque cup (5 cm diameter on top, 7 cm diameter on bottom, 8.5 cm height) with a side opening (3.5 cm width, 4 cm height) on the lower side of the wall, and an opaque cardboard box (25 cm, 23 cm, 8 cm: width, depth, height respectively) below the cup (Figure 1(a)). Bread pieces cut in approximately 1 cm^3 cubic were used as food stimuli. The cup served as an "artificial tree", the side opening as an "artificial hollow", and the bread pieces as "artificial prey", analogically representing the hypothetical foraging paradigm of "Two insects go into a hollow in a tree. One then leaves the hollow. Anything left in the hollow?" The opaque cardboard box containing a slice of the same bread served as an olfactory control device. The amount of food stimuli used for a day, typically between 1 to 3 pieces per individual, was small enough not to interfere with their daily natural foraging.

2.4. Procedure

2.4.1. Experiment 1: One-Step Subtraction.

Experiment 1 was designed to depict basic requisite components for arithmetic-like reasoning using a simple "*one-step subtraction*" task where a quantity is subtracted once (i.e., "1−1").

We placed the apparatus on the windowsill between the veranda and adjoining room and waited for the monkeys to arrive at the testing site (Figure 1(b)). We opportunistically
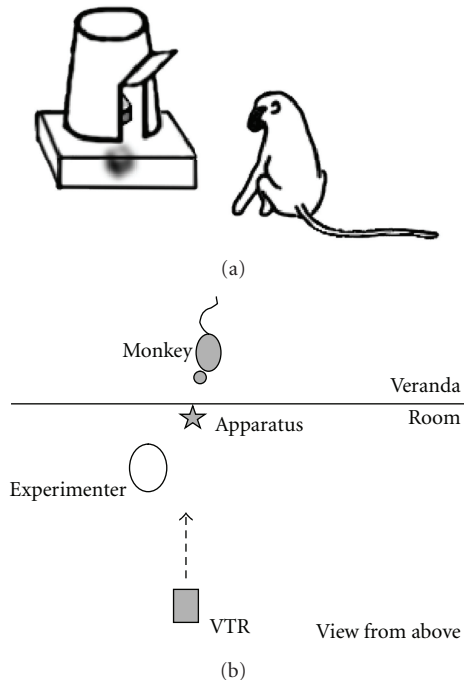
FIGURE 1: (a) Apparatus (not to scale). (b) Testing site (not to scale).

tested them once a monkey sat down on the veranda facing the apparatus within 1 meter (for males) or 2 meters (for females) for 5 seconds. We applied different distance criteria to males and females because the males were more adventurous and approached closer to the apparatus than the females. The monkeys usually came to the testing site individually, but if two or more monkeys were present, the experiment was not carried out until only one monkey remained.

For the test condition "1−1," a human experimenter stood in the adjoining room about 1m away from the apparatus and showed one piece of bread on his palm to the monkey (Figure 2(a)(1)). He then put it into the cup through an opening and rotated the cup 180 degrees so that the monkey could see and confirm what was in the cup through the opening (Figure 2(a)(2)). After making sure that the monkey looked inside the cup, the experimenter rotated the cup 180 degrees back to the original position (Figure 2(a)(3)) and removed the piece of bread from the opening (Figure 2(a)(4)). Then he walked away from the apparatus, still showing the food on his palm to the monkey, and went out of view into another room 2.5 m away from the veranda. In the control condition "1−0," the experimenter performed exactly the same sequence of actions except that he imitated movements of removing a piece of bread by reaching into the opening without actually removing the bread and walked away from the apparatus showing his empty palm to the monkey. Similarly, there were "2−2 (test)," "2−1 (test)," and "2−0 (control)" conditions as subtraction from 2, where two pieces of food were handled at once so that the hand movements were identical across conditions. There was also a "0−0" condition as a baseline where the experimenter made all the same manipulations

of the apparatus without using a piece of bread. This baseline condition was to confirm that the monkeys would not approach the cup when there was no food from the beginning. These 6 conditions were presented once each in random order within a session (6 trials in 1 session). The experimental sessions were recorded by a video camera, and another experimenter coded whether the subject monkey approached and moved the cup to collect food within 30 seconds after subtraction (="foraging attempt made") or not. It was obvious whether the monkey approached and moved the cup or not; thus, coding was very simple. A full slice of the same bread used for the session was concealed in the cardboard box to eliminate the possibility of the monkeys making decisions using olfactory cues. Given the risk involved in approaching human properties, the monkeys should approach the cup only when they decide that the benefit of acquiring food is greater than the cost of a wasteful inspection of the cup. Therefore, it was predicted that if the monkeys perform arithmetic-like reasoning in this experimental situation, they will be more likely to approach the cup when the remainder is greater than zero (i.e., there is some food left in the cup) than when it is zero (i.e., the cup is empty). This was analogically equivalent to a hypothetical situation where the monkeys make a decision on whether or not to forage by weighing the cost (possibility of losing time and energy) and benefit (possibility of foraging success) of a single foraging opportunity.

The six conditions were carefully designed to depict each requisite component for arithmetic-like reasoning; in the "1−1" condition, the monkeys could first see inside the cup through the opening (Figures 2(a)(1) and 2(a)(2)), but then they could no longer see the contents and had to mentally *represent* what they saw—one piece of bread—when the opening was rotated back again (Figure 2(a)(3)). Based on this representation, they were now required to mentally *manipulate* it to solve the subtraction task (Figure 2(a)(4)). In this case, the monkeys could arrive at the correct answer by representing and processing the piece of bread either in the form of *object category* (i.e., bread − bread = nothing), *numerosity* (i.e., one piece of bread − one piece of bread = nothing), or *number* (i.e., one − one = zero). According to Lloyd Morgan's canon [50], we should conclude that they are at least *mentally manipulating* a representation of *object category* if they solve the task. We refer to this as "*category-monitoring subtraction*." The same logic applies to the "1−0," "2−0," and "2−2" conditions.

In the "2−1" condition, the monkeys would be required to *represent* and *manipulate* what they saw as *numerosity* (i.e., two pieces of bread − one piece of bread = one piece of bread left) or *number* (i.e., two − one = one), but not as *object category*, because they would fail the task if they thought "bread − bread = nothing" (Figure 2(b), (1)–(4)). Thus, we may conclude that they are capable of mentally *manipulating* a representation of at least *numerosity* (="*numerosity-monitoring subtraction*") if they attempt to collect the food in the "2−1" condition more often than in the "2−2" condition. If their attempt rate in the "2−1" condition is not different
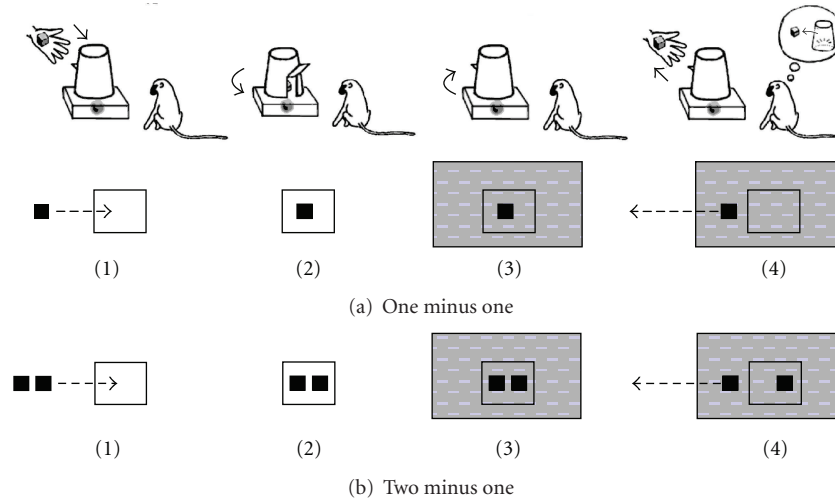
FIGURE 2: Subtraction sequences for the "1−0" (a) and "2−1" (b) conditions. The upper row shows the actual movement of the cup and bread pieces, and the two lower rows indicate the hypothesized view (1, 2) and representation (3, 4) of bread pieces in the monkey's mind.

from the "2−2" condition, we should conclude that their operation is category-monitoring subtraction.

2.4.2. Experiment 2: Two-Step Subtraction. Experiment 2 was designed to depict further components of arithmetic-like reasoning using a "*two-step subtraction*" task where a quantity is subtracted twice (i.e., "(2−1)−1"). In one-step subtraction (i.e., "2−1" condition), the monkeys needed to mentally manipulate the representation of numerosity only once. In two-step subtraction (i.e., "(2−1)−1" condition), monkeys were required to mentally manipulate the representation of numerosity twice. For example, to solve the "(2−1)−1" task, the monkeys would have to first represent the results of "2−1" mental manipulation and then carry out another mental manipulation (i.e., "−1") using that representation.

We examined two-step subtraction in two ways: simultaneous visibility and successive visibility.

Experiment 2-a: Simultaneous Visibility. For experiment 2-a, a separate data sampling period was set 2 years after the data sampling period for experiment 1. Applying the same procedure as in experiment 1, we carried out the "0−0−0," "2−0−0," "2−1−0," "2−0−1," "2−1−1," "2−2−0," and "2−0−2" conditions (1 session = 7 trials, presented in random order within a session). For example, for the "2−1−1" condition, a human experimenter stood in the adjoining room about 1m away from the apparatus and showed two pieces of bread on his palm to the monkey (Figure 3(a)(1)). He then put it into the cup through an opening and rotated the cup 180 degrees so that the monkey could see and confirm what was in the cup through the opening (Figure 3(a)(2)). After making sure that the monkey looked inside the cup, the experimenter rotated the cup 180 degrees back to the original position (Figure 3(a)(3)) and removed one piece of bread from the opening (Figure 3(a)(4)). After confirming that the monkey looked at the removed piece of bread, he removed another

piece of bread from the opening using the other hand, still keeping and showing the previously removed piece of bread on his other palm (Figure 3(a)(5)). Then he walked away from the apparatus, still showing the food on both palms to the monkey and went out of view into another room as in experiment 1. In the control condition "2−0−0," the experimenter performed exactly the same sequence of actions except that he imitated movements of removing a piece of bread by reaching into the opening without actually removing the bread and walked away from the apparatus showing his empty palms to the monkey.

In these simultaneous visibility conditions, the monkeys could either solve the task by performing the "2−2" mental manipulation (=one-step subtraction), the "2−(1+1)" mental manipulation (=two-step subtraction), or the "(2−1)−1" mental manipulation (=two-step subtraction).

Experiment 2-b: Successive Visibility. For experiment 2-b, another separate data sampling period was set 6 months after the data sampling period for experiment 2-a. Applying the same procedure as in experiment 2-a, we carried out the "(0−0)−0," "(2−0)−0," "(2−1)−0," "(2−0)−1," "(2−1)−1," "(2−2)−0," and "(2−0)−2" conditions (1 session = 7 trials, presented in random order within a session). For example, for the "(2−1)−1" condition, an experimenter performed exactly the same sequence of actions until the first piece of bread was removed (Figures 3(b)(1) through 3(b)(4)). After confirming that the monkey looked at the removed piece of bread, he dropped the removed piece into a bucket which was placed in an inaccessible location from the monkeys on the floor and closed the bucket lid by using a foot pedal. He then removed another piece of bread from the opening (Figure 3(b)(5)) and walked away from the apparatus, still showing the food on his palm to the monkey and went out of view into another room as in experiment 1. In the control condition "(2−0)−0," the experimenter performed exactly the same sequence of actions except that he imitated movements of removing a piece of bread by reaching
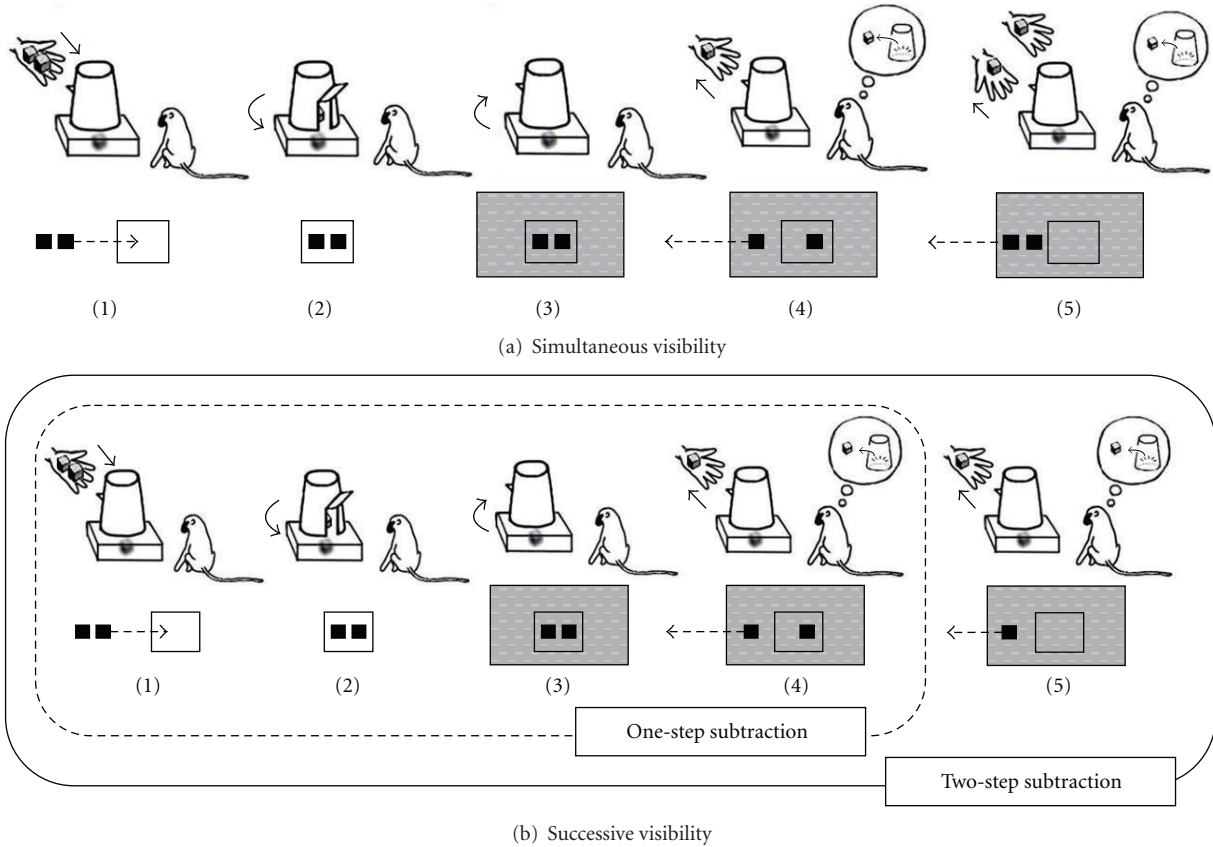
(a) Simultaneous visibility

One-step subtraction

Two-step subtraction

(b) Successive visibility

Figure 3: Subtraction sequences for the "$2-1-1$" (a) and "$(2-1)-1$" (b) conditions. The upper row shows the actual movement of the cup and bread pieces, and the lower row indicates the hypothesized view (1, 2) and representation (3, 4, 5) of bread pieces in the monkey's mind for each condition.

into the opening without actually removing the bread and also imitated movements of placing a piece of bread into the bucket then walked away from the apparatus showing his empty palm to the monkey.

In these successive visibility conditions, the monkeys must solve the task by performing two-step subtraction (i.e., "$(2-1)-1$" mental manipulation) instead of one-step subtraction (i.e., "$2-2$" mental manipulation).

3. Results

3.1. Participation. In the current field experimental paradigm, participation in the experiment depended on the spontaneous choice of the monkeys. During the 2-month data sampling period for experiment 1 (March 2002 to May 2002), four adult monkeys (Mkono: male, Mkia: male, Vidole: male, Mke: female) spontaneously visited the testing site and participated in the experiment. Mkono and Mkia each completed 17 sessions, and Mke completed 12 sessions during the data sampling period. Mke completed fewer sessions because she visited the testing site less frequently. Vidole participated in the experiment much less frequently, completing only 2 sessions. Thus his data were excluded from the analysis.

During the 2-month data sampling period for experiment 2-a (July 2004 to August 2004), another four monkeys (Mr. Funny: male, Meno: male, Macho: female, Matiti:

female) spontaneously visited the testing site and participated in the experiment. Mr. Funny completed 20 sessions, Meno completed 17 sessions, and Macho and Matiti each completed 12 sessions during the data sampling period. The four other monkeys who participated in experiment 1 either did not visit the testing site or they did not spontaneously participate in the experiment during the data sampling period for experiment 2.

During the 1-month data sampling period for experiment 2-b (February 2005), we targeted only one monkey (Mr. Funny) based on his performance in experiment 2-a. During this period, Mr. Funny completed 16 sessions.

3.2. Reaction to "Artificial Foraging Situation"

3.2.1. Experiment 1: One-Step Subtraction. Typically, the monkeys either inspected the cup within 10 seconds or did not approach the apparatus at all after witnessing the subtraction sequences; thus, the 30-second criterion for the "foraging attempt" seemed reasonable. All three monkeys made a "foraging attempt" more often in the "$1-0$" condition than in the baseline "$0-0$" condition (Fisher's exact test; Mokono: $P < .0001$, Mkia: $P < .0001$, Mke: $P < .0001$, Figure 4, all P values are two-tailed in the current paper), meeting the assumption that the monkeys react differently according to whether there was some food or no food from the beginning.
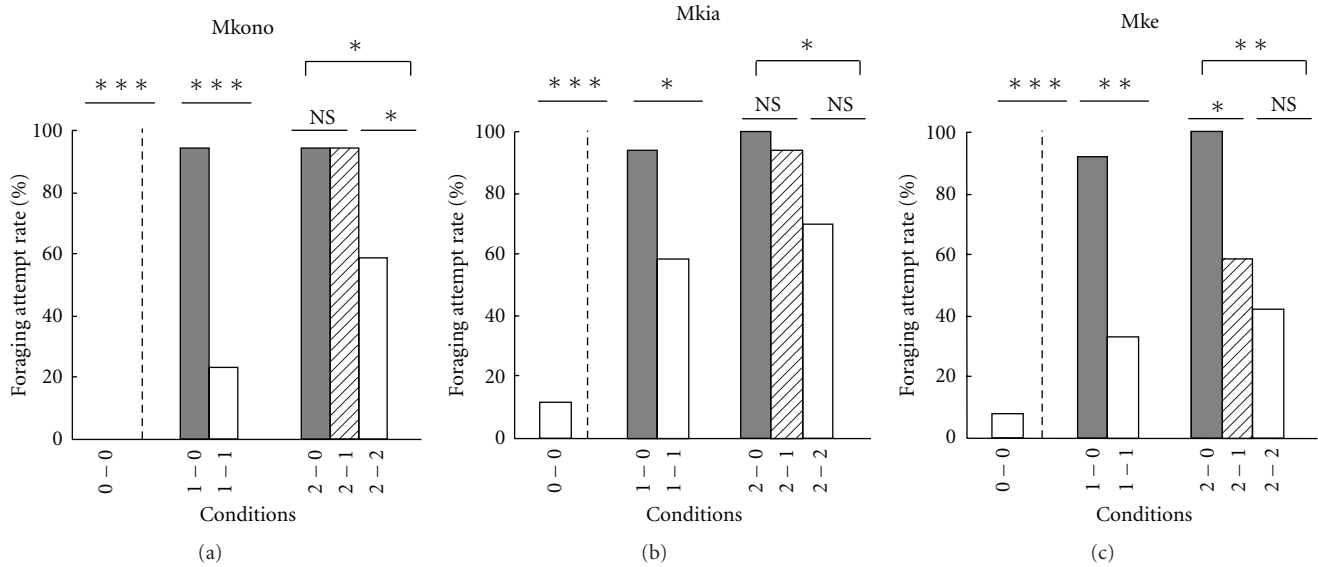
FIGURE 4: "Foraging attempt" rates for one-step subtraction. The "foraging attempt rates" were expressed as the percentage of "attempt made" trials over the total number of trials in each condition for each subject. The number of sessions completed was 17 for Mkono and Mkia, and 12 for Mke. ∗∗∗: $P < .001$, ∗∗: $P < .01$, ∗: $P < .05$. P values are two tailed. Fisher's exact test was conducted only once between the "2−1" and "2−2" conditions for testing differences among the three conditions: "2−0", "2−1", and "2−2" for Mkono, since the frequencies for the "2−0" and "2−1" conditions were identical. The difference between the "2−0" and "2−2" conditions becomes marginally significant when the threshold is set at 2.5% for multiple comparison for Mkia. The difference between the "2−0" and "2−1" conditions becomes marginally significant when the threshold is set at 2.5% for multiple comparison for Mke.

In subtraction from 1, all three monkeys made a "foraging attempt" more often in the "1−0" condition than in the "1−1" condition (Fisher's exact test; Mokono: $P < .0001$, Mkia: $P = .039$, Mke: $P = .009$), suggesting that they were capable of (1) mentally performing category-monitoring subtraction (i.e., bread − bread = nothing) and (2) changing their behavior accordingly when the number of objects *represented* and *manipulated* was one.

In subtraction from 2, again all three monkeys made a "foraging attempt" more often in the "2−0" condition than in the "2−2" condition (Fisher's exact test; Mokono: $P = .039$, Mkia: $P = .044$, Mke: $P = .005$), suggesting that their category-monitoring subtraction extended to a situation where the number of objects *represented* and *manipulated* was two.

Comparison of the three conditions resulting in no remainders (i.e., "0−0", "1−1" and "2−2" conditions) over the three monkeys as a group revealed that there was a pattern of increasing "foraging attempt" rates as the number of objects *represented* and *manipulated* increased (Friedman $\chi^2 = 6.000$, $Df = 2$, $P = .05$). This could either imply that the monkeys' motivation was greater when the number of bread pieces inserted in the cup was greater or the difficulty of performing category-monitoring subtraction increased as the number of objects handled at once increased.

Comparisons of the "2−1" condition with the "2−0" and "2−2" conditions revealed varying "foraging attempt" rates among the three monkeys. Mkono approached the "2−1" cups as often as the "2−0" cups (Fisher's exact test; $P = 1.000$) but more often than the "2−2" cups (Fisher's exact test; $P = .039$), indicating that he was (1) mentally

performing at least numerosity-monitoring subtraction (i.e., two pieces of bread − one piece of bread = one piece of bread left) and (2) changing his behavior accordingly. Mke approached the "2−1" cups less often than the "2−0" cups (Fisher's exact test; $P = .037$) but as often as the "2−2" cups (Fisher's exact test; $P = .684$), suggesting that she applied category-monitoring subtraction instead of numerosity-monitoring subtraction when both types of reasoning are possible. Although the order of attempt rates was the same as the other monkeys, Mkia's reaction to the "2−1" condition did not reveal significant differences compared with the "2−0" and "2−2" conditions (Fisher's exact test; "2−0" versus "2−1": $P = 1.000$, "2−1" versus "2−2": $P = .175$). We have no basis for distinguishing between the two types of reasoning that Mkia might have employed.

The correct response rates for the first session for each monkey were as follows: Mkono: 66.6%, Mkia: 83.3%, and Mke: 83.3% (Figure 5). Group analysis of the correct response rates in the first and the last 6 sessions for the three monkeys did not reveal significant differences ($F_{1,2} = 3.000$, $P = .225$), nor was there any interaction between the order of sessions and conditions ($F_{5,10} = 0.313$, $P = .894$). This implies that the monkeys were less likely to have learned to approach or not in each condition over repeated tests through operant reinforcement. The results therefore appear to reflect spontaneous subtraction.

3.2.2. Experiment 2: Two-Step Subtraction

Experiment 2-a: Simultaneous Visibility. Comparison of the "2−0−0" condition with the "0−0−0" condition revealed
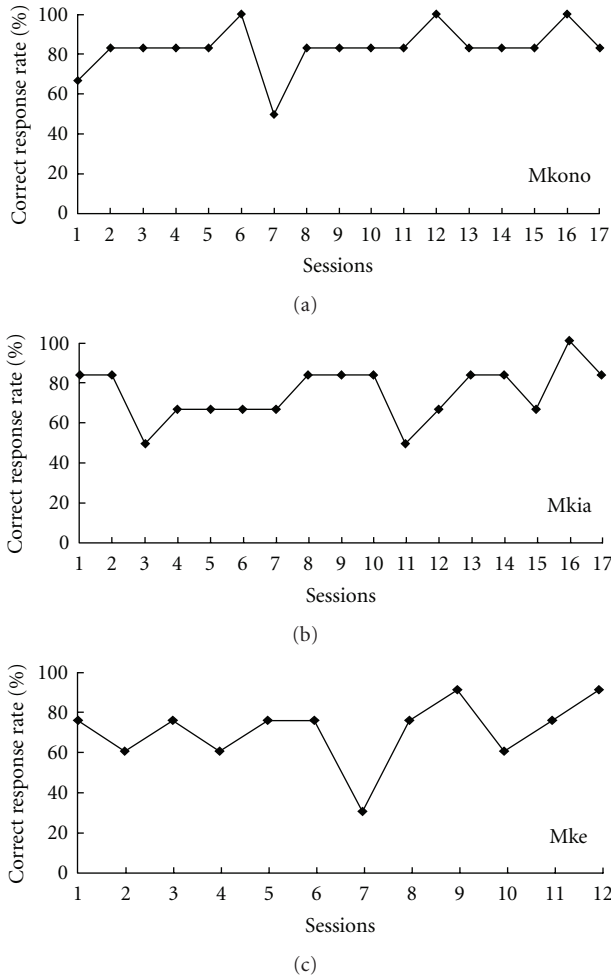
(a)

(b)

(c)

FIGURE 5: Correct response rates over sessions for one-step subtraction. The correct response rates were calculated as the percentage of "attempt made" trials when the remainder was 2 and 1, and "attempt not made" trials when the remainder was 0, over the total 6 trials for each session for each subject.

that one out of four monkeys met the baseline assumption (Fisher's exact test; Mr. Funny: $P = .004$, Meno: $P = .084$, Macho: $P = 1.000$, Matiti, $P = 1.000$, Figure 6). Further analysis on Mr. Funny revealed that he approached the cup equally often when the remainder was two and when the remainder was one, but less often when the remainder was zero (Figure 6; Fisher's exact test; "remainder = two" versus "remainder = one": $P = 1.000$, "remainder = one" versus "remainder = zero": $P < .0001$; N/B: frequencies for "2−1−0" and "2−0−1" conditions were summed to form a "remainder = one" condition, and frequencies for "2−1−1", "2−2−0", and "2−0−2" conditions were summed to form a "remainder = zero" condition). This suggests that at least one monkey inspected the cup more often when there was some food left compared with when there was no food left, when the bread pieces were sequentially removed twice and the animal could see the removed pieces simultaneously. He might have either solved the task by performing the "2−2" mental manipulation (=one-step subtraction), the "2−(1+1)" mental manipulation (=two-step subtraction),

or the "(2−1)−1" mental manipulation (=two-step subtraction) in this case.

Mr. Funny's correct response rate for the first session was 57.1% (Figure 7). The average correct response rates in the first and the last 6 sessions was the same (71.4%), suggesting that he was less likely to have learned to approach or not in each condition over repeated tests through operant reinforcement. The results therefore appear to reflect spontaneous subtraction.

Experiment 2-b: Successive Visibility. Comparison of the "(2−0)−0" condition with the "(0−0)−0" condition for Mr. Funny revealed that he did not meet the baseline assumption for experiment 2-b (Fisher's exact test; $P = .433$, Figure 8); however, comparisons among the test conditions did reveal that he approached the cup equally often when the remainder was two and when the remainder was one but less often when the remainder was zero (Figure 8; Fisher's exact test; "remainder = two" versus "remainder = one": $P = .386$, "remainder = one" versus "remainder = zero": $P < .004$; N/B: frequencies for "(2−1)−0" and "(2−0)−1" conditions were summed to form a "remainder = one" condition, and frequencies for "(2−1)−1", "(2−2)−0", and "(2−0)−2" conditions were summed to form a "remainder = zero" condition). Mr. Funny's correct response rate for the first session was 42.9% (Figure 9). The average correct response rate in the first 6 sessions (57.1%) was not significantly different from the one in the last 6 sessions (66.7%) ($t = -1.348$, $df = 10$, $P = .207$).

The fact that the baseline assumption was not met does not allow us to draw any concrete conclusion, but it still stands true that Mr. Funny inspected the cup more often when there was some food left compared with when there was no food left, when the bread pieces were sequentially removed twice and the animal could only see the removed pieces successively, not simultaneously, except for the case where there was no food from the beginning. We could only speculate, but Mr. Funny might indeed have changed his behavior by performing two-step subtraction (i.e., "(2−1)−1" mental manipulation) instead of one-step subtraction (i.e., "2−2" mental manipulation); however, the tendency to inspect the cup might have generally increased for all conditions as the difficulty and complexity of the tasks developed from simultaneous visibility task to successive visibility task. In other words, he might be capable of performing two-step subtraction, but he could have gradually changed his foraging strategy from "mainly deploying mental manipulation of numerosity" to "a mixture of mental manipulation and inspection anyway" for all conditions.

We could further speculate that in a given population of vervet monkeys more individuals are capable of one-step subtraction and they deploy mental manipulation of numerosity as a foraging strategy, while fewer individuals are capable of two-step subtraction and they start to depend more on other strategies as mental manipulation of numerosity becomes less effective. Several factors could be involved in decreased effectiveness in their mental manipulation; for example, a possible failure in attentional mechanisms or in working memory capacity may have contributed
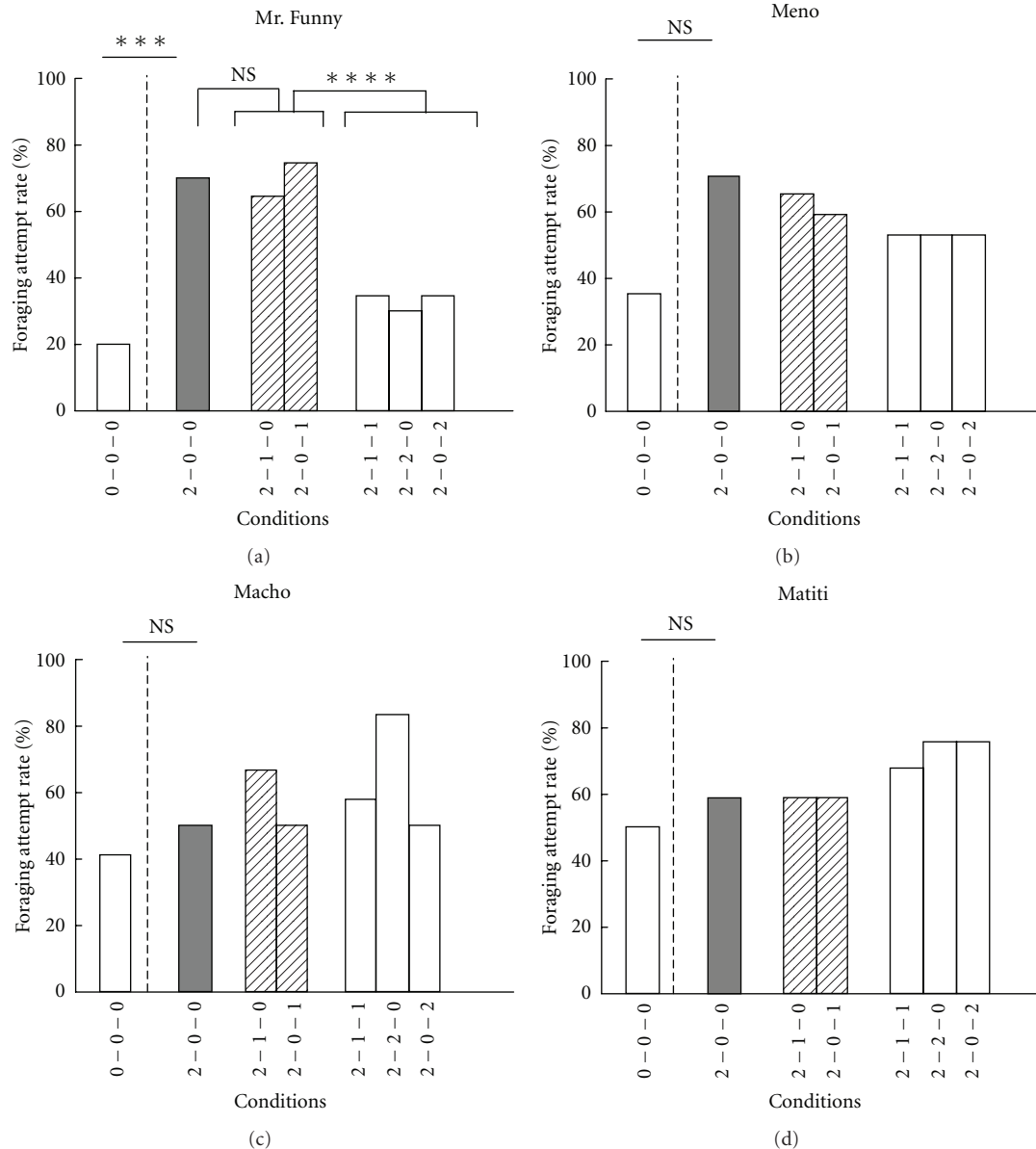
FIGURE 6: "Foraging attempt" rates for simultaneous visibility. The "foraging attempt rates" were expressed as the percentage of "attempt made" trials over the total number of trials in each condition for each subject. The number of sessions completed was 20 for Mr. Funny, 17 for Meno, and 12 for Macho and Matiti. $* * * *$: $P < .001$, $* * *$: $P < .01$. P values are two tailed.

to explain Mr. Funny's behavior in experiment 2-b as well as that of the other three monkeys that failed in experiment 2-a. Also, from an evolutionary perspective, an inspection could be considered worthy whenever a monkey witnesses repeated (i.e., more than one or two) manipulations even though no food is ever visible (such as in the "0−0−0" condition of experiment 2-a and in the "(0−0)−0" condition of experiment 2-b). Unlike other conditions, the "0−0−0" and "(0−0)−0" conditions involve a "peculiar behavior" of the human experimenter repeatedly manipulating the empty cup and the monkeys might have associated such manipulation to the possible presence of food from the previous experience. In any case, more individuals should be tested in the future to further discuss such speculations, as

the current data involve only a few individuals and the result is interestingly pregnant.

4. Discussion

We asked two major questions in the current study: how animals benefit from arithmetic-like reasoning (=*ecological function*), and how such reasoning is conducted (=*mechanism*). The results demonstrated that vervet monkeys spontaneously change their "foraging behavior" according to the quantity of the "artificial prey" in the current experimental setup and that attention to the numerosity of objects guides this behavior in some individuals while other monkeys attend to the category of objects rather than the numerosity.
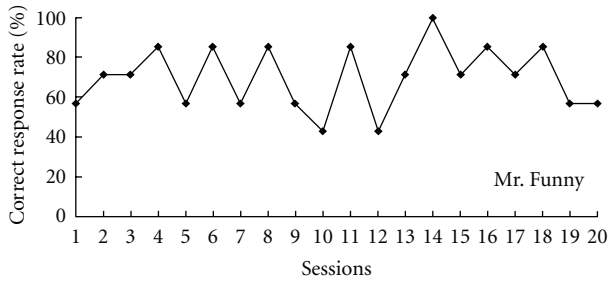
FIGURE 7: Correct response rates over sessions for simultaneous visibility. The correct response rates were calculated as the percentage of "attempt made" trials when the remainder was 2 and 1, and "attempt not made" trials when the remainder was 0, over the total 7 trials for each session.
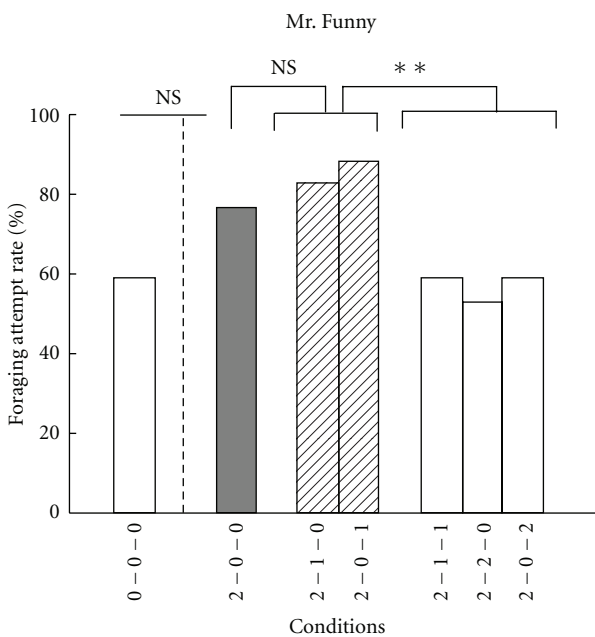

FIGURE 8: "Foraging attempt" rates for successive visibility. The "foraging attempt rates" were expressed as the percentage of "attempt made" trials over the total number of trials in each condition. The number of sessions completed was 16. ∗∗: $P < .01$. P values are two tailed.
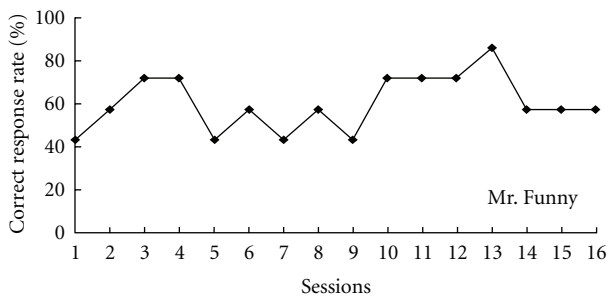

FIGURE 9: Correct response rates over sessions for successive visibility. The correct response rates were calculated as the percentage of "attempt made" trials when the remainder was 2 and 1, and "attempt not made" trials when the remainder was 0, over the total 7 trials for each session.

The increased "foraging efficiency" in the current "artificial foraging paradigm" (i.e., involving a cup, bread pieces, and human experimenter) does not necessarily mean that the monkeys would similarly adjust their foraging behavior in their actual "natural foraging" scenario (i.e., involving a hollow and insects), nor does it imply that they did so in their evolutionary history. This does not allow us to draw any conclusion about whether foraging is one possible factor for the evolution of arithmetic-like reasoning, but the current study sets a platform for future cross-species comparison.

To answer evolutionary questions, we need a cross-comparison of the phylogenic and ecological factors in question (e.g., foraging pattern, social complexity, etc.). We can look for differences in numerical competence between animals with different foraging patterns (i.e., omnivores and carnivores who chase moving objects like insects, birds, mammals, etc. versus herbivores who attend to stable objects like fruits, leaves, etc.). In addition to providing empirical data on one species (i.e., vervets) as a starting point, the current study provids a simple and easily adaptable field technique that would allow comparison across taxa and habitat using a uniform method. Phylogenically, vervets are Old World monkeys (Family Cercopithecidae) whose foraging pattern includes mobile objects (i.e., invertebrates) [45]. Using a comparable "seminatural foraging paradigm," it has been shown that the phylogenically and dietarily similar rhesus macaque is capable of rudimentary subtraction in seminatural settings [36]. The dietary similarities extend to foraging in human residential areas [51]. In addition to this well-matched cross-species comparison, phylogenically similar but dietarily different species can be compared, like the leaf monkey, the most folivorous of Old World monkeys.

Concerning mechanisms, the current study demonstrated that at least some vervets spontaneously engage in mental manipulation of numerosity and that numerosity can mentally be manipulated at least once and potentially twice. The fact there was no extensive training suggests that the ability already existed in the wild. Various models have been proposed for the mechanisms of numerical representation in nonverbal and preverbal mind, including the widely discussed object file model [52] and accumulator model [53], and empirical evidence exists in support of both models as discussed in [36]. In either of the two models it is possible to perform simple arithmetic (i.e., addition, subtraction, multiplication, and division) as long as it involves the first three or four numerosities [36], so the focus of our research was how arithmetic-like reasoning is put into practice in a cost-benefit decision-making situation by referring to more general mechanisms. By considering the elemental distinction between a category and particular instances of a category, we found that monkeys use both category-monitoring and numerosity-monitoring mechanisms for responding to subtraction-like manipulations of objects and that such cognitive processes affect their cost-benefit decision making. We cannot rule out a possibility that the monkeys used estimates of continuous physical variables (e.g., volume, area, perimeter, etc.) for their arithmetic-like reasoning. However the size of bread pieces was not strictly identical, and each piece had a slightly different area, perimeter,

shape, and so forth. While acknowledging that the data only represent instances of magnitude estimation (of which numerosity is just an example), it would be cognitively economical to attend to an overall numerical attribute of an object (i.e., numerosity) rather than to varying physical variables when subtraction-like manipulation is mentally performed. This seems to be in line with the case with other species; for example, lemurs [15] and rhesus monkeys [18] are known to spontaneously attend to numerical attributes when information on both numerosity and other physical variables is available, and in chicks the identification of objects as different and separate individuals is crucial for the computation of number rather than continuous extent [12]. This also seems to be in line with the fact that each prey has different physical features in the actual environment; if foraging did play a role in the evolution of subtraction-like reasoning then such cognitive ability should be applicable to, and functional in, the actual foraging situation. While we leave a distinction between magnitude estimation and strict numerosity to further controlled research, we attach importance of the current data to a demonstration of spontaneous arithmetic-like reasoning in a wild population of monkeys.

It is also interesting to note that at least one monkey responded to both one-step and two-step subtractions according to the numerosity of the remainder but that his performance for two-step subtraction became undistinguishable from the baseline "$(0-0)-0$" condition. The overall effectiveness for his two-step subtraction seems to have decreased compared to one-step subtraction. While acknowledging that sequential steps involved in subtraction manipulations are not immediately comparable to the first-order and second-order representation of social events (i.e., theory of mind, [54]), it is worth noting that in this domain of quantitative cognition the monkeys also showed varying responses towards different number of steps.

Acknowledgments

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