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Can rhesus monkeys spontaneously subtract?

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Abstract

Animals, including pigeons, parrots, raccoons, ferrets, rats, New and Old World monkeys, and apes are capable of numerical computations. Much of the evidence for such capacities is based on the use of techniques that require training. Recently, however, several studies conducted under both laboratory and field conditions have employed methods that tap spontaneous numerical representations in animals, including human infants. In this paper, we present the results of 11 experiments exploring the capacity of semi-free-ranging adult rhesus monkeys to spontaneously compute (i.e. single trial, no training) the outcome of subtraction events. In the basic design, we present one quantity of objects on one stage, a second quantity on a second stage, occlude both stages, and then remove one or no objects from each stage. Having watched these events, a subject is then allowed to approach one stage and eat the food objects behind the occluder. Results show that rhesus monkeys correctly compute the outcome of subtraction events involving three or less objects on each stage, even when the identity of the objects is different. Specifically, when presented with two food quantities, rhesus monkeys select the larger quantity following subtractions of one piece of food from two or three; this preference is maintained when subjects must distinguish food from non-food subtractions, and when food is subtracted from either one or both initial quantities. Furthermore, rhesus monkeys are capable of representing zero as well as equality when two identical quantities are contrasted. Results are discussed in light of recent attempts to determine how number is represented in the brains of animals lacking language. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Number representation; Non-human primates; Rhesus; Math; Evolution

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1. Introduction

Over the past 20 or so years, experimental work in the lab and field has provided considerable evidence that animals have the capacity for numerical representation (for reviews see Boysen, 1997; Gallistel & Gelman, 2000; Hauser, 2000; Shettleworth, 1998). In nature, for example, studies of lions have demonstrated that individuals respond more intensely to the roars of three individuals than to the roars of one individual (McComb, Packer & Pusey, 1994). In the lab, studies of pigeons and rats have demonstrated that subjects can press a lever approximately 20 times (i.e. the number of presses is roughly normally distributed around 20) to obtain food, even when such factors as time, energetic expenditure, and motivational state have been controlled (Gallistel, 1990); moreover, as predicted by Gibbon (1977) and Meck and Church (1983), the standard deviation of the distribution of bar presses by a rat increases as a function of the number of target presses, showing that the representation of large numbers is possible, but only approximately. Finally, studies of an African gray parrot (Pepperberg, 1994) and several chimpanzees (Boysen & Bernston, 1989, 1995; Matsuzawa, 1985) indicate that these extensively trained individuals can learn the meaning of the Arabic numerals, with the highest level of achievement obtained by Matsuzawa's chimpanzee Ai who understands the ordinal relationships between the numbers zero through nine (Biro & Matsuzawa, 1999; Kawai & Matsuzawa, 2000; Matsuzawa, 1985).

1.1. Different models of number representation

Two models have generally dominated current discussions of numerical representation in non-human animals and preverbal human infants, with empirical evidence providing some support for both models (Carey & Spelke, in press; Dehaene & Changeux, 1993; Gallistel & Gelman, 2000; Hauser & Carey, 1998; Wynn, 1998). On the one hand is the Meck and Church (1983) accumulator model which is based on the idea that each object or event is enumerated or represented as an impulse of activation from the nervous system. To extract number (or time), the accumulator stores each impulse until the end of counting (or timing), and then transfers this information into memory where it outputs one value for the impulses counted. As many have articulated, this can be schematically represented as a growing number line with 1 = _, 2 = __, 3 = ___, 4 = ____, … 8 = ________, and so on. Because of variability or noise in the remembered magnitude, the output from the accumulator is an approximation of number, with variability increasing in proportion to magnitude, or what is referred to as scalar variability (Gibbon, 1977; Whalen, Gallistel & Gelman, 1999); studies of animals in particular have demonstrated that subjects can keep track of both time and number in such tasks, with some recent evidence of more accurate computation of time (Roberts, Coughlin & Roberts, 2000). As Gallistel and Gelman (2000) have recently articulated, under this model "numerosity is never represented exactly in the nonverbal or preverbal mind, with the possible exception of the first three or four numerosities". Nonetheless, with number represented as a magnitude with scalar variability it is possible to compute such arithmetical operations as addition, subtraction, multiplication and division.

In contrast to the accumulator model, others have proposed that number, especially small numbers less than about four, may be represented by a different system, one that is used by adults for object-based attention and tracking: the object file model (Kahneman, Treisman & Gibbs, 1992; Scholl, in press; Scholl & Leslie, 1999; Trick & Pylyshyn, 1994). Although the object file model does not provide an explicit representation of number (and was not developed for this purpose), it does provide at least four criteria for constructing numerical representations (Carey & Spelke, in press): (1) using spatiotemporal information, object files are opened based on principles of individuation and numerical identity; (2) if one or more object files are opened, opening a new one provides a mechanism for adding one item to an array of items, an operation that is likely to be important for the successor function that is crucial to the integer count list; (3) object files are based on $1 - 1$ correspondence, and thus contribute to the establishment of numerical equivalence; (4) the number of object files that can be simultaneously opened is limited to about four (at least for adult humans; Trick & Pylyshyn, 1994), but is precise and not subject to Weber's law (distance and magnitude effects; for review see Dehaene, 1997; Gallistel, 1990; Gallistel & Gelman, 2000).

Until recently, these models, and the form of numerical representation that they operate upon, have been pitted against one another. However, theoretical arguments developed by Carey (in press) and Carey and Spelke (in press), together with empirical work on human infants and non-human primates (Hauser, Carey & Hauser, 2000; Uller, Carey, Huntley-Fenner & Klatt, 1999; Uller, Hauser & Carey, 2000), suggest that both models together may provide a more comprehensive explanation of the results to date. In particular, and as Carey and Spelke (in press) have explicitly argued, if number is represented as a magnitude, then it is not possible to account for the fact that human infants successfully discriminate two from three dots, but fail to discriminate four from six and eight from 12 dots (Starkey & Cooper, 1980; Xu & Spelke, 2000); specifically, if infants tapped a magnitude representation of number, in which Weber's law holds (i.e. the discriminability of two perceived magnitudes is determined by the ratio of objective magnitudes), then these pairs should be discriminable since they differ by the same ratio. On the other hand, a magnitude system can account for the fact that human infants are able to discriminate eight from 16 dots, numerical values that well exceed the presumed limits of an object file representation (Xu & Spelke, 2000). Putting these findings together leads to the suggestion that an object file mechanism may underlie success with small numbers, whereas an analog magnitude system may underlie success with larger numbers. More precisely, the object file model provides a mechanism for precise small number quantification, whereas the accumulator model provides a mechanism for approximate large number quantification.

The goal of the present paper is to further explore the extent to which non-human animals can spontaneously compute (i.e. in the absence of training) arithmetic operations over small numbers of objects. More specifically, given the extensive work on the operations of addition (Boysen & Bernston, 1989; Hauser et al., 2000;

Hauser, MacNeilage & Ware, 1996; Olthof, Iden & Roberts, 1997) and ordering (Biro & Matsuzawa, 1999; Brannon & Terrace, 1998), we designed a series of experiments to assess whether rhesus monkeys are capable of computing the outcome of subtraction events, an operation that has been relatively neglected in the animal literature (e.g. Brannon et al., unpublished data; Gibbon and Church, 1981; Hauser et al., 1996). In addition to this general problem, two more specific issues guided the particular details of our experiments. First, current accounts of the object file model are based on featureless object files (Scholl, in press; Scholl & Leslie, 1999; Simon, 1997; Uller et al., 1999). Specifically, to establish or maintain an object file, information about the object's features is not used. The only relevant operation is $1-1$ correspondence. Thus, when a display is occluded and then revealed, the object file system simply checks for a match at the object level, independent of the object's properties or features. However, recent studies of rhesus monkeys, reviewed more completely below, suggest that object features are tracked, remembered, and used to determine the precise number of objects occluded when that number is less than five. These data suggest that either the object file mechanism can, under certain circumstances, keep track of object features or that a different mechanism is in play, one that tracks objects features and is limited to small numbers; the suggestion by Cowan (2001) of a short-term memory mechanism with a limit of four is a candidate mechanism.

The second issue stems from recent studies by Wynn and Chiang (1998). Human infants are surprised (i.e. look longer on an expectancy violation task) by a magical disappearance of an object ($1+1=1$), but are not surprised by a magical appearance ($2-1=2$). Based on these findings, Wynn and Chiang argue that human infants cannot represent zero, a finding that they consider to be consistent with the accumulator model. Specifically, so they argue, the accumulator is not engaged unless there is an object or event to initiate the process of impulse activation. If Wynn and Chiang are correct, then tests involving animals' capacities for subtraction are particularly relevant because subtraction is necessary to get to zero.

1.2. Why rhesus monkeys?

There are two reasons why rhesus monkeys are ideal subjects for exploring the details of non-linguistic numerical representation. First, recent work by Brannon and Terrace (1998) shows that rhesus monkeys trained to discriminate between the numbers one through four can subsequently discriminate – in the absence of training – between the numbers one through nine. On two counts, these data provide support for the accumulator mechanism of analog magnitude representation. Specifically, rhesus monkeys' success in discrimination exceeds the limits of the object file mechanism (i.e. greater than four) and their performance is subject to magnitude effects (i.e. greater accuracy with increasing differences between number pairs); because the animals were trained on one through four, it is not possible to assess whether they would also show scalar variability within this range. Second, using a spontaneous (i.e. no training, one trial per animal) search task involving addition operations, Hauser et al. (2000) provide evidence for the set size signature of the object file model (i.e. a limit of approximately four), one that keeps track of object features. In the basic task, each subject received only one trial in which they watched different quantities of apple placed into one of two boxes. Thus, for example, a subject watched as an experimenter sequentially placed (i.e. consecutive addition operations) three pieces of apple into one box, followed by four pieces of apple into a second box. Subjects were then allowed to approach one box, and eat its contents. Because the pieces of apple are placed out of sight into the boxes, subjects must keep this information in working memory in order to calculate which box has more food. Subjects succeed up to a contrast of four versus three (controlling for time and volume), but fail at larger numbers, including five versus four, six versus four, and eight versus three; these failures are inconsistent with Weber's law, and stand in striking contrast to the results of Brannon and Terrace (1998) using an operant procedure. In controlling for time, we required the rhesus to keep track of the identity of each object placed in the box. Thus, for example, they saw four apple slices placed into one box versus three apple slices and a rock placed into the other box. Once again, they picked four over three slices, showing that they attended to the features of the objects placed, distinguishing between apple slices and rocks.

In a second series of experiments with rhesus monkeys, using the expectancy violation procedure of Wynn (1992), Hauser and colleagues (Hauser & Carey, 1998; Hauser et al., 1996; unpublished data) have also shown the set size signature of the object file mechanism. Specifically, rhesus monkeys pass tests (i.e. look longer at the impossible outcomes) involving $1 + 1 = 1$ versus 2 versus 3, $2 + 1 = 2$ versus 3, and $2 - 1 = 1$ versus 2, but fail with $2 + 2 = 3$ versus 4 versus 5. Thus, using two different tasks, Hauser and colleagues provide converging evidence that rhesus monkeys spontaneously represent the numbers one, two and three.

Given the rhesus monkeys' performance on the spontaneous search tasks involving addition operations, the following experiments were designed to explore their capacity to compute subtraction operations. Specifically, we examine whether rhesus monkeys compute the outcome of subtraction events, attending to the identity of the objects placed out of sight, and contrasting the quantities obtained in two spatially separated locations, following subtraction events. Rather than focus on the upper limit of their capacity to compute the outcome of subtraction operations, we focused instead on their ability to track object identity, compute the precise outcome of a subtraction operation, and represent both zero and equality.

2. Methods

2.1. Subjects

Experiments were conducted on a population of semi-free-ranging rhesus monkeys (*Macaca mulatta*) living on the island of Cayo Santiago, Puerto Rico (Rawlins & Kessler, 1987). This population has been observed for over 60 years, thereby providing considerable information concerning demographic parameters, life history characteristics, social behavior, mating system, and vocal and cognitive behavior. Over the past 5 or so years, researchers have conducted several experiments on this population, using spontaneous methods to determine the nature of their representations. This includes studies of vocal communication (Gouzoules, Gouzoules & Marler, 1984; Hauser, 1998a; Rendall, Rodman & Edmond, 1996), hemispheric asymmetry for vocal perception (Hauser, 1998b; Hauser & Andersson, 1994), object knowledge (Munakata, Santos, O'Reilly, Hauser & Spelke, in press), and number representation (Hauser & Carey, 1998; Hauser et al., 2000, 1996).

At the time of study, the population consisted of approximately 900 individuals divided into seven social groups. Females reach reproductive maturity at approximately 3 years, whereas males reach reproductive maturity at approximately 4 years. All individuals tested in these experiments were adults. Researchers can readily identify individuals by their distinctive chest and leg tattoos, ear notches and facial markings. All animals are well habituated to the presence of human observers, thereby facilitating close observation.

2.2. General experimental procedure

The following experiments are based on the procedures developed by Hauser et al. (2000) to explore spontaneous number representation in semi-free-ranging rhesus monkeys. The overall goal of these experiments is to provide individuals with a semi-natural foraging problem – a choice between two patches or quantities of food. In the original experiments, subjects observed addition operations; here we explore subtraction using the same technique. Specifically, an experimenter searched the island for a lone individual, either an adult female or an adult male. Once a subject was located, the experimenter stood 5–10 m away, and then placed two foam core platforms on the ground, approximately 2 m apart, with a specific number of objects placed on each platform; in each experimental condition, there was always some number of plums (food) on each platform, and in some cases, non-food objects (i.e. a plum-sized metal nut) as well. Once the platforms were in place, we placed an occluder in front of each platform, blocking the subject's view of the objects. Depending on the condition, the experimenter then removed some number of objects from each side, and walked away, thereby allowing the subject to approach. An object was removed by slowly reaching behind the occluder, pulling it out, showing it to the subject, and then placing it inside the experimenter's pocket. For each experiment, we counterbalanced the side on which objects were first subtracted, as well as the side on which there were more objects.

For each trial, the subject was always stationed equidistant between the two platforms, with no obstructions along the path to a platform; by making sure that the path to a platform was clear, we reduced the possibility that one platform was easier to approach than the other. Because of the distance between the platforms, it was not possible for a subject to approach the midpoint and feed at both platforms; moreover, when the subject approached, there was no ambiguity with respect to which platform was approached first. We ran only one trial per subject, with no subject tested in more than one condition. We ran 11 experiments using this general protocol, and in each experiment we tested a total of 15 subjects. Because some

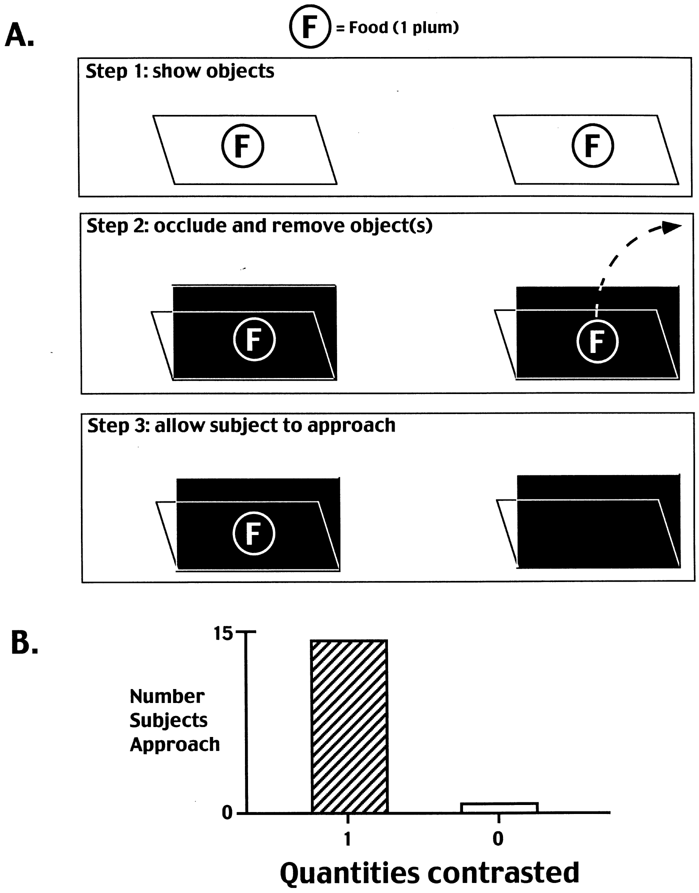

Fig. 1. (A) Procedure for presenting rhesus monkeys with a 1 versus 1 − 1 operation. (B) Results showing the number of subjects out of 15 picking one plum over no plum.

subjects failed to attend to the entire presentation, or were distracted by other group members, we often tested more than 15 subjects for each condition; subjects were considered inattentive if they looked away at any point in the presentation. The range in the number of subjects tested per condition was 15–23.

3. Results

3.1. Experiment 1: 1 versus 1 − 1, single subtraction

Fig. 1A provides a schematic illustration of the experimental design. A subject watched as an experimenter placed two foam core platforms on the ground, with one plum on each platform, lowered an occluder in front of each platform, and then removed one plum from one side. The experimenter then walked away, allowing the subject to approach. Given the initial set-up, this experiment provides each subject with a choice of one plum versus zero plums (i.e. $1 - 1 = 0$).

Results show (Fig. 1B) that 14 out of 15 subjects (sign test: $P < 0.001$) selected the platform with one plum over the platform with zero plums. This suggests that rhesus monkeys can represent the number of plums placed behind an occluder, and can determine which occluder conceals more plums when one plum has been removed. This result also suggests that rhesus monkeys can represent zero, as evidenced by the fact that they consistently pick one plum over no plums; we take up this issue in later experiments.

3.2. Experiment 2: 1 versus 3 − 1, single subtraction

Experiment 2 was conducted to determine whether rhesus monkeys would chose the larger quantity when the initial number of objects was greater than in Experiment 1, and when the quantities left on both platforms were greater than zero. Furthermore, we wanted to establish that success in Experiment 1 was not simply due to animals avoiding the side on which an object had been removed. Fig. 2A illustrates the experimental design. After we placed the platforms on the ground, with three plums on one side and one plum on the other, we occluded both sides. Next we removed one plum from the side with three plums (i.e. $3 - 1 = 2$). Subjects were therefore provided with a choice of two plums versus one plum.

Results show (Fig. 2B) that 13 out of 15 subjects (sign test: $P < 0.008$) selected the platform with two plums over the platform with one plum. This suggests that rhesus monkeys can represent the number of plums placed behind an occluder, and can determine which occluder conceals more plums when one plum has been removed, leaving some number of plums behind each occluder. These results also show that rhesus monkeys do not simply avoid the side on which an object has been removed.

3.3. Experiment 3: 2 − 0 versus 2 − 1, double action

The results from Experiments 1 and 2 can be interpreted as evidence that rhesus monkeys are capable of computing subtractions of small numbers. Can they, however, determine the largest quantity when there has been action at each location? Experiment 3 was conducted to test this possibility (Fig. 3A). After we placed the platforms on the ground, with two plums on each side, we then occluded both sides. Next, we reached behind one occluder and removed one plum, and then reached behind the other occluder and withdrew the hand empty; we clearly showed the subject that one hand held a plum and one hand was empty. Given the initial set-up, this experiment provides each subject with a choice of two plums (i.e. $2 - 0 = 2$) versus one plum (i.e. $2 - 1 = 1$).

Results show (Fig. 3B) that 13 out of 15 subjects (sign test: $P < 0.008$) selected the platform with two plums over the platform with one plum. This suggests that rhesus monkeys can represent the number of plums placed behind an occluder, and

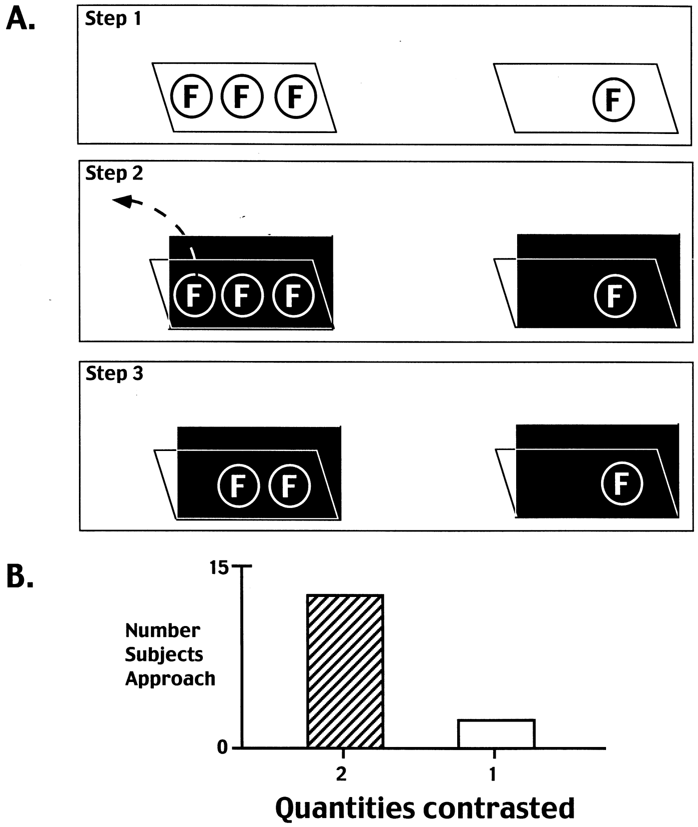

Fig. 2. (A) Procedure for presenting rhesus monkeys with a 1 versus 3 − 1 operation. (B) Results showing the number of subjects out of 15 picking one plum over no plum.

can determine which occluder conceals more plums even when there is action (i.e. a reaching motion) at each occluder.

3.4. Experiment 4: 2 − 1 versus 1 − 1, double subtraction

Results from Experiment 3 indicate that rhesus monkeys can determine the location with more food when there is action at each location. However, they could be avoiding the side associated with object removal. If rhesus monkeys followed this rule – that is, approach the side where nothing has been removed from behind the occluder – they would succeed on Experiment 3. To test this possibility, we conducted Experiment 4 (Fig. 4A). After we placed the platforms on the ground, with two plums on one side and one plum on the other, we removed one plum from each side. Given the initial set-up, this experiment provides each subject with a choice of one plum (i.e. 2 − 1 = 1) versus zero plums (i.e. 1 − 1 = 0). Because a plum is removed from each side, these events on their own can not be used to

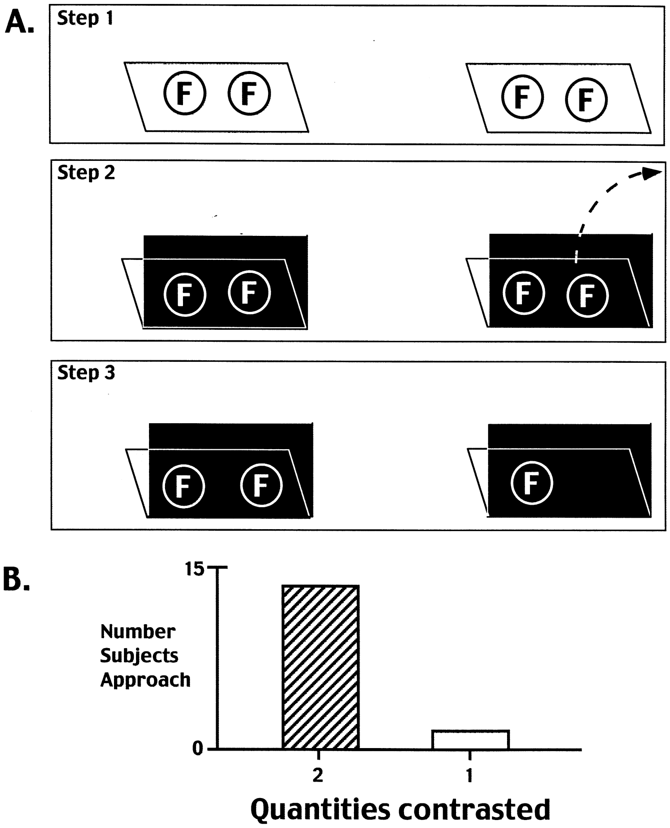

Fig. 3. (A) Procedure for presenting rhesus monkeys with a 2 − 0 versus 2 − 1 operation. (B) Results showing the number of subjects out of 15 picking two plums over one plum.

determine which location has more food. Rather, subjects must attend to the initial differences in food quantity.

Results show (Fig. 4B) that 14 out of 15 subjects (sign test: $P < 0.001$) selected the platform with one plum over the platform with zero plums. This suggests that rhesus monkeys can represent the number of plums placed behind each occluder, and can determine which occluder conceals more plums even when food is subtracted from each side. These results also suggest that rhesus monkeys can represent zero; for further discussion, see Experiment 11.

3.5. Experiment 5: 2 − 1 food versus 2 − 1 non-food, double subtraction and object identity

Based on the results presented thus far, it appears that rhesus monkeys compute subtraction events. What is less clear is the extent to which they attend to the identity of the object(s) subtracted. To probe this issue further, we conducted

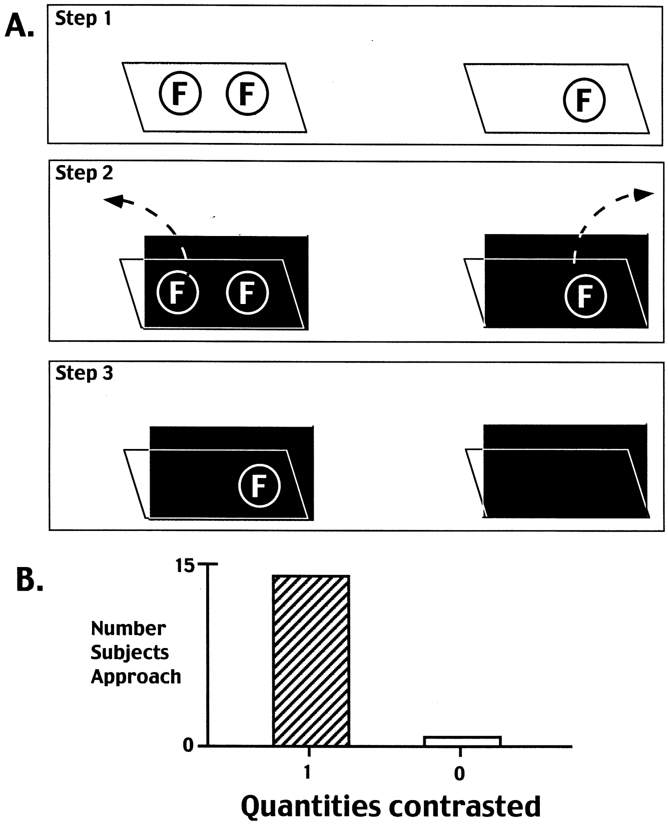

Fig. 4. (A) Procedure for presenting rhesus monkeys with a $2 - 1$ versus $1 - 1$ operation. (B) Results showing the number of subjects out of 15 picking one plum over zero plums.

Experiment 5 (Fig. 5A). After we placed the platforms on the ground, with one plum and one plum-sized metal nut on each side, we then set up the occluders. On one side we removed the plum and on the other side we removed the metal nut. This set-up therefore provides subjects with a choice between one plum and one metal nut.

Results show (Fig. 5B) that 15 out of 15 subjects (sign test: $P < 0.001$) selected the plum over the metal nut. Thus, when rhesus monkeys attend to these subtraction events, they appear to attend to the kind of object removed, or at least, to the salient properties of such objects.

3.6. Experiment 6: 2 − 1 food versus 2 − 1 food, double subtraction and object identity

To push the rhesus monkeys further, we ran a subtle variant of Experiment 5, but this time removed food from both sides. In this situation, therefore, the kind of object removed was not relevant, since it was the same on both sides. Rather, to choose the larger quantity, subjects would have to attend to the kinds of objects on each platform prior to occlusion. More specifically (Fig. 6A), after we placed the platforms on the ground, we placed two plums on one side and a plum and metal nut on the other. We then occluded each side and removed one plum from each. This set-up resulted in one occluded plum on one side and one metal nut on the other.

Results show (Fig. 6B) that 14 out of 15 subjects (sign test: $P < 0.001$) selected the side with one plum over the side with one metal nut. Thus, not only do rhesus monkeys attend to the kinds or properties of objects subtracted (Experiment 5), they also attend to the kinds or properties of objects initially present on the stages, and use such information to determine which platform has more food following a subtraction event.

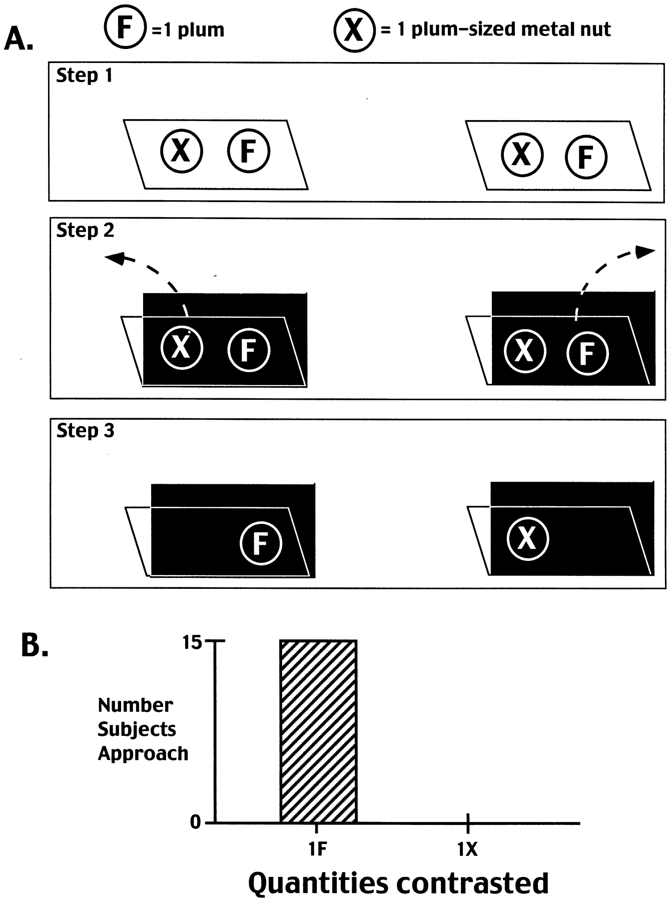

Fig. 5. (A) Procedure for presenting rhesus monkeys with a 2 − 1 food item versus 2 − 1 non-food item operation. (B) Results showing the number of subjects out of 15 picking one plum over metal nut.

3.7. Experiment 7: 3 − 1 food versus 2 − 1 non-food, double subtraction and object identity

The experiments presented thus far show that rhesus monkeys can calculate the appropriate outcome of subtraction events when the numbers are small, and can even do so when the kinds or properties of the objects differ. Experiment 7 attempts to take this claim further by increasing the number of objects (Fig. 7A). After we placed the platforms on the ground, with three plums on one side and one plum and one metal nut on the other, we then placed the occluders in front of each stage. Next, we removed one plum from the side with three initial plums, and the metal nut from the other side. This set of subtraction events resulted in two plums on one side (i.e. $3 - 1 = 2$) and one plum on the other (i.e. [1 plum + 1 nut] − 1 nut = 1 plum).

Results show (Fig. 7B) that 13 out of 15 subjects (sign test: $P < 0.008$) selected the platform with two plums over the platform with one plum. This shows that

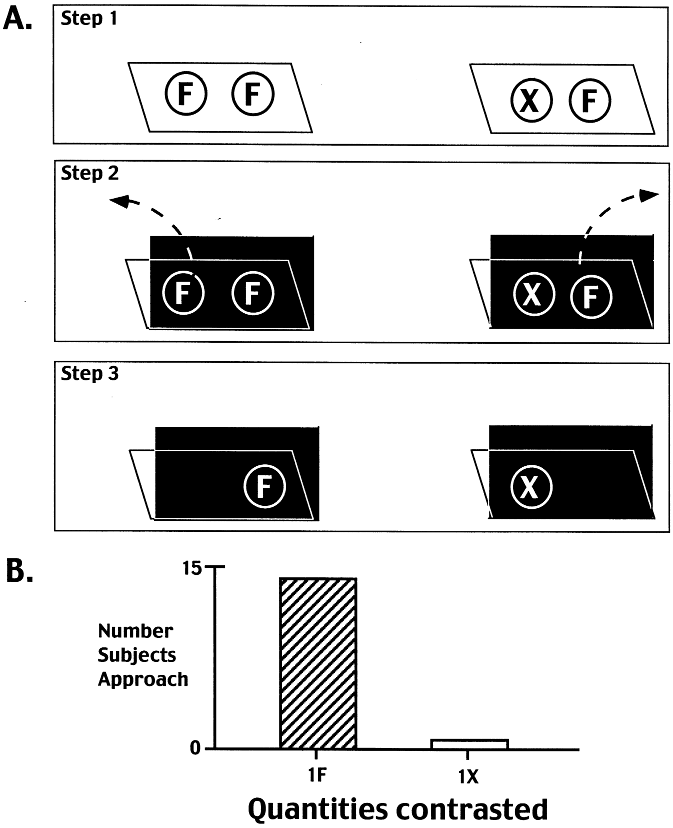

Fig. 6. (A) Procedure for presenting rhesus monkeys with a 2 − 1 food item versus 2 − 1 food item operation; here, one side starts with two plums and the other starts with a plum and a metal nut. (B) Results showing the number of subjects out of 15 picking one plum over one metal nut.

rhesus monkeys attend to the kinds or properties of objects prior to and following occlusion, and use such information to determine which platform has more food, even when the starting numbers are as high as three. These results provide additional support for the claim that rhesus monkeys are not avoiding the side associated with a food subtraction.

3.8. Experiment 8: 3 − 1 food versus 2 − 1 food, double subtraction and object identity

Experiment 7 shows that rhesus monkeys attend to the properties or kinds of objects during subtraction events. They might have solved this problem, however, by ignoring the non-food item. To test this possibility, we ran a subtle variant of Experiment 7, involving food subtraction from both platforms. Specifically (Fig. 8A), after we placed the platforms on the ground, we placed three plums on one side and two plums on the other. We then lowered the occluders, and reached behind

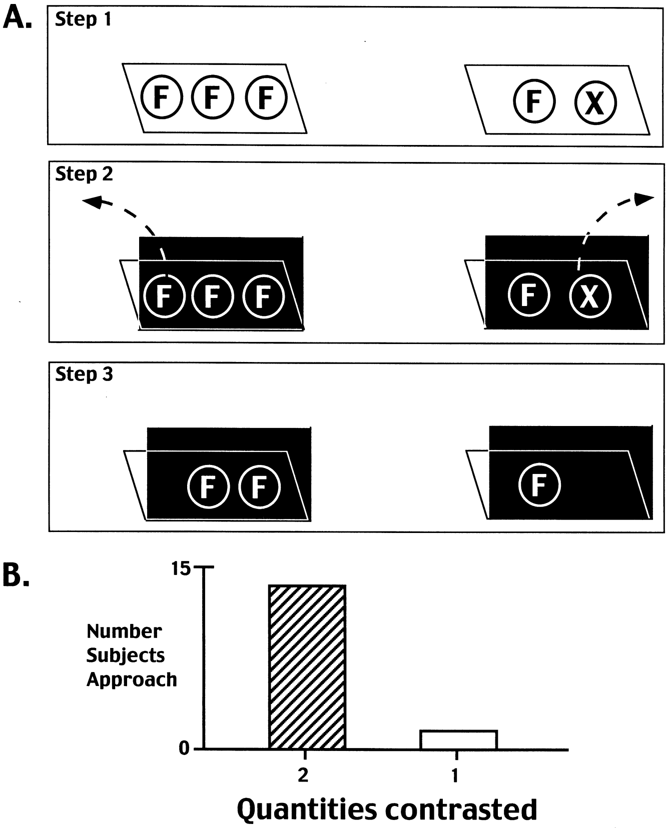

Fig. 7. (A) Procedure for presenting rhesus monkeys with a 3 − 1 food item versus 2 − 1 non-food item operation. (B) Results showing the number of subjects out of 15 picking two plums over one plum.

each side, in turn, and removed a plum. This set-up provided subjects with a choice between two plums (i.e. $3 - 1 = 2$) versus one plum (i.e. $2 - 1 = 1$).

Results show (Fig. 8B) that 13 out of 15 subjects (sign test: $P < 0.008$) selected the platform with two plums over the platform with one plum. Thus, when rhesus monkeys compute a subtraction event, they can do so successfully even when the starting quantities are three versus two, and when one piece of food is removed from both sides.

3.9. Experiment 9: 2 − 1 versus 1 + 1, subtraction and addition without changing the total number of initial objects

The experiments presented thus far show that rhesus monkeys compute subtraction events, attending to the properties or kinds of objects initially presented and subsequently subtracted, when those numbers fall within the range of three or less; at present we do not know whether this represents the limits of their capacity to

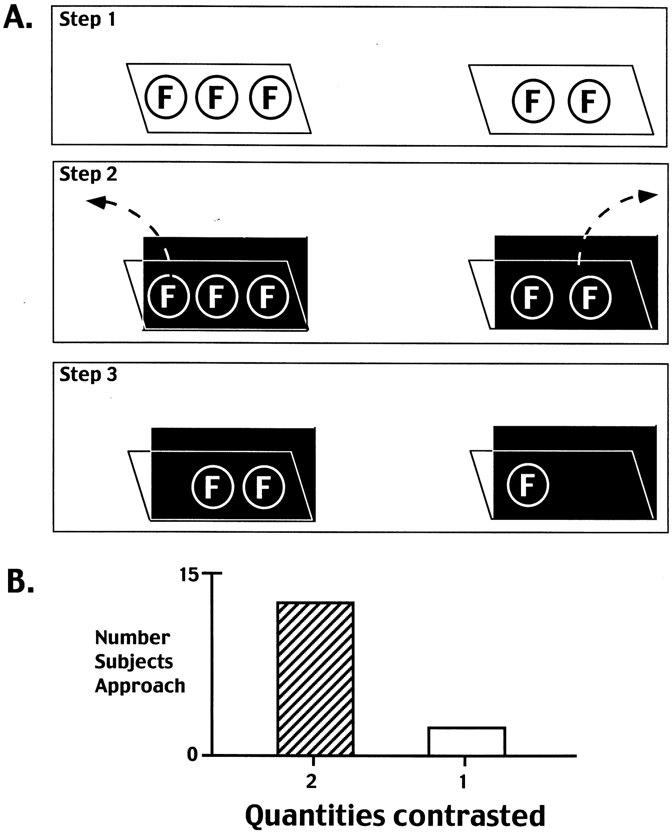

Fig. 8. (A) Procedure for presenting rhesus monkeys with a 3 − 1 food item versus 2 − 1 food item operation. (B) Results showing the number of subjects out of 15 picking two plums over one plum.

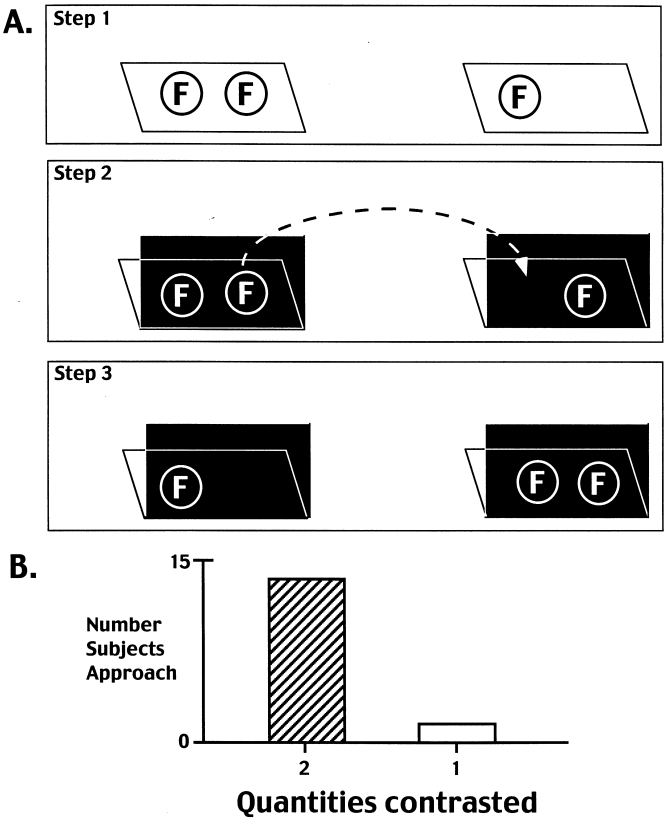

Fig. 9. (A) Procedure for presenting rhesus monkeys with a 2 − 1 versus 1 + 1 operation. (B) Results showing the number of subjects out of 15 picking two plums over one plum.

compute subtraction events (see Section 4). Rather than increase the numbers of objects that can be operated upon, the following experiments explore other properties of the subtraction operation. In Experiment 9, we ask whether rhesus monkeys can track the transfer of an object from one side to the other, creating a subtraction on one side, and an addition on the other. Thus, we placed two platforms on the ground, with two plums on one side and one plum on the other (Fig. 9A). Next, we lowered the occluders, and transferred one plum from the side with two plums to the side with one plum. Thus, we carried out a subtraction event on the side with two plums (i.e. $2 - 1 = 1$) and an addition event on the side with one plum (i.e. $1 + 1 = 2$). In so doing, we preserved the initial number of objects occluded to two versus one, but caused the larger quantity to switch from one side to the other. To solve this problem, and chose the larger quantity, rhesus monkeys must update the number of objects concealed behind both occluders, computing both a subtraction and an addition operation.

Results show (Fig. 9B) that 13 out of 15 subjects (sign test: $P < 0.008$) selected the platform with two plums over the platform with one plum. This shows that rhesus monkeys can update information held in memory by first computing a subtraction operation followed by an addition operation, and then use the output of this computation to determine which platform holds more food.

3.10. Experiment 10: 3 − 1 versus 1 + 1, subtraction and addition leading to equality

In all of the experiments discussed thus far, subjects were presented with a choice between two food quantities, where one quantity always exceeded the other. In Experiment 10 we ask whether rhesus monkeys can compute a subtraction operation followed by an addition operation – as in Experiment 9 – but recognize equality, the fact that some arithmetical operations lead to no net difference. Thus, we placed two platforms on the ground with three plums on one side and one plum on the other (Fig. 10A). Next, we lowered the occluders, reached in and removed one plum from the side with three plums, and transferred it to the side with one plum. Thus, we carried out a subtraction operation on the side with three plums (i.e. $3 - 1 = 2$) and an addition operation on the side with one plum (i.e. $1 + 1 = 2$). In so doing, we created an equality of two plums behind each occluder. In this situation, therefore, we predicted no bias with respect to the occluder approached by the rhesus monkeys.

Results show (Fig. 10B) that eight subjects selected the platform with two plums on the left side and seven selected the two plums on the right side (sign test: $P > 0.05$). This shows that rhesus monkeys can update information held in memory by computing both a subtraction and an addition operation, and use the output of this computation to determine that each platform holds the same number of plums.

3.11. Experiment 11: 0 + 1 versus 1 − 1, subtraction and addition, and the representation of 'zero'

As discussed in Section 1, Wynn and Chiang (1998) have argued that human infants can not represent zero, a finding that they claim is consistent with the accumulator model of Meck and Church (1983). Specifically, Wynn and Chiang claim that the accumulator can only be engaged with a positive integer value (i.e. something to be counted), and thus, zero is not a countable entity. Their evidence comes from a preferential looking time study. In one condition, infants watched as an experimenter occluded two objects (each behind a screen) and then removed one object from one screen. In the expected outcome ($2 - 1 = 1$), the infant saw one object, whereas she saw the same two objects in the unexpected ($2 - 1 = 2$) or 'magical appearance' outcome. In the second condition, infants watched as an experimenter first occluded one object behind a screen and then pushed a second object behind a second screen. In the expected outcome ($1 + 1 = 2$), the infant saw two objects, whereas she saw one object in the unexpected ($1 + 1 = 1$) or 'magical disappearance' condition. Whereas infants looked longer at the magical disappearance than at the other expected conditions, they failed to look longer at the other violation, the magical appearance; Wynn and Chiang obtained the same pattern of results with a $0 + 1 = 1$ versus $1 - 1 = 1$ contrast.

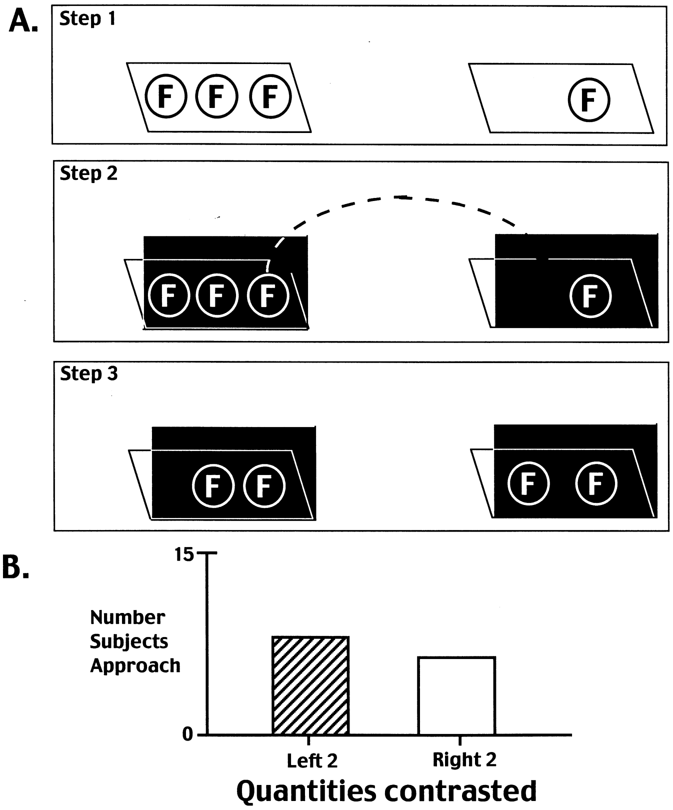

Fig. 10. (A) Procedure for presenting rhesus monkeys with a 3 − 1 versus 1 + 1 operation, yielding equality. (B) Results showing the number of subjects out of 15 picking the two plums on the left over the two plums on the right.

A number of the experiments we have discussed thus far could be taken as evidence that rhesus monkeys can represent zero.[1] For example, in Experiment 1, subjects were given a choice between an occluded plum that was left untouched and an occluded plum that was removed (i.e. $1 - 1 = 0$). Rhesus monkeys consistently approached the platform with one plum over the platform with no plums. Similarly, in Experiment 4, subjects were shown two plums on one side and one plum on the other, and then, following occlusion, observed one plum being removed from each side. Thus, subjects were given a choice between one occluded plum and no plums,

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[1] For both this work and the studies reported by Wynn and Chiang (1998), it is probably more appropriate to use the concept of 'absence' given that an understanding of zero presumably mandates a much richer understanding of number than infants or untrained rhesus monkeys have. For consistency with Wynn and Chiang, however, we will refer to the notion of zero, but acknowledge that it is unlikely to be analogous to our concept of zero.

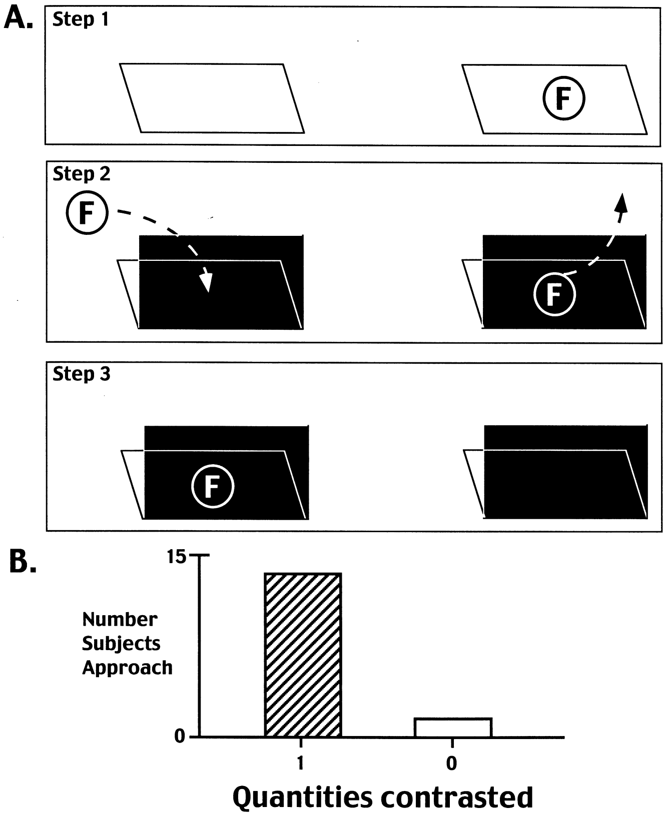

Fig. 11. (A) Procedure for presenting rhesus monkeys with a 0 + 1 versus 1 − 1 operation. (B) Results showing the number of subjects out of 15 picking one plum over no plum.

and consistently selected the platform with one plum. Finally, Experiment 6 shows that rhesus monkeys preferentially select one plum over no plums, even when the platform with no plums holds a non-food object. These data suggest that rhesus monkeys can represent zero, or minimally, the absence of a meaningful, countable object. To push this issue further, we designed Experiment 11. Thus, rhesus monkeys watched as we placed two platforms on the ground, with one plum on one platform, and nothing on the other (Fig. 11A). We then occluded both platforms, added one plum to the side with no objects, and removed the plum from the side with a starting plum; we counterbalanced for the order in which each operation was conducted. Thus, subjects witnessed a $0 + 1 = 1$ addition operation on one platform and a $1 - 1 = 0$ subtraction operation on the other platform; this design is modeled after the second experiment of Wynn and Chiang (1998).

Results show (Fig. 11B) that 13 out of 15 subjects (sign test: $P < 0.008$) selected the platform with one plum over the platform with no plums. This shows that rhesus monkeys can update information held in memory by computing both an addition and a subtraction operation, and use the output of this computation to determine which platform holds a plum and which one does not. These results suggest, together with the data obtained in Experiments 1, 4 and 6, that rhesus monkeys can represent zero, or perhaps more accurately, the absence of a meaningful object. If the failure to represent zero is taken as evidence that is consistent with the accumulator model of number representation, then these data suggest that a different mechanism must underlie the rhesus monkeys' success with small numbers; the object file model is one such mechanism. Alternatively, perhaps the accumulator can represent zero, in which case, our results are consistent with this model and the infant data are in conflict. We return to these issues in Section 4.

4. General discussion

The central aim of these experiments was to determine whether rhesus monkeys can spontaneously compute subtraction operations with small numbers. In contrast to our earlier work with rhesus monkeys (Hauser & Carey, 1998; Hauser et al., 2000; Hauser et al., 1996), where we were able to document the upper limit of spontaneous number discrimination following addition operations, the present studies provide a more in-depth analysis of subtraction. Specifically, studies of addition show that rhesus monkeys spontaneously discriminate between outcomes of four versus three pieces of apple, even when the number of actions (or an approximation of equal time) and the volume of food contrasted have been controlled. The upper limit of four is consistent with the set size signature of the object file model (Carey & Spelke, in press; Hauser et al., 2000) especially since rhesus monkeys failed on conditions involving larger numbers (five versus four) and comparable ratios (e.g. four versus eight), computations that should, in theory, be possible for organisms operating on the basis of mental magnitudes with scalar variability. Based on the present experiments, we cannot yet say whether rhesus monkeys are subject to the same limits for subtraction operations as they are for addition. What we can say, however, is that the capacity of rhesus monkeys to calculate the outcome of subtraction operations is remarkably precise for small numbers (i.e. three or less). While computing subtraction operations, rhesus monkeys identify the properties or kinds of objects initially presented and subsequently removed, keep track, in memory, of the actions performed with objects out of view, and use such information to determine which occluder conceals more food. Furthermore, rhesus monkeys can apparently use their capacity to spontaneously compute the outcome of a subtraction event to represent the absence of a relevant object as well as equality, carrying out a subtraction operation followed by an addition operation.

The studies presented here do not allow us to assess whether rhesus monkeys compute the outcome of subtraction events on the basis of analog magnitude or object file representations. The primary reason for this is that, in contrast to our work on addition, we have yet to determine whether the pattern of successes and failures for subtraction is consistent with the set size signature of the object file system for small numbers. That is, all of our tests involve quantities less than four, and the object file mechanism is claimed to be dedicated to small number quantification. Future experiments involving subtraction will explore numbers greater than four. If subjects fail at larger numbers, especially when the ratios are consistent with Weber fractions (e.g. success at three versus two with failure at six versus four), then our results will provide further evidence for an object file mechanism for quantifying over small numbers.

Although these experiments are insufficient with respect to distinguishing between analog magnitude and object file representations, they do present some challenges for thinking about the nature of spontaneous number representation in rhesus monkeys, and perhaps other animals (humans included) as well. Here, we briefly discuss two such challenges. First, consider the claim by Wynn and Chiang (1998) about the accumulator model and the representation of zero. If infants' failure to detect a magical appearance is considered to be consistent with the accumulator model and analog magnitude representations, and if the accumulator mechanism is considered to be the primary mechanism for non-linguistic representations of number (Dehaene, 1997; Gallistel & Gelman, 2000; Wynn, 1998), then rhesus monkeys must be using a different system. Specifically, our results suggest that rhesus monkeys can represent zero. There are two possible interpretations of these results. On the one hand, some might argue that the accumulator can represent zero. Given that the original Meck and Church (1983) model allows for an empty accumulator state (i.e. no activation), it is not inconceivable that rhesus monkeys use one accumulator to represent one or more plums, and one to represent no plums. Moreover, given the fact that the accumulator can be reset, one could well imagine that following a subtraction of $1 - 1$, that the accumulator resets to a zero state, waiting for the next impulse of activation. At present, we do not believe that the accumulator model is sufficiently well articulated to assess this claim, or the proposal by Wynn and Chiang (1998) that the accumulator can not represent zero. On the other hand, if one rejects the idea of an empty accumulator, then it is necessary to invoke a different mechanism to account for the rhesus monkeys' successes. One possibility is the object file model, which certainly allows for an empty file, or for a file with an object in place to be removed leaving an empty file; with an empty file stored in memory, a magical appearance certainly would be surprising. At present, current theoretical specifications of the accumulator and object file models are insufficiently precise to allow us to distinguish between these alternatives.

Second, we consider our results to provide some evidence against current versions of the object file model of number representation that take, as input, featureless objects (Scholl, in press; Scholl & Leslie, 1999; Simon, 1997; Uller et al., 1999). Specifically, because rhesus monkeys compute, with precision, the outcome of subtraction events involving different kinds of objects, they apparently keep in mind at least some set of features necessary to track occluded objects. Thus, when opening up an object file, rhesus monkeys appear to store information about the object's identity, and this includes a suite of properties that enable either re-identification or retrieval following occlusion. Alternatively, the object file mechanism might only open up files for relevant items such as food. In this case, however, there would have to be some mechanism for distinguishing relevant from irrelevant objects, and gating the relevant ones into working memory. A possible mechanism for this kind of operation has been proposed by Cowan (2001) who invokes short-term working memory to account for the limit of four during object or event tracking. An appealing aspect of Cowan's account is that short-term working memory can take as input information from multiple modalities, and thus provides a basis for the abstract nature of numerical representations; in contrast, the classic object file model is restricted to visual objects. On either count, object features are crucial to the operation of the mechanism. In addition, because our task involves operations at two distinct locations, with the overall number of objects well exceeding four, it is necessary to make a further emendation to these candidate mechanisms. Specifically, if both the object file and short-term working memory models can only operate over numbers between approximately one through four, then our results clearly exceed this range (e.g. three in one box and four in the other). Consequently, it is necessary to invoke at least two separate computational filing or storage systems, each limited to the range of one to four objects, and allowing for independent operations within each system.

Future work must establish whether the limit on spontaneous computations of addition operations is similar to or different from the limits on subtraction operations. By increasing the number of objects, and the difference between the magnitudes, we will be in a better position to evaluate whether the spontaneous representation of number in rhesus monkeys operates over mental magnitudes with scalar variability or on the basis of object files, or a combination of both. At present, results from the current experiments show that rhesus monkeys can calculate, with precision, the outcome of subtraction on small numbers of objects.

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