

Representing Space and Objects in Monkeys and Apes

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Primate foraging can be construed as a set of interconnected problems that include finding food, selecting efficient travel routes, anticipating the positions of moving prey, and manipulating, and occasionally, extracting food items using tools. The evidence reviewed in this paper strongly suggests that both monkeys and apes use three types of representation (i.e., static, dynamic, and relational) to solve various problems. Static representations involve recalling certain features of the environment, dynamic representations involve imagining changes in the trajectories of moving objects, and relational representations involve encoding the properties of objects in relation to other objects. Contrary to previous claims, no clear differences were found between the representational skills of monkeys and apes. Current evidence also suggests that primates may be better at representing general compared to specific problem features. Finally, we have characterized the domains of space and objects as complementary and indicated future lines of research in these domains.

I. INTRODUCTION

Feeding is one of the most time consuming and challenging activities for primates. In order to feed effectively, primates face many challenges associated with finding and processing food. They have to deal with patterns of food distribution in time and space, the accessibility of food items, and the plants' natural defenses against predators. On some occasions, responding to the demands of each of these activities simply entails recalling information that primates have acquired in the past, for instance, where certain food sources are located, or what sort of manipulations are needed to extract the food. On other occasions, however, primates may have to be able to respond appropriately to novel situations by producing novel solutions. For instance, when a route that has been used in the past is currently blocked, individuals may have to use alternative routes, or alternative means to reaching their objective.

The complexity and variety of these problems suggests that primates must possess some cognitive flexibility which enables them to recall, predict, plan, or even understand

the elements that constitute their foraging problems. At the core of this cognitive flexibility is the question of whether primates use representation to solve problems. Some authors have argued that apes, but not monkeys, are capable of representation as evidenced by their ability to solve invisible displacements, organize food processing routines in a hierarchical fashion, understand tool relations and anticipate the best travel routes (Natale, Antinucci, Spinozzi, & Potì, 1986; Byrne, 1994; Visalberghi, 1993; Povinelli & Cant, 1995). On the other hand, other authors are reluctant to accept a clear-cut dichotomous distinction between representational apes on the one hand, and nonrepresentational monkeys on the other (Anderson, 1996; Tomasello & Call, 1997; Vauclair, 1990a). These authors argue that representational skills can be found in both monkeys and apes in various domains. This controversy is partly a consequence of presenting the issue of representation in such a dichotomous fashion, that is, some primates have it (i.e., apes) whereas others do not have it (i.e., monkeys). One major problem of this dichotomous view in comparative cognition is that it presents a misleadingly simple picture of representation, when in reality, representation is a very broad topic that spans across many cognitive abilities. Therefore, focusing on a broader range of abilities is probably more fruitful than just selecting particular domains to resolve the issue of representation in nonhuman primates (and other animals). For purposes of clarity of exposition three types of representation in nonhuman primates will be considered in this paper: static, dynamic, and relational representations.

First, static representations simply have to do with recalling certain features of the environment, for instance, what type of food is under a bowl or where to find a certain object. Second, dynamic representations involve imagining changes in the behavior of objects, for instance, what path a moving target will follow or how an object will look after a spatial transformation (i.e., mental rotation). Finally, relational representations encode the properties of objects in relation to other objects, for instance, by asking what properties an object must have in order to constitute an effective tool to solve a particular problem, or what modifications are necessary to transform an unsuitable tool into a suitable one. Note that in this case, the suitability of a tool is always measured in relation to the demands of the problem.

The aim of this article is to evaluate the evidence of representation in nonhuman primates, and in particular, the putative difference between the representational skills of monkeys and apes. The first part of this article will be devoted to reviewing the evidence available in support of each of the three types of representation previously outlined in the contexts of locating and processing food. In the second part of this article, this evidence will be used to compare the representational skills of monkeys and apes. Furthermore, the differences in representational ability across tasks and the relationship between representing space and objects will be discussed.

II. STATIC REPRESENTATION

Static representations have to do with encoding the various attributes associated with objects. Two of the most basic attributes associated with objects are their location in space

and their physical appearance. Recalling these representations enables individuals to know about important features of the environment, for instance, what type of food is under a bowl or where to find a certain tool. The first two sections provide information regarding the ability of primates to identify objects and recall the location of food. The last section describes how individuals organize spatial information into efficient travel and search patterns.

Identifying Objects

Many primates are capable of recalling a variety of object features. Studies on discrimination learning have shown that numerous species can use various object attributes such as shape, color, size, or weight to obtain food rewards (see Meador, Rumbaugh, Pate, & Bard, 1987; Fobes & King, 1982, for reviews). Discrimination learning involves recalling specific features of objects that are associated with positive consequences. For instance, subjects are presented with a sample object (e.g., triangle) and two alternatives (e.g., triangle and square), and rewarded for selecting the alternative that matches the sample object. Although in these studies the association between object features and their positive consequences usually develops over dozens or even hundreds of trials and is usually restricted to those particular features, other studies have shown very rapid acquisition of these features and extrapolation to novel stimuli. These studies are reviewed in turn.

Numerous primates are capable of very fast object discrimination in the context of learning set formation (Harlow, 1949). This is accomplished by presenting several hundreds of object discrimination problems in succession. Typically, each of these problems involves presenting a pair of novel objects (one designated as positive and one as negative) in six successive trials. Subjects are rewarded for selecting the positive stimulus in each of six trials. After extensive experience with these problems subjects are capable of associating a novel object with the reward after a single exposure. Moreover, some studies based on reversal learning have shown that primates can generate rules of learning, even when novel stimuli are used (Rumbaugh & Pate, 1984). In these studies, associationistic learning based on learning specific stimulus features is directly pitted against mediational learning, which is based on acquiring more abstract rules such as "select the object that was previously incorrect." Rumbaugh and Pate (1984) argued that apes, unlike monkeys, were capable of mediational learning of this sort. However, some studies have also shown that macaques were capable of relational learning (Essock-Vitale, 1978). Moreover, recent studies using a computerized testing paradigm have shown that rhesus and capuchin monkeys also exhibit evidence of mediational learning (DeLillo & Visalberghi, 1994; Washburn & Rumbaugh, 1989).

A second issue that deserves attention in the context of encoding object features is whether individuals are also capable of organizing object features in more abstract ways such as concepts. Various studies have shown that squirrel monkeys, macaques, and capuchin monkeys are capable of selecting novel exemplars of a given category (Schrier, Angarella, & Povar, 1984; Irle & Markowitsch, 1987; D'Amato & Van Sant, 1988). For instance, Schrier et al. (1984) trained stump-tail macaques to respond to pictures of

humans, monkeys, and the letter A. Subjects learned to select these pictures after extensive training and correctly selected novel pictures of both humans, monkeys and letter A during transfer trials. In most of these studies, however, it is difficult to decide whether concept formation or stimulus generalization is responsible for the results.

One way to decide whether individuals operate at a conceptual level involves investigating the classification of novel exemplars based on functional rather than on purely perceptual features. Savage-Rumbaugh, Rumbaugh, Smith, and Lawson (1980) presented language-trained chimpanzees with two sets of objects corresponding to two categories: tools and food. Subjects were trained to sort exemplars of each in separate trays and were then presented with novel exemplars of each category. Subjects were capable of sorting these novel objects into the appropriate tray. Furthermore, subjects were presented with lexigrams (i.e., symbolic and arbitrary representations) of objects corresponding to each of the two categories. As they had done with the novel objects, chimpanzees sorted the lexigrams into the appropriate trays.

Finding Locations

Recalling food locations is one of the most basic cognitive abilities displayed by primates (and many other animals). Research in the wild has suggested that primates know quite a bit about where resources can be found (Boesch & Boesch, 1984; Kummer, 1982; Milton, 1980; Wheatley, 1980). For instance, Wheatley (1980) noted that longtail macaques visited 13 trees of the same species in succession to obtain a certain food item. This behavior suggests that longtail macaques (and other primates) are capable of recalling food locations scattered over large areas (i.e., locomotive space).

Several authors have tested the spatial ability of various primates under more controlled laboratory conditions (Coussi-Korbel, 1994; Cramer & Gallistel, 1997; Menzel, 1973; Vauclair, 1990b). For instance, Vauclair (1990b) investigated the spatial abilities of a group of Guinea baboons living in a large outdoor enclosure. During experimental trials, baboons observed the experimenter placing food under four stones of the 135 available in their enclosure. The baited stones varied from trial to trial and were scattered throughout the enclosure. After witnessing the baiting process from a distance ranging from 5 to 25 m, the baboons were released and allowed to find the pieces of food. In control trials the experimenter also hid four pieces of food but the baboons were prevented from observing the locations where the food was being deposited. Baboons recovered the food in 96% of the experimental trials compared to 69% of the control trials. In addition, the latency to recover the food in experimental trials was lower than in the control trials. These results suggest that baboons were capable of remembering the baited locations in their enclosure. Other studies have also produced positive results for chimpanzees, mangabeys, and vervet monkeys, although Cramer and Gallistel (1997) indicated that vervet monkeys visited fewer baited locations than chimpanzees. In a second experiment, Vauclair (1990b) showed that baboons not only can recall the location of hidden food but are also sensitive to food. Baboons observed the experimenter deposit under stones on each side of the enclosure either two or three pieces of food. Fifteen seconds after their release, subjects

were found to be preferentially foraging in the side of the enclosure with a larger food density.

Previous studies have shown that primates are capable of recovering food after they have seen the experimenter hide the food at a particular location. Another series of experiments has investigated the ability of various primates to return to locations where food was found (and depleted) in the past. Garber and Paciulli (1997) conducted a field experiment with capuchin monkeys in Costa Rica. These researchers built a number of platforms (feeding stations) within the monkeys' home range and observed the behavior of the capuchins after baiting the platforms. Some platforms contained bananas, some contained nonedible bananas (i.e., plastic bananas), and others were left empty. Capuchins quickly (after only 1 trial) learned to visit the platforms that contained food and ignored both the empty platforms and the ones that were baited with nonedible bananas. Similar experiments conducted in captivity have produced similar positive results. Capuchin monkeys, gorillas, common marmosets, yellow-nosed monkeys, and squirrel monkeys all tended to search for food in locations where they had found food in the past (De Lillo, Visalberghi & Aversano, 1997; MacDonald, 1994; MacDonald, Pang, & Gibeault, 1994; MacDonald & Wilkie, 1990; Roberts, Mitchell, & Phelps, 1993).

A number of studies in the laboratory have also investigated the ability of primates to recall the location of food in manipulative space (e.g., within the confines of the WGTA) as opposed to locomotive space. Numerous primates, including prosimians, squirrel monkeys, capuchins, macaques, orangutans, gorillas, and chimpanzees, are capable of recovering food items after the experimenter has placed them under a cover in full view of the subject (see Tomasello & Call, 1997 for a review). Spatial delayed tests have shown that these species are also capable of recovering hidden objects after increasing delays (Harlow, 1932; Harlow & Bromer, 1939; Harlow, Uehling, & Maslow, 1932). Harlow and colleagues found a decrement in retrieval accuracy with increasing delay periods. These and other studies (e.g., Fischer & Kitchener, 1965; Miles, 1957) have found some differences between species, with Old World monkeys (e.g., macaques) and apes outperforming prosimians (e.g., lemurs) and New World monkeys (e.g., marmosets).

Travel and Search Efficiency

Most studies on spatial memory of multiple food locations have also tested the ability to travel efficiently. Fieldworkers often report that several species of primates travel from certain locations to others in an efficient manner, that is, taking the shortest routes possible (Galdikas & Vasey, 1992; Garber, 1989; Mackinnon, 1974; Sigg, 1986). Menzel (1973) tested the ability of four young captive chimpanzees to use least distance strategies, that is traveling the least while obtaining the most food rewards in a large enclosure; he found that chimpanzees minimized the distance traveled. Similarly, Boesch and Boesch (1984) found that wild chimpanzees traveled efficiently when collecting stones needed to crack open nuts, that is, they selected stones that were closer to their current location. Recently, a number of researchers have described the use of least-distance strategies in vervet monkeys, common marmosets, and yellow-nosed monkeys (Cramer & Gallistel, 1997;

MacDonald et al., 1994; MacDonald & Wilkie, 1990). In contrast, MacDonald (1994) has shown that gorillas failed to use efficient travel routes. However, this author argued that a possible explanation for this result was that in this study the food containers were arranged in a way that may have encouraged simple sequential travel.

A related skill to travel efficiency (in which animals have to cover certain distances) is search efficiency when the food sources are relatively clumped. MacDonald and colleagues found that common marmosets, yellow-nosed monkeys, squirrel monkeys, and gorillas searched for food in an efficient and exhaustive manner in these situations (MacDonald et al., 1994; MacDonald & Wilkie, 1990; MacDonald, 1994; Roberts et al., 1993). Roberts et al. (1993) found that one of their two squirrel monkeys used a systematic search strategy consisting of starting his search at the bottom of a tree, climbing it, and collecting the raisins available in each hole. After reaching the top of a tree, the subject jumped onto the next tree and repeated the same operation. Using this strategy allowed the subject to avoid depleted holes and may suggest that squirrel monkeys (and other primates) are capable of organizing their searches by keeping a mental record of the visited (and depleted) locations.

However, Roberts et al. (1993) pointed out that subjects may have simply used external cues such as the position (open) of the hole lids to select what trees to visit next. De Lillo et al. (1997) used precisely this argument to question the conclusions of MacDonald and colleagues regarding the mechanism responsible for efficient searches. Both gorillas and yellow-nosed monkeys modified the position or orientation of the containers after obtaining the food, and consequently, visual cues rather than a mental record of the containers visited may be responsible for the efficient searches observed. De Lillo et al. (1997) administered a search task to four capuchins in which the container's appearance remained unchanged after subjects had depleted its contents. The authors arranged nine containers into two different configurations and baited them in the subject's absence. In the uniform configuration the containers were arranged in a 3×3 matrix whereas in the clustered configuration the containers were grouped in three groups of three forming a triangle. In both the uniform and clustered configurations, nine searches, corresponding to the number of containers available, was the optimal number of searches needed to deplete all containers. Results revealed that the capuchins' search efficiency depended on the type of container configuration. In the uniform configuration capuchins needed approximately 16 attempts (of the 9 searches needed) to deplete all containers, that is, roughly twice the number that would be needed if an efficient search was carried out. In contrast, capuchins only needed an average of approximately 12 searches in the clustered configuration to obtain all the rewards. Moreover, capuchins became more efficient over trials (decreasing their searches from approximately 13 to 10) in the clustered configuration but not in the uniform configuration. In view of these results, it is conceivable that the squirrel monkeys tested by Roberts et al. (1993) viewed their artificial trees as equivalent to clusters, which may explain the good searching efficiency of those monkeys.

In sum, this set of studies demonstrates that various primates are capable of using static representations to recall object features, spatial locations, and to organize their travel efficiently. In some of these studies, this involved recalling multiple food locations after

various delay periods and encoding object features at different levels of abstraction. Finally, some primates may also be capable of organizing efficient searches under some circumstances.

III. DYNAMIC REPRESENTATION

Dynamic representations involve mental transformations of static representations of the kind explored in the previous section. These transformations may take place both in the realm of space and objects and are aimed at inferring or predicting the spatial and/or feature changes of objects before those transformations actually take place. In some cases these transformations involve extrapolating or inferring novel food locations. In other cases, transformations involve tracking object movements and predicting the future positions of targets. Finally, some of these transformations consist of inferring the appearance of objects after spatial rotations have taken place. In the next three sections each of these topics will be reviewed in turn.

Inferring Novel Food Locations

A series of recent experiments by Menzel (1996a,b) has provided some evidence that some primates are capable of inferring the possible locations where food can be found based on various strategies. One of these strategies consists of using the presence of landmarks (e.g., tree logs) that have been associated with food in the past to infer the presence of food in novel locations which are also associated with those specific landmarks. Menzel (1996a) baited some locations adjacent to certain landmarks (e.g., poles) with visible food, and also hid food in similar locations (e.g., other poles) throughout the enclosure. He observed whether long-tailed macaques, upon finding the visible food next to a certain landmark, would search preferentially in locations containing similar landmarks. Menzel (1996a) found that macaques did forage preferentially in those areas associated with those landmarks even after a single exposure. That is, after they found the visible food next to a pole, they searched for food next to other poles in the enclosure. Menzel (1996a) extended those findings further and observed that individuals not only quickly associated certain landmarks with food, but were also sensitive to the quality of the food that could be found in each location. He baited certain structures with low preference foods (e.g., carrot) and other structures with high preference foods (e.g., banana) and observed which structures the monkeys visited. Macaques tended to visit the locations associated with high-preference foods compared to low-preference foods.

Menzel (1996b) also demonstrated another form of food location inference in longtail macaques. He placed food on the ground, forming a straight line but with only some of the reward being visible. The idea was to see if subjects would extrapolate the location of hidden food based on the location of visible foods, in other words, whether macaques would project an imaginary straight line to find hidden foods. Results indicated that monkeys were able to use extrapolation to find the hidden food although their proficiency at this task clearly increased over trials. Hemmi and Menzel (1995) replicated these results

while adding a control. After subjects had experienced finding visible food laid out on a linear trajectory, Menzel introduced two hidden rewards. One of the rewards was a continuation of the linear trajectory whereas the other reward was hidden at the same distance from the visible reward and the hidden reward but at a 60° angle from the linear trajectory. Macaques retrieved significantly more rewards located in the linear trajectory than those located at a 60° angle.

Tracking Objects in Invisible Displacements

Several studies have also investigated the ability of primates to retrieve objects after the objects have undergone visible and invisible displacements. In visible displacements (Stage 5 object permanence, Piaget, 1954), subjects find an object first under cover A, and then on a subsequent trial watches the experimenter move it from under cover A to under cover B. Numerous species of primates including squirrel monkeys, capuchins, macaques, gorillas, and chimpanzees are capable of solving visible displacements (thus avoiding the A-not-B error); that is, they correctly search under cover B even though the object was initially placed under cover A (see Tomasello & Call, 1997 for a review).

Tracking the visible displacements of objects, however, does not require any inferential ability, only remembering where the reward was last seen. In contrast, invisible displacements require some inference of the location of an object by reconstructing its previous path after it moves to different locations. In this task the experimenter places a piece of food under a small container which is displaced invisibly under several other containers with the food left under one of them. To solve this problem effectively, subjects have to search under all and only those boxes where the food might have been deposited given the trajectory of the box that initially contained the food. For instance, the food cannot be located under a box that was not touched by the experimenter. Piaget (1954) argued that solving this task required a mental representation of the trajectory of the food. Numerous authors have claimed the mastery of invisible displacements in a number of primate species including squirrel monkeys, capuchin monkeys, rhesus macaques, stump-tail macaques, chimpanzees, and gorillas (see Tomasello & Call, 1997 for a review). However, Natale et al. (1986) have criticized these studies because no controls were used to ensure that subjects were not finding the hidden food on the basis of simple, practical search strategies. For example, a subject may employ a simple strategy to search under the last of the containers under which the small container passed or under all of the containers available on each trial.

Natale et al. (1986) tested the ability of a Japanese macaque and a gorilla infant to track invisible displacements that included appropriate control tests. In the initial test, subjects were presented with two large boxes and one small one (see Figure 1a). The experimenter placed a food item inside the small box and moved it under one of the large boxes. After the small box emerged from the large box, it was placed beside it. In some trials the food was left in the large box and in other trials it remained in the small box. Natale et al. (1986) reasoned that if subjects understood invisible displacements, they should avoid searching for the food in the large box that had not been visited by the experimenter. Their results

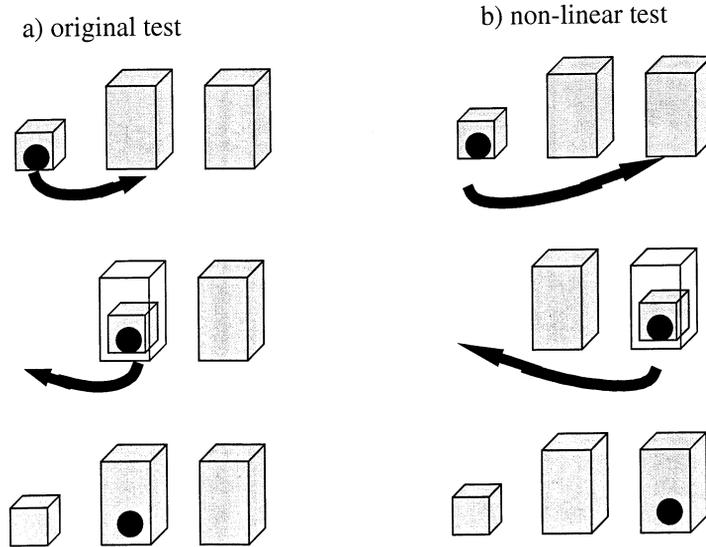


Figure 1. Diagram of two of the tests used by Natale et al. (1986) to test invisible displacements in a macaque and a gorilla infant.

seemed to support the idea that the macaque and gorilla were capable of reconstructing invisible displacements since both subjects responded correctly in the majority of trials by either searching under the small box or the visited large box.

Then, Natale et al. (1986) conducted two control tests to rule out nonrepresentational search strategies. In the false trials test, the authors investigated whether subjects had developed the simple strategy of choosing the box touched by the experimenter regardless of whether the large box was visited by the small box. The experimenter placed food under the small box, as before, but then the small box did not pass under any of the large boxes, and consequently, the food always remained in the small box. The experimenter, however, lifted one of the large boxes as before without passing the small box under it. Results revealed that on half of these false trials the macaque searched under the large box that the experimenter lifted whereas the gorilla never did. The nonlinear trials control test was aimed at investigating whether subjects were capable of following a novel type of invisible displacement which consisted of leaving the small box next to the nonvisited large box (see Figure 1b). Note that in previous trials, the small box had always been left next to the visited large box. This procedural modification forced subjects to skip the middle box in their search. In nonlinear trials, the macaque searched under the incorrect middle box on 70% of the trials whereas the gorilla made the same mistake in only 38% of the trials. The investigators concluded that this gorilla employed a representational search strategy consisting of mentally imagining the object as it passed from location to location whereas the macaque relied upon simpler practical (nonrepresentational) search strategies.

Various studies since then have confirmed the difficulty of invisible displacements in longtail macaques (Natale & Antinucci, 1989; Schino, Spinozzi, & Berlinguer, 1990),

rhesus macaques (De Blois & Novak, 1994), and capuchin monkeys (Dumas & Brunet, 1994; Natale & Antinucci, 1989; Schino et al., 1990). However, Schino et al. (1990) found one capuchin monkey that succeeded both on 1) false trials (he did not search under the large box that was manipulated but was not visited by the small box), and 2) nonlinear trials (his performance was above chance and was comparable to that of the gorilla tested by Natale et al. (1986). Schino et al. (1990) concluded that that this capuchin monkey was representing the invisible displacements of objects. Recently, De Blois, Novak, and Bond (1998) found that orangutans but not squirrel monkeys were capable of solving invisible displacements, although they failed the invisible displacements that involved nonlinear trials.

Target Prediction

A related skill to tracking invisible displacements is predicting the future positions of moving targets. Knowing where a target is headed may be a useful skill in intercepting prey or competitors who hold valuable resources. Using a computerized testing system, Washburn and colleagues have investigated whether rhesus monkeys are able to predict the future locations of moving targets. Washburn (1992) administered two related problems to two rhesus monkeys. In the LASER problem, subjects had to shoot from a stationary location on the bottom of the screen to a target that moved across the screen. Subjects could direct their shots at the target by adjusting the shooting angle which was controlled by the position of a joystick. Washburn (1992) noted that subjects were more successful (and faster) at hitting the target when it moved in a predictable manner as opposed to an unpredictable one, suggesting that subjects were capable of predicting the future locations of the target in the predictable condition. This finding is reinforced by another feature of this task. Subjects were allowed to abort shots during the game. Aborting shots was a good strategy if shots were going to miss the target because then new shots could be taken. However, shots that will hit the target should not be aborted. Macaques aborted 88% (compared to 91% in adult humans) of the shots that would have missed the target. Considering as correct responses both aborting bad shots and not aborting good shots, rhesus monkeys were correct in 65% of the trials. Recently, Filion, Washburn, and Gullledge (1996) have found that rhesus monkeys are capable of shooting moving targets even when they pass behind an occluder that is superimposed to the screen, therefore predicting the likely locations where the target might be. Again, monkeys' accuracy is comparable to that of human adults and reinforces further the notion that they can predict and anticipate the future locations of a moving object even when they are not able to see it directly.

Washburn (1992) used a second task called CHASE to investigate a related skill. Subjects still had to track and chase a moving target, although in this case, subjects were supposed to chase and capture the target with the cursor rather than shoot at it. In order to do so appropriately, subjects not only had to chase the target, but also on many occasions they had to predict its location in order to ambush it since the target speed was equal or superior to the cursor. Washburn (1992) and Washburn and Rumbaugh (1992)

found that subjects again were more effective at intercepting targets when they followed predictable compared to unpredictable paths. Analyses of their responses indicated that in the predictable condition, subjects learned to anticipate the location of the target, whereas in the unpredictable condition, they merely chased after the target. Washburn and Rumbaugh (1992) reasoned that since rhesus monkeys learned to predict the movements of the target over thousands of trials, it was conceivable that they were responding to mere stimulus-response associations between cursor and target and not operating at a more general level of knowledge about the target's travel. In a final experiment, Washburn and Rumbaugh (1992) presented the target moving from the left to the right of the screen. Upon reaching the far right, the target reappeared on the left side. Their results indicated that upon learning one pattern of chasing from left to right, subjects moved in the opposite direction from the target to wait for it on the other side of the screen. But more importantly, when the target movement was changed from left-right to top-bottom, subjects showed no decrease in their performance indicating that they had learned a general rule. Human adults presented with the same task outperformed macaques but the authors argued that this represented a difference in degree not in kind. Filion et al. (1996) also used the CHASE task and found that two rhesus monkeys were capable of intercepting a moving target that disappeared behind a visual barrier and were able to accurately predict the point of exit of a target based on its angle of entry into the opaque region. In this task subjects moved the cursor around the opaque region (that the cursor itself could not enter) and positioned the cursor on the location where they expected the target to reappear. Taken together these studies suggest that monkeys knew where the target was going as well as where the target was, and that they knew this on the basis of more general knowledge about the target's "behavior" rather than mere stimulus response associations.

Mentally Rotating Objects

Menzel, Savage-Rumbaugh, and Lawson (1985) investigated the ability of two language-trained chimpanzees to use televised visual information of their own actions to guide their hands in touching hidden targets. Results showed that both chimpanzees were capable of reaching the targets with the help of the televised information. Moreover, chimpanzees quickly adapted and continued to use this televised information effectively when the image provided was inverted or reversed. This result indicated that chimpanzees were capable of coping with visual transformations to guide their reaching behavior.

Another paradigm that has more directly tested the ability to carry out representational transformations is mental rotation. Vauclair, Fagot, and Hopkins (1993) used a matching to sample paradigm to test the ability of six Guinea baboons to perceive mental transformations. The authors presented a sample and then were presented with two alternatives: a rotated sample (positive stimulus) and an inverted sample rotated the same amount as the positive stimulus (negative stimulus). The rotated sample orientation varied from 0° (no rotation) to 180°. Baboons were successful in selecting the rotated over the inverted sample. Moreover, the response latency to respond to the rotated objects increased linearly as a function of the rotational angle of the rotated object when the stimuli were presented to the right visual half-field of the baboons.

In sum, this set of studies shows that various primates are capable of using dynamic representations to infer the location of objects and to anticipate the movement of objects. Although only one capuchin monkey and one gorilla have responded in a way that is consistent with an ability to represent invisible displacements of objects, computer-based methodologies have suggested that rhesus macaques may be capable of representing invisible displacements of objects. Finally, baboons seem capable of mentally manipulating the orientation of objects in a mental rotation task.

IV. RELATIONAL REPRESENTATION

Relational representations involve encoding the properties of objects in relation to other objects, for instance, by asking what physical appearance an object must have to constitute an effective tool to solve a particular problem, or what modifications are necessary to transform an unsuitable tool into a suitable one. This relational representation is the kind of representation that may constitute the building blocks of cause-effect understanding. Relational representations are based on static and dynamic representations of the kind explored in previous sections. In some cases, relational representations involve relating two simple objects in a relatively simple fashion such as inserting a set of graded cups in the correct sequence of increasing size. In more cognitively demanding tasks, more complex objects relate to one or more objects in more complex ways. A prototypical case of complex relational problems is tool use. In the next two sections we explore the use of representational strategies and causal understanding in the context of simple and complex relational problems.

Simple Relational Problems: Object Manipulation

Several studies have shown that primates often engage in complex forms of object manipulation (see Tomasello & Call, 1997, for a review). These studies, however, mainly dealt with sensorimotor intelligence, as opposed to representational intelligence. One task that may permit the study of representational abilities in the context of object manipulation is the nesting cups task. Greenfield (1991) studied how children assembled cups of different sizes and distinguished various levels of complexity. The simplest level of complexity consisted of placing one or more cups inside a larger one in no particular order. More complex levels involved nesting cups in order of size. For instance, in a set of three size graded cups, this would entail inserting the smallest cup into the intermediate cup, and these two cups as a whole into the largest cup. Greenfield (1991) argued that this method was especially complex because it may require subjects to have a mental representation of the correct sequence of cups.

Westergaard and Suomi (1994) and Matsuzawa (1991) studied 10 capuchin monkeys and 9 chimpanzees (2 adults, 7 juveniles and infants), respectively, in the nesting cup test. Westergaard and Suomi (1994) used a 4-cup set and found that three of their capuchins used both the pot and subassembly methods. Unfortunately, no information was provided regarding how quickly they produced these combinations. Matsuzawa (1991) found that

all chimpanzees used the pot method with a 5-cup set, but only the two adult chimpanzees (who had also received language training) used the subassembly method. Both chimpanzees used the subassembly method relatively quickly, making very few errors in their assemblages which gives some credence to the idea that they were planning the sequences in advance.

In a more naturalistic setting, Byrne and Byrne (1993; see also Byrne, 1994) investigated both the actions used and the sequences of manipulation in the food processing of mountain gorillas. These authors observed that different plants required different manipulations depending on their natural defenses (e.g., thorns or spines). For instance, when eating nettles that are covered with spines, gorillas use both hands, each one performing different actions. Byrne and Byrne (1993) indicated that there was a hierarchical organization in the execution of these manipulations, leading these researchers to postulate that gorillas represented the different steps in the manipulation sequence and executed them as plans. One piece of information that is missing from this naturalistic study is the ontogeny of these manipulations, which could help us understand how the subroutines are established and integrated.

Complex Relational Problems: Tool Use

Primates use tools in a variety of ways and for a variety of purposes. Pulling within reach, extracting, reaching a certain height, knocking down, digging out, or cracking open, just to mention a few, are some of the uses that nonhuman primates make of tools (see Beck, 1980; Tomasello & Call, 1997, for reviews). In addition, monkeys and apes can use multiple tools in sequence to obtain a single goal, and in some cases each of these tools accomplishes different functions. Often tools are modified or even manufactured prior to their use, and there have been some studies in which apes have been trained to use tools to manufacture other tools. Based on this evidence, it is tempting to conclude that primates mentally represent the requirements of the task, plan their solutions beforehand, and have a sophisticated understanding of the causal relations between tool and goal. This assertion, however, needs to be backed up by carefully controlled experiments since successful performance is not always equivalent to understanding (e.g., Visalberghi & Trinca, 1989). We begin our analysis of what primates understand about tools with perhaps the simplest tool-using problem: the support problem.

Support Problem. In this problem a reward is placed on a cloth. The reward itself is outside of the subject's reach but one of the ends of the cloth is within reach. The solution to this problem consists of pulling in the cloth to bring the reward within reach. Piaget (1952) studied this problem in human infants and indicated that by 12 months of age children not only readily pull in the cloth but, more importantly, they withhold pulling when the reward is not in contact with the cloth. This indicates that children at this age understand that spatial contact is necessary for the tool to act on the reward.

Spinozzi and Potì (1989) tested several infant primates (1 Japanese macaque, 2 capuchin monkeys, 2 longtail macaques, and 1 gorilla) on this problem. In one condition

the reward was placed on the cloth whereas in another condition the reward was placed off the cloth to the side. All primates responded appropriately by pulling in the cloth when the reward was on the cloth, and withheld pulling when the reward was off the cloth. In a second experiment Spinozzi and Potì (1989) tested the generality of these findings by modifying the conditions of the off-cloth condition by placing the reward near the end of the cloth rather than to the side of it. The authors reasoned that if subjects had simply learned to respond appropriately to a specific configuration of the cloth and the reward rather than a more general relation between them, they would respond inappropriately to this novel configuration. Results confirmed their previous findings: all subjects pulled in the on-cloth condition but not in the off-cloth condition. Recently, Spinozzi and Potì (1993) administered the same support problem to two infant chimpanzees and only one of them succeeded. Redshaw (1978) reported that 4 infant gorillas passed the support problem but gave no details on the performance of the subjects.

Stick Problem. A more challenging task than the support problem consists of using a tool to bring in a reward that is not in direct contact with the tool. This situation entails putting the tool into contact with the reward and then sweeping the reward within reach. According to Natale (1989a), solving this task demonstrates an ability to understand complex causal relations such as that the stick must be of the appropriate size and material (e.g., long and rigid) and that only certain kinds of contact (e.g., with a certain force and directionality) would be successful.

Natale (1989a) presented 8 subjects from the same four species tested by Spinozzi and Potì (1989) with an out-of-reach reward and a stick, placed in different positions relative to the object in different experimental conditions. Three of the four capuchin monkeys and the gorilla were moderately successful in obtaining the reward in various tool-reward spatial arrangements. These results have been confirmed by other studies (see Beck, 1980; Tomasello & Call, 1997 for a review). Although none of the macaques tested by Natale (1989a) was able to obtain the reward with the stick, other studies have shown that macaques and other primates including baboons, orangutans and chimpanzees are capable of solving the stick problem (see Beck, 1980; Tomasello & Call, 1997 for a review).

Tube Problem. Although previous studies varied the experimental conditions such as the position of the reward, it is not clear that they represent novel situations. Moreover, it can be argued that these situations are not challenging enough to reveal mental manipulation of the elements of the problem to find appropriate solutions. In a series of studies, Visalberghi and colleagues have explored the ability of capuchin monkeys and apes (mostly chimpanzees) to adjust to novel tool use problems using their understanding of the causal relations between the elements of the task.

Visalberghi and Trinca (1989) presented four capuchin monkeys with a transparent tube with food visible inside (Figure 2). To acquire the food, subjects had to poke it out the opposite end with a stick. Three subjects were successful relatively quickly and the researchers presented each of them with three variations of the problem involving different types of tools that required different solutions. In the bundle task, subjects were

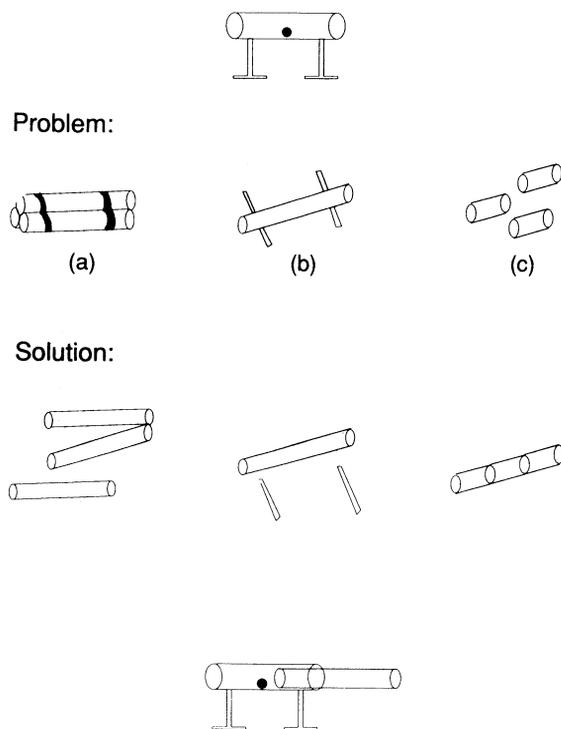


Figure 2. Diagram of the experimental conditions used by Visalberghi and colleagues to test the understanding of causality in capuchin monkeys and chimpanzees.

given a bundle of sticks taped together that as a whole was too wide to fit in the tube; the solution consisted of breaking the sticks apart. In the short-sticks task, subjects were given three short sticks that together added up to the length required; the solution consisting of putting them all in the same end of the tube to displace the food out the other side. Finally, in the H-tool task, subjects were given a stick with transverse pieces on either end that prevented its insertion into the tube; the solution consisting of removing the blocking piece from the tool. Although all three subjects eventually solved these variations of the task, they made a number of errors such as attempting to insert the whole bundle or inserting one short stick in one end of the tube and another short stick in the other end. Moreover, these errors did not decrease significantly over trials, suggesting that capuchins understood little about the causal relations between the elements in the task. Visalberghi, Fragaszy, and Savage-Rumbaugh (1995) essentially replicated the results of the bundle and the H-tool tasks with six other capuchins.

There is one recent study, however, that suggests that some capuchins may understand more about causal relations than previously thought. Anderson and Henneman (1995) tested the ability of two adult capuchin monkeys to anticipate (and solve) a variety of problems associated with using a stick to extract honey from a box with multiple holes. In a series of experiments of increasing complexity, subjects were required to select a stick

of the appropriate diameter to fit the holes, rake in a stick of the appropriate diameter with the help of another tool, modify a stick that was too thick or too twisted to fit the holes, or construct a rake which would permit them to obtain a suitable stick to extract the honey. Results indicated that both capuchins (especially the male) readily selected sticks of a suitable diameter to fit the holes which even included cases when the box and the sticks available were not within the same visual field. This result contrasts with Visalberghi's (1993) findings in which capuchins failed to select appropriate tools to solve the tube task when the tools were left in a room adjacent to the tube with food in it. Moreover, Anderson and Henneman (1995) noted that one capuchin modified tools in a very purposeful manner without committing the sort of errors described by Visalberghi and Trinca (1989). The same capuchin also used a tool (itself not suitable for honey-dipping) to rake in appropriate sticks for honey-dipping. Neither of the subjects, however, was able to construct a rake to obtain honey-dipping sticks.

The tube task has also been administered to apes. First, Bard, Frigaszy, and Visalberghi (1995) administered this task to young chimpanzees (2–4 years old) and found that in the two most difficult versions of the task (i.e., short-sticks & H-tool), the performance of the majority of subjects actually deteriorated over trials, indicating that they may not have come to understand the causal relations involved, although their young age may have explained their poor performance. Visalberghi et al. (1995) presented the bundle and the H-tool tasks to subadult and adult apes (four bonobos, five chimpanzees, and one orangutan). Eight of the ten apes solved the basic tube task on the first trial, and the other two were successful later on. When given a bundle of sticks all subjects immediately disassembled the bundle and unlike capuchins no ape attempted to insert the bundle as a whole. However, apes proved less successful in the H-tool task, making some of the same mistakes as the capuchins. Indeed, a statistical comparison of the two species in this condition revealed no significant differences (see also Khurstov, 1970, whose adult chimpanzee subjects made many of these same kinds of error on a similar task). Although there was an overall group tendency to decrease the number of errors across trials, some subjects increased their errors.

Visalberghi and colleagues argued that chimpanzees (unlike capuchins) were operating with foresight, that is, with a mental representation of the causal relations in the problem. This is based on the chimpanzees' rapid success in the basic task and the absence of errors in the bundle condition. However, Anderson and Henneman (1995) found that the performance of one capuchin monkey was consistent with the use of representation, and that some chimpanzees failed the H-tool task.

Tube-Trap Problem. In order to further probe the understanding of causal relations, Visalberghi and Limongelli (1994) presented a new tube problem that punished subjects who did not foresee the consequences of their behavior. The authors presented four capuchin monkeys with a tube that had a trap in its bottom center, and placed the food next to the trap (see Figure 3a). If subjects pushed the food in the direction of the trap it would fall in it and they would lose it; to get the food they had to push the food away from the trap towards the other end of the tube. Visalberghi and Limongelli (1994) found that only

one subject solved the task, systematically pushing the reward away from the trap. Although this subject seemed to be planning her moves in advance, the authors noted that in half of the trials she inserted the tool in the wrong side of the tube and upon seeing that the reward was moving into the trap, she withdrew the tool, reinserted it in the other end and pushed the reward out. Visalberghi and Limongelli (1994) probed further her understanding of the relation between the trap and the reward by inverting the trap 180° so that the trap was on top of the tube where it was no longer effective (see Figure 3b). The subject, however, persisted in her strategy of pushing the food away from the trap which, the authors reasoned, indicated that the subject had apparently learned to simply push the food away from the trap side without understanding the causal relations between the trap and the reward.

Limongelli, Boysen, and Visalberghi (1995) presented the trap-tube task to five chimpanzees who behaved at chance levels for the first 70 trials, although two of them learned to avoid the trap during 70 additional trials. The authors administered an additional test to assess whether chimpanzees understood the relation between the position of the reward with respect to the trap or whether they were simply using the simple rule of pushing the reward out of the side to which it is closest, thus avoiding the trap. Limongelli et al. (1995) varied the location of the trap in the tube. In some cases the trap was located very close to one end with the food just beyond it, so that subjects actually had to push the food out the end from which it was farthest. In other cases, the opposite arrangement was used. Both subjects solved these variations easily, with almost no errors, and so the researchers concluded that these two chimpanzees understood the causal relations in this task better than the capuchin monkeys. It should be noted, however, that the variations used in this experiment could still be solved by the rule “push the food away from the trap,” which could have been learned during the previous trials. Unfortunately, the authors did not invert the trap as was previously done with capuchins. However, Reaux (1995) used the inverted trap condition with one 6-year-old chimpanzee (the only one of four subjects who was successful in the regular tube trap task at all). Despite her mastery of the basic task, she continued to avoid the inverted trap—in the same manner as Visalberghi and Limongelli’s (1994) capuchin.

In sum, this last set of studies has shown that various primates are capable of using certain relational representations. They are able to foresee the order in which nesting cups should be inserted, they have some basic understanding of physics, such as that objects have to be in contact for a tool to be effective, and some studies even show that they can represent the appropriate dimensions of an effective tool in a particular task. More detailed studies on the understanding of more complex problems such as the tube problems have shown that capuchins and chimpanzees have difficulty representing some of the features of these problems. Although it is true that most of these studies have portrayed chimpanzees as more adept than capuchin monkeys, some chimpanzees do not seem to pass some of these tasks either. Still, avoiding the trap (even after inserting the tool in the wrong end of the tube) may be seen as displaying some elemental form of prediction and foresight.

V. DISCUSSION

Multiple Forms of Representation

Primates of various species display an enormous flexibility in solving problems related to space and objects. They remember multiple food locations, travel to these locations efficiently, and some primates under certain spatial arrangements use efficient search strategies. Moreover, primates use various strategies to infer novel food locations, track some object displacements accurately, and are capable of predicting the movement of targets. Primates can encode the features of stimuli to various degrees of sophistication and abstraction and are capable of imagining how stimuli will look after spatial rotations. Several primate species use and manufacture tools (mostly in the laboratory), which on some occasions are used in organized sequences. On some occasions, these tools are selected or modified in advance to meet the requirements of the task and some primates even have some understanding of some cause-effect relations in simple problems (e.g., contact between tool and reward is necessary for the tool to be effective). Taken together this evidence strongly suggests that primates use mental representation to solve various problems associated with foraging. The use of representational strategies in primates is further reinforced by a growing body of evidence in other cognitive domains such as learning, numerical skills, and transitive inference (see also Boysen, this volume; Tomasello & Call, 1997, for a review).

The three types of representation outlined in this chapter have been useful in organizing the information available in the literature. Mental representation may take many forms including things such as recalling various kinds of information, predicting and inferring outcomes, imagining the appearance of objects, anticipating problems, planning problem-solving sequences, and even having some degree of basic causal understanding of simple problems (see Table 1). This more varied view of representation is deemed more fruitful than the dichotomous characterization of representation (i.e., yes or no) that has prevailed in some discussions of primate cognition. Furthermore, each of these three types of representation is likely to contain various degrees of complexity. For instance, primates may understand some aspects of tool use (e.g., contact between a tool and a reward are necessary for the tool to work) but fail to grasp the significance of more complex aspects such as the importance of the shape or orientation of a tool in trying to obtain a reward. The absence or scarcity of actions aimed at active exploration of object properties and object-object relations (i.e., tertiary circular reactions) in earlier stages of development in nonhuman primates (Antinucci, 1989; Natale and Antinucci, 1989; Spinozzi & Potì, 1993) may be an early indication of a lack of sensitivity to the specific features of the problem. Future developmental studies should focus on the relation between early manipulative skills and the ability to solve the types of problems designed by Visalberghi and colleagues in a variety of primates. Baboons and gorillas are obvious candidates for these kinds of studies due to their highly complex manipulative propensities (Byrne & Byrne, 1993; Westergaard, 1992).

Table 1
Summary of the Types of Representational Skills Observed in Monkeys and Apes

Type of representation	Skill	Species	
		Monkeys	Apes
Static	Recall locations	++	++
	Recall object features	++	++
	Organize travel	++	++
	Organize searches	+	
Dynamic	Infer novel food locations	++	
	Track invisible displacement	+	+
	Target prediction	++	
	Mental rotation	+	+
Relational	Plan nesting cups sequences	+	++
	Hierarchically organize actions		+
	Simple tool use: support problem	++	++
	Simple tool use: stick problem	++	++
	Complex tool use: tube test	+/-	+
	Complex tool use: tube-trap test	-	+/-

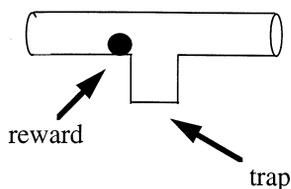
++: convincing evidence, +: some evidence, +/-: mixed evidence, -: negative evidence, blank: no evidence.

See text for references.

Representational Apes and Nonrepresentational Monkeys?

Numerous authors have argued that there is a sharp divide between monkeys and apes in regard to the use of representation (Natale et al., 1986; Byrne, 1995; Povinelli & Cant,

a) tube-trap problem



b) inverted tube-trap problem

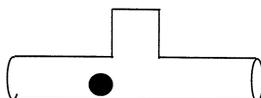


Figure 3. Diagram depicting the tube trap test and the inverted trap tube test used by Visalberghi and Limongelli (1994) to test the causal understanding of capuchin monkeys in tool using problems.

1995; Visalberghi & Limongelli, 1996). In short, these researchers have claimed that apes but not monkeys use representational strategies to solve problems in various domains such as object permanence, object manipulation, travel planning, and tool use. The current review, however, casts some doubt on such claims since there is ample evidence to support the use of representation in monkeys in most if not all of these domains (see Table 1). This conclusion is supported by the work of Anderson (1996), who compared the cognitive skills of chimpanzees and capuchin monkeys on a variety of tasks, and concluded that there were no fundamental differences between them except in mirror self-recognition. Tomasello and Call (1994, 1997) reached a similar conclusion after comparing the cognitive skills of monkeys and apes in domains of physical and social cognition. Tomasello and Call (1997) argued that the current evidence does not justify placing monkeys and apes in different cognitive categories in regard to their ability to use representation.

Perhaps the differences between monkeys and apes would become clear if our attention is focused on particular types of representation rather than on a general ability to represent. One way to organize this analysis is by using the three types of representation outlined in the previous section: static, dynamic, and relational (see Table 1). First, many monkeys and apes showed evidence of various forms of static representation. For instance, squirrel monkeys, capuchin monkeys, baboons, macaques, chimpanzees, gorillas, and orangutans recall the location of food (Harlow et al., 1932); capuchin monkeys and baboons recall quantities associated with each location (Garber & Paciulli, 1997; Vaclair, 1990b); and longtail macaques infer the location of food based on landmarks (Menzel, 1996a). In regard to the use of dynamic representations, macaques and capuchin monkeys have repeatedly failed to represent invisible displacements of objects when tested in the traditional object permanence setting. However, Filion et al. (1996) have recently shown that two rhesus macaques are indeed capable of inferring invisible displacements when tested in a computerized paradigm. Moreover, Washburn (1992) have also shown the ability of rhesus monkeys to predict the future positions of moving targets, and Vaclair et al. (1993) have shown that baboons are capable of mental rotation. Finally, capuchins, macaques, baboons, chimpanzees, orangutans, and gorillas make and use tools and they have some understanding of cause-effect relations (Tomasello & Call, 1997). Moreover, some chimpanzees (Visalberghi & Limongelli, 1996) but not others (Limongelli et al., 1995; Reaux, 1995) also have some understanding of the object-object relations in tool using situations, but so has one capuchin monkey (Anderson & Henneman, 1995)

In sum, the current analysis of the kinds of representational abilities found in monkeys compared to apes does not suggest that the former operate at a different cognitive level than the latter. Perhaps there are some quantitative differences between species, for instance, chimpanzees may remember more locations or for longer delays than marmosets, but these differences may merely be quantitative, not qualitative.

Representation, Inhibition, and Depth of Processing

Although the current review has shown that primates use representation to solve various problems, it is also clear that primates do not seem to use representation with the same

ease in each situation. For instance, in the domain of space we often find efficient travel but not always efficient searches. The fact that most primates struggle with tracking invisible displacements of objects somehow reinforces the special problems associated with search. In the domain of objects, some primates exhibit good hierarchical organization both in object manipulation and tool use, and in some cases this organization is carried out in a manner that suggests planning and foresight, but often subjects have problems with the specific features of certain tool using tasks.

One possible explanation for these discrepancies between domains is to invoke some sort of cognitive deficit. Subjects may be perfectly able to conduct efficient searches, including those involving the invisible displacements of objects, but they may have trouble producing certain responses in particular situations. For instance, in object permanence problems they may have problems inhibiting the choice of boxes that were previously baited (Diamond, 1991), or organizing means-ends sequences (Diamond, 1985). Alternatively, whether or not individuals use of representational strategies may depend on the type of problem. It is conceivable that primates construct and use representations by interacting with particular problems. These representations constitute the emergent properties of an individual's behavioral interactions with those problems. Munakata, McClelland, Johnson, and Siegler (1997) have used this approach to explain the A-not-B error in human children. These authors argue that cognitive deficit/inhibition driven explanations are insufficient to account for children's errors because the errors persist even after training the necessary means-ends skills to solve the problem. Instead they offer the alternative that representations (and knowledge) are part of the behavioral processes particular to each task.

Similarly, it is conceivable that the discrepancies between domains, for instance more positive evidence for travel efficiency compared to search efficiency, may be a consequence of the strength of the static representations that primates possess in each of those domains. Following that same reasoning, we can speculate that the depth of processing within a particular domain (e.g., tool use) may be a result of the differential strength of representations. In general, primates seem more adept at understanding how the different steps in a problem are organized rather than the specific stimuli properties of objects or their object-object relations. For example, in the tube test situation, most primates may realize that they need a tool to obtain the food, and that they need to insert the stick to poke the reward out, but may not think beforehand about the specific features that the tool has to have to be effective or what manipulation would be needed if there is a trap in the tube. This ability to better represent general as opposed to specific features in problems may extend into the social domain. Current research on social learning in primates seems to indicate that primates pay more attention to the overall actions and consequences of a model rather than to the model's specific behaviors. Instead of copying the behavior of a model primates seem at best to be trying to emulate the model's behavior, which results in individual learning (Tomasello, 1996). Furthermore, Byrne (1995) has pointed out that gorillas and other primates may engage in program-level imitation (i.e., copying the hierarchical organization of behavior), rather than imitative learning (i.e., copying the model's actions).

Space and Objects: Two Sides of the Same Coin?

The cognitive domains dealing with space and objects have provided ample evidence for representational strategies in nonhuman primates. In both domains we have discussed various types of representation (i.e., static, dynamic, and relational). Further, we have speculated that primates seem to have a greater facility for dealing with general problems rather than specific details within those problems. It is tempting to establish a parallel between representing space and representing objects. For instance, planning a route could be considered equivalent to planning the steps of a tool using sequence. This equivalence is probably no coincidence but reflects the fact that solving problems associated with space and problems associated with objects produce analogous challenges, and may consequently, be responsible for common cognitive structures.

Piaget (1952) has already argued for a connection between space and objects in human development. Object permanence is about objects but at the same time is about constructing space and what sort of spatial operations objects can undergo. Also, object manipulation is instrumental in constructing causality and object-object relations, which are in a sense spatial relations. That is, for some object-object relations, two objects have to be in contact (a spatial relation) for the tool to be effective. But the connections go beyond the Piagetian framework to include other domains. For instance, mental rotation of objects refers to the ability to perform spatial transformations, which are at the core of being able to decide beforehand what tools may be suitable for a task before attempting to use them. Planning travel routes may be equivalent to planning the steps in object manipulation sequences. Computer tests about chasing or shooting targets belong to the domain of spatial knowledge but they could easily be understood as knowing about the “behavior” of the objects involved. Incidentally, predicting the behavior of moving objects may be the first step in explaining its causes and perhaps even attributing intentions (Rochat, Morgan, & Carpenter, 1997).

A question that remains unanswered is the relation between activities that happen in locomotional space and activities that happen in manipulative space. Of special interest is the use of computer tasks that simulate certain activities that primates engage in with some frequency, for instance, chasing. Conspecifics chase each other and prey and also are chased by predators. It would be very interesting to test empirically the ability of macaques to chase targets on the screen and live targets in order to see if they use the same strategies, or whether the two abilities correlate.

VI. CONCLUSION

Monkeys and apes use flexible foraging strategies. Various primate species recall and infer new food locations, select efficient travel routes, anticipate the positions of moving targets, mentally rotate objects, plan object manipulation sequences, use and manufacture tools, and understand something about the cause-effect relations between tools and goals. All these activities strongly suggest that both monkeys and apes use representation in solving foraging problems. No clear divide has been found between the representational

skills of monkeys and apes. On the contrary, both monkeys and apes use static, dynamic, and relational representations, and we have speculated that primates have a greater facility for representing general as opposed to specific features in problems. Finally, we have characterized the domains of space and objects as complementary and indicated future lines of research both between and within these domains.

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