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Recognition and categorization of biologically significant objects by rhesus monkeys (*Macaca mulatta*): the domain of food

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Abstract

To survive, organisms must be able to identify edible objects. However, we know relatively little about how humans and other species distinguish food items from non-food items. We tested the abilities of semi-free-ranging rhesus monkeys (*Macaca mulatta*) to learn rapidly that a novel object was edible, and to generalize their learning to other objects, in a spontaneous choice task. Adult monkeys watched as a human experimenter first pretended to eat one of two novel objects and then placed replicas of the objects at widely separated locations. Monkeys selectively approached the object that the experimenter had previously eaten, exhibiting a rapidly induced preference for the apparently edible object. In further experiments in which the same objects were used as tools or were manipulated at the face but not eaten, we fail to observe an approach bias, providing evidence that the monkeys' pattern of approach in the earlier experiments was specific to objects that were eaten. Subsequent experiments tested how monkeys generalized their preference for an edible object by first allowing them to watch a human experimenter eat one of two objects and then presenting them with new objects composed of the same substance but differing from the original, edible object in shape or color. Monkeys ignored changes in the shape of the object and generalized from one edible object to another on the basis of color in conjunction with other substance properties. Finally, we extended this work to infant rhesus monkeys and found that, like adults, they too used color to generalize to novel food objects. In contrast to adults, however, infants extended this pattern of generalization to objects that were acted on in other ways. These results suggest that infant monkeys form broader object categories than adults, and that food categories become

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sharpened as a function of maturational or experiential factors.

Keywords: Biologically significant objects; Rhesus monkeys (*Macaca mulatta*); Domain of food

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1. Introduction

To survive, human and non-human animals must classify the rich assortment of physical and social objects that surround them. Discovering appropriate categories is a challenge, however, because there are indefinitely many ways to sort objects in any organism's environment. For example, when encountering a new fruit that turns out to be rotten, an animal might infer that the fruit's unpalatability was signaled by any number of different properties or combinations of properties of the fruit, including its smell, color, texture, shape, size, time of discovery, or proximity to other objects. Some of these properties would be beneficial for distinguishing ripe from rotten fruit, but most properties would not (see Hauser, Kralik, & Botto-Mahan, 1999; Keil, Smith, Simons, & Levin, 1998). Differentiating properties that are relevant for categorization from the many detectable but irrelevant properties is made more difficult by the fact that the properties relevant for categorizing objects in one domain often are not relevant for categorizing objects in other domains. For example, although a chimpanzee could successfully use the feature of smell to judge the edibility of fruits, it could not apply this same feature to determine rank in males or rigidity in rocks. Given these difficulties, how do organisms discover effective ways to sort objects?

Evolutionary biology and psychology suggest that animals may solve this problem by breaking it into parts. Instead of one general-purpose system for learning to categorize objects, animals may possess a set of specialized subsystems for categorizing particular, ecologically significant kinds of objects (Gallistel, 1990; Hauser, 2000). Behavioral ecologists provide numerous examples of domain-specific recognition systems in a wide array of animals, including recognition of competing males by frogs (Ryan & Rand, 1999), recognition of different predator classes by vervet monkeys (Cheney & Seyfarth, 1990), and recognition of edible foods by chickens (Marler, Dufty, & Pickert, 1986). In some cases, domain-specific recognition systems may be largely innately specified; in other cases they depend on innately constrained learning systems (e.g. imprinting in chicks, Horn, 1998; song recognition in sparrows, Marler, 1993; recognition of stellar configurations by migratory birds, Emlen, 1996). If constrained, domain-specific recognition systems allow human and non-human animals to categorize the significant objects in their environment, then primates may form categories of some objects but not others, and they may use different perceptual features to categorize objects of different kinds.

A number of researchers in the field of cognitive development have embraced a similar hypothesis about children's categorization of objects, proposing that humans are born with biases that guide their perception and learning about different object kinds (Carey & Spelke, 1994; Gelman, 1990; Hirschfeld & Gelman, 1994; Keil, 1989; Keil et al., 1998). When children encounter a new animal, for example, they may attend to detailed features of its shape, composition, and manner of motion (Gelman, 1990; Mandler, 1992); when they encounter a tool, they may attend to different shape features and to the actions that others perform upon it (Brown, 1990; Landau, Smith, & Jones, 1988, 1998).

Despite the interest in domain-specific categorization processes, the domain of food has received little attention in human or animal research. Although many investigators of object recognition in humans and non-human primates propose that distinct representational systems underlie recognition of animate objects (of which faces are a prototypical example) and inanimate objects (of which tools or geometric forms are prototypical examples), it is widely thought that a greater proliferation of systems for object recognition and categorization is not necessary (e.g. Biederman, 1987; Farah & McClelland, 1991) and need not be investigated. Three sources of evidence from studies of humans and animals suggest, however, that important distinctions may exist within the domain of inanimate objects, picking out privileged categories of living objects and edible objects. First, studies of learning in humans and other animals suggest that food objects are reasoned about quite differently than objects in other domains (Galef, 1990; Garcia, Hawkins, & Rusiniak, 1974; Garcia & Koelling, 1966; Rozin, 1990). As Garcia's famous experiments on avoidance learning attest, rats and other organisms are more likely to associate nausea with the ingestion of a novel food object than with a bright light or other stimulus; similarly, a variety of organisms fail to learn to avoid eating a food object that is paired with a painful shock (Garcia et al., 1974; Garcia & Koelling, 1966). These results suggest that the types of information organisms attend to when learning about food are different than those attended to when organisms reason about shocks and other kinds of stimuli. Second, there is evidence from studies of neurological patients for selective impairment of the category of food objects (Caramazza, 1998; Hart, Berndt, & Caramazza, 1985). Third, there is evidence from studies of humans in technologically remote cultures for processes of categorizing foods and other living kinds that differ considerably from the processes for categorizing and reasoning about technologically advanced artifacts (Lucy, 1992; Medin & Atran, 1999). All these studies raise the possibility that organisms have a number of domain-specific systems for recognizing and categorizing objects, including a system for categorizing objects that are potentially edible.

Do organisms possess a domain-specific system for categorizing edible objects? We sought to investigate this question in a non-human primate. Like research on humans, a growing body of research has investigated non-human primates' categorization of animate objects (e.g. Hauser, 1998a; Perrett, Hietanen, Oram, & Benson, 1992) and artifacts (e.g. Hauser, 1997; Hauser et al., 1999; Povinelli, 2000; Santos, Miller, & Hauser, 2001; Visalberghi & Tomasello, 1998), but there has been little investigation of possible domain-specific recognition systems beyond these two global domains. In an initial attempt to fill this gap, we examined how free-ranging rhesus macaques (*Macaca mulatta*) categorize novel food objects in the absence of training.

2. Experiment 1

In our experiments, we first showed a monkey two novel food objects of different shapes and colors. One object was then eaten while the other was held but not otherwise acted on. Finally, the monkey was presented with two other food objects and his selective approach to one of the objects was observed. Since many monkey species are initially neophobic (see Visalberghi & Fragaszy, 1995), we developed a paradigm that facilitated subjects' interest in the novel food: a social facilitation choice paradigm in which subjects watched a human experimenter eat a piece of food and then were allowed to choose between two foods. We reasoned that watching a human experimenter eat the food would make subjects more interested in investigating the food that they had watched the experimenter eat. This type of social facilitation effect on food consumption has been documented for at least the past 50 years. A wide range of animals have been shown to eat more food when a conspecific is present and to reverse food aversions if that individual eats the aversive food (rats: Galef, 1988; hyenas: Yoerg, 1991). Most importantly, social interaction makes normally neophobic animals more likely to sample a novel food (rats: Galef, 1988, 1993; marmosets: Vitale & Queyras, 1997; capuchins: Visalberghi & Fragaszy, 1995; but see Visalberghi, Valente, & Fragaszy, 1998; and macaques: Johnson, 2000). To our knowledge, this social facilitation effect has never been observed across two different species, but there is anecdotal reason to believe that rhesus macaques will become more interested in a food they have seen human experimenters eat. Rhesus monkeys on the island of Cayo Santiago frequently observe human experimenters eating and show much interest in the novel foods that humans eat.

In Experiment 1, we examined whether or not rhesus macaques, when presented with two novel food objects, would selectively choose a new food item that was perceptually indistinguishable from one that they had previously seen a human experimenter eat.

2.1. Method

2.1.1. Subjects

We tested 20 adult free-ranging rhesus macaques (*Macaca mulatta*) living on the island of Cayo Santiago, Puerto Rico (Rawlins & Kessler, 1987). The Cayo Santiago field site is run and maintained by the Caribbean Primate Research Center and the University of Puerto Rico School of Medicine. The population currently consists of about 1000 individuals divided into nine social groups. Subjects can be easily identified using tattoos and ear marks. Due to the long history of research on this island, subjects are well habituated to human observers. In addition, the authors who ran the experiments have had extensive experience working with this population and in running similar choice experiments (Hauser, 2001; Hauser, Carey, & Hauser, 2000; Hauser, MacNeilage, & Ware, 1996; Sulkowski & Hauser, in press).

On the island, water is provided ad libitum throughout the day at a number of sources. The island is provisioned with Purina monkey chow at three feeding stations. This provisioned chow represents approximately 50% of the monkeys' diet, depending on dominance rank. Individuals supplement their diet by foraging on leaves, small berries, flowers, and soil. In addition, although researchers on the island are typically not allowed to feed the monkeys, subjects do watch the researchers eat and often show great interest in the foods that they typically see humans eating (e.g. apples, oranges, etc.). Using this natural interest in the researchers' foods, Hauser and his colleagues have successfully run several experiments in which subjects from this population are given a choice of different numbers of food objects (see Hauser et al., 2000; Santos, Sulkowski, Spaepen, & Hauser, 2001; Sulkowski & Hauser, in press). In all of these past studies, subjects in this population were motivated to obtain the novel foods that the experimenters presented them with and normally consumed the foods immediately after obtaining them.

2.1.2. Displays

Food objects consisted of the following items: baby carrot pieces, whole cherry tomatoes, lemon chunks, lime chunks, and celery pieces. Each food item was approximately 4 cm long. None of these items are available on the island so monkeys' experience with these objects is minimal. All food objects were carried by the experimenter in a small opaque waist pouch and were presented to the animal on white foamcore platforms (25×25 cm).

2.1.3. Design

Each monkey was given a single approach trial, starting with the experimenter eating one of the two objects and then placing one object on the left platform and one on the right. All ten possible pairings of the food items were tested twice, for a total of 20 subjects and test trials. The particular object that the experimenter ate and the lateral positions of the two objects were counterbalanced across subjects.

2.1.4. Procedure

Subjects were tested opportunistically by finding individuals who were completely alone and in a sitting, resting position. The experimenter was careful to test each subject on a flat, clear terrain such that no obstacles would impede the subject's approach. At the beginning of each trial, a human experimenter approached the subject and crouched down approximately 7 m away (see Fig. 1). The experimenter first placed the two platforms down on either side (approximately 1.5 m away from the experimenter and thus over 3 m apart from each other). The experimenter made sure that the subject was stationed equidistant between the two platforms to eliminate the possibility that one platform was easier to approach than the other. This set-up therefore established a triangle with the subject at one point and the two platforms at the other two points; the experimenter was positioned midway between the two platforms. The experimenter then removed the two food items from the waist pouch and held them up at eye level for 3 s. Once the subject had viewed both foods, part of one of the foods was eaten. The experimenter then put both foods back into the waist pouch and removed two new food items from the same two categories. Both foods were held up at eye level for 3 s and then placed on the foamcore platforms. The experimenter then stood up, turned around, and walked away thereby allowing the subject to approach. Because of the distance between the two platforms, the subject was forced to approach one of the two platforms first. In past experiments involving similar choices (Hauser, 2001; Hauser et al., 2000; Sulkowski & Hauser, in press),

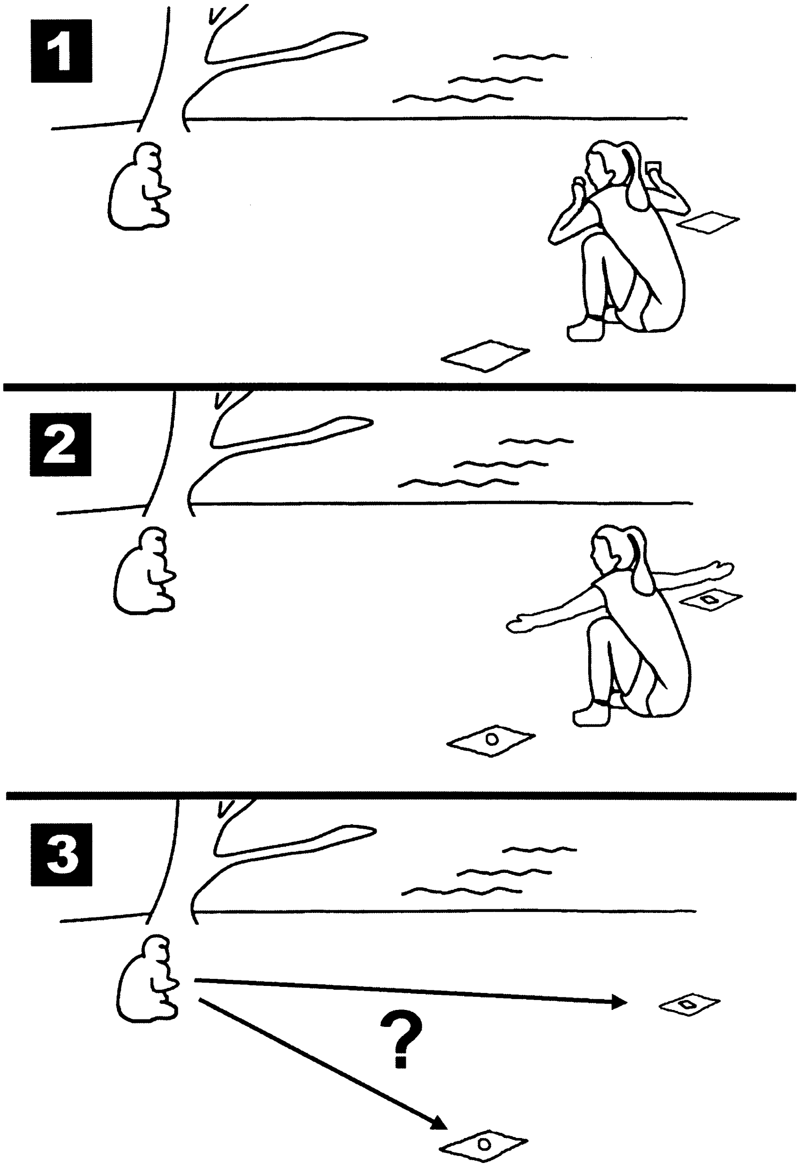

Fig. 1. Procedure for Experiment 1.

subjects typically approached the chosen platform in an unambiguous straight line. As such, the subject's choice was scored as the first platform approached within less than 1 m. This criterion was used because we did not want subjects to actually obtain the food. First, we feared that monkeys might spread the novel food across the island such that untested monkeys would no longer be naive. Second, we feared that possession of a novel food might cause fights between animals. Finally, in later experiments using non-food stimuli, we did not want the subjects to attempt to eat the inedible objects. We dropped from the experiment trials in which the subjects were not being completely attentive, approached prior to the completion of the presentation, failed to approach immediately after the experimenter walked away, or failed to make a clear, straight approach.

2.2. Results

Nineteen out of 20 subjects approached the platform holding the food object that the experimenter had eaten (one sample sign test, $P < 0.0001$; see Fig. 2). There was no systematic bias to approach one food object over the other and no side bias.

2.3. Discussion

After watching a human experimenter eat a novel food object, rhesus macaques selectively approached a replica of that object in preference to a replica of a second object that the experimenter had presented but not acted upon. This finding provides evidence both for a social facilitation effect from humans to monkeys and for rapid learning about novel food objects in monkeys.

Having established this effect using real foods, we next turned to artificial objects.

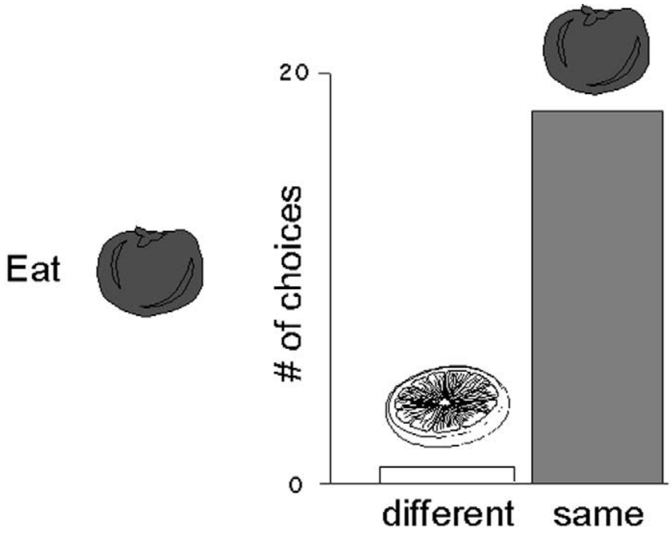

Fig. 2. Number of subjects who chose the eaten object in Experiment 1.

The potential advantage of artificial objects is that they lack any distinctive odors, are certain never to have been experienced by the monkeys as food, and provide an opportunity to control and systematically manipulate particular object features. We investigated monkeys' reactions to small, manipulable objects made of Play-Doh™ modeling clay and molded into distinctive shapes. Because the clay is non-toxic, comes in a variety of colors, and can be molded into a variety of shapes, we thought it the ideal stimulus for our experiments on monkeys' learning and categorization of food objects. In Experiment 2, we investigated whether the social facilitation effect observed in Experiment 1 would hold for non-food clay objects that a human experimenter pretended to eat.

3. Experiment 2

3.1. Method

3.1.1. Subjects

Subjects were 15 adult rhesus macaques from the Cayo Santiago population. We chose to use this number in all subsequent experiments because of the size of the effect observed in Experiment 1 and because it is the number of subjects typically tested in choice experiments of this kind (see Hauser et al., 2000; Sulkowski & Hauser, in press).

3.1.2. Displays

The displays consisted of 16 different objects of four different colors (pink, purple, green, and orange) and four different shapes (flat rectangle, cylinder, sphere, and ring). All objects were approximately 5 cm long. To be sure that the color and shapes of these objects were distinguishable, we presented them to five human subjects at twice the distance (15 m away) and asked subjects to identify the color and shapes. All human subjects could easily identify both the color and shape of all 16 objects. Given the similarity between human and rhesus monkey vision (see DeYoe & Van Essen, 1988), we assume that our rhesus subjects were readily able to discriminate our test objects at shorter distances. As in Experiment 1, all objects were carried by the experimenter in a small waist pouch and were presented to the animal on white foamcore platforms.

3.1.3. Design

Experiment 2 started approximately 5 months after Experiment 1. Each monkey was presented with two objects that differed in both color and shape (e.g. green ring and pink cylinder), one of which the experimenter pretended to eat. The color and shape of the apparently edible object and the side that object was placed on (left or right) were randomized across subjects such that each particular configuration of objects was used at most once.

3.1.4. Procedure

The general procedure for Experiment 2 was the same as in Experiment 1. A single experimenter presented each monkey with two objects differing in shape and color, pretended to eat one of the objects, placed both objects back inside the waist pouch, removed two more identical objects from the waist pouch, held them up at eye level for 3 s, and then placed them on the foamcore platforms. The experimenter then stood up, turned around, and walked away, allowing subjects to approach one of the two platforms. Again, once a choice was scored, the experimenter attempted to scare the subject away from the platform before he obtained the object on his chosen platform. As in Experiment 1, trials in which the subject was not completely attentive, began approaching before the completion of the presentation, failed to approach immediately, or failed to make a clear, straight approach were aborted and were dropped from the experiment.

3.2. Results

Twelve out of 15 subjects selected the previously eaten object (one sample sign test, $P = 0.04$; see Fig. 3). There were no systematic color, shape, or side preferences.

3.3. Discussion

When presented with non-food clay objects of simple shapes, uniform colors, and no distinctive odors, monkeys selectively approached the object that looked identical to the one previously eaten by the experimenter. This result replicates and extends the findings of Experiment 1, providing evidence that the social facilitation effect found in that study is not specific to real food items or to odorous substances,

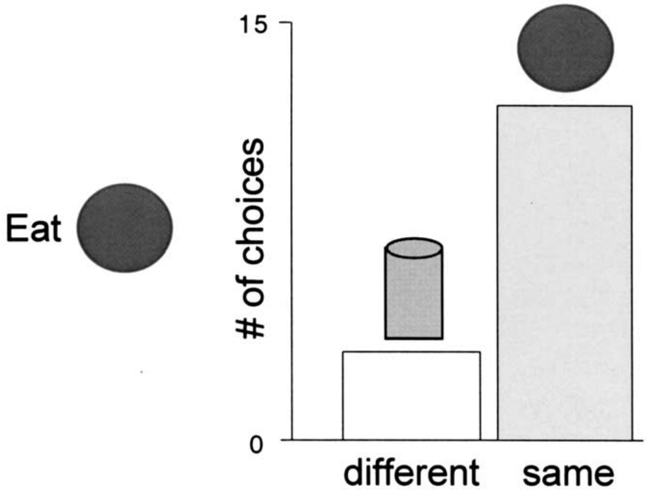

Fig. 3. Number of subjects who chose the eaten object in Experiment 2.

and that the generalization observed during the test was based purely on the visual attributes of the objects.

Together, Experiments 1 and 2 provide evidence that monkeys who view a person apparently eating an object change their representation of that object in ways that make that object, and other objects with the same visual features, more attractive to them. These experiments do not reveal, however, whether the change in the attractiveness of the object has anything to do with its apparent edibility. It is possible that monkeys are attracted to any object that a person acts upon, regardless of the nature of that action. To distinguish between these possibilities, the next set of experiments investigated whether monkeys selectively approach an object that is identical in visual features to one that a person has acted on in other ways.

4. Experiment 3

In this experiment, an experimenter introduced monkeys to the same pairs of objects used in Experiment 2. Instead of pretending to eat one of the objects, however, the experimenter manipulated one of the objects in a different way (for example, by twirling the ring on her finger or rolling the sphere on a foamcore platform). After this presentation, monkeys were given the same selective approach test as in Experiment 2. If monkeys selectively approach any object that a person acts upon independently of the kind of action performed, then the results from Experiment 3 should mirror those obtained in Experiment 2. In contrast, if monkeys only evidence selective approach for apparently edible objects, and edibility is functionally defined as objects placed in the mouth, then rhesus should show a relatively more random pattern of approach.

4.1. Method

Experiment 3 started approximately 5 months after Experiment 2. Subjects who had been previously tested in Experiment 2 were not retested. The method was the same as Experiment 2 with the following exceptions. After presenting a monkey with two objects differing in both shape and color, the experimenter then acted on one of these objects: she pounded the cylinder on the ground, spun the ring around her finger, scratched her hand with the rectangle, or rolled the sphere on the ground. Then the experiment proceeded as in Experiment 2.

4.2. Results

In contrast to Experiment 2, subjects showed no selective approach to the object with the same visual features as that which the experimenter had acted on. Only seven out of 15 subjects approached the same-colored, same-shaped object over the different-colored, different-shaped object (one sample sign test, $P > 0.99$; see Fig. 4).

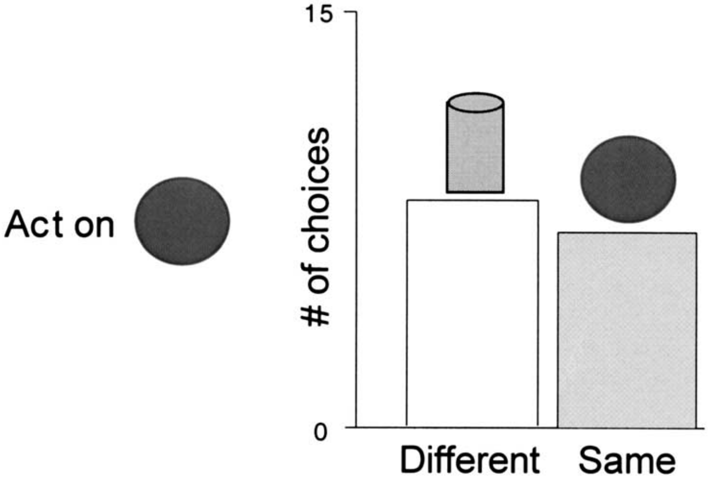

Fig. 4. Number of subjects who chose the acted on object in Experiment 3.

4.3. Discussion

Monkeys who viewed a person manipulating an object without eating it subsequently showed no selective approach to a visually identical object. Their behavior contrasted with that of the monkeys in Experiment 2, who selectively approached an object that was visually identical to one that an experimenter had pretended to eat. Because the monkeys in Experiments 2 and 3 were tested by means of the same procedure, the contrasting findings of those experiments provide evidence that the selective approach observed in Experiment 2 does not stem from a general tendency to approach any object that a person acts upon.

Nevertheless, Experiments 2 and 3 do not reveal whether the monkeys' selective approach is guided specifically by a categorization of an object as potentially edible. It is possible, in contrast, that monkeys selectively approach any object that they perceive to be of interest to humans. If monkeys attend more to human faces than to human hands, then they will be more likely to categorize an object as "interesting" if a human acts on the object at her face than if she acts on the object with her hands, and they will selectively approach any object that is manipulated at the face. The next experiment was undertaken to distinguish this possibility from the thesis that selective approach depended on a rapidly learned categorization of an object as edible.

5. Experiment 4

The monkeys in Experiment 4 were presented with the same pairs of objects as in Experiments 2 and 3. Instead of pretending to eat or manipulate an object, however, the experimenter first looked at one of the objects and then used it to scratch her ear.

Monkeys' selective approach to the object was then tested by means of the same procedure as in the previous studies. If monkeys selectively approach any object that a person acts on at her face, then the patterns of selective approach observed in Experiment 2 also should occur in Experiment 4. In contrast, if monkeys specifically approach objects that they categorize as edible, then the pattern of approach observed in this experiment should be random.

5.1. Methods

Experiment 4 started approximately 9 months after Experiment 3. Subjects who had been previously tested in Experiments 2 and 3 were not retested. The experiment used the same method as in Experiments 2 and 3. After showing a monkey two objects differing in both shape and color, the experimenter scratched her ear with one object, using motions that were as large in extent and duration as those used in the pretend eating actions of Experiment 2. The procedure then continued as in Experiments 2 and 3.

5.2. Results

When the experimenter scratched her ear with one object, only seven out of 15 subjects approached this object (one sample sign test, $P > 0.99$; see Fig. 5).

5.3. Discussion

The findings of Experiment 4 are similar to those of Experiment 3 and contrast with those of Experiment 2. Although monkeys selectively approach an object that has apparently been eaten, they fail to selectively approach when an object has been manipulated by an experimenter's hands or at her face. Experiments 3 and 4 there-

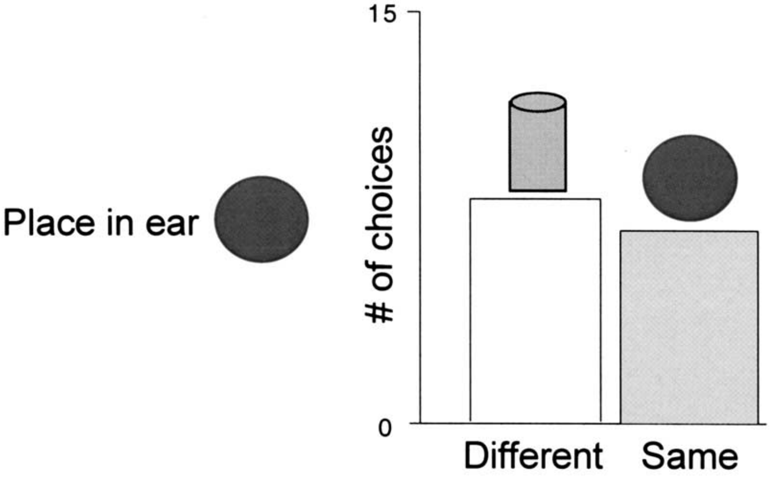

Fig. 5. Number of subjects who chose the object placed in the ear in Experiment 4.

fore provide evidence that the pattern of selectivity observed in Experiment 2 is relatively specific to objects that have been eaten. Monkeys who view an object being eaten appear to categorize that object as edible and to extend the property of edibility to other objects with the same visual features.

In Experiments 1 and 2, monkeys generalized the property of edibility from one object to another object that looked just like it. In natural scenes, however, distinct members of a single food category do not look exactly alike but rather vary, to some degree, in their visual attributes. Do monkeys generalize categories of edible objects to new objects with distinctive visual features? If so, what features are the most important guides to categorization?

Investigations of the features that monkeys use to categorize novel objects bear directly on the issues of domain-specific systems for recognizing objects discussed in Section 1. It has often been proposed that objects are represented and recognized primarily by their shapes (Biederman, 1987; Farah & McClelland, 1991; Gross, 1992; Logothetis & Sheinberg, 1996). Shape-based object recognition is highly effective for recognizing individual members of one's own species (Perrett et al., 1992), other species of animals (Biederman, 1987), and tools (Keil et al., 1998; Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). If a single system of recognition and categorization serves to identify all kinds of objects, therefore, we might expect monkeys to categorize food objects by their shape as well. Contrary to this expectation, an ecological analysis suggests that food objects should be categorized differently. The edibility of an object depends on the stuff of which it is made, not on its form. If an object is cut or broken so that it changes radically in form, that change is not likely to affect its edibility. Transformations that alter the substance of a food object, in contrast, may well affect edibility. These changes are more likely to be signaled by changes in the color or texture of an object than by changes in its shape. If a domain-specific system underlies monkeys' categorization of food objects, therefore, then we might expect monkeys to weight color more strongly than form in categorizing novel objects as food. The next four experiments tested these contrasting predictions.

6. Experiment 5

Experiment 5 used the same method as Experiment 2 except for properties of the objects presented. In one condition (color), both objects presented had the same shape and differed in color (e.g. pink sphere vs. green sphere). In the other condition (form), both objects had the same color but differed in form (e.g. pink sphere vs. pink ring). If monkeys' categorization of edible objects is sensitive to the color and shape, then monkeys should selectively approach the object with the same color and shape as the previously eaten object.

6.1. Method

Thirty adult monkeys from the Cayo Santiago population participated in this experiment which began about 1 month after Experiment 2 and about 4 months before Experiment 3. Subjects who had been previously tested in Experiments 2–4 were not retested. The 15 monkeys in the *color* group were presented with two objects of the same shape and different colors (e.g. green ring and pink ring). The 15 monkeys in the *shape* group were presented with two objects of the same color and different shapes (e.g. green ring and green sphere). The methods were otherwise the same as in Experiment 2.

6.2. Results

In the color condition, 13 out of 15 monkeys approached the object with the same features as the one that was eaten (one sample sign test, $P = 0.007$). In the form condition, in contrast, only seven out of 15 monkeys approached the object with the same features as the one that had been eaten ($P > 0.99$). Performance in the color condition was significantly different from that in the form condition ($\chi^2(1) = 5.4$, $P = 0.02$; see Fig. 6). There were no systematic shape, color, or side preferences in either of the groups.

6.3. Discussion

When given a choice between clay objects of different colors but the same shape, monkeys selectively chose the object with the same color as the one that a human demonstrator had pretended to eat. This finding suggests that monkeys form categories on the basis of color, at least in the presence of objects of identical texture and consistency. In contrast, rhesus monkeys failed to generalize to the same-shaped object when choosing the object which the demonstrator had eaten. This failure

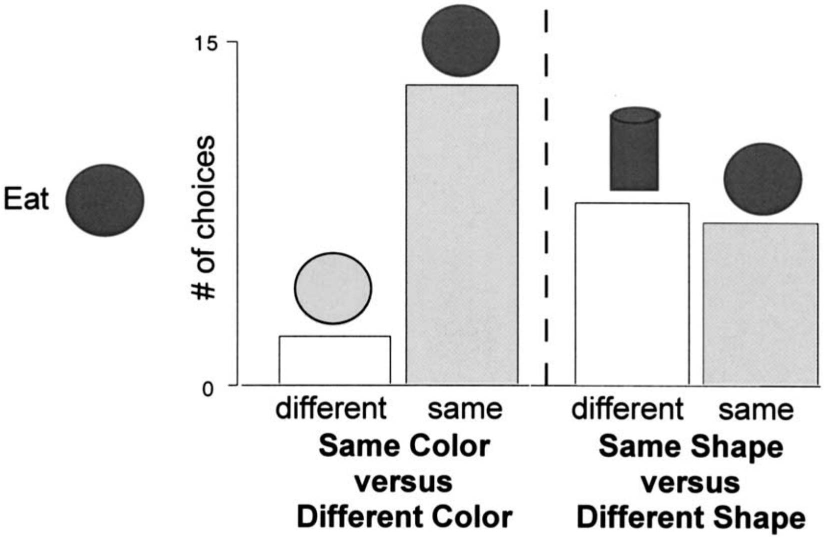

Fig. 6. Number of subjects who chose the eaten object in Experiment 5 across same shape and same color conditions.

suggests that rhesus monkeys do not form food categories on the basis of shape, at least in the presence of objects of identical texture and consistency.

The finding that rhesus monkeys use color to generalize across edible food items contrasts with a large literature on object recognition suggesting that monkeys and humans tend to categorize objects by shape (Biederman, 1987; Perrett et al., 1992; although see Sands, Lincoln, & Wright, 1982; Spinozzi, 1996 for evidence that macaques are able to use color as well). Very little work on object recognition, however, has looked at food objects. Our results therefore support the thesis that object recognition and categorization depend on domain-specific systems for representing ecologically significant objects. To further explore this claim, we investigated the generality of color-based categorization in three additional experiments. In Experiment 6, we showed monkeys one eaten food object and allowed them a choice between an object of the same shape but different color or an object of the same color but different shape. If monkeys generalize to new edible objects by color more than by shape, they should selectively choose the same-colored object over the same-shaped object.

7. Experiment 6

The monkeys in this experiment were presented with a single object (e.g. green ring) by an experimenter who pretended to eat it. Then the experimenter removed that object and presented two new objects, one with the same shape (e.g. pink ring) and one with the same color (e.g. green sphere). Monkeys' selective approach to these objects was observed as in past experiments. If monkeys categorize edible objects by their color, then they were expected to approach selectively the object with the same color as the one they had observed being eaten.

7.1. Method

Experiment 6 began approximately 1 month after Experiment 5 and used the same objects. Subjects who had been previously tested in Experiments 2–5 were not retested. The procedure differed slightly from that of Experiments 2–5 because the experimenter familiarized subjects with only one object. After pretending to eat this object, the experimenter returned it to the waist pouch and removed two new objects. One of these objects had the same shape as the original object but differed in color. The other object had the same color as the original object but differed in shape. The experimenter held these objects up at eye level for 3 s, and then placed them on the foamcore platforms. The design and procedure were otherwise the same as Experiments 2–5.

7.2. Results

Monkeys selectively approached objects of the same color as the one eaten by the experimenter. Twelve of 15 subjects approached the same-colored, different-shaped

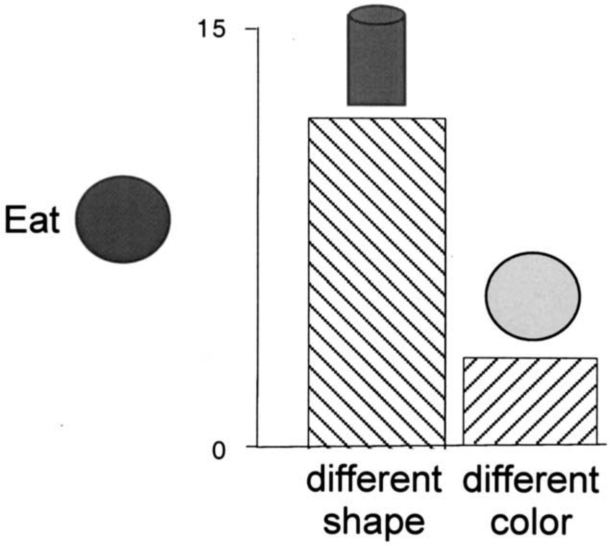

Fig. 7. Number of subjects who chose the same color/different shape objects over different color/same shape objects in Experiment 6.

object rather than the same-shaped, different-colored object (one sample sign test, $P = 0.04$; see Fig. 7).

7.3. Discussion

Paralleling the pattern obtained in Experiment 5, the monkeys in Experiment 6 selectively approached an object of the same color as the one that was eaten by the experimenter. This result provides further evidence that monkeys weight color above shape when generalizing about novel food objects.

Why did the monkeys in Experiments 5 and 6 not use shape information when categorizing novel objects as edible? As we have noted, one possible explanation appeals specifically to the importance of color in the domain of food. Although food objects can vary both in color (as they ripen) and in shape (as they are torn or eaten), the former variation is more relevant to their edibility than is the latter. Pieces of melon or apple do not vary in palatability as they vary in shape, but they typically do vary in palatability as they vary in color. More generally, edibility is a substance property, and surface color and texture are more informative about substances than is surface form. On this view, the color-based generalization observed in Experiments 5 and 6 should be specific to the domain of food (and, perhaps, to other biologically significant domains of objects whose functional properties depend primarily on their substances).

A contrasting explanation appeals to a general perceptual bias. It is possible that adult monkeys weight color above shape in generalizing about all kinds of objects, not just in generalizing about food. Monkeys may have found the color of the clay objects more salient than their shapes. If this is the case, then the pattern of results we obtained would reflect an attentional bias: a predisposition to preferentially attend to the color of the objects used in the experiment.

An attentional bias seems unlikely to explain our findings, given results of other experiments on object recognition and categorization in primates (Biederman, 1987; Hauser, 1997; Hauser et al., 1999; Visalberghi & Tomasello, 1998), including one series of experiments on the same population of rhesus monkeys (Santos et al., 2001). In the latter studies, monkeys from the Cayo Santiago population were tested using an expectancy violation procedure in which they witnessed a small hockey stick shaped tool push a grape into a well. Monkeys tested in this situation generalized to new tools based on shape rather than color. Similar evidence has been obtained for a different monkey species – cotton-top tamarins (*Saguinus oedipus*) – tested on a different tool-use task (Hauser, 1997; Hauser et al., 1999). However, because we failed to elicit a pattern of selective approach to non-food objects in Experiments 3 and 4, we cannot test directly for domain-specific recognition and generalization with the present paradigm. It is possible, therefore, that the color-based generalization observed in Experiments 5 and 6 depended on idiosyncratic features of the stimulus objects or experimental procedure rather than a domain-specific system for categorizing objects as edible.

The next experiments investigated this possibility by introducing two innovations into the methods of the previous studies. First, we asked whether monkeys would show generalization by color when they were presented with objects that looked very different from the Play-Doh objects used in the previous studies. Second, we asked whether monkeys would show such generalization when the edibility of an object was revealed in a very different way from that of the previous studies. In Experiment 7, monkeys were presented with real food – pieces of pineapple – that was dyed different colors and cut into different shapes. Moreover, monkeys discovered the edibility of a food object not by observing the eating of others but by eating it themselves. If monkeys have a domain-specific system for representing and categorizing food, then they should generalize to new food objects on the basis of color in these experiments as well.

8. Experiment 7

At the start of the study, a monkey was given a small piece of pineapple of a particular shape and color and was allowed to eat it. After he had eaten this object completely, the experimenter presented two new pieces of pineapple – one differing in color and the other differing in shape from the original object – and the monkey was allowed to approach one of them. If monkeys tend to make generalizations about edible objects on the basis of color, then they should approach the object with the same color as the previously eaten object, despite its different shape.

8.1. Method

Experiment 7 began approximately 7 months after Experiment 5 and used pine-

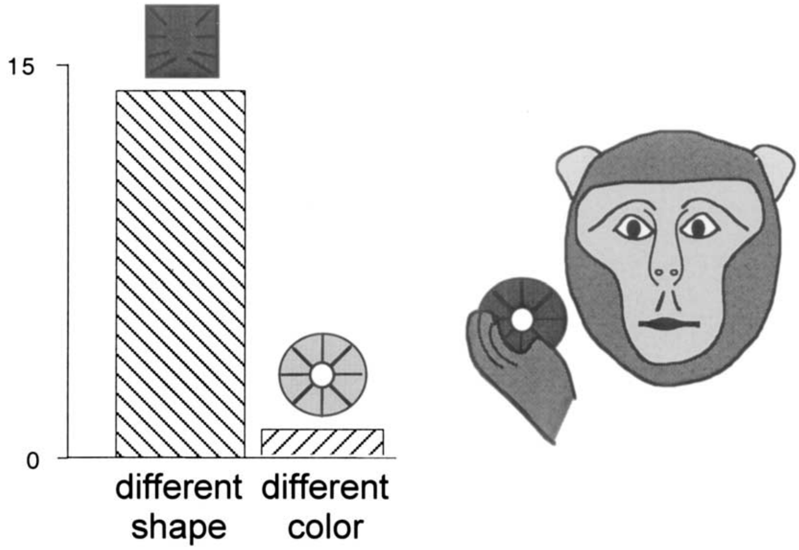

Fig. 8. Number of subjects who chose the same color/different shape pineapple over different color/same shape pineapple in Experiment 7.

apples of two colors (either dyed blue or red) and two shapes (a rectangle cut from a whole pineapple or a ring shape) as stimuli. In this experiment, we followed the same procedure as Experiments 1–6 except as follows: instead of eating the food object in front of the monkey, the experiment gave the monkey a single piece of pineapple and allowed him or her to eat it before presentation. To accomplish this, she presented subjects with one pineapple object (e.g. blue ring), holding it up for 2 s. She then slowly approached the monkey, placed the pineapple approximately 1 m in front of him and allowed him to approach and eat it completely. After the subject had finished eating, the experimenter then took out two other pineapple objects, one differing in shape, the other differing in color (e.g. red ring and blue rectangle), held the objects up at eye level for 3 s, and then placed them on the foamcore platforms. The experiment then proceeded as did Experiments 2–6. Trials in which the subject failed to completely eat the original object, walked away before the completion of the presentation, or failed to make a clear approach during the test were dropped from the study.

8.2. Results

Fourteen of 15 monkeys approached the object of the same color as the food item that they had previously eaten ($P < 0.001$; see Fig. 8). There was no systematic color, shape, or side preference.

8.3. Discussion

After eating a piece of pineapple, rhesus monkeys selectively approached an object of the same color as the one they had previously eaten over an object of the same shape. This result suggests that the generalization pattern observed in previous experiments was not an artifact of the fact that objects were made of clay. Moreover, the generalization observed in previous experiments was not restricted to situations in which monkeys observed a human eating an object. Even with truly edible, differently colored and shaped pieces of pineapple that the subjects ate themselves, monkeys categorized the food items using color as the most salient feature. Whether monkeys' knowledge of edibility is direct or indirect, they use color to generalize to new exemplars of the same food.

In the last set of experiments, we began to investigate the development of this domain-specific system. Specifically, we used the same approach paradigm with infant rhesus monkeys in order to investigate whether they too rapidly learned about edible objects by attending to the actions of a human actor, and whether they used color as the most dominant feature in categorizing a new object as edible.

9. Experiment 8

In this experiment, infant rhesus monkeys were presented with the novel objects used in Experiments 2–6. They observed a human experimenter who presented them with two objects of different colors and shapes and then either pretended to eat one of the objects as in Experiment 2 or manipulated one of the objects as in Experiment 3. Then infants were shown two new objects with the same features as the original pair of objects and were allowed to approach one of them. If infants learn rapidly about the edibility of the objects, those who view the eating of an object should selectively approach the object with the same features in the visual test. A comparison of infants' selective approach in the two conditions should reveal whether such learning is specific to the action of eating or is more general.

9.1. Method

Subjects were 30 monkeys from the Cayo Santiago population between 6 months and 2 years of age. Most subjects were between the ages of 1 and 2 years. The displays and procedure were the same as for Experiments 2 and 3 except as follows. Trials began by finding a single infant who was on its own or whose mother was not attending to him or her (e.g. involved in a grooming bout with another individual, foraging, etc.). Infants were divided into two groups. The *food* group was given the same procedure as for Experiment 2, in which the experimenter presented each infant with two differently colored and differently shaped objects (e.g. pink ring and green sphere) and pretended to eat one. The *artifact* group was given the same procedure as in Experiment 3, in which the experimenter presented two differently colored and differently shaped objects and then manipulated one object. Approach was measured in the same way for infants as for adults.

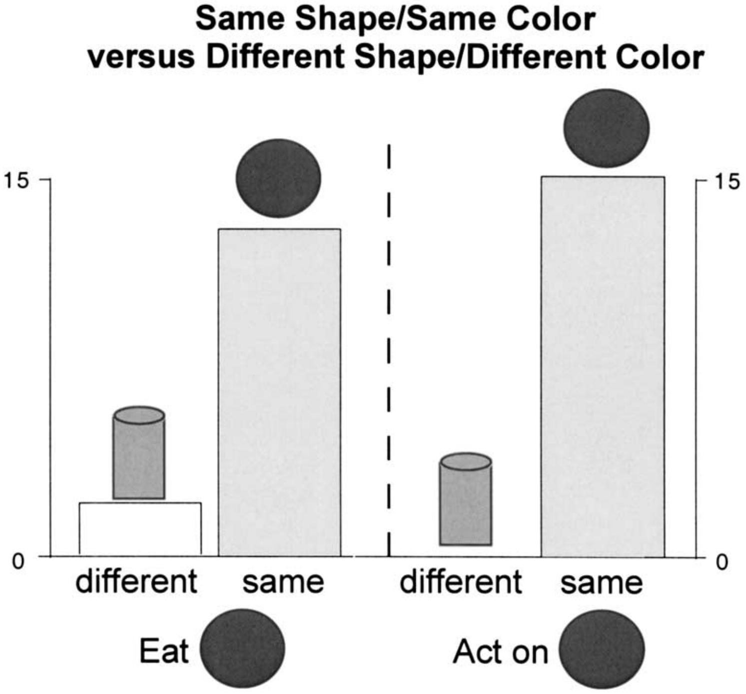

Fig. 9. Number of subjects who chose the acted on object across artifact and food conditions in Experiment 8.

9.2. Results

In all, 28 out of 30 infants approached the same-colored, same-shaped object over the different-colored, different-shaped object (one sample sign test, $P < 0.0001$; see Fig. 9). All 15 infants in the artifact group approached the object with the same properties as the one that had been manipulated ($P < 0.0001$) and 13 out of 15 infants in the food group approached the object with the same properties as the one that had been eaten ($P < 0.007$). Rates of approach in these two conditions did not differ from one another ($\chi^2(1) = 2.13$, $P = 0.14$). Infants' rates of approach in the food condition also did not differ from the performance of adults in Experiment 2 ($\chi^2(1) = 0.24$, $P = 0.624$). In contrast, infants and adults did reliably differ on performance in the artifact condition, with infants having a consistent approach to the manipulated object ($\chi^2(1) = 10.9$, $P = 0.001$).

9.3. Discussion

Like adults, infant rhesus macaques demonstrate a social facilitation effect for objects they witnessed being eaten by a human experimenter. Unlike adults, however, this facilitation effect also was obtained for objects that were manipulated in other ways. Infant monkeys reliably approached the object of the same shape and color as the object an experimenter had previously manipulated without eating. Infant monkeys therefore showed selective approach on the basis of a broader array of actions by the human demonstrator.

To begin to investigate the perceptual basis of infants' rapid learning about objects, we next tested infant macaques on the same procedure as Experiment 6, in which the experimenter acted on one object and then gave the infants a choice between an object of the same shape but different color or an object of the same color but different shape. We again divided infants into two groups and varied the manipulation they saw the experimenter perform on the objects: either eating the object (food group) or manipulating it (artifact group).

10. Experiment 9

Infant monkeys were presented with a single object of a given color and shape, as in Experiment 6, that the experimenter either pretended to eat or manipulated in other ways, as in Experiment 9. Then monkeys were presented with new objects that differed from the original object either in color or in shape, and their selective approach to these objects was measured. If infant monkeys already have a domain-specific system for recognizing and categorizing food, and if categorization depends on the most reliable information for palatability, then subjects who view the experimenter eating the original object should selectively approach the novel object with the same color. If such a system is specific to food, then subjects who view the experimenter manipulating the original object should show a different pattern of generalization.

10.1. Method

Experiment 9 began approximately 1 week after Experiment 8 and followed the same method except as follows. As in Experiment 6, the experimenter presented only one object to each subject and then acted on it either by pretending to eat it or manually manipulating it. The selective approach test was the same as in Experiment 6 and involved two new objects, one with the same shape but different color from the original object, and one with the same color but different shape.

10.2. Results

Twenty-four out of 30 infants approached the object that was the same color as the one that had been eaten ($P < 0.001$; see Fig. 10). In each of the two groups (food and artifact), 12 out of 15 individuals ($P < 0.04$) approached the object of the same color over the object of the same shape. Performance in each condition of this experiment was similar to that of adults in Experiment 6.

10.3. Discussion

Like adults, infant rhesus macaques used color as the basis for generalizing about

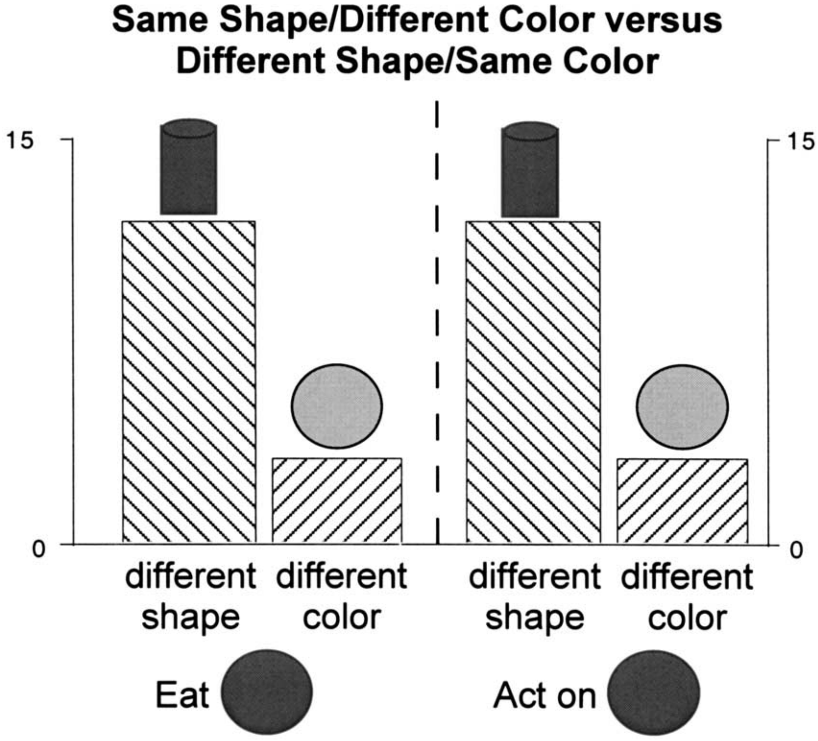

Fig. 10. Number of subjects who chose the same color/different shape object over the different color/same shape object across artifact and food conditions in Experiment 9.

new food objects. After seeing a human experimenter pretend to eat an object, they selectively chose objects of the same color as the one eaten. In contrast to adults, however, infants also showed this pattern of generalization for non-eaten objects. After seeing a human experimenter manipulate an object without bringing it anywhere near the mouth, they too tended to approach an object of the same color in preference to an object of the same shape.

These findings could be interpreted in either of two ways. First, it is possible that infant monkeys are predisposed to learn about all kinds of novel objects that are manipulated by human beings and to generalize their learning to new objects in a manner that weights color above shape. However, this possibility contradicts evidence suggesting that in other situations, infant rhesus macaques will weight the feature of shape over color. Rhesus macaques of the same ages as those tested in these studies and younger have been shown to use shape to recognize faces and other objects in object discrimination tasks (see Rodman & Nace, 1997). These findings suggest that it is unlikely that rhesus infants are predisposed to generalize using the feature of color over shape for all kinds of objects.

An alternative possibility is that infant monkeys have a domain-specific system for learning about edible objects, but they consider a broader range of actions by other animals as relevant to an object's potential edibility. Although adult monkeys do not consider object manipulations such as rolling and twirling as relevant to the object's potential edibility, infant monkeys may infer that any object acted on by another primate is more likely to be edible than an object that is not acted upon.

The second possibility is not wholly implausible when one considers the natural environment of rhesus monkeys. Most of the inanimate objects that adult monkeys manipulate in an attentive manner are edible: untrained monkeys show little interest in tools, rocks, or other inedible objects. A learning system that considered any object that an adult monkey acted on as potentially edible would likely allow infant monkeys to learn about many of the foods that monkeys eat. As they observed other monkeys, moreover, they would be in a position to learn to narrow the range of actions and events that are informative about edibility.

The idea that infants consider a broader range of objects as edible is also consistent with what has been observed in human infants. As most new parents quickly learn, human infants are willing to put almost any object in their mouths. Rozin, Hammer, Oster, Horowitz, and Marmara (1986) documented this behavior systematically and found that before the first 2 years of life, human infants show mouthing of nearly all objects except hair. Over the next year, toddlers begin to narrow the range of objects they will place in their mouths and start to show an adult-like pattern of selectivity for edible objects by 3 years of age. A similar developmental narrowing of natural object categories appears to occur in a different primate species and domain: vervet monkeys show a very early development of categories of predators, and the basis by which they categorize objects as predators becomes more specific and restricted with development (Cheney & Seyfarth, 1990). Thus, for example, vervet infants begin life giving eagle alarm calls to all objects in the air that appear to frighten them. Over the course of approximately 1 year, infants give eagle alarm calls to only those species that prey on them. This gradual development toward selectivity may be an important feature of these and other domain-specific recognition systems.

11. General discussion

After learning about a novel food object, rhesus monkeys selectively approach objects of the same color, but not objects of the same shape. This pattern is robust over changes in the food stimuli used and the method by which subjects learn about the edibility of the objects. For adult monkeys, however, this pattern only holds when the object is viewed as edible; adult monkeys approach randomly when they have seen an object acted on or inserted in an experimenter's ear. For rhesus monkeys of all ages, moreover, color is a more salient property of food categories than is shape.

These results parallel recent work examining word learning in human children. Ordinarily, children demonstrate a shape bias when learning new words; that is, they will generalize a word used to label a novel object to all objects of a similar shape (see Jones, Smith, & Landau, 1991; Landau et al., 1988, 1998). Recent work suggests, however, that 3- and 4-year-old children do not show a shape bias for food objects (Lavin & Hall, 1999; Macario, 1991; Santos, Miller, & Hauser, 1999). Children selectively use color and texture information when categorizing novel food objects, ignoring information about the object's form. Like rhesus monkeys, children seem to value the property of color over shape when generalizing to novel food objects.

Why do children and rhesus monkeys selectively attend to color when categorizing food objects? As mentioned earlier, it is unlikely that children and monkeys have a general perceptual bias for the feature of color and selectively attend to this property when generalizing about all kinds of objects in light of the wealth of evidence that human and non-human primates of all ages selectively attend to an object's form when categorizing and recognizing objects (Biederman, 1987; Hauser, 1997; Hauser et al., 1999; Landau et al., 1998; Rodman & Nace, 1997; Santos et al., 2001). An alternative possibility is that humans and non-humans categorize foods and non-foods at different categorical levels (see Rosch et al., 1976). Researchers have found that objects with the same shape tend to be categorized at the same basic level (Rosch et al., 1976). In contrast, when researchers have focused on subordinate level categorizations, the property of color is shown to be important (Logothetis, Pauls, Bulthoff, & Poggio, 1994; Vogels, 1999). It is possible, therefore, that rhesus monkeys use the feature of color to categorize the food objects in our study because they place all the stimuli in our experiment into the basic level category "food" and then learn about the edibility of different subordinate categories of food objects. Although our research does not rule out this possibility, we view it as unlikely for two reasons. First, human primates do not place all food objects into one basic level category (see Rosch et al., 1976). Second, when rhesus monkeys communicate about available foods, they use distinct vocalizations for high quality (e.g. coconut) and low quality (e.g. monkey chow) food objects rather than a single vocalization for all food objects, suggesting that they find a lower level of abstraction most useful when categorizing food objects (Hauser, 1998b; Hauser & Marler, 1993). These considerations suggest that for monkeys, as for humans, the category "food" is a superordinate category rather than a basic level category.

The alternative explanation we propose for why monkeys selectively attend to color information when classifying food objects is that the color-based generalization pattern for food objects results from a specialized subsystem for classifying and recognizing foods, an ecologically-significant subclass of inanimate objects that are edible, and that is shared across the primate order. On this view, the monkeys who ate or observed the eating of a food object categorized the object as edible and applied this categorization to other manipulable objects of the same color and texture irrespective of shape. It is possible that color-based generalization is specific to the category of edible objects for monkeys. Alternatively, color-based generalization may be applicable to a broader class of objects that includes other natural kinds or living kinds but excludes artifacts (see Keil et al., 1998). In either case, a domain-specific system would serve to interpret acts of eating, categorize edible objects, and guide subsequent actions toward those objects.

If our account is correct, why would a separate representational system for food objects have emerged in primate evolution? With the possible exception of breathing, eating is the most critical of all biological needs, and unlike respiration, the process of eating requires a host of goal-directed actions (foraging, selection, preparation, etc.) which animals must quickly master in order to survive (Rozin, 1990). In addition, learning to find nutritional and non-toxic foods is more than just a cognitively daunting task; it is a dangerous one. The cost of error in food selection is very high and negative evidence needed for effective learning can easily lead to death (Galef, 1988, 1990; Rozin, 1990).

In general, natural selection is likely to favor highly-constrained domain-specific systems over domain-general ones when there are high costs associated with making errors, and where the window for learning about the domain is relatively brief. In the case of food, a domain-general object recognition system that focused critically on object form would miss out on the properties that are most relevant to food selection, such as color which can signal toxicity. In addition, the costs of learning about the properties that are important for food selection are high. While organisms have the luxury to learn about categorizing most objects, the ability to generalize to new kinds of edible food items often must be learned immediately after weaning and thus without the opportunity for much experience (Rozin, 1990).

Such costly learning predicts that domain-specific categorization of food objects should begin to operate very early in ontogeny, as soon as an animal begins to forage. This pattern accords with the finding that infants systematically categorize edible objects; like adults, they generalize new food objects using the feature of color. Even though they show the adult pattern of generalization for edible objects, however, there are important differences in the types of objects infant and adults consider to be edible. Infants, unlike adults, selectively approach objects that are not eaten, but are merely manipulated. This pattern suggests that rhesus infants begin life with a broader range of objects they will consider food and gradually narrow this category as they gain more experience with the objects in their environment.

The macaques tested in this experimenter are far from naive about categorizing foods. By about 6 months of age, infant rhesus macaques begin eating many types of solid food, such as monkey chow, soil, and various plants (see Roemer & Marriott, 1982). Even before 6 months of age, a rhesus infant has had considerable opportunity to gain indirect experience about what is edible by observing its mother's foraging and feeding behavior. Because of this wealth of prior experience, it is difficult to tease apart the origins of this color-based generalization pattern for foods. Unfortunately, it is not possible to test more inexperienced infants using this current paradigm because infants younger than those tested spend the majority of their time on their mother's backs and thus cannot be tested in the kind of search experiment we have developed here.

There is similarly little work examining the development of the domain-specific food recognition system in human children (see Macario, 1991; Rozin, 1990; Rozin et al., 1986). As previously noted, children as young as 3 years of age selectively attend to the color of food objects during word learning, but children younger than toddlers have yet to be tested. Fortunately, the paradigm that we have used to test rhesus macaques can easily be applied to test human infants. Feigenson, Carey, and

Hauser (in press) have successfully tested human infants as young as 12 months of age using a crawling paradigm in which infants are allowed to crawl towards one of two boxes containing food; results show that by 1 year of age, infants selectively approach the box with more food. This type of crawling procedure could easily be adapted to questions of categorization of edible objects. Testing younger human infants, who have not had direct experience with solid foods, using a similar paradigm would be a crucial next step to test how domain-specific systems such as this are shaped by experience.

It is also important to note that organisms clearly use more than the feature of color to classify food objects. In our experiments, we controlled for the texture and smell of our objects, two features that human children use to distinguish food kinds (Lavin & Hall, 1999). It is likely that these features are used by non-human animals as well. Future research with humans and non-human animals would profit from teasing apart the influences of more complex features and their interrelationships as well.

In conclusion, we suggest that rhesus monkeys possess a domain-specific mechanism for categorizing the ecologically-significant subset of inanimate objects that are edible. This mechanism appears to be shared across the primate order, and it provides primates with an effective generalization strategy for tackling the daunting task of food selection.

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