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How Social Influences Affect Food Neophobia in Captive Chimpanzees: A Comparative Approach

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1 Introduction

Humans, chimpanzees, and capuchin monkeys are all species facing the “omnivore’s dilemma” (Rozin 1977), that is, their success depends both on the propensity to eat novel foods and on the caution to explore and sample them. On the one hand, an omnivorous species should look for novel foods to enlarge its diet, to adapt to different environments, and to overcome shortage; on the other hand, it should detect and avoid the risk of ingesting poisonous substances (Freeland and Janzen 1974; Glander 1982; Milton 1993).

Food neophobia, that is, the hesitancy to eat novel foods so that only a small amount is tasted or ingested, is often viewed as a strategy to reduce the risk of being poisoned by ingesting too-large quantities of a novel food (Barnett 1963; Freeland and Janzen 1974; Glander 1982) while learning about its toxicity by ingesting a small amount and experiencing the consequences (Garcia et al. 1955; Garcia and Koelling 1966; Matsuzawa and Hasegawa 1983; Matsuzawa et al. 1983). This behavioral trait is common to many animal species, from birds to humans (warblers, *Dendroica castanea* and *D. pensylvanica*: Greenberg 1990; rats, *Rattus norvegicus*: Barnett 1958; Galef 1970; lambs, *Ovis aries*: Burritt and Provenza 1989; Provenza et al. 1995; capuchin monkeys, *Cebus apella*: Visalberghi and Fragaszy 1995; Visalberghi, et al. 2003a; rhesus macaques, *Macaca mulatta*: Weiskrantz and Cowey 1963; Johnson 1997, 2000; bonobos, *Pan paniscus*: Kano 1992; humans, Rozin 1976). In nonhuman primates, food neophobia is usually low in infants and juveniles (tufted capuchin monkeys: Fragaszy et al. 1997; Visalberghi et al. 2003a; chimpanzees: Ueno and Matsuzawa 2005) and such age differences are also evident in humans, where 4- to 7-month-old infants are less neophobic than 2- to 5-year-old children (Sullivan and Birch 1994; Birch et al. 1998).

However, because omnivores increase their chances of survival through a varied diet, food neophobia in the long run might be maladaptive and should be overcome. In fact, in primates food neophobia is influenced by several factors, such as the type of food (tufted capuchin monkeys: Visalberghi and Fragaszy

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1995; chimpanzees: Visalberghi et al. 2002), the number of exposures to a novel food (tufted capuchin monkeys: Visalberghi et al. 1998; children: Birch and Marlin 1982; Sullivan and Birch 1990; Wardle et al. 2003), and the postingestion consequences (Japanese macaques: Matsuzawa and Hasegawa 1983; Matsuzawa 1983). Moreover, there is a large body of evidence that in nonhuman primates social influences increase the acceptance of novel foods (chacma baboons, *Papio ursinus*: Cambefort 1981; tufted capuchin monkeys: Visalberghi and Fragaszy 1995; Visalberghi et al. 1998; marmosets, *Callithrix jacchus*: Vitale and Queyras 1997; Yamamoto and Lopes 2004; Schrauf et al. 2004). Similarly, when children observe a familiar adult eating an unfamiliar food, they tend to eat more food compared to the situation in which the food is simply offered to them (Harper and Sanders 1975). Moreover, in adult humans the observation of the behavior of a model reduces food neophobia (Hobden and Pilner 1995).

Group living can be of great advantage in learning when, how, and on what to feed (Giraldeau 1997), and most research concerning social influences on feeding behavior has focused on the widely expressed view that social animals gain knowledge about food from conspecifics (Galef and Giraldeau 2001). However, it should be noted that if relying on others' eating behavior helps the individual to deal safely with novel foods, then it is mandatory that learning takes into account food specificity. For example, if artichokes are a novel food for individual A, then watching group members eating artichokes should affect A's likelihood of eating artichokes and not A's likelihood of eating beets; in other words, watching group members eating artichokes is a congruent source of information only about the safety of eating that same food, and not another one. Given this, to support the view that social influences foster a safe diet, we should reject two alternative explanations: the acceptance of a novel food increases (1) because of the mere presence of group members or (2) because group members are eating, regardless of what they are eating.

Surprisingly, only recently has the question of what exactly is learned from others about novel foods been experimentally addressed. We recently demonstrated that capuchins are more likely to eat a novel food when seeing group members eating (but not when group members are merely present) than when alone (Visalberghi and Addessi 2000, 2001; see also Addessi and Visalberghi 2001). However, this increase in acceptance occurs regardless of the color¹ of the food eaten by the group members. Therefore, at least in capuchins, the influence of group members allows an individual to overcome neophobia but not to learn that a food is safe. In contrast, children tested with a similar experimental paradigm are selectively oriented toward specific food targets, that is, they eat more of a novel food only when their food and the models' food are identical

1 (Addessi et al., in press).

The present study investigates how social influences affect neophobia and food choice in young and adult captive chimpanzees, a species more cognitively

¹To make the observer's and the demonstrators' foods look very different from one another, they were dyed two strikingly different colors.

advanced than capuchin monkeys but less so than children (Tomasello and Call 1997). Similarly to capuchin monkeys, chimpanzees adapt to a wide range of different habitats and to food seasonality (Goodall 1986; Teleki 1989; Sugiyama and Koman 1992) by exploiting a great variety of food sources. However, very little is known about how chimpanzees respond to novel foods. According to Nishida et al. (1983), wild chimpanzees are conservative and unwilling to taste novel foods, although young individuals seem more likely to do so. When Matsuzawa and Yamakoshi (1996; see also Matsuzawa 1999) provided Bossou chimpanzees with coula nuts (*Coula edulis*) in the area where they usually spend their time cracking oil-palm nuts (*Elaeis guineensis*), some chimpanzees sniffed the coula nuts, picked them up, and tried to bite them, whereas others simply ignored them. Coula nuts (whose appearance is rather different from that of oil-palm nuts) are not available in the home range of the Bossou chimpanzees but they are present in a nearby area, where the Nimba chimpanzee community lives. Only one female, probably born in the Nimba community, and therefore probably familiar with coula nuts, cracked the coula nuts open with a tool. Her behavior elicited great interest from a group of juvenile chimpanzees, some of which successfully cracked open the coula nuts in the following days.

Captive chimpanzees as well are cautious toward novel food, although in infants novel foods elicit more interest than familiar ones (Ueno and Matsuzawa 2005; see also Chapter **; for similar findings in capuchins, see Fragaszy et al. 1997; Drapier et al. 2003). In a recent experiment, eight adult chimpanzees were offered 16 novel foods (Visalberghi et al. 2002). Marked interindividual differences in food acceptance and consumption emerged, and chimpanzees ranged from being almost completely neophobic to accepting almost all foods. Moreover, to assess whether seeing the novel food eaten by a human demonstrator affects its consumption, each novel food was presented twice with the experimenter eating the food in the presence of the chimpanzee (demonstration). Although chimpanzees were always attentive to the human eating the novel food, the demonstration did not affect the acceptance of the novel foods. The negative outcome of this study could be attributed to the type of demonstrator used, namely, a human subject. In fact, a human demonstrator may lack the salience of a conspecific demonstrator (see also Whiten and Ham 1992), and a chimpanzee-human dyad is not the setting in which information about food is expected to be transferred (although for captive chimpanzees, interactions with humans are important). Therefore, in the present study we aimed to investigate whether chimpanzees learn about food safety from the behavior of their group members (as in the capuchin monkey studies; for a review see Visalberghi and Addessi 2003; Addessi and Visalberghi, in press). By increasing the salience of the visual input provided by the conspecific, we expected chimpanzees to pay attention not only to the behavior of the demonstrators but also to what they were eating and to behave accordingly. We tested this hypothesis both when the observer encountered only one food (experiment 1) and when the subject was presented with a choice between two novel foods (experiment 2), of which only one matched the color of the food eaten by the demonstrator. These two

experiments simulate rather common situations in nature (Goodall 1986). A wild chimpanzee may well encounter a novel food while her or his group members are eating the same food, a different food, or when she or he is alone. Similarly, the chimpanzee can encounter two or more novel foods while her or his group members are selectively eating only one food.

2 Experiment 1: Does the Observation of Group Members Eating Affect the Observer’s Acceptance of a Novel Food?

2.1 Methods

2.1.1 Subjects

As observers, we tested nine captive-born chimpanzees (one adult male, two adult females, two juvenile males, and four juvenile females; Table 1) living in the same group at the Wolfgang Köhler Primate Research Center/Leipzig Zoo, Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany).

They were housed in indoor–outdoor areas. The indoor area consists of an indoor enclosure (430 m²) and sleeping and observation booths (47 and 25 m², respectively). The outdoor area (4000 m²) and the indoor enclosure contain natural vegetation, climbing structures, trees, water streams, and various other natural features.

Chimpanzees were fed three times a day, and browse was provided on a regular basis. In addition, they received other foods according to seasonal availability (e.g., chestnuts); other opportunities for special foraging activities (e.g., at artificial termite mounds) were also made available on a regular basis.

Table 1. Experiment 1. Assignment of foods to the experimental conditions within each block of subjects

| | Experimental conditions | Subjects | Sex | Age (years) |
|-----------------------------|-------------------------|----------|-----|-------------|
| Experimental group 1 | | | | |
| yellow food | Alone | Robert | M | 26 |
| green food | Different color | Trudi | F | 8 |
| red food | Same color | Fifi | F | 8 |
| Experimental group 2 | | | | |
| yellow food | Same color | Ulla | F | 24 |
| green food | Alone | Frodo | M | 8 |
| red food | Different color | Jahaga | F | 8 |
| Experimental group 3 | | | | |
| yellow food | Different color | Patrick | M | 4 |
| green food | Same color | Sandra | F | 8 |
| red food | Alone | Fraukje | F | 25 |

In the “different-color” and “same-color” conditions (see following), the observer was tested with two demonstrators. All the subjects acted both as observer and as demonstrator, except one adult female who acted as observer only.

2.1.2 Apparatus

Chimpanzees were tested in two adjacent booths. Each booth had a Plexiglas window (73 cm × 60.5 cm × 2 cm) on its side through which the observer and the demonstrators could see each other. Between these two windows there was a space of 94 cm, in which a wooden table (93 cm × 78.5 cm × 44 cm) was inserted. The foods (see following) were placed on the wooden table. The observer and the demonstrators could reach the food through three holes (diameter, 6 cm; the holes were 23 cm apart from each other) made in their Plexiglas window.

2.1.3 Foods

We used three foods never previously tasted by the observers. They were colored green, red or yellow with Brauns Heitmann’s Crazy Colors food coloring (2 ml/100 g): mashed canned green peas, colored green, mashed boiled lentils, colored red, and mashed boiled beans, colored yellow; the caloric content was 285 kJ/100 g for green peas, 386 kJ/100 g for lentils, and 380 kJ/100 g for beans. Both sexes can discriminate these colors (Jacobs et al. 1996). Novel foods were blended in a food processor. They were all of similar texture and not particularly attractive to the apes.

The familiar food for the demonstrators was a mixture of peeled, boiled, and mashed potatoes and yogurt (in ratio 4:1; total, 500 g). In the same-color condition (see following) the potatoes were colored yellow, red, or green with Brauns Heitmann’s Crazy Colors food coloring (3 ml/100 g), whereas in the different-color condition the potatoes were not colored. All the subjects liked this food very much, regardless of its color.

2.1.4 Procedure

As shown in Fig. 1, there were three experimental conditions, as follows. (a) Alone: the observer was in one booth and received the novel food, while the demonstrators were not in the adjacent booth. (b) Different color: the observer was in one booth and received the novel food, while two demonstrators were in the adjacent booth and received the not-colored familiar food. The colors of the familiar and the novel food were clearly different from one another. (c) Same color: the observer was in one booth and received the novel food, while two demonstrators were in the adjacent booth and received the familiar food of the same color as the novel food. The colors of the familiar and the novel food were identical. In each condition, the observer was given 250 g novel food; in the different-color and same-color conditions, the demonstrators were given 500 g familiar food.

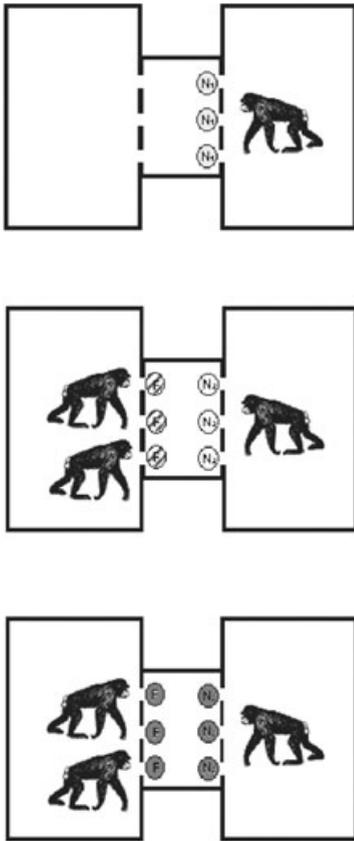


Fig. 1. The three experimental conditions of experiment 1. In the alone condition (a), the subject (on the right, in its booth) receives a novel food (*N1*) while its group members are not present in the opposite booth (on the left). In the different-color condition (b), the subject (observer, on the right) receives a novel food (*N2*), while in the opposite booth two of its group members (demonstrators) are eating a familiar food (*F*) of a color different from that of *N2*. In the same-color condition (c), the observer receives a novel food (*N3*), while its demonstrators are eating a familiar food (*F*) of the same color as *N3*

Trials were conducted at 9 a.m., 11 a.m., or 4 p.m. Chimpanzees were not food deprived; they routinely received a light meal in the early morning and in the early afternoon, so thus received this food before testing.

3 Because a food can be novel only once, we assigned each of the three foods to one of the three conditions within each block of three observers. Block 1 received the beans in the alone condition, the green peas in the different-color condition, and the lentils in the same-color condition; block 2 received the lentils in the alone condition, the beans in the different-color condition, and the green peas in the same-color condition; and block 3 received the green peas in the alone condition, the lentils in the different-color condition and the beans in the same-color condition (see Table 1). Observers belonging to each block were balanced for age and sex and these assignments were counterbalanced across observers.

We tested every observer in each of the three conditions once; presentations occurred on different test days. The order in which the three conditions were presented was counterbalanced across observers and blocks. Each session lasted 5 min and started as soon as the observer entered its booth and, in the

different-color and same-color conditions, could see the demonstrators, which were already in their booth, eating the familiar food. We carried out the experiment between December 2001 and January 2002.

2.1.5 Behaviors Scored

An experimenter scored the behavior of the observer with instantaneous sampling every 10 s, while a fixed video camera was set to record the area by the panel in the demonstrators' booth. The following observer behaviors were scored: (1) eating behavior, that is, putting food in the mouth and chewing it or chewing food already in mouth; (2) exploration, that is, sniffing the food; (3) and visual attention to the demonstrators, both when they were eating and not eating. In addition, the latency to ingestion was scored. The novel food given to the observer was weighed before and after the session to measure the amount of food eaten.

To assess the input the observer received from its demonstrators, we scored their behavior from videotapes every 10 s (at the same sample point as the observer's behavior was scored). We counted the number of demonstrators eating in the area in front of the panel.

2.1.6 Analysis

For each behavior scored, for the latency to ingestion and for the amount of food eaten, we carried out the Friedman analysis of variance (ANOVA) for comparisons across conditions and the Wilcoxon signed-ranks test for comparisons between conditions. Moreover, we used the Mann-Whitney U test to assess whether age and sex affected observers' behavior toward novel food. Given our small sample size, we used the exact variant of each statistical test.

For the different-color and the same-color conditions, we ran Spearman correlations to evaluate (1) the relationship between the average number of observers showing visual attention to the eating demonstrators at each sample point and the average number of demonstrators eating at the same sample point, and (2) the relationship between the average number of observers eating at each sample point and the average number of demonstrators eating at the same sample point.

2.2 Results

2.2.1 Behavior of the Demonstrators

Demonstrators spent most of the session eating in the area in front of the observer. In the different-color condition there was at least one demonstrator present and eating the familiar food in 96.3% of the samples. In the same-color condition, the corresponding value was 99.0%. In fact, at the end of each session, no potato leftovers were found.

2.2.2 Behavior of the Observers

Observers showed more visual attention for the demonstrators when the demonstrators were eating than when they were not eating (different-color condition: $T = 0, P < 0.05$; same-color condition: $T = 0, P < 0.05$). In both conditions, the average number of observers showing visual attention to the eating demonstrators at each sample point was correlated with the average number of demonstrators eating at the same sample point (different-color condition: $r_s = 0.42, n = 30, P < 0.05$; same-color condition: $r_s = 0.5, n = 30, P < 0.01$). Observers' visual attention to the eating demonstrators did not differ between the different-color and same-color conditions ($T = 9.5, n = 9$; NS).

Observers' behavior toward the novel food did not significantly differ across conditions (latency to ingestion: $\chi^2 = 0.97, n = 9$; NS; exploration: $\chi^2 = 1.0, n = 9$; NS; eating: $\chi^2 = 0.62, n = 9$; NS; food eaten: $\chi^2 = 0.76, n = 9$; NS). Moreover, the average number of observers eating at each sample point was not significantly correlated with the average number of demonstrators eating at the same sample point (different-color condition: $r_s = -0.32, N = 30$; NS; same-color condition: $r_s = -0.29, n = 30$; NS).

Similarly, observers' behavior did not differ across trials (exploration: $\chi^2 = 5.29, n = 9$; NS; eating: $\chi^2 = 0.83, n = 9$; NS; food eaten: $\chi^2 = 0.06, n = 9$; NS), the only exception being latency to ingestion ($\chi^2 = 6.61, n = 9; P < 0.05$). In particular, it was significantly shorter in trial 3 than in trial 2 ($T = 0, P < 0.05$). Further analysis showed that this was the result of an age difference; in particular, in the third trial, juveniles showed a shorter latency to ingestion than adults ($U = 1.0, n_1 = 3, n_2 = 6; P < 0.05$). In the alone condition, age significantly affected also eating behavior and food eaten, with the juveniles eating and ingesting more novel food than the adults (eating behavior: $U = 1.5, n_1 = 3, n_2 = 6; P < 0.05$; food eaten: $U = 1.0, n_1 = 3, n_2 = 6; P < 0.05$). Sex did not significantly affect observers' behavior.

3 Experiment 2: Do Social Influences Affect the Observer's Choice Between Differently Colored Novel Food?

3.1 Methods

3.1.1 Subjects

As observers, we tested eight captive-born chimpanzees, the same subjects as in experiment 1, except for the alpha male. Each observer was tested with one demonstrator, and all the subjects acted both as observer and as demonstrator.

3.1.2 Apparatus

The experiment took place in the same booths as in experiment 1. All features of the apparatus were as described in experiment 1.

3.1.3 Foods

As novel food for the observer, we used mashed boiled chickpeas, a food never previously tasted by the subjects. The caloric content was 417 kJ/100 g. According to the experimental group (Table 2), it was colored brown and violet or orange and blue with Brauns Heitmann's Crazy Colors food coloring (4 ml/100 g). Both sexes discriminate these colors (Jacobs et al. 1996). Novel foods were blended in a food processor. They were all of similar texture and not particularly attractive to the apes.

The familiar food for the demonstrators was a mixture of peeled, boiled, and mashed potatoes and yogurt (in ratio 4 : 1; total, 500 g). According to the experimental group (see following), it was colored brown, violet, orange, or blue with Brauns Heitmann's Crazy Colors food coloring (4 ml/100 g).

3.1.4 Procedure

The observer was in one booth and received chickpeas colored brown and violet or orange and blue, according to the experimental group. The demonstrator was in the adjacent booth and received potatoes colored brown, violet, orange, or blue, according to the experimental group (see Table 2). The observer was given 125 g each novel food; the demonstrator was given 250 g familiar food. In a session, the observer had simultaneous access to chickpeas whose color matched the color of the food eaten by the demonstrator (hereafter called "matching-color food") and to chickpeas whose color did not match the color of the food eaten by the demonstrator (hereafter called "nonmatching-color food") (Figs. 2, 3).

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We divided the eight subjects into four experimental groups ($n = 2$ each) and assigned each group to one matching color. Experimental group 1 had access to brown and violet chickpeas while the demonstrator was given brown potatoes; experimental group 2 had access to brown and violet chickpeas while the demonstrator was given violet potatoes; experimental group 3 had access to orange and blue chickpeas while the demonstrator was given orange potatoes;

Table 2. Experiment 2. Assignment of the observers to the experimental groups

| Observers | Colors of the observer's novel foods | Experimental groups (defined by the color of the food eaten by the demonstrator) |
|-----------|--------------------------------------|--|
| Fraukje | Brown-Violet | Brown |
| Fifi | Brown-Violet | Brown |
| Sandra | Brown-Violet | Violet |
| Patrick | Brown-Violet | Violet |
| Ulla | Orange-Blue | Orange |
| Jahaga | Orange-Blue | Orange |
| Trudi | Orange-Blue | Blue |
| Frodo | Orange-Blue | Blue |



Fig. 2. Experiment 1. Demonstrators are eating the familiar food, positioned on the table in front of the holes present in their window

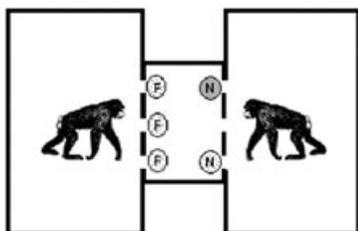


Fig. 3. Experiment 2. The observer (on the *right*, in its booth) receives a novel food of two different colors, while its demonstrator (on the *left*, in its booth) is eating a familiar food whose color matches the color of one of the two observer's foods

experimental group 4 had access to orange and blue chickpeas while the demonstrator was given blue potatoes (see Table 2). The position of the colored chickpeas was counterbalanced across subjects.

We tested every subject once. The session lasted 5 min and started as soon as the observer entered its booth and could see the demonstrator, already in her/his booth eating the familiar food. We carried out the experiment in January 2002.

3.1.5 Behaviors Scored

Behaviors scored were the same as in experiment 1. In addition, we scored the first choice of the observer, that is, which of the two foods the observer chose first.

3.1.6 Analysis

For each behavior scored, for the latency to ingestion and for the amount of food eaten, we carried out the Wilcoxon signed-ranks test for comparing the behavior between the matching-color food and the nonmatching-color food. As in experiment 1, we used the Mann–Whitney U test to assess whether age and sex affected observers' behavior toward novel food. Moreover, we ran Spearman correlations to evaluate (1) the relationship between the average number of

observers showing visual attention to the eating demonstrators at each sample point and the average number of demonstrators eating at the same sample point, and (2) the relationship between the average number of observers eating the matching-color food or the nonmatching-color food at each sample point and the average number of demonstrators eating at the same sample point. Given our small sample size, we used the exact variant of each statistical test.

3.2 Results

3.2.1 Behavior of the Demonstrators

As in experiment 1, demonstrators gave to the observers the input requested by the experimental design and they ate in front of the observer in 99.6% of the sample points, on average.

3.2.2 Behavior of the Observers

Observers showed more visual attention for the demonstrators when the demonstrators were eating than when they were not eating ($T = 2.0$, $n = 8$; $P < 0.05$). However, the average number of observers showing visual attention to the eating demonstrators at each sample point was not significantly correlated with the average number of demonstrators eating at the same sample point ($r_s = 0.12$, $n = 30$; NS).

Observers' behavior toward the novel food did not significantly differ between the matching-color food and the nonmatching-color food (latency to ingestion: $T = 16.0$, $n = 8$; NS; exploration: $T = 0$, $n = 8$; NS; eating: $T = 10.0$, $n = 8$; NS; food eaten: $T = 13.0$, $n = 8$; NS) and the number of times in which the observers chose to eat first the matching-color food rather than the nonmatching-color food first was equal. The average number of observers eating at each sample point was not correlated with the average number of demonstrators eating at the same sample point (matching-color food: $r_s = 0.25$, $n = 30$; NS; nonmatching-color food: $r_s = 0.10$, $n = 30$; NS). Age and sex did not significantly affect observers' eating behavior.

4 Discussion

Chimpanzees eagerly ate the familiar food given to them when they played the role of demonstrators. In addition, we never witnessed a case in which they did not accept and eat a familiar food. Therefore, although we lack a control condition in which each observer is individually presented with familiar food, we can argue that captive chimpanzees are cautious toward novel food (see also Visalberghi et al. 2002). Moreover, in the absence of group members young chimpanzees are less neophobic than adults, which in agreement with the observation that infant chimpanzees are more interested in novel foods than in familiar ones (Ueno and Matsuzawa 2005; see also Chapter ••). Therefore, age seems to

affect food neophobia in chimpanzees, as it does in capuchin monkeys both in captivity (Fragaszy et al. 1997) and in the wild (Visalberghi et al. 2003a). According to Janson and van Schaik (1993), age differences in neophobia are the result of the youngsters' low foraging efficiency and great risk of starvation, which makes them willing to try new food. Many years ago, Itani (1958) had argued that by being more explorative young individuals might discover food sources or feeding strategies not yet exploited by their group members.

Regardless of age, chimpanzees having group members as demonstrators were not more inclined to accept novel foods or to choose a food matching in color the demonstrator's food. Surprisingly, this lack of social influence occurs despite the demonstrators eating and the observers monitoring with attention the demonstrators' behavior and food choice. Chimpanzees behaved differently from both children and capuchins. Preschool children tested with a similar paradigm were socially facilitated only when their food matched the food of the demonstrator; that is, they were sensitive to what the demonstrator was eating (Addessi et al., in press). Capuchin monkeys accepted and ate novel foods more when facing group members eating than when alone, even if social facilitation of eating (i.e., the increased likelihood to eat when somebody else is eating; see also Clayton 1978) occurred regardless of what the demonstrators were eating (for a review, see Visalberghi and Addessi 2003; Addessi and Visalberghi, in press). In other words, in children social influences might serve to learn about a safe diet, whereas in capuchin they serve to reduce neophobia without necessarily leading to a safe diet.

Overall our experiments with chimpanzees led to negative results, which by itself is unfortunate. However, we can rule out the possibilities that a poor experimental design and/or a small sample size accounted for the lack of the significance of most results. In fact, in other primate species the same paradigm has been successful (Visalberghi and Addessi 2003; Addessi and Visalberghi, in press; Addessi et al., in press). Then, how can we explain our results? First, it is possible that social facilitation of eating behavior necessitates the subjects to be hungry; this was certainly not the case in our present experiment, as well as in our previous ones, because our subjects were never food deprived before testing. However, individuals of other species did not need to be hungry for social facilitation of eating to occur. Therefore, this hypothesis is unlikely as well as impossible to test for ethical reasons. Second, captive chimpanzees might be prone to accept any food either because they are rarely, if ever, faced with potentially poisonous substances or because they do not distinguish novel from familiar foods. The behavior of our subjects did not support this second claim. Chimpanzees were cautious toward novel foods despite being in captivity (see also Visalberghi et al. 2002) and clearly treated them very differently from the familiar food they received as demonstrators. A third possibility is that eating behavior was socially facilitated and that chimpanzees inhibit such response, regardless of the type of food eaten by the demonstrator. This hypothesis is very speculative but worthwhile discussing because it allows us to interpret our data within a comparative framework.

In macaques, the observation of actions related to eating behavior activates motor representations similar to those observed. The basic mechanism underlying this phenomenon has to do with a class of visuomotor neurons, named mirror neurons, found in the macaque's premotor and parietal cortex (Gallese et al. 1996, 2002; Fogassi et al. 2005). The mirror neurons become active both when the monkey makes a specific action with its hand (or mouth) and when the monkey observes similar hand (or mouth) actions performed by another individual. Several brain imaging studies support the existence of a mirror system in humans involving the frontal and parietal areas, which are homologous to those in which mirror neurons have been found in macaques (see Rizzolatti et al. 2001). Other evidence in support of the existence of this system in humans derives from transcranial magnetic stimulation (TMS). By using this technique it has been shown that the observation of others' actions increases motor corticospinal excitability measured from various arm, hand, and mouth muscles (see Fadiga et al. 2005 for a review).

Based on the properties of mirror neurons, it was suggested that they are part of a neural system implicated in the process of action recognition, in which the visual description of an action is matched with its motor outcome (Gallese et al. 1996; Rizzolatti et al. 2001). More recently, Ferrari et al. (2005) argued that mirror neurons could be also involved in the process of response facilitation, that is, the repetition of an observed action already part of the observer's motor repertoire (as, for example, eating behavior). The property of mirror neurons to couple observed and executed actions would be suitable to allow them to participate in the response facilitation phenomenon by means of a "resonance" mechanism in which the motor system of the observer is activated specifically by observing others' actions. Evidence that this may occur derives from the TMS studied already mentioned in which action observation may increase the excitability of the corticospinal tract as a consequence of the enhancement of the motor cortex excitability.

However, with the exception of very few behaviors recently described (e.g., eating behavior; see Ferrari et al. 2005), the observation of others' behavior in primates, although this activates motor representation in the premotor cortex, does not lead to overt movement. This apparent discrepancy between neurophysiological data and behavioral data can be partly explained by the fact that during action observation the modulation pattern of corticospinal excitability can be suppressed at the spinal level, as recently demonstrated in humans using TMS (Baldissera et al. 2001; Fadiga et al. 2005). This effect has been interpreted as the expression of a mechanism serving to block overt execution of seen actions. In humans it is likely that inhibition mechanisms suppressing overt movement during action observation could involve cortical frontal areas. Support for this point comes from patients suffering from lesions in cortical frontal regions of the brain. Patients with this lesions (echopraxia) repeat automatically any action seen made by another individual, without any possibility of inhibiting repetition (Dromard 1905; Stengel et al. 1947; Lhermitte et al. 1986); it has been proposed that this uncontrolled repetition probably occurs because

of a lack of inhibition at the level of the mirror system (see Rizzolatti et al. 1999). It is also possible that during development this inhibitory system require months to be fully developed. Thus, some behavioral phenomena in infants, such as the repetition of mouth movements after having observed them in adults (i.e., newborn imitation; Meltzoff and Moore 1977) could reflect this phenomenon.

Given the foregoing findings, it can be hypothesized that capuchins, chimpanzees, and humans differ in their capability to inhibit responses, with capuchins being unable to inhibit facilitated eating responses, chimpanzees being capable of inhibiting facilitated eating responses but incapable of selective inhibition, and, finally, young children being capable of selective inhibition. Future research should better investigate whether selective inhibition is affected by neuroanatomical–neurophysiological complexity and the extent to which different primate species (and individuals of different age) are able to selectively inhibit facilitated eating responses.

Finally, the following three questions still remain to be answered. (i) How can nonhuman primates learn so little by watching the behavior of others but still learn what to eat and what not to eat? (ii) How can they detect and avoid noxious foods? (iii) Why is there a strong convergence on what the individuals in a group feed on? The flavor and nutrient content of foods play an important role in determining individual choices and preferences (Simmen and Hladik 1998; Laska et al. 2000; Hladik et al. 2002; Visalberghi et al. 2003b). Taste perception provides an immediate and powerful feedback, allowing assessment of food quality (Dominy et al. 2001). Primates dislike bitter flavors, which are associated with the presence of secondary compounds (such as alkaloids and glycosides) and that can cause severe illness or even have lethal effects (Freeland and Janzen 1974; Ueno 2001). Conversely, all primate species tested so far readily accept sugars, a very important energy source (Glaser 1993). Both in human and in non-human primates, acceptance and rejection responses are evident already in newborns, before experiencing any consequences from the ingestion of sweet or bitter substances (gustofacial reflex; Steiner and Glaser 1984; Ueno et al. 2004).

However, taste perception is not always a reliable cue for selecting what to eat and what to avoid; in fact, some substances, as for example the lethal alkaloid dioscorine, are almost tasteless (Hladik and Simmen 1996). Therefore, it is not surprising that an additional system comes into play. Nutrients and/or toxic compounds provide a feedback that animals are able to associate with the sensory properties of the food, and the metabolic consequences of eating a food efficiently directs animals' future food selection (Forbes 2001). A recent study demonstrated that after a few encounters with novel foods capuchins preferred those with a high sugar content (which is readily perceived through taste). Nevertheless, if capuchins keep encountering these same foods, their preferences become correlated with the foods' energy content. Therefore, after experiencing the consequences of ingesting the novel foods, capuchins responded to the feedback coming from the foods' energy content, and by doing so they maximize the net gain of energy (Visalberghi et al. 2003b). Similarly, preschool children learn to prefer food with a high caloric content over food with a low caloric content

and use different flavors as immediate cues to distinguish foods (Birch et al. 1990).

Nevertheless, although the individual's physiology and behavior have an important role in determining diet acquisition, proximity to more knowledgeable individuals, interest in their activities, and/or opportunity to take food remains from them may foster occasions for experiencing what they eat (for a discussion, see Fragaszy and Visalberghi 2004; for a similar view in chimpanzee mother-infant pairs, Ueno and Matsuzawa 2004; see also Matsuzawa et al. 2001). Moreover, behavioral coordination, that is, the tendency to coordinate activities in space and time with those performed by group members (Coussi-Korbel and Fragaszy 1995), increases the individual's chance to engage in the same activities as its group members and thus serves as a simple and powerful social bias on individual learning.

In conclusion, these findings warn us to believe "by default" that the social context is crucial for the acquisition of a safe diet. Taste perception, a neophobic tendency toward unknown foods, and conditioned aversions and preferences seem very helpful in enabling the individual to select an adequate diet and efficiently reduce the risk of making fatal mistakes. However, group members' presence and behavior bias the individual's learning opportunities, and the combination of social facilitation, local enhancement, and stimulus enhancement does increase the chances that the food choices of a naïve individual will be canalized toward those of its group members.

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