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NEWS AND PERSPECTIVES

Reactions to novel objects in monkeys: what does it mean to be neophobic?

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Abstract
Animals' reactions to novel objects vary not only with zoological taxa and their ecology but also in the types of presented stimuli, the context, and individual characteristics. Behavioral reactions can vary from extremely neophobic (avoiding novel objects) to extremely neophilic (intense exploration of novel objects); most often, a mixture of these behavioral patterns appears. In primates, reactions toward novel objects vary according to species, age, sex, population, and the types of objects. Most experiments in this field have used a free exploration design with food or non-food objects. Here, we tested the reactions of captive male rhesus macaques using various stimuli, motivation levels, rewards, and time limits. We found that the monkeys explored and manipulated novel objects in various contexts, with little evidence of a neophobic response; however, environment, types of stimuli, and other parameters of the test can significantly affect monkeys' reactions.

Keywords Novelty response · Exploration · Neophobia · Neophilia · Rhesus macaque (*Macaca mulatta)*

Introduction

Humans and animals are often confronted with unfamiliar objects, food, and situations. Their reactions vary across species and individuals, as a function of situational variables such as the context of the experiment, the type of stimuli, and personality or motivation of the individual. Variations may also be related to species' ecology and ethology (e.g., Day et al. 2003; Addessi et al. 2007; Gustafsson et al. 2014), and sex and age differences (e.g., Menzel 1966; Visalberghi 1988; Visalberghi et al. 2003). Moreover, reactions may be influenced by individual experiences (Jones 1986) or social hierarchical position (e.g., Chamove 1983).

A novel object might elicit a neophobic or neophilic reaction, or a mixture of both (Russell 1973). Neophobia can be described as heightened alertness, suspicious, or even fearful behavior, while neophilia refers to curiosity and a spontaneous attraction towards a novel object, environment, or food (Greenberg and Mettke-Hofmann 2001). At first sight, neophobia and neophilia can be seen as opposite poles of the same axis. The Halliday–Lester theory proposes a common origin for both these reactions—fear (Lester 1967; Russell 1973 for summary). Depending on its level, fear can initiate curiosity and approach (low-level fear), or anxiety and avoidance (high-level fear). The alternative "two-factor" theory suggests that novelty can lead to both curiosity and fear. The displayed reaction results from competition between these two motivations (Russell 1973; Fu et al. 2013; Sabbatini et al. 2007). However, it is not always easy to identify an individual's motivation, as the same behavioral pattern (e.g., approaching or manipulating an object) may

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be motivated by both curiosity and fear. Some authors distinguish between explorative behavior (curiosity)—when an animal approaches and explores a novel object presented in a neutral location and context, and neophobia—when a novel object is placed near food and the animal has to approach it (e.g., Exnerova et al. 2015; Mettke-Hofmann et al. 2002).

Reactions toward novelty may also be affected by species' food-related behavior. For example, the wide geographic distribution of rhesus macaques—a predominantly frugivorous omnivore—means that the diet of subpopulations is likely to vary. One might predict that rhesus feeding behavior would be either less neophobic than that of more highly specialized species (the neophobia threshold hypothesis) or more neophobic, due to conditioned taste aversion. Interestingly, field and laboratory studies of rhesus and other macaques have found evidence of neophobia towards novel food (Itani 1958; Kawai 1960; Weiskrantz and Cowey 1963; Johnson 2000a), even when food is in short supply (Kawai 1960), but also neophilia towards novel food sources, as in a translocated group that was starving due to a lack of provisioned food (Fedigan and Asquith 1991). Food neophilia was present in corral-housed rhesus macaques but not in a semi-free island population (Johnson 2000b).

In macaques, reactions to novelty have been studied mainly with food (Hikami et al. 1990; Johnson 2000a, b, 2007; Santos et al. 2001; Weiskrantz and Cowey 1963). Some studies have tested preferences for novel non-food objects, but mostly focused on neuronal and physiological mechanisms; relatively little is known about intact animals (Drea 1998; Kinnally et al. 2008; Menzel 1966). In primates more generally, few studies have used different methods with the same subjects. Some have presented food with or without non-food stimuli (Sabbatini et al. 2007), or used food motivation in non-food experiments (Day et al. 2003; Kendal et al. 2005). New World primates have been especially studied, including marmosets and tufted capuchins (*Sapajus apella*) (Byrne and Suomi 1996; Visalberghi et al. 2003). To our knowledge, only one study has tested Old World monkeys (chacma baboons, *Papio ursinus*), in a study of their reactions toward both food and non-food (predator) stimuli (Carter et al. 2012).

Here, we tested reactions to novelty in rhesus macaques (*Macaca mulatta*) in various contexts, manipulating the types of stimuli, motivation level, and time limits. We tested whether different procedures would lead to different reactions in the subjects (i.e., different levels of neophobia/neophilia). We also assessed individual differences. We believe this is the first study of reactions of single individuals in multiple contexts.

Methods

We tested rhesus macaques (*Macaca mulatta*) in two types of experimental settings, namely free exploration and two-choice tests. In the free exploration tests, both food and non-food objects were placed inside the monkey's home cage, but not in the regular feeding place. In the two-choice tests, both food and non-food objects were placed for a limited time on a platform outside the home cage, within the monkey's reach. The food and non-food objects were paired only with objects of the same category.

Subjects

The subjects were four male rhesus macaques (*Macaca mulatta*), two adults (10 years old) and two subadult/young adults (4 years). At the beginning of the experiments, they were housed in pairs in indoor cages with visual, auditory, and olfactory contact with the other pair. During these experiments, the housing consisted of two connected cages for each pair ($124 \times 142 \times 260$ cm and $200 \times 100 \times 260$ cm; $150 \times 110 \times 260$ cm and $180 \times 86 \times 260$ cm), furnished with shelves and swings; various enrichment objects were occasionally placed in the cages. Their diet consisted of standardized granulated feed with daily supplements of fresh fruit and vegetables, and free access to water. During the experiments, the monkeys had free access to water, and food was offered after each experimental session. The older monkeys had experience of various cognitive tasks (touch screen spatial-cognition tasks, object permanence; Nekovarova et al. 2006, 2009, 2013; Nedvidek et al. 2008); the younger monkeys had participated only in object permanence tests.

Free exploration tests

In the free exploration object/food test, the monkeys were presented with novel objects or food in their home cages (online supplementary materials, Table Sup. 3). The object experiment consisted of six sessions, and the food experiment consisted of two parts, each with six sessions. In each session, one novel object or food was presented.

Stimuli

The objects varied in shape and color. We used durable objects that would survive manipulation by the monkeys, such as baby and dog toys, and common household objects. In each session, the object was placed on the floor of the cage by a familiar experimenter. The food stimuli were divided into two categories: (1) high protein/fat and (2) high saccharide (carbohydrate-rich foods; fruit). In each session, the food was placed in a familiar bowl on the floor of the cage by the experimenter. The amount of food presented was the same for each monkey.

Procedure

In both free exploration object and food tests, the monkeys were tested while temporarily isolated in their home cages. The other monkeys were in the same room, with limited visual contact, and occupied by other enrichments. For the food test, the high-protein foods were presented first, for six consecutive days, followed by the high-saccharide foods, presented in the same way. Every free exploration session was video recorded and the first 15 min was analyzed from the moment the object or bowl was placed in the cage.

Two-choice tests

In the two-choice tests, the monkeys could choose spontaneously from two objects placed outside the home cage. In contrast to the free exploration tests, there was a time limit for making a choice (30 s). We used both food and non-food objects, always in same-category pairs. In the non-food tests, monkeys could choose between two cups, each of which covered a small piece of the same food to maintain motivation to manipulate them (Table Sup. 3); thus, the monkey received the same food whether it chose a novel cup or a familiar one.

In each of the 12 sessions, we presented one novel and one familiar cup, for 12 consecutive trials. The “novel” cup from one session became the “familiar cup” in the following session, paired with another novel cup. We used two sets of seven cups. When starting with each set, as the familiar cup we used one that had been used in extensive previous testing on object permanence.

The two-choice food tests were similar to the two-choice non-food tests, but used food instead of cups. Two same-sized pieces of food, one familiar and one novel, were presented (Table Sup. 3), fully visible to the monkey. We conducted six sessions of 12 trials each.

Stimuli

The objects in the non-food tests were plastic or paper cups (8 cm diameter) covered with material differing markedly in texture and color (paper, plastic, textile, fabric, sisal rope, aluminium foil, etc.) (see supplementary materials: Graphics Sup. 1). Three categories of food were used in the food tests: (1) high-protein (2) high-fat, and (3) high-saccharide, with each category represented by three different types of food. Each food stimulus was visually distinctive from the other types of same-category food. We also controlled for the predominance of one nutritional component (fat, saccharides, and proteins) and a relatively low content of the other two nutritional components. The high-fat food category consisted of almonds, avocado, and coconut. The high-protein category consisted of egg white, turkey ham, and tofu. The high-saccharide category consisted of pear, mango, and fig. However, as the data analysis revealed no behavioral differences in relation to food category, we present only the results concerning food vs. non-food objects.

Procedure

All monkeys were tested individually in their home cages. Before the start of testing, we attached a horizontal wooden desk to the outside of the cage for presenting the stimuli so that monkeys could easily reach and manipulate them. For the food tests, we first familiarized the monkeys with one type of food from each category by giving them a sample (repeatedly in small pieces) 3 days prior to the whole experiment; those samples were also given to the monkeys 1 day before testing of each category. During trials, only foods from one category were presented together, to avoid preferences based on different macronutrient content. The order of the tests was high-fat, followed by high-protein, and finally high-saccharide food.

Analysis

In the free exploration test, we analyzed “time to approach”, i.e., time elapsed from when an object was presented until the monkey approached it to within reach, and “time to manipulation”, defined as the time elapsed until the monkey grabbed the object. We also analyzed “time between approach and manipulation”, defined as the interval between when the object was approached until it was touched. In the two-choice test, we analyzed the percentage of choices of novel objects. We also analyzed the number of sessions in which the novel object was chosen at least once, and the number of sessions in which the novel object was chosen in the first trial.

To analyze the effect of object type (food vs. non-food) in the free exploration tests, we used a non-parametric Wilcoxon test, with p values adjusted according to the Holm–Bonferroni correction for multiple comparisons. For analysis in the free exploration tests and the two-choice tests, we used logistic regression. We used R-project version 3.0.0 (2013-04-03)—“Masked Marvel” Copyright (C) 2013 The R Foundation for Statistical Computing Platform: i386-w64-mingw32/i386 (32-bit) and other versions of R-project.

Results

Free exploration tests

The means, medians, and neophilia ranking for each subject in the parameters analyzed in the free exploration and two-choice tests are shown in the online supplementary materials (Table Sup. 1 and Table Sup. 2).

In the free exploration tests, the monkeys showed interested in the objects, approaching and visually exploring them in all sessions, although monkey Puck (a submissive male) did not approach one non-food item. Time to approach was less than 1.25 min in 90% of the sessions. In only three sessions out of 68 (4.4%), approaching the object occurred after 4 min, and in one session (1.5%) the object was not approached at all (by monkey Puck).

There were two types of presented objects: non-food objects and food items. The latter had two subcategories: protein-rich food items and carbohydrate-rich food items. The upper plot in Fig. 1 shows approach latencies for each monkey and for each object type. The monkeys approached food and non-food items with similar latencies, except that Puck was slower to approach non-food objects than the food items (Wilcoxon rank-sum test performed separately for each monkey: Puck: $W=1$, $p<0.009$; Attila: $W=37$, $p=0.40$; Dante: $W=28$, $p=0.87$; Vergilius: $W=27$, $p=0.87$). No differences were found between the two categories of food items.

After a monkey approached an object, it either grasped the object (in 77.6% of the sessions) or did not touch it, exploring only visually (in 22.4% of the sessions). The probability of touching and manipulating was different for food- and non-food items (Table Sup. 4). The monkeys touched food items (83.4%) significantly more frequently than non-food objects (63.6%). The logistic regression with the factors "object type" and "monkey" showed an effect of "object type" [$\chi^2_{(1)}=4.03$, $p<0.045$], but not "monkey", or an interaction ["monkey": $\chi^2_{(3)}=6.67$, $p>0.083$; interaction: $\chi^2_{(3)}=1.92$, $p>0.58$]. In the case of the food objects, the monkeys manipulated the saccharide foods more frequently than the protein foods ["object type": $\chi^2_{(1)}=12.70$, $p<0.001$].

Any touching of the object occurred shortly after approach (Table Sup. 5). In 63.5% of sessions, the object was touched within 1 s, and in 90% of sessions, within 13 s. The longest latency was 1 min 51 s (by Vergilius, a submissive male). The bottom plot in Fig. 1 shows the individual differences in time between approach and manipulation. When the monkey Attila touched an object, it was always within 1 s of approaching it. The other monkeys frequently visually explored the objects before touching them. To see whether some object types were touched earlier than others, we compared sessions in which the object was touched in the first second after approach vs. later. Table Sup. 5 shows the percentages of the sessions in which the object was touched in the first second. The logistic regression with the factors "object type" and "monkey" showed an effect of "monkey" [$\chi^2_{(3)}=20.28$, $p<0.0001$] but not "object type" [$\chi^2_{(1)}=0.07$, $p>0.79$], and no interaction [$\chi^2_{(3)}=1.03$, $p>0.79$]. Concerning food objects, the effect of "monkey" was also significant [$\chi^2_{(3)}=20.78$, $p<0.0001$], but there was no effect of "object type" [$\chi^2_{(1)}=1.77$, $p>0.18$] or interaction [$\chi^2_{(3)}=3.87$, $p>0.27$].

Two-choice tests

In the two-choice tests, the monkeys selected the novel object at least once in 82.2% of the sessions. Table Sup. 6 shows the percentages of the sessions in which the novel object

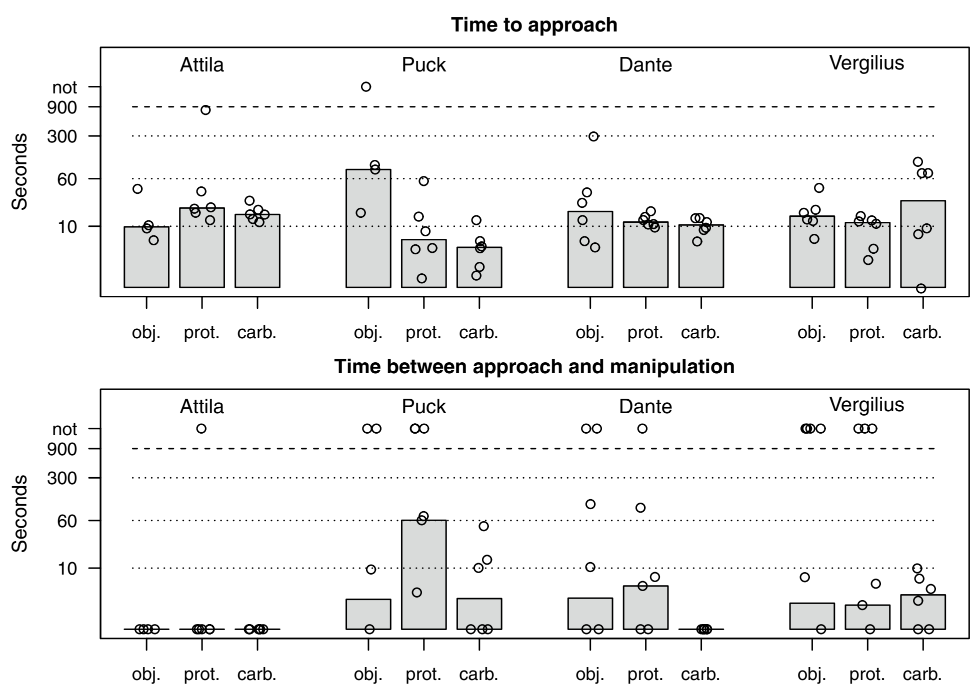

Fig. 1 Free exploration tests. "Time to approach": time elapsed from when an object was presented until the monkey approached it. "Time between approach and manipulation": time elapsed from when the object was approached until it was touched. "not" denotes not approached in the upper plot and not manipulated in the bottom plot. The bars represent medians calculated only from sessions in which the objects were approached (upper plot) or were manipulated (bottom plot). *Obj.* non-food objects, *Prot.* protein-rich food items, *Carb.* carbohydrate-rich food items

was chosen for each monkey and for object type. The monkeys picked up the novel food items (95.8%) significantly more frequently than the novel non-food items (75.5%). The logistic regression with factors "object type" and "monkey" showed an effect of "object type" [$\chi^2_{(1)} = 63.87$, $p < 0.019$] but not "monkey" [$\chi^2_{(3)} = 57.18$, $p > 0.12$], and no interaction [$\chi^2_{(3)} = 53.40$, $p > 0.28$].

When the novel object was chosen during the sessions, it occurred most frequently in the first trial (Fig. 2, and Table Sup. 7). The percentages ranged from 44.4% for Dante and Vergilius to 68.4% for Puck and between the two object types from 49.0% for non-food items to 58.3% for food items. The logistic regression with factors "object type" and "monkeys" showed no effect of either factor, and no interaction ["object type": $\chi^2_{(1)} = 0.57$, $p > 0.45$; "monkey": $\chi^2_{(3)} = 3.03$, $p > 0.38$; interaction: $\chi^2_{(3)} = 4.03$, $p > 0.25$].

Discussion

In the present study, we tested the reactions of rhesus macaques to novel objects using various type of stimuli, different time limits, and motivation levels of the monkeys. We used two experimental settings: free exploration and a two-choice experiment, each with food and non-food objects. In the free exploration tests, the objects were presented in sequence, separately—one object per session, whereas in the two-choice tests two objects of the same type (familiar vs. novel) were presented simultaneously in one session.

We found that the monkeys generally explored and manipulated novel objects; we found no clear evidence of a neophobic response. However, the context of object presentation and types of the stimuli used, along with the monkeys' motivation, individual experience, and personality may significantly affect the reactions observed. Thus, neophobia/neophilia is not one stable individual characteristic; it may differ in individuals in various contexts—e.g., concerning food or non-food. Moreover, the types of behavioral parameters used to assess neophobic or neophilic behavior (e.g., time to approach or time to manipulate with an object) may also vary among individuals.

When the behavior of all subjects was analyzed together, the monkeys were generally interested in novel objects, both in free exploration and the two-choice experiment. This finding agrees with previous studies showing neophilic behavior in captive primates (e.g., Forss et al. 2015; Gustafsson et al. 2011; Hardus et al. 2015; Visalberghi and Fragaszy 1995; Visalberghi et al. 2002 for differences between captive and wild populations), although we also found differences across experiments. In the free exploration tests, approach time was very short in most of the sessions for all types of stimuli, which may also suggest a limited neophobic reaction. However, the probability and latency touching the objects differed depending on the stimuli presented, (food

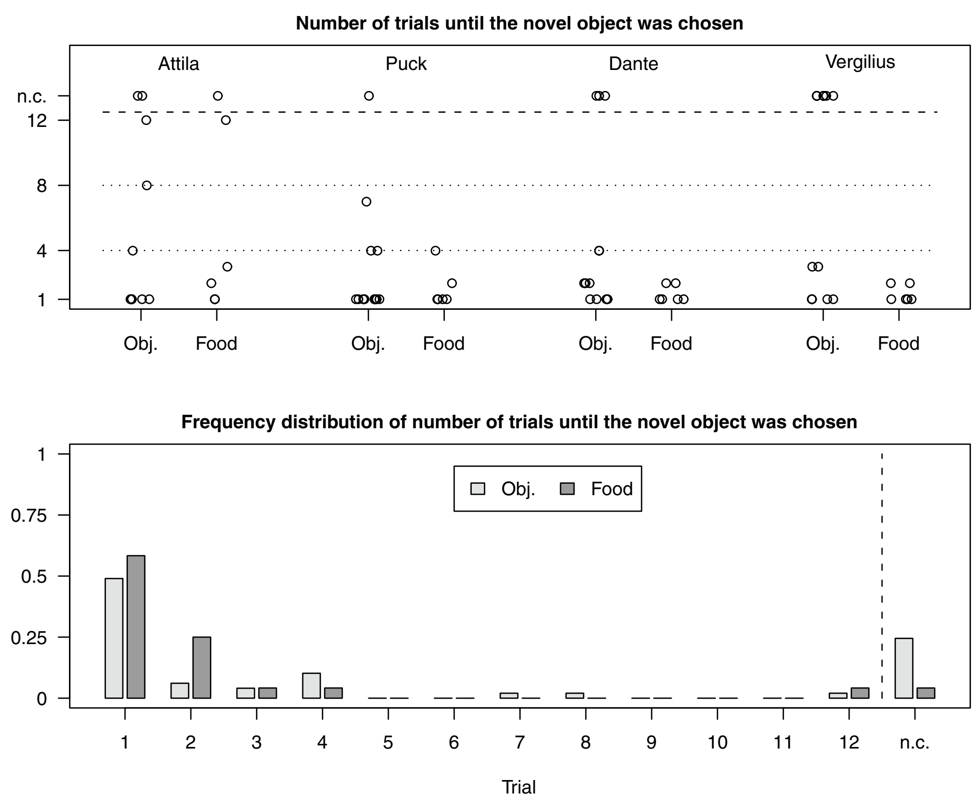

Fig. 2 Two-choice tests. The number of trials in the session until the novel object was chosen and the frequency distribution of the number of trials until the novel object was chosen. *n.c.* not chosen

vs. non-food, and also different food objects), and also in individual monkeys.

After initial exploration, the monkeys were more likely to manipulate and taste the saccharide food than the protein food or non-food objects. This strongly suggests that nutritional content influences the food preferences of primates (with a preference for sweet food), as Laska (2001) and Glaser et al. (1996) confirmed, not only in macaques.

In the two-choice tests, the monkeys selected the novel object at least once in 82.2% of sessions. As in the free exploration test, there were also significant differences in reactions towards different types of stimuli. The level of neophilia was also higher for food stimuli, with three of the four monkeys choosing the novel food at least once in each session. Although approach times for the novel food stimuli were similar to those for non-food objects in the free exploration tests, food stimuli were touched or picked up more frequently in both the free exploration and two-choice tests.

Reactions towards novel food or non-food objects may differ markedly in many species (e.g., wild rats: e.g., Barnett 1958; Meddock and Osborn 1968, also monkeys: Sabbatini et al. 2007; Visalberghi et al. 2003). Neophobia towards novel foods is often present in wild macaques (Itani 1958; Kawai 1960; Johnson 2000a, b), but less so in captive macaques (Weiskrantz and Cowey 1963), (but see Fedigan and Asquith 1991 for a wild reintroduced group). In captive macaques, neophilic reactions towards food predominate (Johnson 2000b, 2007), which was also suggested by our results. Unlike wild populations, our captive macaques routinely receive novel foods from caregivers, they have not had food aversion experiences, and have never suffered from food poisoning. In the wild, stimulus generalization can lead to food neophobia after repeated exposure to unpalatable or toxic foods (Johnson 2000a). Moreover, the fact that we tested monkeys in their familiar environment (home cages) likely decreased the level of stress, and hence neophobic reactions ("learned safety").

To summarize, our results indicate an important effect of the types of object used in tests of reactions to novelty, as we found significant differences in rhesus monkeys' behavioral reactions to various object types (food x non-food) in two separate experiments. Our findings also emphasize the need to properly select the experimental settings and behavioral measurements for analysis even within a single experiment. Such considerations probably extend beyond behavioral experiments to include physiological research and other projects.

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