SHORT-TERM LEARNING OF OLFACTORY DISCRIMINATION TASKS IN COTTON-TOP TAMARINS (*SAGUINUS OEDIPUS*)

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Abstract

After years of near absence from the literature, olfaction is finally beginning to be recognized to have an important role in primate feeding ecology. Yet even though it is already clear that primates' olfactory acuity is higher than previously thought, it is still unclear upon which parameters of the olfactory system selection pressures have worked to produce an efficient lineage-specific sense of smell. Here, we report experiments in which we presented a generalist primate, the cotton-top tamarin (*Saguinus oedipus*), with a series of olfactory discrimination tests in order to examine whether its generalist diet also yielded a general olfactory system. We show that tamarins are capable of discriminating between novel odors of several categories, learning to associate them with positive and negative rewards and use them as food selection cues. Although odors were from varying levels of ecological relevancy (fruity, herbal, and seafood), no differences in discrimination performance between were observed. Combined with partial learning and memorizing abilities, these results demonstrate a generalist olfactory system whose range of detectable compounds is not restricted to ecologically relevant odors and which relies on learning rather than innate responses.

Key Words: Food selection, foraging, frugivory, generalist diet, olfaction, sense of smell, sensory ecology.

Resumen

Después de años de casi total ausencia en la literatura, el olfato finalmente empieza a reconocerse que el olfato tiene un papel importante en la ecología alimentaria de los primates. Aun cuando es ya claro que la agudeza olfatoria de los primates es más alta de lo que antes se pensaba, no es aún claro sobre qué parámetros del sistema olfativo las presiones de selección han trabajado para producir un sentido del olfato eficiente específico al linaje. Aquí reportamos experimentos en los cuales sometimos a un primate generalista, el tití cabeza blanca (Saguinus oedipus), a una serie de pruebas de discriminación olfativa con el propósito de examinar si su dieta generalista también se correspondía con un sistema olfativo general. Mostramos que los titi cabeza blanca son capaces de discriminar entre olores nuevos de varias categorías, aprendiendo a asociarlos con recompensas positivas y negativas, y a usarlas como pistas para la selección del alimento. Aunque los olores fueron de variada relevancia ecológica (frutales, herbales y de comida de mar), no se observaron diferencias en el desempeño de discriminación entre ellos. Combinado con aprendizaje parcial y habilidades de memorizar, estos resultados demuestran un sistema olfatorio generalizado cuyo rango de compuestos detectable no está restringido a olores ecológicamente relevantes y el cual depende del aprendizaje más que de respuestas innatas.

Palabras Clave: Selección de alimento, forrajeo, frugivoría, dieta generalista, olfato, sentido del olfato, ecología sensorial.

Introduction

Primates are one of the most vision-oriented taxonomic groups (Fobes and King, 1982) and are the only eutherian mammal order which includes lineages with habitual or partial (polymorphic) trichromacy (Jacobs, 2009). This elaboration of visual capacities has long been considered to have come with a price – a continuous reduction in olfactory capacities which rendered them in effect "microsmats", whose olfactory capacities are reduced to almost negligible levels (Le Gros Clark, 1971). These notions begun shifting when social functions of olfaction were identified (Michael et al., 1976; Epple et al., 1993) but mostly after Laska and colleagues (e.g., Laska et al., 2000, 2004, 2005) demonstrated that primates of several lineages possess olfactory capacities that are in line with, and sometimes even superior to, those of traditionally "macrosmats" such as dogs or rodents. This, in turn, led to a proliferation of studies that emphasized the roles of olfaction in primate feeding ecology. In frugivory – the main dietary modality of many primate species – few managed to demonstrate the ability of any species to locate fruiting trees from afar. In contrast, the majority of studies observed that primates tend to employ their sense of smell in the food selection phase, to assess the quality of individual fruits before ingestion (Nevo and Heymann, 2015). Whereas the importance of the sense of smell may be minor to vision when selecting fruits that provide clear visual signals, some fruit species are visually cryptic (i.e. their fruits do not change their color when ripening) and thus require reliance on olfactory cues (Hiramatsu et al., 2009; Melin et al., 2009). Here, the sense of smell may acquire the foremost position and provide crucial information otherwise unobtainable, regardless of color vision capacities.

In the food selection phase, the main challenge primates face is to quickly and accurately determine whether a fruit is ripe or unripe. Frugivorous primates are usually generalists: they may consume the fruits of up to hundreds of species (Van Roosmalen, 1985; Buzzard, 2006; Culot, 2009; Beaune et al., 2013), some of them providing fruits only every other year or even less (Chapman et al., 2005). Thus, primates may encounter certain fruits only at long intervals. Furthermore, the odor of ripe fruits of different species can be qualitatively and quantitatively different (Hodgkison et al., 2013) and even within species may change over the dial cycle (Borges et al., 2013) and according to the availability of nutrients (Mattheis and Fellman, 1999). As a result, it is unlikely that efficient recognition of ripe fruits can be based on a few compounds that characterize fruits of all, or many species. Therefore, along with some more general decision rules (e. g. ripe fruits tend to be softer, Dominy, 2004), this context strongly favors reliance on fast and accurate learning of the visual and olfactory cues associated with each consumed species (Schaefer et al., 2014). However, this stored information may be relevant only for few hours or days in which the species provides fruits, but possibly becomes obsolete fast when fruiting ceases and the primates shift their foraging effort to other species.

Thus, an efficient use of the olfactory system can be predicted to encompass discriminating between the odors of desired (ripe) and undesired (unripe) items, and based on trial-and-error, quickly learning to associate the positive and negative stimuli with their respected rewards to allow quicker and more correct choice during forthcoming encounters. Further, given that memory formation and its storing are not cost-free (Dukas, 1999), it is likely that they would take place only when the stimulus becomes regular. Indeed, previous studies demonstrated that continuous exposure to such challenges over many days allows primates to learn the tasks up to a point where their success rates are approaching 100% (Laska et al., 1996; Hübener and Laska, 1998). In addition, even if generalist frugivores are under selection to retain a generalist olfactory system which can allow response and quick learning of diverse stimuli, over time it can be expected to evolve to be more sensitive to odorants that are "ecologically relevant" – odorants or odorant classes that are common in their feeding items. The olfactory receptors of primates have experienced positive selection (Dong et al., 2009) and primates of several lineages possess high olfactory sensitivity to odorants common in fruits (e.g., Laska et al. 2006). Not surprisingly, capuchin monkeys (Cebus apella) have been shown to be better to discriminate between odors of ecologically-relevant fruits as opposed to ecologically-irrelevant seafood odors (Ueno, 1994).

Here, we report a short experiment which focused on the early stages of olfactory learning in food selection tasks in cotton-top tamarins (Saguinus oedipus), a generalist New World frugivorous-insectivorous primate (Neyman, 1978; Rylands and Mittermeier, 2013). We asked the following questions:

1. Can cotton-top tamarins quickly learn to associate novel odors with positive and negative rewards, and consequently learn to use the ability to discriminate between the odors in food-selection tasks?

2. Does olfactory memory form after short, abrupt, exposure to the stimuli?

3. Do tamarins perform better when the stimuli are ecologically-relevant?

To address these questions, we exposed captive cotton-top tamarins to a series of experiments that required them to discriminate between novel odor stimuli associated with positive or negative rewards, simulating an unfamiliar plant species that presents ripe and unripe fruits which carry different odors. In order to answer question (3), we repeated the experiments three times, using three sets of odorants of decreasing levels of ecological relevancy: fruity, herbal and seafood.

Methods

Study animals

Experiments were conducted on a group of 7 adult and subadult male cotton-top tamarins hosted at the German Primate Center, Göttingen, Germany in March 2012. The group lived in two connected cages, totaling at about 9 m^2. The tamarins were normally fed with a mash of rice flour, various fruits and vegetables, dried fruits such as raisins or apricots, rusk and boiled eggs. Once a week, mealworms or grasshoppers were provided.

Experimental procedure

Each of the four experiments was conducted over 2 h over 3 consecutive days in the following order: control, fruity, herbal, seafood odors (Table 1). For each experiment, on

Table 1. Odors used in all experiments

Conditions	Assigned odors	
	Odor indicating positive reward (S+)	Odor indicating negative reward (S-)
Control	-	-
Fruity	Cherry[1]	Grapefruit[1]
Herbal	Lavender[1]	Eucalyptus[1]
Seafood	Eel[2]	Shrimp[2]

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Figure 1. Experimental station.

each day, 4 identical experimental stations were placed in the enclosure at the same time. Each contained 2 familiar drinking bottles (Fig. 1). The bottles were filled with either sugar or salty water, which served as positive (S+) and negative (S-) rewards respectively. Next to the opening, each bottle was marked with a 1.5 ml Eppendorf vial containing 20 drops of commercially obtained aromatic oils (empty in the control experiment). Odors were assigned randomly in the beginning of the experiment and were not switched afterwards (i. e., a single odor was always associated with either a positive (S+) or a negative reward (S-). Preliminary experiments confirmed that the sugar water is a positive reward for the tamarins while salty water is never drank after an initial contact. The tamarins had not been exposed to these odors prior to the reported experiments. To ensure correct scoring, the bottles were marked with red and green markers. Male tamarins are dichromats (Jacobs, 2009) and could therefore not use this as a cue.

In each experimental session the tamarins were allowed to freely approach any of the four identical stations, examine the bottles and attempt drinking. Once an attempt was made (defined as physical contact of the tongue or lips with the bottle), the observer (E-M.R.) called individual's name, allowed the tamarin to drink or switch to the other bottle in case of an incorrect first choice, and then removed and re-placed the bottles in quasi-randomized order to annihilate location within the station as a cue. This also ensured that observing group members did not provide any useful cue in identifying the S+ bottle, and also that spatial preference of right or left could not affect the overall success rates. Thus, the chance level for correct choice was 50%. The experiments were recorded with a video camera. Scoring was conducted by the experimenter after all experiments were completed based on the color marks on the bottles. We recorded only the first choice (S+ or S-) in each interaction with the experimental station. To ensure that scoring was accurate, a second observer scored one of the video footages (150 datapoints). Inter-observer reliability was 96% (i.e. the second observer agreed with the experimenter in 96% of the scoring during analysis of one video).

Statistical analysis

Due to variation in the number of tamarin-bottle interactions between individuals and days and since no significant differences between days were found, we lumped all data points for each individual in each experiment (e. g., individual A, fruity) to a single figure depicting its success rate (share of correct decisions) in that experiment. One individual was excluded due to very low participation rate, thus reducing the sample size to N = 6. For the remaining individuals, the number of interactions with the experimental devices in any of the experiments ranged between 10 and 257. In each of the four experiments, we used one-tailed Wilcoxon tests to test whether the tamarins scored higher than the baseline chance level of 0.5. We used one-tailed tests because preliminary experiments showed that the tamarins avoid drinking salty water and thus the minimum theoretical success rate was 50% (Ruxton and Neuhäuser, 2010). To compare success rates between conditions we applied the Wilcoxon signed-rank test when comparing two groups and Friedman's test for more. We used paired tests to model the average within-individual difference in performance between treatments. Data were analyzed on R 3.0.1 (R Core Team 2013) and graphs were made using the package Plotrix (Lemon, 2006).

Results

Discrimination performance

Tamarins scored significantly above chance level in all experiments (Wilcoxon tests, one tailed, Fruity: N = 6, V = 15, p = 0.03; herbal: N = 6, V = 15, p = 0.03; seafood: N = 6, V = 24.5. p = 0.045), showing that, as a group, they could discriminate between the odors and choose the correct drinking bottle above chance level (Table 2). Since we found no significant differences in discrimination performance between treatments, we further summed the scores of the three treatments (fruity, herbal, seafood) to a single "stimulus" figure, which increased the number of data points (79–257) per individual and substantially reduced inter-individual variation. This "stimulus" was also significantly larger than the 0.5 baseline (N = 6, V = 27, p = 0.017). Success rates in the control condition were not different than 0.5 (N = 6, V = 15, p = ns), indicating the subjects could not identify the S+ bottle based on cues other than the olfactory stimuli tested (Table 2, Fig. 2).

Short-term learning and memory formation
To examine memory formation of the stimuli we compared success rates between the 3 consecutive days of experiments, with the expectation that memorizing would result in increased success rates in days 2 and 3. Since performance in the three odor categories was indistinguishable, we lumped them to a stimulus to increase the number of observations per individual and the test's robustness. Success rates did not vary between days (N = 6, Friedman's X^2 = 4.33, df = 2, p = ns), indicating that a 2 h exposure was not sufficient for effective memory formation. Nonetheless, short-term learning was apparent: tamarins scored above chance level in both first and second halves of the sessions, but significantly more in the latter (stimulus, all days lumped – Wilcoxon test, two-tailed, N = 6, W = 2, p = 0.013) (Fig. 3).

Differences in discrimination performance between treatments
We found qualitative differences in discrimination performance between the three treatments. Performance was lowest for the fruity stimuli and highest for the herbal stimuli (Fig. 2). However, none of these differences are statistically significant (N = 6, Friedman's X^2 = 1.33, df = 2, p = ns).

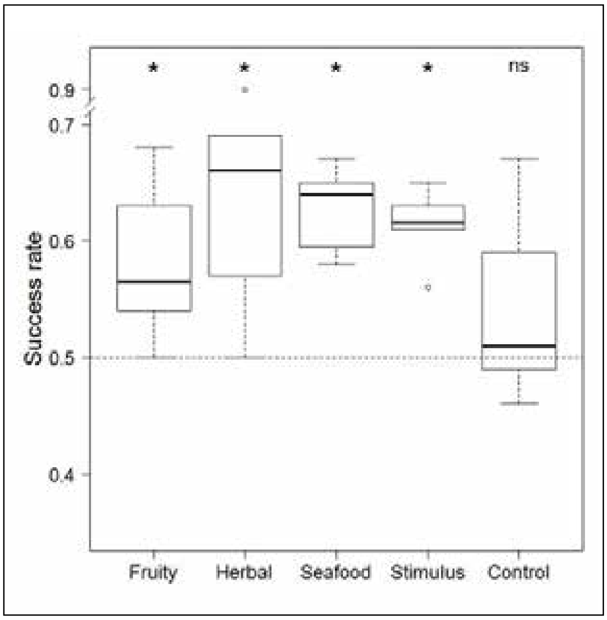

Figure 2. Success rates in all experiments. Stimulus is the success rates in all experimental conditions lumped (fruity, herbal, seafood). Asterisks denote significance at p < 0.05 in one-tailed Wilcoxon tests comparing success rates to the 0.5 chance level. N = 6 individuals in all experiments.

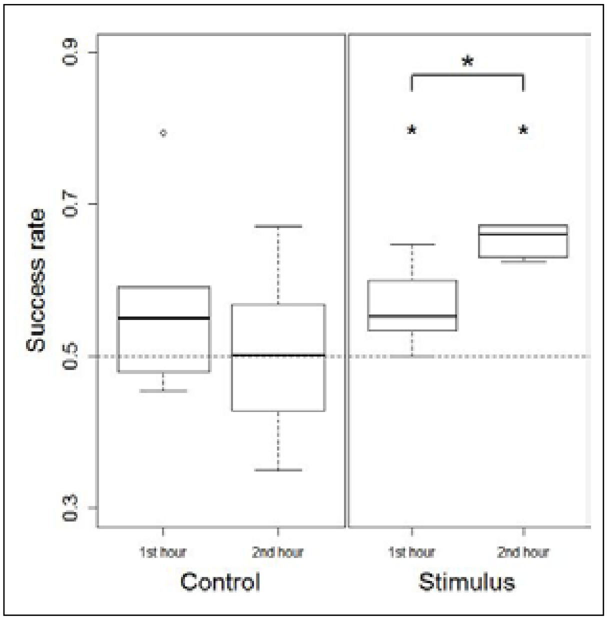

Figure 3. Success rates in early and late phases of the experiments. Results from all days are lumped. Stimulus is fruity, herbal and seafood lumped. Asterisks above boxes denote significance at p < 0.05 in one-tailed Wilcoxon tests comparing success rates to the 0.5 chance level. Asterisk above arch denotes significance at p < 0.05 in a two-tailed Wilcoxon paired test. N = 6 individuals in all experiments.

Table 2. Mean individual success rates (correct / total choices) in all conditions. Stimulus: fruity, herbal and seafood combined.

Individual	Conditions				
	Control	Fruity	Herbal	Seafood	Stimulus
B	0.59 (91/153)	0.68 (58/85)	0.67 (31/46)	0.63 (79/126)	0.65 (168/257)
G	0.46 (29/63)	0.54 (19/35)	0.91 (10/11)	0.57 (19/33)	0.61 (48/79)
J	0.51 (59/115)	0.63 (49/78)	0.65 (24/37)	0.59 (81/136)	0.61 (154/251)
L	0.49 (26/53)	0.58 (14/24)	0.5 (5/10)	0.67 (34/54)	0.62 (53/85)
O	0.67 (52/78)	0.5 (20/40)	0.57 (8/14)	0.65 (17/26)	0.56 (45/80)
R	0.51 (22/43)	0.55 (26/48)	0.68 (37/54)	0.65 (41/63)	0.63 (104/165)

Discussion

The first questions we asked were whether cotton-top tamarins, a generalist frugivore, can learn to use random novel odors as reliable cues in food selection tasks, and whether abrupt exposures would lead to memory formation. We focused on limited and fast exposure which mimics fruit species whose yield and fruiting time are relatively low and unpredictable. All three experiments (fruity, herbal, seafood) demonstrated this capacity. Within two hours the animals scored significantly above chance level in all conditions, and they clearly improved towards the end of each session. Thus, abrupt exposures of 2 h are sufficient for effective association of novel odors with positive and negative rewards, and the ability to discriminate between the odors allows cotton-top tamarins to identify desired feeding items and avoiding undesired items. In the wild, this ability is expected to translate into the ability to identify ripe fruits and avoiding unripe or overripe fruits. At the same time, the lack of difference in performance between experimental days indicates that this short-term learning process does not translate into effective memory formation. Although the tamarins systematically improved in solving the task within session, success rates in the following morning always decreased and indicate that the tamarins had to learn the task anew. So, it appears that while very short-term memory formation took place, it was not consolidated and could not be used after a day's break. However, it is likely that had the experiments been prolonged for more days or more hours per day, the tamarins would have begun storing the learned information rather than learning it every day anew, as demonstrated in previous studies (Laska and Hudson, 1993; Laska et al., 1996; Hübener and Laska, 1998).

Taken together, these results provide support for the validity of the characteristics we expected to find in the generalist's olfactory system – quick adjustment and ad hoc learning to deal with novel stimuli to make food acquisition more efficient, but lack of memory formation when the stimulus is irregular. This system is likely to be favored in generalist frugivores, which feed on hundreds of plant species whose fruit yield is irregular and unpredictable. On one hand, the frugivore would benefit from the ability to quickly learn to identify ripe over unripe or overripe fruits. On the other hand, when it is unknown whether or when and fruits of the same species would be encountered again, the costs of memorizing odors of ripe and unripe fruits of hundreds of species may exceed the benefits.

The third question at hand was whether tamarins would perform better when the challenge entails discrimination of ecologically relevant stimuli as opposed to irrelevant such as the seafood condition. We chose novel stimuli with which the tamarins had been unfamiliar in order to examine whether the ability to learn to associate novel odors with positive and negative rewards (question 1), increases when the stimuli are more ecologically relevant. Plant volatile compounds tend to be very different than those present in seafood (cf. Hiatt, 1983; Hodgkison et al., 2013; Knudsen et al., 2006). Therefore, if the tamarin olfactory system has been under selection to emphasize detection and discrimination of fruity/herbal volatile compounds, it was predicted that this should translate into higher ability to learn to use novel fruit or herbal odorants as food selection cues. This was intended to attempt to partially replicate a study which demonstrated that capuchin monkeys possess higher discrimination abilities when facing "fruity" rather than "fishy" odors (Ueno, 1994). Our results failed to record this pattern. In fact, fruity odors were qualitatively the most difficult to discriminate, although this trend was not supported by the statistical tests. This, however, should be taken with great care because it is practically impossible to standardize the "olfactory distance" between odor pairs in the experiments. There are genetic, neurological and ontogenetic factors which determine whether discrimination between two odor mixtures is easier or more difficult. As a result, it is possible that tamarins indeed possess higher olfactory discrimination capacities to "fruity" odor mixtures, but that the single odor pairs used here are not fully representative of odor mixtures from their respective categories. It is therefore likely that repeating these experiments with many different odor pairs would yield significant differences in discrimination performance between odors from categories of varying ecological relevance. Nonetheless, it is also possible that generalist species, and especially taxa such as tamarins, which rely on olfaction for intraspecific communication as well (Heymann, 2006), have retained a very general olfactory system which can respond to many different stimuli, even if ecologically less relevant.

In conclusion, these short experiments demonstrate two characteristics of the olfaction system of a frugivorous generalist primate: the ability to quickly learn to use arbitrary olfactory cues as food selection guides and the lack of clear specialization on odors strictly ecologically relevant. They further indicate that under abrupt and irregular exposure memory formation does not take place – a phenomenon that may be adaptive under such conditions. Time and budget limitations forced this to be an exploratory experiment which we hope would encourage other groups to examine similar questions using different settings and model species.

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adhered to the ASAB guidelines for the use of animals in research and teaching.

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