Influence of visual information on sniffing behavior in a routinely trichromatic primate

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Abstract

Most catarrhine primates are considered to be strongly visually oriented animals, obtaining information about conspecifics and their environment from a diversity of visual cues. Other sensory modalities may provide information that is redundant and/or complimentary to visual cues. When cues from multiple sensory modalities are available, these may reinforce or suppress each other, as shown in a range of taxa from insects to humans. In the present study, we tested how the presence and ambiguity of visual information affects the use of olfactory cues when exploring food and non-food items in semi-free ranging Barbary macaques at Affenberg Salem, Germany. In experiment 1, we presented monkeys with pipes containing food (peanuts, popcorn), non-food (stones, feces) or no items. The ends of the pipes were either transparent or opaque, and we assessed whether animals looked, sniffed and/or grabbed into the pipes depending on visibility of the contents. In experiment 2, we manipulated the visual appearance of familiar food items (popcorn) with food colorant and scored if monkeys sniffed at and/or ate the popcorn depending on whether it was uncolored or dyed. In both experiments, the available visual information modulated sniffing behavior. Both visual as well as olfactory information further affected, whether or not monkeys attempted to retrieve the items from the pipes in experiment 1, while data were insufficient to assess this in experiment 2. Hence, reliance on the olfactory sense was modulated by the available visual information, emphasizing the interplay between different sensory modalities for obtaining information about the environment.

Keywords: multimodal information, olfaction, vision, food assessment, Barbary macaques

Introduction

Animals gain information about their physical and social environment using different sensory channels. Information can be conveyed via vision, audition, olfaction or other sensory modalities either by a single or multiple sensory channels in combination. In fact, sensory information is frequently multi-modal (i.e. encompassing more than one modality) in nature and integrating information from multiple modalities is widespread throughout the animal kingdom (e.g. Rushmore et al. 2012; Higham and Hebets 2013). Well-known examples include aposematically colored insects, which typically also emit an odor or sound when approached by a predator, or courtship signals encompassing combinations of visual, acoustic, tactile and/or chemical elements in a range of taxa (e.g. insects, fish, birds, see review in Hebets and Papaj 2005). The different modalities may thereby provide redundant or complimentary information simultaneously or sequentially, which may reinforce or in other ways interact with each other, and/or act at different spatial or temporal scales (Hebets and Papaj 2005). As a result, multimodal information may be more accurate, salient or diverse, more robust to noise, more memorable or available across a larger range than information conveyed via a single modality (Hebets and Papaj 2005; Higham and Hebets 2013; Leonard and Masek 2014). For instance, juvenile zebra finches (*Taeniopygia guttata*) responded more to zebra finch models which showed audio-visually synchronized beak movement than to models with unsynchronized or no beak movement during song playbacks (Simon et al. 2023), and wild chimpanzees (*Pan troglodytes*) used combinations of vocal and gestural signals more frequently after vocal signals alone failed to elicit a receiver response (Hobaiter et al. 2017).

Many multimodal studies focus on relatively easily recordable modalities like vision and audition, but an increasing number of studies show multimodal interactions involving olfaction as well (reviewed in Hebets and Papaj 2005). The interplay of olfaction with other senses has been studied relatively well in insects and insect-plant interactions (reviewed for bees in Leonard and Masek 2014), but rather little in vertebrates (see Melin et al. 2019). In the lizard *Liolaemus pacha*, for instance, the overall response towards conspecific stimuli was similar towards chemical cues presented in isolation compared to multimodal stimuli containing visual and chemical cues, but the specific reactions (tongue flicks or head-bob displays) depended on the sensory channel(s) available (Vicente and Halloy 2017). In two species of frugivorous bats (*Artibeus watsoni* and *Vampyressa pusilla*) Korine & Kalko (2005) manipulated the sensory cues available during foraging and showed that bats relied little on vision, but on echolocation and odor during foraging for figs. Notably, bats of both species required odor cues for determining the approximate location of figs in an environment full of leaves, but seemed to rely more on echolocation at a close distance for fine-scale localization and selection of fruits. Moreover, humans asked to detect an odor in an experimental context

reacted quicker when the odor was paired with a semantically congruent picture than when no or an incongruent picture were shown, with certain brain regions specifically activated when both modalities were presented together rather than in isolation (Gottfried and Dolan 2003). Hence, there is evidence that the availability and salience of information in one modality may affect to what extent animals attend to other sensory modalities in various contexts.

Vision and olfaction have been suggested to be the main senses in primate foraging ecology (e.g. Dominy 2004; Rushmore et al. 2012; Veilleux et al. 2022). Most diurnal primates are strongly visually oriented animals (see overview in Veilleux et al. 2022). They have three-dimensional vision and are the only eutherian mammals to have developed trichromatic vision, albeit not in all taxa (see Nevo and Heymann 2015; Niimura et al. 2018). More specifically, catarrhine primates (Old World monkeys and apes) and howler monkeys have routine trichromacy, while many platyrrhine species (New World monkeys) show a polymorphism that results in heterozygous females being trichromatic and homozygous females as well as all males being dichromatic (Niimura et al. 2018). Catarrhines and diurnal platyrrhines further show a high degree of visual acuity (Veilleux et al. 2022). Furthermore, it is now well-established that primates in all taxa also routinely rely on olfaction in a variety of contexts (e.g. Drea 2015; Vaglio et al. 2016; Jänig et al. 2018; Kücklich et al. 2019). Reliance on olfaction, in particular, has been suggested to be related to their general feeding ecology, with frugivore species relying more on olfactory cues than folivores, but also to the availability of visual cues in strepsirrhine and platyrrhine primates (Nevo and Heymann 2015). For instance, dichromatic white-faced capuchins (*Cebus imitator*) were reported to sniff fruits more often than trichromatic conspecifics (Melin et al. 2019), although no clear relationship between sniffing and chromacy had been found in an earlier study in black-handed spider monkeys (*Ateles geoffroyi*, Hiramatsu et al. 2009). Black-handed spider monkeys, however, were found to sniff more at fruits not changing color during ripening, and how much they sniffed was negatively correlated with the proportion of fruits consumed (rather than discarded, Hiramatsu et al. 2009). In contrast, the sniffing behavior of white-faced capuchins appeared to be unrelated to color conspicuity (red-green, blue-yellow or luminance) of the fruits they were feeding on (Melin et al. 2019). In humans, the sense of smell was reported to have higher subjective value in blind than sighted people and olfactory bulb size was found to be larger in early blind people (reviewed in Sorokowska et al. 2019). A recent meta-analysis, however, provided no robust evidence for a behavioral difference in olfactory abilities (olfactory thresholds, discrimination or identification) between blind and sighted people when corrected for publication bias (Sorokowska et al. 2019).

Some studies further assessed to what extent the availability and reliance on one sense or the other translated into foraging outcome. Rushmore et al. (2012) compared the reliance on vision

and/or olfaction for selecting preferred (i.e. ripe/more nutritious) over less preferred (i.e. unripe/less nutritious) food in three lemur species with different diets. While all species appeared to rely more on vision than olfaction during food selection, the folivore species (*Propithecus coquereli*) required visual and olfactory cues together to reliably identify their preferred food, the generalist species (*Lemur catta*) could identify preferred food using either modality alone, and the frugivore species (*Varecia variegata*) could identify preferred food using olfactory, but not visual, cues alone. Similarly, nocturnal grey mouse lemurs (*Microcebus murinus*) were able to detect their insect prey using either visual, acoustic or olfactory cues in isolation but performed best when cues from all three modalities were available together (Piep et al. 2008). Hence, current evidence points towards olfaction in primate feeding ecology being relevant primarily for food selection and when visual information about food quality is lacking or ambiguous, although the overall evidence is mixed and data are still too scarce for robust conclusions (Hiramatsu et al. 2009; Nevo and Heymann 2015). Furthermore, with the exception of a few studies in humans, data on the interplay between vision and olfaction are lacking for species that are routinely trichromatic. Within a project on the role of olfaction in a catarrhine primate, the Barbary macaque (*Macaca sylvanus*), we therefore investigated how attending to olfactory stimuli is affected by the availability and salience of visual information in two experimental feeding contexts and how reliance on vision and/or olfaction affected the experimental outcome. Like all catarrhine primates, Barbary macaques have trichromatic vision (Niimura et al. 2018). They are feeding generalists that feed on plant items such as leaves and fruit, but also on insects and scorpions (Fooden 2007). As such, they might be expected to be able to use visual as well as olfactory cues for food selection. Indeed, behavioral observations further showed that they routinely rely on olfaction, with the vast majority of sniffs (~80%) being directed at food, and to a lesser degree at the environment and conspecifics (Simon et al. 2022). In experiment 1 of the present study, we provided Barbary macaques with food or non-food items in either a visible or non-visible condition. We generally expected the monkeys to rely more on olfaction if visual information was absent, and to use the olfactory information gained in the non-visible condition to inform subsequent behavior (i.e. attempting to retrieve the content or not). In experiment 2, we provided familiar food in a novel color. We expected that unnaturally colored food items would be inspected by sniffing more frequently than naturally colored items, and that colored items would be discarded more frequently than naturally colored ones but only if the monkeys did not sniff the item.

Methods

Study population

The study was conducted at Affenberg Salem, Germany in February and March 2021. Affenberg Salem is home to ~ 200 Barbary macaques in three naturally formed social groups that range freely year-round within a 20ha forested enclosure. The park is open to visitors from spring to autumn, and is an active site of research year-round. Visitors are restricted to a designated path, while researchers have access to the entire park area. As a result, the monkeys are well-habituated to human presence (see de Turckheim and Merz 1984 for details on the park). The monkeys feed on plants and insects found naturally within the park and are supplemented daily with fruit, vegetables and grain. Water is available ad libitum in ponds and water troughs throughout the park. Individuals are identifiable from natural markings such as facial pigmentation patterns, coat color and stature as well as an alphanumeric code tattooed on the inner thigh. Individual life histories, group memberships and maternal relatedness are known from near-daily monitoring by staff.

Experiment I: transparent *vs.* opaque pipes

Setup

We experimentally presented the monkeys with different food and non-food items in a visible and non-visible condition at 12 sites throughout the park. Hence, experiments took place in a near-natural environment without spatial or temporal restrictions of access. For logistic reasons, we split the experiment into three blocks, during each of which four sites were active simultaneously. In each block, the four active sites were distributed across the home ranges of all three groups. Sites were set up in locations routinely used by the monkeys but not directly at the feeding areas.

At each site we fixed a grey drainage pipe (11cm diameter) with a 90° angle to the bottom of a tree. One, open end of the pipe faced upwards, the other to the right (when viewed from the front) as depicted in Fig. 1. The end pointing to the right was closed with a transparent or an opaque food storing can (made of hard plastic, 11cm diameter) using cable ties. The opaque storing can was identical to the transparent one but coated with a layer of grey duct tape on the inside. Due to the angle and dimensions of the pipe, items placed into the can were not visible (as assessed separately by 3 different human experimenters) from the top opening of the pipe, but only through the walls of the can if this was transparent (Fig. 1). All cans were punctured three times at the bottom to allow the odors of the content to be perceivable not only from the top opening of the pipe but also when sniffing the can (see Fig. 1). Pipes were fixed to trees with black belt straps (38mm width, polypropylene), with the opening at a height of 30-40cm. The dimension and height of the setup allowed monkeys to inspect the setup and also to grab into it from the top to retrieve items from the can.

Figure 1: Setup for the pipe experiment with a transparent (left) or an opaque (right) storage can affixed to a drainage pipe. In the example shown, both cans are baited with popcorn, but the popcorn is only visible from the outside when the can is transparent. The setup is open at the top; and storage cans are punctured at the bottom to allow for olfactory investigation from either the top or the can.

At each site, approaches to and interactions with the setup were continuously monitored with two wildlife cameras (Crenova 4K 20 MP) mounted to neighboring trees to cover the setup from two different angles. Cameras were set to record a full HD video (avi format with 1920x1080p resolution) for 1min without sound whenever detecting movement with their motion detectors. We set the break between consecutive videos of the same camera to the minimal possible setting of 5sec. Individuals interacting with the setup for longer than one minute were thus not consistently covered by a single camera. However, as the two cameras at a given site were affixed to different trees and monitored slightly different angles/ranges, monkeys came into their range at slightly different times and thus triggered the two cameras with an offset of a few seconds from each other, thereby allowing continuous monitoring of the setup by at least one of the cameras nonetheless. Cameras were equipped with a night mode which used infrared light, allowing for 24/7 monitoring. Pipes and cameras were oriented in a way to avoid strong backlight and a background with much activity (e.g. feeding area, visitor path) to improve image quality and reduce the number of false triggers of the cameras.

Experimental design

At each site we first conducted a 2d habituation phase to familiarize the monkeys with the setup and its location. During the entire habituation phase a transparent can was attached to the pipe, and the pipe was filled with food items (3-6 pieces of peeled peanuts or popcorn) at random intervals 6-8 times per day.

The habituation phase was followed by a 7d test phase. In the test phase, the transparent can was exchanged with an opaque can every few hours and the can was filled with different food or non-

food items or was pretended to be filled but left empty (see details below). At each site, the setup was filled 6x/d using the following semi-randomized manner: we divided daylight hours (7 a.m. to 7 p.m.) into six 2h time slots. In each slot, a given setup was filled once within the first hour of the slot, whereby we randomly determined the start time (0, 15, 30 or 45 min of the first hour) for filling the first setup and the order in which the four sites deployed simultaneously were visited. This ensured that the experiment covered the different daytimes evenly without making the visits to the respective setups easily predictable. In this way there further was at least one hour between consecutive visits to the same site, thereby increasing chances that one or several monkeys passed the setup while filled with a given content.

At each visit, the can was filled with one of 7 possible contents. As food items we either used pieces of peeled peanuts or popcorn, which were provided in two different quantities (3 or 6 pieces) to vary the intensity of their odor. As non-food items we either used 3 stones or 3 small pieces of Barbary macaque feces. Stones with an approximate size of the peanut pieces were collected within the park area, washed with a neutral soap & water and rinsed with distilled water before use in the experiment. Feces were used as a potentially aversive item, as contact with feces may increase the risk of contracting infections and is avoided in numerous species (see e.g. Case et al. 2020 and references therein). Feces were collected opportunistically whenever individually identified, adult monkeys were seen to defecate. Feces were stored in 30ml glass vials with screw top sealed with parafilm and were frozen at -20°C within 2h after collection. Feces were defrosted ~30min before use and sized to approximately match the size of the peanut pieces. We used feces from both sexes but from other groups than the group using the area of the experimental site. As the experiment was conducted in a near-natural environment without spatial or temporal restrictions in access to the setup, monkeys could potentially observe the filling of the setup. To better disentangle whether a filling event or the items in the setup affected exploratory behavior, we therefore included a 7th possible content, for which the can was pretended to be filled by reaching into it, but was left empty. All items were handled with disposable gloves, and the experimenter wore a medical mouth-nose cover. At each visit potential remains of the previous filling were removed, the inside of the setup was wiped first with 70% Ethanol (Carl Roth) and then with distilled water to remove residues of the ethanol before being refilled.

Over the course of the 7 test days, each of the 7 possible contents was presented once in the transparent and once in the opaque condition in three of the six 2h time slots: one of the first two, one of the middle two and one of the last two slots of the day (i.e. 7 contents x 2 conditions x 3 daytimes = 42 times). The order of these 42 filling events was randomized conditional on the following rules: a maximum of 3 consecutive fillings without edible items and no empty conditions

twice in immediate succession at a given site (to keep the incentives up), and at least one but a maximum of three changes between transparent and opaque cans per day and site (to balance randomization with feasibility). This randomization procedure was done separately for each site, so that the order of conditions and contents was also randomized across sites.

Coding

We first screened all recorded videos and discarded the "false alarms", in which the cameras were triggered by movement in the background or other animals than the monkeys (e.g. mice at night). We kept a total of 6570 videos in which one or more monkeys approached (i.e. interacted with or passed within 1m of) the setup. This number comprises the videos recorded from both angles/cameras at a given site and thus represents a lower number of events that triggered one or both cameras. It further comprised a small fraction of videos recorded in the early morning hours after the end of the 7d test phase but before the setup was dismantled.

From the videos we scored each individual monkey's approach, which was defined as a monkey coming to within 1m of the setup. Videos could encompass multiple approaches per video or multiple, successive videos per approach, if the monkey remained at the setup for more than 1 minute. Whenever an approach could be fully coded (see below) from one camera angle, we did not analyze the simultaneously recorded video of the other camera. Due to the large amount of data and limited manpower we only analyzed 3590 videos, which corresponded to 1556 different approaches. To ensure sufficient data for all contents and visibility conditions, we focused on analyzing the videos from all 12 sites triggered after filling events, and thereby on those approaches in which the setups were likely still baited. Nonetheless we also included approaches after (other) monkeys had already retrieved the items, as these represented additional cases of an empty setup similar to when the setup was only pretended to be filled. In fact, for 7 of the 12 sites, the coded videos encompassed all monkey approaches to the setup (viewed from one or both angles), irrespective of whether the content in the setup had already been retrieved by one or several monkeys or not. This allowed us to also take into account information on previous visits to the setup by the approaching or other monkeys (see details on statistical analysis below). At the remaining 5 sites coding all approaches was not feasible because they were visited too frequently.

For each approach we scored from the video the date and start time as well as the behavior of the monkeys towards the setup. All approaches took place during full daylight (98%) or late dawn (2%). More specifically, we scored whether or not the individual looked, sniffed or grabbed into the setup. Looking was scored when the approaching animal oriented its eyes towards or into the opening or can of the setup. This was typically accompanied by a clearly noticeable movement and re-orientation of the head from a distance of less than 50cm. Sniffing was scored when an animal placed

its nose within 5cm of the opening or can. We distinguished it from looking by the position and angle of the head, with the snout and nose stretched forward and placed closest to the setup in the case of sniffing but pulled back towards the neck, with the eyes closest to the setup, in the case of looking from a close distance. For both looking and sniffing we differentiated which part of the setup (opening or can) the behavior was directed at. Grabbing was defined as moving the hand (and arm) into the opening of the pipe so that at least the entire hand was inside the pipe. If a grab occurred, we also scored whether the monkey successfully retrieved anything from the setup. We scored any other interactions of the monkeys with the setup (e.g. climbing, tugging, biting into it) as "other", and further coded the order of the respective behaviors. In the transparent condition, we also scored whether any items were visible in the can. All individual identities were scored from video by an observer (B.M.W.) with 2yrs experience in identifying the study animals. As the manipulation of the setup by the monkeys sometimes led to a slight shift in the pipe's orientation we also scored the angle of the opening to statistically take into account the possibility that items may have become visible from the top opening. We scored the orientation from -5 to +5, with 0 resembling the opening pointing straight to the top. Positive numbers reflected the opening tilting to the right (i.e. no possibility of dislodging contents from the can), and negative numbers to the left (i.e. a possibility of items shifting towards the bend and thus being visible from the opening). The position of the opening was positive or neutral (0) in 83.9% of approaches used for analysis (see below), tilted marginally to the left (-1) in 15.2% of approaches and tilted more strongly to the left (-2 to -5) in only 0.9% of approaches.

Based on the experimental schedule and notes taken in the field, we further added information on condition (transparent or opaque), site, and the exact time and content of the preceding filling for each approach. By combining information on what was filled into the setup when, what was visible in the can on the video, what monkeys retrieved and what was left in the setup at the next filling we were further able to deduce the actual content of the setup at the time of each individual approach.

Videos were coded by a total of 6 different observers blind to the content of the setup, at least in the opaque condition. Four of these observers had previously worked with Barbary macaques at Affenberg Salem, while two had no prior experience with observing nonhuman primates. Before coding, pairs or trios of observers were trained together. In a subset of 396 approaches, behavior was independently coded by two observers, which showed an inter-observer agreement of 87.4% for looking, 74.7% for sniffing and 94.2% for grabbing into the setup. To assess the reliability of identifying individuals, identities were coded by a second observer (with 6 months experience with the study population) in 70 approaches. The two observers agreed in their assessment of individual identities in 67 (95.7%) of these approaches.

Statistical analysis

To assess the role of visibility on sniffing behavior as well as the consequences of olfactory inspection for further interactions of monkeys with the experimental setup, we constructed four generalized linear mixed models (GLMMs) in R (version 4.2.2, R Core Team 2022) using the function glmer in package lme4 (version 1.1-31, Bates et al. 2015). All 4 models were run with binomial error structure with logit link function. For these analyses, we only considered approaches in which the animals interacted with the setup by looking, sniffing, grabbing or any other form of inspection (i.e. 1431 of 1556 scored approaches, excluding those in which animals just passed by). To be able to account for repeated observations of the same individuals we further used only those approaches for which we could identify the involved individual , i.e. max. 1399 approaches by 126 different individuals (which interacted with the setup 1-84 times). The sample sizes actually used differed between models for analytical reasons as described below.

Model 1 was formulated to investigate the **influence of the visibility condition** (i.e. transparent or opaque can) **on the propensity to sniff** at the setup during any stage of exploring it. This model tested the prediction that visibility affects sniffing behavior. We fitted the model with sniff (yes/no) observed as response variable. As fixed effects test predictors, we modelled the visibility condition (transparent vs. opaque can), the actual content of the setup at the time of the approach (i.e. peanuts, popcorn, stones, feces or nothing) and the interaction between visibility condition and content to account for the possibility that different items were more or less likely to elicit sniffs in the transparent condition. We also fitted interactions between visibility condition and two control predictors, namely cohort (i.e. birth year of approaching individual), and, to account for a potential learning effect across time, the number of days a given site was already active. As fixed effects control predictors, we further included sex (male/female), group (C, F or H), the experimental block (1-3, fitted as a covariate), the time (in min) since the last filling, the orientation of the pipe's opening (from -5 to +5, see above) and, to account for potential differences in activity patterns, the hour of the day (all approaches used in the analysis took place during daylight hours). We further fitted the identity of the coder, the monkey ID, the date and the site as random intercepts to account for repeated measures and the random variation imposed by these grouping factors. To facilitate accurate estimation of random variation, we excluded 45 of the 1399 cases from the analyses that represented rare levels of grouping factors (i.e. fewer than 3 observations per level), which was the case for one date with only 2 scored approaches and 29 individual monkeys with one or two scored approaches. The remaining 1354 approaches used in the analysis represented 853 cases with and 501 cases without sniffs by a total of 97 different individuals. To achieve reliable estimates for fixed effects predictors, we further fitted all theoretically identifiable random slopes of fixed effects within

the grouping factors (Schielzeth and Forstmeier 2009; Barr 2013, see Supplement S1). To maintain an adequate balance between sample size and model complexity, we did not fit any random correlations between random slopes terms. Hence, this model included a total of 75 estimated terms (fixed effects, random intercepts and random slopes).

Model 2 used only data for the 7 sites for which all approaches had been coded. Coding of all approaches allowed us to also determine the time (min) since the previous approach to the setup by the approaching or other individuals, as well as to number the times the approaching individual had previously been at the setup. The motivation of this model was to take into **account some of the individual information monkeys may have had available** (from own experience or observing others) **in addition to visibility of the content** to guide their (olfactory) exploration of the setup.

The model was constructed like model 1, but additionally included as fixed effects predictors the time (min) since approach by another monkey (delta other), time (min) since own previous approach (delta self) and n^{th} approach to the setup as well as the two-way interactions of these terms with the main test predictor, i.e. visibility condition. For the first approach of an individual to a setup, we imputed the data by using the average time between approaches as time since own previous approach. As in model 1, we excluded rare levels of date and individual, resulting in 973 approaches (609 with and 364 without sniffs) by 80 different individuals being used for this model. Because of the lower sample size but higher number of predictors for this model we slightly simplified the random slope structure by fitting all theoretically identifiably random slopes for test predictors but only slopes for control predictors if predictors varied in at least two thirds of the levels of the respective grouping factor (see Supplement S1), resulting in a total of 92 estimated terms.

Model 3 was formulated to investigate whether the **visibility condition affected if the monkeys used olfaction at the beginning of the exploration or later**. Specifically, we expected the monkeys to sniff first when the content was not visible but later during the exploration if it was visible. Hence, this model used only those approaches in which the monkeys did sniff. As binary response variable we fitted whether a sniff occurred first or later in the exploration sequence. Similar to model 1, we fitted the visibility condition, the content of the setup and their interaction, as well as the interaction between visibility condition and the control predictor day (i.e. number of days the site had already been active) as fixed effects test predictors. As fixed effects control predictors, we further included sex, cohort, group, block and the hour of the day. We further fitted the identity of the coder, the monkey ID, the date and the site as random intercepts. To facilitate accurate estimation of random variation, we excluded 69 of the 882 approaches with sniffs from the analyses that represented rare levels of grouping factors in date and individual. Hence, 813 approaches by 71 individuals were used in this analysis. These represented 158 cases in which sniffs were the first behavior at the setup and

655 cases with sniffs at later stages of the exploration. As in model 2, we fitted all theoretically identifiably random slopes for test predictors, but only slopes for control predictors if predictors varied in at least two thirds of the levels of the respective grouping factor (see Supplement S1), and no random correlations between random slopes terms. This model included a total of 61 estimated terms before and 40 after exclusion of non-significant interactions (see general procedures below).

Model 4 specifically investigated the **interplay between visual condition, olfaction and the (attempted) retrieval of items** from the setup. We expected that in the transparent condition vision will primarily guide the decision as to whether individuals would grab or not, while in the opaque condition olfaction should do so, and that in either case the decision would depend on the content. We therefore fitted grab (yes/no) as binary response variable, and the visibility condition, the content of the setup, whether or not monkeys first sniffed (yes/no), and their 2-way and 3-way interactions as test predictors. In this model, "sniff first" referred to the order of a sniff relative to the first grab to assess whether olfactory information may have guided the decision to grab. Hence, approaches with sniffs before the first grab, or sniffs not followed by a grab, would be denoted as "yes, and approaches with sniffs after the first grab, or without any sniffs as "no". As fixed effects control predictors, we further included sex, cohort, group, block, the day of the experiment, the time since the last filling of the setup and the hour of the day. We also fitted the interaction between orientation of the pipe and content to account for the possibility that food items (but not non-food items) having shifted into the bend could elicit more grabs. As in the other models, we further fitted the identity of the coder, the monkey ID, the date and the site as random intercepts and excluded rare levels of grouping factors from the analysis to facilitate accurate estimation of random variation. Hence, this model was run with 1354 cases (the same cases as in model 1), of which 510 were approaches with, and 844 without grabs. We further attempted to fit all theoretically identifiably random slopes, but this model did not converge. We therefore ran the model with a simplified slope structure containing only slopes of predictors varying in at least 3/4 of the levels of the respective grouping factor (but all the slopes for the main terms of test predictors, see Supplement S1), and no random correlations between random slopes terms. This model included a total of 105 estimated terms before and 71 after exclusion of non-significant interactions (see general procedures below).

General model procedures

For all models, we z-transformed covariates to a mean of 0 and an SD of 1 prior to fitting the model to facilitate convergence and interpretation of model estimates (Schielzeth 2010). To facilitate comparisons between studies, means and SDs of the untransformed covariates are provided in supplement S2. As the time since the last filling (delta fill) and since approach by another monkey (delta other) were strongly right-skewed, we log-transformed these variables after adding the

constant 1 (to avoid 0-values) to improve model fitting. In these cases, the log-transformation was performed first and the z-transformation last. Furthermore, we manually dummy-coded categorical fixed effects predictors if involved in model interactions to be able to include their respective random slopes.

We checked for collinearity between predictors by using the function vif of the package car (version 3.1-1, Fox & Weisberg 2019). There were no issues with collinearity in any of the models (largest VIF in model 1: 1.15, model 2: 1.36, model 3: 1.25, model 4: 1.32). We further assessed the stability of the models by excluding each grouping factor level one at a time and comparing model estimates, using a function provided by R. Mundry. In model 1, estimates for the test predictors and some control predictors were rather wide, but generally had the same sign or were close to 0, suggesting stable model results with respect to the sign of effects, but some uncertainty in the magnitude. This was also the case in model 2, with the exception of the interaction between visibility condition and cohort, which varied moderately between positive and negative values depending on the levels of random effects included in the model. In model 3, stability was estimated based on 111 models lacking one single level of a grouping factor. These estimates were generally stable with the exception of 4 out of 111 estimates for content and one out of 111 estimates for group, where the removal of a random effects level resulted in highly deviating estimates. In all 5 cases, deviations in the estimates were explicable by considerably smaller sample sizes due to the removal of the respective random effects level and/or complete separation, suggesting that the overall results were stable. Because of the long computation time we did not assess model stability for model 4 (estimated to take >60 days).

For inference, we compared the full models comprising all predictors with the corresponding null models, which excluded the test predictors but included all control predictors and all random intercepts and slopes. Hence, full-null model comparisons are indicative of whether one or more test predictors, but not whether control predictors significantly affect the response. Full-null model comparisons were conducted with Likelihood Ratio Tests (LRTs) using the R function anova. Only if the full-null model comparison was significant ($p < 0.05$), we assessed significance of the individual (test and control) predictors with LRTs using the function drop1. In case of non-significant full-null model comparisons we assessed significance of control predictors using Wald statistics provided by the glmer function, but did not consider results of test predictors. Accordingly, in contrast to test predictors, results of individual control predictors are not controlled for cryptic multiple testing. If a model contained non-significant interactions involving test predictors, we excluded the non-significant interactions from the model to facilitate interpretation of the main terms.

Experiment II: colored popcorn

In the second experiment, conducted after the pipe experiment, we manipulated the visual appearance of a familiar food item, i.e. popcorn. This experiment was conducted with 32 adult focal animals of both sexes (16 males with ages of 7 to 21 years, 16 females with ages of 6 to 21 years) from two of the three study groups. All focal animals were already habituated to retrieving peanuts from a shallow plastic container in the course of another study.

With each of these individuals, we conducted two sessions (with 1-3d between sessions), in which popcorn was offered in a grey plastic container (the socket plug of a drainage pipe with 7.5cm diameter and 3 cm height) fixed to a horizontal branch or wooden rail with a belt strap. Each session consisted of a warm-up and a test trial. In the warm-up trial, a single piece of un-manipulated, white popcorn was offered in the container. If the animal participated in the warm-up trial, the container was filled with 4 pieces of popcorn simultaneously, 2 of which were unmanipulated and 2 were dyed blue with diluted food coloring (Dr. Oetker). Popcorn was dyed by dissolving a drop of the viscous food dye in the same amount of water. The diluted dye was soaked up with a paper towel and softly dabbed over the entire surface of the popcorn, then left to dry. In blind tastings of dyed and undyed popcorn, three experimenters (each tasting 3 pieces) were not able to distinguish between dyed and undyed popcorn.

To avoid interference by other monkeys, sessions were conducted when the respective focal animal had voluntarily separated from group members and was either out of sight of any other monkeys, or was at least 3m away from other monkeys and all individuals in the vicinity were lower-ranking than the focal animal. All sessions were conducted by the same experimenter and recorded with a handheld video camera (Panasonic HC-V180), with the experimenter commenting on the observed behaviors and colors of the retrieved popcorn pieces while recording. All 32 focal animals could be successfully tested in this manner.

From the videos, we scored for each session the date and time, and for each piece of popcorn the order of retrieval, its color, whether or not it was sniffed at and/or eaten. All videos were coded by the same observer.

Statistical analysis

We analyzed the effect of popcorn color on sniffing behavior by fitting a GLMM with sniff (yes/no) as the binomial response variable with logit link. The unit of analysis was each single piece of popcorn offered to the 32 focal individuals in the test trials (N = 32 individuals x 4 pieces per session x 2 sessions = 256). As fixed effects test predictor, we fitted the color of the popcorn (white/blue). To account for the possibility that monkeys might get used to the novel coloration over the course of

the experiment, we further fitted the interaction between color and the nth piece of popcorn retrieved (continuous variable from 1 to 8). We controlled for sex (male/female), cohort, hour of the day and group (C or F) by fitting these terms as fixed effects control predictors, and for monkey ID and date by fitting them as random intercepts. We further fitted all identifiable random slopes of fixed effects predictors within ID and date (see Supplement S1), but no random correlations, as this caused non-convergence of the model. Checks of model assumptions and stability as well as determination of p-values for the full model and individual predictors were conducted as described for the models in the pipe experiment. There were no issues with collinearity (largest VIF 1.31). Estimates for the effect of nth piece of popcorn were rather wide and overlapped 0, but the model was stable with respect to the test predictor and the other control predictors.

Results

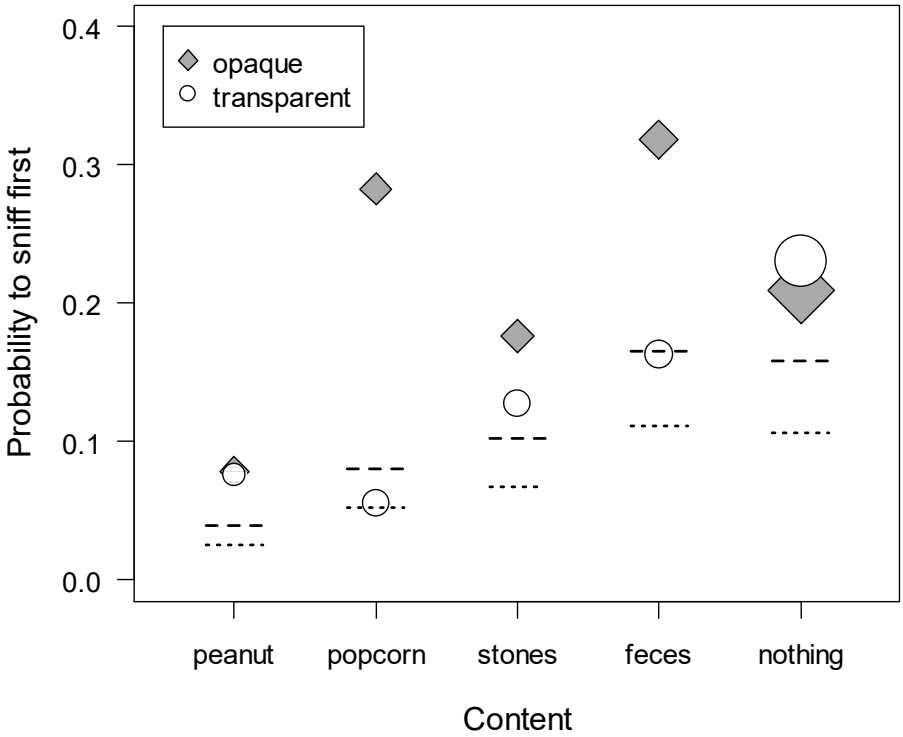
Experiment 1: transparent vs. opaque pipes

In the 1399 approaches with interactions by identified individuals the monkeys sniffed in 439 (59.1%) of 743 approaches when the transparent can was attached to the pipe, and in 443 (67.5%) of 656 approaches when the can was opaque. However, although the proportion of sniffs in the opaque condition was slightly higher, the visibility condition had no significant impact on the propensity to sniff when the other predictors were controlled for (Model 1 on 1354 approaches by 97 individuals: full-null model comparison, LRT, $\chi2 = 11.747$, df = 11, P = 0.383, see Tab. 1). This remained qualitatively the same when accounting for potential additional information on the contents from own or others' prior approaches to the setup (Model 2 on 973 approaches by 80 individuals: full-null model comparison, LRT, $\chi2 = 17.807$, df = 17, P = 0.401, see Tab. 1). While this was not addressed by the full-null model comparison, model results were suggestive of a significant effect of cohort, with younger individuals being more likely to sniff than older ones in Model 1 (Wald test, z = 3.032, P = 0.002) and an interaction between cohort and visibility condition in Model 2 (Wald test, z = 2.015, P = 0.044), although the latter result was not very stable across models with different random level effects included (see details on model stability in the methods).

Table 1: Estimates of the GLMMs investigating the propensity to sniff for all experimental sites (Model 1, N = 1354 approaches) and for fully-coded experimental sites only (Model 2, N = 973 approaches). Values in parenthesis indicate levels relative to the respective reference level (content peanuts, condition opaque, sex female, group C). SE = standard error. P-values not shown because full-null model comparisons were non-significant.

	Model 1		**Model 2**	
Term	*Estimate*	*SE*	*Estimate*	*SE*
Intercept	1.137	0.407	1.156	0.577
Content				
(feces)	0.119	0.411	0.000	0.541
(nothing)	-0.301	0.347	-0.417	0.484
(popcorn)	-0.664	0.406	-1.085	0.523
(stones)	-0.384	0.415	-0.580	0.544
condition (transparent)	-0.485	0.426	-0.572	0.599
delta_other			-0.117	0.125
delta_self			-0.222	0.138
n^{th}_approach			-0.054	0.302
Cohort	0.328	0.108	0.287	0.129
Day	0.131	0.164	0.351	0.150
sex (male)	-0.128	0.179	-0.045	0.200
Group				
(F)	-0.114	0.265	0.185	0.410
(H)	0.164	0.327	0.125	0.578
Block	-0.079	0.102	-0.084	0.140
delta_fill	-0.159	0.124	-0.128	0.121
Orientation	-0.081	0.071	0.008	0.081
hour of day	-0.102	0.080	-0.165	0.101
content:condition				
(feces:transparent)	-0.138	0.547	-0.108	0.725
(nothing:transparent)	0.148	0.461	0.318	0.621
(popcorn:transparent)	0.691	0.584	0.927	0.836
(stones:transparent)	0.304	0.554	0.190	0.745
condition (transparent):cohort	0.172	0.136	0.351	0.174
condition (transparent):day	-0.131	0.149	-0.245	0.227
condition (transparent):delta_other			0.271	0.183
condition (transparent):delta_self			0.232	0.195
condition (transparent):n^{th}_approach			0.120	0.190

495 In the 882 approaches during which the monkeys were observed to sniff, sniffing was the very first
496 behavior directed towards the setup in 172 (19.5%) of cases. More specifically, monkeys inspected
497 the setup first by sniffing in 76 (17.3%) of 439 cases in the transparent condition, and in 96 (21.7%) of
498 443 cases in the opaque condition, whereby both content and visibility condition significantly
499 affected the propensity to sniff first (Model 3 on 815 approaches by 71 individuals, full-null model
500 comparison LRT, $\chi 2 = 24.782$, df = 10, P = 0.006, see Tab. 2). Specifically, monkeys were slightly more
501 likely to sniff first if the can was opaque, irrespective of content, and were more likely to sniff first
502 when non-food items or nothing was in the pipe (Fig. 2).



503

504 Figure 2: Proportion of approaches with sniffs in which the first interaction with the setup was a sniff
505 depending on content and visibility condition (white symbols: transparent, grey symbols: opaque). Symbols are
506 scaled by sample size (range 38 – 205). Lines depict model estimates (dashed: opaque, dotted: transparent
507 condition).

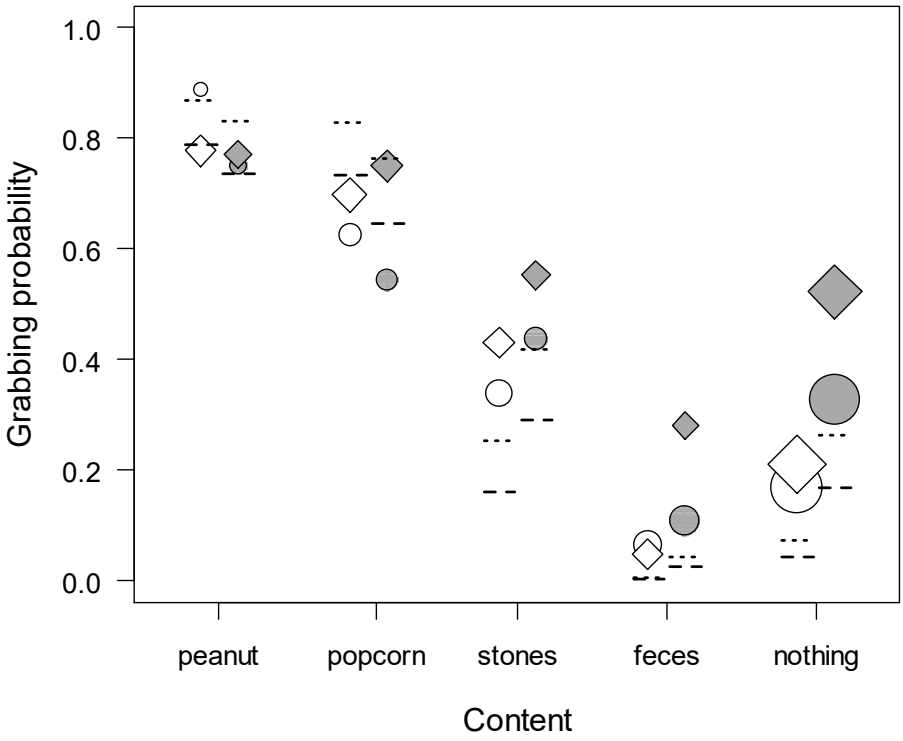
508

509 Table 2: Estimates of the GLMM investigating the propensity to sniff first (N = 882 approaches with sniffs).
510 Values in parenthesis indicate levels relative to the respective reference level (content peanuts, condition
511 opaque, sex female, group C). Values for non-significant interactions are marked in grey and represent values
512 before removal of the respective terms from the model, all other terms represent values after the removal of
513 the non-significant interactions. SE = standard error. χ^2 and P values are derived from LRTs to determine the
514 significance of the individual test predictors. Significant effects are marked in bold.

term	*Estimate*	*SE*	χ^2	*df*	*P*
Intercept	-3.061	0.787			
content			14.061	4	**0.007**
(feces)	1.582	0.536			
(nothing)	1.529	0.507			
(popcorn)	0.766	0.574			
(stones)	1.025	0.566			
condition (transparent)	-0.458	0.209	4.213	1	**0.040**
cohort	-0.283	0.185	1.735	1	0.188
day	0.101	0.141	0.482	1	0.487
sex (male)	-0.408	0.231	2.933	1	0.087
group			3.569	2	0.168
(F)	-0.013	0.354			
(H)	0.622	0.409			
block	-0.209	0.150	1.837	1	0.175
hour of day	0.084	0.163	0.281	1	0.596
content:condition			7.305	4	0.121
(feces:transparent)	-0.673	1.181			
(nothing:transparent)	0.240	1.034			
(popcorn:transparent)	-3.144	2.300			
(stones:transparent)	-0.569	1.229			
condition (transparent):day	-0.326	0.247	1.530	1	0.216

Finally, in the 1399 approaches with interactions by identified individuals the monkeys grabbed into the setup in 516 (36.9%) of cases. Whether or not the monkeys did grab was affected by the content, the visibility condition and whether or not the monkeys had sniffed at the setup (Model 4 on 1354 approaches by 97 individuals: full-null model comparison, LRT, $\chi2 = 94.424$, df = 23, $P < 0.001$). In particular, the effect of the visibility condition depended on the content of the setup (Tab. 3). Specifically, monkeys showed a similar propensity to grab for food items irrespective of the visibility condition, but a reduced propensity to grab for non-food items or into an empty pipe in the transparent versus the opaque condition (Fig. 3). Sniffing generally decreased the propensity to grab into the setup (Tab. 3). Although this decrease appeared to be more pronounced in the opaque condition (Fig. 3), the interaction between sniffing and visibility condition or content was not

526 significant. Furthermore, the propensity to grab inside was higher in younger animals and later in the
527 experiment (Tab. 3).



528

529 Figure 3: Proportion of grabs into the setup depending on content, visibility condition (white symbols:
530 transparent, grey symbols: opaque) and whether or not monkeys had sniffed first (yes: circles, no: diamonds).
531 Symbols are scaled by sample size (range 18 – 201). Lines depict model estimates (dashed: sniffed first, dotted:
532 no prior sniff).

533 Table 3: Estimates of the GLMM investigating the propensity to grab into the setup (N = 1354 approaches).
534 Values in parenthesis indicate levels relative to the respective reference level (content peanuts, condition
535 opaque, sniff first yes, sex female, group C). Values for non-significant interactions are marked in grey and
536 represent values before removal of the respective terms from the model, all other terms represent values after
537 the removal of the non-significant interactions. SE = standard error. χ^2 and P values are derived from LRT to
538 determine the significance of the individual test predictors. Significant effects are marked in bold.

term	*Estimate*	*SE*	χ^2	*df*	*P*
Intercept	0.522	0.647			
content					*
(feces)	-4.687	0.766			
(nothing)	-2.622	0.521			
(popcorn)	-0.424	0.613			
(stones)	-1.917	0.596			

condition (transparent)	0.294	0.630			*
sniff first (no)	0.568	0.274	4.348	1	**0.037**
cohort	0.971	0.230	10.366	1	**0.001**
sex (male)	0.186	0.375	0.248	1	0.619
group			2.134	2	0.344
(F)	0.492	0.451			
(H)	0.789	0.579			
day	0.243	0.139	3.125	1	0.077
block	0.713	0.147	14.216	1	**< 0.001**
z.delta_fill	-0.163	0.099	2.695	1	0.101
orientation	0.073	0.142	0.269	1	0.604
hour of day	-0.152	0.102	2.140	1	0.144
content:condition			15.018	4	**0.005**
(feces:transparent)	-2.173	1.009			
(nothing:transparent)	-1.791	0.688			
(popcorn:transparent)	0.124	0.886			
(stones:transparent)	-1.047	0.781			
content:sniff first			3.170	4	0.530
(feces:no)	1.118	0.918			
(nothing:no)	1.088	0.734			
(popcorn:no)	0.372	0.860			
(stones:no)	0.765	0.794			
content:orientation			1.549	4	0.818
(feces)	0.365	0.645			
(nothing)	0.225	0.536			
(popcorn)	0.198	0.630			
(stones)	0.534	0.564			
condition(transparent):sniff first (no)	-0.224	0.387	0.327	1	0.567
content:condition:sniff first			4.425	4	0.352
(feces:transparent:no)	-1.088	1.969			
(nothing:transparent:no)	1.248	1.458			
(popcorn:transparent:no)	0.874	1.714			
(stones:transparent:no)	2.015	1.633			

* not presented because terms comprised in significant interaction and thus having a very limited interpretation

Experiment 2: colored popcorn

The 32 focal animals retrieved all of the 256 pieces of popcorn and sniffed at 58 (22.7%) of them. The color of the popcorn had a clear impact on the probability of sniffing (full-null model comparison, LRT, $\chi2 = 10.77$, df = 2, P = 0.005). More specifically, blue popcorn was sniffed at significantly more often (50 times) than white one (8 times), irrespective of how many pieces had already been retrieved (see Tab. 4). Furthermore, females generally sniffed at a higher proportion of popcorn than males (Tab.4, 5). Finally, the sniffing frequency appeared to decrease slightly over the course of the experiment irrespective of color, but this was only a statistical trend and not very robust (see details on model stability in the methods).

Table 4: Number (N) and fitted values for proportion (prop. fit) of white and blue popcorn pieces sniffed by female and male Barbary macaques. The total number of popcorn pieces per sex and color was 64 (16 individuals x 2 pieces x 2 sessions).

	white		blue	
	N	prop. fit	N	prop. fit
female	6	0.044	34	0.490
male	2	0.008	16	0.148

Table 5: Estimates of the GLMM investigating the propensity to sniff at popcorn (N = 256 pieces of popcorn). Values in parenthesis indicate levels relative to the respective reference level. Values for the non-significant interaction are marked in grey and represent values before removal from the model, all other terms represent values after the removal of the non-significant interaction. SE = standard error. χ^2 and P values are derived from LRTs to determine the significance of the individual test predictors. Significant effects are marked in bold.

term	*estimate*	*SE*	χ^2	*P*
Intercept	-3.274	0.729		
color (blue)	3.037	0.675	9.550	**0.002**
popcorn_nr	-0.829	0.507	3.325	0.068
sex (male)	-1.709	0.637	7.894	**0.005**
group (F)	0.334	0.584	0.314	0.576
cohort	0.043	0.347	0.015	0.902
hour of day	0.006	0.259	0.001	0.982
color (blue):popcorn_nr	-0.742	0.596	1.747	0.186

561 The monkeys ate the vast majority of popcorn pieces (232) and only discarded 24 of them (23 blue, 1
562 white). They had sniffed at 13 of the discarded blue and at the one piece of white, discarded
563 popcorn. Due to the low number of discarded pieces (especially white ones), we did not assess the
564 interplay between visual and olfactory cues on the decision to eat or discard the popcorn statistically.

565

566 Discussion

567 We assessed the role of visual information on the use of olfaction (i.e. sniffing) and how the available
568 sensory information affected subsequent behavior in a highly-visually oriented primate species with
569 routine trichromatic vision and a generalist diet. The presence or absence of visual information about
570 the contents (food, non-food or nothing) of an experimental setup (experiment 1) did modulate
571 sniffing behavior, but differences between visibility conditions (transparent vs. opaque) were small
572 and only significant for the timing of olfactory inspection. Both visual and olfactory information,
573 however, affected the likelihood to grab for items. Ambiguous visual information (i.e. familiar food in
574 an unfamiliar color, experiment 2) increased olfactory inspections of items considerably more than
575 the presence/absence of visual information. Color further appeared to affect the consumption of
576 items, but as the monkeys ate the vast majority of the offered food items we could not statistically
577 assess the consequences of color and sniffing on their consumption.

578 *Experiment 1: Effects of visual information on olfactory behavior*

579 Sniffing probabilities in experiment 1 were generally rather high and only little affected by the
580 visibility condition: monkeys sniffed in more than half of the approaches even if the content was
581 visible through the transparent can. Notably, sniffing occurred throughout all phases of interacting
582 with the setup. While an initial assessment of the setup using olfaction was slightly more pronounced
583 when cans were opaque than when they were transparent, the majority of sniffs in either visibility
584 condition occurred after the monkeys had actively looked, grabbed or in other ways interacted with
585 the setup. Hence, as suggested for various strepsirrhine and platyrrhine primates (reviewed in Nevo
586 and Heymann 2015), sniffing in Barbary macaques may be more relevant *after* an item is located
587 using other sensory modalities, and thus function primarily in quality assessment and the food
588 selection process rather than in the search for food. Similar patterns can be observed in e.g. swamp
589 wallabies, *Wallabia bicolor*, which used olfaction to differentiate low and high-nutrient seedlings of a
590 highly preferred food source, *Eucalyptus pilularis*, in the absence of visual cues, but visual cues
591 overrode olfactory ones in detecting seedlings (Stutz et al. 2017). In contrast, eastern grey kangaroos,
592 *Macropus giganteus*, which graze on a variety of grasses and forbs, did not appear to use olfaction to
593 differentiate between *Eucalyptus pilularis* seedlings of different quality (Stutz et al. 2017).

Indeed, species differences in the interplay between vision and olfaction in food search and assessment have been associated with evolutionary adaptations to aspects such as diet or sensory abilities of foragers. In procellariform ("tube-nosed") sea birds, for instance, burrow-nesting species, which develop in the dark until fledging, were found to be sensitive to more prey-related odors than surface-nesting species, in which chicks experience light from early on (Van Buskirk and Nevitt 2008). The authors suggest that this difference in light exposure in early development led to surface-nesting birds also having developed a stronger visual or multimodal (visual and olfactory) dependence during foraging at sea. In primates, the reliance on olfaction in food selection has been attributed to both diet and chromacy. In particular, studies suggest that routine trichromacy was favored by folivory, while a potential advantage for the detection of fruits or flowers is still debated (reviewed in Veilleux et al. 2022). Nonetheless, studies indicate that more frugivorous species are more likely to sniff food items, while species that feed less on fruits rely more on visual or other sensory cues (reviewed in Nevo and Heymann 2015). The sensory cues provided by food items and the sensory capabilities of individuals may thereby interact in an intricate manner to affect the reliance on one or the other sense. In spider monkeys, Hiramatsu et al (2009) found no robust differences in sniffing rates between di- and trichromatic individuals, but monkeys generally sniffed more at those fruit species whose color was less conspicuous, with sniffing indices decreasing from 40-45% in fruit species with rather cryptic coloration to 0 for the most conspicuous fruit species. In contrast, Melin et al. (2019) found that trichromatic capuchin monkeys sniffed more at fruits than dichromatic ones irrespective of the conspicuity of the visual cues provided by the fruits, although differences in sniffing rates of di- vs. trichromatic individuals varied greatly between fruit species and the overall difference was small (8% vs. 7% sniffing in di- vs. trichromatic individuals). Our study animals presumably all had highly similar visual capabilities with the one known exception of a subadult male with one blind eye from birth on. He sniffed in 70% of 37 approaches to the transparent and 73% of 22 approaches to the opaque setup and thus more frequently than the average. In humans, blind people evaluated olfaction as more important to them than sighted people (reviewed in Sorokowska et al. 2019), but in the present study, we are not able to assess whether the male's high sniffing rates were really related to his visual impairment, his rather young age of 4 years (as younger individuals were also more likely to sniff or grab into the setup) or just chance.

Overall, our results corroborate findings in primates and other mammals that vision modulates aspects of sniffing behavior, although a direct comparison to other studies is difficult owing to the fact that we provided different food and non-food items (including potentially aversive feces) rather than different kinds of fruits (as in most primate studies), and that we dynamically modulated visual information of the same items rather than assessing natural variation in visual information or sensory ability. Further studies incorporating a wider range of species are certainly

needed to address how aspects such as dynamic vs. stable differences in visual information, diet and other aspects of species ecology or individual differences in sensory capabilities affect to what extent vision affects olfactory behavior.

Experiment 1: Effects of sensory information on grabbing for items

Monkeys grabbed into the setup in a little more than one third of the approaches. As expected, whether or not monkeys grabbed was modulated by the content and its visibility. When the can was transparent, monkeys preferentially grabbed for food items (peanuts in 80% and popcorn in 66% of cases), but only rarely grabbed inside when nothing was visible through the transparent can (18%) and seemed to avoid feces (6%). The latter was to be expected, as contact with feces bears the risk of contracting infections, and numerous species avoid contact with feces (see e.g. Case et al. 2020 and references therein). Monkeys grabbed in about one third of cases when stones were inside, potentially pointing towards some uncertainty in the monkeys' ability to visually distinguish stones, which were of similar size and shape as peanuts, through the transparent plastic can.

Notably, monkeys were still most likely to grab for peanuts and least for feces when the can was opaque, although the differences in grabbing between contents were less pronounced in the opaque condition (76% for peanuts vs. 17% for feces). This suggests that the absence of visual information limited the monkeys' ability to distinguish the contents of the setup, but also that they did have other sensory information than the items' visibility available to guide the decision as to whether or not to grab inside. Our prediction that olfaction would mediate further exploration of the setup in the absence of visual information was only partly supported though. Results indeed indicated a significant effect of prior sniffing on the propensity to grab. Based on grabbing rates (see Fig. 3), this effect appeared to be more pronounced in the opaque condition, particularly when feces, nothing or popcorn was inside. However, statistically an interaction between sniffing, visibility condition and content could not be confirmed; model results rather suggest that monkeys that had sniffed the setup were generally less likely to grab inside irrespective of content or visibility condition. At first glance, statistical power seems to be an unlikely explanation for the lack of a significant interaction, as we scored well over 1000 approaches. The model design was complex though, as we accounted for the different contents, visibility conditions and sniffing behavior, but also for numerous control predictors such as sex and age, experimental day and daytime, different individuals, experimental sites and coders. Furthermore, the number of actual approaches to a given content and condition as well as the (sniffing) behavior shown by the monkeys upon approach was not controllable by us, so that for particular combinations of predictors, cases may have still been too rare to detect statistically robust patterns. Another explanation could be that some residues of aversive fecal odor remained in the setup even if other contents were inside, although we took great

care to thoroughly clean the setup between fillings. Given the pronounced avoidance of grabbing for feces, this could explain a generally lower propensity to grab after sniffing irrespective of visibility condition and content, but if this was the case, we would have expected a much more pronounced decrease in grabs after sniffing than actually observed.

Furthermore, even if monkeys had not sniffed, grabbing rates differed between contents in the opaque condition (see Fig. 3), suggesting that the monkeys may have had other sources of information about the contents than anticipated. One possibility is that the odors of the contents may have been perceivable from a greater distance and without requiring the active sniffing movement that we scored, so that we may have underestimated the number of approaches in which olfactory information was available and used by monkeys. Although the majority of studies point towards primates primarily using olfaction for the close-up assessment of food items (Nevo and Heymann 2015), at least some species of strepsirrhines and platyrrhines appear to be able to detect and locate food sources from up to several meters distance using olfactory cues (Bicca-Marques and Garber 2004; Cunningham et al. 2021). Monkeys also sometimes pulled at the setup, which may have dislodged items from the tip of the can into a position visible from the top opening of the pipe. We controlled for this possibility by including the orientation of the pipe into the models, but could not unambiguously determine for each approach whether or not monkeys could have seen the contents even in the opaque condition. Although pulling at the setup likely caused harder items like peanuts or stones to rattle slightly, sound is unlikely to have provided salient information about the contents (other than that there is something inside). Touch, on the other hand, has been suggested to be an important sense for evaluating food quality in primate feeding ecology (Dominy 2004; Veilleux et al. 2022). For instance, results by Dominy et al. (2016) suggest that the ingestion of green figs, *Ficus sansibarica*, by chimpanzees was elicited by fig toughness rather than their color or size. Along similar lines, the Barbary macaques in the present study may have grabbed inside the setup to gather tactile information about the items. In fact, monkeys actually retrieved peanuts and popcorn in almost all instances of grabbing (peanuts: 95 out of 96 times, popcorn 115 out of 119 times), but only in half of the 80 cases in which they grabbed stones and never in the 24 grabs when feces were inside the can. While these numbers support the idea that the monkeys may also have used tactile cues, a systematic assessment of possible information from other sensory channels such as touch, and the interplay with vision and olfaction would require a much more detailed analysis of behavioral sequences shown at the setup, which is beyond the scope of this paper. Finally, the high propensity to grab for food items even in the opaque condition and when monkeys had not sniffed may also be explicable by a generally higher incentive of gaining a favorite food item than costs for an unsuccessful grab revealing no food or even an aversive item like feces. Peanuts, in particular, are not routinely provided by the park but are highly favored, so at least some individuals may have

698 pursued the strategy to grab inside as long as there was no obvious cue suggesting feces or other
699 non-food content. Furthermore, only about half of the monkeys ever approached a setup containing
700 feces, and those not having made the experience may have been more prone to grab inside
701 irrespective of visual or odor cues to the content. Again this would have required a much more
702 detailed investigation taking into the account the prior setup experience of each individual and
703 additional individual characteristics such as rank, which was not feasible for the given study design.

704 Taken together, our data suggest that both vision and olfaction guided Barbary macaques in
705 their decision to grab into the setup. As such, these results corroborate findings by Rushmore et al.
706 (2012), who found that ring-tailed lemurs, who – like Barbary macaques – have a generalist diet,
707 were able to use both visual and olfactory cues to select preferred foods. Barbary macaques
708 appeared to depend more on visual than olfactory information to distinguish between items,
709 although question marks remain as to whether or how visual and olfactory information interact to
710 guide exploratory behavior in an experimental feeding context.

711

712 *Experiment 2:*

713 The second experiment addressed a different aspect of visual information. By presenting blue and
714 white pieces of popcorn, visual information was constantly available but while size and shape were
715 familiar, the color of dyed popcorn was not and thus represented a source of ambiguity. Indeed,
716 monkeys sniffed at popcorn in a novel (blue) color considerably more often than at the familiar,
717 white popcorn. This matches results in spider monkeys and squirrel monkeys, who used olfaction and
718 other non-visual senses more when presented with novel food (i.e. entirely unfamiliar or with
719 unfamiliar color or scent), while relying primarily on vision for assessing familiar food items (Laska et
720 al. 2007). Color has also been suggested to be particularly salient in affecting olfactory & flavor
721 perception in humans (reviewed in Thesen et al. 2004) and although we assessed the use of olfaction
722 rather than perception thresholds or discriminatory ability, color also appeared to be particularly
723 salient for sniffing behavior in Barbary macaques and elicited stronger changes in olfactory
724 inspections than the presence or absence of visual cues in experiment 1. In spider monkeys and
725 squirrel monkeys, the non-visual inspection of novel food items by sniffing or touching also
726 decreased rapidly over the course of the experiments (Laska et al. 2007). In the Barbary macaques,
727 the propensity to sniff also tended to decrease the more pieces of popcorn an individual had
728 retrieved, but this effect was not significantly different between blue and white popcorn.

729 Novel colors have also been shown to affect the acceptance of food items. In zebra finches,
730 for instance, familiar food dyed red increased latencies to approach and eat the items (Kelly and
731 Marples 2004). This effect was even more pronounced when the novel color was paired with a novel

732 odor, while novel odor alone did not affect latencies. Similarly, spider monkeys and squirrel monkeys
733 showed longer manipulation times until consumption for novel food items or food items whose color
734 and odor had been manipulated (Laska et al. 2007). In the popcorn experiment, we only scored if
735 pieces were consumed at all, as exact latencies to approach would have been difficult to score in the
736 near-natural environment in which the experiment was conducted. In fact, the monkeys consumed
737 such a large proportion of the popcorn pieces (91%) that we did not have a sufficient number of
738 discarded pieces to statistically assess how the interplay between visual information and sniffing
739 behavior affected consumption. It is noteworthy though that 23 of the 24 discarded pieces were
740 blue, suggesting that color, at least, affected acceptance.

741 A potential limitation of the popcorn experiment was that we had no white food coloring of
742 the same brand as the blue one available and thus compared dyed with undyed popcorn. Although
743 different humans were not able to detect a difference in smell or taste of the dyed and undyed
744 popcorn, we cannot exclude that the monkeys may have been able to perceive a difference. If that
745 was the case though, this information should only have become available after sniffing or tasting the
746 popcorn. Accordingly, a potential difference in the smell or taste of blue popcorn should have been
747 of little relevance for the question if an unusual color elicits olfactory investigation, but might have
748 had an effect on the consumption of the popcorn.

749 Hence, this experiment provides first indications that the color of food items affects olfactory
750 investigations and probably also acceptance of food items in Barbary macaques in a similar manner
751 as in other primate taxa and non-primate species. Follow-up studies should incorporate different
752 colors as well as combinations with odors (as done in e.g. Kelly and Marples 2004; Laska et al. 2007)
753 to get a better understanding how color and olfactory information interact in catarrhine primate
754 food choice.

755 *Conclusions*

756 The present study provided evidence that Barbary macaques used visual and olfactory information to
757 guide exploratory and feeding behavior in experimental feeding contexts. As a highly visually
758 oriented species with acute color vision it comes as no surprise that the presence or absence of visual
759 information as well as coloration of items clearly affected how monkeys responded to different food
760 and non-food items. Monkeys also routinely used olfaction to inspect items, and olfactory inspection
761 affected subsequent behavior to some degree, albeit less than vision. As such, this study also adds to
762 the increasingly comprehensive evidence that olfaction plays a prominent role in the lives of
763 catarrhine primates, which were historically regarded to rely only little on the sense of smell.
764 Importantly, by taking a multimodal approach we were able to show that the availability and salience
765 of information in one sensory modality affects the reliance on other sensory modalities, potentially

leading to a complex, multisensory interplay affecting behavior. As also pointed out by various authors (e.g. Smith and Evans 2013; Leonard and Masek 2014; Valenta et al. 2015; Wilke et al. 2017; Veilleux et al. 2022), our results highlight the importance of a multimodal perspective, as examining single modalities may be insufficient to explain behavioral decisions. How such multisensory interactions guide behavior in a feeding or other contexts requires further studies and across a wider range of species to understand how (socio)ecological traits shape sensory ecology.

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