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Successful acquisition of an olfactory discrimination test by Asian elephants, *Elephas maximus*

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ABSTRACT

The present study demonstrates that Asian elephants, *Elephas maximus,* can successfully be trained to cooperate in an olfactory discrimination test based on a food-rewarded two-alternative instrumental conditioning procedure. The animals learned the basic principle of the test within only 60 trials and readily mastered intramodal stimulus transfer tasks. Further, they were capable of distinguishing between structurally related odor stimuli and remembered the reward value of previously learned odor stimuli after 2, 4, 8, and 16 weeks of recess without any signs of forgetting. The precision and consistency of the elephants' performance in tests of odor discrimination ability and long-term odor memory demonstrate the suitability of this method for assessing olfactory function in this proboscid species. An across-species comparison of several measures of olfactory learning capabilities such as speed of initial task acquisition and ability to master intramodal stimulus transfer tasks shows that Asian elephants are at least as good in their performance as mice, rats, and dogs, and clearly superior to nonhuman primates and fur seals. The results support the notion that Asian elephants may use olfactory cues for social communication and food selection and that the sense of smell may play an important role in the control of their behavior.

1. Introduction

Behavioral evidence suggests that Asian elephants *(Elephas maximus)* strongly rely on their sense of smell in a variety of contexts including foraging, social communication, and reproduction [1–3]. In fact, the Asian elephant is one of the few mammal species so far for which a sex pheromone has been chemically identified and functionally verified [4,5]. Anatomical evidence of well-developed olfactory and vomeronasal systems [6–8] as well as of specialized scent glands [9,10] further supports the idea that the sense of smell plays a crucial role in regulating the behavior of Asian elephants.

However, until now no behavioral test exists which would allow us to systematically assess the olfactory capabilities in this species. Asian elephants have successfully been trained in two-choice visual [11,12], auditory [13], and tactile [14] discrimination tasks. It was therefore the aim of the present study to develop and apply an olfactory discrimination test for Asian elephants and to collect first data on olfactory learning speed, olfactory long-term memory and olfactory discrimination performance. The test is based on a food-rewarded two-alternative instrumental conditioning procedure. The animals learn to sniff at two odor ports and are food-rewarded when they perform an operant response (putting the trunk at a certain position of the experimental set-up) upon correctly identifying the rewarded odor stimulus.

Similar instrumental conditioning procedures to assess olfactory learning capabilities and olfactory long-term memory have been employed with other mammals such as mice [15], rats [16], dogs [17], squirrel monkeys [18], spider monkeys [19], pigtail macaques [20], and South African fur seals [21]. This allows us to directly compare the speed of initial task acquisition, the ability to master intramodal stimulus transfer tasks, and olfactory long-term memory performance between species.

Using a set of structurally related odorants that has been used with humans [22], mice [23], squirrel monkeys [24], and South African fur seals [25] allows us to compare discrimination performance between species and to assess the mechanisms underlying between-species differences and similarities in this basic measure of olfactory capabilities.

2. Materials and methods

2.1. Subjects

Testing was carried out using three adult female Asian elephants *(E. maximus)* maintained at Kolmården Wildlife Park, Sweden. Bua, Saonoi, and Saba were 13, 14, and 42 years old at the start of the study. The animals were kept as a group in two indoor enclosures (approximately 150 m^2 and 250 m^2) but were let outside into an

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outdoor back enclosure (750 m^2) or an outdoor exhibit (3000 m^2) for a larger part of the day or at least once a day and when the weather was appropriate. The elephants were fed pellets in the morning and roughage and branches were provided ad libitum. Environmental enrichment in the form of scattered and hidden fruits and vegetables throughout the enclosure was provided at least once a day and no food deprivation was required during the study. The elephants were kept in a hands-on system in which the keepers have full access to the animals and they were therefore accustomed to follow commands and perform certain motor patterns upon demand.

The experiments reported here comply with the *Guide for the Care and Use of Laboratory Animals* (National Institutes of Health Publication no. 86–23, revised 1985) and also with current Swedish laws.

2.2. Odor stimuli

A set of 11 monomolecular odorants was used (Table 1). The rationale for choosing these odorants was that the same set of stimuli has been used in previous studies with other species and thus allows for direct comparisons of learning speed and discrimination performance. All odorants were obtained from Sigma-Aldrich (St. Louis, MO) and had a nominal purity of at least 99%. They were diluted using near-odorless diethyl phthalate (Sigma-Aldrich) as the solvent. The level of dilution was chosen to provide stimuli that were easily detectable and of approximately equal subjective intensity for humans (Table 1).

2.3. Experimental set-up

For the presentation of odorants two high density polyethylene (HDPE) boxes with removable lids (35×35×20 cm, Rubbermaid Cooling Bags, Huntersville, NC) were used. The tight fitting lid of each odor box was equipped with a ventilator (6 cm diameter, RS Components, Malmö, Sweden) powered by a lead accumulator (12 V, 1.3 Ah, Clas Ohlson, Stockholm, Sweden), which provided an ingoing airflow of approximately 0.58 $m^3\,min^{-1}$. A total of 130 holes of 3 mm diameter placed in intervals of even distance forming a filled circle with a diameter of 7.5 cm were drilled in an exact pattern in the middle of one of the front sides of each odor box, serving as an outlet for the airflow provided by the ventilator.

In order to present an odorant a circular filter paper of 9 cm diameter (Grycksbo Paper, Grycksbo, Sweden) was placed into an open Petri dish and 1 ml of the odorant was pipetted onto it. The petri dish, in turn, was placed into an open white plastic HDPE box (12×20×12 cm) inside the odor box to avoid contamination. The odor boxes were cleaned with warm water and perfume-free detergent after the completion of each session.

Testing was carried out in a separate indoor enclosure in which the animals could be trained individually. The trainer was positioned in the experimental room on the second floor where an opening in the wall was fitted with a service door (106×90×5 cm) made of steel. The door was modified to hold a window (45×75 cm) in its upper part which was covered with a steel grid (with a mesh width of 4×4 cm) that physically separated the trainer from the animals while allowing the trainer to observe and interact with the animals and to present the food reward (Fig. 1). The grid also served as a barrier that kept the elephants from reaching and grabbing the odor boxes. The location of the door allowed the trainer to observe the animals while the animals had a very limited opportunity to see the trainer.

The service door was located approximately 3 m above the ground of the testing enclosure and was divided by a vertical bar (105×20×5 cm) in the middle into a left and a right section. Each section contained an odor port, that is, a round opening with a diameter of 21 cm, at the lower half part of the door. Both odor ports were covered with a steel grid (with a mesh width of 4×4 cm) on the experimenter's side allowing the animals to sample the odorized airstreams provided by the odor boxes, but preventing them from making physical contact with the boxes. Above the odor ports was the rectangular grid-covered window where the animals had to place their trunk in order to indicate their decision and to receive their food reward (Fig. 1). A wooden platform on the floor inside the experimental room ensured that the odor boxes were placed with their outlets congruent with the odor ports of the experimental set-up.

Table 1
Odorants used and their concentrations.

Odorant no.	Odorant name	CAS#	Dilution[a]
1	n-pentyl acetate	628-63-7	1:5
2	anethole	104-46-1	1:10
3	1,8-cineole	470-82-6	1:10
4	(+)-limonene	5989-27-5	1:3
5	(+)-α-pinene	7785-70-8	1:5
6	(−)-carvone	6485-40-1	1:3
7	ethyl butyrate	105-54-4	1:3
8	2-phenyl ethanol	60-12-8	1:3
9	ethyl acetate	141-78-6	1:10
10	n-propyl acetate	109-60-4	1:10
11	n-butyl acetate	123-86-4	1:5

[a] Note that the headspace above these liquid dilutions was further diluted by the airstream provided by the odor boxes (see Materials and methods section).

2.4. The behavioral test

The behavioral test was based on a food-rewarded two-choice instrumental conditioning procedure. The animals were trained to sniff at the two odor ports and then to indicate which of them held the rewarded odor stimulus (S+) by placing the tip of their trunk onto a defined position above the corresponding odor port.

At the beginning of each trial, the two odor boxes were placed with their outlets towards the odor ports and after a verbal command (the loudly spoken word “now”) an animal was allowed to sample the two stimuli as often as it liked. Immediately following the animal's decision, the two odor boxes were removed and, in the case of a correct response (placing the tip of the trunk onto a defined position above the odor port bearing the S+), the animal was rewarded with a carrot presented through the grid at the position where the animal had placed the tip of its trunk. In the case of an incorrect response (placing the tip of the trunk onto a defined position above the odor port bearing the S−) no reward was given to the animal. Thirty such trials were performed per session and usually two sessions were performed per animal and day. Care was taken to present the rewarded stimulus to the right or the left odor port adopting a pseudorandomized sequence with the limitation that the same option was not used more than three times in a row.

2.5. Experimental design

A total of 10 experiments were conducted (Table 2). Experiments 1 and 2 were performed to assess whether elephants can be trained to respond to an odor stimulus and to discriminate between two odor stimuli. Experiments 3–7 were performed to assess the elephants' ability to perform intramodal stimulus transfer tasks. This type of task assesses an animal's ability to master a discrimination task when either the rewarded stimulus is exchanged for a new one while the unrewarded stimulus is kept constant (tasks 4 and 6 in Table 2), or the unrewarded stimulus is exchanged for a new one while the rewarded stimulus is kept constant (tasks 3 and 5 in Table 2), or both the rewarded and the unrewarded stimuli are exchanged for new ones simultaneously (task 7 in Table 2). Experiment 8 was performed to assess the ability of the animals to discriminate between structurally related odorants that only differ from each

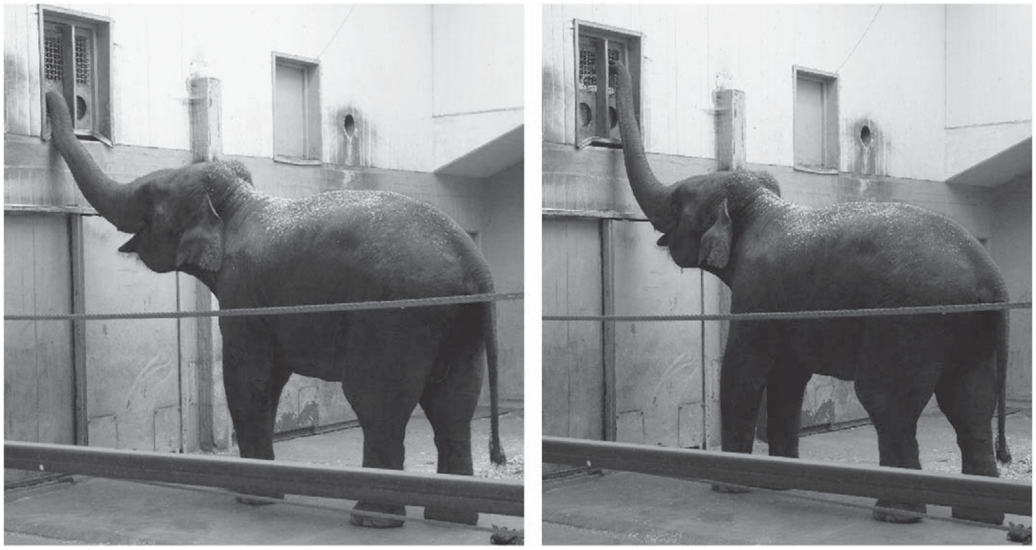

Fig. 1. The experimental set-up. Left panel: an elephant sampling one of the two round odor ports at the lower part of the experimental set-up. Right panel: an elephant performing the operant response, that is, putting its trunk onto the rectangular grid above the odor port bearing the rewarded odor.

other in their respective carbon chain length. Experiment 9 was performed to assess the long-term odor memory of the animals for a given odorant combination after a recess in training for a given period of time. Experiment 10 was performed as a control in which the lids and ventilators of the odor boxes were switched between sessions while the odor boxes and odor stimuli were kept constant.

2.6. Data analysis

In the method described here, the animal had two options: (1) to correctly respond to the rewarded stimulus (hit), and (2) to falsely respond to the unrewarded stimulus (false alarm). The percentage of hits was taken as the measure of performance. In all tasks, the criterion was set at 70% hits in two consecutive sessions of 30 decisions each (corresponding to $p<0.01$, two-tailed binomial test). The rationale for choosing this criterion was that similar standards have been used in previous olfactory studies allowing for direct comparisons of performance across species.

Correlations between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length were evaluated using the Spearman rank correlation coefficient. Comparisons of performance across individuals were made using the Mann–Whitney *U*-test for independent samples. Comparisons of individual performance in the first and second transfer tasks (negative and positive) as well as before and after recess in training were made using the Wilcoxon signed-rank test for related samples.

3. Results

3.1. Initial acquisition of the discrimination procedure

Fig. 2 summarizes the performance of the elephants in the first two experiments which assessed their ability to reliably respond to the presentation of an odor stimulus (when tested against a blank stimulus as the alternative) and to discriminate between two simultaneously presented odor stimuli. In both experiments, all three animals reached the learning criterion of 70% correct decisions in two consecutive sessions of 30 trials each (two-tailed binomial test, $p<0.01$) within the first two sessions. This corresponds to 60 trials or approximately 120 stimulus contacts (as the animals usually sampled both alternatives before making a decision). In both experiments,

Table 2
Experimental design.

Experiment		Odorant	
No.	Task	S+	S−
1	Initial training	1	Blank
2	Initial odor discrimination	1	2
3	First negative stimulus transfer	1	3
4	First positive stimulus transfer	4	3
5	Second negative stimulus transfer	4	5
6	Second positive stimulus transfer	6	5
7	Double stimulus transfer	7	8
8	Discrimination of structurally related odorants		
8a	Difference in carbon chain length = 3	1	9
8b	Difference in carbon chain length = 2	1	10
8c	Difference in carbon chain length = 1	1	11
9	Long-term odor memory tests		
9a	2 week recess	7	8
9b	4 week recess	4	5
9c	8 week recess	1	2
9d	16 week recess	6	5
10	Control experiment	1	2

Odorant numbers as in Table 1.

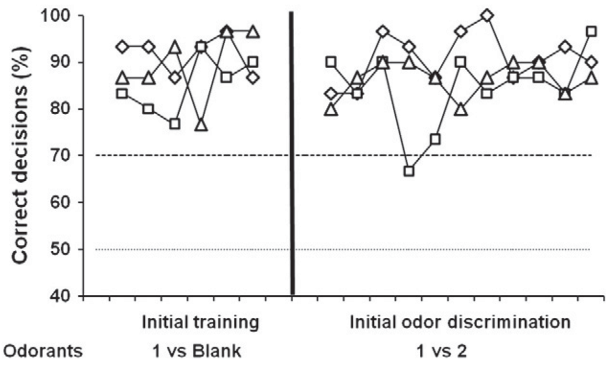

Fig. 2. Performance during initial acquisition of the olfactory discrimination procedure. Each data point represents the percentage of correct decisions per session (of 30 trials each). The three different symbols represent data from each of the three individual animals tested (Saba: diamond; Saonoi: square; Bua: triangle). The horizontal dotted line indicates chance level (at 50%) and the horizontal dashed line indicates criterion level (at 70%). The solid vertical line indicates the switch between tasks. Odorant numbers are explained in Table 1.

performance was relatively stable and with only one exception (Saonoi in session 4 of experiment 2) all animals performed above criterion in all sessions.

A comparison of performance across individuals during the initial acquisition of the discrimination procedure showed that Saba performed significantly better than Saonoi (Mann–Whitney, $p<0.01$), but no such difference in performance was found between Saba and Bua or between Saonoi and Bua, respectively (Mann–Whitney, $p>0.05$).

3.2. Intramodal stimulus transfer tasks

Fig. 3 summarizes the performance of the elephants in the experiments which assessed their ability to perform intramodal stimulus transfer tasks. All three animals successfully mastered the two negative stimulus transfer tasks (tasks 3 and 5 in Table 2) and reached the learning criterion within two sessions (two-tailed binomial test, $p<0.01$). Thus, the learning speed of the animals did not differ significantly between the first and the second negative stimulus transfer task (Wilcoxon, $p>0.05$). Similarly, all three animals successfully mastered the two positive stimulus transfer tasks (tasks 4 and 6 in Table 2) (two-tailed binomial test, $p<0.01$). However, the animals needed four (Bua), five (Saonoi), and ten (Saba) sessions, respectively, to reach the learning criterion in the first positive stimulus transfer task, whereas they needed only two sessions to do so in the second task of this kind. Thus, the learning speed differed significantly between the first and second positive stimulus transfer task (Wilcoxon, $p<0.05$). All three animals also successfully mastered a double transfer task (task 7 in Table 2) and reached the learning criterion within two (Bua) and three (Saba and Saonoi) sessions, respectively (two-tailed binomial test, $p<0.01$). Thus, the learning speed in the double transfer task did not differ significantly from that in the two negative stimulus transfer tasks and the second positive stimulus transfer task (Wilcoxon, $p>0.05$).

A comparison of performance across individuals in the intramodal stimulus transfer tasks showed that Saonoi performed significantly better than Saba and Bua (Mann–Whitney, $p<0.01$) whereas no significant difference in performance was found between Saba and Bua (Mann–Whitney, $p>0.05$).

3.3. Discrimination of structurally related odorants

Fig. 4 shows the performance of the elephants in discriminating between structurally related odorants. All three animals were clearly able to discriminate between all three odorant pairs (two-tailed binomial test, $p<0.01$) and already performed above the criterion of 70% correct decisions in the first session of 30 trials (as depicted in Fig. 4). There was a significant negative correlation between discrimination performance and structural similarity of the odorants in terms of differences in carbon chain length (Spearman, $r_s = 0.905$, $p<0.05$).

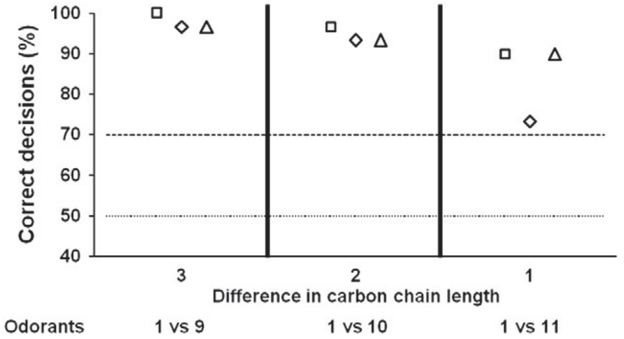

Fig. 4. Performance in the odor discrimination tasks with structurally related odorants. Each data point represents the percentage of correct decisions during the first session (of 30 trials) with a given stimulus pair. The three different symbols represent data from each of the three individual animals tested (Saba: diamond; Saonoi: square; Bua: triangle). The horizontal dotted line indicates chance level (at 50%) and the horizontal dashed line indicates criterion level (at 70%). The vertical solid lines separate the different tasks. Odorant numbers are explained in Table 1.

A comparison of performance across individuals in the discrimination of structurally related odorants showed no significant differences between the three animals (Mann–Whitney, $p>0.05$).

3.4. Assessment of long-term odor memory

Fig. 5 summarizes the performance of the elephants in tests of long-term odor memory. With all three animals and all four recess intervals tested (2, 4, 8, and 16 weeks, respectively) there was no significant difference in performance between the last two sessions before and the first two sessions after a given recess interval (Wilcoxon, $p>0.05$). To exclude the possibility that the high degree of performance that the elephants showed in the first session after a given recess interval was due to fast re-learning instead of long-term memory we additionally analyzed the first six trials in each of these first after-recess sessions separately. In all 12 cases the animals made at least five correct decisions in the first six trials (in six cases even 6/6), and in 10 out of

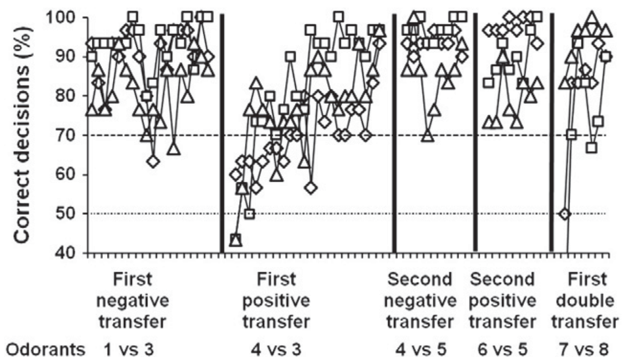

Fig. 3. Performance in the intramodal stimulus transfer tasks. Each data point represents the percentage of correct decisions per session (of 30 trials each). The three different symbols represent data from each of the three individual animals tested (Saba: diamond; Saonoi: square; Bua: triangle). The horizontal dotted line indicates chance level (at 50%) and the horizontal dashed line indicates criterion level (at 70%). The solid vertical lines indicate the switch between tasks. Odorant numbers are explained in Table 1.

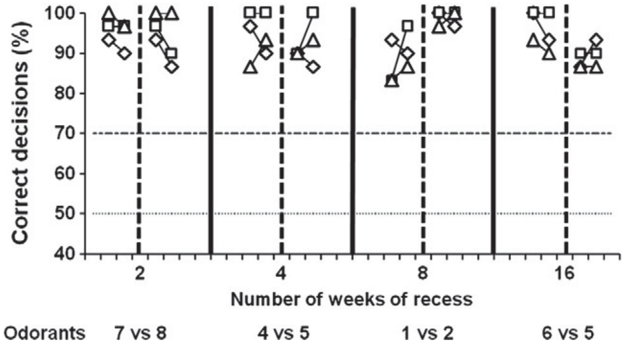

Fig. 5. Performance in the long-term odor memory tasks. Each data point represents the percentage of correct decisions in the last two sessions (of 30 trials each) before and the first two sessions after the recess in training, respectively. The vertical dashed lines indicate the recess in training, and the vertical solid lines separate the different recess intervals. The three different symbols represent data from each of the three individual animals tested (Saba: diamond; Saonoi: square; Bua: triangle). The horizontal dotted line indicates chance level (at 50%) and the horizontal dashed line indicates criterion level (at 70%). Odorant numbers are explained in Table 1.

12 cases they even correctly decided for the S+ in the very first trial after a given recess interval.

No significant correlation between performance in the first two sessions after a given recess and the length of the recess interval was found (Spearman, $p>0.05$).

A comparison of performance across individuals in the long-term odor memory tasks showed no significant differences between the three animals (Mann–Whitney, $p>0.05$).

3.5. Control experiment

In this experiment the lids and ventilators of the odor boxes were switched between sessions while the odor boxes and odor stimuli were kept constant. The performance of the animals during the session with switched lids and ventilators did not differ significantly from their performance during the sessions before and after this switch. This was true with all three animals (Wilcoxon, $p>0.05$).

4. Discussion

An increasing number of behavioral observations suggest that Asian elephants strongly rely on their sense of smell. However, in order to understand olfactory function and to fully appreciate the role that olfactory stimuli may play in regulating the behavior in this proboscid species, it is necessary to gain knowledge as to the animals' basic perceptual capacities. Although observations of spontaneous preferences or olfactory-related behaviors are clearly important they are limited in their validity with regard to olfactory performance due to their dependence of responding on experience and motivational state of the animals and due to a lack of stimulus standardization and control. It was therefore the aim of the present study to develop a means of reliably assessing olfactory performance in Asian elephants using a method that was not based on spontaneous preferences or behaviors and that allows for standardization and control of odor stimuli.

The results of the present study demonstrate that Asian elephants can successfully be trained to cooperate in an olfactory discrimination test based on a food-rewarded two-alternative instrumental conditioning procedure. The animals readily acquired the basic principle of the test, mastered intramodal stimulus transfer tasks, showed well-developed olfactory discrimination skills with structurally related odorants, and displayed an excellent long-term odor memory.

An across-species comparison of olfactory learning performance between the Asian elephants tested here and other species trained in two-odor discrimination tests using food-rewarded instrumental conditioning procedures shows that the speed of initial task acquisition (120 stimulus contacts till criterion with the elephants) was at least as good as that found with mice [15], rats [16], and dogs [17] which all needed <150 stimulus contacts, respectively. The elephants' learning speed in the initial task was clearly superior to that reported in nonhuman primates such as squirrel monkeys [18], spider monkeys [19], and pigtail macaques [20] which needed 450–750, 660–720, and 960–1800 stimulus contacts, respectively, to reach criterion. South African fur seals that were trained with a method very similar to the one used here [21] needed 480–880 stimulus contacts to reach criterion in the initial task and thus also a considerably higher number than the elephants. (Please note that the number of stimulus contacts rather than the number of trials are compared as some of the species mentioned above were tested using simultaneous presentation of odorants – in which one trial comprises at least two stimulus contacts – whereas other species were tested using sequential presentation of odorants – in which one trial comprises only one stimulus contact prior to an animal's decision.)

A comparison with learning speed in visual tasks obtained in various species lends support to the idea that Asian elephants appear particularly well prepared to use the sense of smell in learning tasks: whereas an Asian elephant needed 330 trials to reach learning criterion in a first visual discrimination task [26], and thus a considerably higher number than the 60 trials that our elephants needed in the present study with odor stimuli, squirrel monkeys and pigtail macaques needed <100 trials each to reach criterion in corresponding visual tasks, while mice and rats needed >700 trials [27]. (Please note that here the number of trials are compared as all species mentioned were tested using simultaneous presentation of visual stimuli.)

When comparing the speed of initial task acquisition among different species, one must keep in mind that the specific methods employed in two-choice odor discrimination tests necessarily differ to some extent in order to meet the motoric, physiological, and cognitive requirements of the species under investigation and the numbers mentioned above should therefore not be taken as absolute measurements. Nevertheless, the performance of the elephants in acquiring the initial task suggests that their learning speed with odor stimuli is comparable to that of species known to strongly rely on their sense of smell and that they readily learn to use olfactory stimuli when solving a discrimination task. This suggestion is further supported by the elephants' ability to quickly master intramodal stimulus transfer tasks (see Fig. 3). Here, too, the performance of the elephants in terms of number of stimulus contacts needed to reach criterion was generally comparable to the numbers reported in mice [15] and rats [16] and superior to that reported in nonhuman primates [18–20] and in South African fur seals [21].

Our finding that the elephants did not only succeed in discriminating between odorants that were structurally different from each other and, at least for humans, evoke clearly different odor qualities (as the ones used in the intramodal stimulus transfer tasks), but also readily discriminated between structurally similar odorants that belong to the same chemical class and only differed from each other in their respective carbon chain length suggests that *E. maximus* is also capable of distinguishing between fine nuances of odor qualities. Similar to humans [22], mice [23], and squirrel monkeys [24], the elephants displayed a significant negative correlation between discrimination performance and structural similarity in terms of differences in carbon chain length of the aliphatic esters used (see Fig. 4). This suggests that Asian elephants may use molecular structural features such as carbon chain length for odor quality perception and discrimination in a manner that is comparable to that of other, non-proboscid, mammals.

Although the size of the olfactory receptor repertoire of the Asian elephant has not been determined yet (a draft genome is currently compiled), another proboscid species, the African elephant, has recently been shown to have ≈1500 functional genes coding for olfactory receptors [28], and thus a higher number of such genes than the mouse, the rat, or the dog [29], all species presumed to have a highly developed sense of smell. In line with these genetic findings, a recent neuroanatomical study found that the olfactory bulbs of the African elephant display an unusual feature as their glomerular layer is composed of 2–4 layers of glomeruli instead of the mammal-typical 1–2 layers suggesting an unusually high degree of connectivity between the olfactory receptor cells and secondary neurons such as mitral and tufted cells [30]. Given that phylogenetically closely related species often share a similar number of functional olfactory receptor genes [31] this suggests that the Asian elephant might also possess a large repertoire of olfactory receptors. Further studies systematically assessing the elephants' discrimination performance with structurally related odorants will allow us to test the hypothesis that the efficiency of the olfactory system is correlated with the size of its receptor repertoire [32].

Throughout training and testing it was notable that weekend breaks, far from having detrimental effects on performance, only seemed to increase the animals' interest in the task, and in no case was there any evidence of short-term forgetting. Our results demonstrate that the elephants have an excellent long-term odor memory as they displayed no sign of forgetting of the reward values of odor stimuli after 2, 4, 8, and even 16 weeks of recess (see Fig. 5). This finding is in line with the general notion that elephants have an outstanding long-term memory [32] although only few studies so far directly assessed this cognitive ability [33]. McComb et al. [34] reported that family groups of free-ranging elephants recognized the calls of group members that had been absent for up to two years suggesting an excellent long-term auditory memory. Markowitz et al. [35] reported that a captive Asian elephant re-tested on a visual discrimination task after an eight year recess displayed retention of the reward value of the stimuli suggesting an excellent long-term visual memory. Given their longevity and their presumed reliance upon odor stimuli in different behavioral contexts it should not be surprising that elephants also possess a highly developed long-term odor memory. However, it should be mentioned that not only species presumed to strongly rely on their sense of smell such as mice [15], rats [16], gerbils [36], and guinea pigs [37] have been shown to display excellent retention of the reward value of odor stimuli over periods of weeks and months, but also species such as squirrel monkeys [38], spider monkeys [19], pigtail macaques [39], and South African fur seals [21]. Thus, further studies are needed to elucidate whether the elephants' long-term odor memory is superior to that in other species.

Taken together, the results of the present study demonstrate the suitability of the food-rewarded two-alternative instrumental conditioning procedure developed and employed here for assessing olfactory function and cognitive abilities in Asian elephants. The ease with which the animals learned the basic principle of the method and their apparent willingness to cooperate in all tasks with odor stimuli suggests that the experimental set-up, the use of positive (rather than negative) reinforcement, and the lack of restraint all met the motoric, physiological and cognitive capabilities and limitations of *E. maximus* which are a prerequisite for successful training. The excellent performance of the elephants in tasks of odor learning, odor discrimination, and long-term odor memory supports the assumption that the sense of smell plays an important role in regulating the behavior in this proboscid species. Future studies should systematically explore the discriminative abilities of the elephants as well as their sensitivity for odors to further our understanding of the role of olfactory information for foraging, food selection, and social communication in Asian elephants.

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