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Cover Page Footnote
This study would not have been carried out without the generosity of the Chicago Zoological Society and the cooperation of the staff of the Brookfield Zoo, especially Peter Crowcraft, George Rabb, Benjamin Beck, Mary Nichols, Gay Kuester, and the keepers at the Pachyderm Building — Dennis Houdek, Charles Pankow and Leroy Woodruff, Jr. Robert Hoffmann, Gunther Schlager and two anonymous reviewers provided helpful comments after reading earlier versions of the manuscript. One of the reviewers informed me of Fred Kurt's data. Financial support was provided by the Chicago Zoological Society through its Summer Program in Behavioral Research. This paper is part of a thesis submitted in partial fulfillment of the M.A. degree in the Department of Systematics and Ecology, The University of Kansas, Lawrence.

BEHAVIOR ASSOCIATED WITH FEEDING IN CAPTIVE AFRICAN AND ASIAN ELEPHANTS

Richard N. Racine

Abstract: Elephants' use of their trunks during feeding in captivity is described. African and Asian elephants differ not only in trunk morphology but also in trunk behavior. African elephants pick up objects using a "pinch" while Asians rely mostly on a "grasp." Asians normally use their feet to secure objects while Africans use their tusks. The first documented case of Africans using their feet is reported. Laterality or "handedness" is also reported for the first time in elephants. A survey of several zoos and circuses showed this phenomenon to be widespread in captivity. A female African elephant who was intensively studied showed lateral preferences for many different components of her feeding behavior.

Introduction

The most striking feature of modern elephants, besides their great size, is the proboscis or trunk. This organ, a prolongation of the nose and upper lip, performs a variety of functions including breathing, detecting odors and determining scent direction. The trunk is a formidable weapon as well as a highly sensitive tactile instrument (Crandall, 1964) and is also used in contact promoting behaviors, especially during sexual reproduction (Eisenberg, McKay and Jainudeen, 1971). Elephants can use their trunks to manipulate and use tools (Douglas-Hamilton and Douglas-Hamilton, 1975; Hall, 1963; Rensch and Altevogt, 1954; Steinbacher, 1965), mostly branches and twigs used for scratching and swatting flies. The trunk is most often used for securing and transferring food to the mouth, for squirting drinking water into the mouth and for spraying water or throwing dust over the body.

Morphologically, the trunk is annulated, especially in the African species (Loxodonta africana), and covered with sensory hairs. The tip of the trunk in the Asian elephant (Elephas maximus) has a single finger-like process on the dorsal edge while the ventral edge is flattened, usually with a faintly indicated division in the middle. The trunk tip of the African elephant differs in that it has both dorsal and ventral finger-like processes (Fig. 1). Unlike other mammals, the nasal cartilage does not extend into the septum of the trunk, and for this reason the trunk has great flexibility (Boas and Pauli, 1908). The septum between the nostrils stops a little short of the end of the trunk, facilitating use of the dorsal and ventral processes (hereafter called fingers) in apposition.

This study was undertaken to observe how captive elephants use their trunks and to compare the behavior of the two species.

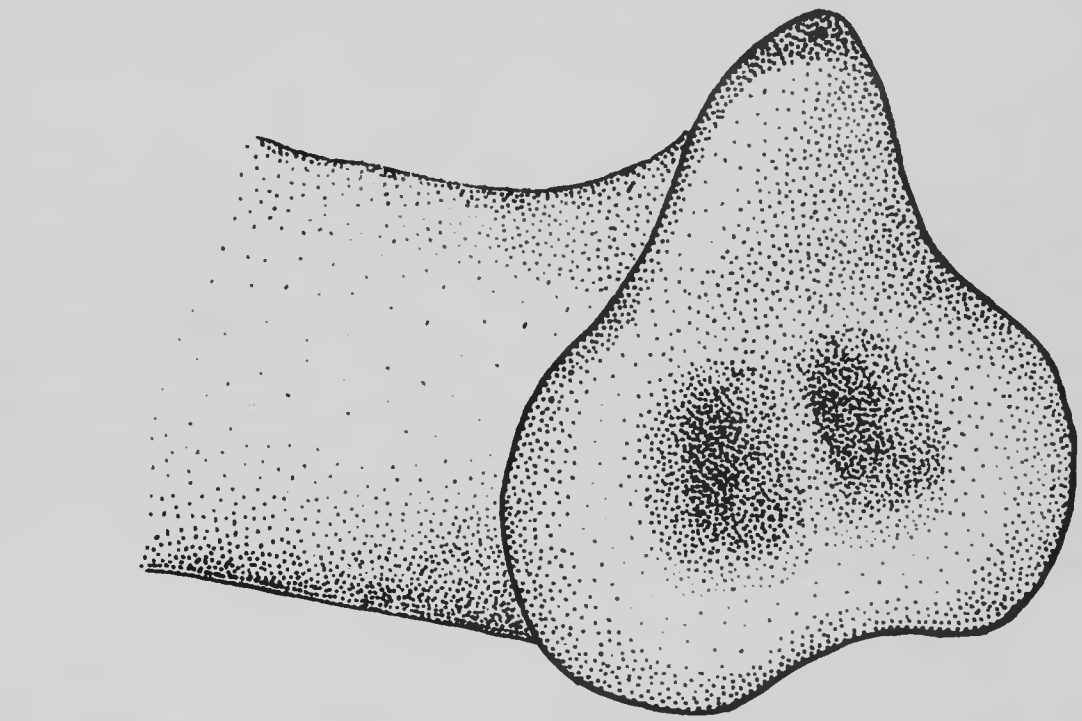

Figure 1. Elephant trunk tips -- a single "finger" in the Asian species (top) and two "fingers" in the African species (bottom).

Methods

This study was conducted from June through August, 1975 primarily at the Chicago Zoological Park (Brookfield Zoo), Brookfield, Illinois.

The Brookfield Zoo maintained six elephants (Table 1) during this study. The elephants were normally kept indoors during the night and allowed outside in moated enclosures between 0830 and 1600 hours (Minnie remained inside all the time). Each elephant was given a bale of hay when it first went out in the morning and later would forage for weeds and grass in the pen and surrounding moat for leaves on low hanging branches of trees on the opposite side of the moat. When the elephants were brought indoors they were each fed a large bucket of grains, bread, fruits and vegetables. They also received hydroponically grown grass and more hay. Water was always available.

Much of this study focused on Widget and Minnie since they were the only adults with fully functioning trunks. Babe and Ziggy both had injured trunks and, although they had adjusted their behavior accordingly, these behavicrs were clearly different from those seen from normal elephants. Mame and Patience had not yet fully developed their trunk behavior repertoires. Observations at other zoos and circuses (see Table 4) confirmed that Minnie and Widget were quite representative of their respective species.

To observe object manipulation, a variety of fruits and vegetables (see Table 2) was presented to the elephants on an irregular basis. The smaller items were presented in greater quantities because they were more readily available. Cut tree branches were also provided.

Results

PICKING UP OBJECTS

Elephants use several methods for picking up and holding objects, and there was a clear difference between the two species (Fig. 2). The size of the object influenced the method employed since smaller objects could be more easily pinched and large objects could only be grasped (see Table 2). The Africans almost always tried to use a pinch while the Asians were more variable but definitely preferred the grasp. A pinch-grasp, in which the item was first pinched and then the trunk curled around the item while it remained secured between the fingers was also used by the Africans. This might be repeated until several items accumulated. It was not necessary for a grasped item to be completely encircled by the trunk. The Asians were quite capable of holding small or thin items in a very shallow grasp by apparently constricting the surface of the skin that was in contact with the item.

Several other methods were seen. One I call "vacuum cleaning," in which the trunk tip was moved over the surface of the ground while the items were sucked into the trunk. This was normally used with very fine materials and, of course, this was the normal method for picking up water. These items had to be blown out of the trunk. Elephants with tusks can also secure items between one tusk and the side of the trunk, a process termed tusking. Tree branches are often picked up, pulled and/or broken with this method. Tusking is also a

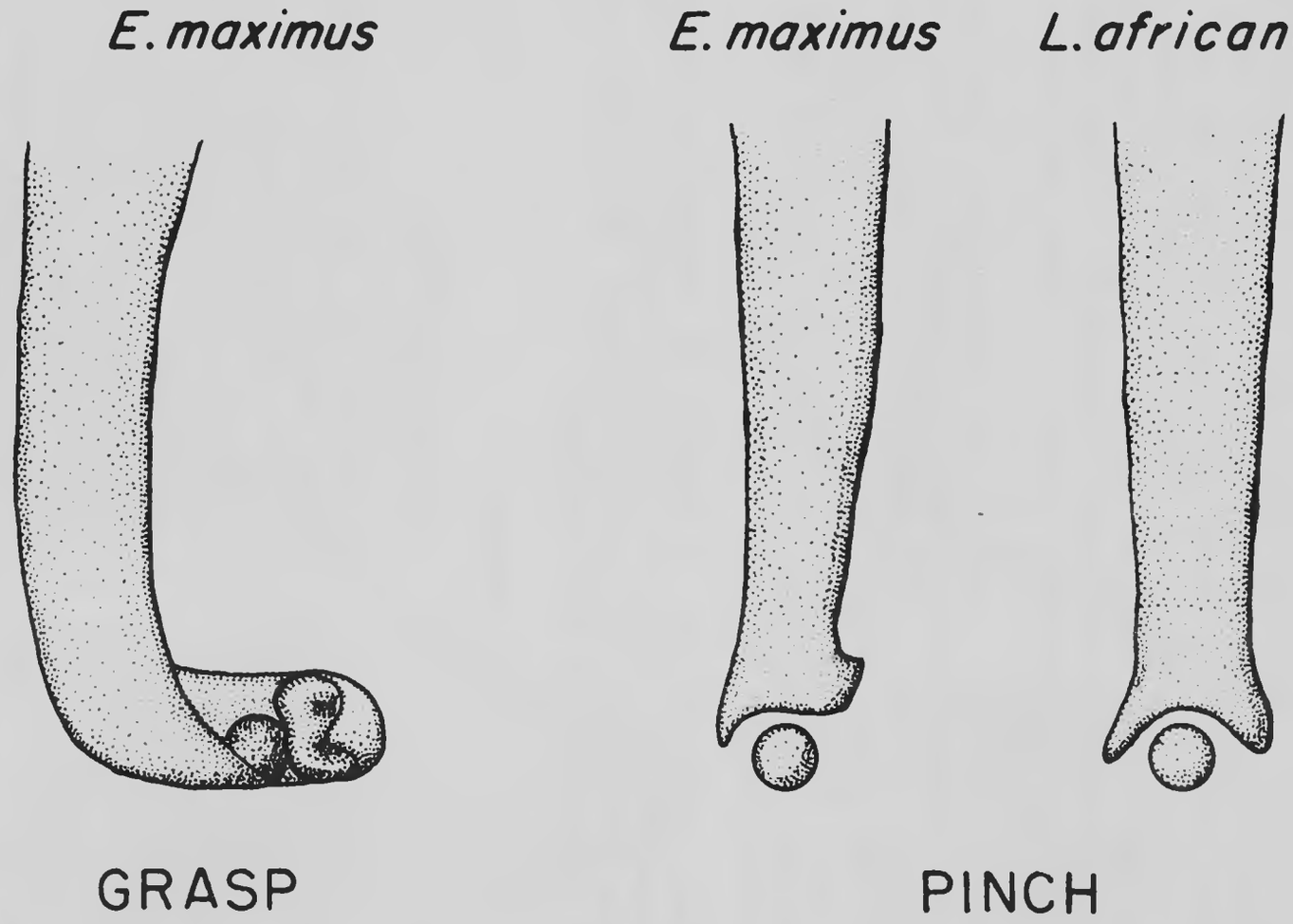

Figure 2. The two primary methods for picking up objects. A lateral view of the left side of the trunk is shown (i.e., the elephant would be facing to the left).

useful method for carrying items. Very large or bulky items were grabbed by wrapping the whole trunk around the object with the trunk going over the top of the item and then coming back underneath to support the bottom. If tusks are present, they are often used to help support the bottom of the item.

To get a better perspective on the differing pickup styles, a variety of fruits and vegetables was presented to the elephants and the method of pickup recorded (Table 2). If the item was crushed (see below), only the pickup (or attempted pickup) prior to the crushing was recorded.

Widget pinched everything but watermelons. When first presented with a watermelon, however, she always tried to pinch it and only after several unsuccessful attempts to lift it did she finally resort to grabbing it with her whole trunk; this was scored as a grasp.

The African preference for pinching was clearly shown with a large item like a honeydew melon. After placing her fingers over the top of the melon, Widget pressed them tightly onto the melon and at the same time applied considerable suction with her trunk. She was able to lift the melon in this manner but had difficulty maneuvering it to her mouth. She lifted her head and tilted it backward so as to swing the melon toward her mouth. She sometimes twisted her trunk as she tried to get the melon higher up, her trunk looking like a corkscrew. She was not always successful and dropped the melon which split open. She would then pick up the pieces by pinching each. She did not appear to be deliberately trying to break the melon.

Mame, with her smaller trunk, had to resort to grasping items as small as large apples and oranges, after she had first tried to pinch them. Although size class two (Table 2) did not show a significant difference in method for Mame, it was actually composed of two significant differences in opposite directions which canceled out. Mame pinched most of the apple halves (28 out of 32, $P < 0.01$) but grasped most of the whole items (20 out of 25, $P < 0.01$).

After lifting a large item off the ground, Mame adjusted her grip so that she had it positioned between her fingers and cradled at the same time. She then pushed the item up along the ventral surface of her trunk towards her mouth, positioning the item on the trunk tip like a golf ball on a tee. The ventral surface of the trunk was used to keep the object properly balanced.

Widget also balanced large items on her trunk tip. She initially pinched the object and then quickly swung it up while rotating her trunk tip beneath and then pushed the object straight to her mouth. She did not require the ventral side of her trunk for support because the spread of her fingers was wide.

Minnie used both methods (Table 2), particularly with long, thin items (size class 1), but grasped significantly more often. The method chosen seemed to be a function of distance, close items usually were grasped and items farther away either pinched or swept in closer and then grasped. Items against a wall were usually pinched. She never tried to pick up a large item but instead grasped it, pulled it in closer and then crushed it with one forefoot (see below).

Grain was handled in much the same manner as hay scraps. The Asians normally grasped and sometimes used a series of rapid multiple grasps that resembled "squeezing" and this appeared to be a method of gathering an appropriate amount in a pile before finally picking it up. After a portion of grain had been picked up it was transferred to the mouth by inserting the "hand" either straight in or over one lip. The "hand" was then rotated slightly so that the "palm" opened downwards. The tongue was pulled back so that it hooked the "hand" and when the grip was released, the tongue caught the grain and pulled it into the back of the mouth. As the grain pile disintegrated and spread out during eating, they repeatedly swept the contents back into the single pile by laying their trunk flat on the ground around the loose grain and then curling the trunk in towards themselves. As the curl became tighter, they would slowly lift the trunk off the ground, forming a conical pile from which they took small handfuls.

The Africans pinched as long as there was enough remaining that could be swept into a pinchable pile. When only fine residue remained, they spread their fingers wide apart and sucked the residue into the nasal tubes while moving the tip over the area. The grain was then blown into the mouth.

The Africans did not normally sweep in the same manner as the Asians. They usually used the inside surface of the dorsal finger to pull the scraps in towards themselves, repeating this procedure until a new pile had been formed.

Both species draw up water into their trunks and normally discharge it by blowing; the trunk of an adult holding about five liters (Benedict, 1936). To drink, the head was slightly elevated and the tip usually inserted straight in and rested on the tongue while the water ejected into the back of the mouth. Some elephants placed the tip over one lip in the corner of the mouth rather than straight in. Usually the fingers were closed together to hold the water in. The tip was then inverted so that it pointed up. Since the water can be retained in the trunk even when the fingers are not tightly closed, this would imply that suction is sufficient to hold water in the trunk.

Objects were often held in a cradle which freed the tip for other purposes. The cradle was formed by the inward curling of the trunk so that a loop was formed by the mid-section of the trunk. An item held by the tip was placed in this loop.

Cradling was used for adjusting a grip or removing unwanted portions from the amount held, such as dirt or rocks. Cradling was often seen when the elephant held something but wanted to test for scent without dropping the item on the ground. The cradle was also useful for simply carrying objects.

USE OF FEET

Another behavioral difference between the two species involved use of the feet. Asian elephants consistently use trunk-foot coordination while they eat (McKay, 1973), employing their feet to hold down items while they tear off portions with their trunk, and crushing items to make them more easily handled. Almost all large items were stepped on, and even small items, like apples and oranges, were frequently crushed. After the item was crushed, it was felt by

the tip, which was then inserted into the mouth. This behavior was presumably used to test food before eating it. The crushing might also be done to release the fragrances of the item (Sikes, 1971).

In contrast, African elephants are reported not to use their feet in this manner (Sikes, 1971; but see Buss, 1972 for a slightly contrary view).

Mame frequently used her feet to hold down sections of "hydrograss" while she tore off portions and on one occasion was seen holding down a pineapple while she tore out the crown. She also used her foot and toenails to break open a watermelon while bracing the melon with her trunk. She did not attempt to crush anything as do Asians. She broke open two other watermelons by kneeling down and driving her two little tusks (about 3" long and barely perceptible beyond the folds in her trunk) down into the melon, splitting it open, with considerable crushing. She remained on her knees and used her trunk to push pieces of melon into her mouth. These pieces would have been too large for her to pick up. Eventually she got up and finished eating in a normal fashion, with no further crushing.

Widget never deliberately stepped on a food item to crush it. She never held down items with her foot while tearing off portions although she did tusk items and then tear off portions. However, she did make one attempt to use her feet with a tree branch. After having disposed of most of the limbs and all of the leaves, she was left with a branch about five feet long. She had some difficulty in trying to break it into smaller pieces. She began trying to hold down one end with her foot while pulling up on the other end with her trunk. She also had a fork of the branch tusked and was pulling up with her head. Her actions were very uncoordinated. She did not have her foot far enough up on the branch to act as an effective fulcrum. She did not succeed in breaking the branch using her foot, despite several attempts, and finally gave up. Babe was then given the branch and broke up most of it.

LATERALITY

During the course of this study it appeared that the elephants were displaying lateral preferences with their trunks. Laterality can be defined as a significant preference for one side over the other in a bilateral situation. Normally the choice is between left and right, manifested with paired appendages during manipulatory situations (Brookshire and Warren, 1962; Cole, 1957). This phenomenon has previously been shown in monkeys (Brookshire and Warren, 1962; Kounin, 1938), rats (Tsai and Maurer, 1930), cats (Cole, 1955) and birds (Fisher, 1957; Friedman and Davis, 1938).

The trunk is a symmetrical organ with a right and left side. It was previously shown that elephants, especially Asians, grasp objects using the ends of their trunks like hands. This grasp has motions similar to those made by organisms with true hands. If we start with the palm facing down and the fingers pointing straight out, a right-handed grasp is performed by rotating the hand clockwise around its longitudinal axis for one-quarter turn and then curling the fingers in a counter-clockwise direction around the object. A left-hand grasp is just the mirror image of the right-hand. Fig. 2 shows a "left-handed" elephant.

Africans' preferred tendency to pinch objects when picking them up gives very little indication of laterality. However, if the item is too large or too firmly attached to be picked up by only a pinch, they will use a pinch-grasp which does show the lateral preference.

Hay eating, the most commonly observed behavior, was normally used for checking laterality. Sometimes other behaviors had to be used, particularly with Africans since they pinch most of the time. In some cases a lateral preference was never clearly determined.

Although there are no physical constraints on the laterality of a grasp, Table 3 shows that each elephant had a preference and maintained this preference in a variety of situations. The two elephants which displayed variability, Babe and Ziggy, had injured trunks, but whether this affected laterality is not known.

To check for the generality of this phenomenon in elephants, other zoos and circuses were visited to determine if laterality was shown and maintained (Table 4). It was possible to check individual elephants for consistency over a period of days and, in some cases, weeks. Some variability was noted but the elephants generally maintained a lateral preference.

Widget showed lateral preferences for several other behaviors that she used while eating hay (Table 5). Double folding was usually initiated with the opposite laterality of the other behaviors and was much less variable. Starting with a left fold meant finishing with a right fold. Possibly the second fold was more important since the ending positions for the two different types of folds were consistent with each other and this may have been the important factor prior to inserting the hay into her mouth.

BEGGING

A behavior observed on one occasion was a watermelon eating episode in which Widget had been given half a watermelon. She picked up the whole thing and put it into her mouth when Mame approached and stuck her trunk tip into Widget's mouth. Mame withdrew her trunk and laid it back on her forehead with the tip extended over her back. She opened her mouth and elevated her head. Widget ignored her so Mame repeated the entire sequence. Widget finished eating the melon and walked away while Mame went over and searched the ground for scraps. The posture that Mame used appeared to be very similar to the posture of a nursing baby elephant.

Discussion

The two elephant species can be distinguished not only by their trunk morphology but also by their trunk behavior. The major behavioral difference is the African elephant's use of a pinch (or pinch-grasp) to pick up objects, while the Asian elephants rely primarily on a grasp.

The morphology of the tip may account for this difference. The Asian elephant, with only one flexible finger, is quite capable of pinching and does so quite often. However, the African's two fingers encompass a much larger area

than the Asian's and the African's fingers appear to be better suited for pinching since both are flexible.

Another morphologic difference gives the Asians the advantage in grasping. Although the ventral finger does not extend out very far, it is expanded and fleshy. It actually forms a stop or hook which projects slightly back and this facilitates holding objects in a grasp. The musculature and skin in this "palm" area may also be specially developed to enhance grasping. In Africans, the ventral surface of the trunk runs straight out to the end of the finger. The ventral finger could be bent backwards and used as a hook but Africans usually use the inside surface of the dorsal finger (i.e., a pinch-grasp) when a grasping behavior is needed.

There has been some disagreement as to whether African elephants show trunk-foot coordination. Sikes (1971) says they do not. Buss (1972) and Wing and Buss (1970) state that Africans do show coordinated use of trunk and forefoot but the examples cited are trivial. Africans have not been reported using their feet to any degree equal to Asians except in pushing dirt onto their trunks for dusting.

Widget only made one unsuccessful attempt (with a tree branch) and appeared very uncoordinated in her actions. Mame, who never crushed food items with her feet, did show coordinated trunk-foot behavior during eating. It is unlikely that Mame learned this behavior from Asian elephants as an artifact of captivity because: (1) she was initially kept alone in the Children's Zoo for three years, (2) she had been with Widget at the Pachyderm Building for only a few months prior to the start of this study, and (3) she was isolated from the Asians.

Nevertheless, captivity may have been responsible for Mame's behavior. The types of foods given elephants in captivity may provide opportunities for learning trunk-foot coordination, especially by young elephants. The food is not attached to the substrate and is often difficult to handle. Because of their small size, young elephants must stand close to their food, if not on top of it. Without tusks the only way to secure an item is to hold it down with a foot. Under these conditions, young elephants could easily learn to use their feet. Patience, who was less than one year old, had already learned this behavior in isolation, at a period when most young elephants are totally dependent upon their mothers. It is always possible that this behavior is genetically determined in Asian elephants but that would not explain Mame's behavior. Given the elephant's hign degree of intelligence (Eisenberg, 1972), it is capable of learning this behavior when the opportunity is right.

This behavioral difference between the two species can also be related to their morphological differences. Female Asian elephants rarely have large tusks so they must rely on their feet to hold down objects, whereas Africans of both sexes have tusks and use them to hold items. However, Asian males in captivity use both methods. McKay (1973) was unable to confirm that wild Asian males use their tusks, primarily because he saw so few feeding male tuskers. Sikes (1971) reported that only Africans use their tusks and that they have a preferred tusk for stripping bark from trees, called the servant tusk. She

believed it was the stronger of the two, but this could have been a manifestation of a lateral preference.

Laterality, sometimes called handedness, is biologically important because functional asymmetries in the activities of the dominant and subdominant cerebral hemispheres have been demonstrated and related to the lateralization of speech and motor controls in man (Brookshire and Warren, 1962). Cole (1955) believed that the pyramidal systems of the cerebral cortex were the important determinants of handedness, and in elephants, the large motor-nerve fibers extending up and down the trunk correspond to the pyramidal tracts in humans (Altevogt, 1975). Warren (1958) showed that environmental factors and learning were as important as the anatomical explanation given by Cole and these factors became more important in determining laterality in the higher mammalian orders. Laterality in Asian elephants may well be learned (Fred Kurt, unpublished data from Sri Lanka). Although Hecaen (1969) stated that functional dominance by one hemisphere had never been shown in any non-human species and, therefore, laterality in animals should not be considered as homologous with manual preference in man. Other studies have provided evidence that cerebral dominance may occur in other species (Hamilton, Suzannah and Farrel, 1974; Warren, Abplanalp and Warren, 1967).

For whatever reason, the elephants in this study clearly showed lateral preferences with their trunks.

Acknowledgments

This study would not have been carried out without the generosity of the Chicago Zoological Society and the cooperation of the staff of the Brookfield Zoo, especially Peter Crowcraft, George Rabb, Benjamin Beck, Mary Nichols, Gay Kuester, and the keepers at the Pachyderm Building -- Dennis Houdek, Charles Pankow and Leroy Woodruff, Jr. Robert Hoffmann, Gunther Schlager and two anonymous reviewers provided helpful comments after reading earlier versions of the manuscript. One of the reviewers informed me of Fred Kurt's data. Financial support was provided by the Chicago Zoological Society through its Summer Program in Behavioral Research.

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TABLE 1

Brookfield Zoo elephants (Summer, 1975)

Species	Name	Sex	Age (years)	Tusks
African (Loxodonta africana)	Widget	F	22	Y
	Mame	F	4	Y**
Asian (Elephas maximus)	Ziggy*	M	59	Y
	Minnie	F	49	N
	Babe	F	26	N
	Patience	F	1	N

NOTE: Ages are approximate.

*Died October 27, 1975.
**Her tusks were barely visible.

F = Female, M = Male
Y = Yes, N = No

TABLE 2

Method of picking up food items in different size classes
Pinch versus Grasp

Size Class+	0		1		2		3		4		Total	
Method	**P**	**G**	**P**	**G**	**P**	**G**	**P**	**G**	**P**	**G**	**P**	**G**
Widget	23**	0	33**	0	72**	0	18**	0	0	4	146**	4
Mame	15**	0	37**	1	33	24	0	6*	0	2	85**	37
Minnie	15	60**	32	21	24	47**	0	10**	0	4	71	142**
Babe	16**	0	8**	0	9**	0	1	4	0	2	34**	6

NOTE: Significance determined with a binomial test of P(pinch) = G(grasp) = 0.50 (Siegal, 1956).

* = $P < 0.05$
** = $P < 0.01$
+0 = peanuts, grapes
1 = carrots, bananas, corn
2 = oranges, apples, (whole and halves), hard rolls
3 = coconuts, grapefruits, melons
4 = watermelons

TABLE 3

Lateral preferences shown by the Brookfield Zoo elephants when picking up a variety of different objects. Left vs. Right

Class+	1		2		3		TOTAL	
Preference	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
				Elephas maximus				
Patience (♀)	12**	0	13**	0	12**	0	37**	0
Babe (♀)	18**	2	1	8*	9**	1	28**	11
Minnie (♀)	22**	0	9**	0	7**	0	38**	0
Ziggy (♂)	4	2	5	0	3	0	12**	2
				Loxodonta africana				
Mame (♀)	7**	0	23**	4	3	0	33**	4
Widget (♀)	11**	0	4	0	5	0	20**	0

NOTE: Significance determined with a binomial test of P(left) = P(right) = 0.5 (Siegal, 1956).

* = $P < 0.05$
** = $P < 0.01$

+1 = grass, hay, tree branches
2 = grains, fruits, bread
3 = dirt, rocks, other inedible objects

TABLE 4

Survey of elephant laterality

	Elephas maximus		Loxodonta africana	
	Left	Right	Left	Right
Brookfield Zoo	4	0	2	0
Milwaukee Zoo	2	1	2	1
St. Louis Zoo	4	3*	1	0
Topeka Zoo	2	0	0	1*
Circus Vargas	2	6	0	1*
Carson and Barnes Circus	12	9	0	1*
Ringling Bros. and Barnum & Bailey Circus	10	8	0	0
Total+	36	27(1)	5	4(3)

*An elephant which could not be positively categorized was tentatively included in this class. +The number in parentheses indicates the total number of elephants included but not positively categorized.

TABLE 5

Widget's lateral preferences during hay eating

Behavior	Left	Right
Tusk	53*	32
Carry	14**	1
Test for scent	28**	4
Fold	126**	55
Double fold	7	94**

NOTE: Significance determined with a binomial test of P(left) = P(right) = 0.5 (Siegal, 1956).
* = $P < 0.05$ ** = $P < 0.01$

Editor's note: This paper, by Richard N. Racine, was reviewed by William H. Elder and John F. Eisenberg. Elder writes: "The observations were carefully conducted and the paper is well written, but my general feeling is that there will be little that is new to people familiar with elephants. The left and right handedness is a new and interesting observation. . . I am uneasy about conclusions drawn strictly from animals in confinement for two reasons: (1) the numbers were too few (really only one adult of each species was studied in detail) and (2) the repertoire of zoo animals must be limited by lack of normally diverse objects and actions frequently pursued in the wild (like picking fruit from trees, digging bulbs and roots, pulling clumps of grass and knocking off dirt against a leg, etc.). Eisenberg indicated that ". . . in spite of the frequent references in the popular literature to the trunk of the elephant as being employed as an offensive and defensive weapon, I have very little direct information to confirm this. Elephants will strike with their trunks in known circumstances, such as when an adult pushes at a younger animal. But in extremely dangerous situations during attack, the trunk is generally coiled. In Asian elephants an attack is pressed home by kicking, especially in those forms where tusks cannot be brought into play (i.e., females and tuskless males). . . . On balance, I think this is a well written paper."