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Review

Large brains and cognition: Where do elephants fit in?

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Abstract

Among terrestrial mammals, elephants share the unique status, along with humans and great apes, of having large brains, being long-lived and having offspring that require long periods of dependency. Elephants have the largest brains of all terrestrial mammals, including the greatest volume of cerebral cortex. In contrast to what one might expect from such a large-brained species, the performance of elephants in cognitive feats, such as tool use, visual discrimination learning and tests of "insight" behavior, is unimpressive in comparison to the performance by chimpanzees and, of course, humans. Where elephants do seem to excel is in long-term, extensive spatial-temporal and social memory. In addition, elephants appear to be somewhat unique among non-human species in their reactions to disabled and deceased conspecifics, exhibiting behaviors that are mindful of "theory-of-mind" phenomena. Information gleaned from studies on the neural cytoarchitecture of large brains reveals that the neurons of the cerebral cortex of elephants are much less densely populated than in large-brained primates. The interactions between cortical neurons would appear to be more global and less compartmentalized into local areas, and cortical information processing slower, than in great apes and humans. Although focused neural cytoarchitecture studies on the elephant are needed, this comparative perspective on the cortical neural cytoarchitecture appears to relate to differences in behavior between elephants and their primate counterparts.

Keywords: Elephants; Cognitive behavior; Large brains; Memory; Higher order brain functions

Contents

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1. Introduction

Elephants, perhaps more than any other non-primate group of wild species, have intrigued naturalists and popular writers for centuries. While this influence undoubtedly reflects their large size and strength, the alleged memory and complex social behavior of elephants have also contributed to this impact. Among terrestrial mammals elephants share the unique status, along with great apes and humans, of having large brains, being long-lived and having offspring that require long periods of dependency. Elephants not only have the largest brains but also the greatest volume of cerebral cortex of all terrestrial mammals.

When delving into what information is available regarding the performance of elephants in some aspects of cognitive behavior, namely feats of tool use, tests of so-called insight behavior and visual discrimination learning, one finds them unimpressive in comparison to chimpanzees and, of course, humans. Where elephants do appear to excel is in long-term, extensive spatial-temporal and social memory. Elephants also appear to be unusual among non-human animals in exhibiting behaviors that could potentially be related to "theory-of-mind" phenomena, particularly with regard to mirror self-recognition, attempts to assist injured or disabled conspecifics and ceremonial-like investigation of the remains of deceased conspecifics.

Reflection upon the anatomical, physiological and life-style (ecological) differences between elephants and great apes provides a perspective to explain the somewhat paradoxical relationship between the large brains of elephants and their relatively weak performance on cognitive tasks. For example, in great apes and humans, digestive physiology and feeding behavior are oriented on consuming foods rich in protein and energy. Relatively small volumes of food are highly valued and there are logically fitness benefits for cognitive behaviors that increase the availability of foods such as insects, nuts and fruits. Elephants, in nature, customarily consume a diet with the lowest concentration of calories and protein of any mammalian species and their digestive system is adapted for the ingestion of large volumes of forage with low nutritive value. Elephants spend an estimated 60–80% of each 24-h day obtaining this low quality forage (Owen-Smith, 1988). For elephants, meeting foraging and water requirements does not involve coordinated, fine-grained cognitive responses but rather an ability to reliably locate scattered, distant foraging and water resources. Not surprisingly, therefore, the types of cognitive behavior where chimpanzees seem to greatly outperform elephants are those in which highly coordinated, fine-grained cognitive responses would appear to be paramount.

Another biological difference influencing cognitive behavior involves those responses where binocular vision could play a major role. Elephants have much less binocular overlap and possibly weaker visual resolution than primates (Rensch and Altevogt, 1955). While the tip of the trunk is capable of fine manipulations, one cannot expect analogous vision-dependent behavioral performance in elephants as in chimpanzees with relatively complete binocular overlap and elaborate digital manipulation abilities.

It is acknowledged that natural selection can be expected to influence brain organization to support behaviors with the greatest fitness consequences (Balda and Kamil, 2002; Hofman, 2003). Elsewhere we have discussed the available neurobiological studies on the anatomy and cytoarchitecture of the brains of elephants and large-brained primates, introducing the perspective that elephants differ from primates in the way in which cerebral cortical neurons interact (Hart and Hart, 2007). This perspective suggests that while the elephant brain effectively mediates long-term, extensive information storage, their brains have more limited capacity for some types of cognitive tasks such as highly coordinated or fast-action tool use, simultaneous visual discriminatory learning and insight behavior, which are behaviors in which chimpanzees, with a cerebral cortical volume one-tenth that of elephants, perform well. In this review, we expand on this perspective by first reviewing the studies that show that elephants fall short of the performance of chimpanzees in primate-like tests of cognitive behavior but excel in capacity for extensive long-term memory. We introduce the concept that some theory-of-mind-like behaviors, that appear unique to elephants among non-human animals, may also relate to the unique cytoarchitecture of the brains of elephants.

There are currently three recognized species of elephants. The African savannah elephant (*Loxodonta africana*) is the largest species. The forest elephant, *Loxodonta cyclotis*, previously considered to be a subspecies of the African savannah species, is now classified as a separate species (Comstock et al., 2002; Roca et al., 2001). Given that so little behavioral information exists about the forest elephant, our review covers only the African savannah elephant (which we will refer to as the African) and the Asian elephant (*Elephas maximus*) which may be divided into subspecies related to Asian locations (Sukumar, 2003).

2. Behavioral comparisons between elephants and great apes

We will sometimes use the term often used by neurobiologists, "higher order brain functions," to refer collectively to cognitive behavior, extensive long-term memory and theory-of-mind-like behaviors in elephants. With the possible exception of tool use, various aspects of cognitive behavior are not without controversy with regard to the tests required to meet specific criteria and interpretation of results (Boysen and Himes, 1999). This controversy would not seem, however, to preclude a meaningful discussion of various aspects of cognitive behavior as they apply to comparing large-brained primates and elephants.

The perspectives under the heading, "Comparative Aspects of Cognitive Behavior," that deal with tool use, insight behavior and visual discrimination learning in elephants are derived from published experimental tests on captive Asian elephants. The perspectives under the headings "Elephants and Long-term, Extensive Memory" and "Elephants and Behaviors Suggestive of Theory of Mind Phenomena" reflect both opportunistic observations of relatively rare events, mostly in wild African elephants, and sound scientific studies supporting these opportunistic observations. The opportunistic observations mentioned here represent valuable anecdotal data with high external validity, as recently discussed by Bates and Byrne (2007). We have been guided by their principles in establishing criteria for determining credibility of the anecdotal data set. Briefly stated, these principles involved: (1) utilizing observations by experienced field investigators familiar with the species; (2) using directly observed behavior, presumably reflected in field notes and subsequently published; and (3) discussing only phenomena for which there are multiple records of relevant anecdotal data from different authorities. Because of the highly species-specific nature of the long-term memory and theory-of-mind-like events, these headings do not include specific comparisons with great apes or humans.

2.1. Comparative aspects of cognitive behavior

The overriding interest in the cognitive behavior of great apes, especially chimpanzees (*Pan troglodytes*), is understandable given the interest in achieving insights into the biological underpinnings of human cognitive and social behavior. Tool use is increasingly studied, at least partially, because the behavior has quantifiable parameters and can be studied conveniently in captive animals.

2.1.1. Tool use and tool manufacture

The use of tools by wild chimpanzees is epitomized by the modification and use of sticks to fish termites out of underground nests or to probe inside bones to extract marrow (Matsuzawa, 2003; van Schaik et al., 1999). A particularly complex and coordinated example of tool use by chimpanzees is holding a nut against an anvil stone and hitting the nut with a hammer stone to crack it open (Humle and Matsuzawa, 2001). Tool use and modification are not, of course, just the prerogative of great apes or large brained mammals, and are fairly common across a range of animal taxa (e.g. Beck, 1980). Noteworthy in this regard are observations on New Caledonian crows (*Corus moneduloides*) that have long been known to forage using twigs cut so that a short projecting piece forms a hook to drag out invertebrates (Hunt, 1996). In experimental documentation of tool modification behavior in captive members of this species, investigators made only a straight wire available as a potential tool. The crows in most trials bent the wire to form a hook that was used to pull a food-containing bucket out of a transparent tube (Weir et al., 2002).

2.1.2. Tool use by elephants

Fly switching with branches in elephants may represent the first documented example of tool use in any non-human animal, dating back to 1838 when wildlife adventurer Harris (1838) wrote of seeing elephants emerging into an open glen which were "bearing in their trunks the branches of trees with which they indolently protected themselves from flies" (p. 169). Fly switching in elephants was mentioned by Darwin (1871) in discussing the intelligence of beasts, in the *Descent of Man*. In an 1879 issue of *Nature*, Peal (1879) describes a captive Asian elephant modifying a branch before using it as a switch. More recently, studies have documented the efficacy of fly switching in repelling flies (Hart and Hart, 1994) and the modification of branches to use as switches (Hart et al., 2001). The repertoire of tool use in Asian and African elephants also includes scratching with a stick and throwing sticks or stones at rodents competing for fruit beneath a tree (Chevalier-Skolnikoff and Liska, 1993; Hart and Hart, 1994; Kurt and Hartl, 1995; Wickler and Seibt, 1997). Despite the historical significance of elephant tool use (possibly reflecting the fact that in such a large animal the behavior would be hard to miss), the level and complexity of tool use in elephants does not compare with the repertoire of highly coordinated tool use described for chimpanzees.

2.1.3. Insight behavior and visual discrimination learning

One area of cognition where elephants have been compared with great apes is in tests of so-called insight behavior. The studies, though quite limited, reveal that elephants perform rather poorly. Two captive Asian elephants studied by Nissani (2004) for their ability to catch on to pulling a retractable cord thrown over a bridge to obtain a desirable object, did not perform in a manner where chimpanzees, rhesus monkeys, and even several species of birds, do quite well in comparable tests. Recently an experiment on 15 captive Asian elephants to test for their ability to apply "causal reasoning" to retrieve food from an uncovered bucket after being trained to remove a lid from the bucket to obtain food also revealed limitations (Nissani, 2006).

An illustration of the disappointment one finds in trying to document "insightful" tool use in elephants is an unpublished experiment we conducted several years ago on captive Asian elephants. We placed a favorite food used by elephant handlers on a platform suspended from a tree, initially allowing elephants to tip the platform with their trunk and be reinforced with access to the food. We then raised the platform just beyond the reach of the trunk and put a long stick in a prominent place that we assumed the elephant could see. We expected they might grasp the stick and tip the platform thus releasing the food reward. Several attempts at offering this puzzle to five elephants yielded no success. A similar test by Nissani (unpublished communication) produced the same result.

Visual discrimination learning is another area where the performance of elephants does not meet standards set by other mammals. Working elephants in Burma, maintained under semi-natural conditions, were tested for their ability to learn simultaneous black/white or large/small discrimination tasks. While some learned in a few trials, others never learned the discrimination and the performance of even the fastest learning elephants was unremarkable compared with other mammals in similarly designed tests (Nissani et al., 2005).

2.2. Elephants and long-term, extensive memory

Reflecting upon the extensive foraging demands, which are met by travel over long distances, along with family and clan associations which are maintained at long distances, one would expect fitness benefits for long-term memory about details of the environment regarding food and water resources, as well as social relationships, to be accumulated within the brains of single individuals that may live for 60–70 years or more. The documentation in this area comprises both careful observations (anecdotal data; see above) by seasoned investigators as well as experiments. In this section only elephants are dealt with because comparable behaviors on the part of great apes, or even humans, are not documented.

2.2.1. Spatial-temporal memory

Reflecting the large amount of forage that elephants consume, they must constantly move to new foraging grounds, with movements being influenced by rainfall and geographical barriers.

A recent detailed study of home range and seasonal movements of eight African elephants of the Kunene Region of the Namib desert area, using GPS/telemetry collars, revealed movements of up to 473 km in one group and up to 625 km in another group over 5 months (Leggett, 2006).

Previous studies by Viljoen (1989) of movements of radio-tagged elephants in the northern Namib Desert showed large home ranges during the dry season in which the elephants visited, every 4 days or so, water holes which could be more than 60 km apart. The ability of a family to head unerringly over huge distances towards one of several isolated water holes, after a stressful 4 days without water, is obviously an important element to survival.

Viljoen (1989) also noted that elephants of the Namib Desert travel, on an annual basis, from their home ranges to locations up to 195 km away in response to localized rainfall, arriving within 3 days after the start of the rains. Similarly, elephants at Tsavo were observed to travel up to 85 km to areas of localized rainfall (Leuthold and Sale, 1973). Given the precise and extensive observations by Leggett (2006) using GPS telemetry, the legendary travel by African elephants for hundreds of kilometers towards distant geographical targets is no longer in doubt.

The above studies of long distance movements, while not specifically testing memory of travel routes to distant locations, imply a memory of the locations to which the elephants travel over hundreds of kilometers. An illustration of the fitness benefits of long-term spatial-temporal memory comes from a study by Foley (2002) in Tarangire National Park in Tanzania during the severe drought of 1992–94. Clans with older matriarchs left the Park to forage in non-park areas but clans in which older matriarchs had been lost to poaching stayed in the Park, and with insufficient water and forage, suffered infant mortality and all-age mortality that was more than double that of normal clans. Matriarchs would have had to be at least 35 years old to have experienced at least one other equally severe drought and successfully travel outside the park. The matriarchs of the clan that remained in the park were too young to have experienced such a severe drought.

2.2.2. Social memory

Two areas in which one may expect long-term or detailed social memory to occur, and that can be experimentally verified, are recognition of individual acoustic characteristics and recognition of individual chemosensory signatures. Using playback experiments of recordings from family members or unfamiliar wild elephants at Amboseli National Park (Kenya), McComb et al. (2003) found that elephants could recognize individual calls from typically 1–1.5 km away. Nine acoustic features were important in distinguishing individual calls. However, the attenuation that occurs over distance is not consistent across all frequency domains of the acoustic signature of individuals. Because elephants can recognize calls of about 100 other elephants from various families and clans (McComb et al., 2000), one cannot help but be impressed by the memory capacity of an individual that can recognize the acoustic characteristics of 100 individuals, sometimes relying on just a fraction of the acoustic signature that is otherwise present at close range.

Families with older matriarchs, who have had time to accumulate a great deal of such social memory, are more adept at discriminating between familiar and unfamiliar individuals than families with younger matriarchs. A measure of the fitness benefit of the long-term memory ability was evident in that the age of the matriarch was a

significantly positive predictor of the number of calves produced in a family per female reproductive year (McComb et al., 2001).

Chemosensory characteristics of urine allow an animal to recognize individual conspecifics, possibly even decades after the last encounter. Urine of females is typically investigated by adult male elephants through the process of flehmen behavior which, presumably, is involved in the transport of fluid material taken into the mouth during flehmen to the vomeronasal organ for chemosensory analysis (Hart et al., 1989). Tests on captive Asian elephants reveal that young males flehmen selectively to the urine of their mothers and retain memory of chemical characteristics of their mother's urine for decades after they have been separated from their mothers (Rasmussen, 1995; Rasmussen and Krishnamurthy, 2000). This chemosensory memory could act as a means to avoid future inbreeding by adult male elephants which leave their natal families at a juvenile age.

2.3. *Elephants and behaviors suggestive of theory-of-mind phenomena*

The descriptive literature on great apes contains numerous references to behaviors that one may refer to as theory-of-mind-like responses. The definition of theory of mind and interpretation of experimental results are controversial. For our purposes, we will refer to two aspects of theory-of-mind behavior: (1) indications that the animal under consideration exhibits self-awareness and (2) indications that an animal's behavior is guided by an attribution of a mental or biological state to another animal. As with our discussion of long-term memory, the documentation in this area comprises careful observations (anecdotal data) by experienced investigators as well as experiments. In this section, with the exception of self-recognition, only elephants are dealt with because comparable behaviors on the part of great apes are not documented.

2.3.1. *Self-awareness and recognition*

The classical experiment that addresses this topic is the mirror test in which a spot is painted on the head of the animal and it has access to a mirror in which it can see itself. If the animal spontaneously uses the mirror to touch the spot on its head, this is considered evidence of self-awareness and recognition. Until recently, mirror self-recognition was documented only for humans and great apes. One paper now describes mirror self-recognition in dolphins (*Tursiops truncatus;* Reiss and Marino, 2001). The reaction in front of mirrors generally involves the following stages: (1) social responses or interaction with the reflected image; (2) physical inspection of the mirror such as looking behind it; (3) mirror testing behavior such as movements made only in front of the mirror; and (4) self-directed behavior indicating recognition of the mirror image of self; this is typically verified if the subject spontaneously uses the mirror to touch a mark on its body (Gallup, 1970). Animals without self-recognition tend to not progress beyond stages 1 and 2. In a carefully designed test of seven chimpanzees, three met the stage-4 criterion of self-recognition (Povinelli et al., 1993).

In a recent test of mirror self-recognition in three captive Asian elephants of the Bronx Zoo, New York City, a large mirror was placed in the enclosure of the elephants (Plotnik et al., 2007). Over the next several days, all three elephants progressed through the first three stages of mirror-related behavior. When an odor-free visual mark was applied to the heads of the elephants, along with a sham mark on the other side, one elephant progressed to stage 4 on the first day and used the mirror to touch the mark on her head. The other two did not progress to the fourth and definitive stage of mirror self-recognition. Progression of all elephants through stage 3 and one through stage 4 is roughly comparable to the performance of chimpanzees in which fewer than half pass the mark test of stage 4 (Povinelli et al., 1993; Swartz and Evans, 1991). Previous attempts to uncover mirror self-recognition in elephants were unsuccessful (Povinelli, 1989), possibly due to use of a small mirror. The authors of the recent paper on mirror self-recognition in elephants relate the concept of self-recognition to the phenomenon of sympathetic concern, including targeted empathic helping of conspecifics (de Waal, 2003). The topic of targeted empathic helping of conspecifics in elephants is taken up in the next section.

2.3.2. *Reactions to disabled conspecifics*

If one were to conjecture where the attribution of a mental state to another individual might play out in nature, one situation would be the reaction of able-bodied animals to injured or disabled conspecifics guided by an attribution of a state of disablement to the other animal. Such "targeted empathic helping" is a frequently noted behavior in African elephants in their reactions to conspecifics disabled by immobilization drugs or bullets. Table 1 lists examples of firsthand accounts (anecdotal data) of such observations by wildlife authorities. Typical of such accounts, occasioned by immobilization of African elephants for translocation, is a description by wildlife veterinarian, Harthoorn (1970, p. 205). Following the darting of an elephant, "there was an indescribable melee of screaming, trumpeting beasts... The young immobilized animal was lifted repeatedly on the tusks of the big older cows, until after two hours it began to stand and eventually... was marched off into the forest."

A recent observation by Douglas-Hamilton et al. (2006) provides missing pieces with regard to documentation of a naturally occurring disablement and whether or not assistance may be provided by elephants unrelated to the disabled animal. Relying upon GPS radio-tagged animals, field observations and photo documentation, the investigators were able to follow reactions of elephants to a matriarch, referred to as Eleanor, who had been severely injured in a fall and was seen with a swollen trunk.

Table 1
Opportunistic observations, comprising anecdotal data (see text) of targeted helping behavior of disabled conspecifics and investigation of deceased conspecifics in African elephants

Description of event	References
Assistance of injured or disabled elephants	
Lifting injured elephant (bullet)	Blunt (1933, pp. 97–98)
Protection and lifting of immobilized elephant	Douglas-Hamilton and Douglas-Hamilton (1975, pp. 109–110)
Attempt to lift fatally injured mother	Douglas-Hamilton and Douglas-Hamilton (1975, p. 235)
Attempts to lift fatally injured female	Moss (1988, pp. 73–74)
Attempts to pull calf from deep hole	Buss (1990, p. 26)
Attempts to lift family members	Foley (2002, p. 97)
Attempts to lift injured non-family matriarch	Douglas-Hamilton et al. (2006)
Investigation of deceased elephants	
Cover over feet, ears with vegetation	Harthoorn (1970, p. 207)
Investigate decomposing corpse	Douglas-Hamilton and Douglas-Hamilton (1975, p. 237)
Investigate bones	Douglas-Hamilton and Douglas-Hamilton (1975, p. 239)
Cover body of recently dead elephant	Moss (1988, pp. 73–74)
Cover head and shoulders of recently dead daughter with vegetation	Buss (1990, p. 34)
Investigate deceased elephants	Payne (2003, pp. 80–85)
Investigate clean bones and ivory of elephants	McComb et al. (2006)
Investigate corpse of recently dead matriarch	Douglas-Hamilton et al. (2006)

The matriarch's family was at least 1.5 km away, but 2 min after Eleanor fell to the ground an unrelated matriarch from another family rapidly approached Eleanor in some degree of excitement, sniffed and touched Eleanor's body with her trunk and foot and then, with her tusks, lifted Eleanor, back to her feet. When Eleanor began to collapse again the strange elephant pushed her in an attempt to get her to walk. Eleanor died the next day. This study provides evidence of attempts of an unrelated, relatively strange elephant to help a disabled elephant and stands in contrast to other instances of animals helping conspecifics where the assistance is offered by close relatives of the disabled member (Hart, 1990).

2.3.3. *Reactions to the remains of dead conspecifics*

More than any other aspect of elephant theory-of-mind-like behavior, accounts of investigation and ceremonial handling of recently deceased conspecifics abound in the literature. Table 1 provides examples of firsthand (anecdotal data) reports of observations by experienced investigators. The accounts lead one to conclude that the reactions to the remains of dead conspecifics, whether related to theory-of-mind phenomena or another syndrome, are population wide, at least among African elephants.

The study mentioned above regarding the fatal injury of a matriarch allowed the investigators, using GPS radio-tagged animals and direct observations, to record travels of elephants to the corpse of Eleanor over the subsequent 7 days. On the day of her death, a tagged family member that had been 2 km away from Eleanor spent 7 h in the vicinity of the corpse. During that time a female from another family, and relatively unfamiliar to Eleanor, "hesitantly" approached Eleanor's body, extended her trunk, sniffed the body, and then touched it. She hovered her right foot over and nudged the body, and with her left foot and trunk, rocked the body to and fro. The tagged member of Eleanor's family, accompanied at least on some occasions by the rest of her family, visited the body on the second and fourth days after her death. During the 5 days after her death the body was visited by unrelated elephants from three other families, providing clear evidence of the interest elephants have in the bodies of dead conspecifics, whether a family member or not.

Elephants differ from other non-human animals not only in their investigation of elephant corpses, but also in the bones of long dead elephants. Fig. 1 illustrates the nature of this interaction. This phenomenon was systematically investigated by McComb et al. (2006) who presented 17–19 family groups of elephants at Amboseli choices of three objects which had been dried, bleached and thoroughly cleaned. When offered ivory, an elephant skull and a piece of wood, the elephants significantly spent about six times longer investigating the ivory as the piece of wood and three times longer than the skull. In a second experiment, family groups were presented with skulls of an elephant, a buffalo or a rhinoceros. They spent, significantly, twice as much time investigating the elephant skull as either of the other two skulls. In a third experiment, elephants of three families, which had lost their matriarchs 1–5 years previously, were presented with the dried, bleached and washed skulls of their deceased matriarch and similarly treated skulls of matriarchs of the other two families. Elephants spent virtually the same amount of time investigating the skulls of non-related matriarchs as their deceased family matriarch. One could argue that while elephants identify the skeletal remains as members of their own species, interest in the remains is not linked to relatedness, a behavior that is mindful of the interest humans have in skeletal remains, especially skulls.

3. Comparative aspects of brain information processing

As mentioned, elephants have the largest brain of all terrestrial animals. Figures reported in the literature vary considerably and obviously depend on sex, age, species and the amount of brain stem and dura matter that were included in the measurement. Averaging across these variables, a common estimate for brain mass of adult elephants is 4700 g, ranging from 4050 to 5220 g (Shoshani et al., 2006). This is about 13 times the common estimate of

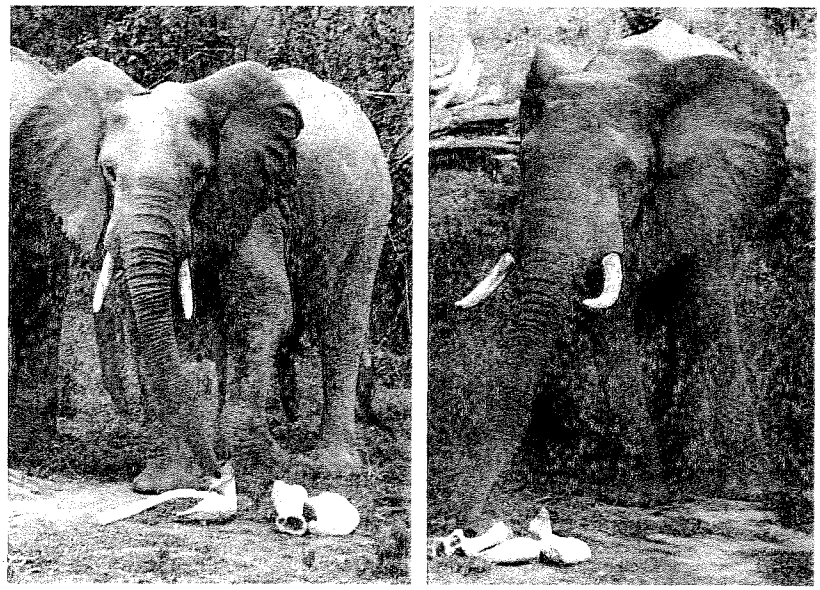

Fig. 1. Illustrations of examination of skeletal remains of elephants as described by field investigators working in Africa (see text). Photos by N. Pinter-Wollman.

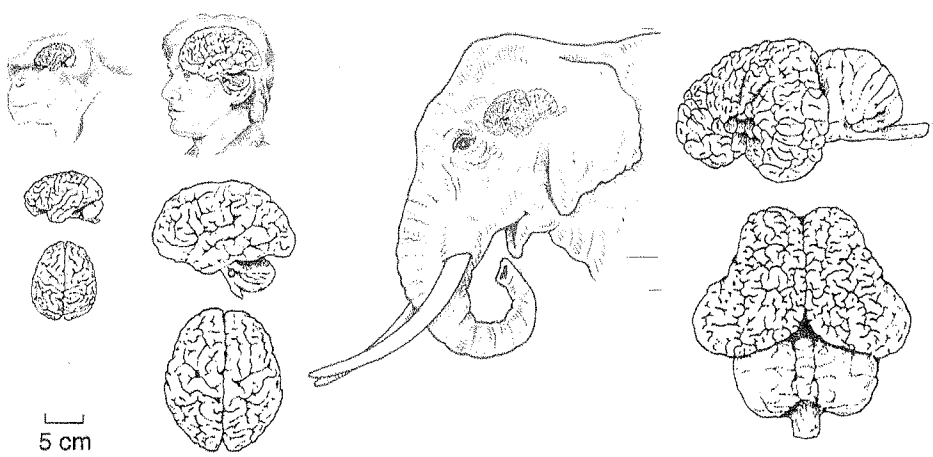

Fig. 2. Relative size, shape and surface convolutions of the cerebral cortex of the brains of elephants, humans and chimpanzees as seen in lateral and dorsal views. The brains are depicted in the same scale. Note the enlarged temporal lobes of the elephant brain. Images used with permission from the Comparative Mammalian Brain Collections (brainmuseum.org) with support from the National Science Foundation.

350 g reported for chimpanzees and 3.4 times the common estimate of 1400 g reported for humans (Hofman, 1985; Shoshani et al., 2006). Of course, any comparisons among species with regard to capacity for higher order brain functions must take into account differences in body mass, which varies greatly among individuals, as well as with age, sex, and in the case of elephants, species.

The conventional approach to grasping the relationship between brain size and higher order brain functions is through calculation of an encephalization quotient (EQ), which is a derivation of the ratio of brain mass to body mass to the 3/4 power, with EQ representing a measure of how far above the best fit regression is the data point for the species in question (Jerison, 1973). Correspondingly, the EQ of humans is represented as 7.5 compared to 2.5 for chimpanzees (Jerison, 1973). The EQ mentioned for elephants varies from 1.3 (Jerison, 1973) to 2.3 (Cutler, 1979).

We argue here that more relevant for understanding the higher order brain capacities than EQ is the total amount of cerebral cortex that is not dedicated to body size-related functions and various sensory systems. Neurobiological investigators refer to this as the nonsomatic or nonsensorimotor cerebral cortex. While the volume of cerebral cortex in the elephant exceeds that of all terrestrial animals (Fig. 2), there is no generally accepted model for estimating

nonsomatic cerebral cortex across species as divergent as primates and elephants. One model has involved scaling cerebral cortical volume to body mass by reference to a primitive marsupial, the opossum (*Didelphis marsupialis*), which reportedly has the lowest relative brain size for living mammals, and assuming that almost all of the cortex is involved in body size-related functions and sensory systems (Hofman, 1982). Using this scaling formula, one can then estimate the amount of somatic cortex needed to support a given body mass in larger-brained species and subtract this from the total volume of cerebral cortex to arrive at an estimate of the volume of nonsomatic cortex. With this model, the chimpanzee is estimated to have 161 cm^3 of total cortex of which 156 cm^3 is nonsomatic. The human is estimated to have 682 cm^3 of total cortex of which 660 cm^3 is nonsomatic, while the Asian elephant is estimated to have 1800 cm^3 total cortex of which 1600 cm^3 is nonsomatic (Hofman, 1982).

One problem with this approach to estimating nonsomatic cortex is species differences in cerebral cortex dedicated to various sensory systems. For example, in primates the visual system is extensive while in elephants the auditory system is extensive, as evident by the massive temporal lobes (Fig. 2; Shoshani et al., 2006). Also, the volumetric scaling method based on a "primitive" mammal does not take into account differences in cortical neuron densities across species as well as possible species differences in the relationship between cortical neuron numbers and somatic components such as muscle, viscera and skin.

Another approach to estimating the volume of nonsomatic cortex of elephants refers to differences in body mass between African and Asian elephants and assumes that most of the difference in brain volume between the two species can be attributed to the additional somatic cortex needed to support the difference in body mass. Reliable, agreed upon, figures for multiple comparisons between genders of the two species, with regard to brain volume and body mass, do not exist. That said, using figures for typical body mass for males of both species from Owen-Smith (1988) and an estimate of brain volume differences between species from several sources (Jerison, 1973; Cozzi et al., 2001; Altman and Dittmer, 1962), one can determine that for a species difference in body mass of 1000 kg, and a species difference in brain volume of 200 cm^3, that 1 cm^3 of cerebral cortex services about 5 kg of body mass. Thus, for an Asian female elephant with a body mass of 2500 kg (Owen-Smith, 1988) about 500 cm^3 of cerebral cortex would be needed for somatic functions. With an estimated cerebral cortex volume of 1800 cm^3, this would leave 1300 cm^3 for nonsomatic functions. By this calculation the elephant has about eight times the volume of nonsomatic cortex as chimpanzees and twice the volume of humans. The volume of nonsomatic cortex calculated by this method would be less if the reference were to an adult Asian male or if one used a smaller species difference in body mass.

3.1. Neuronal density, number, size and interconnections

A greater volume of cerebral cortex does not translate into a proportionately greater number of information processing neurons. There is a well-established negative correlation between brain size and cortical neuron density. Tower (1954) first estimated the neuron densities of the cerebral cortices (rounded to nearest 1000) of chimpanzees at 15,000, humans at 9000 and Asian elephants at 7000 per mm^3. A more recent comparative study by Haug (1987) is based on the mean of samples from four areas of the cerebral cortex and 10–20 rows of neurons perpendicular to the cortical surface. Haug placed the approximate densities of cortical neurons for chimpanzees at 41,000, humans at 26,000 and African elephants at 7000 per mm^3. Although he calculated a greater density of neurons for the large-brained primates than did Tower, Haug did not differ from Tower in estimating the neuron density of elephants, suggesting that the figure of 7000 per mm^3 may be an accurate representation for both species of elephant. The markedly reduced density of cortical neurons, compared to primates, described by Haug agrees with the more recent observations of Cozzi et al. (2001) on an Asian elephant, although the latter paper does not give specific numbers for cortical neuron density.

Using the neuronal density counts from Haug (1987) and the cerebral cortical volume data derived from Hofman (1982), one can estimate the number of neurons in the total cerebral cortex. With 682 cm^3 of cerebral cortex, humans are estimated to have 17.4 billion neurons in the cerebral cortex, elephants with 1800 cm^3 of cerebral cortex, 12.5 billion and chimpanzees with 161 cm^3 of cerebral cortex, 6.7 billion. A more updated technique of neuron counting estimated the human cortex to have a range of 19–23 billion neurons (Pakkenberg and Gundersen, 1997). Comparative data with the newer technique are not available for the elephant and chimpanzee.

The number of neurons in the nonsomatic cortex of humans, elephants and chimpanzees would appear to give at least a rough estimate of the number of neurons available for higher order brain functions. Correspondingly, with the Haug neuron density data and nonsomatic cortex volume calculations from Hofman, based on scaling from a primitive mammal, the 660 cm^3 of nonsomatic cortex in humans has about 17 billion neurons and the 156 cm^3 of nonsomatic cortex in chimpanzees, 6.5 billion. A calculation based on scaling from the marsupial brain estimates 11.2 billion neurons in the nonsomatic cortex of the elephant (1600 $cm^3 \times 7000$). For humans, if one uses the calculation of Pakkenberg and Gundersen, an estimate for nonsomatic cortex would be about 20 billion neurons.

Using the volumetric approach, scaled from a primitive mammal, makes sense for comparisons between primates with a high cortical neuron density and equivalent sensory systems. With regard to elephants, for reasons cited above, a calculation of volume of nonsomatic cortex based on comparing body mass and brain mass differences between

the two species may make more sense. Estimated in this manner, the 1300 cm^3 of nonsomatic cortex in Asian female elephants has 9.1 billon neurons. Recognizing that this is only a rough estimate for volume of nonsomatic cortex, and that new methods may eventually show that the neuron density in the elephant cortex is actually higher, we are using a figure of 10 billion neurons as a working number for the elephant. With available information, the defining difference between elephants and large-brained primates is in cortical neuron density, and thus, the relatively similar result obtained by two, quite divergent methods of determining the number of nonsomatic cortical neurons, suggests that regardless of method of calculating the volume of nonsomatic cortex the comparative picture, with regard to number of information-processing cortical neurons, would probably not change in a meaningful way. Fig. 3 portrays an estimate of the number of nonsomatic neurons for humans at 20 billion, Asian elephants at 10 billion and chimpanzees at 6.5 billion.

Along with reduced cortical neuron density there is generally an increase in overall neuron size. The elephant was reported by Haug (1987) to have a mean neuron size of 4200 μm^3, and a size distribution towards large and very large neurons, primarily pyramidal cells. The size of neurons in the elephant cortex exceeded that of all species measured by Haug except one species of cetaceans. In the same study, the human and chimpanzee cortical neurons were estimated to have a mean size of 1200 μm^3 with a high proportion of small neurons, primarily granular cells. The characteristics of elephant cortical neurons, described in detail by Haug, were also mentioned by Cozzi et al. (2001) for the elephant brain they examined.

The space between neurons is filled with neuropil, which is the substrate for incoming nerve fibers, synapses, glial cells and capillaries. Elephants have a greater density of glial cells than primates (Haug, 1987). Given that larger, less dense neurons generally have greater numbers of synapses and interconnecting axons per neuron (Harrison et al., 2002), one would expect the cortical neurons of elephants to have a greater number of synapses and interconnecting axonal ramifications than large-brained primates.

Cortical neurons maintain connectivity with distant cortical areas through the cortical white matter which is mostly made up of long axons traversing between distant cortical regions (Zhang and Sejnowski, 2000). Several papers have shown that the underlying white matter of the neocortex increases disproportionately with cerebral cortical volume (Hofman, 1989, 2001; Allman, 1998; Zhang and Sejnowski, 2000; Bush and Allman, 2003). With an increasing expansion of the cerebral cortex and disproportionate expansion of underlying white matter, the point is reached where there is a limitation on interconnectivity among neurons (Hofman, 2001; Changizi, 2007; Changizi

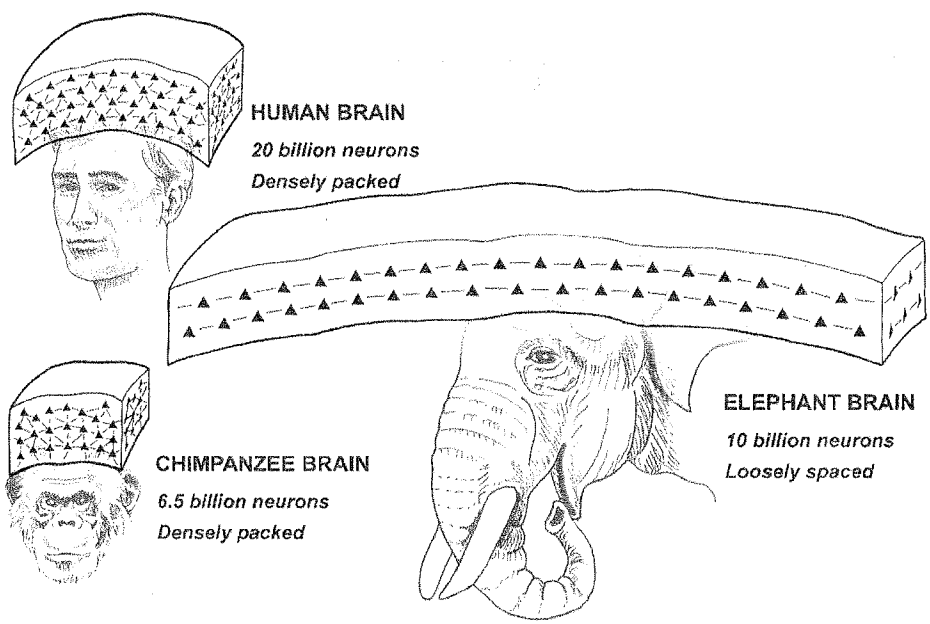

Fig. 3. Comparative cytoarchitectural aspects of the human, chimpanzee and elephant nonsomatic cerebral cortex. The nature of information processing capacity for higher order brain functions is a reflection of the number of the neurons, size of neurons, degree and type of interconnections and average distance between interacting neurons. In this model the neurons in the elephant cerebral cortex are envisioned as less densely packed but much larger than those in the cortex of the comparison primates. Representing a bias toward more global transcortical connections, compared to the highly compartmentalized local circuit interactions of primates, information processing in the elephant brain is proposed to be much slower, with less local interconnectivity. This figure portrays an estimate of neuron density for humans according to Pakkenberg and Gundersen (1997) and for the chimpanzee and elephant according to Haug (1987). Calculation of the volume of nonsomatic cerebral cortex used to estimate the total number neurons in the nonsomatic cortex for humans and chimpanzees is from Hofman (1982) and for elephants by a body mass/brain volume comparison between species (see text).

and Shimojo, 2005). In addition, nerve impulses between distant regions of the cortex must travel increasingly farther, resulting in increased elapsed time for information processing because conduction time is the main limiting factor in information processing speed (Harrison et al., 2002).

To maintain an optimal level of interconnectivity and a minimal nerve impulse conduction time, cortical neurons of great apes and humans have evolved to become less global in cortical connections and increasingly compartmentalized with more local circuit or modular connections (Kaas, 2000, 2007; Changizi and Shimojo, 2005). There is also an increase in multiple cortical areas in large brains (Krubitzer, 1995; Krubitzer and Hoffman, 2000; Krubitzer and Hunt, 2007). By shifting neuronal information processing to circumscribed areas the efficiency of interconnectivity, and speed of processing, within a sub-population of neurons is maintained. This principle of increasing localization of neuronal interactions, with increasing cerebral cortical volume, is revealed by the proportion of neurons within a module that are local circuit neurons (LCNs) connecting only to other neurons in the same or adjacent modules (Hofman, 1985). In going from chimpanzee to human, where there is a fourfold increase in cortical volume, LCNs increase from 93% to 98%.

The issue of constraints imposed by the disproportionate increase in white matter to grey matter volume raises a question about neuronal interconnectivity in the elephant cerebral cortex. Recent magnetic resonance imaging of the elephant brain reveals that the ratio of white matter to neocortical grey matter is in keeping with the disproportionate scaling of white to grey matter seen in primate brains (Hakeem et al., 2005). Given that elephant cortical neuron density is less than one-third that of the human, and about one-seventh that of the chimpanzee, it seems possible that a larger proportion of cortical neurons in the elephant brain send axons through the white matter to distant cortical neurons than in large-brained primates. This could be the case even though the larger neurons of the elephant cortex should have axons of larger diameter traversing the white matter. A bias towards a proportionately greater projection to distant cortical areas would involve a commensurately reduced participation in local circuit connections. Data supporting this conclusion come from the study by Hofman (1985) on LCNs of neuronal modules. Recall that in going from the chimpanzee brain to the human brain with four times the cortical volume, the proportion of neurons which are LCNs increase from 93% to 98%. In going from the human brain to the elephant brain with 2.6 times the volume of cerebral cortex, LCNs actually decrease from 98% to 91%.

Thus, based on several lines of evidence, one could predict that the continuum towards increasing compartmentalization and reduced global interconnections, which characterizes the evolution of large brains in primates, is not necessarily appropriate to apply to the evolution of the large brains of elephants (Hart and Hart, 2007). Rather there may be a neural cytoarchitectural bias in elephants towards maintaining long distance global connections (Fig. 3). A departure from this primate, large-brain continuum would be easier to entertain if elephants arose through a different evolutionary history. This appears to be true. As pointed out recently by Glickman et al. (2005), the evolution of elephants now appears almost certainly to have proceeded from aquatic rather than terrestrial mammalian lines. There is strong paleontological evidence, reinforced by histological studies on the testes and kidneys, as well as mitochondrial DNA analyses (De Jong, 1998), that elephants have an aquatic evolutionary history that is even different from that of cetaceans.

3.2. Relating brain information processing to behavior

Undoubtedly, by any quantitative method used, the number of nonsomatic cortical neurons available in the elephant for higher order brain functions, including extensive long-term memory, is large. Even with a little over half the number of neurons estimated in Fig. 3, the elephant would have a number comparable to chimpanzees. This cognitive neuronal capacity, if coupled with a bias towards maintaining global connections throughout the cerebral cortex, could be reflected in an exceptional ability to integrate information from a wide variety of spatial-temporal and social domains. This is evident from the documented accounts discussed above of remarkable feats of long-term, spatial-temporal and social memory. The cost of maintaining such global connections is a prolonged cortical information processing time and reduced intensity of interconnections within a subset of cortical neurons in the same or adjacent areas or modules. Indeed, this cost may be evident in the relatively weak performance of elephants on tests of cognitive behavior with a reference to cognitive performance of primates that is characteristically time-sensitive and/or involves intricate or complex behaviors.

The apparent outstanding ability of elephants in the area of long-term, spatial-temporal or social memory does not mean that their ability necessarily exceeds that of humans. Using the method of calculating numbers of neurons portrayed in Fig. 3, humans have at least twice as many cortical nonsomatic neurons available for higher order brain functions as elephants. One could argue that humans have sufficient white matter for involvement of a large number of cortical neurons in long distance global communication, leaving a high proportion for local circuit processing.

An emphasis on long-term, spatial-temporal memory ability in elephants brings up the question of whether the hippocampal complex, which is crucial for the formation and retention of cognitive maps that code for unfamiliar spatial-temporal relationships that are viewpoint-independent representations of the environment (Burgess et al., 2002; Sweatt, 2004), is proportionately larger in elephants

than in large-brained primates. The African elephant brain that was examined by magnetic resonance imaging revealed that the hippocampus is unusually large and convoluted and proportionately slightly larger in comparison to brain size than in the human (Hakeem et al., 2005). This observation contrasts with another report, however, based on dissection of African and Asian elephant brains, indicating that the hippocampus is somewhat disproportionately smaller than in the human (Shoshani et al., 2006). It seems possible that a comparison of brain structures by dissection could be a little distorted compared with modern imaging techniques applied to intact brains (Hakeem et al., 2005). Although more definitive studies are needed, a larger and more complex hippocampus in the elephant brain than would be predicted by brain size, would be consistent with the viewpoint that the information processing of the cerebral cortex in elephants is adaptively biased towards facilitating long-term, spatial-temporal information acquisition and storage.

The emphasis on long-term extensive memory ability, coupled with convincing evidence of relatively poor performance in conventional tests of cognitive performance of elephants, brings to mind studies on the rare savant syndrome in humans which is often associated with autism (Heaton and Wallace, 2004). The syndrome features extraordinary rote memory ability, especially of numbers, names and dates, often in the context of intellectual impairment (Miller, 1999). Because most authorities relate the occurrence of the savant syndrome in humans to brain injury (Heaton and Wallace, 2004), one is tempted to wonder if, on occasion, some types of brain injury might have induced regeneration and reorganization of information processing capacities of the cerebral cortex somewhat along the lines typical of normal elephants.

The cytoarchitecture of the elephant brain, characterized possibly by a global connection bias, may also be related to the behavioral phenomena suggestive of some types of theory-of-mind-like events. The mirror self-recognition performance would appear to be shared with great apes, humans and dolphins. The interest in the corpses and skeletal remains of conspecifics with an apparent concept of death, and the behavior of helping related and unrelated conspecifics, that is so highly profiled in elephants, would seem to set them apart from all other species except humans.

4. Concluding comments

Throughout human history the elephant, particularly Asian elephant, has played a major cultural, religious, political and economic role in human affairs. Even today, in Asian countries images of the elephant are ever-present in commerce, art and in public places. It is one of the major features in Hinduism and Buddhism, two of the world's great religions. The reputation for intelligence of elephants extends back to the ancient philosophers. Pliny, the elder, for example, says of terrestrial animals, "The elephant is the largest of them all, and in intelligence approaches the nearest to man" (Bostock and Riley, 1855).

From a diverse set of neural cytoarchitectural studies of large brains, we have pulled together a perspective on elephant brains that may have implications for understanding differences in behavior between elephants and primate counterparts. Namely, the interactions between neurons of the cerebral cortex of elephants may be much less compartmentalized and the interaction times slower than in primates, putting them at a disadvantage in primate-like, time-sensitive or intricate tests of higher order brain functions. A possible global bias of cortical neuron interconnections of elephants may be an adaptation for other aspects of higher order brain functions, particularly long-term, spatial-temporal and social memory. The neural cytoarchitecture of the elephant brain, if indeed unique, may relate to the behavioral reactions to the remains of dead conspecifics, and in helping others that are reminiscent of some aspects of theory-of-mind phenomena. The elephant has been neglected in neural cytoarchitectural studies of large brains and we hope to stimulate focused studies on elephants that may support or refute the concepts presented in this review.

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