

# Von Economo Neurons in the Elephant Brain

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## ABSTRACT

Von Economo neurons (VENs), previously found in humans, all of the great ape species, and four cetacean species, are also present in African and Indian elephants. The VENs in the elephant are primarily found in similar locations to those in the other species. They are most abundant in the frontoinsular cortex (area FI) and are also present at lower density in the anterior cingulate cortex. Additionally, they are found in a dorso-lateral prefrontal area and less abundantly in the region of the frontal pole. The VEN morphology appears to have arisen independently in hominids, cetaceans, and elephants, and may reflect a specialization for the rapid transmission of crucial social information in very large brains. *Anat Rec*, 292:242–248, 2009. © 2008 Wiley-Liss, Inc.

**Key words:** elephant; Von Economo neuron; frontoinsular cortex; cetacean; large brains

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The Von Economo neurons (VENs) are large, bipolar neurons located in layers 3 and 5 of frontoinsular (FI) and anterior cingulate cortex (ACC) in great apes and humans, but not in other primates (Allman et al., 2005; Nimchinsky et al., 1999). The VENs have also been discovered in regions corresponding to FI and ACC in the humpback, fin, sperm, and killer whales (Hof and Van der Gucht, 2007). Morphological, biochemical, and neuropathological evidence suggests that VENs are part of the neural circuitry involved in social awareness and may participate in fast, intuitive decisions in complex and rapidly changing social situations (Allman et al., 2005). The VENs are more numerous in humans than in apes and may be part of the neural circuitry supporting complex social behavior in hominids (great apes and humans). The large size of the VENs, the morphological simplicity of their dendritic architecture, and many other features suggest that they are specialized for rapid transmission of information over long distances (Hofman et al., 1987; Nimchinsky et al., 1995; Allman et al., 2002). The bipolar dendrites of VENs are shaped and positioned to integrate information from an entire cortical minicolumn and to rapidly relay output to other brain structures (Watson et al., 2006). The VENs are selectively affected in a variant of frontotemporal de-

mentia (FTD) that causes the loss of social awareness and the capacity to self-monitor in social situations (Seeley et al., 2006), and thus are implicated in social functioning. We sought to determine whether a similar neuronal morphological specialization was present in elephants, which have independently evolved large brain size and the capacity for highly complex social behavior (Balfour and Balfour, 1997; Moss, 2000; Sukumar, 2003).

## MATERIALS AND METHODS

The African elephant brains were obtained from the Cleveland Metroparks Zoo. Elephant 1 was a female of

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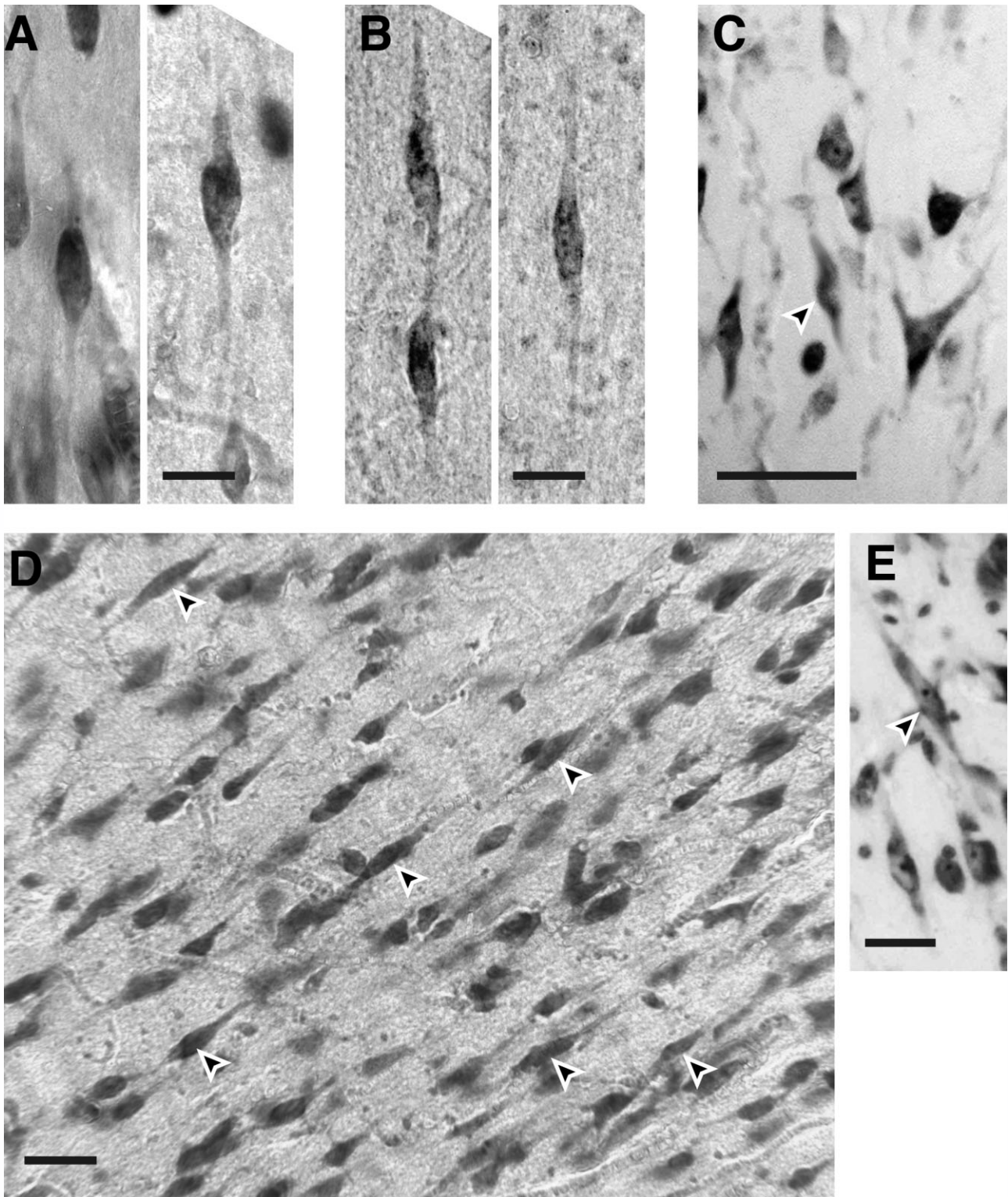


Fig. 1. Photomicrographs of VENs in the brain of the African elephant. **A:** VENs in frontoinsular cortex (area FI). Scale = 25  $\mu$ m. **B:** A pair of VENs and a single VEN in dorsolateral frontal cortex (DL). Scale = 25  $\mu$ m. **C:** A VEN (arrow) and nearby layer 5 neurons in ACC of an

Indian elephant. Scale = 70  $\mu$ m. **D:** A lower magnification view of area FI in Elephant 1 (an African elephant). VENs are indicated by arrows. Scale = 50  $\mu$ m. **E:** A VEN (arrow) in area FI in the brain of a bottlenose dolphin. Scale = 60  $\mu$ m.

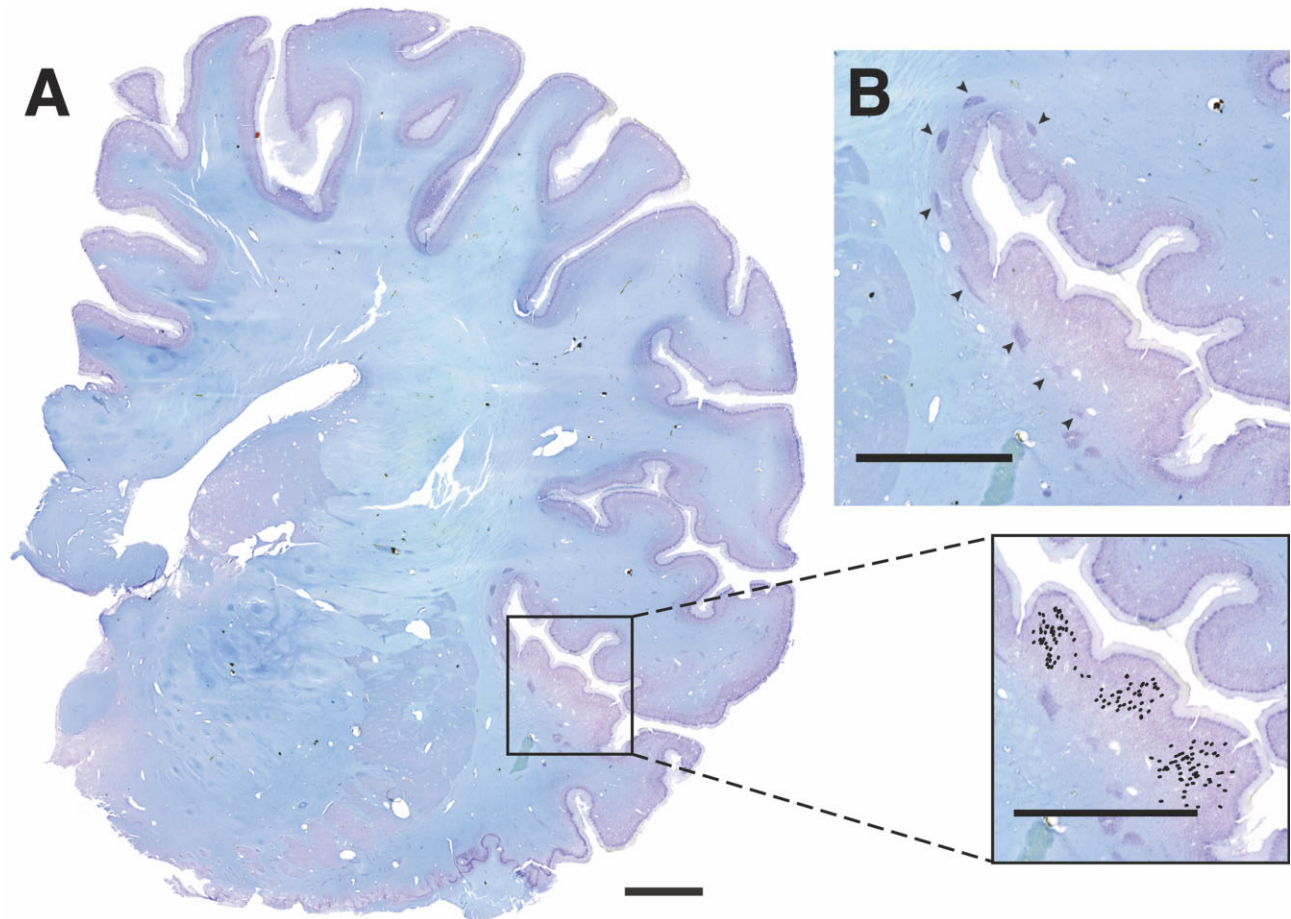


Fig. 2. **A:** A scan of a Nissl-stained coronal section through the right hemisphere of the brain of Elephant 1 at the level of area FI. The inset tracing shows the distribution of VENs in area FI. Each dot corresponds to one VEN. The VENs are more prevalent at the crowns of

the gyri and are absent at the bases of the sulci. **B:** A magnified view of area FI showing the locations of the "claustral islands," dense clusters of cells found between the cortex and white matter in this region. All scales are 1 cm.

~42 years of age at the time of death. This individual was wild-born and was acquired from Africa in 1955. At death, she had a pheochromocytoma (tumor of her adrenal medulla). She probably died of a sudden hypertensive crisis from hormone release by the tumor (Bonar et al., 2005). Elephant 2 was a female of 16 or 17 years of age, wild-born and acquired from Africa around 1980. Probable cause of death was a sudden cardiac arrhythmia. Histologic examination of every major organ was negative, as was serologic testing for encephalomyocarditis virus. Cortical samples were obtained from the brain of an adult female Indian elephant (*Elephas maximus*) that died of natural causes in a zoologic park. The brain was fixed at necropsy by immersion in a large volume of formalin. The specimen was kept in formalin in the collection of the Department of Anatomical Sciences, University of Adelaide, Australia.

The African elephant brains were cut into ~20-mm-thick coronal slabs at necropsy and fixed in 10% formalin. Each slab through the frontal lobes of the right and left hemispheres of Elephant 1 and the left hemisphere of Elephant 2 was placed on a specially machined micro-

tome stage containing a large reservoir of dry ice. The slabs were frozen and cut with a sliding microtome into 120- $\mu$ m-thick coronal sections. The exposed block face was photographed before each section was sliced from the frozen slab. Every 20th section through the frontal lobes was mounted on a gelatin-coated slide. Sectioning photographs were used to ensure the sections were mounted in the correct orientation. For higher resolution in the region of FI, every 4th section was mounted. The sections were dried, stained with a cresyl violet Nissl stain, and protected with a coverslip. The entire frontal cortex was examined for the presence of VENs. The plotting of the VENs in Figs. 2 and 4 was done at 400 $\times$  using the program NeuroLucida (MBF Bioscience, Williston, VT). The stereological counting was performed using StereoInvestigator (MBF Bioscience).

We also studied histological sections made in the 1960s from the brains of three adult male bottlenose dolphins (*Tursiops truncatus*, brain weights 1420–1585 g) that had been gravity-perfused *in situ* through the descending aorta with 40 L of heparinized Windle's fluid following lethal anesthesia (McFarland et al., 1969).

Mantee, rock hyrax, tenrec, and armadillo brains examined are part of the Welker Collection at the National Museum of Health and Medicine. These brains were celloidin embedded, sectioned at 35  $\mu$ m, and stained with a thionin Nissl stain.

From the brain of the Indian elephant, we collected 5- to 6-mm-thick surface samples from the anterior and posterior cingulate cortex, the frontal polar region, various sites over the temporoparietal convexity, and the hippocampal formation. These blocks were cryoprotected, sectioned at 40  $\mu$ m on a cryostat, and 1:20 series of sections were stained with cresyl violet.

The brains of the bottlenose dolphins were embedded in celloidin, sectioned at 35  $\mu$ m on a large specimen microtome, and every 5th and 6th sections were stained with either the Loyez-Weigert method for myelin or the Bielchowsky-Plien cresyl violet for cellular architecture (Jacobs et al., 1971; Hof et al., 2005).

Whole brains of rock hyrax (N = 2), giant elephant shrew (N = 1), two-toed sloth (N = 2), lesser anteater (N = 1), giant anteater (N = 1), and bontebok (N = 1) were obtained from the Cleveland Metroparks Zoo or the Philadelphia Zoo and came from animals that had died of natural causes. Considering the species-specific age of sexual maturity, the giant anteater and one of the two-toed sloths were juveniles; all other specimens were from adults. The entire left cerebral hemisphere of each brain was sectioned for histology and a 1:10 series of sections was stained for Nissl substance with a solution of 0.5% cresyl violet. In addition, immunohistochemistry was performed on an adjacent series of sections in these brains with a monoclonal antibody against a nonphosphorylated epitope on the neurofilament H protein (NPNFP) (dilution 1:2,000; SMI-32 antibody; Covance International, Princeton, NJ). Immunostaining with the SMI-32 antibody labels the soma and dendrites of a subset of projection neuron types, including VENs in humans (5).

## RESULTS

We sectioned the brains of two female African elephants (*Loxodonta africana*). We examined a series of Nissl-stained sections from both hemispheres of the brain of one elephant (Elephant 1) and the left hemisphere of the other elephant (Elephant 2). In several locations in these brains we discovered neurons with the same morphology as the VENs seen in humans, great apes, and cetaceans (Nimchinsky et al., 1999; Allman et al., 2005; Watson et al., 2006; Hof and Van der Gucht, 2007). These large neurons have an elongated, spindle-shaped soma, a single large apical dendrite, and a single large basal dendrite with no branching near the soma. In hominids they are found primarily in layer 5 of area FI and anterior ACC, but smaller numbers are also present in dorsolateral prefrontal cortex in humans (Fajardo et al., 2008). Cetaceans have VEN populations in FI and ACC, but mysticetes also have numerous VENs in frontopolar cortex (Hof and Van der Gucht, 2007). Figure 1 shows photomicrographs of VENs in area FI (Fig. 1A,D) and a dorsolateral frontal area (Fig. 1B) in the African elephant. We also have evidence for VENs in ACC of an Indian elephant (*Elephas maximus*) (Fig. 1C).

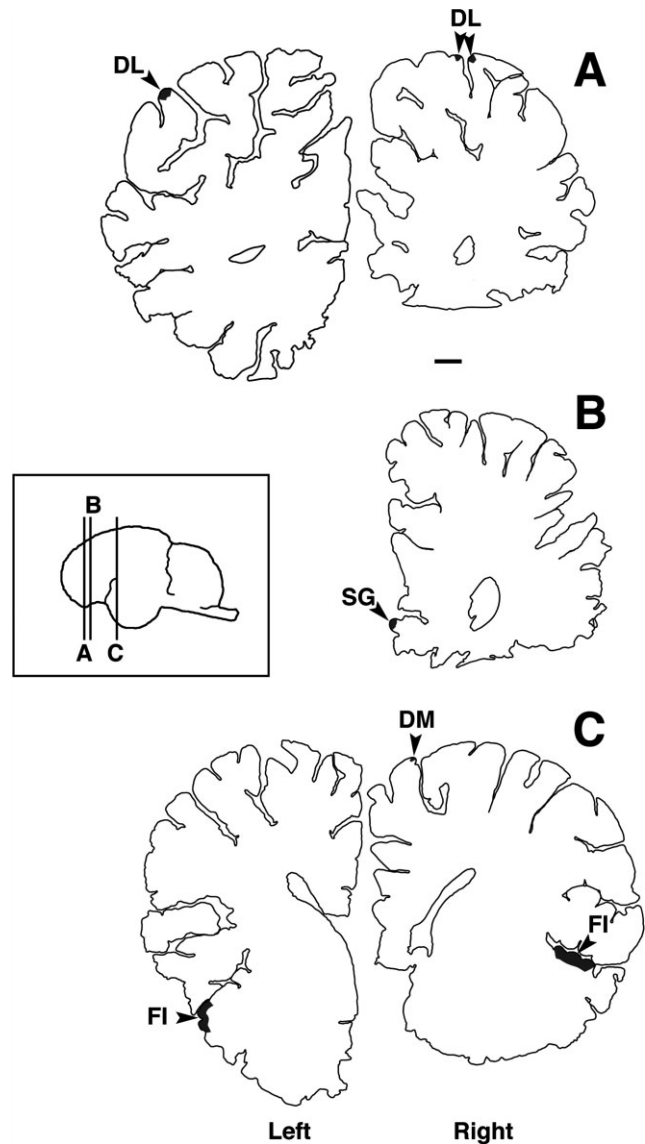


Fig. 3. VEN-containing regions of the elephant brain indicated on coronal section outlines. The locations of the sections are indicated by the vertical lines on the inset tracing of the medial aspect of the brain. The left hemisphere is on the left side of the figure. **A:** We found VENs in a dorsolateral frontal cortical area in all three hemispheres examined. **B:** VENs were present in subgenual anterior cingulate cortex (ACC). Because of previous removal of tissue from these brains in the region of ACC, we were unable to plot their locations in dorsal ACC or in the left hemisphere. **C:** Area FI, in which VENs were abundantly present. Scale = 1 cm.

The main concentration of VENs in the elephant brain is in a cortical domain similar in location to area FI of humans and apes. Figure 2 illustrates a section through area FI of the right hemisphere of Elephant 1. We plotted the location of each VEN in the area corresponding to FI in this section. The inset tracing of Fig. 2A shows the VEN distribution map. Note that the VENs are more numerous at the crowns of the gyri and are nearly absent in the cortex below the fundus of each sulcus. This is a characteristic pattern that we have also

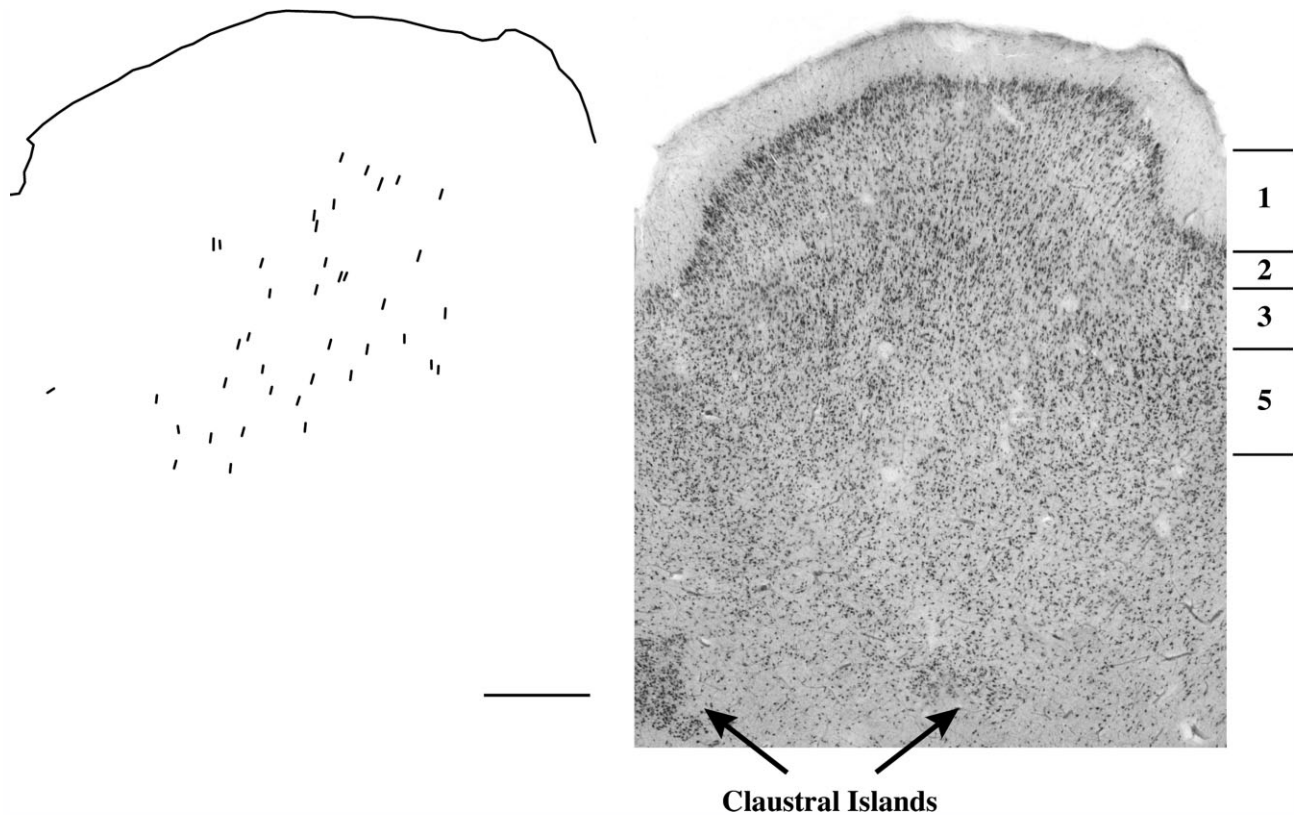


Fig. 4. A tracing (left) showing the distribution of VENs in one gyrus of area FI in the right hemisphere of Elephant 1. The VENs occur primarily in layer 5 and are more prevalent at the crown of the gyrus than in the adjacent sulci. In the photomicrograph (right) of the

corresponding region of the section the layer structure (indicated at extreme right) can be observed, as well as two of the dense "claustrial islands" found between the cortex and the white matter. Scale = 250  $\mu$ m.

**TABLE 1. Results of stereological counts of VENs and total neurons in area FI of the left and right hemispheres of Elephant 1**

	VENs in FI	VEN CE Gundersen $m = 1$	VEN CE Schmitz-Hof 1st	Neurons in FI	Neuron CE Gundersen $m = 1$	Neuron CE Schmitz-Hof 1st	VEN %
Elephant 1 right hemisphere	10,200	0.05	0.05	1,300,000	0.05	0.04	0.78%
Elephant 1 left hemisphere	9,110	0.08	0.08	348,000	0.06	0.09	2.6%

observed in FI in human, ape, and cetacean brains. The location of the FI VENs was similar in all three hemispheres examined. Figure 3 uses section outlines to illustrate the locations of right and left FI in Elephant 1, as well as the locations of smaller number of VENs in the subgenual anterior cingulate cortex (SG), and in a dorsolateral frontal area (DL). We additionally observed VENs in a dorsomedial area (DM) in the right hemisphere of Elephant 1, but not in the left. There were a small number of VENs located near the frontal pole, a region in which a more substantial amount of VENs have also been observed in the humpback whale (*Megaptera novaeangliae*), in the fin whale (*Balaenoptera physalus*), in the sperm whale (*Physeter macrocephalus*), and in the killer whale (*Orcinus orca*) (Hof and Van der Gucht, 2007). The VENs in elephant ACC occur at lower density than in humans and great apes (Nimchinsky et al., 1999).

As has been observed in humans, great apes, and cetaceans, the VENs of the elephant are primarily found in layer 5 of the cortical regions that contain them, along with populations of other large pyramidal neurons with distinctive morphologies such as the compass cells, which were also described by Von Economo (Von Economo and Koskinas, 1925). This typical layering can be seen in Fig. 2, which shows a magnified portion of area FI. As in Fig. 2, the tracing indicates the locations of all the VENs in the photographed region. In this region of FI, there are a series of dense clusters of cells in the subcortical white matter (see Fig. 2B). We believe these clusters may possibly correspond to the claustrum, and we suggest the term "claustrial islands" to refer to them.

To quantify the number of VENs in area FI in the African elephant, we performed stereological counts on a series of sections through area FI from the left and right hemisphere of Elephant 1. Table 1 contains the results

of these counts. The number of VENs found in Elephant 1 (19,310) is lower than the number in adult humans (average total 193,000 VENs), but is higher than the average number found in great apes (average total 6,950 VENs) (Allman et al., 2005). We also counted the total number of neurons in the VEN-containing region and found that VENs make up 0.78% of the total neurons in layers 3 and 5 of FI in the right hemisphere and 2.6% of total neurons in these FI layers in the left hemisphere, reflecting a smaller but more densely populated left FI.

Whereas humans and great apes have VENs, monkeys and strepsirhine primates do not (Nimchinsky et al., 1999). VENs are also present in areas corresponding to FI and ACC in humpback, fin, sperm, and killer whales. We have recently found them in the bottlenose dolphin (*Tursiops truncatus*) as well (see Fig. 1E). To determine whether any of the closest relatives of the elephant have VENs, we examined brains from the rock hyrax (*Heterohyrax brucei*), manatee (*Trichechus manatus latirostris*), and giant elephant shrew, as well as xenarthrans (one species of sloth, one of armadillo, two species of anteaters, and three species of tenrec). We also examined an ungulate, the bontebok (*Damaliscus pygargus*), because some alternative phylogenies maintain a close relationship between ungulates and elephants (Eisenberg, 1981). No VENs can be found in the cortex of these animals except for manatee, in which an occasional isolated VEN-like cell can be observed, but without significant VEN populations in either FI or ACC. Two species of rodents, the brown rat (*Rattus norvegicus*) and the paca (*Cuniculus paca*), were also found to lack VENs. These data are summarized in Fig. 5, a cladogram based on extensive molecular genetic evidence showing the relationship of various mammalian groups to the elephant (Murphy et al., 2001).

**DISCUSSION**

The VEN morphology appears to have arisen independently in hominids, cetaceans, and elephants. The VEN specialization may parallel the emergence of very large brain size in these mammals. The evolution of large brain size may place a special premium on overcoming geometric constraints to maintain rapid transmission of crucial information, and this need may explain the independent emergence of the VENs in these species. There are a few mammals apart from hominids, cetaceans, and elephants that have brains somewhat larger than the apes. It would be interesting to determine whether or not these mammals, such as the giraffes and hippopotamuses, have VENs in parts of the brain corresponding to FI and ACC. If they are present, it would suggest that the VEN morphology may be primarily related to absolute brain size. If not, it would suggest that the VENs may be related to behavioral specializations common to hominids, whales, and elephants. One such behavioral specialization could be mirror self-recognition (Reiss and Marino, 2001; Plotnik et al., 2006). However, this awaits confirmation from further studies.

From a functional viewpoint, in humans, FI is strongly activated by negative social feedback in the form of frowning faces and by the command to end an ongoing activity (Ullsperger and von Cramon, 2003;

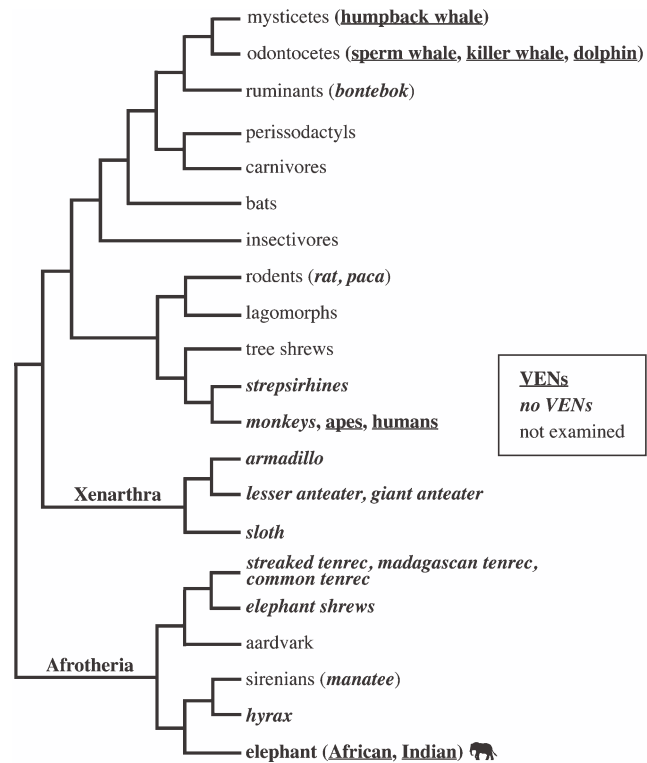


Fig. 5. The phylogenetic distribution of the VENs. Species in which VENs have been observed are indicated by underlines; species which have been examined and found to possess no VENs are indicated by italics. Note that while the African and Indian elephants have VENs, they share this trait only with other large-brained groups (the cetaceans and humans/great apes) and not with their nearest relatives, the rock hyrax, manatee, giant elephant shrew, and tenrecs.

Aron and Poldrack, 2006). FI is activated in a number of social situations in which empathy, guilt, embarrassment, and resentment are strongly present (Shin et al., 2000; Berthoz et al., 2002; Sanfey et al., 2003; Singer et al., 2004). Each of these situations involves negative feedback with respect to some aspect of the social network in which an individual is participating. FI is activated when subjects scrutinize a face to determine the intentions of another individual (Baron-Cohen et al., 1999). The anterior insula and adjacent cortex is involved in many aspects of self-awareness of bodily states including heart rate and pain (for review see Craig, 2003) and in the conscious awareness of having committed an error (Klein et al., 2007). Thus the VENs and related insular circuitry may be involved in monitoring changes in the physiological network of an individual's own body and that individual's social network. In each case, the VENs may be involved in initiating homeostatic corrections to changes in network states. This conceptualization resembles the "somatic marker hypothesis" of Damasio (1994) in linking bodily awareness to social functioning, although it places more emphasis on specialized circuitry within FI, ACC, and related brain structures and the role of this circuitry in initiating error-correcting responses.

There are well-documented instances in which elephants appear to respond empathically to situations in which other group members are threatened (Poole and Moss, 2008). In one incident, a drowning elephant calf was saved when the matriarch and another adult female climbed into a lake, positioned themselves on each side of calf, and, using their tusks and trunks, lifted the calf to safety on the shore (Reflections on Elephants, 1994, National Geographic Video). In another example, a male elephant was observed for several hours providing care to a dying companion by trying to force him to stand when he fell down and bringing him water to drink (Balfour and Balfour, 1997). The VENS may enhance the functioning of the circuitry within FI, ACC, and related structures involved in social awareness, heightening alertness to the distress of others and resulting in such instances of empathy and other complex social behaviors.

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