

1-1-2000

# Do elephants feel pain and if so, how do we know this?

Jeheskel Shoshani

*Elephant Research Foundation; Department of Biology, University of Asmara, jshosh@sun.science.wayne.edu*

Lois E. L. Rasmussen

*Department of Chemistry, Biochemistry & Molecular Biology, Oregon Graduate Institute, betsr@admin.ogi.edu*

William J. Kupsky

*Pathology Department, School of Medicine, Wayne State University, wkupsky@dmc.org*

Dalen W. Agnew

*Detroit Zoological Institute, dwagnew@ucdavis.edu*

George S. Borszcz

*Psychology Department, Wayne State University, gborszcz@sun.science.wayne.edu*

Follow this and additional works at: <https://digitalcommons.wayne.edu/elephant>

## Recommended Citation

Shoshani, J., Rasmussen, L. E. L., Kupsky, W. J., Agnew, D. W., & Borszcz, G. S. (2000). Do elephants feel pain and if so, how do we know this?. *Elephant*, 2(4), 48-52. Doi: 10.22237/elephant/1521732222

This Article is brought to you for free and open access by the Open Access Journals at DigitalCommons@WayneState. It has been accepted for inclusion in Elephant by an authorized editor of DigitalCommons@WayneState.

---

# Do elephants feel pain and if so, how do we know this?

## **Cover Page Footnote**

Detective David Smithers, Ian Redmond, Gary H. Marchant, Jann S. Grimes, Eleanor C. Marsac, Jules L. Pierce, and Sandra L. Shoshani helped in various aspects of this investigation. Bucky Steele donated Tulsa's brain for research.

Elephant, Volume 2, Number 4, pages 48-52  
Copyright © 2000 Elephant Research Foundation

### DO ELEPHANTS FEEL PAIN AND IF SO, HOW DO WE KNOW THIS?

by Jeheskel Shoshani [1], Lois E. L. Rasmussen [2], William J. Kupsky [3], Dalen W. Agnew [4], and George S. Borszcz [5]

[1] Elephant Research Foundation, 106 East Hickory Grove Road, Bloomfield Hills, Michigan 48304 USA, and Department of Biology, University of Asmara, P. O. Box 1220, Asmara, Eritrea, e-mail addresses: jshosh@sun.science.wayne.edu, and hezy@eol.com.er; [2] Department of Chemistry, Biochemistry & Molecular Biology, Oregon Graduate Institute, P. O. Box 91000, Portland, Oregon 97291-1000, USA, e-mail address: betsr@admin.ogi.edu; [3] Pathology Department, School of Medicine, Wayne State University, Detroit, Michigan 48201, USA, e-mail address: wkupsky@dmc.org; [4] Detroit Zoological Institute, 8450 West Ten Mile Road, P. O. Box 39, Royal Oak, Michigan 48068-0039, USA (current address: Anatomic Pathology, Veterinary Medical Teaching Hospital, University of California - Davis, One Shields Avenue, Davis, California 95616-8747, USA, e-mail address: dwagnew@ucdavis.edu; [5] Psychology Department, Wayne State University, Detroit, Michigan 48202, USA, e-mail address: gborszcz@sun.science.wayne.edu.

#### DEFINITIONS \*

Endorphins = A class of hormones known to serve as neurotransmitters, and to function as natural analgesics.

Nociceptors = Naked nerve endings in the skin, known to be associated with the ability to sense pain. These nerve endings respond to mechanical, thermal, or chemical stimuli.

Pain = The sensation or feeling resulting from or accompanying some injury, derangement, overstrain, or obstruction of the physical condition. Pain may cause stress and suffering. Sensations of external and internal pain result from impulses reaching the cerebral cortex via specific nociceptors neural pathways.

Receptor = This is usually a modified neuron, which occurs singly or in groups, along with other cell types within sensory organs, such as the eyes and ears. It is a structure that transmits information in the external and internal environment of an animal.

Reception = The ability of a cell in an animal body to absorb the energy of a stimulus.

Stimulus = An agent that produces a temporary change in physiological activity in an organism or any of its parts.

\* Compiled from different sources including Campbell (1993), Andrews *et al.* (1993).

#### INTRODUCTION

Among the physiological changes that animals experience are those for which one can clearly observe associated behavioral changes. In the case of humans, where the subject can communicate with the examiner, it is easy to understand which physiological changes are associated with a particular behavior. Examples: a person may lift a foot from the ground and when asked to explain this behavior, explains that there is a thorn in that foot. On the other hand, if an animal raises a foot from the ground, it may not be possible to determine the reason. It may be that the animal was tired of standing on that foot and shifted its weight to the other, or there may be a thorn

in that foot. In the first example, the person experienced or sensed pain, and that stimulus caused him to lift that foot.

When working with animals, therefore, one has to infer their behaviors and possibly interpret them based on anatomical and physiological evidence. Sensations, and the perceptions they evoke, begin with excitation of sensory receptors. They are specialized to respond to various stimuli, including heat, light, pressure, and chemicals. These stimuli represent forms of energy. Functions of receptor cells include converting the energy of stimuli into the electrochemical energy of action potentials and carrying those action potentials into the nervous system. The five functions common to all receptor cells are: reception, transduction, amplification, transmission, and integration (modified after Campbell, 1993, p. 1016). In this study, we focus on reception of pain.

According to Andrews *et al.* (1993), there are two broad categories of pain: SENSORY-DISCRIMINATIVE and MOTIVATIONAL-AFFECTIVE. Sensory-discriminative pain indicates the site of origin of the stimulus giving rise to the pain. In the motivational-affective pain, the strength of the stimulus is perceived and the animal's response to the pain is determined. Sensory-discriminative pain is most likely to be mediated by subcortical and somatosensory cortical mechanisms that provide the individual with information on intensity, duration, location, and quality of the stimulus. On the other hand, motivational-affective processing involves the forebrain and limbic system for perceptions such as discomfort, fear, anxiety, and depression, and it also includes strong inputs to the hypothalamus and the autonomic nervous system for reflex activation of the cardiovascular, pulmonary, and pituitary-adrenal system. Based on Kitchell *et al.*'s (1983) report on neurosurgical observation conducted on humans, it is possible to differentiate between the sensory-discriminative and motivational-affective components of pain.

This investigation was launched in response to David Smithers, a detective at the Hampshire Constabulary (Andover, Hampshire, England) who has been pursuing factual details in preparation for a court case on an elephant named "Flora". Results of this investigation may reach beyond the courtroom (Anonymous, 1999).

#### HYPOTHESIS

Our hypothesis is: both African and Asian elephants (*Loxodonta africana* and *Elephas maximus*) are capable of experiencing the same dimensions of pain as do humans (i.e., sensory-discriminative and affective-motivational).

#### MATERIALS AND METHODS

We studied preserved tissues of extant elephants — *L. africana* and *E. maximus* — including skin from different areas of the body and brains (complete and sectioned) and consulted the available literature. Our investigation included gross anatomy as well as microscopic examinations of histological slides.

#### RESULTS AND DISCUSSION

*Skin* — Rasmussen and Munger (1996) described histology of the skin on the trunk tip. They depicted and described Pacinian corpuscles, Merkel terminals, and free nerve endings. Based on human anatomy, Pacinian corpuscles and Merkel discs respond to pressure and touch, whereas, free or naked nerve endings are associated with pain (e.g., Campbell, 1993; Kitchell *et al.*, 1983;

Kitchell and Johnson, 1983; Willis, 1985; Zimmerman, 1984).

*Brain* — Two of us (WJK and JS) identified the nucleus accumbens (nAcc) in the brain of an Asian elephant, as was previously reported by Koikegami *et al.* (1967) and Koikegami and Ozaki (1967). We also identified other structures important in the pain system, such as the periaqueductal gray matter (PAG), hippocampus, amygdala, septum, hypothalamus, medial thalamus, and orbitofrontal/medial frontal cortical areas. Among these structures, the nAcc is thought to occupy a pivotal position in the interface between the sensory-discriminative and motivational-affective components of the pain system. The nAcc is believed to be associated with affective experiences, including pleasure sensation, and by implication, also with experiencing pain in humans. Koikegami and Ozaki (1967, p. 131) noted that the nAcc in elephants has functions associated with olfacto-visceral or olfacto-sexual correlation centers. Our interpretation of this statement, as well as data from the work of Rasmussen and her colleagues (Rasmussen and Hultgren, 1990; Rasmussen *et al.*, 1982, 1996), indicate that one of the functions of the nAcc is related to chemical cues and subsequent behavioral repertoire is possibly associated with mating.

The nAcc has complex connections in humans and other mammals which include a limbic-motor interface, channeling information to the thalamus and frontal lobe of the cerebrum. This connection is thought to be involved in goal-directed or exploratory behavior. A second pathway involves channeling information from the amygdala, hippocampus, entorhinal cortex (smell), and cingulate gyrus, all limbic structures, to the septum, hypothalamus, and frontal lobes, areas associated with various visceral and autonomic as well as affective behaviors (cf. Fig. 1F). This pathway is the one postulated as having a role in reward behavior (“pleasure”), and has also been implicated as a putative pathway in pain perceptible and response.

Text in this and the following three paragraphs is based primarily on the work summarized by Nieuwenhuys (1988) on humans, but it also includes observations on primates, cats and rodents, and, by inference, also on elephants. The nAcc is thought to play a role in the initiation of movements in response to emotionally or motivationally powerful stimuli (Nieuwenhuys, 1988, p. 322). The nAcc is part of the ventral or “limbic” striatum and appears to serve a function for the limbic system analogous to the function subserved by the dorsal striatum (basal ganglia system) for other cortical areas. It receives afferents from limbic structures including the limbic areas of the frontal lobe (medial frontal), temporal lobe (perirhinal, entorhinal), and insula (posterior insula) as well from the hippocampal formation (subiculum), the amygdaloid nuclear complex (basolateral nuclear group), and various subcortical nuclei (bed nucleus of stria terminalis, midline thalamic nuclei). The nAcc also receives afferents from brainstem centers including nuclei of the midbrain reticular formation (nucleus centralis superior, nucleus dorsalis raphes) and the PAG.

The PAG is thought to play an important role in a variety of functions and behavioral patterns including nociception (pain perception), defense reactions, vocal expression of emotion, and reflexes related to sexual function (Nieuwenhuys, 1988, p. 322). The PAG receives afferents from many different brain structures, including the spinal cord. It projects, in turn, via ascending pathways to diencephalic and telencephalic structures and via descending pathways to various brainstem and spinal cord structures (cf. Fig. 1F). Its ascending projections include projections to the frontal cortex, nAcc, septum, and olfactory areas along with various hypothalamic nuclei. Its brainstem projections include projections to the ventral tegmental area in the midbrain tegmentum, the nucleus raphes magnus in the pons, and the nucleus ambiguus in the medulla. The nucleus raphes magnus is

thought to be a relay between the PAG and spinal cord neurons in a descending pain-control system which serves to inhibit noxiously evoked activity in spinal cord neurons in the dorsal horn. The nucleus ambiguus innervates striated muscle fibers in the pharynx and larynx, and the PAG-nucleus ambiguus connection appears to convey the impulses which elicit vocal expression of emotion. Difference concerning pathways of pain among man, cat, and pig include transmission of painful stimuli in the spinal cord of the cat is more diffuse than in man (Kennard, 1954). According to Breazile and Kitchell (1968) in the pig the ascending pain fibers system which convey impulses from stimuli are composed of two systems: one unilateral and the other bilateral with reference to the spinal cord.

The efferent connections of the nAcc include a circuit analogous to the principal basal ganglia circuit: frontal cortex → nAcc → ventral pallidum → medial thalamus → frontal cortex (cf. Fig. 1F). A circuit analogous to the striatonigral reciprocal pathway connects the nAcc with the substantia nigra and ventral tegmental nucleus. Additional efferent pathways connect the nAcc to the septal nuclei, hypothalamus, and midbrain tegmentum including the pedunculopontinus nucleus.

The role of the nAcc in pain thus appears to be that of an effector, receiving information related to nociception from the PAG, integrating it with affective information from limbic areas such as the frontal cortex, amygdala, and hippocampus and translating it into motor responses through the pallidothalamocortical and descending brainstem tegmental pathways. Although much of the specific connective anatomy among these structures remains to be established in the elephant brain, the presence of these connections in other mammalian brains suggests that the general pattern should be present in the brain of an elephant.

There is ample evidence that animals do experience pain (Andrews *et al.*; 1993; Bateson, 1991; Borszcz, 1995; Franklin and Abbott, 1989; Hammond, 1989; Kitchell *et al.*, 1983; Kitchell and Johnson, 1983; Vierck *et al.*, 1989; Willis, 1985; Zimmerman, 1984). Animals tested include rodents, primates, and carnivores, and observations were reported on neurosurgical, behavioral responses (including Pavlovian responses), and assessments of analgesic drugs on nociceptive responses.

*Hormones* — Specific kinds of hormones, classified as endorphins (e.g., met-enkephalin and beta-endorphin), have been known to serve as neurotransmitters and function as natural analgesics. The presence of endorphins in the dorsal horn of the spinal cord, substantia gelatinosa of the trigeminal nerve, PAG, medial and interlamina thalamic nuclei is probably related to analgesia. Their presence in other brainstem nuclei is probably related to other functions, such as cough, vomiting, and hormonal regulation (Simon and Hiller, 1994). Thus, one of the functions of these hormones is to act as “painkillers” by decreasing the perception of pain by the central nervous system (Campbell, 1993, pp. 920, 998-9; see also discussion in Franklin and Abbott, 1989). Elephants have been reported to have about eight times the amount of beta-endorphin, the antinociceptive potency, of humans (Cheng and Yamashiro, 1991). The fact that elephants produce these hormones could be interpreted as evidence that they do feel pain, for otherwise, why would they need “painkiller”? How and when elephants secrete this hormone is not known, but it is entirely possible that this hormone is released in response to severe environmental stimuli associated with pain. From an evolutionary perspective, this kind of hormone would be extremely important for the adaptation of a species, for it would provide a higher tolerance and thus a better chance for survival.

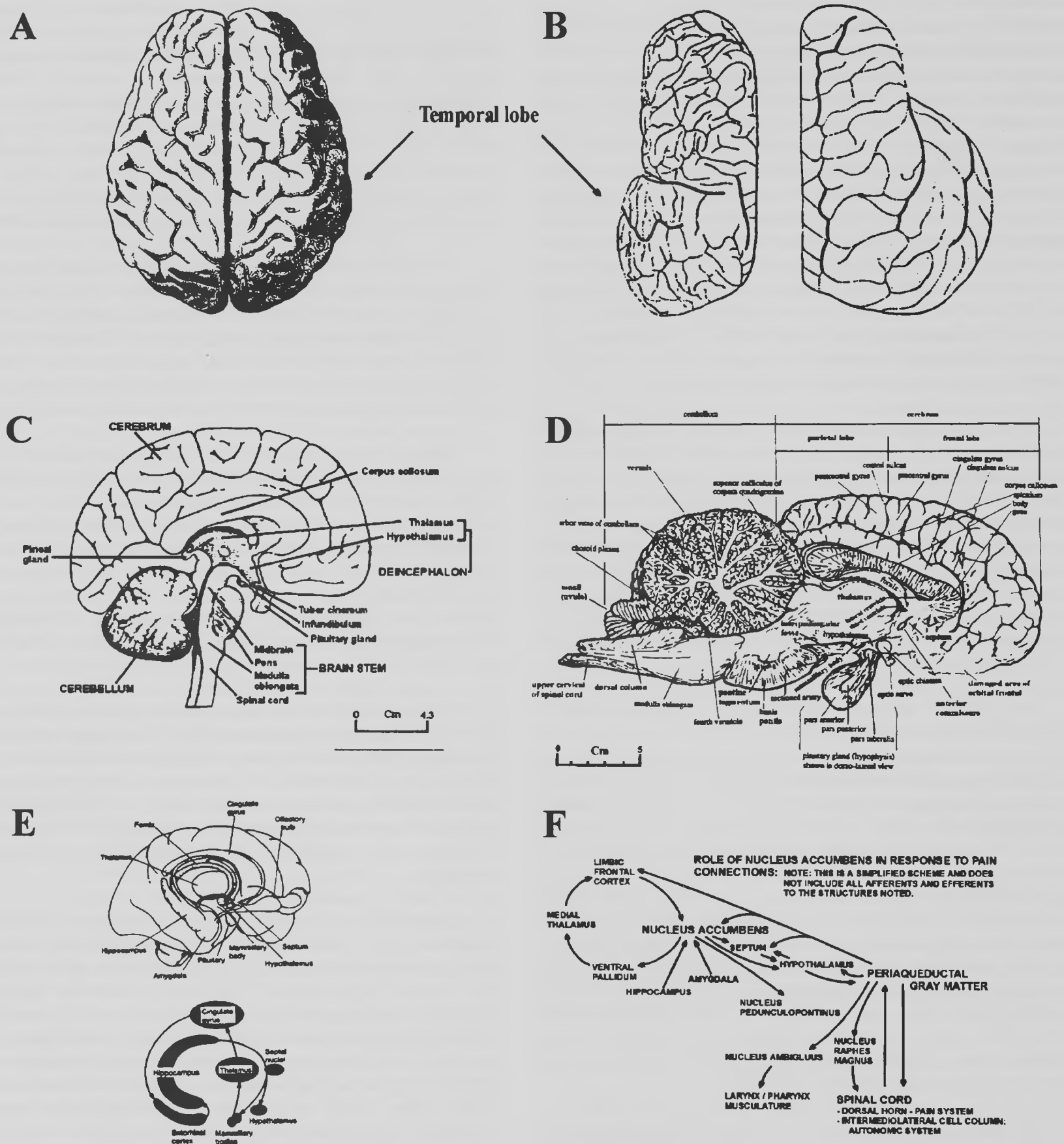


Figure 1. A composite figure depicting structures of the nervous system of humans and elephants, with emphasis on the limbic system. A — dorsal view of human brain (after Gray, 1901); B — dorsal views of cerebri, left side: of African elephant hemi-brain, and, right side: Asian elephant hemi-brain (after Krueg, 1880, taf. xxxviii); C — mid-sagittal view of human brain (drawn by Gary H. Marchant); D — mid-sagittal view of Asian elephant brain (drawn by Brian Cressmann, from specimen of "Tulsa", a 34 year old female); E — top illustration: limbic system; bottom illustration: flow of information through the limbic system (after Kardong, 1995, p. 659; reproduced with permission of the McGraw-Hill companies); F — a diagram showing areas in the limbic system that are associated with pain in humans (drawn by William J. Kupsky). Note that in a broad sense, structures of human brains are similar in gross anatomy to those of elephants, as observed by researchers cited in this paper, and by W. J. Kupsky and J. Shoshani (the temporal lobes in elephants, especially those of the Asian, are much larger than in humans, cf. Figs. A and B). The nucleus accumbens is not seen in illustrations C-E but its approximate location is near the septum shown in Figs. D and E.

## QUESTIONS/PROBLEMS ENCOUNTERED

**QUESTION:** Is it correct to assume from a behavior of animals, elephants in particular, that, if they do not respond to a specific environmental stimulus (e.g., having been poked or hit by a sharp object), they do not have the receptors to feel that stimulus?

**ANSWER:** The short reply is no, it is not correct to assume from a behavior of elephants that, if they do not respond to a specific environmental stimulus, they do not have the receptors to feel that stimulus. A long reply follows. Skin in certain parts of the body may be richer in some types of receptors than skin in other parts. The reaction of the animal will depend on many variables, such as the general health of the animal (including age and sex), thickness of the skin where the impact was made, and the strength and duration with which an elephant was hit. Thickness of the skin in adult elephants varies from 1.8 millimeters (less than 1/8 of an inch) on the medial side of the ear to 32 millimeters (about 1.3 inches) on the dorsum [these measurements include dermis and epidermis; see Shoshani *et al.*, 1982, p. 60, and Shoshani 1992, p. 66]. There are different kinds of receptors associated with different stimuli, and each one is distributed at various depths and positions in the skin. Receptors are grouped according to their functions: mechanoreceptors, chemoreceptors, electromagnetic receptors, thermoreceptors, and pain receptors. Some pertinent examples include: Pacinian corpuscles — found deep in the skin which respond to strong pressure; Meissner's corpuscles and Merkel's discs — found close to the surface of the skin which can detect light touch; Ruffini's end organs — found close to the surface which are sensitive to heat; end bulb of Krause — found close to the surface which is sensitive to cold; nociceptors — found very close to the surface which are sensitive to pain. As noted above, Rasmussen and Munger (1996) depicted and described Pacinian corpuscles, Merkel terminals (discs), and free nerve endings (nociceptors) in the skin of elephants, especially in the tip of the trunk.

**QUESTION:** Is it correct to assume from a structure of a tissue present in humans and elephants that this structure has the same function in humans and elephants?

**ANSWER:** If the structure is fairly common among the animals being investigated, and if its function is unequivocally agreed upon by all investigators, and if such a structure has been shown to be associated with a particular behavior (e.g., withdrawal of a hand or a leg when having been poked by a sharp object), then it is probably correct to assume that such a structure of a tissue present in humans and elephants has a similar or analogous function in human and elephants.

## CONCLUSIONS

Mice, rats, monkeys, humans, and elephants are all mammals. The available experimental evidence indicates that these mammals have nociceptors in their skins. They have been observed to respond to stimuli associated with the sensation of pain as it is known in human subjects. Nociceptors have also been found in elephants along with the central nervous system structures thought to be implicated in the processing and interpretation of pain information. We thus infer that elephants are capable of experiencing pain as are humans.

In addition to citations given above, we note that one of the most convincing arguments is the heavy use of analgesics and pain management in veterinary, and of course, in human medicine (Baumans *et al.*, 1994; Flecknell, 1997/1998) and the reliance of animal models in pain research (Stevens, 1997/1998). Web site

addresses that may be useful are given below under "Web sites".

It is often stated that animals experience pain. For example, Campbell (1993, p. 1019) wrote: "Virtually all animals experience pain, although we cannot say what perceptions they actually associate with stimulation of their pain receptors". Haas (1978, p. 298) reported that an elephant, which used to be easy to handle, suddenly showed signs of dangerous and abnormal behavior. Postmortem examination showed bony structures that pressed on nerves, damaged them, and "caused pain", which was inferred to be the reason for the change in behavior. Based on the evidence we provide from histology (presence of free nerve endings and their interpreted functions as pain receptors), from neurology (presence of nucleus accumbens and other structures thought to be associated with response to pain), and from endocrinology (presence of hormones known as endorphins that function as natural analgesics or "painkillers"), in our professional opinion, elephants are able to experience pain at a level and extent similar to that which humans experience.

## ACKNOWLEDGMENTS

Detective David Smithers, Ian Redmond, Gary H. Marchant, Jann S. Grimes, Eleanor C. Marsac, Jules L. Pierce, and Sandra L. Shoshani helped in various aspects of this investigation. Bucky Steele donated Tulsa's brain for research.

## LITERATURE CITED

- Andrews, E. J., Bennett, B. T., Clark, J. D., Houpt, K. A., Pascoe, P. J., Robinson, G. W., and Boyce, J. R. (1993). 1993 Report of the AVMA panel on euthanasia. *Journal of the Veterinary Medical Association*, 202(2):230-249.
- Anonymous. (1999). Circus "trainer" and zoo inspector guilty of cruelty. *The Animal Welfare Institute Quarterly*, Spring:5.
- Bateson, P. (1991). Assessment of pain in animals. *Animal Behavior*, 42:827-839.
- Baumans, V., Benson, G. J., Flecknell, P., Morton, D., and Short, C. (1994). Detecting and alleviating pain in non-human animals. *Humane Innovations and Alternatives*, 8:580-586.
- Borszcz, G. S. (1995). Pavlovian conditional vocalizations of the rat: a model system for analyzing the fear of pain. *Behavioral Neuroscience*, 109(4):648-662.
- Breazile, J. E. and Kitchell, R. L. (1968). A study of fiber systems within the spinal cord of the domestic pig that subserve pain. *Journal of Comparative Neurology*, 133:373-382.
- Campbell, N. A. (1993). *Biology* (third edn). The Benjamin/Cummings Publishing Company, Inc., Redwood City (California), xxx + 1190 pp. + 3 appendices, glossary, acknowledgments, and Index, all numbered separately.
- Cheng, H.C. and Yamashiro, D. (1991). Synthesis and receptor activity of elephant Beta-endorphin, a beta-endorphin homolog with highly potent analgesic activity. *International Journal of Peptide & Protein Research*, 38:66-69.
- Flecknell, P. (1997/1998). Assessment and alleviation of post-operative pain. *Animal Welfare Information Center Newsletter* [Winter 1997/1998], 8(3-4):8-14.
- Franklin, K. B. J. and Abbott, F. V. (1989). Techniques for assessing the effects of drugs on nociceptive responses. In *Neuromethods: Vol. 13. Psychopharmacology I* (eds. A. A. Boulton, G. B. Baker, and A. J. Greenshaw), pp. 145-216. Humana Press, Clifton (New Jersey), xxiv + 821 pp.
- Gray, H. (1901). *Gray's Anatomy, descriptive and surgical*. (1974 printing edited by T. P. Pick and R. Howden) Running Press, Philadelphia, 1257 pp.
- Haas, G. (1978). Verhaltensstörungen durch Knochenauflagerungen um den Nervus intermediofacialis und statoacusticus bei einer Indischen Elefantenkuh (*Elephas maximus bengalensis*) [loosely translated as "Behavioural disorders associated with bony structures on the intermediofacial and stratoacoustic nerves, in an Indian elephant (*Elephas maximus bengalensis*)"]. *Zoologische Garten*, 48(4):297-298.

- Hammond, D. L. (1989). Inference of pain and its modulation from simple behaviors. In Issues in pain measurement (eds. C. R. Chapman and J. D. Loeser), pp. 69-91. Raven Press, Ltd., New York, xviii + 570 pp.
- Kardong, K. V. (1995). Vertebrates: comparative anatomy, function, evolution. Wm. C. Brown Publishers, Dubuque (Iowa), 777 pp.
- Kennard, M. A. (1954). The course of ascending fibers in the spinal cord of the cat essential to the recognition of painful stimuli. Journal of Comparative Neurology, 100:511-524.
- Kitchell, R. L. and Johnson, R. D. (1983). Assessment of pain in animals. In Animal stress (ed. G. P. Moberg), pp. 113-140. American Physiological Society, Bethesda (Maryland), viii + 324 pp.
- Kitchell, R. L., Erickson, H. H., Carstens, E., *et al.* (eds.). (1983). Animal pain: perception and alleviation. American Physiological Society, Bethesda (Maryland), viii + 324 pp.
- Koikegami, H. and Ozaki, N. (1967). Studies on the paralimbic brain structures. 3. On the nucleus accumbens and on the olfacto-segmental tract in the Indian elephant. Acta Medica et Biologica (Niigata), 15(2):131-140.
- Koikegami, H., Hirata, Y. and Oguma, J. (1967). Studies on the paralimbic brain structures — I. Definition and delimitation of the paralimbic brain structures and some experiments on the nucleus accumbens. Folia Psychiatrica et Neurologica Japonica, 21(3):151-180.
- Krueg, J. (1880). Ueber die Furchen auf der Grosshirnrinde der zonoplacentalen Säugethiere. Zeitschrift für wiss. Zoologie, 33:595-672 + Mit Tafel XXXIV-XXXVIII.
- Nieuwenhuys, R., Voogd, J., and van Huijzen, C. (1988). The human central nervous system (third edn). Springer Verlag, New York, 437 pp.
- Rasmussen, L. E., Schmidt, M. J., Henneous, R., Groves, D., and Daves, Jr., G. D. (1982). Asian bull elephants: flehmen-like responses to extractable components in female elephant estrous urine. Science, 217(4555):159-162.
- Rasmussen, L. E. L. and Hultgren, B. (1990). Gross and microscopic anatomy of the vomeronasal organ in the Asian elephant (*Elephas maximus*). In Chemical Signals in Vertebrates 5 (eds. D. W. MacDonald, D. Müller-Schwarze, and S. E. Natynczuk), pp. 154-161. Oxford University Press, Oxford, xxi + 659 pp.
- Rasmussen, L. E. L. and Munger, B. L. (1996). The sensorineural specializations of the trunk tip (finger) of the Asian elephant, *Elephas maximus*. The Anatomical Record, 246(1):127-134.
- Rasmussen, L. E. L., Hall-Martin, A., and Hess, D. L. (1996). Chemical profiles of male African elephants, *Loxodonta africana*: physiological and ecological implications. Journal of Mammalogy, 77(2):422-439.
- Shoshani, J. (1992). Anatomy and physiology. In Elephants: majestic creatures of the wild (consult. ed. J. Shoshani), pp. 66-80. Rodale Press, Emmaus (Pennsylvania), 240 pp. Also, Simon & Schuster, London, pp. 66-81.
- Shoshani, J. *et al.* [76 co-authors]. (1982). On the dissection of a female Asian elephant (*Elephas maximus maximus* Linnaeus, 1758) and data from other elephants. Elephant, 2(1):3-93.
- Simon, E. J. and Hiller, J. M. (1994). Opioid peptides and opioid receptors. In Basic neurochemistry (fifth edn) (eds. G. J. Siegel, B. W. Agranoff, R. W. Albers, and P. R. Molinoff), pp. 321-339. Raven Press, New York, 1080 pp.
- Stevens, C. W. (1997/1998). A whole-animal alternative model for pain research. Animal Welfare Information Center Newsletter [Winter 1997/1998], 8(3-4):3-5.
- Vierck, C. J., Jr., Cooper, B. Y., Ritz, L. A., and Greenspan, J. D. (1989). Inference of pain sensitivity from complex behaviors of laboratory animals. In Issues in pain measurement (eds. C. R. Chapman and J. D. Loeser), pp. 93-115. Raven Press, Ltd., New York, xviii + 570 pp.
- Web sites on pain and related matters: <[www.nal.usda.gov/awic/](http://www.nal.usda.gov/awic/)>; <[altweb.jhsph.edu/science/meetings/pain/program.html](http://altweb.jhsph.edu/science/meetings/pain/program.html)>; <[www.psyeta.org](http://www.psyeta.org)>.
- Willis, W. D. (1985). The pain system. The neural basis of nociceptive transmission in the mammalian nervous system. S. Karger, Basel, Switzerland.
- Zimmerman, M. (1984). Neurobiological concepts of pain, its assessment and therapy. In Pain measurement in man. Neurophysiological correlates of pain (ed. B. Bromm), pp. 15-35. Elsevier Publishing Co., Amsterdam, xvi + 511 pp. ■