tests, and identical procedures were followed. The data suggest a tendency toward exclusiveness. A presentation area was entered on less than 50 percent of the trials compared to 89 percent for trials with the familiar dog ($P < .01$, combined preference tests). The dog stranger was contacted on only 25 percent of the trials in this test compared to 72 percent for the familiar dog ($P < .02$, combined tests). Even though the stranger was much less effective than the familiar dog, it received substantially more approaches and contacts than did the inanimate surrogate. On 84 percent of the trials in which a presentation area was entered, the dog stranger was chosen first, and it received 88 percent of total time in proximity and 95 percent of total time in contact.

These results bear directly on several important issues related to early social attachments. First, they emphasize the fundamental importance of distinguishing between the attributes of strength, specificity, exclusiveness, and permanence (that is, irreversibility) in discussions of attachment behavior. Conceivably, these attributes can vary independently. We have found that an existing attachment may be strong, specific, and exclusive, and yet can be redirected to an object that is physically quite different from the original attachment figure. Eventually, the new attachment also becomes strong, specific, and exclusive. In addition to the evidence presented, we separated five of the monkeys from their original dogs and housed them with new canine companions. In every case the new dog became an effective parent substitute. Clearly, a prior bond does not preclude the formation of a strong new attachment by young rhesus monkeys.

Second, conclusions that the original attachment abides indefinitely in rhesus monkeys and shows little or no reduction in strength (*4*) must be reexamined in the light of the evidence presented here. The four monkeys in this experiment that were raised with conspecifics consistently preferred the familiar dog over an unfamiliar young monkey. Furthermore, subsequent tests indicated that the two peer-raised monkeys preferred the dog over the original cage mate.

Third, the suggestion that the capacity to form new filial attachments diminishes sharply during the first 2 months of life and all but disappears by 250 days of age is clearly at variance with our results (*5*). All of our subjects, including two that were raised individually in enclosed isolation cages until 10 months of age, showed unequivocal evidence of infantile attachment to the dog—including approach, following, a sharp increase in vocalization upon separation, and active clinging to the dog in situations eliciting fear or distress.

Finally, our data suggest that the ease with which new attachments will be formed depends upon properties of the social substitute which are yet to be fully determined. Although a large measure of stimulus equivalence may be expected in the earliest stages of ontogeny, it seems unlikely that all claspable objects will support the development of strong filial attachments in older infant monkeys. In another experiment in which rhesus monkeys were given cloth surrogates at 10 months, no evidence of attachment formation was obtained (*5*), whereas our monkeys of a comparable age showed strong attachment to their canine companions. A dog obviously provides more varied stimulation and subtle feedback during the affiliation process than an inert cloth surrogate. This probably accounts for the discrepant results. In any event, a gentle, accepting dog can be a highly effective mother substitute for young rhesus monkeys, even for those that have had experience with the real mother.

WILLIAM A. MASON
M. D. KENNEY
Department of Psychology and
California Primate Research Center, University of California, Davis 95616

References and Notes

1. J. P. Scott, *Science* **138**, 949 (1962); D. Morris, *The Human Zoo* (Dell, New York, 1969).
2. J. Bowlby, *Attachment and Loss*, vol. 1, *Attachment* (Basic Books, New York, 1969), pp. 180–187.
3. R. B. Cairns, in *Attachment and Dependency*, J. L. Gewirtz, Ed. (Winston, Washington, D.C., 1972), pp. 29–80.
4. H. F. Harlow, in *Am. J. Orthopsychiat.* **30**, 676 (1960); ——— and S. J. Suomi, *Am. Psychol.* **25**, 161 (1970).
5. H. F. Harlow, *Sci. Am.* **200**, 68 (June 1959); ———, in *Determinants of Infant Behavior*, B. M. Foss, Ed. (Wiley, New York, 1961), pp. 75–97.
6. Supported by NIH grants HD06367 and RR00169.

20 June 1973

Site of Neural Attenuation of Responses to Self-Vocalized Sounds in Echolocating Bats

Abstract. *Bats of the genus* Myotis *emit intense orientation sounds for echolocation. If such sounds directly stimulated their ears, the detection of echoes from short distances would be impaired. In addition to the muscular mechanism in the middle ear, the bat has a neural mechanism in the brain for attenuation of responses to self-vocalized orientation and nonorientation sounds. This neural attenuating mechanism operates in the nucleus of the lateral lemniscus, reducing its activity by about 15 decibels, and it is synchronized with vocalization.*

Sensory systems often receive stimulation produced by the animal's own activities. For instance, the retina is stimulated by movement of images introduced by eye and head movements, and the lateral-line system of fish is activated by water displacement caused by body movement. Such self-stimulation may not be absolutely necessary for monitoring the movements of the eye or body, and it may even disturb the perception of external sensory stimuli. Apparently, the visual and lateral-line systems have mechanisms for attenuating such self-stimulation. Visual perception in humans is suppressed before and during eye movements (*1*). A comparable phenomenon has also been observed in arthropods (*2*). When fish and aquatic frogs move, the activity of sensory cells in the lateral line organ is suppressed by efferent fibers before and during body movements (*3*).

The auditory system is stimulated by the animal's self-vocalized sound. This self-stimulation is important in controlling vocalization, as evidenced by the abnormal variability in intensity of speech sounds from deaf persons (*4*) and by the interference with normal development of songs in birds that are deafened (*5*). Acoustic self-stimulation, however, would be unnecessarily intense for simple monitoring of vocalization, if the auditory system were not equipped with mechanisms for attenuating its sensitivity. Attenuation of self-stimulation appears essential to hearing; such attenuation occurs both at the receptors and in the brain. In humans, cats, and bats, the muscles of the middle ear have been shown to contract synchronously with vocalization to attenuate self-stimulation (*6, 7*). In addition to this muscular attenuation, neural attenuation by the olivo-

cochlear bundle is conceivable, but this has not yet been proved. Data on the brain of gray bats (*Myotis grisescens*) have been obtained which indicate the presence of a neural attenuating mechanism operating synchronously with vocalization (*8, 9*). This neural attenuation in the brain was found by comparing the summated responses of primary auditory and lateral lemniscal neurons to self-vocalized frequency-modulated (FM) sounds with those evoked by the same sounds played back through a tape recorder (*10*). The responses of lateral lemniscal neurons to the self-vocalized sounds were found to be much smaller than those evoked by the playback sounds, even when the response of the primary auditory neurons was nearly the same for both types of sounds. It is clear that the neural attenuation takes place between the auditory nerve and the inferior colliculus (IC), but its specific location has been unknown. Between these two sites, there are the cochlear nucleus, superior olivary complex, and nucleus of the lateral lemniscus. Each of these nuclei is further divided into subnuclei. Since the auditory pathway is complicated, the origin of the neural attenuation appeared difficult to identify; nevertheless we have now identified it in the nucleus of the lateral lemniscus. We report here the data which lead us to this conclusion.

The gray bat was anesthetized with ether, and a smooth head of a nail (1.8 cm in length) was mounted on its skull with dental cement. A few hours after surgery, the awake animal was placed on a plastic ball floating on water in a soundproofed room, the inner wall of which was covered with fiber glass sheets. The shank of the nail was locked into a metal rod with a set screw. Two small holes were then made in the skull without anesthesia. Tungsten-wire electrodes were inserted into the brain through these holes to record summated activity of auditory neurons (*8*). Seventeen bats were used.

When recording and indifferent electrodes are placed on the dorsal surface of the IC and exposed temporal muscles, respectively, one can easily record auditory evoked potentials with five positive peaks, called N_1, N_2, N_3, LL (N_4), and IC responses to acoustic stimuli (*11*). With the recording electrode placed in the auditory nerve, the S-segment (that is, the lateral superior olivary nucleus), or the nucleus of the lateral lemniscus, the N_1, N_3, or LL responses, respectively, became diphasic or triphasic and became as large as 1 to 3 mv peak to peak, while others remained less than 0.2 mv. The N_1, N_3, and LL responses were apparently the summated action potentials mainly originating from the auditory nerve, the S-segment, and the nucleus of the lateral lemniscus (*12*). It was not easy to separately record a large N_2 response. The origin of N_2 was not clear, but it may have been the cochlear nucleus (*13*). Since selective recording of an N_1, N_3, or LL response was possible, we recorded these evoked potentials in different combinations with two recording electrodes and examined combinations in which the neural attenuation was found.

To elicit vocalization, the bat was mechanically stimulated by touching its back or its tail (or both) with a brush or by moving the plastic ball on which the bat rested. Thirty-two different FM orientation sounds or squeaks emitted by the bat were monitored with a quarter-inch (~ 6-mm) microphone (Brüel & Kjaer, 4135) placed about 10 cm in front of the bat's mouth and about 30° down from the eye-nostril axis, and were recorded on a magnetic tape with an Ampex FR-100 tape recorder, which has a frequency response of 50 to 300,000 hertz at a tape speed of 60 inches per second (152 cm/sec). The microphone has a frequency response which is flat from 50 to 120,000 hertz within ± 1.0 db. The sounds emitted by the bat ranged between 100 and 115 db SPL (sound pressure level referred to 0.0002 dyne/cm^2 root-mean-square). The responses (for example, N_1 and N_3) evoked by these 32 emitted sounds were stored and averaged by a computer (Nicolet, 1070). The averaged response was plotted with an X-Y recorder. These are called "the self-evoked responses." The tape-recorded sounds were played back at different amplitudes through a loudspeaker placed 68 cm in front of the

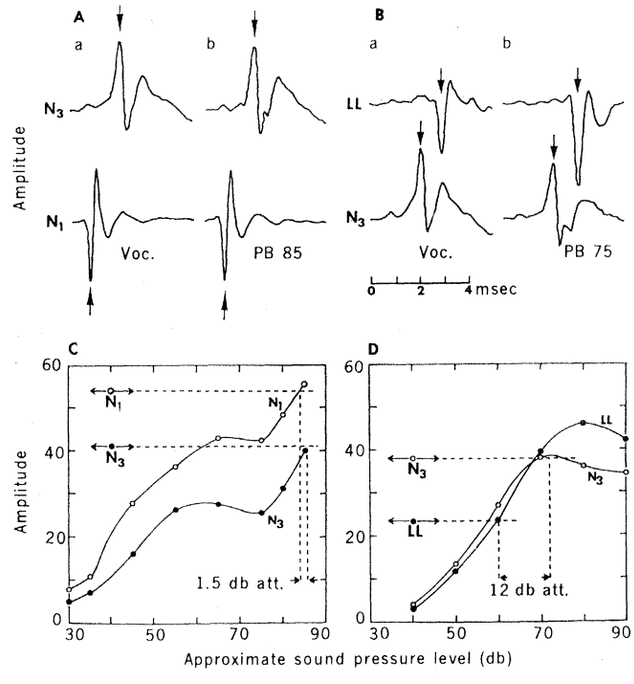

Fig. 1. Summated responses of the auditory nerve (N_1), S-segment (N_3), and nucleus of the lateral lemniscus (LL) evoked by 32 self-vocalized sounds (Voc.) (a) and by these sounds played back (PB) with a tape recorder (b). Each response indicated by an arrow is the average of 32 samples. The slow potential change following N_3 probably originated from the nucleus of the lateral lemniscus and the inferior colliculus. (A) N_1 on the left side and N_3 on the right side are simultaneously recorded. The self-evoked N_3 is very similar to the playback N_3 whenever the self-evoked N_1 is nearly the same as the playback N_1. The amplitudes of the playback sounds are approximately 85 db SPL. (B) LL on the left side and N_3 on the right side are simultaneously recorded. The self-evoked LL is significantly smaller than the playback LL although the self-evoked N_3 is nearly the same as the playback N_3. The amplitudes of the playback sounds were approximately 75 db SPL. The sounds produced by the bat were weaker than those in (A). (C) and (D) Relation between the amplitudes of the playback N_1, N_3, and LL (ordinates) and the approximate pressure level of the playback sounds (abscissas). Each point represents the average of 32 responses. The ordinates represent the peak-to-peak amplitudes of the evoked responses plotted with an X-Y recorder. Ten units in the ordinates correspond to 0.2 to 0.3 mv. The amplitudes of the self-evoked N_1, N_3, and LL are indicated by the horizontal arrows and dashed lines. The graphs in (C) and (D) were obtained in the same recording conditions as those for the evoked potentials in (A) and (B), respectively. The amount of neural attenuation (*att.*) is 10 to 14 db, with an average of 12 db in (D). (The bat was not anesthetized or immobilized during the experiments.)

bat's mouth between 4 and 60 minutes after the self-vocalized sounds were recorded. The output of the playback system, consisting of the tape recorder, amplifiers, and loudspeakers, had a flat frequency-response curve from 20 to 100 khz within ± 2 db. The responses (N_1 and N_3) evoked by these played back sounds were averaged and plotted. These are called "the playback responses." The self-evoked response (for example, N_3) was compared with the playback response (N_3) in order to determine whether there was a difference in amplitudes when N_1 was the same for both types of sounds. Since the computer was synchronized with the onset of either the self-vocalized or the playback sounds, fluctuations in time were always present in averaging the responses, but the amount was the same for both the self-evoked and playback responses. The standard deviation of the amplitudes of these evoked potentials was about ± 5 percent.

When N_1 and contralateral N_3 were simultaneously recorded for self-vocalized and playback sounds, the self-evoked N_3 was nearly the same as the playback N_3 whenever the self-evoked and playback N_1's were the same (Fig. 1A). In Fig. 1C, the relationship between the pressure level of the playback sounds and the amplitudes of the evoked potentials is shown. The horizontal arrows and dashed lines represent the amplitudes of the self-evoked N_1 and N_3. These lines cross the curves for playback N_1 and N_3 at about 85 db SPL. Therefore, there is no neural attenuation between the cochlear nerve and the S-segment.

As another combination, the N_3 and contralateral LL were simultaneously recorded for self-vocalized and playback sounds. As shown in Fig. 1B, the self-evoked and playback N_3's are the same in amplitude, but the playback LL is much larger than the self-evoked LL (t-test for amplitude difference, $P < .01$). This indicates that the response of the nucleus of the lateral lemniscus is suppressed when the animal vocalizes. An alternative explanation could be the facilitation of responses to the playback sounds following vocalization. This, however, appears unlikely because the time interval between vocalization and playback sounds ranged between 4 and 60 minutes. If such a long-lasting facilitation occurs, responses to self-vocalized sounds would also be facilitated.

In Fig. 1D, the relationship between pressure level of the playback sounds and the amplitudes of the evoked potentials is shown. The dashed line indicating the amplitude of self-evoked N_3 crosses the curve for playback N_3 at 70 and 74 db SPL, while the dashed line indicating the amplitude of self-evoked LL crosses the curve for playback LL at 60 db SPL. Thus, the amount of attenuation observed in Fig. 1B is equivalent to either 10 or 14 db, with an average of 12 db.

We repeated these experiments with 17 bats. The neural attenuation observed for the emission of FM orientation sounds or squeaks was 0.0 ± 6.2 db between N_1 and N_3 (16 animals) and 16 ± 12 db between N_3 and LL (17 animals). In previous experiments (*8, 9*), vocalizations were mainly evoked by electrical stimuli applied to the midbrain, and the neural attenuation between N_1 and LL was studied. In the experiments reported here, however, vocalizations were elicited without electrical stimulation. Consequently, the neural attenuation between N_1 and LL was remeasured; it was 15 ± 10 db (11 animals).

Nerve impulses are transmitted from the auditory nerve to the cochlear nucleus, then to the superior olivary complex containing the S-segment, to the nucleus of the lateral lemniscus, and to the inferior colliculus. Our data indicate that the amount of neural attenuation found between the responses of the auditory nerve and the nucleus of the lateral lemniscus was not different from that between the responses of the S-segment and the nucleus of the lateral lemniscus. The neural attenuation did not occur in either the cochlear nucleus or the S-segment, but it occurred in the nucleus of the lateral lemniscus. Further data supporting this conclusion remain to be obtained by recording single unit activity from the nucleus of the lateral lemniscus.

As already mentioned, the middle-ear muscles attenuate the self-stimulation by 20 to 25 db (*7, 14*). Thus, the total attenuation by both the muscles and the neural events is 35 to 40 db. This is a surprisingly large attenuation. We believe that similar muscular and neural attenuation mechanisms also exist in our communication system, because we never perceive our own speech sounds to be disturbingly loud, unless our eustacian tubes are abnormally patent (*15*).

NOBUO SUGA
TATEO SHIMOZAWA*
Department of Biology, Washington University, St. Louis, Missouri 63130

References and Notes

1. P. L. Latour, *Vision Res.* **2**, 261 (1962); F. H. Duffy and C. T. Lombroso, *Nature (Lond.)* **218**, 1074 (1968).
2. J. Palka, *Am. Zool.* **12**, 497 (1972).
3. R. Klinke and C. L. Schmidt, *Pfluegers Arch. Gesamte Physiol. Menschen Tiere* **318**, 325 (1970); I. J. Russell, *J. Exp. Biol.* **54**, 621 (1971).
4. H. Davis and S. R. Silverman, *Hearing and Deafness* (Holt, Rinehart & Winston, New York, 1970), pp. 361-364.
5. M. Konishi, *Z. Tierpsychol.* **20**, 349 (1963); *ibid.* **22**, 770 (1965); *Condor* **66**, 85 (1964).
6. P. W. Carmel and A. Starr, *J. Neurophysiol.* **26**, 598 (1963); G. Salomon and A. Starr, *Acta Neurol. Scand.* **39**, 161 (1963); W. M. Shearer and F. B. Simmons, *J. Speech Hear. Res.* **8**, 203 (1965).
7. O. W. Henson, Jr., *J. Physiol. (Lond.)* **180**, 871 (1965).
8. N. Suga and P. Schlegel, *Science* **177**, 82 (1972).
9. ———, *J. Acoust. Soc. Am.* **54**, 174 (1973).
10. As described previously (*8*), playback sounds at the inner ear are similar, but not identical, to the self-vocalized sounds, because (i) the output of the loudspeaker is not completely flat for all frequencies but uneven within ± 2 db between 20 and 100 khz; (ii) the signal-to-noise ratio of the playback sounds was 30 to 40 db, much smaller than that of the self-vocalized sounds (for which it was more than 60 db), and (iii) self-stimulation always consisted of both bone and air conductions, but the playback sounds consisted solely of air conduction.
11. J. H. Friend, N. Suga, R. A. Suthers, *J. Cell Physiol.* **67**, 319 (1966); A. D. Grinnell, *J. Physiol. (Lond.)* **167**, 38 (1963); N. Suga, *ibid.* **203**, 707 (1969).
12. Since neurons in the cochlear nucleus [N. Suga, *J. Physiol. (Lond.)* **172**, 449 (1964); *ibid.* **179**, 26 (1965)], the S-segment (P. H. Jen, unpublished), and the nucleus of the lateral lemniscus (*9*) of bats commonly show tonic on-responses to tonal stimuli, any evoked potential after N_1 could originate from one or more nuclei. Thus, the origin of a summated evoked potential is very difficult to analyze. Nonetheless, the statements on the origin of N_1, N_3, and LL are still valid, because only well-synchronized action potentials can produce a large summated potential change. For instance, primary auditory neurons fire repetitively during tonal stimuli, but these action potentials do not electrotonically contribute to the LL response which appears with a latency of 2.8 to 3.5 msec. Therefore, it is correct to describe the LL response as mainly originating from neurons in the nucleus of the lateral lemniscus. In the superior olivary complex of *Myotis*, the S-segment and the nucleus of the trapezoid body are large, while the accessory nucleus is absent [J. M. Harrison and M. L. Feldman, in *Contributions to Sensory Physiology*, W. D. Neff, Ed. (Academic Press, New York, 1970), p. 95]. From the measurements of the depth and orientation of the recording electrode, it is more likely that the N_3 response mainly originates from the S-segment. The nucleus of the trapezoid body and the preolivary nuclei, respectively, are too medial and ventral to the tip of the recording electrode to be considered sources. The latencies of single-unit and mass responses of the S-segment of *Myotis grisescens* and *M. lucifugus* are 1.8 to 2.2 msec (P. H. Jen, unpublished). We believe that the N_3 response with a peak latency of 1.8 to 2.1 msec mainly originates from the S-segment, although further experiments are required to confirm its origin by depositing metal ions or dyes at the tip of the recording electrode.
13. A. D. Grinnell, *Z. Vgl. Physiol.* **68**, 119 (1970).
14. N. Suga and P. H. Jen, in preparation.
15. G. M. Coates, H. P. Schenck, M. V. Miller, *Otolaryngology* (W. F. Prior Co., Hagerstown, Md., 1955), p. 17; M. M. Paparella and D. A. Shumrick, *Otolaryngology* (Saunders, Philadelphia, 1973), p. 82.
16. Supported by grant GB-13904-A1 from the National Science Foundation. We thank J. Simmons for reading this manuscript and T. Gass for his assistance.
* Present address: Department of Zoology, Hokkaido University, Sapporo, Hokkaido, Japan.

26 December 1973