crocapsule suspensions in bottles containing copepods with control bottles containing no animals. Each set of experiments (including those with enriched and nonenriched microcapsules) were carried out simultaneously to ensure identical environmental conditions for all bottles.

When the copepods were fed with large microcapsules, net ingestion could be measured only for the enriched capsules (Table 1, experiment B-1) even though debris particles of smaller size were produced (Fig. 1, experiment B-1). There was little or no net ingestion of the unenriched particles but very intense production of particle debris (Table 1; Fig. 1, experiment B-2); in this case, there was considerable modification of the particle size distribution as shown by the experimental curve appearing at the left of the control curve. This was presumably a result of mastication followed by rejection (*5, 7*). The ingestion rate of experiment B-1 was significantly different from that of experiment B-2 (*t*-test, $P < .05$).

The particle size distributions in nature are not as simple as those shown in Fig. 1. Generally particle size distributions in seawater are bi- or polymodal, and thus copepods are able to choose particles from among several sizes (*3*). We created this condition artificially in a second series of experiments in which bimodal particle size distributions with peaks of approximately equal concentration alternately contained the enriched particles of either the large size (Fig. 2, experiment C) or the small size (Fig. 2, experiment D). In experiment C, ingestion occurred in both particle size peaks but it was four times higher for large enriched particles than for large nonenriched particles. Moreover, the production of particle debris was negligible (Table 1). Because of the large production of small-sized particle debris in type D experiments which always masked the feeding responses of copepods to particles smaller than 20 μm, the net ingestion rates of small capsules could never be measured. We then replaced the large-sized microcapsules with beads of similar sizes (Sephadex G-75) in order to reduce the production of debris. We assumed that this substitution did not affect the feeding mechanisms, provided that copepods can ingest hard plastic beads within this size range (*4*). Moreover, if the copepods select only on the basis of size, beads should be ingested about as readily as microcapsules (*4*). The production of debris was then negligible (Table 1, experiment D), and preferential feeding could be observed in the size range corresponding to the small enriched particles (Fig. 2, experiment D).

In experiments A, B, C, and D, copepods always preferentially consumed microcapsules that were enriched with homogenate of naturally occurring phytoplankton. Feeding on large particles, whether enriched or not, corresponds to raptorial behavior (*5*). This behavior was particularly intense with nonenriched capsules, judging from both the greater production of particle debris and the low or even zero rate of ingestion. Small particles are easily ingested by the copepods; large particles have to be broken up by the copepods first, and their ability to do this presumably depends on the size of the mouth aperture. Copepods are able to distinguish between "good" food and "nonfood," by "tasting" either the outside (before mastication) or the inside (after mastication) of the particles (Fig. 1, experiments A and B). The copepods discriminated between two types of particles on the basis of their chemical "scent," independent of their size. Therefore, filter-feeding by copepods is a sensory-determined behavioral process.

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Copulatory Vocalizations of Chacma Baboons (*Papio ursinus*), Gibbons (*Hylobates hoolock*), and Humans

Abstract. *The copulatory vocalizations of female baboons* (Papio ursinus) *are more complex than those of female gibbons* (Hylobates hoolock) *or human females. Adult males of all these species begin calling later than the female, but subordinate baboon males do not call. Copulatory vocalizations may serve to mutually stimulate the mating partners or to incite male competition.*

Vocalizations during copulation are widespread among primate species, from prosimians (*1*) to the apes (*2, 3*) and man (*4–9*), yet their significance is seldom discussed. Before now no sonagraphic analyses of human copulatory sounds have been available. When compared with the extensive details of the physical and physiological features of human coitus (*7*), this omission seems surprising. Either the clinical circumstances required for observations of some aspects of coitus (*7*) inhibited vocalizations or they were simply not reported. Interpretations based upon the concepts of orgasm and pleasure intrude into the human-oriented literature, providing little insight into the meaning of these sounds. Here we contrast copulatory vocalizations by humans, monogamous gibbons (*Hylobates hoolock*), and promiscuous troop-dwelling baboons (*Papio ursinus*) and evaluate their possible significance relative to their social setting.

Sexual arousal and orgasm in humans may be communicated by verbal or nonverbal sounds (or both), including changes in respiratory rate (*7*), moans, and gasps (*4–9*). Some individuals sob or laugh uncontrollably during orgasm (*6, 9*). Individually or culturally improvised verbalizations may also accompany coitus and orgasm (*5, 6, 9*).

Individuals may suppress all copulatory vocalizations, usually from fear of being overheard (*9*). Humans may also vocalize to mimic orgasm (*8*).

Sonagrams of human copulatory vocalizations (Fig. 1) obtained from films and a tape (*10*) show that female sounds gradually intensified as orgasm approached and at orgasm assumed a rap-

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id, regular (equal note lengths and internote intervals) rhythm absent in the males' calls at orgasm. At climax, the sounds of both females and males are explosive bursts that are more structurally complex at this time than elsewhere in the copulatory sequence. Neither sex, however, showed the complexity of note structure characteristic of baboon copulatory vocalizations.

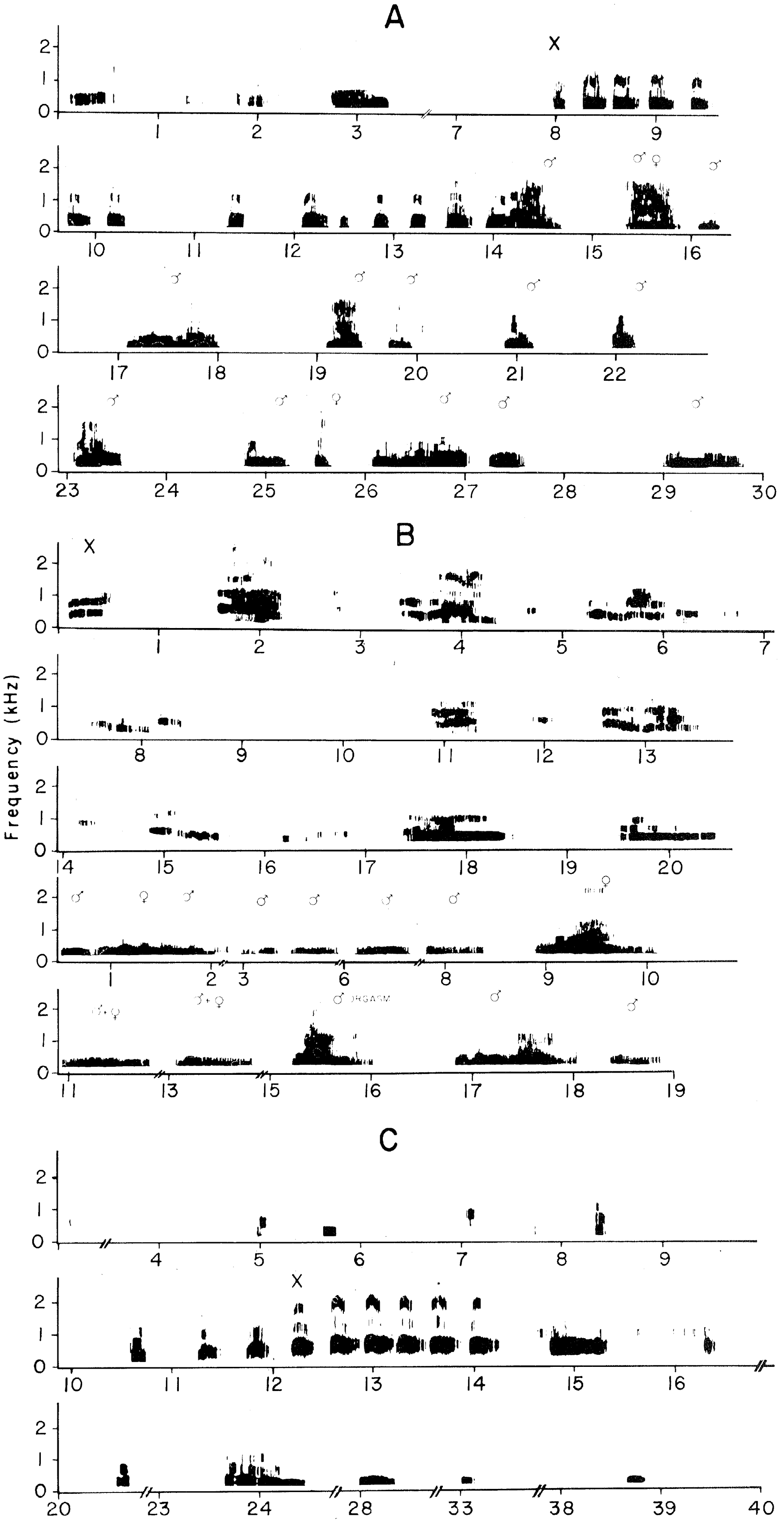

Fig. 1. Sonagrams of the copulatory sounds of human females and males. A male symbol above a note indicates the male's contribution; all other notes are the female's. Onset of the female's orgasm is indicated by an *X*. (A) Human female and male, both about 35 years of age, in a mutually climactic sequence. The first male note indicates the onset of his orgasm. (B) Human female and male, both about 50 years of age. The woman here was multiorgasmic. This sequence reflects only one of her orgasms, early in copulation. The male vocalized much later. (C) Human female, 50+ years of age (postmenopausal). This was the first of a multiorgasmic sequence for this female. Here the male did not vocalize (*25*).

Verbal descriptions of chacma baboon copulatory vocalizations vary. Males are reported to lip-smack (*11*), to give "ech-ech" vocalizations (*12*), or to grunt (*11, 12*) before and during copulation. Female vocalizations are variably described as staccato grunts (*12*), intermittent roars (*11*), or gurgling or muffled growls (*13, 14*), yet all investigators have recognized a copulatory call as a distinct vocalization (*12–15*). Females call with their mouths almost closed and cheeks blown out (*12, 13*).

We observed and recorded individually known adult male and female chacma baboons (*16*) over a series of estrous cycles from May through August 1973. These individuals were members of a troop of 72 baboons living along the Boro River in the Okavango Swamp, Botswana. In every mating with vaginal penetration by a male, several hundred observations in all, the female vocalized. This included matings with juvenile males as young as approximately 2.5 years. Both female and male vocalizations erupted towards the end of copulation as pelvic thrusting ceased and the pair separated (*17*). Both sexes sometimes continued calling for a brief interval after separation.

These chacma female calls (Fig. 2, A to E) are loud and structurally complex, showing a high degree of intraindividual note variation. The notes are usually emitted in a rapid, regular rhythm but diminish in loudness, cadence, and complexity at the sequence's end. The calls also vary among females in note type, note modulation, harmonic structure, and duration (*18*).

Juvenile males did not vocalize when copulating, and the calls given by females during matings with juvenile males are with one exception shorter (*19*) and less complex than those given during adult male matings (Fig. 2, F and G). The female calls maintained their individual character, however.

Adult males always vocalized when copulating with females (*17*) (Fig. 3). These rhythmical low-frequency vocalizations began a few seconds after the female's vocalizations and continued after she ceased vocalizing. In only one case did a male begin vocalizing before the female. The copulatory sounds of males are also individually distinctive (Fig. 3).

Saayman (*12*) found that chacma female copulatory calls occurred more frequently during inflation and maximum turgescence than during deturgescence. Female calls also occurred more often with adult male mountings than with subadult male mountings and much less frequently with juvenile male mountings (*12*). All copulations we observed included female vocalizations.

Chacma females may run away from males following copulation (*14*). We sometimes saw tentative movements away but usually the female did not move more than 1 to 5 m from the male, who immediately followed her. These withdrawals played no discernable role in the change of associations during a female's estrous cycle. Mutual grooming by sexual partners often follows copulation (*14, 15, 20*).

Gibbon calls were recorded from a pair of gibbons living in the Jakarta Zoo, Java. The female called first during copulations (Fig. 4). Her copulatory notes were emitted rapidly and covered a wider frequency range than baboon or human calls, but like human copulatory vocalizations, they are much less structurally complex than female baboon calls. The male gave low-frequency grunts.

Several hypotheses can be offered in explanation of coital vocalizations of primates.

1) The vocalization may be an incidental by-product of the sexual act. Copulatory vocalizations of baboons, gibbons, and man are in part the product of rhythmical labored exhalations. In a copulatory sequence these exhalations become more frequent and intense. This physiological response is the precursor of the call and for some species may be the entire explanation of the vocalization. For the species we studied, however, the vocalizations are more elaborate than exhalations, and the transition from rapid, labored breathing to distinctive and often loud vocalizations suggests a communicatory function.

2) Mutual signals to indicate arousal and orgasm might be advantageous. In humans, after the female's orgasm the anterior vaginal walls and the cervix quickly return to prestimulation positions, immersing the cervix into the seminal pool (*7*). Females may have a greater chance of sperm escape after orgasm due to a relaxed orgasmic platform (*7*). Thus, vocalizations that could stimulate the male or be mutually stimulatory and thus aid in close coordination of ejaculation and female orgasm might improve chances of conception. The extent to which this holds true for other primates remains unknown.

3) Copulatory vocalizations may increase the probability that the same individuals will mate again later. For instance, the association of rewarding sexual activity with individually distinctive calls may strengthen current and future pair relationships. Monogamous primates might then be expected to have elaborate sex calls. The calls of neither monogamous gibbons nor humans are complex compared with those of baboons. Gibbon pairs remain together throughout extended periods of sexual inactivity (*3*), and human pairs persist even though one or both partners may not vocalize.

4) Copulatory vocalizations may serve to expose matings and to identify the copulating partners to other group members. Thus alerted, males may be incited to compete for females (*21*). The fe-

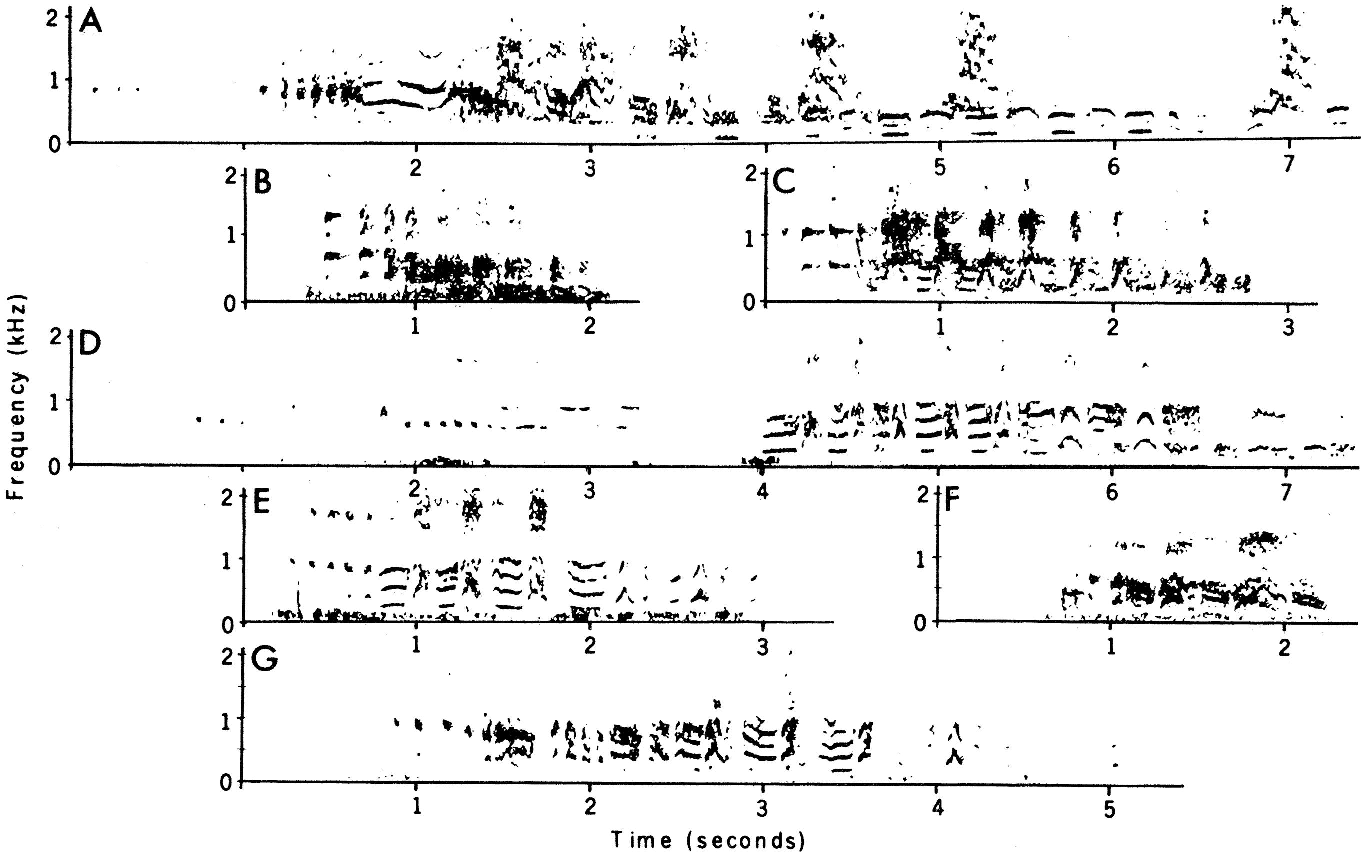

Fig. 2. Sonagrams of the copulatory calls of adult female chacma baboons. (A to E) Representative samples of calls by specific females during matings with adult males. The note characteristics differ among females. (Although the low-frequency male sounds are evident in some sonagrams here, they are not necessarily shown in their entirety.) (A) Heady. (B) Dawn. (C) Prudence. (D) Lightning Tail. (E) Zebra. (F and G) Samples of calls given by two females during matings with juvenile males. Here note structures and durations of calling change yet still remain characteristic of individual females. (F) Heady. (G) Lightning Tail.

male chacma baboons we observed always gave these highly distinctive and loud [audible as far as 200 to 300 m (*12, 15*)] calls when copulating. All chacma troop members are seldom in visual contact since they commonly spread out through vegetation over a space 300 m in diameter. Since in spite of the risk of exposure of individuals and the troop to predators these baboons habitually call during copulation, the calls must have some adaptive value. The value of females mating with high-ranking males has been emphasized in numerous studies of baboons and other polygamous animals (*22*). Female baboons have a series of sexual partners during the estrous cycle and on the average mate with higher-ranking males at ovulation (*23*). Consort pairs, often on the troop's periphery, may be out of sight of other troop members. Thus, a mating can be identified by the presence of loud female copulatory calls and the participants identified by their individually distinctive vocalizations. In contrast with chacma baboons, olive baboons (*Papio anubis*) vocalize during only 10 percent of copulations (*14*). These baboons live in more open savannah and plains environments than chacma baboons, and the identity of matings and participants may thus be determined visually.

For chacma baboons there has been little attention to male interference with copulations. In an early report, Hall (*13*) observed that mating sometimes attracted the attention of the dominant male of one troop, but he witnessed no direct interference with mating. In a later description of the same troop (*14*) he noted one instance of an interference by the alpha male, which succeeded in driving away the copulating male. Ugandan olive baboon males were keenly interested in the sexual activities of others, dancing around a copulating pair, coughing, and touching them (*24*).

Other features of the reproductive cycle reinforce the incitement hypothesis. Female baboons may mate 100 times or more in the course of an estrous cycle (*14*), so the average importance of each mating is low. The estrous swelling provides information about the timing of ovulation, and as the time of ovulation approaches the rank of attending males increases (*23*). The value of vocalizations specific to copulation is that they reveal any mating attempts during receptive periods. The elaborate sex skin cycle and vocalizations of females may thus be adaptations to enhance the probability of mating by dominant males. Individually distinctive calls also identify males and their matings with particular females. Higher-ranking males may be able to complete a greater percentage of their copulations than lower-ranking males [(*14*) but see also (*23*)]. The absence of vocalizations by the lowest-ranking juvenile males suggests that male copulatory vocalizations play a role in preventing interference with copulations.

Human and primate copulatory calls are elaborations of the rhythmic, rapid breathing associated with intense sexual activity. For the three species described, the copulatory vocalizations of females are more complex than those of males and begin earlier in the copulatory sequence. Because of the wide range of ecological and social situations among primates, as exemplified by the three species studied here, unitary explanations of the adaptive significance of copulatory vocalizations may not be possible.

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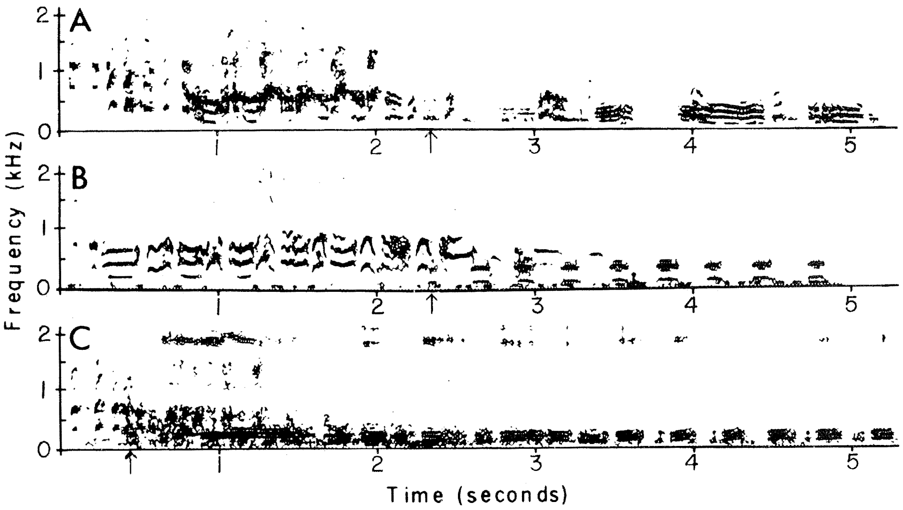

Fig. 3 (A–C). Sonagrams of the copulatory calls of three adult male and female chacma baboon pairs. An arrow indicates the beginning of the low-frequency male calls. (A) male Consort and female Prudence, (B) male Blue and female Lightning Tail, (C) male Blue and female Dawn.

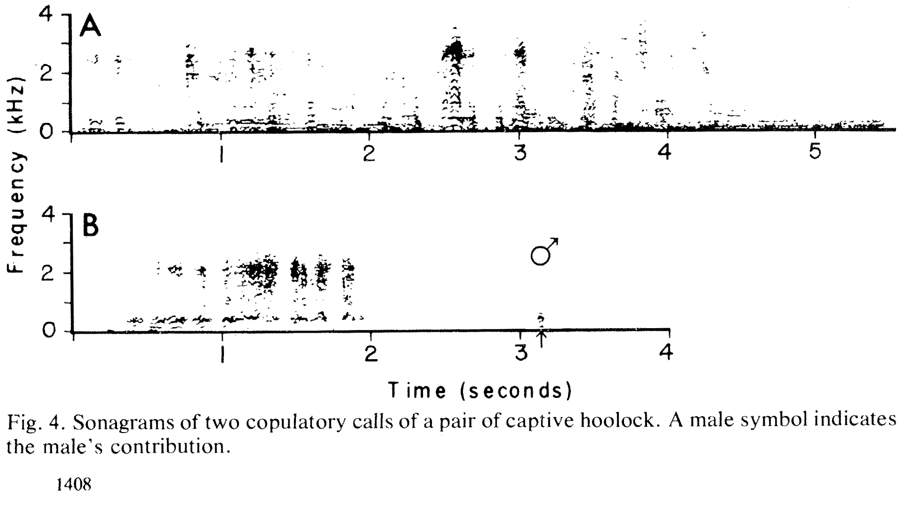

Fig. 4. Sonagrams of two copulatory calls of a pair of captive hoolock. A male symbol indicates the male's contribution.

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10. Sonagrams A and B were made from the soundtracks of two films, *The Squeeze Technique* and *Effective Sexual Functioning*, respectively. These films are used in sexual education and therapy. A tape used in private sexual counseling provided the material for sonagram C. The partners in all three cases were married and were aware they were being filmed or recorded. The first filmstrip is distributed by the Multi Media Resource Center, San Francisco, Calif., and the second was contributed by the Center for Marital and Sexual Studies, Long Beach, Calif.
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16. Adult males, $N = 5$; adult females, $N = 5$; juvenile males, $N = 6$. An adult male is here defined as a male larger than a female.
17. A female chacma baboon in another troop in the Okavango Swamp, Botswana, was recently observed to give copulatory calls when defecating, and, on one occasion, a female gave a copulatory call when a high-ranking male walked nearby. Hall (*13*) also reported that females sometimes gave copulatory calls while defecating. For males, recent observations in Botswana (S. K. Smith, personal communication) suggest that only the more dominant adult males vocalize when copulating.
18. Durations of female calls in seconds: Heady, 6.85 (S.D. = 0.32, $N = 2$); Lightning Tail, 4.47 (S.D. = 0.94, $N = 6$); Zebra, 4.07 (S.D. = 1.19, $N = 4$); Prudence, 3.14 (S.D. = 0.51, $N = 4$); Dawn, 1.94 (S.D. = 0.16, $N = 6$).
19. Duration (in seconds) of female calls over all 22 matings with adult males: 3.68 (S.D. = 0.44). Duration of female calls over seven matings with juvenile males: 3.68 (S.D. = 0.89). Durations of individual female calls during matings with juvenile males: Lightning Tail, 4.65 (S.D. = 0.94, $N = 3$); Heady, 3.42 (S.D. = 1.84, $N = 3$); Dawn, 1.55 ($N = 1$).
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25. We used a tape recorder (Uher 4000 Report-L), microphone (Uher M514), and 60-cm parabola to record baboon vocalizations and the same equipment, without the parabola, to record the gibbon and human vocalizations. Sonagrams were made with a sonagraph (Kay Elemetrics model 6061B) on narrow band filter. (For the human sounds, the wide-band filter was used.) An accessory unit, a 6076C scale magnifier, allowed us to expand the width of these low frequency sounds over the entire 10-cm width of the sonagram paper, thus providing a clearer picture of the complex structure of these sounds.
26. We thank C. D. Busse and Drs. A. B. Clark, G. Hausfater, G. W. Salt, W. A. Mason, and B. S. Orlove for critical reviews of the manuscript; the Anthropology Department, University of California, Davis, for the use of their sound spectrograph; V. Hildebrand for numerous helpful suggestions; and Multi Media Resource Center and the Center for Marital and Sexual Studies for the use of their filmstrips.

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Commissural Transmission: Maturational Changes in Humans

Abstract. *Latency differences between ipsilateral and contralateral somatosensory evoked potentials show maturational trends in keeping with the myelogenic timetable and development of the corpus callosum. The distribution and modality-specific projection of early ipsilateral activity suggests an origin in the contralateral posterior-parietal area.*

In humans and other mammals, the commissures of the forebrain are poorly established at birth (*1*). Their growth parallels that of the neocortex, building up as medullary sheaths (myelin) are deposited. Culmination of the myelogenic cycle in a given pathway has been taken as an index of its functional maturity (*2*). The corpus callosum and other association bundles as well as the intracortical plexus of the parietal lobe are among the last cortical zones to begin and complete the process of myelination.

The evoked potential has been widely used to track the development of interhemispheric communication in animals. Recordings obtained directly from the pial surface in a number of species (*3*) show that the latency of the transcallosal response decreases as a function of age. Detailed electron microscopic examination of the corpus callosum has revealed a strong inverse relationship between the emergence of myelinated callosal axons and the latency of the interhemispheric evoked potential (*4*).

Topological studies of human evoked potentials to sensory stimulation have shown that the ipsilateral response following unilateral stimulation is consistently slower and of smaller magnitude than the contralateral response (*5*). The latency difference between selected components of ipsilateral and contralateral responses has been interpreted as representing the commissural delay (*6*). In the visual modality, a stimulus falling on the left hemiretinae projects exclusively to the right occipital lobe and one on the right hemiretinae projects to the left lobe. Thus commissural transmission can be directly inferred from ipsi-contralateral differences. In this respect, significantly longer latencies and lower amplitudes have been observed over the homolateral cortex after hemifield stimulation (*7*).

Since strict fixation is required for unilateral visual activation, this modality is not suitable for testing young children and infants. Behavioral determinants such as dichotic listening or tachistoscopic reaction time have provided unreliable and often contradictory results regarding commissural transfer (*8*).

I have studied the somatic afferent system in order to derive an objective measure of commissural transmission in humans irrespective of age. Differences found in the latency, distribution, and development of ipsilateral and contralateral responses indicate that the evoked potential recorded from the scalp's surface can provide valuable information regarding myelogenesis and maturation of the corpus callosum.

Sixty healthy subjects ranging in age from 2 years to adulthood (*9*) received tactile stimulation of the left or right index finger (counterbalanced). The stimulus was produced by an Optacon reading aid for the blind. The Optacon consists of a 24 by 6 array of probes covering an area of 28 mm by 14 mm; it generates a 250-Hz vibrotactile pulse. The intensity of the stimulus was a 65-μm indentation for a duration of 50 msec. Cortical potentials evoked by 25 stimuli delivered at a rate of one every 2 seconds were automatically summated with a special-purpose (Nicolet 1070) or general-purpose (PDP 8/E) computer. Bioelectric activity was recorded bilaterally from symmetrical placements 6 to 7 cm lateral to the midline in the interaural plane and 1 to 3 cm posterior to this point. In several subjects, recordings were obtained from multiple parasagittal locations. The vertex (Cz) served as a common reference. Preamplifiers (Grass P511) set for a bandpass of 3 to 100 Hz amplified the signal. The average evoked potential waveform was read out, on line (Hewlett-Packard XY plotter), and the latency of the initial positive-negative-positive complex was digitized.

Representative ipsilateral and contralateral evoked potentials for several age groups are presented in Fig. 1. The peaks of interest, P1, N1, and P2, are identified (top tracings). These peaks were selected for their high within-and-between subject reliability. Since they constitute the earliest deflections of the response, their accurate recognition across age and between ipsilateral and contralateral potentials was simplified. Repeated measurements taken within a session or over the course of 2 years in several adults showed a high degree of replicability. Notice the reduced amplitude and prolonged latency of the early components of the ipsilateral response (Fig. 1). With increasing age there is a progressive decline in the ipsi-contralateral difference. Prior to 3.5 years of age, reliable ipsilateral activity could not be obtained. Figure 2 shows the mean