secured by a ligature, and a second ligature closed the biliary duct just before its opening into the duodenum. Other experiments were conducted in which injections were made into the ducts only (not their respective regions of drainage) with a mixture of India ink and latex (50 : 50 by volume). Following the injections, the mixture was hardened with acetone; the resulting casts were revealed by digesting the exocrine tissue surrounding the ducts with concentrated HCl.

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6. After immunofluorescent staining with the specific antiserums, each section of the islet was photographed on Kodak color slide film at a final magnification of ×80 in a Zeiss photomicroscope (Zeiss, Inc., Ober Kochen, West Germany) equipped for fluorescence. Each color slide was projected onto a 245 by 330 by 4 mm Lucite sheet at a final magnification of ×1200. A colored pen was used to transfer the fluorescent image of each cell to the Lucite sheet. The same color was used to represent cells stained by a particular antiserum. In the reconstructed islet, every fourth Lucite sheet represented the staining by the same antiserum.
7. A morphometric analysis (*8*) of human pancreases obtained from autopsies and stained by the immunofluorescent techniques used for the rat pancreases has revealed similar heterogeneity among the populations of endocrine cells depending on their location within the gland. Of the endocrine cell volume in sections of the posterior part of the pancreatic head in normal adults, about 76 percent contained pancreatic polypeptide, 21 percent contained insulin, 2 percent contained somatostatin, and 1 percent contained glucagon. However, of cells in the body of the pancreas, about 85 percent contained insulin, 11 percent contained glucagon, 3 percent contained somatostatin, and only 1 percent contained pancreatic polypeptide. Moreover, the pancreatic polypeptide–rich region in the head of the pancreas was separated from the remainder of the gland by a plane of connective tissue [L. Orci, F. Malaisse-Lagae, D. Baetens, A. Perrelet, *Lancet* **1978-II**, 1200 (1978); F. Malaisse-Lagae, L. Orci, A. Perrelet, *N. Engl. J. Med.* **300**, 436 (1979); F. Malaisse-Lagae, Y. Stefan, J. Cox, A. Perrelet, L. Orci, *Diabetologia*, in press]. Independent evidence for a partition of the pancreas in pancreatic polypeptide-rich, glucagon-poor and pancreatic polypeptide–poor, glucagon-rich regions in human and canine pancreases was recently described by using radioimmunoassay to assess the hormone concentrations and immunoperoxidase to detect the respective endocrine cell populations [D. J. Gersell, R. L. Gingerich, M. H. Greider, *Diabetes* **28**, 11 (1979)]. These data correlate well wth ours, except for a few human cases in which high concentrations of pancreatic polypeptide were not accompanied by numerous pancreatic polypeptide–containing cells. This discrepancy is explained by the fact that in the human pancreas, the pancreatic polypeptide–rich islets are often contained only in the posterior part of the pancreatic head rather than in the entire head. If the anterior part of the head is radioimmunoassayed for hormonal concentrations and the posterior part for immunoperoxidase staining (or the reverse), then the discrepancy may arise.
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9. Series of four successive serial sections were obtained in dorsal and ventral regions of the pancreas of two male rats (250 g), stained sequentially with the four antiserums, and evaluated morphometrically as described in (*8*). Values pooled from 20 islets studied in each pancreatic region of each rat, expressed as volume density and percentage of each cell type, are:

Hormone	Volume density (by volume)	Percentage
Dorsal islets		
Insulin	0.618	82.5
Glucagon	0.111	15.0
Somatostatin	0.015	2.0
Pancreatic polypeptide	0.004	0.5
Ventral islets		
Insulin	0.600	82.0
Glucagon	0.010	1.3
Somatostatin	0.018	2.4
Pancreatic polypeptide	0.106	14.3

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13. Supported by Swiss National Science Foundation grant 3.120.77 and U.S. National Institutes of Health grant N01-AM-7-2213. We thank P. H. Wright, R. H. Unger, R. E. Chance, R. A. Donald, and S. Ito for providing the antiserums, and I. Bernard, I. Fuglister, A. M. Lucini, and M. Sidler-Ansermet for expert technical assistance.

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Sex Discrimination in *Gerris remigis*: Role of a Surface Wave Signal

Abstract. *Even when blinded with masks, adult male water striders* (Gerris remigis) *accurately ascertain the sex of other adult water striders in the laboratory. Freely moving females that were artificially made to play back computer-generated male surface wave and body-contact signals of about 90 waves per second were treated as males by the masked males and as females when no such playbacks were made. Thus, the males can use presence or absence of the male signal as the sole means for sex discrimination.*

Gerris remigis is a large riverine water strider (body length, 12 to 14 mm)—the most widely distributed North American species of the insect family Gerridae (*1*). Adults and nymphs produce intraspecific surface wave signals during spacing and mating behavior by vertical oscillations of their legs in a fashion similar to that used by adults of the Old World species *Rhagadotarsus kraepelini* (*2*). *Gerris remigis* males (third-instar nymph through adult stage) can produce high-frequency (HF) surface wave signals of 80 to 90 waves per second (Fig. 1) and low-frequency signals of 3 to 10 waves per second. Females (third-instar nymph through adult stage) produce only low-frequency signals. Previously, I demonstrated that, in *R. kraepelini*, signals from males attract receptive females and may induce oviposition (*2*). I now report experiments in which an unusual playback technique is used to show that adult *G. remigis* males can discriminate adult sex solely by whether or not other adults produce HF signals.

During many field trips in Kansas and New York from 1975 to 1978, I saw *G. remigis* males in their mating season repeatedly approach to within a few centimeters of other adults and apparently test each adult by producing HF surface wave signals or by grasping them. If a male was grasped, the two males exchanged HF signals while in contact, and then the grasping male disengaged and moved away. Males in close proximity (a few centimeters) generally exchanged HF surface wave signals, whereupon the approaching male would either grasp the other or move away. If the approaching male encountered a female, however, he usually attempted to copulate after testing her with an HF surface wave signal or grasping her (attempted copulations were easily distinguished from male-male encounters). Males also tested adults by approaching closely and remaining briefly without signaling. If the approached individual did not produce an HF signal, the approacher would usually attempt copulation. When approached, males generally maintained their position and, if grasped, raised their bodies and signaled immediately. However, females often moved away when approached and, if grasped, reacted with anything from passive acceptance of copulation to violent attempts to dislodge the male.

From these observations I hypothesized that males can use presence or absence of the HF signal to discriminate adult sex. In trial series 1 and 2, I tested this hypothesis by determining whether sighted and masked males discriminate sex in the laboratory during their mating season. Trial series 3 was designed to ascertain whether males can use only presence or absence of the HF signal to discriminate sex.

In trial series 1 and 2, three males were placed in an aquarium (surface area, 18 by 30 cm) (*3*) and were then required to discriminate between visitor males and females. Each visitor was introduced in random order with respect to sex at intervals of at least 10 minutes. The resident males were scored according to whether or not they attempted to copulate with a visitor (*4*). In trial series 2, each resident male was blinded with a removable rubber mask (*5*).

Table 1 shows that, in all 120 trials of series 1 and 2, sighted and masked males always discriminated the sex of visitors correctly. Also, in all introductions of males, HF surface wave or contact signals were always exchanged between resident and visitor males. Thus males can discriminate sex accurately and without visual cues.

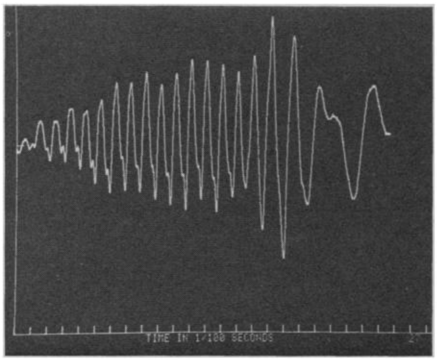

Fig. 1. High-frequency signal of adult male *G. remigis* during spacing behavior, recorded in the field by the galvanometer technique of Wilcox (*2*). The analog signal on magnetic tape was digitized at a sample rate of 4000 per second (8 hits per sample) by the analog-to-digital board in an IMSAI 8080 microcomputer and then displayed on a Tektronix 4006-1 graphics display terminal. For the central, stable-frequency group of waves, peak-to-peak analysis of the signal gives an average of 90.4 waves per second. This signal was used for the playback experiments.

Table 1. Responses of resident male *Gerris remigis* to visitor males and females (trial series 1 and 2) and to females through whom high-frequency signals were or were not played back (trial series 3, a to e).

Trial series	Situation	*N*	Number of trials	Attempts to copulate		Playbacks*		No playbacks†	
				With female	With male	Attempts to copulate with female	No copulation with female	Attempts to copulate with female	No copulation with female
1	Sighted residents Sighted visitors	3 20	60	30	0				
2	Masked residents Sighted visitors	3 20	60	30	0				
3a	Masked male Masked female	1 1	54			0	25	29	0
3b	Masked male Masked female	1 1	10			0	8‡	2	0
3c	Masked male Masked female	1 1	20			0	11	9	0
3d	Masked male Masked female	1 1	20			0	10	10	0
3e	Masked male Masked female	1 1	20			0	11	9	0

*Experimental condition. †Control condition. ‡Male was already grasping female when playbacks began.

In trial series 3, I ascertained whether the HF signal is sufficient for sex recognition by noting how the male responded to freely moving females through whom computer-generated HF signals were or were not sent. Each female thus became her own control, without interrupting the flow of interactions. The technique included gluing a tiny samarium-cobalt magnet to the top of the femur of a female's foreleg, letting her move about inside a coil of magnetic wire (28 cm in diameter), and then using an IMSAI 8080 microcomputer to play the HF signal (shown in Fig. 1) through an amplifier into the coil. The vertically oriented electromagnetic fluctuations oscillated the magnet vertically, making the foreleg produce a surface wave signal with frequency and amplitude characteristics that appeared from recorded playbacks and photographs to be very similar to the normal male HF signal (see cover) (*6*). Neither the presence of the magnet on the foreleg nor the playbacks appeared to affect the behavior of the females. With due caution (behavioral responses to strong electromagnetic fluctuations are always possible), the coil-and-magnet playback system appears well suited for experimentation on various substrate communication modes—for example, web communication among spiders (*7*).

In trial series 3, I allowed a masked male and a masked, magnet-bearing female to encounter each other repeatedly as they moved about inside the coil (*8*). (Such repeated encounters occur commonly under natural conditions.) I randomly played signals (experimental condition) or did not play signals (control condition) when the male showed interest in copulating with the female by closely approaching her head on and either attempting to grasp her or succeeding. In all playback encounters except trial series 3b (see below), I played the signals when the male was within about 2.5 cm of the female, just before he would have grasped her. Thus these males could discriminate sex only through the presence or absence of playback surface wave signals (*9*). This procedure also tested whether males remembered the (apparent) sex of individuals from the preceding encounter.

All trials were videotaped and then reviewed for scoring. I scored only those encounters in which males approached slowly to within about 2.5 cm of females, so that the males would be able to clearly sense the presence or absence of playback signals. In trial series 3, a to e, males always treated females as males when signals were played and as females when signals were not played. Males always replied to playbacks with HF signals. In the first trial of series 3b (a nonplayback trial), the female copulated readily. In eight of nine subsequent trials I played signals only after the male had grasped the still-receptive female, but before copulation had occurred. The male dismounted each time (*10*).

These experiments demonstrate that the HF signal is sufficient for *G. remigis* males to discriminate sex. Even if normally involved, visual cues and body postures and movements are not necessary for sex discrimination. Chemical cues also appear unimportant, since contact playbacks in series 3b repulsed the male even after he had had opportunity to receive possible pheromones from the same female he had copulated with shortly before. Males appear not to remember the sex of individuals involved in previous encounters once close contact is broken.

The coil-and-magnet playback system should help to elucidate the role of frequency and wave-form characteristics of the HF signal in sex discrimination as well as in examining HF signal functions in the other contexts in which it occurs, such as in individual distance maintenance, territoriality, and food defense. *Gerris remigis* produces other surface wave signals, and at least four coexistent species of *Gerris* near Binghamton, New York, produce such signals, providing an opportunity for interspecific studies. The occurrence of surface wave signals in at least 2 of 53 Gerridae genera suggests that further comparative and experimental studies on the many species not yet examined may reveal patterns lending insight into the evolution of surface wave communication.

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3. This area seemed large enough for one or two *G. remigis* to act normally, but was small enough for encounters to occur reasonably often. In all trials of series 1 to 3, males and females were acclimated for at least 24 hours.
4. An encounter was scored as a copulation attempt if the resident male grasped the other individual, held on, and attempted to insert his aedeagus. An encounter was scored as not a copulation attempt if the resident male did not grasp the individual but instead exchanged HF surface wave signals and then turned away from the visitor; or if he released his grasp after a second or two without attempting to copulate. In all trials of series 1 and 2 each visitor had never before encountered the resident male.
5. Masks were made by applying black liquid-silicone rubber to the head of a dead male, peeling the cured mask from the dead male, and slipping it over the head of a live male of the same size. After a day of acclimation, the behavior of masked individuals was very similar to that of sighted individuals.
6. The electromagnetic force decreased in strength toward the center of the coil, so that a female would receive playback signals of different amplitudes depending on her position in the coil. Accordingly, I adjusted playbacks so that all amplitudes visually appeared to be within the normal signal amplitude range. Such variation of amplitude did not appear to influence the outcome of playback trials.
7. For recent reviews of substrate-transmitted communication, see R.-G. Busnel [*Acoustic Behavior of Animals* (Elsevier, Amsterdam, 1963)], T. A. Sebeok [*Animal Communication* (Indiana Univ. Press, Bloomington, 1968); *How Animals Communicate* (Indiana Univ. Press, Bloomington, 1977)], H. Markl [*Naturwissenschaften* **56**, 499 (1969)], and P. H. Brownell [*Science* **197**, 479 (1977)].
8. I masked females as well as males because blinded females are less prone to swim away from approaching individuals, making playback trials easier to conduct.
9. I controlled for direct effects of electromagnetic fluctuations on the behavior of males by comparing responses of a masked male to HF playbacks when the magnet (i) was attached to the female (result of ten trials: male was repelled as usual), (ii) was absent (result of ten trials: male always attempted copulations—as though no playbacks had been made), and (iii) was held in the air near the female on a nylon whisker, which controlled for the magnet's movement per se (result of ten trials: male always attempted copulation).
10. I interrupted the copulations several seconds after the male had achieved insertion. The fact that this masked female was sexually receptive during the trials does not imply a connection between blindness and her receptivity. After trial series 1 to 3 were completed, playbacks were made after the male had achieved insertion. They did not cause the male to dismount. Sometimes a male grasped the female after dashing up from 3 to 4 cm away, and during the usual ensuing struggle, playbacks had no apparent effect on the male (except in trial series 3b). This suggests that differences in body movement sensed when they are struggling may also enable males to discriminate sex. In the field, males occasionally attempted to copulate with other males, regardless of the HF contact signals probably produced initially. Such homosexual attempts may have occurred because the grasping male interpreted the violent movements of the grasped male as female in character, or because the grasping male was sexually deprived.
11. I thank R. Hoy, D. Otte, D. Madison, and J. Shepherd for critical reading of the manuscript; S. Rosenberg for patient and capable help in data gathering; W. Kashinsky for designing the basic computer system and other equipment; W. Kashinsky and T. Apalanek for suggesting the use of a coil-and-magnet system for playbacks; and K. Kafka, T. Apalanek, and D. Gelbman for computer programming and equipment building. Supported by grant BNS77-24708 from the National Science Foundation.

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Shifts in Perception of Size After Adaptation to Gratings

Abstract. *After viewing a suitable grating of vertical stripes for 5 minutes, subjects overestimated the width of a rectangle by 6 percent. The shifts in perception of size occurred whether individual stripes in the grating were narrower than, equal to, or wider than the rectangle. Rectangle width was underestimated only if the grating stripes were extremely wide, with a spatial frequency lower than most of the effective amplitude spectrum of the rectangle. These findings (and complementary ones with horizontal gratings) suggest that the visual system codes size on the basis of spatial frequency components, rather than directly in terms of width.*

Two hypotheses currently address size coding in the visual system. One is that the visual system codes the local feature of size per se. The other, less intuitive hypothesis is that the visual system codes size by doing something like a crude Fourier or spatial frequency analysis of patterns into the appropriate spatial frequency components. We here present findings that are more consistent with coding in terms of spatial frequency components.

Others have shown that, after viewing vertical gratings in which intensity varied sinusoidally across the stripes, observers perceived spatial frequency of other vertical sinusoidal gratings as shifted (*1*, *2*). Gratings higher in spatial frequency (the number of cycles of the grating per degree of visual angle) than the adapting grating appeared higher still, while gratings of lower frequency appeared lower still. Thus, adaptation tends to make gratings appear more different from the adapting frequency than they really are.

If information regarding size or frequency (or both) is carried by channels selectively tuned to spatial frequency (*1*-*3*), adaptation to a particular grating would depress the sensitivity of the channels maximally responsive to that spatial frequency. The central tendency of the distribution of responses of all spatial frequency channels would thus be shifted away from the adapting frequency, and the perceived frequency would also be shifted.

Alternatively, spatial vision may be mediated by size-specific rather than by frequency-specific mechanisms (*4*). Under a size-specific model, the visual field is assumed to be made up of small, overlapping regions (receptive fields), each sensitive to objects of a particular size (such as the width of a single light or

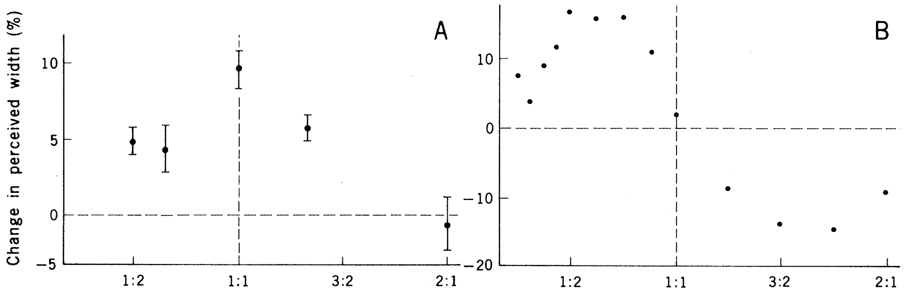

Fig. 1. (A) The perceived widening of a rectangle observed by one subject after adaptation to vertical gratings with sinusoidal intensity distributions. A ratio of 1:1 on the *x*-axis indicates equal widths for adapting bars and test rectangles; on the *y*-axis, 0 indicates no change in perceived size. The width for an adapting stimulus is a half cycle of the grating. Bars indicate standard errors. (B) A subject's matches of the apparent spatial frequency of two vertical gratings, only one of which fell on the retinal region previously exposed to the adapting grating [replotted from figure 2 of (*1*)]. If a size-specific model were correct, the perceived size shift of a rectangle (Fig. 1A) should resemble that for gratings (Fig. 1B).

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