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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2. R. S. Wilcox, *J. Comp. Physiol.* **80**, 255 (1972).
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

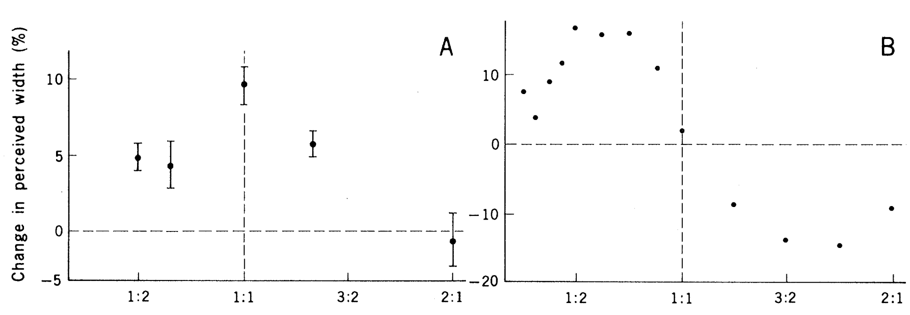

Fig. 1. (A) The perceived widening of a rectangle observed by one subject after adaptation to vertical gratings with sinusoidal intensity distributions. A ratio of 1:1 on the *x*-axis indicates equal widths for adapting bars and test rectangles; on the *y*-axis, 0 indicates no change in perceived size. 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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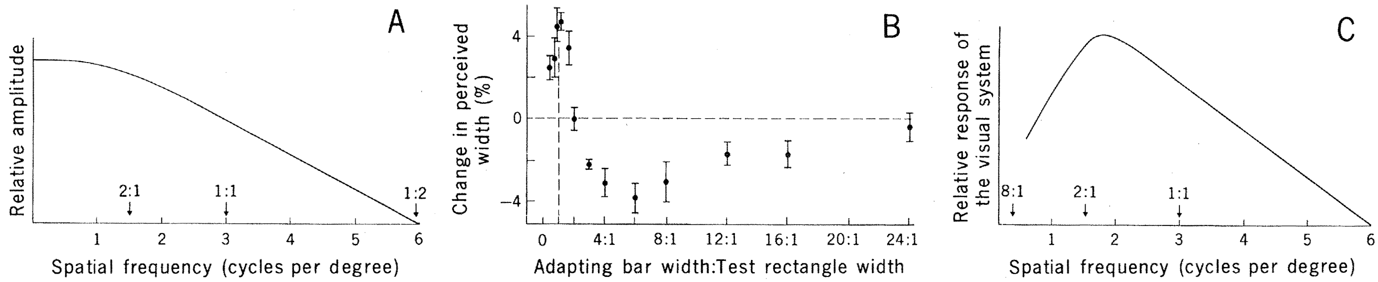

Fig. 2. (A) The lower frequency end of a one-dimensional amplitude spectrum of a 10′-wide rectangle. The arrows represent some of the adapting grating frequencies used in experiment 1; the corresponding size ratios from Fig. 1 are indicated. (B) Percentage change in the perceived width (based on the adjusted height) of a rectangle after adaptation [one subject's data from experiment 2 (*10*)]. Each point is the mean of two sessions and average standard errors are shown. These data are consistent with a spatial frequency model of perceived size. (C) The response of the visual system to the lower frequencies in a 10′-wide rectangle. The arrows show three representative grating frequencies, and the corresponding size ratios are indicated.

dark bar of a grating). Adaptation to a particular grating would fatigue the mechanisms that respond best to objects the size of that grating's bars. After adaptation, these mechanisms would be less responsive to objects the size of the adaptation bars, and the perceived size of other gratings would be shifted accordingly.

The experiment on perceived frequency shifts (*1*) could not distinguish between the size-specific and the frequency-specific hypotheses, because the stimuli used were sine wave gratings, in which there is only a single bar width and a corresponding single spatial frequency. The distinction can be made by using a single uniform bar (or rectangle). Multiple bars in a sine wave grating do not have the same spatial frequencies as a single homogeneous bar of the same width. The fundamental frequency, f, of a grating with bars of width w degrees is $1/(2w)$ cycles per degree of visual angle. A single bar, however, has a broad frequency distribution (*5*).

We used a single bar (rectangle) as an aperiodic test stimulus, which allowed us to disentangle the explanations specific to size and to spatial frequency. If bar width is what matters psychophysically, adapting to a sinusoidal grating will have the same effect on a single bar as on a grating. But if spatial frequency is the determining variable, the effect on a bar and on a grating should be different.

The test bar was a solid luminous rectangle of fixed width but adjustable height. Three subjects reported perceived width by adjusting the height to produce perceived squareness—an adjustment that subjects make with considerable precision. Another seven subjects indicated their judgments by saying whether or not each of the sequence of rectangles appeared square [random, double-staircase procedure (*6*)]. Subjects made judgments before and after viewing a vertical sinusoidal grating for 5 minutes.

The effect of adaptation to the grating on the perceived width of the rectangle was measured as the mean of the ratios between the settings after adaptation and the mean setting before adaptation. After inspecting vertical sine wave bars anywhere between half and one and a half times the rectangle width, the rectangle looked wider (Fig. 1A) (*7, 8*).

If the size model were correct, the results would look not like Fig. 1A, but like Fig. 1B. The size model predicts no size shift when the adapting stimulus and test stimulus are equal in width (1:1 on the abscissa). It predicts perceived widening when the test stimulus is wider than the adapting stimulus and perceived narrowing when the test stimulus is narrower.

The differences between our data (Fig. 1A) and the predictions of the size model seem sufficient to rule out a size-specific model for results with rectangular test objects. [The function on Fig. 1B, which fits the prediction from a size-specific model, consists of data obtained in the perceived frequency shift experiment (*1*), which used sine wave gratings as both adapting and test stimuli. Because only sine wave stimuli were used, the results are consistent with both a size-specific and a frequency-specific model.]

Are the data we obtained (Fig. 1A) consistent with a frequency-specific model? Figure 2A shows the relation between three different adapting gratings and the test rectangle in the spatial frequency domain. The curve is the one-dimensional amplitude spectrum of a 10′ rectangle. The arrows represent some of the adapting grating frequencies used in experiment 1. (The corresponding size ratios from Fig. 1 are indicated.)

According to the spatial frequency explanation, adaptation to a grating makes the spatial frequency channels less responsive to frequencies near the adapting frequency. Therefore, perceived widening should occur when there is relatively less response from the higher frequency channels. Accordingly, the perceived widening we obtained after adaptation to gratings (Fig. 1A) would result from a relative decrease in the effectiveness of higher spatial frequencies. Thus, although our results are not consistent with a size-specific model, they are consistent with a spatial frequency model.

In addition to the widening we observed, the frequency-specific model would also predict perceived narrowing after adaptation to a grating whose frequency is below the equilibrium point of the effective amplitude spectrum of the rectangle—that is, the product of the amplitude spectrum of the physical spatial frequency of the rectangle and the spatial modulation transfer function of the visual system. Thus to obtain perceived narrowing we would either have had to use very small test rectangles or adapting gratings of very low frequency. Because subjects could not make meaningful judgments of squareness for rectangles smaller than 5′ of arc, we used gratings ranging in frequency from 8 cycles per degree to as low as 1/8 cycle per degree and large adapting fields ranging in size from 7° to 23° (*9*).

The predictions from the spatial frequency hypothesis were supported (for example, Fig. 2B) (*10*). Adapting to low-frequency gratings led to perceived narrowing, as indicated by the points lying below zero. After adaptation to very low-frequency gratings, low-frequency channels contributed relatively less to the final judgment, and the observer therefore saw the rectangle as narrower. The points lying above zero corroborate our earlier findings of perceived widening (Fig. 1A) (*11*).

Figure 2C gives a more detailed analysis of the spatial frequency explanation. It shows the distribution of response to the 10′ rectangle, calculated by multiplying the rectangle's frequency spectrum by the modulation transfer function of the visual system (*12*). The arrow at the right (bar and rectangle width equal) shows that adaptation to a grating at this frequency will make the spatial frequency channels less responsive to the high-frequency components of the rectangle and should make the rectangle appear wider; in fact, in our experiment this adaptation did produce perceived widening (as opposed to no change as predicted by the size-specific model). The center arrow shows a possible equilibrium grating bar size. Although adaptation should reduce sensitivity at this frequency, there should be no subsequent size changes; none were observed. The arrow at the left shows that adaptation to a grating at this frequency (bars eight times wider than the rectangle) should make the spatial frequency channels less responsive to the low-frequency components of the rectangle, and should make the rectangle appear narrower; this adaptation produced the predicted narrowing.

Thus, in our investigation of how prior viewing of a grating affects the perceived size of a rectangle, we found support for the hypothesis that the visual system codes size on the basis of the spatial frequency components rather than the width of the stimulus per se (*13*).

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4. I. D. G. MacLeod and A. Rosenfeld, *Vision Res.* **14**, 909 (1974); J. P. Thomas, *Psychol. Rev.* **77**, 121 (1970).
5. A single bar has a continuous frequency distribution proportional to $(\pi f w)^{-1} \sin(\pi f w)$. For simplicity of exposition the effect of finite grating size is not discussed, nor are harmonics mentioned.
6. T. N. Cornsweet, *Am. J. Psychol.* **75**, 485 (1962).
7. All ten subjects observed widening up to a ratio of 4:3. Horizontally oriented gratings used as adapting stimuli yielded essentially the same results: After adaptation, the rectangle appeared broader on the dimension orthogonal to the bars of the grating; in other words, the rectangle appeared taller.
8. Eleven additional subjects have shown similar shifts when run under somewhat different conditions [F. S. Frome, C. S. Harris, J. Z. Levinson, *Bull. Psychon. Soc.* **6**, 433 (1975)].
9. In experiment 1 the height of the adapting stimuli was the same for all spatial frequencies.
10. Similar results were obtained for two other observers and for both 10′ and 7.5′ rectangles.
11. It is not obvious what to call this or other aftereffects. In order to relate our findings to a wide variety of previous ones, we have referred to our results interchangeably as a size or width aftereffect. Further tests would be necessary to determine if the aftereffect reported here is a shift in perception of size, shape, height, width, squareness, extent, or some still-undetermined factor.
12. D. H. Kelly has noted (personal communication) that on a log-frequency plot, the rectangle's spectrum extends endlessly toward lower frequencies. It would thus appear impossible to find an effective adapting frequency lower than the "center of gravity" of such a distribution. Weighting the rectangle's spectrum by a modulation transfer function bounded on the lower frequency end would provide a solution, but one that raises the question of the appropriate frequency scale altogether. In thinking of a spectrum, one may use any arbitrary frequency scale for reasons of convenience, mathematical simplicity, or physical or psychological relevance. Because we do not yet have a rational choice, there is no way to make this discussion more quantitative.
13. For other kinds of data consistent with a similar conclusion, see, for example, N. Weisstein and J. Bisaha [*Science* **176**, 1047 (1972)] and C. S. Harris [*J. Opt. Soc. Am.* **61**, 689 (1971)].
14. F.S.F. was employed by the National Institute of Mental Health Section on Perception early in the course of this work. Data from the first experiment were collected at the University of Maryland and the University of Massachusetts and were reported at the 1974 annual meeting of the Association for Research in Vision and Ophthalmology. Data from the second experiment were collected at the University of California at San Diego and were reported at the 1976 annual meeting of the Optical Society of America. This report was written at SRI International and Bell Laboratories. Partially supported by NIH grant EY01640 to J.Z.L. and NIH research fellowship award EY05116 to F.S.F. We thank N. Weisstein for suggesting the conditions which produce apparent narrowing, D. H. Kelly for discussing appropriate frequency scales, and the late Brian J. Murphy for support and useful suggestions throughout the course of this work. We also thank C. S. Harris for his helpful suggestions on the manuscript.

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Genetic Resistance to Aflatoxin in Japanese Quail

Abstract. *Progress was rapid in attempts to develop lines of quail resistant to acute aflatoxicosis induced by oral dosing with aflatoxin. After five generations of selection, 8- and 11-fold differences were present in mortality between two selected lines and their respective control lines. These quail lines should be of value in investigating the physiological basis of resistance to aflatoxin.*

Aflatoxin, a carcinogenic metabolite, is produced by the filamentous fungi *Aspergillus flavus* and *Aspergillus parasiticus* (*1*). Because this mycotoxin contaminates a number of feedstuffs that enter into the food chains of humans, its long-term influences on human health are of concern. The economic impact of aflatoxin is evident from reduced growth and productivity resulting from ingestion of this mycotoxin by domestic animals.

Genetic variation for resistance of animals exposed to aflatoxin is suggested by differences noted between the New Hampshire and other breeds of chickens (*2*). Through artificial selection, it may be possible to not only demonstrate genetic variation to aflatoxin, but also to develop populations of domestic animals resistant to the adverse effects of aflatoxin. Such animals would be useful for the investigation of the physiological differences between resistant and nonresistant populations and serve as a model to study the mechanism of aflatoxin toxicity within the organism. The objectives of our study were to investigate the genetic factors of selection for resistance to aflatoxin with the Japanese quail as a model and to develop resistant lines for determining systems influenced by the selection process.

Aflatoxin was produced on polished rice (*3*), with incremental increases in temperature during the incubation period (*4*). After the rice was autoclaved to kill the mold, it was ground to a fine powder, and the aflatoxin was extracted from the substrate (*5*) and quantified by high-pressure liquid chromatography. The fer-

Table 1. Mortality of Japanese quail from acute aflatoxicosis by line (control and selected) and generation.

Generation	Aflatoxin at 2.5 mg/kg					Aflatoxin at 3.0 mg/kg				
	Control		Selected			Control		Selected		
	N*	Mortality (%)	N*	Mortality (%)	Ratio†	N*	Mortality (%)	N*	Mortality (%)	Ratio†
S_1	65	40.0	139	14.4	2.8	74	71.6	121	39.7	1.8
S_2	91	72.5	179	36.9	2.0	87	88.5	157	42.0	2.1
S_3	119	79.0	152	22.4	3.5	100	97.0	163	35.6	2.7
S_4	69	78.3	129	11.6	6.8	69	78.3	185	12.4	6.3
S_5	75	75.0	175	6.3	11.9	70	82.9	180	10.0	8.3

*Total number of birds challenged. †Control mortality:selected mortality.

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