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Speculations about noise and the evolution of vertebrate hearing

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Two of the most conspicuous and celebrated properties of human hearing – the abilities to discriminate pitch and to localize sound sources, may have been secondary derivations to which the ear was preadapted by having evolved in the inevitable presence of noise.

noise, spectral filter, spatial filter, temporal resolution, hair-cell resonance, evolution

I base this paper on two propositions: (1) that the acoustical (auditory and seismic) senses of the vertebrate ear arose in response to their adaptive value in remote detection of predators (or other dangers) and prey, and (2) that the vertebrate nervous system was preadapted to the task of parallel computing. If proposition 1 is correct, then sensitivity per se would have been the design parameter sculpted by evolution; one's survival is more likely if he senses the tiger before the tiger senses him. Noise is the principal enemy of sensitivity – amplification alone does not help one separate the tiger's footfall from the sounds of the wind; and acoustical sensors inevitably face noise not only from the world around, but also from the world within the ear. The micromechanical structures of the ear superimpose their random thermal motions on the acoustical signals passing through them, as do the ion channels and synapses of the hair cells (Crawford and Fettiplace, 1981; Ashmore, 1982; Bialek, 1983; Lewis and Hudspeth, 1983; Bialek and Schweitzer, 1985; Hudspeth, 1985). The ionic and molecular messengers of the hair cell also add their random motions to the signals they bear (DeFelice, 1981).

How could the evolving acoustical sensor cope with such noise? There are several solutions, well known to communications engineers. Noise energy generated by random thermal motion com-

monly is distributed more or less uniformly over a very broad frequency spectrum. In principle, therefore, with appropriate spectral filtering, signals with nonuniform spectral structure can be separated from noise. A spectral filter suppresses noise simply by removing most of the noise power at frequencies outside the filter's own pass band. Spectral filtering is especially effective if the spectrum of interest is sorted into many bands spanning different frequency ranges, and the (noise plus signal) power components in all bands are analyzed in parallel. This is the basis of the modern spectrum analyzer; and the parallel-computing capability of the vertebrate nervous system is well suited to it.

For sensing spatially discrete acoustical sources in a noisy world outside the ear, spatial filtering is a most effective means of suppressing noise. Such a filter could pass acoustical signals and noise emanating from the general direction of the tiger's footfall, while removing most of the noise power emanating from other directions. When it operates in the manner of an ear trumpet, the mammalian pinna is a spatial acoustical filter. It is, however, aimed in only one direction at a time, leaving acoustical shadows in which the tiger's footfall would be suppressed along with the noise. An animal could scan the world around it systematically, but this would cost time. On the other hand,

preadapted to parallel computing, the evolving vertebrate auditory system had the potential for simultaneous spatial filtering over the entire outside world – eliminating the time cost of scanning. For this purpose it would need two or more spatially separate sensors, a requirement evidently met as a consequence of bilateral symmetry. Signals and noise coming from a specific range of azimuths exhibit a specific range of differences of arrival times at the two ears. By cross-correlating the signals and noise from the two ears over a particular range of temporal separations, a computational channel would selectively enhance signals and noise components coming from a particular range of azimuths and suppress those from other directions. Each computational channel in the auditory portion of the brain could be listening selectively to a different part of the outside world. This indeed seems to be one of the mechanisms of binaural interaction in man, frogs, barn owls, and other vertebrates (Feng et al., 1976; Hafter et al., 1980; Knudsen, 1982; Konishi and Knudsen, 1982). In fact, the resolution of time separations between the two ears apparently is approximately 20 μ s in man, 10 μ s in barn owls.

Thus we have two filtering schemes: spectral filtering – which is especially effective in suppressing broad-band noise such as that arising from random thermal motion of components within the ear, and spatial filtering – which is effective in suppressing noise in the world outside the ear. Thus propositions 1 and 2 lead to the following principle of evolutionary design: ‘Whenever the power level of ambient acoustical noise is sufficiently high to limit sensitivity, the spectral filters of the ear should operate in a manner that preserves the temporal resolution of the signals and noise passing through them.’

For a spectral filter with a single pass band, two parameters – the bandwidth and the white-noise rejection ratio, summarize its ability to suppress noise¹. As its bandwidth decreases, a spec-

tral filter passes less and less of the noise power impinging upon it. As the filter’s rejection ratio increases, the signal and noise power being passed is increasingly confined to frequencies within the filter’s pass band. Thus the filter’s ability to resolve harmonic constituents of signals and its ability to suppress noise both are enhanced by decreased bandwidth and increased rejection ratio.

There is an approximately reciprocal relationship between the temporal resolution provided by a spectral filter and the bandwidth of that filter. For ideal spectral filters, which transmit all power at frequencies within their pass bands and reject all power at other frequencies, reciprocity becomes precise in the form of the uncertainty relation of Fourier transform theory (Bracewell, 1978). For real spectral filters with finite rejection ratios, the uncertainty relation is approximate but applicable, telling us that ‘narrow band spectral filters do not preserve temporal resolution’. Therefore, narrow band spectral filters evidently are inappropriate for the vertebrate ear whenever sensitivity is limited by ambient noise (rather than internal noise). The filter parameter remaining to be sculpted by evolution, in that case, would be the rejection ratio.

Several investigators recently have found strong evidence of local mechanical and electrical resonances in individual acoustical hair cells, and have suggested that these may serve as spectral filters of acoustical signals and noise (Crawford and Fettiplace, 1981, 1985; Ashmore, 1983; Frishkopf and DeRosier, 1983; Holton and Hudspeth, 1983; Lewis and Hudspeth, 1983; Ashmore and Pitchford, 1985; Roberts et al., 1986). The second-order (two-pole) resonance is an instructive example of the trade-off between bandwidth and temporal resolution. The quality factor (Q), a resonance parameter with many interpretations, is defined to be the ratio of the total (kinetic and potential)

defined as $f_2 - f_1$, where – when white noise is applied, f_1 and f_2 are the frequencies on each side of the pass band at which the power spectral density is half its maximum value. The white-noise rejection ratio is the time-average filter output power over all frequencies within the pass band (f_1 to f_2) divided by the time-average output power over all frequencies outside the pass band – both measured with white noise applied to the filter input.

¹ White noise has constant power spectral density (on average, equal amounts of power per unit frequency at all frequencies). When such noise is applied to the input of a single-pass-band filter, the power spectral density of the output is maximum near the center of the pass band and declines at the edges of the band. The bandwidth conventionally is

energy stored in the resonance to the average energy dissipated by it during each radian of oscillation at the resonant frequency, f_0 . When the resonance is serving as a filter, Q is approximately equal to the filter's white-noise rejection ratio. The bandwidth of the filter is approximately f_0/Q and the time required for the filter to respond fully to a constant amplitude sinusoid at the resonant frequency is approximately Q/f_0 . Thus, in two-pole resonance filters, the properties of bandwidth and rejection ratio cannot be manipulated independently²; for a given center frequency (f_0), narrowing of the bandwidth and increasing of rejection ratio both are accomplished by increasing Q . Furthermore, for a given center frequency, increased Q increases the response time – and thus decreases the temporal resolution, of the filter.

With respect to temporal resolution, the critical fact about a two-pole resonance acting as a spectral filter is its accumulation of energy in one locale (the stored energy is passed back and forth between two local reactive processes). The energy from each incoming half cycle is merged with that left over from all preceding half cycles – there is no cycle-by-cycle resolution of time or phase! When a resonance is responding fully to a constant-amplitude sinusoid at the resonance frequency, each incoming half cycle provides only π/Q ths of the total stored energy (approximately $\pi/2Q$ ths of the total amplitude). Therefore, as the quality factor of a two-pole resonance filter increases, it becomes increasingly sluggish – increasingly less responsive to the phase (timing) and amplitude of the half cycle presently entering it. Because of this, and because the bandwidth and rejection ratio of a resonance filter cannot be manipulated independently, resonances are inappropriate for spectral filtering whenever high temporal resolution and high spectral resolution are both required.

We seek spectral filters whose rejection ratios

can be increased indefinitely while their bandwidths remain wide enough to yield high temporal resolution. In such filters, high rejection ratios are accomplished by high-order dynamics (large numbers of spectral poles and zeros) rather than simply by high Q . To be effective over their entire ranges of input intensities, spectral filters must have rejection ratios comparable to those ranges. Otherwise, strong signals or noise in one filter band will invade the filters covering neighboring bands. The acoustical sensors of the vertebrate ear evidently function over many orders of magnitude of input power (e.g., the nominal 120 dB range of human audition corresponds to a power operating range of $10^{12}:1$). Thus, one would expect exactly what one finds, namely log-amplitude vs log-frequency characteristics (i.e., the amplitude Bode diagrams) of acoustical spectral filters of the ear with band-edge slopes of the order of 100 or more decibels per octave.

Achieved with high-order, non-resonant, linear filters, slopes of this magnitude require as many as sixteen or more discrete reactive (energy-storing) processes³. The ideal amplitude characteristics of classical analog filter theory were those of the low-pass, band-pass, or high-pass filter that passes all signal and noise power falling within its band and rejects all of that outside its band. A central problem addressed by the theory was design of real linear filters whose amplitude characteristics closely approximated that ideal. The best approximations by far (e.g., by Butterworth, Chebyshev, and elliptical approximations) all were

² The behavior of a linear two-pole resonance is described completely by the second-order harmonic oscillator equation. Appropriately normalized in time and amplitude, that equation is $d^2x/dt^2 + 2\delta dx/dt + \beta x = f(t)$, where $f(t)$ is the normalized input and β is equal to ± 1 . In stable resonances, β is $+1$, leaving δ as the single adjustable parameter. Q is approximately equal to $1/2\delta$.

³ In the general terms of nonequilibrium thermodynamics, two classes of discrete reactive processes are defined as follows: let J be the rate of flow of some entity (e.g., particles, charge, energy), and let F be the free energy change per unit measure of flowing entity. A discrete capacitive reactance is a volume of state space over which F is assumed to have a single value, instantaneously and uniquely determined by the integral over all time of the total, net flow into the volume. Examples include discrete chemical states and discrete physical locations, such as particle or energy reservoirs. A discrete inertial reactance is a flow path over which J is assumed to have a single value, instantaneously and uniquely determined by the integral of F_{i0} over all time, where F_{i0} is the free energy loss that occurs when a unit measure of flowing entity is transferred from one end of the path to the other. Examples include paths over which particles flow with shared momentum.

achieved with spectral poles and zeros that were complex numbers rather than negative real numbers (Guillemin, 1957). For high rejection ratios, therefore, one expects evolution to have sculpted spectral filters with large numbers of complex spectral poles and zeros. This would require large numbers of paired complementary reactive processes⁴. However, analog filters designed to provide the best fits to the ideal amplitude characteristics inevitably distort nonsinusoidal waveforms, such as pulses. In this manner, they fail to provide good temporal resolution. In analog filter design, this distortion is reduced by means of phase correction, often provided by all-pass, non-minimum-phase networks. Minimum distortion of nonsinusoidal waveforms is accomplished by filters with phase vs. frequency characteristics that are as close as possible to being linear over the pass band. Therefore, one expects evolution to have sculpted spectral filters with large numbers of complementary reactive processes and with nearly linear phase characteristics.

In that case, how can one explain the extensive evidence of simple resonances (which inherently are low-order, narrow-band filters) in the neuro-electric and mechanical properties of individual acoustical hair cells of lower vertebrates? One answer is suggested by Lighthill's (1981) summary of modern models of the mammalian cochlea and by the recent observations of spontaneous and evoked acoustical emissions from various vertebrate ears (Kemp, 1978; Palmer and Wilson, 1982). Lighthill showed that most of the recent cochlear models derive the high-order cochlear filter characteristics from critical-layer resonance phenomena. The basilar membrane is represented as a continuum of shunt resonances, coupled by the distributed series inertial reactance of the cochlear fluid⁵. When the shunt resonances are excited at

frequencies lower than their resonance frequencies, each behaves as a shunt capacitive reactance; signals and noise at those frequencies propagate as traveling waves through the structure. Signals and noise at frequencies increasingly close to, but slightly below the resonance frequency propagate at increasingly slower velocities; while signals and noise at frequencies equal to or greater than the resonance frequency do not propagate at all. In this way, local resonances are coupled by inertial reactive processes to provide a broad-band, low-pass filter with very high order and very high rejection ratio. Gradation of the shunt resonances from one end of the filter to the other allows different frequency components to propagate different distances along the filter, leading to tonotopy. If the local phase velocity everywhere along the structure is independent of frequency, then the spectral filter will exhibit the desired linear phase vs frequency relationship over the pass band at each locale.

Acoustic emissions are widely regarded as evidence of bidirectional coupling between the mechanical sensory structures of the ear and the neuro-electric components within the sensory cells (Weiss, 1982; Flock, 1983; Brownell et al., 1985). When bidirectional coupling is present, two-port network theory tells us that, from the mechanical side, electrical resonances within the cell will appear as mechanical resonances, and vice versa. In other words, the reactances derived from neuro-electric processes will merge with those derived from mechanical processes, into a single filter network. Thus, with bidirectional coupling, the neuro-electric resonances of lower-vertebrate hair cells could serve the same role as the basilar membrane of mammals – providing a shunt (critical-layer) resonance. Coupled by inertial reactances (fluids or tectorial masses), these resonances also could yield high-order, broad-band spectral filters. If that were so, one would expect the characteristics of the linear spectral filtration seen in VIIIth nerve acoustical afferent responses to reflect high order.

⁴ Two reactive processes are complementary if all of the energy from one can, in principle, be transferred to the other. Capacitive reactances are complementary to inertial reactances but not to each other, and vice versa. Coupled to active processes, or to a passive two-port device known as a gyrator, a capacitive or inertial reactance can become complementary to its own kind.

⁵ Lord Rayleigh (1894) was among the first to point out that systems comprising large numbers of reactive processes often are most easily analyzed in terms of continuous rather than

discrete models. In such models, the reactive processes become infinitesimal in extent, infinite in number. Viewed in this manner, the low-pass filter with complex poles becomes a traveling-wave structure.

This possibility has already been tested and verified in two of the four acoustic sensors in which local resonances have been found – namely the amphibian papilla and the sacculus of the American bullfrog (*Rana catesbeiana*). It remains to be tested in the other two sensors – the basilar papillae of the red-eared turtle (*Pseudemys scripta*) and the alligator lizard (*Gerrhonotus multicarinatus*). In the bullfrog sacculus and amphibian papilla, the linear filter properties were studied by

means of intracellular recording of action potentials from single afferent axons in the VIIIth nerve as it emerged into the cranial cavity from the intact otic capsule with intact circulation. The methods are described in detail in Lewis (1983, 1986). In axons from both sensors, cycle (phase) histograms reveal spike-rate components that are directly proportional to the instantaneous amplitudes of low-intensity, sinusoidal stimuli. The relationships between these response components

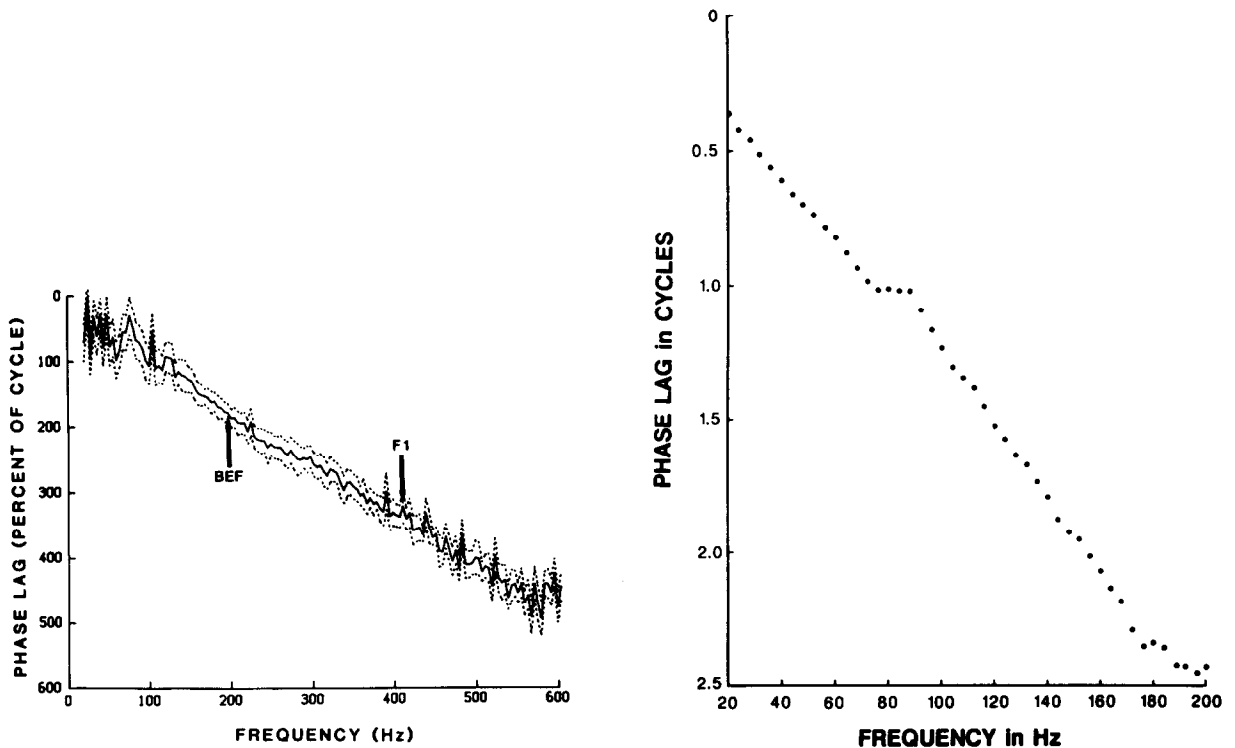


Fig. 1. Phase lag plotted against frequency for the linear, sinusoidal steady-state responses of a bullfrog amphibian papillar axon (left) and bullfrog saccular axon (right). (Left) The solid line shows the mean phase of spikes relative to the stimulus sinusoid, taken at frequency intervals of 4 Hz; the dashed lines are the loci of standard error. BEF (best excitatory frequency) denotes the center of the pass band of the spectral filter associated with this axon. F_1 denotes an amplitude-dependent transition frequency for the lowest order (dc) nonlinear response component; at frequencies higher than F_1 , this response was negative (mean spike rate decreased with increasing stimulus amplitude); at lower frequencies it was positive. In this way, responses to low frequency stimuli were diminished by the responses to higher frequencies (see Lewis, 1986). The amplitude and phase relationships of the linear response component exhibited no discontinuities at F_1 . (Right) The filled circles are mean phases of spikes, taken at 4-Hz intervals. This seismic axon exhibited nearly constant linear gain (linear-response amplitude divided by stimulus intensity) from 20 Hz to 150 Hz; above 200 Hz, the linear gain declined with a slope of 100 dB or more per octave. The plateau in the vicinity of 80 Hz corresponds to a 2-pole antiresonance, whose effects varied from axon to axon – occasionally being very strong in one saccular axon and absent in its neighbor. Although both phase plots are nearly linear with frequency, when viewed almost on edge both can be seen to deviate from linearity with short-range trends – such as one might expect in a phase-compensation network comprising a finite number of discrete elements. Thus neither plot appears to be the consequence of a simple time delay – such as one would expect in a traveling-wave structure with frequency-independent phase velocity. In this regard, both plots are representative of all phase data we have obtained from the bullfrog saccule and amphibian papilla.

and the stimulus sinusoids are robustly linear and thus provide an indirect window on the linear dynamical properties of the spectral filters associated with the sensors. Fig. 1 shows the phases of the response sinusoid (relative to the stimulus) plotted against stimulus frequency. The data were taken at very small (4 Hz) frequency intervals in order to avoid the ambiguities that arise when the phase shift increment exceeds a half cycle. The results are representative of almost all of a very large number of axons that we have examined from these sensors, and also representative of results obtained by Hillery and Narins (1984) from the amphibian papilla of another frog species. At 500 Hz, the data from this particular amphibian papillar axon show phase accumulation of more than four full cycles. This implies the presence of sixteen or more pole-zero pairs in the underlying dynamics. The data from the saccular axon (representative of those from over 100 bullfrog saccular axons examined so far), show a phase accumulation of at least two full cycles at 200 Hz – implying at least eight pole-zero pairs in the underlying dynamics. If the phase-frequency relationships of Fig. 1 were truly linear, they would correspond to those expected from a traveling-wave structure in which phase velocities are independent of frequency. The phase delays implied by the data of Fig. 1 would be approximately 7.5 ms for the amphibian papillar axon and approximately 12 ms for the saccular axon. Phase delays implied in this manner vary from axon to axon, ranging from 1 to 10 ms for bullfrog amphibian papillar afferents and from 10 to 20 ms for bullfrog saccular afferents. The sum of axonal time delays from sensor to electrode and acoustical time delays outside of the sensors themselves are approximately 1 ms (Lewis, 1984). Thus, almost all of the phase shift displayed in Fig. 1 is attributable to the sensors and their spectral filters. Dye filling of axons with Lucifer yellow provided definitive evidence of their afferent nature and their peripheral sources (Lewis et al., 1982).

The chief distinction between the critical-layer resonance filter and the simple (local) resonance filter is the mode of energy storage. I have already pointed out that the simple, local resonance accumulates the input energy from many stimulus cycles in two reactive elements. In this way, much

of the same energy is returned to a single reactive process cycle after cycle. In a critical-layer resonance filter this does not happen. The coupling reactances pass the energy from resonance to resonance, as water would be passed along a bucket brigade. In this way, the energy from the present stimulus half cycle is never merged with that from any previous half cycle. For example, when the phase lag in Fig. 1 was two full cycles, the axon responded to the stimulus four half cycles earlier. The three intervening half cycles were stored individually, somewhere between the input and the output of the filter, then passed along in correct order toward the output. In a simple two-reactance resonance, the energies from all of these half cycles would have been merged; and the absolute maximum phase lag would have been one-half cycle.

When the power level of acoustical noise in the outside world is sufficiently low, the sensitivity of acoustical sensors will be limited by internal noise; and spatial filtering will not be useful for noise reduction. Under those circumstances, the performances of the spectral filters of the ear could be enhanced markedly by bandwidth reduction – without calamitous consequences. This evidently is what happens in the mammalian cochlea. At very low sound levels (the lowest 30 or 40 dB of the audible range), the spectral filters exhibit sharp tuning peaks, with narrow bandwidths (Evans and Wilson, 1973; Kiang and Moxon, 1974). At higher sound levels, the peaks disappear, and spectral filtration appears to be accomplished by broadband, high-rejection-ratio, traveling-wave filters (Russell and Sellick, 1978). The cochlea thus appears to have adaptive spectral filters, with properties appropriate for high and low ambient sound levels. A similar phenomenon may occur in the basilar papilla of the red-eared turtle, where efferent feedback evidently leads to broadening of the bandwidths of the spectral filters (Art and Fettiplace, 1984). If auditory efferent activity in that animal increases with ambient sound level – a premise so far untested, then we again would have an appropriately adaptive filter.

If the premises and conclusions presented in this paper are correct, then as a consequence of their primary adaptations for dealing with internal and external noise, the two vertebrate ears were

preadapted for pitch discrimination (through their parallel, peripheral spectral filters) and for sound localization (through their parallel, central spatial filters)⁶. Both of these phenomena have been observed in fish, amphibians, reptiles, birds and mammals (Fay and Popper, 1980; Feng et al., 1975, 1976; Helmholtz, 1862; Knudsen, 1982; Konishi and Knudsen, 1982; Schuifj and Buwalda, 1980; Turner, 1980). Indeed, there is even now evidence of seismic (surface-wave) source localization by the sacculi of the European fire-bellied toad, *Bombina bombina* (Walkowiak and Munz, 1985).

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⁶ In an insightful and instructive paper, Békésy (1962) considered the problem faced by an ear that must sense external sounds in the presence of internal noise and interference (such as vocalizations by the listening animal). He concluded that predictable internal interference might be suppressed by neural inhibition. In their fascinating paper on the evolution of hearing in mammals, Masterton et al. (1968) concluded that high-frequency sensitivity in those animals arose principally as a consequence of the marked improvement it provided in sound localization. The basis for spatial filtering at very high frequencies is interaural intensity difference rather than interaural time difference. The same thing may have taken place in birds as well (Konishi and Knudsen, 1982). In the lower vertebrates and in birds and mammals confronting low-frequency sound sources, on the other hand, spatial filtering based on interaural time differences undoubtedly provided great selective advantage. An improvement of only 1.0 dB in signal to noise ratio would have extended the range of the auditory early warning system by more than 12% (i.e., it would have provided a 12% greater headstart on the tiger), and increased the area covered by the warning system by more than 25%!

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