The senses of deer

For social communication, detecting predators, and reproduction, the deer probably relies on its sense of smell more than on any other sense.

Imagine standing 75 yards away from someone. You cannot see him—he has concealed himself in a dense fir thicket. He stands downwind of you, facing you, with his hands behind his back. Would you hear him clicking his fingernails?

You wouldn't, but a black-tailed doe actually did.

That report, from Linsdale and Tomich, is not unusual in the annals of deer sensorial feats. Deer are well known for keen senses of hearing, sight, and smell—so keen that mere humans can scarcely measure their extent.

Hearing

Like a satellite dish pointed to the heavens, collecting signals for the owner to sort out and tune in, a deer's ears point toward the source of sound and gather essential information.

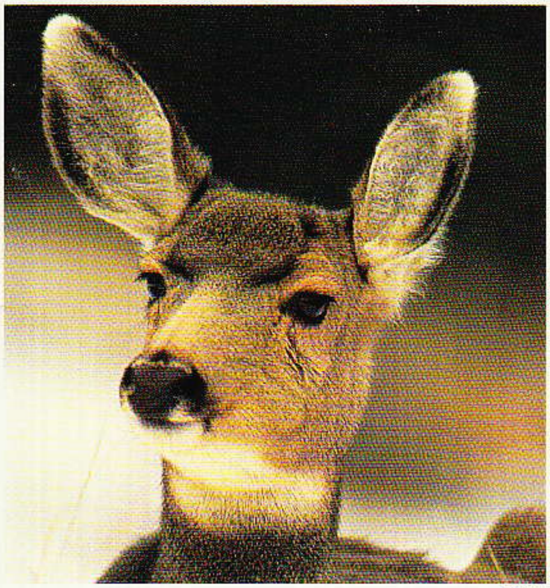
When the ears, or pinnae, are stationary and at rest, the deer can tell whether the sound comes from ahead or behind. The pinnae can move independently of each other; by comparing the signals each ear receives, the deer locates the source of the sound. One measure of comparison is intensity: a louder signal in the right ear indicates that the sound comes from that direction. But deer use another measure as well. They can evaluate the difference in time it takes the sound to reach each ear, especially if the frequency, or pitch, of the sound is high.

The deer can also evaluate sounds with just one ear. Monaural hearing helps the deer locate sounds in the horizontal plane, revealing whether the source of the sound is near or far. By swiveling one pinna toward the source of a sound, the deer effectually amplifies the signal. Although monaural hearing is also essential in determining vertical location, deer usually pay little attention to what is above them: in their natural world, predators from the sky are not to be feared. Increasingly, this predator is man, hunting from a tree stand, but even this development seems to have had little effect on deer behavior. In Europe, tree stands have been used successfully by generations of roe deer hunters who have seen no need to change their strategy.

Deer are able to hear frequencies higher than those audible to human beings but not as high as those perceived by dogs—or so researchers infer from studies of the taxonomically and ecologically not-too-distant domestic goat. Goats pick up sounds from 78 Hz to 37 kHz and are most sensitive at 2 kHz. This places them between the ranges of human hearing—16 Hz to 20 kHz with greatest sensitivity at 2 to 2.3 kHz—and dogs—15 Hz to 40 kHz.

Thus equipped with sensitive ears, deer rely primarily on hearing to detect the presence of animals around them, Linsdale and Tomich concluded. Anatomy, behavior, and habitat all work together here. Red deer, Darling observed, live in "zones of silence" with little or no wind and can therefore detect the sounds of approaching creatures

The pinnae can swivel in all directions, enabling the deer to hear a disturbance from one direction while she is looking in another. This protection is important when the animal is in a vulnerable position, as while grazing, with the head down. The mule deer's ears are especially large; the doe on the right is a Sitka blacktail.



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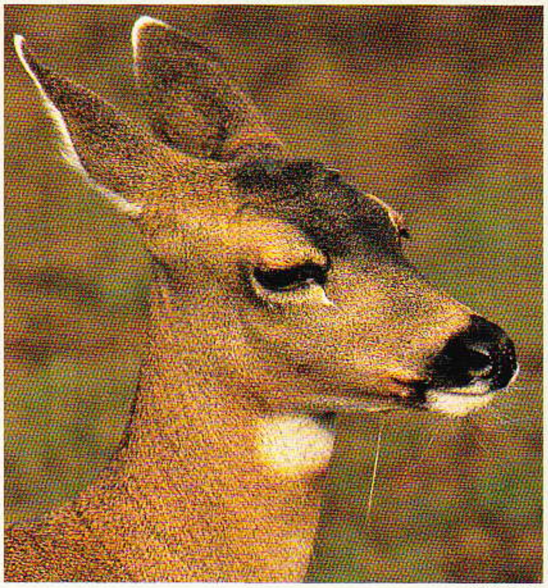

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while they have time to take evasive action. North American deer that live in the midst of constant background noise–the rustling leaves of Northeast woodlands, the patter of raindrops in the Pacific Northwest, the winds and whispering grasses of the West–learn to listen for alien sounds. Habituated to the familiar sounds of their environment, they filter out all but the significant, potentially threatening auditory signals.

Deer whistles, devices mounted on vehicles to warn deer of the machine's approach, are designed to take advantage of the animal's sensitive ears, but their effectiveness has yet to be determined accurately. These whistles produce sound at a frequency between 16 and 20 kHz, but Stattleman, testing a single white-tailed deer, determined that the animal could not hear sounds in that range. Muzzi and Bisset reported that, in Ontario, railroad engines equipped with these whistles struck fewer moose than did engines without them; the engine crews also had to perform fewer moose-warning maneuvers–blowing whistles, ringing bells, dimming lights, changing engine noise–than did the crews of engines without whistles. On the other hand, Romin and Dalton reported that free-ranging mule deer in Utah reacted no differently to a test truck when it traveled with or without a deer whistle.

Vision

Astute early naturalists noted that deer see very well at night and can detect the slightest movement. And indeed, deer are often active after sunset, even in the darkest hours. Like other animals that are adapted for crepuscular and nocturnal behavior, deer have a membrane in the back of the eye that reflects light back through the receptor layer of the retina. This *tapetum lucidum,* like that of many hoofed animals, is made up of tendonlike collagen tissue. By passing light through the receptor layer a second time, the *tapetum* improves the deer's vision in dim light and also produces the eyeshine of nocturnal animals caught in automobile headlights.

Deer are active in daytime as well. Their ability to see well in bright light may be explained by a ring of pigment surrounding the cornea in the eye. This pigment, according to Duke-Elder, is most likely an antiglare device, since it is not found in mammals that are strictly crepuscular and nocturnal.

Day or night, a deer's visual acuity is excellent. Under strong light, the pupils of the eye close into a slit, focusing light onto a horizontal band across the eye's retina. In exactly this streak are clustered the nerve cells that function as signal conductors, carrying messages from the photoreceptors to the brain. The arrangement and density of the nerve cells, called ganglion cells, in the visual streak account for the deer's ability to detect danger from afar. Bruckner, in fact, suggested that the visual streak corresponds to the horizon that dominates the world view of open-country ungulates. If so, the

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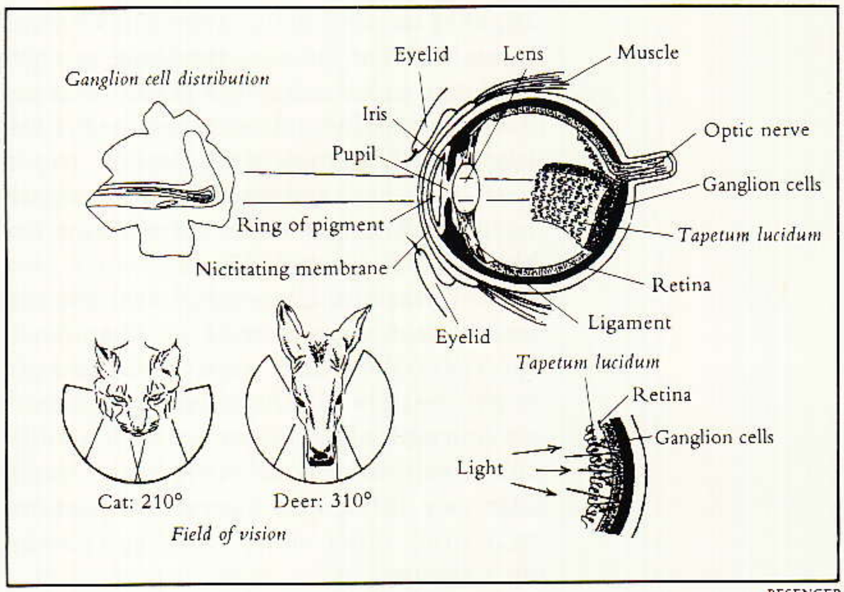

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The tapetum lucidum, *a thin layer of reflective tissue, bounces light back across the receptor cells, effectively brightening a dimly lit image; it accounts for this axis doe's eyeshine. The eye's visual streak–the concentration of ganglion receptor cells–focuses visual acuity in a linear pattern. This, along with the wide field of vision, lets the deer see across a wide area and focus on the horizon, where predators might appear–all without turning its head.*

vision of deer is particularly suited to observing intruders in flat country. The theory would also account for the observation that mountain mammals–Dall sheep, mountain goats, chamoix, and ibex among them–tilt their heads when focusing on a distant disturbance, presumably to align the visual streak with the slanted horizon of the slope on which they stand.

Other herbivores–sheep, goats, cattle, horses, red kangaroos–have a similar arrangement of ganglion cells in a horizontal visual streak. In bovines the streak is most distinct. In carnivores such as wolves and mountain lions the streak is more diffuse, with the density of receptor cells per area gradually decreasing into the surrounding areas. In human beings, there is no visual streak at all: the human eye focuses on just one spot at a time and cannot take in the whole horizon without movement of the eyes or head.

The visual acuity of deer is well demonstrated by an experiment known to researchers as the minimum separable. An animal is trained to distinguish stripe patterns so that the researchers can determine how fine a stripe can be seen at how great a distance before the pattern blurs: it's the animal equivalent of the doctor's eye chart. Red deer can distinguish 1.4 millimeter (0.056 inch) wide black-and-white stripes from gray from 0.8 meters (2.6 feet) away. This indicates a visual resolution for deer similar to that of other hoofed mammals, greater than a nilgai antelope but less than a goat. Humans have a visual resolution about twelve times better than that of deer.

Deer see well, but do they see colors? Experiments to determine the answer to this question have to be carefully constructed: just as it is possible for us to distinguish the yellow car from the red in a black-and-white photo, so animals may use brightness (the intensity of light) to discriminate what human beings see as color (different wavelengths on the spectrum).

In an outdoor test that did not control for brightness, elk distinguished fluorescent orange from other colors and from white; the colors were painted on food buckets.

Behavioral findings indicate that red deer can discriminate colors. Each deer in the study learned to press a lever when a light came on to signal that food was available; press the right-color lever and food appears. The deer distinguished red, orange, yellow, yellow-green to green, and blue both from one another and from gray. A red deer hind spontaneously was attracted to green but, in the words of Backhaus, "disliked" blue and "threatened to become neurotic" when he tried to condition her to prefer blue over shades of gray.

In another study, red deer were found able to see colors in very dim light. Landscape painters have long observed that colors fade into gray at dusk, when, physicists tell us, light measures a mere 0.01 Lux. Paint the same scene at high noon on a sunny day–at

10,000 Lux—and the palette must be vivid. But what is the intensity threshold at which deer start to see color? For yellow, it is just 0.007 to 0.01 Lux. Humans require 0.1 Lux (about the brightness of a full moon) to perceive color. Reds and greens require a slightly higher level of light before they become visible to deer as spectral colors.

Two whitetails, in an experiment like that for the red deer, learned to discriminate spectral colors that were controlled for brightness. They distinguished orange (with a wavelength of 620 nanometers) from other colors with long wavelengths more readily than they distinguished green (500 nanometers) from other short-wavelength colors, such as blue.

This difficulty in picking out green is surprising, considering that deer forage among myriad shades of grassy and leafy green. Perhaps color is not important for white-tailed deer after all. Noting that the doe took only seven days to discriminate between the presence and absence of light but needed twenty-six days to learn color (the buck was slower: twenty-eight days and forty-four days, respectively), Smith and his colleagues concluded that deer may not need to distinguish colors in their natural environments, even though they can do so in the laboratory.

Deer appear to have the anatomical apparatus for color vision, though again, not all studies agree. In vertebrate eyes there are two kinds of photoreceptors: rods, which respond to single photons and enable vision in dim light, and cones, which account for color and daylight vision. The mix of rods and cones—or the absence of one form altogether—determines what kind of vision an animal has.

Cones have been found in the retinas of elk and whitetails. For whitetails, Witzel and his colleagues counted 10,000 per square millimeter, compared with 20,000 cones per square millimeter for monkeys and human beings, and 25,000 for cats.

According to a different study, however, whitetails do *not* have cones. Using scanning and transmission electron microscopy, Staknis and Simmons clearly distinguished cones and rods in the retina of the pig but found no cones in whitetail eyes. Because deer are well adapted for low-light vision and thus have many rods in the retina, it may be that the cones were not easily detected, especially if not all sections of the eye were scanned. Unlike some mammalian eyes (including the human eye), in which the cones are concentrated in a central area called the fovea, the deer's eye could have them spread across a larger area.

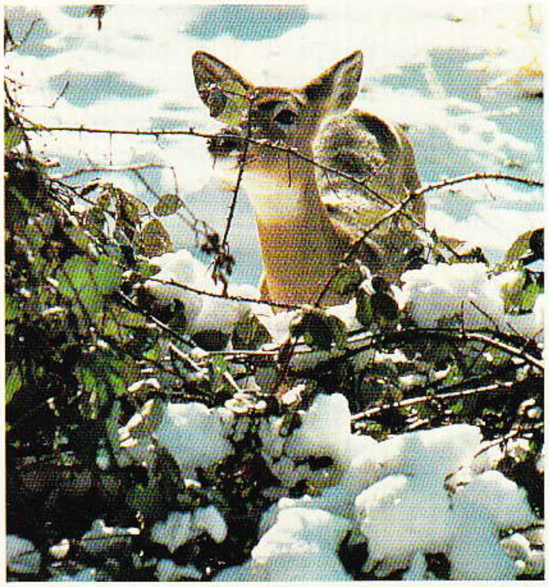
In another study, Murphy and colleagues measured the electrical activity of the photoreceptors in the retinas of nine whitetails to find not only cones, but their photopigments and the specific colors to which they respond. Pigments in the cones responded to light with a wavelength of 537 nanometers (yellow-green) and 455 nanometers (blue); pigment in the rods was most responsive to light with a wavelength of 496 nanometers (blue-green). These findings suggest that deer are less sensitive to light of long wavelengths (orange and red) and actually rely upon their perception of only two colors—yellow and blue.

Deer can become blind. Cervid eyes are susceptible to cataracts, which accounted for the visual impairment in ten of seventeen apparently blind moose in a Swedish study. The lenses were deformed, reduced, and milky white or brownish gray, with granular and uneven surfaces. A microscope revealed fluid accumulation between the lens fibers, according to Kronevi et al.

Chemical Senses

What we refer to as the senses of taste and smell is the reception of molecules of chemical compounds. When the molecules of food or odor bind with receptor molecules in the animal's tongue or nose, a response is triggered. It's no longer enough, however, to talk about a deer's senses of taste and smell; there is another sense that guides numerous aspects of deer behavior, a true sixth sense unknown to early deer researchers. Vomolfaction, like taste and smell, is a chemical sense involving, in this case, the vomeronasal organ.

Taste. A deer's sense of taste is the important gatekeeper for food ingestion. Deer drop undesirable plants from their mouths, along with saliva. Bitter forage is known to be unpalatable, but a better understanding of taste sensitivity and selectivity would en-



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able researchers to develop repellents to protect agriculture, from backyard gardens to cornfields to vast forest plantations. Byers et al. found that various repellents kept white-tailed deer from feeding on apples and apple shoots, but only for a time. After one to six days the deer overcame their reluctance to feed on the treated forage. The effectiveness of chemical repellents may depend on how many deer are competing for how much food: if deer are few and other food is available, the treatments are likely to work longer.

Like other ruminants, deer have long, mobile tongues. The tastebuds are arranged in groups on fungiform (mushroom-shaped) or circumvallate (moated) papillae. The circumvallate papillae, which contain more tastebuds, run in two rows on either side of the midline of the tongue. Just behind the highest point of the upper surface of the tongue is a prominent cluster of fungiform papillae. Elsewhere, papillae are scanty.

The significance of the arrangement and forms of tastebuds is unexplored, but it is known that ruminants have more circumvallate papillae (sheep and ox, twenty-four; antelope, fifty-two) than carnivorous mammals (dog, four to six; cat, seven; skunk, two).

Smell. The hunter whose quarry is downwind knows all too well the deer's keen sense of smell. The animal's sense of smell aids in finding and selecting food, detecting predators, alerting other deer, identifying members of the herd, attracting mates, determining the sexual readiness of potential mating partners, bonding between doe and fawn, tracking of mates and mothers and fawns – in short, as Cowan put it, "This is the paramount sense of the deer."

Yet little is known of thresholds of olfaction. Only one species, the black-tailed deer, has been studied for olfactory performance. Findings by Müller-Schwarze et al. indicate that deer are capable of three levels of olfactory discrimination. All the experiments involved Z-4-hydroxydodec-6-enoic acid lactone, a thick, oily, unsaturated liquid that naturally occurs in deer urine and tarsal gland excretions.

In one experiment, a biological dose (an amount similar to that found in the wild) of natural lactone was applied to the hock of a fawn and the responses of its penmates – five- to twelve-month-old fawns – were recorded. The fawns sniffed and licked the spot: they had smelled it. Then the researchers applied comparable amounts of very similar synthetic lactones. Three other unsaturated lactones were sniffed and licked significantly

Foraging begins with smell. Once a deer has tested food with the nose, it takes an experimental nibble. The long, mobile tongue has taste buds that test for toxins; bitter and otherwise unpalatable plants may be spit out. The deer at the left is an endangered Columbia whitetail.

WERNER

Compounds of low volatility cannot be smelled; they must be examined with the vomeronasal organ. Having licked a sample of a doe's urine, this mule deer buck uses a lip curl to pump the compounds into the VNO duct in the upper palate.

less, and three saturated lactones prompted even less response. When the amounts were increased a hundred-fold, the fawns still ignored the saturated lactone but responded to the unsaturated ones just as they would to an actual tarsal scent comprising urine, bacteria, and tarsal secretions.

In a second experiment, blacktails discriminated between two versions of lactone, the naturally occurring Z form and the synthetic E form, whose only difference, chemically speaking, is the position of one hydrogen atom at the molecule's double bond.

Some pairs of molecules, called enantiomers, differ only in the arrangement of four groups of atoms around a carbon atom. Mirror images of one another, such molecules are said to have "handedness" by analogy to a pair of hands: Because of their orientation one cannot be superimposed on the other,

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just as a person's right hand cannot be superimposed on his left. These two versions of the same molecule have identical physical and chemical properties, except for their ability to rotate polarized light in different directions, denoted by (+) or (−). To humans and animals, however, enantiomers can appear quite different. For example, the (−) form of carvone has a distinct spearmint odor, but the (+) form has an odor of caraway. When the deer were challenged to differentiate between a pair of such molecules of a lactone that both occur in the natural tarsal scent, they could smell both versions, albeit to different degrees. The natural scent of the deer's lactone contains 11 percent (+) lactone and 89 percent (−). When the two forms were separated, deer were found capable of distinguishing between them by responding more to the (−) form than to the (+).

Besides lactone, deer respond to other social odors produced by their skin glands, urine, and feces. Response may be to each compound individually, or perhaps the compounds in a mix of deer excretions may interact in ways as yet unknown. In other mammals, chemical signals called pheromones often consist of mixtures of compounds, in which the effect of one substance depends on the admixture of another, or in which two compounds have little effect on their own but a synergistic effect when combined, or in which two compounds are basically redundant.

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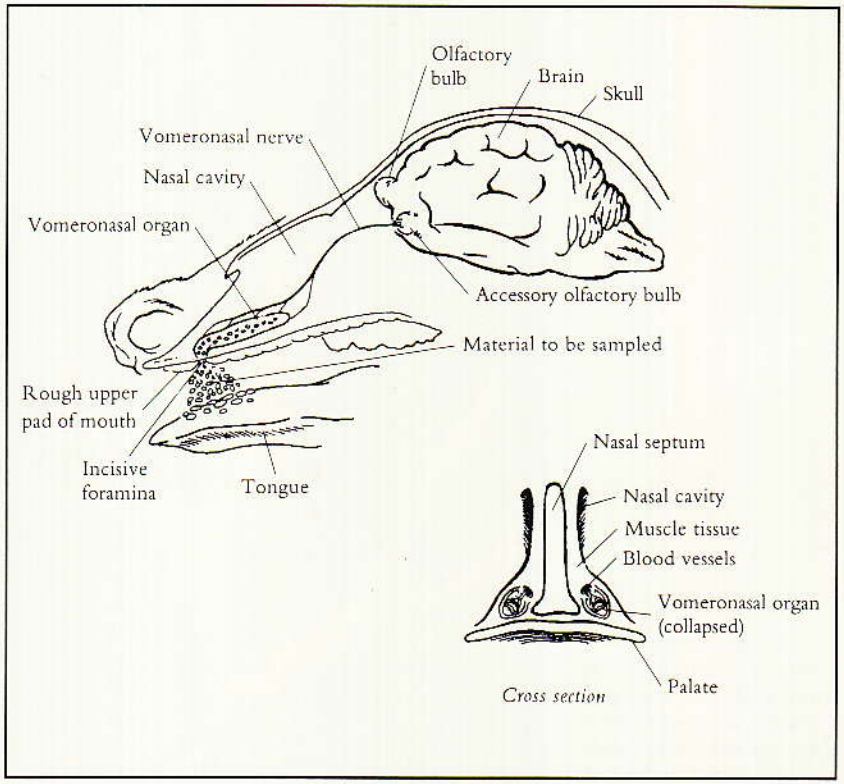
The best example of vomolfaction occurs during the rut, when bucks appear to lick fresh urine from a doe approaching estrus. The buck's grimacing flehmen, or lip curl, mechanically transfers the odoriferous material to a pair of pores, called the incisive foramina, in the roof of the mouth. Tongue movements are important in this mechanical process, but the deer also has a vomeronasal pump. Small muscles contract to empty blood vessels around the vomeronasal organ, exerting negative pressure on the organ, in effect, creating a weak vacuum. A narrow tube leading into the dead-end organ widens and sucks in material to be tested. Once the chemical analysis is done, the muscles relax, the blood vessels engorge with blood, and the resultant pressure forces the material out of the vomeronasal organ. The organ is then ready to sample the next batch.

Unlike olfactory receptors, which detect molecules in vapor, the receptors in the vomeronasal organ are sensitive to nonvolatile compounds. Not being airborne, these compounds must come into direct contact with the chemoreceptors. When the buck seeks to ascertain the readiness of the doe he is pursuing, then, he must examine her urine at close range by licking it.

—Dietland Müller-Schwarze



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The lip curl causes the blood vessels around the vomeronasal organ to empty, creating a vacuum that the sample rushes in to fill; the compounds then are read by chemoreceptors in the olfactory bulb of the brain.