Chapter 13. Sensory Systems and Communication

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The Theory of Communication

The classic definition of communication involves an action on the part of one animal that alters the behavior of another (Wilson 1975). In this definition one should include self since many behaviors are refined in a looping that involves neural circuits in self (Chapter 17). However, the transmission of information to others, which trigger behaviors, is what makes behaviors strikingly different than say simple morphological traits. Behaviors can invoke emergent properties that are properties of groups of communicating individuals.

The essence of communication is the relationship between signaler and receiver. We have already discussed many kinds of signaler-receiver relationships in some detail:

1. signals of greenbeard recognition (Chapter 4)
2. signals of speciation (Chapter 5)
3. signals involved in male-male competition, (Chapter 8)
4. signals between males and females in mate choice (Chapter 10)
5. Signals of antagonistic selection (Chapter 11)

In both cases of sexual selection that we covered, we discussed honesty in signal design. Implicit in the notion of honesty is the idea that signaler and receiver benefit in some way from the act of communication. For example, the female peacock that choose males on the basis of good genes, may gain material benefits for her offspring. The male that avoids conflict by advertising his supremacy in battle by a badge avoids unnecessary conflict in battle and the male that is repelled by the badge avoids a costly loss.

Recall that ESS theory in mate competition (Chapter 8), which involves the war of attrition, suggests that rival males should conceal information regarding intent. However, data on animals suggests anything but concealment of intent when you look at males in the wild and during escalated conflict. Males advertise constantly, and it is thought that such advertising may be related to neighbor or individual recognition. An important component of animal communication is the idea that animal displays usually have a unique "signature" to them that allow conspecifics to identify one another. This allows animals to focus on new rivals rather than waste energy on the dear "enemies".

Signal Content and Structure

Transmission and reception of the signals are of paramount importance in the design of a visual system (Endler 1992). Guilford and Dawkins (1991) also breakdown a signals design into:

1. **tactical components** that refer to ease of transmission, detection, discrimination (e.g., from other similar signals), and ease of storage in memory;
2. **strategic components** that refers to the signals function in a natural selection framework such as a signal that benefits the sender in some way.

Animal communication is typically thought of as being adaptive. Why else should a signaler communicate unless they are going to receive some benefit from their behavior. The benefits for signalers have already been outlined for the signals many situations. The adaptive value of signals has been broken down into the following classes:

1. recognition of species, individuals, neighbors, castes (social insects), kin, or demes (Chapter 4, 19),
2. reproduction which involves courtship by males, female choice, or female receptivity (e.g, acceptance or rejection) (Chap. 10)
3. agonistic interactions and the establishment of social status (Chapter 8, 9, 19),
4. antagonistic selection of genomic imprints (e.g., progeny allocation, Chapter 11),
5. alarm calls among group dwelling animals (e.g., ground squirrels, Holekamp and Sherman 1989),
6. coordination among hunting animals (Chapter 7),
7. parental care -- parent offspring recognition (Chapter 11, below).

While the benefits to the signaler are fairly intuitive, the benefits to the receiver can be intended or unintended. Communication with an intended receiver usually will be mutually beneficial. However, they may be many unintended receivers intercepting the signals.

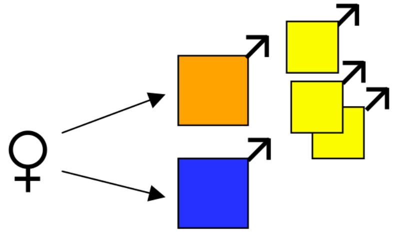
Unintended Receivers and Dishonest Signaling

Even though signaler may receive benefit, many animals can receive the signal. A receiver could in fact be a predatory species (Chapter 14). Even though sexual ornaments are intended for the female, they also make the male more obvious to a predator and thus they entail costs. Advertising calls make males of many species vulnerable to a predator's detection mechanisms. Suffice it to say that there may be costs to signaler's that arise from predators that can also receive the signals.

Costs of signaling can also be found in conspecific interactions. Recall the example of alternative male strategies (Chapter 9). Dominant males put out signals, and such signals might attract alternative morphs to the dominants. The sneakers can also manipulate signal reception mechanisms of the dominants by mimicking the displays of females.

i) Intended receivers:

1) badge of status in male-male conflict: O beats B
2) badge also used in female choice



ii) Unintended receivers

Sneaker males (Y) can also cue in on the honest O badge, but rather than use cooperation like B, they exploit O with cryptic behaviors involving mating system tradeoffs of monogamy vs polygamy Strategies of mate-guarding are resistant to sneakers, but may require cooperation.

Such dishonest signaling presumably arises because of constraints on the signal reception, and processing machinery of the dominant males.

One unique constraint on dominants may arise from the hormone Testosterone. Administering testosterone to appears to make vertebrates more far sighted than near sighted. They see objects at greater distances, at the expense of close range visual acuity. Improved vision at great distance may be a tremendous advantage for a highly territorial male that has to deal with conspecific territorial males. However, far-sightedness and poor short-range visual acuity could be a distinct liability in the inspection of a female mimic at close range. Perhaps testosterone results in a perceptive cost that allows sneaker males to co-opt the signal mechanisms involved in male-female interactions to their advantage and a dishonest signaling strategy can be quite successful.

There are even certain situations where animals use a dishonest signal intentionally to manipulate conspecifics. Consider male vervet monkeys that have a language consisting of a number of words for objects in the environment. Males will try to entice females into their vicinity by saying the vervet monkey word for food. The male will attempt to engage the female in copulation after this verbal sleight of hand.

We will not explore this coupling in complete detail in this Chapter, but it should be kept in the back of your mind. At the end of the next chapter (14), where I consider predator-prey systems, we will generate a more synthetic view of sensory systems. Our goal in this chapter is to assess how sensory systems are built. We focus on vision because it is so well characterized. We have in fact consider other sensory modalities in previous chapters, and others we will explore in future chapters:

1. Vision (Chapter 5, 8)
2. Sound (Chapter 5, 10)
3. Scent (Chapter 16, 18)
4. Feel (Chapter 16)
5. Taste (Chapter 14)
6. Phermomones via the vertebrate VNO (Chapter 10), which interfaces with HP system, or analogues in insects (Chapter 16)
7. Electromagnetic detection (Chapter 8, weakly electric fish) and avian migration that uses photoreceptors (Side Box 13.2).

Physics of Light, Sound, and Smells

The medium and sensory modalities used in the transmission of signals all seem to have a common feature -- the signals typically travel in some waveform. In the case of light, color properties of light are encoded in different wavelengths of light. In addition, many visual signals that animals produce also have a waveform that is generated by the body movements. In the case of sound or sonar, signals travel in waves that have different frequencies. Even olfactory cues may have a waveform associated with them as the source of the cue trails the signal somewhere downstream, the signal becomes degraded by turbulent flow, and the turbulent flow appears to impart a wavelike quality to the smell. The waves involved in olfaction could also impart information to the recipient concerning the distance that of the signaler. Waves are used everywhere in animal communication.

Light and The Visual System

Understanding vision and visual systems involves an understanding of the properties of light. While humans can see light from sun in the visible range, many animals can see light in both the infrared, and into the ultraviolet spectrum. Some animals have exquisite color vision, others poor color vision. Other animals have exquisite night vision. Where do these differences originate? Are there constraints placed on the structure of a sensory system? These questions are best answered with reference to the visual system, given that the molecular and neural mechanisms are so well characterized, but they apply to all the senses. Recall that in the case of avian migration (Chapter 13, Side Box 13.2), birds use the visual photopgiments to pick up the electromagnetic field lines generated by the earth.

Side Box 13.1. Primate color vision and photoreceptor systems

The processing of a color signal in the brain requires cells that are sensitive to different wavelengths of light (e.g., photoreceptors in the eye), and a mechanism for integrating the information from different receptors that have different sensitivities. The core theory for understanding how this comparison works in the cone photopigment system is centered on the concept of **visual opponency**, in which special integrating neurons compare the signal comparing from two different photoreceptor cells. The differences between long wavelength (L) photoreceptors are compared to medium (M) wavelength receptors. The long wavelength system is of more recent phylogenetic origin (in primates at least) than the Short (S) and Medium systems. The neurons of the M system also integrate information from the L system. These systems are also called red-green-blue based on the peak wavelength of the photopigments. The 3 phosphors of RGB computers are tuned to maximally stimulate our eyes, as is a color television. Vertebrates like birds or reptiles possess yet a 4th photopigment in the UV spectrum, and thus these vertebrates can integrate across a larger spectrum.

The **spectral sensitivity** of a photoreceptor cell is defined as the probability of a photon of light with wavelength λ being transduced to generate a neural signal. The photopigment consists of two pieces:

1) an opsin protein, which generates the spectral tuning of the photopigment (i.e., in mammals)
2) a prosthetic retinal group that absorbs the light (like an antenna)

The maximum wavelength, λ_{max}, of a photopigment is used to categorize the different opsins. For example one photopigment has a λ_{max}=565, but the precise location of this peak varies considerably among species.

Evolution of opsin number. The signal processing of an opponency mechanism allows for color discrimination to occur regardless of brightness (intensity of photon flux), since opponency involves a subtraction between neural signals. Thus, ***information*** in a visual system can be reduced to one ‘achromatic’ brightness mechanism, which sums all receptors outputs (e.g., area under all 3 curves, Fig. 13 a), and n-1 ‘chromatic’ mechanisms. These rules apply for **trichromats**, which have a 3-photopigment system, as well as **dichromats**, which have only 2-photopigment system (“color-blind mammals), and **tetrachromats** (lizards, birds), which have a 4-pigment system. In addition, if there are 2 alternative alleles segregating at one locus, which vary in spectral sensitivity, these generalizations also apply. Therefore, it is entirely possible to generate trichromat vision from 2 photopigment genes, if one has segregating alleles that vary in their spectral sensitivity. A heterozygote would have both alleles, each of which might be turned on in different photoreceptor cells, in addition to the other photopigment (functional trichromat). Homozygotes in such species would be colorblind. These kinds of species are called **polymorphic** and reflect an intermediate stage in the evolution of higher levels of color acuity with more photopigments. All that is required is a duplication of the polymorphic locus, and fixation of each for one different allele.

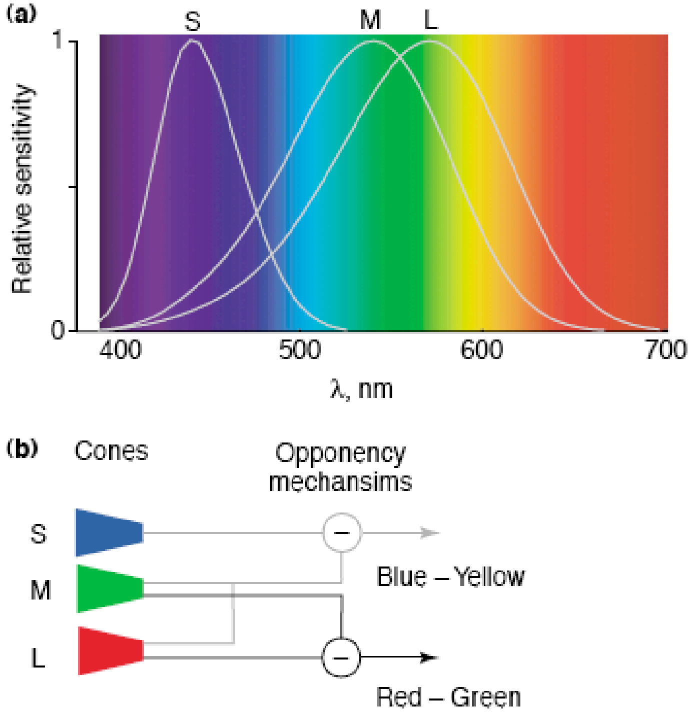


Figure 13.2. a) Typical spectral sensitivities for a primate (in this case a Howler monkey). The approximate colors of the spectrum are also depicted. The sensitivities have all been normalized to 1. b) The theory of visual opponency includes integration neurons that subtract one color channel from another to produce the output of a given comparison circuit. For example M-L is the red-green color comparison circuit and M-S is the green-blue circuit. Primates also have another comparison circuit between the L-and SM system. From Schaefer et al. (2004).

The simplest constraints on receiver systems may involve interactions of light with the different photoreceptors (see Side Box 13.1) in a given species (e.g., rods *versus* cones, 2, 3, or 4 types of cones). The packing of rods *versus* cones in the fovea of the vertebrate eye may set up a simple constraint on signal detection -- visual acuity and night vision *versus* color vision. Visual acuity is also a function of eye size. A larger eye casts a larger image on the retina and on a correspondingly greater number of photoreceptors (Fleishmann, 1992).

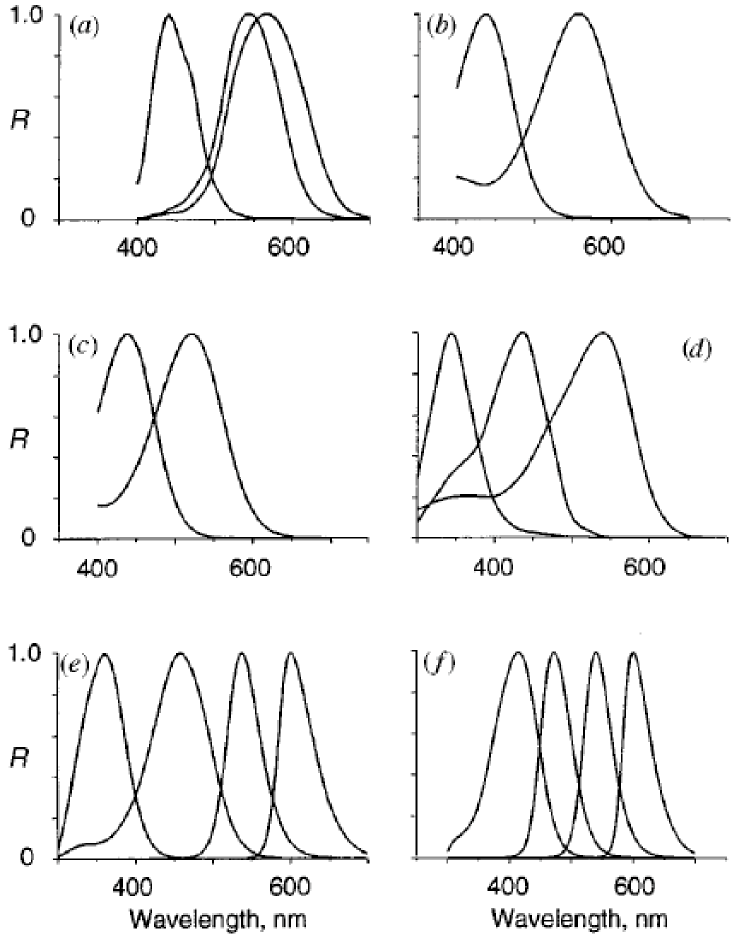


Figure 13.3. Receptor spectral sensitivity in different organisms: a) a human (Smith and Pokorny 1972), b) tree shrew (*Tupaia belangeri*; Petry and Harosi 1990); c) ground squirrel (*Spermophilus beechyi*; Jacobs et al. 1985); honeybee (*Apis millifera*; Menzel and Backhaus 1991); Pekin robin (*Leiothrix lutea*; Maier and Bowmaker 1993) and f) pigeon (*Columba livia*; Bowmaker et al. 1997).

Additional acuity can also be obtained via concentrating photoreceptors in a **fovea**. Lets consider lizards as a case study (Fleishman, 1992). Some lizards, like *Anolis* spp., have a unique eye, which has two fovea. The only other vertebrate group that has two foveas is the raptors. The central fovea of lizards is used for detection of prey or reception of signals from conspecifics at larger distances. Because lizard eyes are laterally placed, the central fovea for each eye takes in a broad field of view from one side of the animal. Given the placement of the eyes, there is very little dead space, which isn't taking in an image. Each eye takes in a field of view that is 200°. There is a 20° region of overlap at the front of the animal. This is where the temporal fovea comes into play. The temporal fovea of each eye is situated near the back of the eye (relative to the body axis) and the 2 temporal foveas are used in binocular vision during prey capture. Just before lunging (in anoles) or in the final dive (in raptors), the temporal fovea fixates the prey in the binocular field of vision, and this enhances depth perception.

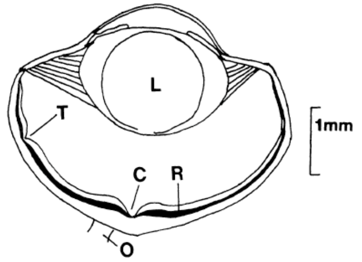


Figure 13.4. The left eye of a typical Anole: C – central fovea, L – lens; O – optic nerve; R – receptor layer of the retina; T – temporal fovea. The white aera in front of the photoreceptor layer (in black) is the neural layer (Based on Underwood 1970, after Fleishman 1992).

Additional constraints arise from the number of photopigments (see figure 13.3 for various vertebrates and the honey, an invertebrate). At a more detailed level, we must also understand a little bit about the photopigments used in detecting light waves. It turns out that many vertebrates have a three-photopigment system. Other animals have a four-pigment system. Any photopigment has a maximum wavelength at which they operate and sensitivity of a pigment drops off to either side of the maximum wavelength. However, the actual *optimum* area in which sensitivity is greatest is the region of the curve with steepest descent (the shoulder), which is where one photopigment overlaps with another photopigment, and the opponency is greatest between a pair of photopigments (see Side Box 13.1 for a description of opponency mechanisms). With more and more photopigments, the eye presumably has better color detection mechanisms as the coverage of the wavelengths is enhanced by the presence of more pigment optima, which in reality increases the area that is crisscrossed by pairs of photopigments generating greater coverage of the **opponency fields**.

Phylogenetic history may also constraint the senses. For example, most vertebrates use a system of photoreceptors that is based on the cone. However, the source of mammalian rods may be different from rods found in other groups. Mammals are thought to have evolved from a small nocturnal ancestor that would have needed excellent acuity under the difficult lighting conditions at night. Geckos, which are also active at night, have converged on the mammalian rod receptor, but there are several interesting differences, which point to an independent origin to the gecko "rod". The primates illustrate the origins of trichromatic color vision from dichromatic vision, with intermediary steps of polymorphic vision, in which dichromatic loci contain additional color alleles, which gives heterozygotes trichromatic vision (the evolution of trichromats from polymorphic forms is discussed in Side Box 13.1).

In general signals in the visual realm involve reflection or refraction for displaying color, although there are a few animals that produce light by bioluminescent processes. In addition, animals add motion, or postural changes to communicate, which is discussed in greater detail below. Thus, while this chapter mainly focuses on color and movement that is sensed by the visual system, many of the principles of communication described for vision may apply to other sensory modes.

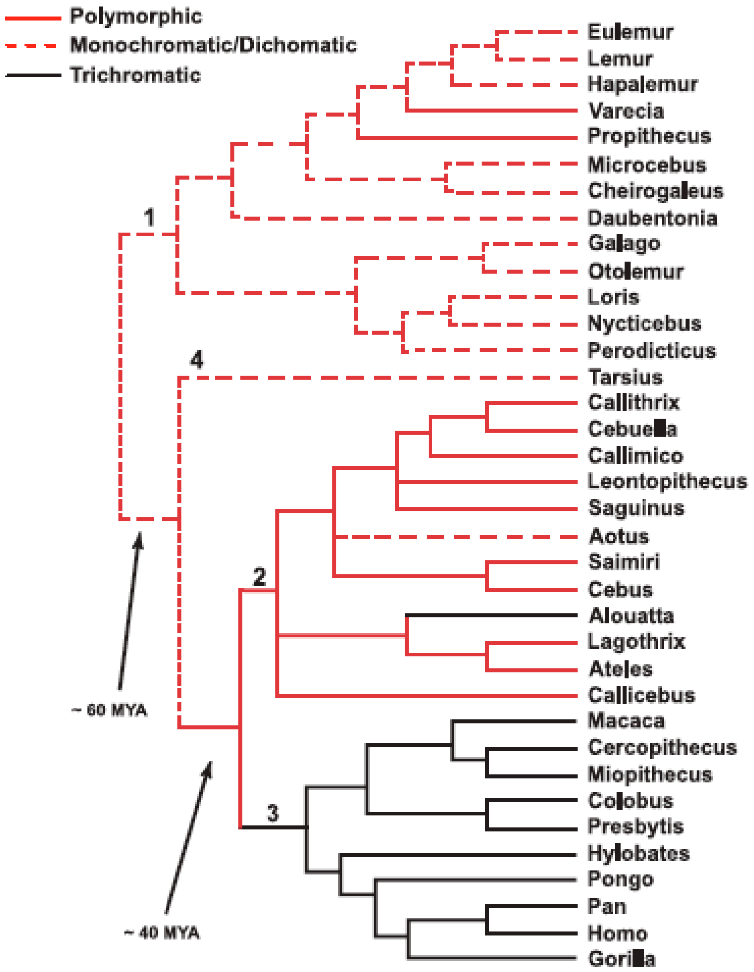


Figure 13.5. The distribution of color vision among primates. The nature of color vision measured or inferred fro a number of extant genera has been divided into three categories: routinely trichromatic; polymorphic; routinely dichromatic or monochromatic (see definitions; Side Box 13.1). the numbers identify the 3 taxonomic groupings (1 – strepsirrhines, 2 – platyrrhines, 3 – catarrhines). Tarsius (4) is currently considered as belonging in the same sub-orer (Haplorhini) as the platyrrhine and catarrhine monkeys (from Surridge et al. 1998).

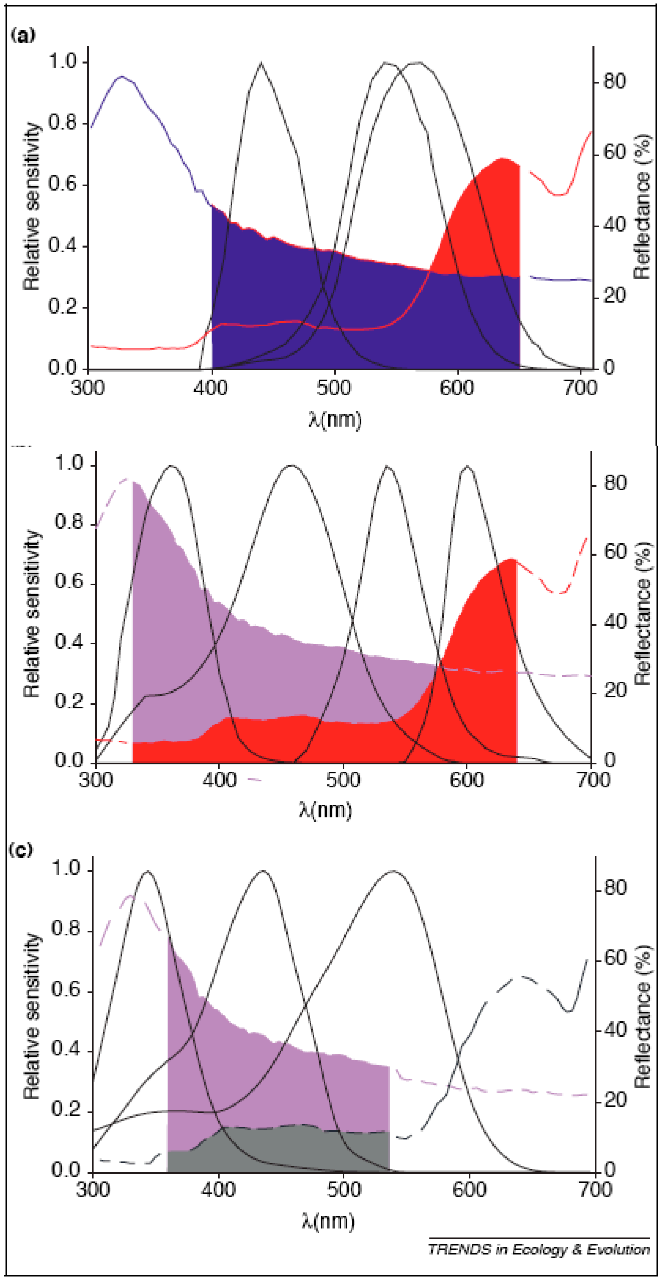


Figure 13.6. The reflectance spectra of a blueberry, which is given by the dashed line (*Vaccinium* sp.), has a UV peak, and willowleaf cotoneaster, which is given by the 2nd dashed line (*Cotoneaster salicifolia*) has a peak in the red part of the spectrum. The photoreceptor pigments (and opponency) integrate each of these colors differently depending on spectral sensitivities of a) a trichromatic human lacking a peak in the UV, but with a conspicuous photopigment peak in the red spectrum b) a tetrochromatic bird with relatively good coverage across the spectrum, or c) trichromatic bee with a photopigment peak in the UV. In order to 'see' a color, an organism must have two photopigments in operation in the area of the spectrum that is an emitted by the object, which in this case is two different flowers (blueberry bright in UV vs. willowleaf bright in red). Thus, the bee can see a peak in the UV but it cannot see red, while a human can see the red peak but not the UV, but still resolves the blueberry as blue. The bird can see both prominent peaks (from Schaefer et al. 2004).

The Physics of Air and Water

Air and water are both similar in that sound travels in a wave. Because of the nature of air and turbulence, a signal projected in air is degraded quite rapidly with distance from a source. In contrast, signals in water can travel great distances before they degrade in a significant way. The best times for signal transmission at great distance in the air is undoubtedly during the still morning when the air is also a little denser. The tendency for territorial birds to begin their singing in the morning is undoubtedly related to the distance that such songs travel in the morning. We will explore more on air *versus* water when we discuss bat *versus* dolphin sonar in Chapter 14. The wavelike properties of air, water, or even light are thus key in the design of all signal systems.

Principles of Signal Design and Detection

Input Matching

The concept of **input matching** is central to understanding how receivers collect information. If certain colors are important from the point of view of signal origin and reception then the visual system may be fine-tuned such that only a small signal needs to be used to affect the detection mechanisms of the receiver. The spectra of light produced by the signaler may match the optimum detection areas of the receiver.

For example, stickleback males put out a red signal to females. The visual system of female sticklebacks is fine-tuned such that the emission spectra (in water) closely matched the sensitivity of the visual system of a male stickleback (see below, Boughman 2001). Input matching may also found in the auditory system. For examples, certain calls maximally stimulate the nerves that project from the ear. In the examples in Figure13.6), the color vision for a) humans, b) birds, and c) bees, lead to differences in their ability to “see” two different kinds of plants. Plants might often signal to animals to have seeds eaten and dispersed or pollen moved among plants. Thus, colors of plants may evolve to better allow for detection by their coevolutionary partner(s).

Many plants that are pollinated by hummingbirds are red in color, while those pollinated by bees are UV in color, which we cannot see so they often appear to be white or blue to our eye. We actually do not see the beautiful UV patterns on flowers that attract bees to the center of the flower where it can land and load up on nectar (and pollen).

Motion Detection and Habituation

The **motion detector** in most vertebrates arises from integration between the visual system and the optic tectum or in mammals the superior colliculi (Chapter 14). Most of the retinal ganglion cells, which are hooked up to photoreceptors in the eye also project into the optic tectum. Neural output from the optic tectum is very sensitive to novel visual stimuli. The central part of the visual field and the visual neurons that project back into the optic tectum are motion sensitive to receptive fields of 0.5°. In contrast the most peripheral visual fields are only sensitive to motions in excess of 40°. Specific cells in the visual field respond best to a narrow range of angular velocities.

There is a reflex in most vertebrates that is sensitive to the motion detection mechanisms described above. When an object is detected in the periphery, particularly moving objects, the eye shifts such that the image becomes fixed on the central fovea -- the **visual grasp reflex**. Habituation mechanisms are used to shut out objects that are moving with a wavelike motion such as blowing branches. However, the eye of lizards is very sensitive to square wave patterns that lizards make during pushups and head-bobs. Lizards are very responsive to square waves, produced by conspecifics, but not very responsive to sine wave motion.

Finally **habituation** is a key concept in motion detection (and indeed in other sensory modalities). If the motion is periodic and the motion cycles through 2-3 cycles, the response of the motion detector neurons becomes habituated and the response is turned off (Fig. 13.7). Such habituation mechanisms allow the animal to shut out noise such as the period movements found in vegetation blowing in the wind. Similar habituation mechanisms are found in the auditory system for removing white noise (noise of random frequency and amplitude).

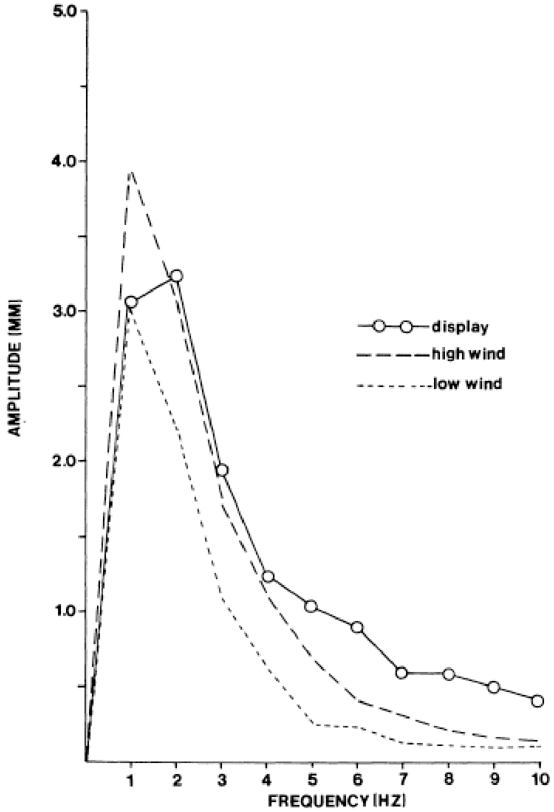


Figure 13.7. A fourier analysis of the wave properties of motion patterns in a typical *Anolis auratus* assertion display (connected circles) compared to motion found in windblown vegetation typical of the vegetation in the habitat of *Anolis*. Plant motion was measured by directing a fan at potted plants (3 grass species). Two wind speeds are shown (0.9 m/s and 0.6 m/s). Notice that the display is shifted in frequency, particularly in the high frequency part of the motion spectrum. (from Fleishman 1988).

Long-range signature displays and close range communication

Lizards periodically send out a square wave signal (push-up or head-bob) during their territorial patrols. The signature display that they use is of very large amplitude (e.g., head displacement height). The signature display of many lizards that have been studied include unique individual components to them much like bird song or whale song has an individual component to it. In addition, the signature display in most organisms is usually designed to function as a species recognition signal so it is also very conserved in other key respects (Chapter 1). Finally the signature display is designed to be received at fairly large distances. In lizards the signal is intended to be used across a few territorial diameters. Bird song signatures are intended to be heard over several territory diameters. The nature of the ocean as a medium for the transport of signals allows whales to transmit their signature displays over hundreds of and perhaps thousands of kilometers (for blue whales).

Signature displays are meant to get an individuals attention. Once the other animal is listening or watching, the animals will typically move in to closer range, and begin signaling with smaller amplitude or more quiet signals. In the case of lizards, two males that are at close range use much smaller amplitude "challenge displays". In the case of a male and female making contact, the courtship song at close range is much more quiet (intimate) than the territorial signature display, which is meant for long range reception.

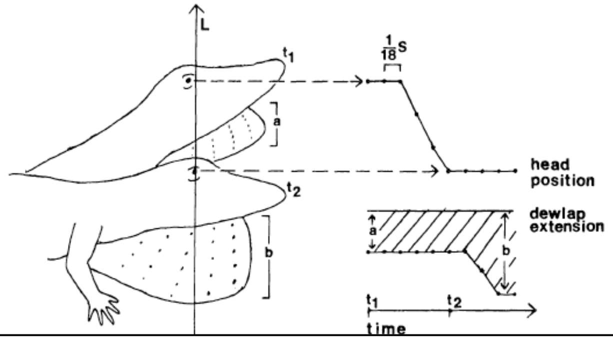


Figure 13.8. Head movement and dewlap extension a complex multipart signal used in Anolis lizards. (From Fleishman 1988).

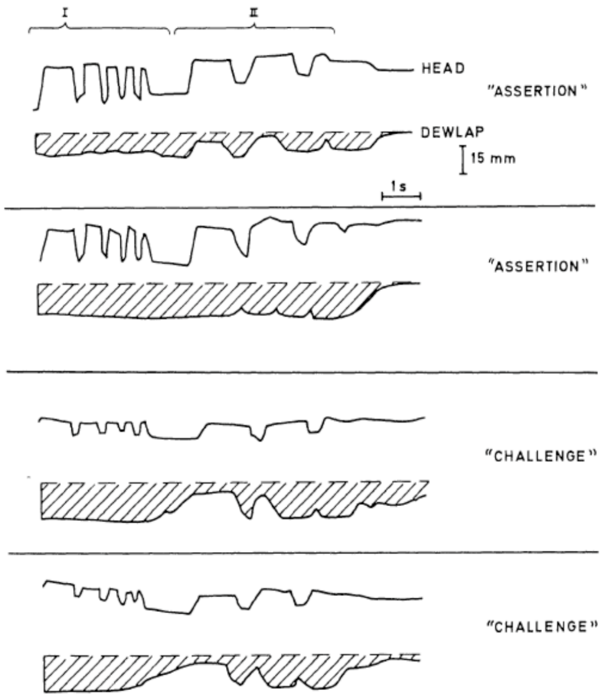


Figure 13.9. Four typical displays by an individual lizard. The first two displays are assertion displays (given spontaneously at long distance), and the last two are challenge displays (given at close range to a 2nd individual). Note that the temporal patterns of the two types of displays are the same, but the amplitudes of head movements are much larger for the long-distance assertion displays. (from Fleishman 1988).

Complex Signals and Multiple Sensory Modalities

Many of the important signals that animals do not rely on just a single sensory modality (e.g., vision *versus* sound), but can use a number of modalities. Large herbivores give a "pursuit invitation display" that involves two visual cues. When they detect a distant predator, deer (and gazelles) lift their tail to reveal a white patch of fur and they also move away with a stiff legged stotting gait. The signal is presumably used to signal the predator a message of which would have the following effect (e.g., in anthropomorphic terms): "you have been detected and the jig is up -- pursuit is futile." Birds often use multi-modal signals.

The lekking behavior in many species of manakin, a small tropical bird, involves different 3 sensory modalities:

1. the visual grasp reflex as males move on their perch
2. auditory system that is synchronized with the visual; a male leaps and makes a loud snapping sound with its wings.
3. the visual photopigment system and feather colors.

Movies of manakin behavior are available on at JEB: http://jeb.biologists.org/cgi/content/full/206/20/3693/DC1

The manakins have evolved elaborate displays and even coordinated behavior among males to attract females. The feather colors among different manakin species are produced by different mechanisms. Pigments and structures give rise to color in all animals so this group is very useful to not only investigate structure of color pigments, but also the structure of complex signals in multiple modalities.

Color can be produced by 3 basic mechanisms. **Structural colors** are produced by microstructure of the a biological feature, which generate colors much like a prism splits light into constituent colors, while other structures filter and let through certain colors. Bird feather colors in the blue and ultraviolet are often produced by ultrastructure. **Pigment colors** and spectra are produced by the differential absorption and reflectance of a given pigment. Carotenoids reflect in the red, while melanins tend to absorb all colors. In addition to structural and pigment colors, **iridescence** mechanisms can generate a change in the colors that are emitted from a surface, by altering the actual quantum properties of photons (via, 1) the changes that occur when photons are first absorbed by pigments, which increase the energy of the pigment, 2) that subsequently re-radiates a photon, which is changed in wavelength spectra).

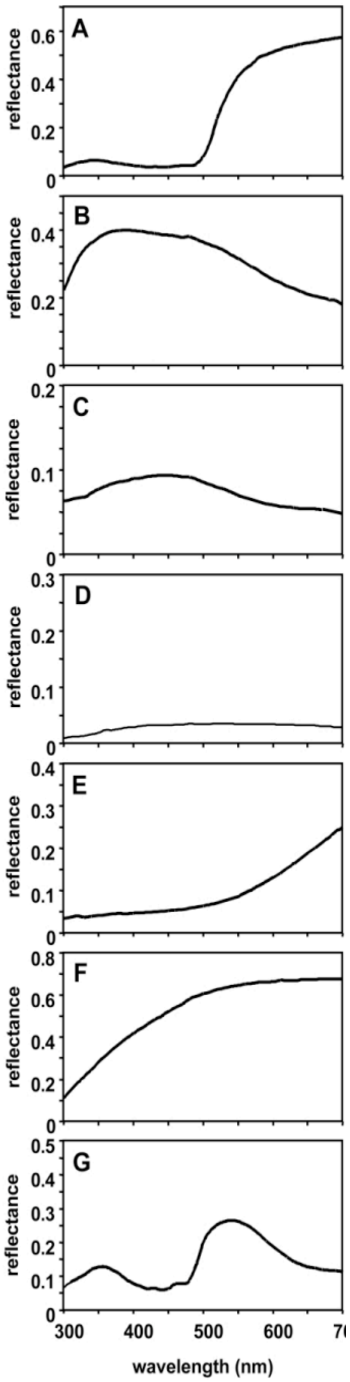


Figure 13.10. Representative reflectance spectra of plumage colors produced by 3 mechanisms. A, Orange carotenoid crown reflectance of *Pipra erythrocephala*. B, Ultraviolet/blue noniridescent structural mantle reflectance of *Chiroxiphia linearis*. C, Blue black iridescent structural mantle reflectance of *Corapipo gutturalis*. D, Black eumelanin breast reflectance of *C. linearis*. E, Rufous brown phaeomelanin mantle reflectance of *Machaeropterus deliciosus*. F, Structural white throat reflectance of C. gutturalis. G, Green carotenoid/structural rump reflectance of *Lepidothrix* iris.(from Doucet et al. 2007).

Long-tailed manakins (*Chiroxiphia linearis*) have a social system in which teams of 2 males display cooperatively in dispersed lek arenas, but only the alpha partner mates with visiting females. One benefit of performing as a nonmating partner might be to gain experience as an "apprentice" to improve the performance of the complex duet song and joint dance. Trainer et al. (2002) found that (1) singing competence, including consistent singing and frequency matching, increased as a function of the age of the subordinate partner and (2) frequency matching by established teams was greater than the random expectation. Because frequency-matched songs attract more females (Trainer and McDonald, 1995), any process that improves frequency matching enhances the mating success of males.

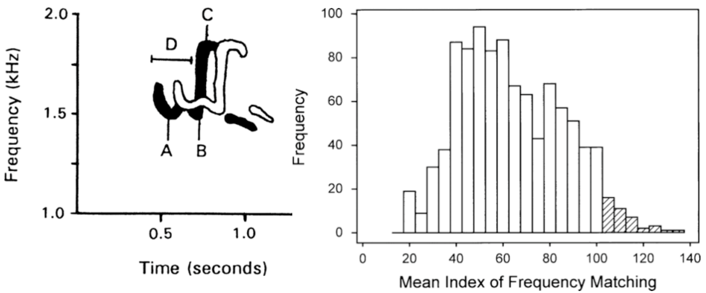


Figure 13.11. Four variables illustrated in sonograms were measured for each male's contribution to the dual toledo song of the long-tailed manakin. The contribution of 1 male is solid black, and the other male is outlined. The songs of established teams of definitive males were more congruent than expected by chance. Out of 999 artificial assemblages, each containing seven randomly paired teams, only 33 (shown hatched) had a mean index of frequency matching greater than that of the focal teams (from Trainer et al. 2002).

Side Box 13.2. What colors do animals really see in a messy world?

The processing of color signals by the retina involves not only the reflected light of the viewed object, but also the background behind the object, the opponency mechanisms generated by the photopigment system (e.g., tetrachromatic, trichromatic, dichromatic, monochromomatic), and the ambient light striking the object and other aspects of the visual system that might differentially attenuate light like lenses and cornea. These structural attenuation mechanisms (e.g., oil droplets above retinal cells) are important in enhancing visual discrimination of color. For example, oil droplets deposited above the photopigment cells narrow photoreceptor spectral sensitivities (Hart et al. 2000; Hart 2001) and thereby improve color discriminability (Vorobyev et al. 1998; Vorobyev 2003).

Figure 13.12. Data used in formulating an avian color-space model. Calculations are based on models by Vorobyev et al. (1998). A color-space model requires:

1) A) **the available light in the environment**, which in the case of manakins is average reflectance spectrum of green vegetation surrounding 14 *Chiroxiphia linearis* leks in bottomland evergreen forest in Costa Rica
2) B) **the background forest**, which is normalized forest-shade irradiance spectrum from an average of five spectra collected at each of 14 *C. linearis* leks in shady conditions,
3) C) **Normalized spectral sensitivities** including the effects of oil droplets for the four photopigment cone types in *Parus caeruleus* (from left to right: UV sensitive, S sensitive, M sensitive, L sensitive).
4) D) **Transmission spectrum** for the ocular media of *P. caeruleus*.

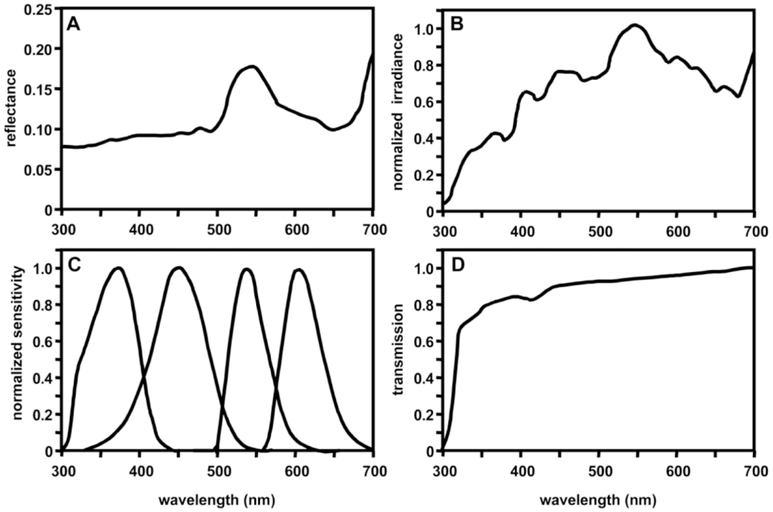


Figure 13.13. Light environments in the forest. The spectra shown are plots of the intensity of light as a function of wavelength (from Endler 1990). Forest shade is rich in middle wavelengths (green and yellow); Small gaps are rich in longer (redder) wavelengths; Woodland shade is rich in shorter (blue) wavelengths; Large gaps exhibit essentially white light. When the sun is obscured by clouds, spectra of the 4 habitats converge on large gaps or non-forested areas. In twilight conditions (early/late), spectra of habitats converge on purplish light, deficient in middle wavelengths of available light.

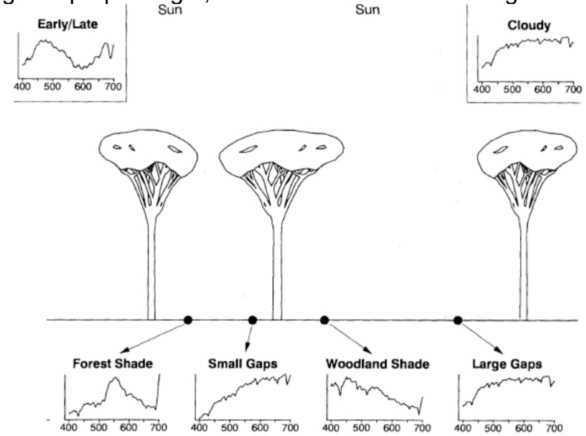
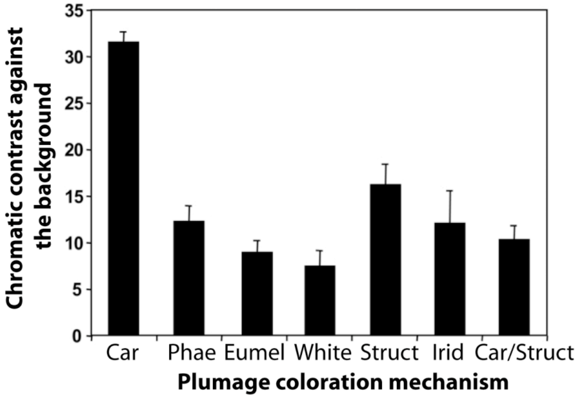


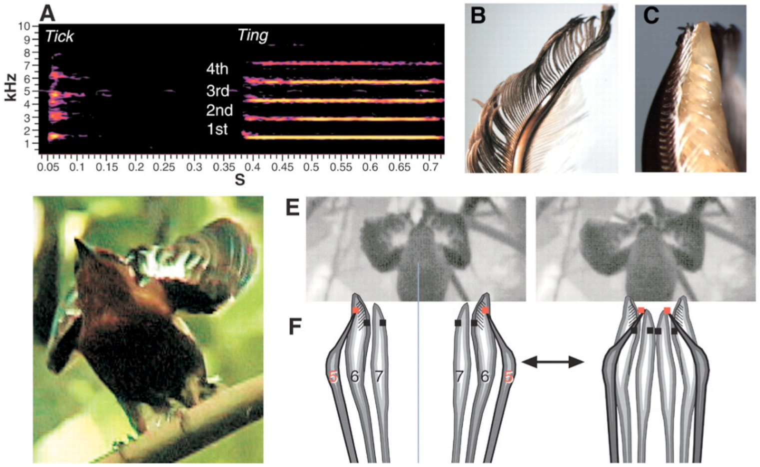
Figure 13.14. Integrating these properties of the visual system, the object, and the background, one can estimate the chromatic contrast, to determine what really stands out against the background for a visual manakin. Carotenoids and structural colors (like blue and UV) stand out against the green forest background. Interestingly, manakins also use light gaps to amplify the signals on their feathers (see Fig. 13.10 for color mechanisms) as do other lekking birds.



Moving on to the sound production systems of manakins, the wings snap sounds can be quite simple or very elaborate. In vertebrates, moving air through a vocal apparatus produces most acoustic signals. Bostwick and Prum (2005) describe a unique mechanism used to produce a tonal acoustic signal in male club-winged Manakins, *Machaeropterus deliciosus* that can sustain harmonic tones via interactions among oscillating secondary wing feathers (Fig. 13.15). This mechanism of sound production shows morphological and mechanistic convergence with arthropod stridulation (which is discussed in Chapter 14).

In summary, the complex signals of manakins involve a coordination that even transcends individuals and involves an apprentice. Other species use combinations of color and movement. One of the most spectacular examples is the moonwalking dance of the crimson hooded manakin: http://www.youtube.com/watch?v=i-wtO7pjJKk&eurl

Figure 13.15. Spectrogram of a *Tick-Ting* sonation of one male *M. deliciosus*, showing signal energy in integer-related harmonic bands (labeled 1 to 4). S, seconds. (B) Dorsal surface of the right fifth secondary feather of a male *M. deliciosus*, distal tip bent medially at 45°. (C) Medial surface of the thickened distal end of the right 6th secondary, showing regular, raised ridges. (D) Conventional and (E) high-speed video of *M. deliciosus* during *Ting* production. (F) Graphical depiction of distal ends of the 5th secondary (the pick) moving across the ribbed surface of the 6th secondary (the file) to create stridulatory impulses that sustain resonance of the enlarged 6th and likely 7th secondary shafts. Relative motion of the pick and file is indicated by red and black blocks, respectively (from Bostwick and Prum (2005).



Signal Design and Background "Noise"

Animal signals are tuned to the environmental conditions. Why make a big or "noisy" signal when a small signal will suffice. Not all animals will evolve to be as gaudy and showy as manakins. For example, squirrels found in woodland habitats use a large "tail flagging" motion, where the tail is moved from the back to nearly ground level. In contrast, a squirrel species found in rocky habitats use a short jerky tail flick. Similarly, sticklebacks in dense weeds court females with a jump dance to attract the attention of the female, whereas sticklebacks found in barren environments do not appear to use the jump dance at all (Fleishman, 1992).

The environmental lighting conditions (see Side Box 13.2, Fig. 13.13) that animals are found in also affect signal design structure (Endler 1992). The most striking differences are predicted to occur with:

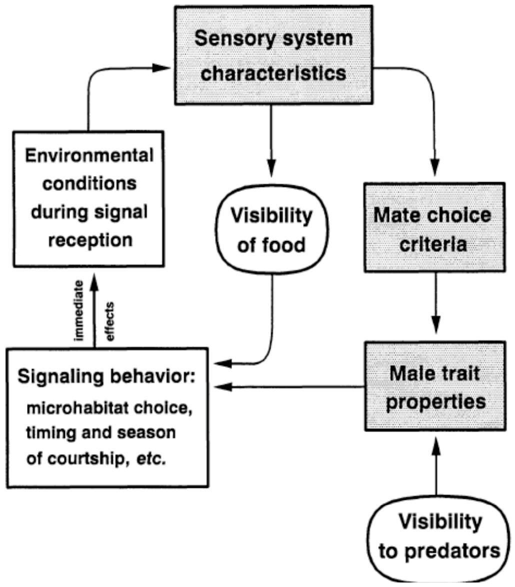
1. time of day when spectra appears purplish (blue + red) because intermediate wavelengths are absorbed by ozone as the light rays travel through a longer atmosphere,
2. the amount of foliage cover, which in the case of forest shade appears greenish because of the reflection and transmission properties of light,
3. cloud cover, which tends to reflect red light back to the earth.

Sensory Drive vs. Exploitation: How do female preferences evolve?

A recent theory (Endler, 1992, Ryan 1990) suggests that there exist sensory biases in the nervous/sensory receptors of females that pre-disposes them to pick some male traits, not because they perceive them as sexy *per se*, but because they are "attracted to them", probably for reasons other than mate choice. **Sensory traps** (West-Eberhard 1984) discussed in reference to mechanisms of genomic imprinting (Chapter 11) are related to concepts of **sensory drive** and **sensory exploitation**.

Certain stimuli (e.g., colors, shapes, movement) may be useful in other contexts (e.g., feeding and foraging). The nervous systems of females (and males) are honed by natural selection to be efficient at picking out food items from a world that is overly rich in extraneous stimuli. Parts of the nervous system/sensory system may be co-opted by sexual selection and males that show a trait that triggers a heightened response in females may have an advantage. A male's signal should become fine-tuned such that it maximally stimulates the female sensory system. **Sensory drive** is the integrated evolution of communication signals, perceptual systems and communication behavior because of the physics of signal production and transmission, and the neurobiology of perception (Boughman 2002). **Sensory exploitation** is a subset of these interactions restricted specifically to female preference (Fig. 13.16).

Figure 13.16. Processes of Endler's process of **sensory drive**. Arrows indicate evolutionary influences except for the one labeled immediate effects. The shaded portion of the figure is equivalent to Ryan's (1990) concept fo **sensory exploitation** (from Endler 1993).



Inherent properties of signals, such as their color, intensity, or size, affect signal conspicuousness and detection. Three interrelated processes affect detection: (1) habitat transmission (passage of signals through the habitat); (2) perceptual tuning (perceptual adaptation to local habitat); and (3) signal matching (matching of male signals to female perception). The sensory drive hypothesis describes how these three processes shape the evolution of inherent signal properties (Boughman 2001, 2002).

Does sensory exploitation of females by males take place?

Basalo studied a genus of sword-tailed fish, *Xiphoporus*, which have elongate swords. A phylogeny of *Xiphophorus* indicates that most recent members of the "clade" have swords (T+). One member of the genus, the most "ancestral" type lacks a sword (T-). Basalo tested if females from this ancestral species preferred males of their own species, which lack a sword, or males of their own species with swords tied on. The overwhelming choice was for males that had a of their own species with swords tied on (P+/T-). She interpreted these results to imply that there existed an "ancestral" bias, for sword preference in these fish that in turn led to a Runaway Process (Fig. 13.17B)

Ryan (1999) argues that sensory exploitation is likely to be quite common in animals and cited a number of

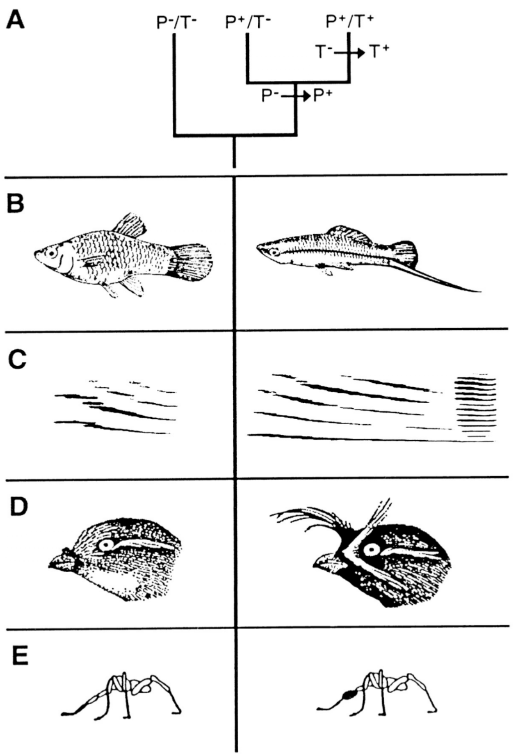


Fig. 13.17. (**A**) A hypothetical phylogenetic tree showing the distribution of absence (-) and presence (+) of female preferences (P) and male traits (T) consistent with the sensory exploitation hypothesis. The most parsimonious explanation is that the preference existed before the trait evolved (see Chapter 18). (**B** to **E**) Studies supporting the sensory exploitation hypothesis show that females prefer traits absent in their own males (left panels) but present in males of other species (right panels), and also offer phylogenetic evidence that supports the scenario shown in (A). These include preferences for sword in poeciliid fish (B), call suffixes in *Physalaemus* frogs (C) [sonogram, frequency versus time], feather ornaments in auklets (D), and hair tufts in wolf spiders (from Ryan 1999). See also Chapter 18.

examples (Fig. 13.17B-E). However, Sherman and Reeve (1999) countered that in many of the examples cited, female benefit may be due to generalized preference for high-quality males. For example, sword preference may be because females benefit from large male size. The only way to resolve this controversy is with more detailed information on female sensory mechanisms (Chapter 14, 18).

Speciation mediated by environment effects

The environment can have a profound effect on the ability of signals to be properly discriminated by a receiver. One of the best demonstrations of this principle is observed in the species radiation of African Cichlids, which radiated into several hundred species in as little as 12400 years. However, in the past two decades species of cichlids have been disappearing at an alarming rate. Seehausen et al. (1997) suggest that turbidity changes in the past two decades, due to eutrophication have led to environmental constraints on the mate preferences that now allow species to hybridize, which could properly discriminate before eutrophication took hold in the lakes. Seehausen et al. (1997) show that transmission spectra at several research stations vary a lot (Fig. 13.19). Furthermore, the bandwidth of transmission spectra (defined in Fig. 13.19) varies in an exponential fashion with the width of the transmission spectra (Fig. 13.20). This relationship is not only true of for the number of coexisting species, but it also holds for the number of co-existing color morphs with a species (Fig. 13.20). They also demonstrate that mate choice arises directly as a function of these color differences among species.

Figure 13.19. Transmission spectra at a water depth of 2 m at the 13 research stations. Numerals indicate the number of coexisting haplochromine species for each station. The width of spectra at 10% transmission (nanometers), defined as the **bandwidth**, is related to turbidity (centimeter Secchi disc).

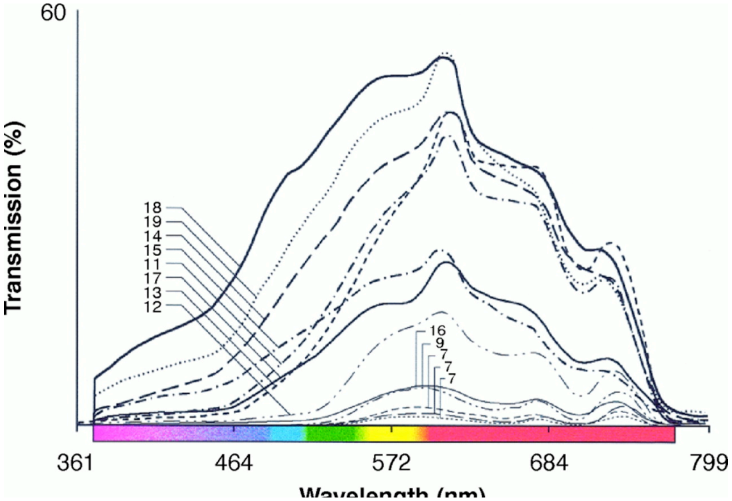
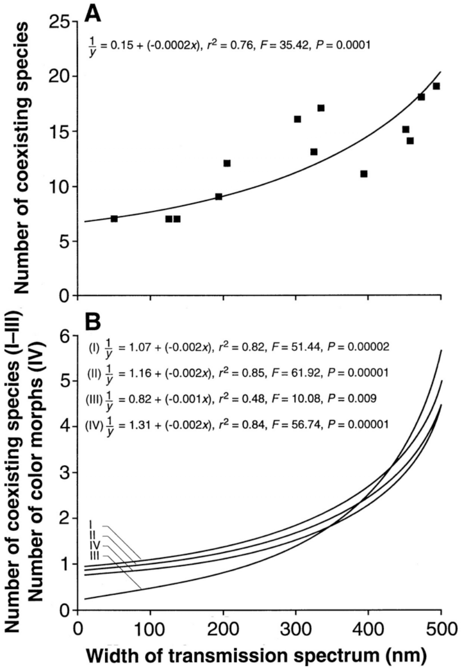


Figure 13.18. Relation between bandwidth of the transmission spectrum and cichlid diversity. (**A**) Spectral bandwidth at 2 m water depth (31) and the number of coexisting haplochromine cichlid species. Each point represents one of 13 rocky islands along a south-north transect. (**B**) The same relation for the genera *Neochromis* (I), *Nyererei* complex (II), *Paralabidochromis* (III), and for the number of color morphs of *Neochromis* "velvet black"/"blue scraper" (IV) (from Seehausen et al. 1997).



Boughman (2001) tested the three key precepts of the sensory drive hypothesis (listed above) in speciation process in stickleback species. Sticklebacks have noteworthy differences due to ecological speciation between limnetic forms that live in the open water column, which have structures for raking plankton, and benthic forms which forage near the bottom, and towards the shore, where they prey on benthic crustaceans. Hyridization of these two forms leads to fish with an intermediate morphology and reduced fitness (Schluter 1995, Fig. 13.22). The lighting environments in each of the habitats stickleback species breed should have a profound effect on speciation processes that drive the radiation of sticklebacks into their respective ecological niches.

As noted above, the sensory drive hypothesis predicts that three factors underlie divergence in sexually selected species: 1) habitat-specific transmission of male signals, 2) adaptation of female perceptual abilities to local environmental conditions, and 3) matching of males signals to female perceptual ability (e.g., coevolution of the sexes).

The lakes clearly vary in transmission of male signals. As the lakes become more red-shifted males display less red, because red will be quite ineffective against the red-shifted background (Fig. 13.19), they display with nuptial colors that are likely to contrast with the water color confirming the 1st prediction of the sensory drive hypothesis.

Boughman then scored the optomotor response and found differences between the detection thresholds for red light, with a low threshold implying higher sensitivity. The limnetic females are more sensitive to red than benthic females, and females from populations with red males are more sensitive to red light than females from populations with black males. This perceptual ability correlates with variation in water quality (Fig. 13.20b), suggesting that the environment influences perceptual sensitivity, confirming the 2nd prediction of the sensory drive hypothesis.

Finally, the area of red in males correlated negatively with the detection threshold in females (Fig. 13.21) confirming the 3rd prediction, male signals are matched to female perceptual ability.

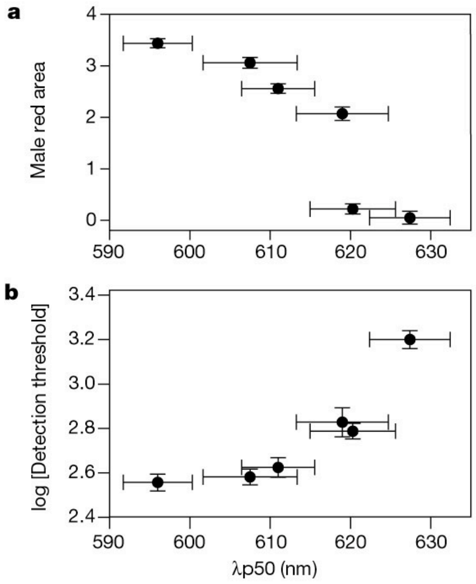


Figure 13.20. Influence of water color (λp50 values for the nesting habitat) on sexually selected traits in males and females. Population means are shown. A) Area of red coloration is negatively correlated with λp50, and as the light becomes red-shifted males display less red. B) Female detection threshold shows a positive correlation with λp50. Females with high detection threshold (low sensitivity) to red light mate in more red-shifted habitats. Sensitivity to red is high when the detection threshold is low and is measured in log photon flux). (from Boughman 2001).

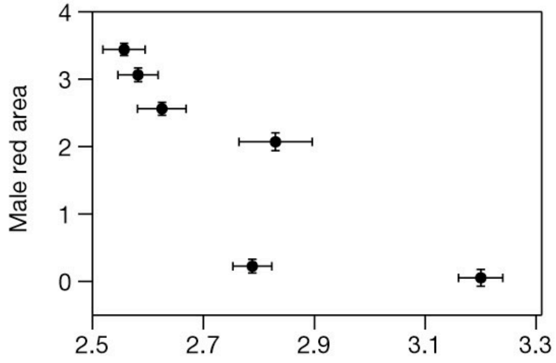
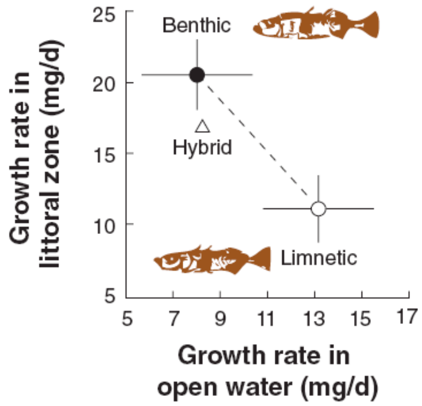


Figure 13.21. Relationship between female detection threshold and amount of red in males is negative indicating that signal and receiver are tightly matched.

The notion of environment in driving the evolution of sexual selection and speciation process has a lot of merit. The list for the number of species in which sensory drive seems to have played a role in speciation processes is growing (Table 13.1). Boughman (2002) suggests that the environment can play a very important role, but that ecological differences must go hand in hand with the evolution of sensory systems and signals, such that hybrid unfitness will reinforce the divergence in sexual signals due to sensory drive (Fig. 13.22). Case studies like the cichlids illustrate this process in reverse. Genetic differences between species begin to unravel as the environment begins to limit the ability of the sexes to make species discrimination (Seehausen et al. 1997).

Figure 13.22. Tradeoffs in growth of limnetic, benthic, and hybrid forms of stickleback, *Gasterosteus* spp. in 2 different habitats. Hybrids are inferior to the trade-off line for feeding in littoral versus feeding in open water, indicating that hybrids do poorly. These ecological differences work in conjunction with sensory drive to generate differences in nuptial coloration of benthics *versus* limnetics (from Schluter 1995)



Taxon	Signal	Habitats differ in transmission of signals	Signals vary with habitat	Perceptual sensitivity varies with habitat	Signals match perceptual sensitivity	Preference varies with perceptual sensitivity or habitat	Divergent signals correlate to R.I.	Divergent preferences correlate to R.I.	Low levels of genetic divergence	Refs
Vogelkop bowerbirds Amblyornchus inornatus	Bower shape and decoration color	Y	Y	U	U	U	U	U	Y	[38]
Warblers Phylloscopus spp.	Color patches	Y	Y	U	U	U	U	U	N	[26]
Cricket frogs Acris crepitans	Call	Y	Y	P	Y	P	P	P	Y	[30,43] [24,29]
Lizards Anolis spp.	Dewlap color	P	P	N	P	U	Y	U	N	[44–47]
Anolis cooki and A. cristatellus	Dewlap color	Y	Y	Y	Y	U	U	U	Y	[48]
Haplochromine cichlids Haplochromis spp.	Color	Y	Y	Y	P	P	Y	Y	Y	[49 –51]
Threespine stickleback Gasterosteus spp.	Throat color	Y	Y	Y	Y	Y	Y	Y	Y	[39]
Snappers (Lutjanidae)		Y	U	Y	U	U	U	U	U	[27]
Ermine moths Colias eurytheme , C. philodice	Pheromones	U	U	P	Y	P	P	P	N	[52]
Drosophila mojavensis , Baja and Sonoran populations	Epicuticular hydrocarbons	Y	P	U	P	P	Y	Y	Y	[53 –57]
Wolf spiders Schizocosa ocreata , S. rovneri	Vibration pattern and leg tufts	Y	Y	P	Y	Y	P	P	Y	[58 –60]

* Columns correspond to predictions of the hypothesis that sensory drive promotes speciation through divergence of mating traits and concomitant reproductive isolation. Key: Y, yes; N, no; P, possible but unconfirmed; U, unknown or no data; R.I., reproductive isolation.

Parent-offspring communication

The generalizations about sensory drive extend to all forms of communication, including parent-offspring signals and reception. In many avian species, nestlings have evolved striking plumage, behaviors and mouth colors to obtain a greater share of parental investment (e.g., see Chapter 11). Great tit nestlings exhibit color inside their mouths. When they gape they show parents the contrasting colors and two hypotheses have been proposed to explain these signaling structures. Red mouth color in songbirds can act as a signal of nestling need or condition. Alternative hypotheses suggest that bright nestling mouths in cavity-nesting birds evolved to increase nestling detectability by the parents. Heeb et al. (2003) tested this hypothesis by painting the interior *versus* exterior of the mouths YY, YR, or RR. In nests with low luminosity, red mouths decreased nestling detectability to the feeding parents and supports the hypothesis that poor luminosity in nesting cavities can select for pale mouths. Additional studies on great tits reveals that the colors also include a UV component (Jourdie et al. 2004), which when eliminated by UV blocker reduce nestling weight gain. UV is conspicuously reduced in the environment, suggesting a role for *sensory drive* in parent-offspring communication.

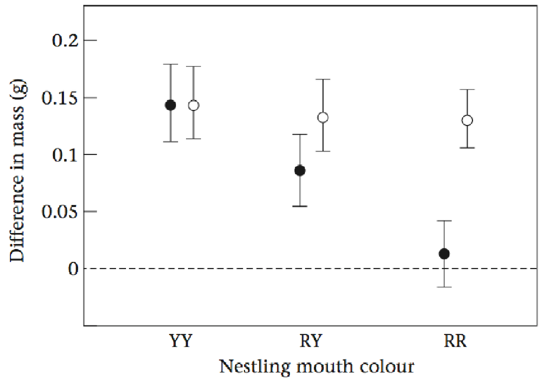
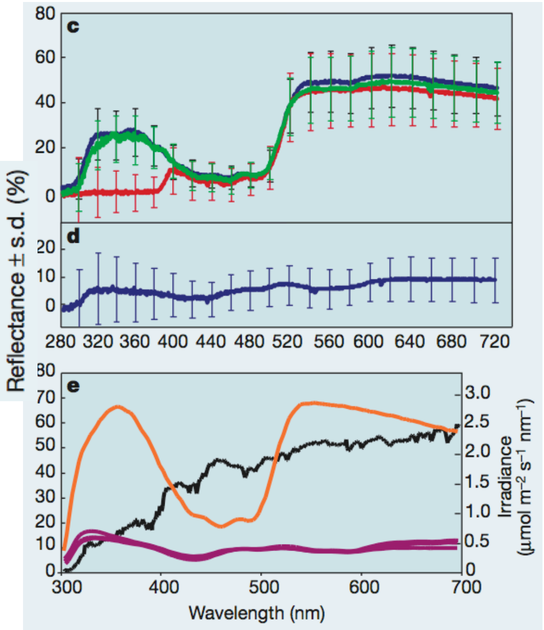


Figure 13.23. Observed changes in nestling mass of great tits in relation to modifications of nest luminosity and nestling mouth color (open circles high luminosity, closed circles low luminosity. (from Heeb et al. 2002)

Figure 13.24. Reflectance spectra of the mouth flanges of great tit nestlings (top panel) and body skin (middle panel). Blue is untreated skin, red is treated with a UV blocker. (bottom panel) The nest irradiance is shown in black, nestling skin in purple and mouth flanges in orange (from Jourdie et al. 2004).



Study Questions for Sensory Systems and Communication

1. Apply the principles of tactical and strategic signal components to:

a) male male competition

b) sensory drive and female choice.

2. Is the phenomenon of sensory drive more related to runaway process or indicator models of sexual selection? Justify your answer.

3. Why are cut and paste experiments especially useful in understanding the communication between signaler and receiver?

4. Why are playback experiments useful in decoding the strategic components of a signal? (see the material on information in male contests as well).

5. Discuss the concept of honesty and dishonesty in male-male and male-female relations. (there are many places where honesty and dishonesty is discussed in previous Chapters).

6. How do animals cope with noise (visual and auditory) in decoding signals?

7. A juvenile bird that is learning a song squawks a song in the woods but no other bird or animal is around to hear it. Is it communicating? Why or why not?

8. Distinguish between sensory bias and sensory exploitation.

9. Describe input matching with respect to visual pigments. Must include both signaler and receiver in your answer.

10. Draw diagrams of a di-, tri- and tetrachromatic animal? What is a hypothesized intermediate step between di- and trichromatic vision (what is a polychromat)?