3
Perception and Attention

To a bat or an owl, a summer evening is full of sounds of which we are only dimly aware. A honeybee sees patterns on flowers that are invisible to us. That every kind of animal has its own *umwelt* or self-world, formed by the kinds of information its senses can process, was one of the fundamental insights of the founders of ethology. The ethologist Von Uexküll (1934/1957) attempted to capture this insight in pictures of how the world might seem to other species (Figure 3.1). A great deal is now known about how animals process sensory information even if most contemporary behavioral scientists do not attempt to translate it into such depictions of subjective experience.

The study of comparative cognition begins with sensation and perception for two reasons. First, it is important to keep in mind that adaptive behavior can result from specializations in perception as much as from higher-level learning or decision processes. Second, perception provides some excellent examples of modularity and adaptation in information processing. This chapter begins with a few illustrative examples of sensory specialization, then looks at how perception can be studied in animals and introduces the important ideas of signal detection theory. Armed with this information, we can see how "receiver psychology" (Guilford and Dawkins 1991; Endler and Basolo 1998; Rowe and Skelhorn 2004) has influenced the evolution of animal signals. And at the end of the chapter we look at how sensory information is filtered by attention and how attentional processes can explain the classical ethological phenomenon of search image formation.

3.1 Specialized sensory systems

Every animal must be able to respond appropriately to its own food, mates, young, and predators. The cues it can use are determined by the environment characteristic of its species (Dusenbery 1992). Species active at night have a different set of cues available to them from those active during the day; those that live underground, different cues from those that live in the treetops; creatures of the deep sea, different cues again from creatures of clear streams. Sensory systems and their sensitivities tend to be matched to lifestyle and environment.

The sensory specializations we find most impressive are those allowing animals to respond to forms of energy that an unaided human cannot detect. The ultrasonic

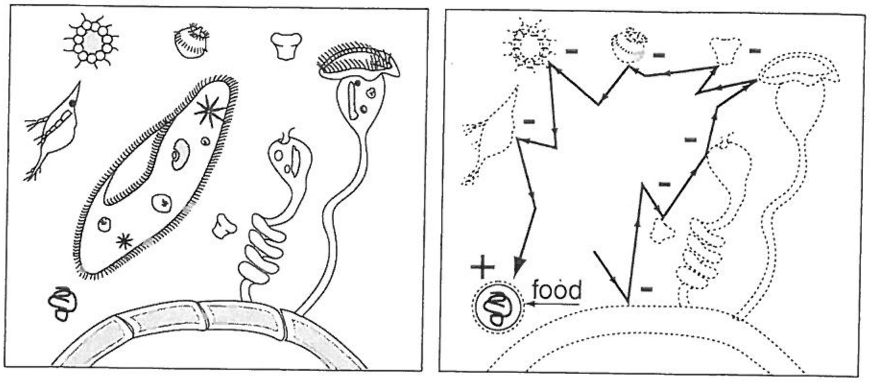
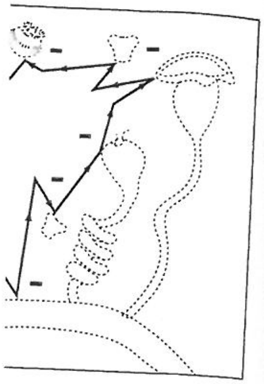


Figure 3.1. Von Uexküll's conception of the *umwelt* of a paramecium (the large gray blob in the left panel). The environment in all the complexity perceived by humans is depicted on the left, the same environment as perceived by the paramecium on the right, with + and—_ showing what attracts and repels it, respectively. Redrawn from von Uexküll (1934/1957) with permission.

hearing of bats is one well-studied example (Figure 3.5). Many bat species find prey in the dark using a kind of sonar. They continually emit ultrasonic cries, and the echoes from flying insects enable the bats to locate their prey in complete darkness. Some snakes locate live prey by homing in on warm objects, using infrared detectors in their snout. The platypus feeds underwater at night using sensitive receptors in its bill to detect the electric fields generated by movements of its prey (Manger and Pettigrew 1995). Using mechanisms that are still somewhat mysterious, some birds, mammals, reptiles, and other animals navigate by means of the intensity and/or inclination of the Earth's magnetic field (Wiltschko and Wiltschko 2006).

Many animals with color vision, such as honeybees and most birds, have a different pattern of wavelength sensitivity from humans. Thus they do not necessarily see prey items or potential mates (or images we create to mimic them) the way we do (Box 3.1). For example, wavelength sensitivity of many birds extends into the ultraviolet (UV), and some feathers reflect UV light (Cuthill et al. 2000). This discovery has led to some striking observations which illustrate very compellingly how we need to understand an animal's species-specific perceptual world to understand its behavior. For example, blue tits and starlings are bird species in which males and females look the same color to humans. But to a blue tit or starling, males look very different from females because they have conspicuous patches of UV-reflecting feathers, patches which are larger or better developed in males. In such species, females may base mate choice on the brightness of these patches, rejecting males treated with UV-blocking sunscreen in favor of untreated males (review in Cuthill et al. 2000). To take an example from prey-catching, kestrels locate places where voles can be found using the UV reflectance of the urine that the voles deposit as they run along their habitual trails (Viitala et al. 1995). Honeybees also have UV vision, which they use to discriminate among flowers (Section 3.5.1).

The foregoing are but a few examples of striking species differences in what animals sense. The sensitivity of particular systems also may differ among closely related species or even individuals of the same species. For example, optimal visual sensitivity is different for fish dwelling at different depths because the distribution of wavelengths illuminating objects changes with depth as sunlight is filtered by seawater. Sensitivity may change with age if the same fish lives at different depths at



(the large gray blob in the left
depicted on the left, the same
—_ showing what attracts and
ermission.

ny bat species find prey in
nic cries, and the echoes
omplete darkness. Some
nfrared detectors in their
ve receptors in its bill to
(Manger and Pettigrew
, some birds, mammals,
and/or inclination of the

nd most birds, have a
s they do not necessarily
ic them) the way we do
s extends into the ultra-
. 2000). This discovery
npellingly how we need
to understand its beha-
hich males and females
ales look very different
JV-reflecting feathers,
h species, females may
nales treated with UV-
ill et al. 2000). To take
les can be found using
n along their habitual
n, which they use to

s differences in what
differ among closely
ample, optimal visual
se the distribution of
ght is filtered by sea-
at different depths at

Box 3.1 Color Vision

Color resides not in objects but in the observer's perception of wavelength differences and similarities. To a color blind animal, objects differ visually only in brightnesss. What this means is illustrated by a classic demonstration of color vision in honeybees (Frisch 1914, as cited in Kelber, Vorobyev, and Osorio 2003). Bees trained to find sugar water on a blue or a yellow card showed that they were using wavelength and not brightness by choosing their training color over all shades of grey, from very light to very dark. The first stage in responding to wavelength is the reaction of photopigments to light; in vertebrates these are in the retinal cone cells (cones). Each photopigment has a unique profile of responsiveness as a function of wavelength. Behavioral discriminations are based on a neural comparison of the responses of different photoreceptor types (for further details see Cuthill et al. 2000; Kelber, Vorobyev, and Osorio 2003).

The kind of color vision available to different species is revealed by the relative sensitivities, or absorption spectra, of the animals' photoreceptor types (Figure B3.1). Honeybees, like many other insects (Briscoe and Chittka 2001), have three photoreceptor types all near the blue-green end of the spectrum. One is sensitive in the ultraviolet. Pigeons have three photoreceptor types (retinal cone cells, or *cones*) with sensitivities similar to those of humans' and a fourth with maximum sensitivity in the ultraviolet (UV). Many other birds have UV vision, as discussed in the main text. Humans and many other primates have three cone types, with maximum sensitivities in red, green, and blue wavelengths. Primates are unique among mammals in having color vision, and there is some debate about why such trichromatic color vision evolved (Surridge, Osorio, and Mundy 2003). Red-green discrimination is thought to be useful for detecting ripe fruits in the forest, but it could be equally useful for folivorous (leaf-eating) primates because the freshest and most nutritious leaves tend to be red. Color also plays a role in social communication in some primates (Ghazanfar and Santos 2004), but whether it evolved first in that context or in the context of foraging is still debated. Selection for enhanced visual capabilities, including color vision, may have played a role in the evolution of relatively large brains in primates (Chapter 12; Barton 2000).

Behavioral tests of color matching are important in showing how photoreceptors are actually used: any wavelength can be matched with a mixture of the primary colors for that species (i.e., those at the peak sensitivities for the different photoreceptors). This principle is made use of in video screens that generate colors by activating red, green, and blue phosphors in different proportions for different colors. As a result, most animals do not see the colors on conventional TV the way we do because their peak sensitivities and/or distributions of different receptor types are different from ours (Box 6.1; Oliveira et al. 2000).

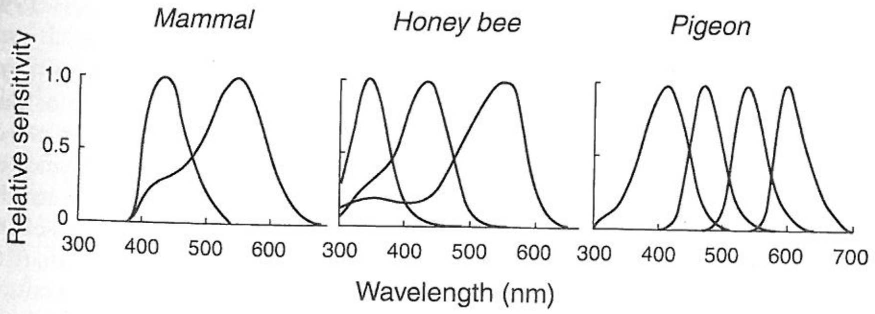


Figure B3.1. Relative wavelength sensitivities of photoreceptors in a representative nonprimate mammal, honeybees, and pigeons. In terms of human perception, red is toward the right on the x-axis. Relative sensitivity, on the y-axis, is the proportion of maximum responsiveness that the given receptor type shows at each wavelength. Human sensitivity is similar to that of pigeons except that we lack the very short-wavelength, UV, receptor. Adapted from Kelber, Vorobyev, and Osorio (2003) with permission.

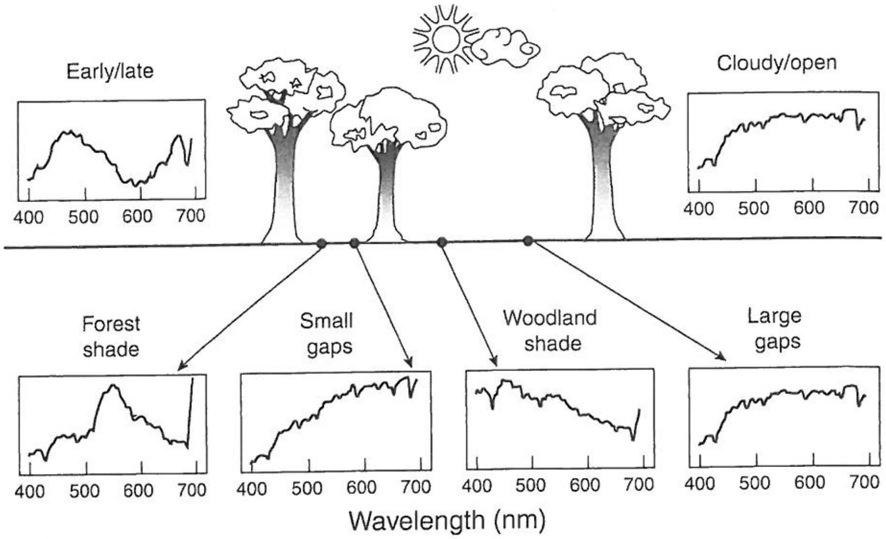
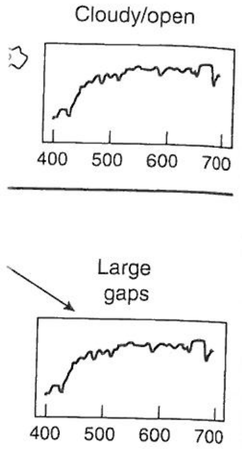


Figure 3.2. The relative intensities of different wavelengths of light in different parts of a forest and under different conditions. Forest shade, for instance, has a relatively high proportion of wavelengths from the middle (greenish) part of the spectrum, whereas small gaps are rich in longer (redder) wavelengths. Redrawn from Endler (1992) with permission.

different stages of its life cycle (Lythgoe 1979). As shown in Figure 3.2, the light environment also differs in different parts of the forest and at different times of day. The nuptial plumage of male forest birds and the times and places at which they display may be matched to the available light in such a way as to maximize the males' conspicuousness (Endler and Thery 1996; Endleret al. 2005). The sound frequencies that travel farthest are determined by factors such as atmospheric conditions and type of vegetation. These physical constraints have affected the evolution of animal sound production and reception mechanisms. For example, the songs of forest birds tend to have a different distribution of frequencies from the songs of birds from open habitats. Regardless of habitat, many birds choose to sing from high, exposed, perches, from which sound travels furthest (Catchpole and Slater 1995; Slabbekoorn 2004).

How much of the environment an animal can see at once depends on where its eyes are. Animals with eyes on the sides of their heads can see a wider arc of their surroundings than animals with frontally placed eyes. The placing of the eyes reflects the extent of binocular vision required by the species diet and the extent to which the animal is predator as opposed to prey, as illustrated in Figure 3.3 with the striking contrast between an owl and a woodcock. The most important things may be near the horizon or above or in front of the animal, and this feature of ecology may be matched by greater visual acuity in some parts of the visual field than others. For example, pigeons view a small area in front of them binocularly. Binocular vision and concomitantly good depth perception are important for accurate pecking at seeds, whereas the lateral field of view is important for detecting predators. Accordingly, pigeons have two "foveas," areas of maximally dense photoreceptors, one in the binocular field and one on which objects to the side are focused (see Roberts et al. 1996). Species of birds with different lifestyles also have different retinal distributions of photoreceptors (Nalbach, Wolf-Oberhollenzer, and Remy 1993). For example,



ferent parts of a forest and
h proportion of
all gaps are rich in longer

n Figure 3.2, the light
different times of day.
l places at which they
o maximize the males'
The sound frequencies
ric conditions and type
ution of animal sound
of forest birds tend to
; of birds from open
from high, exposed,
and Slater 1995;

ends on where its eyes
a wider arc of their
ing of the eyes reflects
he extent to which the
3.3 with the striking
hings may be near the
ology may be matched
others. For example,
cular vision and con-
ite pecking at seeds,
edators. Accordingly,
receptors, one in the
ed (see Roberts et al.
t retinal distributions
1993). For example,

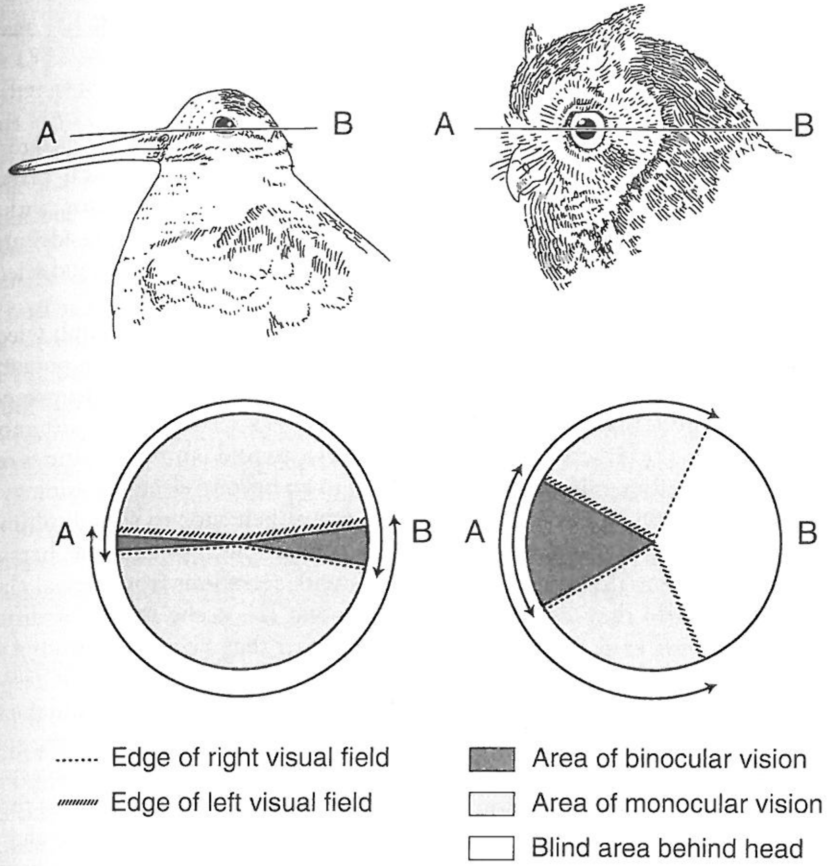


Figure 3.3. Differences in the placement of the eyes and visual fields for different lifestyles, prey animal (wood cock) versus visual predator (owl). Redrawn from Evans and Heiser (2004) with permission.

seabirds tend to have a central horizontal strip of high density photoreceptors. Owls and other birds of prey have the densest photoreceptors in the part of the retina that views the ground. They may have to turn their heads almost upside down to see something approaching from above.

In many situations animals respond to a very narrow range of stimuli. For example, male moths of species like *Bembyx mori* are sexually attracted to a particular molecule contained in a pheromone emitted by the female of their own species (see Hopkins 1983). A hungry baby herring gull pecks at a red spot near the end of its parent's beak and less at other colors in other locations (Tinbergen and Perdeck 1950). The first step in analyzing such an example of selective behavior is to find out whether it can be explained by the responsiveness of the sensory system involved. In the case of the moth, the characteristics of the olfactory system completely account for the male's selective sensitivity. The male moth's antennae are covered with receptors selective for the female's sexual pheromone. In contrast, the herring gull's selective pecking at red spots on beaklike objects reflects processing at a higher level (Delius et al. 1972). Both the female pheromone and the red spot would be classified as sign stimuli (Chapter 6), but one reflects a purely sensory filter, the other a more central processing mechanism.

3.2 How can we find out what animals perceive?

3.2.1 Studying perception in animals

Three approaches can be taken to analyzing perception in animals: *(1)* electrophysiology and related methods of neuroscience, *(2)* studying how natural behavior changes with changes in stimulation, and *(3)* testing learned behavior with the methods of animal psychophysics. Each one of these approaches has its advantages and disadvantages. Two or three of them can be used together to understand selective responsiveness in natural situations.

Recording electrical responses of sensory neurons to controlled stimuli (electrophysiology) is the most direct way to find out what sensory information is potentially available to an animal. In the case of the moths described in the just-preceding section, such methods make clear that the "decision" to approach and court another moth is reached by the olfactory receptors. However, to find out what features of the world are behaviorally significant, it is necessary to go beyond electrophysiology and look directly at behavior. Often, an animal's natural behavior to stimuli of importance to it can be used to test simple sensory discriminations. For example, hamsters, like many other mammals, mark their territories with secretions from special glands. To find out whether they can discriminate among the scent marks of different individuals, Johnston et al. (1993) made use of the fact that a hamster spends a great deal of time sniffing a glass plate scent marked by another hamster. This response decreases as the hamster encounters successive marks of the same kind from the same hamster, that is, the response *habituates* (see Chapter 5). However, once the subject hamster has habituated to the scent from one hamster, it still vigorously investigates scent from a second hamster (Figure 3.4). Such renewed investigation shows that the animal discriminates the second scent from the first. As we will see in later chapters, this is a powerful way to discover what stimuli all kinds of subjects, including humans, discriminate. It is generally called the *habituation/dishabituation method,* but it should be noted that renewal of an habituated response in the presence of a new stimulus is not strictly the same as what is referred to as dishabituation in the analyses of the habituation process discussed in Chapter 5.

The differences animals perceive among behaviorally relevant stimuli can be studied in the field as well as in the laboratory. For example, many territorial songbirds learn the characteristics of their neighbor's songs and where those neighbors typically sing (Box 5.1). A familiar neighbor singing from a new location is treated as

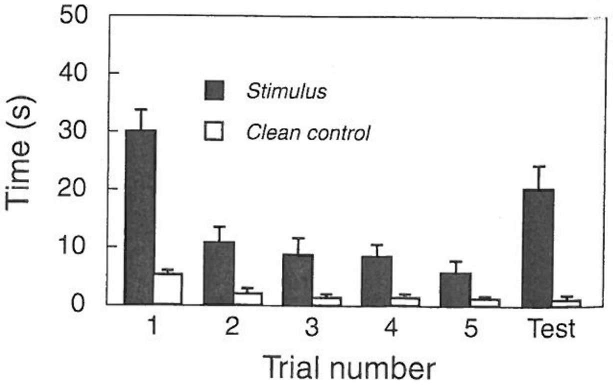
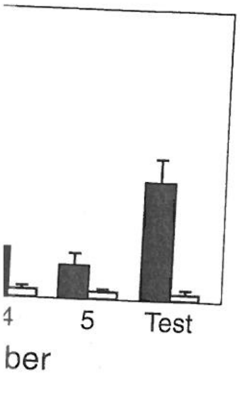


Figure 3.4. Data from a habituation/dishabituation test of olfactory discrimination in male golden hamsters. Time spent sniffing the scented (stimulus) half of a glass plate is compared to time spent sniffing the clean half. The stimulus was the same in Trials 1–5 and different in Trial 6. Redrawn from Johnston et al. (1993) with permission.

animals: *(1)* electrophy-
; how natural behavior
ned behavior with the
ches has its advantages
to understand selective

trolled stimuli (electro-
formation is potentially
d in the just-preceding
oach and court another
out what features of the
electrophysiology and
or to stimuli of impor-
For example, hamsters,
ns from special glands.
nt marks of different
amster spends a great
amster. This response
ne kind from the same
ever, once the subject
igorously investigates
gation shows that the
see in later chapters,
of subjects, including
habituation method,
the presence of a new
uation in the analyses

vant stimuli can be
any territorial song-
ere those neighbors
location is treated as



---

a threat and attacked. A novel conspecific song from a loudspeaker is also attacked (Falls 1982), making it possible to present songs in a controlled way in the field to find out what aspects of this complex auditory stimulus birds are sensitive to. Experiments of this kind have shown, for example, that great tits can discriminate among the voices of their neighbors (Weary 1996).

A limitation of using natural responses to natural stimuli is that there are at least two reasons why an animal may respond in the same way to two or more stimuli. It may not be able to discriminate among them or the differences it discriminates may have no behavioral significance for it. In the example above, for instance, a territorial male bird might be equally aggressive toward two very different novel songs, but he might later show that he could discriminate them if one was the song of a neighbor while the other remained relatively novel (for further discussion see Collins 2004; Dooling 2004). Late in the breeding season, when sex hormone levels are lower, he might respond equally little to all songs. A good understanding of the behavior of the species being tested is clearly necessary to ensure that tests of discrimination are being done in a meaningful way. In general, because natural responses to natural stimuli may reflect so many motivational and other variables, electrophysiological or psychophysical methods must be used to study sensory ability separately from responses to the signals of interest.

3.2.2 Animal psychophysics

One of the oldest areas of experimental psychology is *psychophysics,* the study of how information is processed by the senses. For example, what is the smallest amount of light energy, at each wavelength, that can be seen in total darkness? Or, with a given background sound, what increase in sound pressure level is required for subjects to report an increase in loudness? The former is a question about the *absolute threshold;* the latter, about the *relative* or *difference threshold.* Data from psychophysical investigations typically consist of plots of absolute or relative thresholds as a function of a physical stimulus dimension.

A psychophysicist interested in absolute auditory thresholds can tell a human subject, "Press this button whenever you hear a tone." Visual acuity can be tested by instructing a person, "Press the left button when you see stripes; press the right when you see a gray patch." Animals, in contrast, have to be given their instructions by careful training, using the methods of operant or classical conditioning. Figuring out how to ask nonverbal subjects the questions one wants to ask in a way that yields unambiguous answers is one of the biggest challenges in any area of comparative cognition. With operant methods, the animal is placed in a situation where it can obtain reward or avoid punishment only by using as a cue the stimulus the experimenter is interested in. Since animals seem to have an uncanny knack of latching onto subtle irrelevant cues, being sure the animal responds only to the stimulus of interest is not as easy as it sounds. Well-designed psychophysical experiments include stringent controls for possible influences of extraneous cues.

A typical procedure for investigating animal sensory abilities is one used for testing bats' ability to discriminate distances by echolocating (Figure 3.5). The basic idea is to reward a bat for making one response when it detects an object moving rapidly back and forth (a "jittering" target) and another response when the target is stationary. As long as the bat can make the correct choice at above the chance level of 50%, it must be discriminating between the two distances from which it hears the jittering target's echoes, that is, between the two echo delays. Since all bats are not really "as blind as a

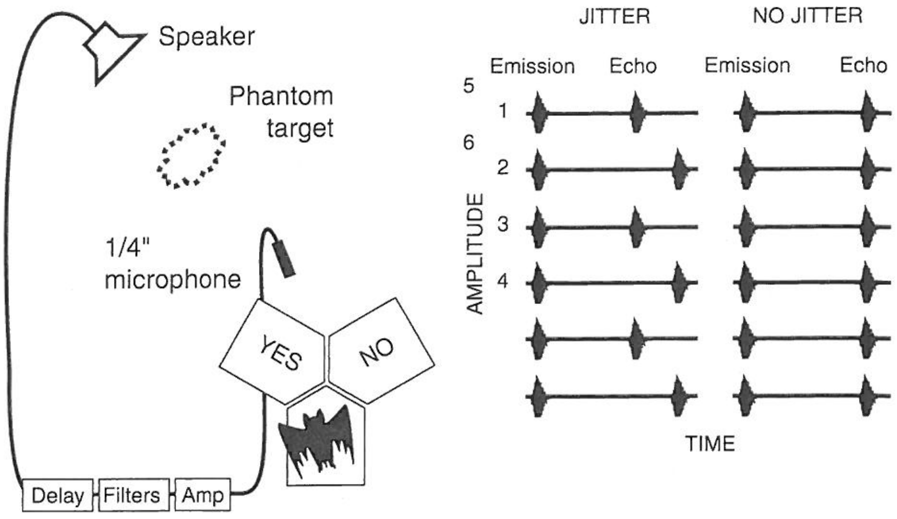
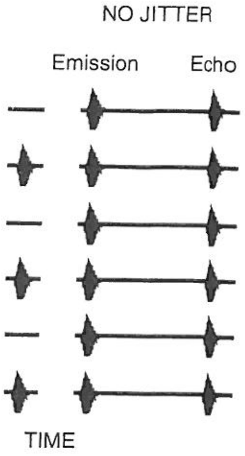


Figure 3.5. Schematic view of a setup for testing temporal discrimination in bats. The bat was reinforced for moving onto the left platform for a jittering target ("yes, jitter present") and onto the right platform when no jitter was present. Redrawn from Moss and Schnitzler (1989) with permission.

bat," the experiment depicted in Figure 3.5 had to eliminate visual cues to motion. This was done by using virtual rather than real targets. The bat's cries were picked up by a microphone near its mouth and broadcast back to it either with a fixed delay, as if reflected by a stationary object, or with alternating short and long delays, as if coming from a jittering object. The bat sat on a Y-shaped platform and was rewarded with a mealworm for crawling onto the left arm when a (virtual) jittering target was presented and onto the right arm for a stationary one. To ensure that the animal learned the required discrimination, training began with large jitters. When the animal performed correctly a large proportion of the time on this easy task, the task was made more difficult, and so on. The bats were eventually making extremely fine discriminations.

This elaborate instrumentation and training procedure may suggest that psychophysical experiments can be done only in the laboratory, but this is not so. Classic field studies of bees' color and shape perception were done by von Frisch (1967) and similar methods have been used with hummingbirds (Goldsmith, Collins, and Perlman 1981). Animals that return repeatedly to one food source as bees and hummingbirds do are particularly good candidates for field tests of sensory abilities because the animal is using the sense for the job it has most likely evolved to do. Not all training methods used in animal psychophysics are so obviously related to the subjects' natural behaviors. It might be assumed that any arbitrary training procedure may be used to tap the capabilities of any sensory system, but the results of psychophysical studies could be influenced by the motivational and response systems used. For example, pigeons attend more to lights than tones when working for food but the reverse is true when they are avoiding shocks (Foree and LoLordo 1973). This could mean that subtle auditory discriminations are easier to teach to frightened than to hungry pigeons. The kind of behavior guided by a given sensory system should be taken into account in psychophysical tests of that system.



n in bats. The bat was
tter present") and onto the
itzler (1989) with

visual cues to motion.
:'s cries were picked up
r with a fixed delay, as
and long delays, as if
orm and was rewarded
al) jittering target was
nsure that the animal
rge jitters. When the
on this easy task, the
ally making extremely

y suggest that psycho-
this is not so. Classic
von Frisch (1967) and
ldsmith, Collins, and
d source as bees and
sts of sensory abilities
ely evolved to do. Not
viously related to the
ary training procedure
the results of psycho-
esponse systems used.
rking for food but the
rdo 1973). This could
to frightened than to
ory system should be

3.3. Some psychophysical principles

All sensory systems have some basic properties in common (Barlow 1982), many of them shared by instruments designed to detect physical energies. As we have already seen, the senses are characterized by specificity in the kinds of energies they detect: the visual system is specific for electromagnetic radiation in a certain range of wavelengths; the auditory system for changes in sound pressure; the olfactory system for airborne chemicals. Moreover, most sensory systems are not equally sensitive to everything they detect. Rather, each system can be characterized electrophysiologically and behaviorally by a tuning curve. The plots of visual sensitivity as a function of wavelength in Box 3.1 are examples.

In addition to quality ("what is it?") an important feature of stimuli is intensity ("how much is it?"). Brightness, sweetness, and loudness are examples of perceptual intensity continua. An important psychophysical principle that emerges from research on perception of intensity or size continua is Weber's Law, which describes the difference threshold (or *just noticeable difference,* the *JND*) between two stimuli as a function of their magnitude. The JND is a constant proportion across a wide range of base values. This proportion, the Weber fraction, depends on the species and sensory channel. For example, suppose a 10-gram weight has to be increased by .5 grams in order for a person consistently to detect the change. Weber's Law says that if we ask for the same judgment starting with a 20-gram weight, the difference threshold will be 1 gram, whereas it would be .25 grams if we started with a 5-gram weight. Examples of Weber's Law in animals' time and number discrimination are discussed in Chapters 9 and 10.

Three other psychophysical principles have important implications for animal behavior. First, sensory neurons tend to respond more to physically more intense stimuli. Therefore, more intense or reliable behavioral responses can be expected to stimuli that are brighter, louder, or bigger in some other way. This seems so obvious and right as hardly to need stating, but animals need not have been designed this way. One could build, say, a sound meter that gave high readings to soft sounds, and none at all to loud ones. An animal built like it would react to things far away from it and ignore predators or conspecifics close by. In fact, the opposite is generally the case, and it does make functional sense that animals should react more intensely to things that are larger and/or closer.

A second general feature of sensory or perceptual systems is a tendency to habituate (or show adaptation) to prolonged unchanging stimulation. We have seen in the last section how this feature has been put to use to test hamsters' odor sensitivity. It has been suggested that the tendency for listeners to habituate explains why some bird species have repertoires of many different songs. Females, it is suggested, will be more stimulated by a constantly changing series of songs than by one song sung monotonously over and over, and indeed in some species males that sing more different songs are more successful in obtaining mates (Collins 2004).

Third, in many systems response to a given stimulus depends on its contrast with the background. A quiet tone is more easily heard in silence than in soft noise. To a person with normal color vision, a red spot looks redder on a green than on an orange background. The tendency of sensory systems to respond more strongly to stimuli that contrast with what surrounds them in time or space appears to have shaped the evolution of animal color patterns, auditory signals, and the like. For example, many animals that are food for other animals resemble the substrate on which they typically rest, that is, they minimize contrast so as to be cryptic rather than conspicuous. Such

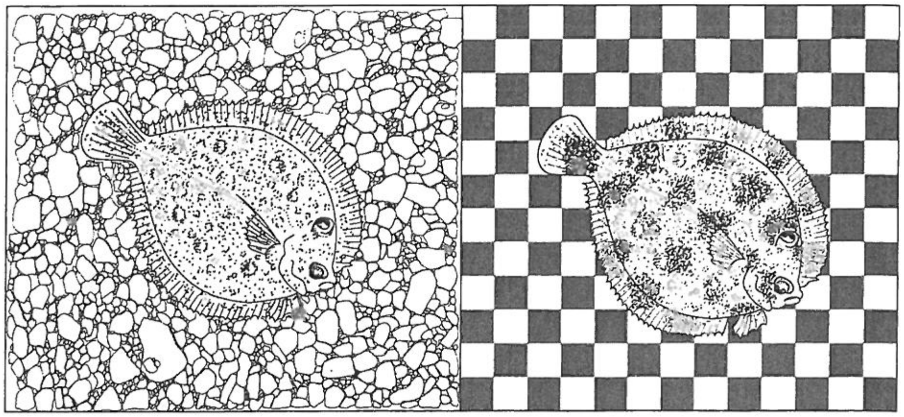


Figure 3.6. Examples of camouflage, showing how a tropical flounder changes its pattern to match the substrate. From photographs in Ramachandran et al. (1996) with permission.

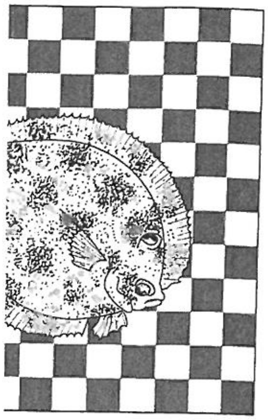
animals sometimes behave so as to enhance their resemblance to their surroundings. For instance, moths that resemble birch bark not only choose birch trees to rest on, they rest so that their stripes are in the same orientation as the black patches on the bark (see Figure 3.18). Flounders, fish that lie flat on the bottom of the sea, provide one remarkable example of how animals can change their appearance to match the substrate (Figure 3.6). Cephalopods (octopus, squids, and cuttlefish) show truly amazing control over not only the color and pattern but the texture of their skin, and the neural and visual control of their elaborate camouflage is beginning to be understood (Hanlon 2007). However, although many details of animal color patterns have long been thought to aid in camouflage, there is surprisingly little experimental evidence for most of these suggestions (Ruxton, Sherratt, and Speed 2004). A recent exception is a demonstration that color patches that break up the outline of a moth's body ("disruptive coloration") do in fact reduce predation by birds compared to the same patches entirely within the body contours (Cuthill et al. 2005).

Far from being cryptic, some animals have what would appear to be the maximum possible contrast with their typical backgrounds. Red rain forest frogs and bright yellow-and-black striped caterpillars seem to be advertising their presence to predators. However, many such warningly colored, or *aposematic,* species sting, prickle, taste bad, or otherwise cause their attackers to reject them. Their bright colors may help predators to learn to avoid attacking them and others like them (see Chapter 6). Contrast with the background is also important in intraspecific communication, as exemplified by the colorful plumage and loud songs of many male birds (see also Section 3.5)

3.4 Signal detection theory

3.4.1 Detecting signals in noise: Theory

In Section 3.3, threshold was mentioned as if it were a definite quantity above which a stimulus is always detected and below which it never is. Even in the best-controlled psychophysical experiment, however, data do not fit this pattern. Observers report



changes its pattern to match
ermission.

ce to their surroundings.
se birch trees to rest on,
the black patches on the
ttom of the sea, provide
ppearance to match the
d cuttlefish) show truly
he texture of their skin,
flage is beginning to be
of animal color patterns
singly little experimental
d Speed 2004). A recent
p the outline of a moth's
y birds compared to the
l. 2005).
pear to be the maximum
forest frogs and bright
g their presence to pre-
ic, species sting, prickle,
Their bright colors may
ke them (see Chapter 6).
cific communication, as
ny male birds (see also

quantity above which a
n in the best-controlled
ttern. Observers report

---

detecting a constant stimulus only a proportion of the time. Threshold is calculated as the value detected a fixed proportion of the time, often 75% or 80%. Variation in response to a constant stimulus is thought to be due to inevitable changes in the observer's state, perhaps lapses in attention or spontaneous firing of sensory nerves, and to uncontrollable fluctuations in the stimulus. In addition, data from different observers can vary because people vary in how willing they are to say "it's there" when they are unsure. Thus the idea of an observer with an absolute threshold must be replaced by the idea that a stimulus has a distribution of effects. The observer's problem is to detect that signal against a fluctuating background with which the signal can be confused (noise). An animal's problem in nature is essentially the same: to detect biologically important signals in an environment filled with unimportant stimuli (see Wiley 2006). For both the psychophysical observer and the animal in the field a certain proportion of mistakes is inevitable, and their cost must be kept to a minimum. Signal detection theory quantifies this fundamental tradeoff.

Signal detection theory (Figure 3.7) was originally developed to tell radar operators the best way to decide which blobs to treat as planes on a noisy radar screen. It has been used extensively in the analysis of human psychophysical data (Macmillan and Creelman 2005), but the ideas it embodies apply to any difficult discrimination performed by any creature. Signal detection theory conceptualizes the perceiver as faced with the task of discriminating some signal from a noisy background (which could be another signal). Signal and noise both have a distribution of effects. The

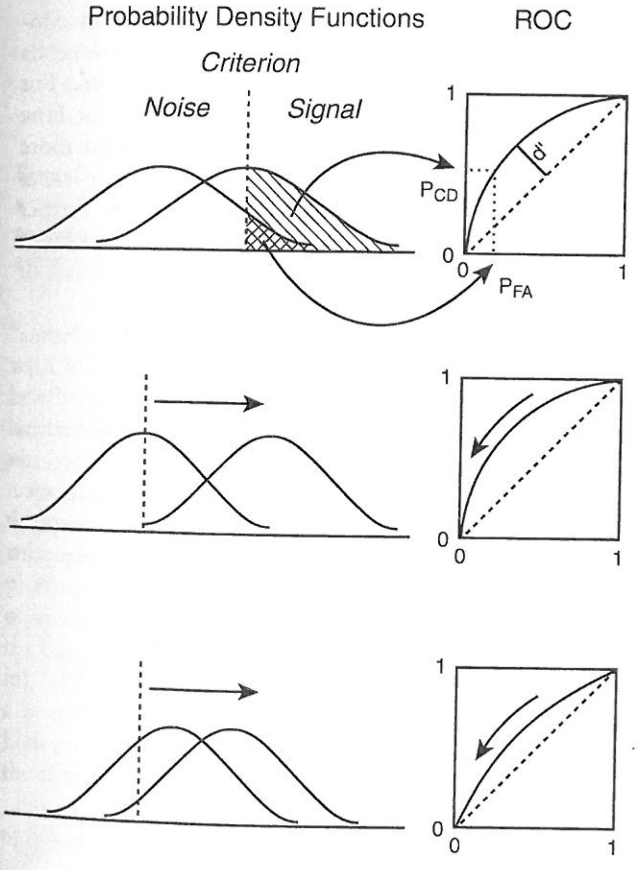


Figure 3.7. The elements of signal detection theory. Hypothetical normal probability distributions of the effect of signal and of noise along some stimulus dimension together with the placement of the criterion for classifying stimuli as "signal" vs. "noise" translate into ROC curves. As the criterion moves from left to right, as shown in the two lower panels, correct detections (CD) and false alarms (FA) move along the ROC curve in the direction of the arrows. As signal and noise become less discriminable, in the bottom panel, performance moves onto an ROC curve with a smaller d.' After Wiley (1994) with permission.

computations are simplest if these distributions are normal with the same variance, as in Figure 3.7. The essential features of these distributions, regardless of their shape, are that *(1)* they overlap, more so the more similar are signal and noise; and *(2)* the value along the stimulus continuum (x-axis) represents the only information about the signal that is available to the perceiver. Thus, many stimuli are inherently ambiguous: the perceiver cannot know whether they represent the noise alone or the signal. All the perceiver can do is to set a decision criterion, a value along the stimulus dimension above which to say "signal" and below which to say "no signal." Once the criterion is set, any of four things can happen: the observer can say "signal" when there is in fact a signal; these responses are termed *correct detections* or *hits.* Inevitably, however, the observer will sometimes say "signal" when there is no signal; such responses are *false alarms.* Saying "no signal" when the signal is in fact absent is a *correct rejection;* "no signal" when a signal is there is a *miss.* Thus there are two kinds of correct responses, and two kinds of errors (Table 3.1). The probability of each is related to the location of the criterion and the overlap between the two distributions as shown in Figure 3.7.

With fixed characteristics of the signal, the background, and the sensory system, correct detections and false alarms change together in a way described by the receiver operating characteristic, or *ROC curve* (Figure 3.7). ROC curves are characterized by their distance from the diagonal that bisects the plot of p(correct detection) versus p(false alarm), represented by the parameter *d′* ("dee prime"). A perceiver with a lower criterion, saying "signal" more often, has more correct detections but necessarily more false alarms (and concomitantly fewer correct rejections) as well. A conservative observer will make few false alarms but concomitantly fewer correct detections. The optimal location of the criterion depends on the relative payoffs for the four possible outcomes described above. For instance, as the payoff for correct detections rises relative to the penalty for false alarms, the criterion should be lower, that is, the observer should respond more often as if the signal is present. The same thing should happen if the observer learns that signals are relatively common. Observers can move onto a ROC curve further from the diagonal, with higher d′ and higher sensitivity, only if the stimuli become more discriminable. This can happen because of changes in the signal, the noise, or the observer's sensory system.

3.4.2 Data

Humans and other species do perform in psychophysical experiments as predicted by signal detection theory. For example, Wright (1972) tested pigeons' ability to discriminate wavelengths in the way depicted in Figure 3.8a. This two-alternative forced-choice experiment was designed to ask the bird whether it perceived both halves of a central pecking key as the same color or as different colors. It pecked a left side key to report

Table 3.1 Possible responses in a signal detection task

		Signal	
		Present	Absent
Response	Yes ("Signal there")	Correct Detection (Hit)	False Alarm
	No ("No signal")	Miss	Correct Rejection

h the same variance, as
gardless of their shape,
and noise; and *(2)* the
nly information about
stimuli are inherently
ent the noise alone or
ion, a value along the
ich to say "no signal."
server can say "signal"
rect detections or *hits.*
vhen there is no signal;
gnal is in fact absent is
s. Thus there are two
1). The probability of
lap between the two

d the sensory system,
vay described by the
7). ROC curves are
the plot of p(correct
ter *d′* ("dee prime").
en, has more correct
itantly fewer correct
alse alarms but con-
the criterion depends
escribed above. For
the penalty for false
hould respond more
if the observer learns
a ROC curve further
f the stimuli become
signal, the noise, or

nents as predicted by
ns' ability to discrimi-
rnative forced-choice
th halves of a central
eft side key to report

bsent
alse Alarm
Correct Rejection

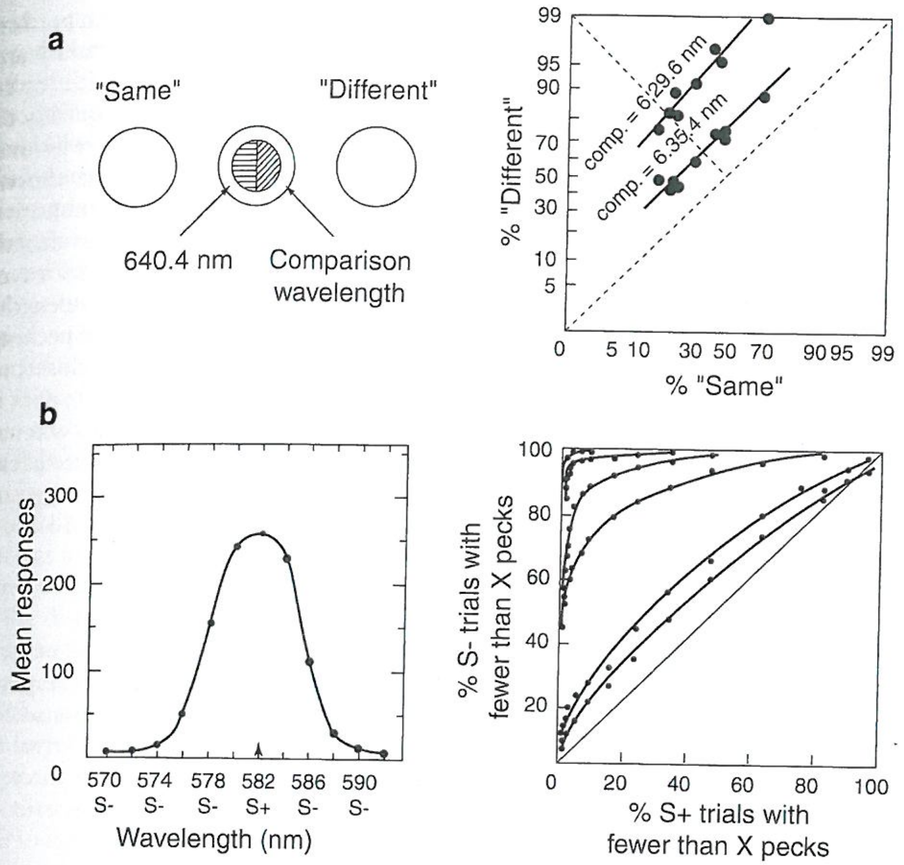


Figure 3.8. a. Method and results of Wright's (1972) experiment on wavelength discrimination in pigeons. The discs are the pecking "keys" referred to in the text. The ROC curves described by the results are plotted as as straight lines on logarithmic coordinates. b. Pigeons' wavelength generalization gradient and derived ROC curves from Blough (1967). Redrawn with permission.

"same" and the right side key to report "different." A bird was occasionally rewarded with food for reporting "same" or "different" correctly. Feedback was always given by briefly turning on a light above the feeder after correct responses but extinguishing all lights in the test chamber after incorrect responses. The bird's criterion for pecking left vs. right was manipulated by varying the probability of reward for correct left vs. right responses. On some sessions it was more profitable to report "same" correctly than it was to report "different," and on other sessions the opposite was true. The pattern of results was exactly as predicted by a signal detection analysis. For each pair of wavelengths, plotting the probability of correctly reporting "different" (i.e., hits) versus the probability of incorrectly reporting "different" (i.e., false alarms) traced out a single ROC curve as the payoffs were varied. For example, when the probability of reinforcement for reporting "different" (pecking the right key) was relatively high, the birds behaved as if adopting a liberal criterion, with a relatively high p(correct detection) accompanied by relatively high p(false alarm). And as indicated in Figure 3.8 a, the more the wavelengths differed, the further from the diagonal was the ROC plot (i.e., the higher the d′).

Wright's procedure for varying the birds' criterion required each bird to complete many trials at each combination of wavelengths and reinforcement probability, but human observers can be asked to apply several criteria simultaneously by reporting the certainty with which choices are made. Responses given with high certainty are assumed to have exceeded a more stringent criterion than those given with lower certainty. Animals can reveal their "certainty" about their choices by how quickly or how much they respond. If the choice keys in a psychophysical experiment are lit for a fixed amount of time on each trial, the number of responses made to the chosen alternative in that time behaves like the human observers' report of subjective certainty. For example, Blough (1967) trained pigeons on a difficult wavelength discrimination. A central pecking key lit up for 30-second trials with one of 13 wavelengths. Pecks at 582 nm were reinforced, but pecks at any of 12 other wavelengths ranging between 570 and 590 nm were never reinforced. The birds' rates of pecking traced out a typical *generalization gradient,* with more pecking to stimuli closest to the positive, or reinforced, stimulus (Figure 3.8b). One way to interpret these data is to say that the lower the rate, the more certain the bird was that the stimulus was not 582 nm. For each nonreinforced stimulus, the proportion of trials with fewer pecks than each of a series of criteria did trace out a ROC curve, just as this notion suggests, with stimuli further from 580 nm giving ROC curves of higher d′ (Figure 3.8b).

3.4.3 Implications for the evolution of animal signals

The examples presented so far have been framed in terms of psychophysical experiments, but signal detection theory applies to any decision whether or not to respond to a signal. The "decision" need not involve performing a learned response for reward. The criterion can represent the threshold for attacking a possible rival or prey item or for displaying to a female. The threshold might be adjusted through evolution or through individual experience. Likewise, evolution and/or experience might adjust the distributions of signal or noise effects, by altering some aspect of the signaler or the sensitivity of the receiver. The payoffs may be in terms of energy wasted, injury risked, food items or mating opportunities gained or lost. Here we consider an example from animal signaling systems. In later chapters we will see how signal detection theory can be applied to other animal decisions (for further discussion and related models see Getty 1995; Sherman, Reeve, and Pfennig 1997; Bradbury and Vehrencamp 1998; Phelps, Rand, and Ryan 2006; Wiley 2006).

Suppose the perceiver is a female bird in the spring, living in an area inhabited not only by males of her own species but by males of another species that look and sound very similar to her species male. Natural selection will have ensured that she is more likely to mate with a male of her own species than with males of other species. To emphasize how signal detection theory applies here, the following discussion refers to the female's decision to mate or not to mate. This means only that the female performs or does not perform some behavior leading to successful copulation and production of young. It does not necessarily mean that she decides in the same way a human observer in a psychophysical experiment decides how to classify a light or a tone. The female's decision mechanism might be as simple as the evolutionarily determined threshold for performing a display that in turn elicits copulation by the male.

The female's problem can be translated into the language of signal detection theory as shown in Figure 3.9 (see also Wiley 2006). Here the signal and noise distributions represent the sensory effects of some male feature or features such as plumage color or song. The "signal" is the distribution from males of the female's own species; "noise" is signals from the other species. The criterion represents the female's threshold for mating

taneously by reporting
with high certainty are
hose given with lower
ices by how quickly or
experiment are lit for a
s made to the chosen
' report of subjective
a difficult wavelength
s with one of 13 wave-
12 other wavelengths
birds' rates of pecking
ng to stimuli closest to
interpret these data is
at the stimulus was not
trials with fewer pecks
as this notion suggests,
r d′ (Figure 3.8b).

psychophysical experi-
ther or not to respond
learned response for
ing a possible rival or
it be adjusted through
tion and/or experience
ring some aspect of the
be in terms of energy
ained or lost. Here we
apters we will see how
ons (for further discus-
e, and Pfennig 1997;
06; Wiley 2006).
n an area inhabited not
ies that look and sound
nsured that she is more
es of other species. To
ing discussion refers to
only that the female
cessful copulation and
cides in the same way a
to classify a light or a
as the evolutionarily
elicits copulation by

gnal detection theory as
and noise distributions
ch as plumage color or
own species; "noise" is
e's threshold for mating

with a male, although in fact successful copulation is not usually the result of a single response on the part of either male or female. Correct detections result in viable, fertile offspring, the ultimate evolutionary payoff. False alarms waste reproductive effort. Because many birds lay just one clutch of eggs in a season and may not live long past their first breeding season, incubating eggs and feeding young that do not eventually put their parents' genes into the next generation does represent a considerable cost, putting pressure on females to adopt high criteria. On the other hand, too many missed detections of conspecific males means that the breeding season may pass or all males become mated before the female mates at all, so some false alarms may be worth the risk. In cases where the costs and benefits of each possible outcome can be quantified, the optimal criterion can be derived (see Chapter 14 in Bradbury and Vehrencamp 1998). An informal analysis nevertheless provides two important insights (Wiley 1994).

First, whatever their criterion, females are stuck with at least some false alarms and missed detections unless something reduces the overlap of the signal and noise distributions, that is, moves the female onto an ROC curve of higher d′. This can occur in two ways. The two distributions can stay the same shape while their means move further apart (Figure 3.9). This might represent the case of males of the two species in our example evolving more differentiated songs or displays, a phenomenon referred to as *character displacement.* The female's discrimination will also improve if the distributions become narrower while the means remain the same. This might represent the case of changes in the female's sensory system that, for example, sharpen her sound or color discrimination ability. She might also pay more attention to the parts of the signal that best differentiate the species. The distributions of sensory effects from the males could also sharpen if the males evolve to broadcast their signals more effectively. For example they might sing from more exposed perches so their songs are degraded less before reaching the female.

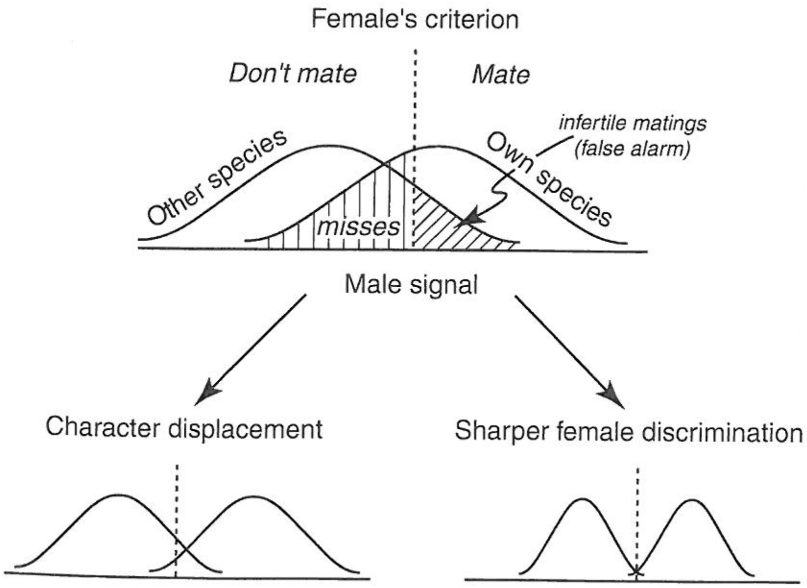


Figure 3.9. Signal detection theory applied to mate choice, showing how false alarms (infertile matings) can be reduced either by males evolving more discriminable characteristics or by females evolving better discrimination.

The second insight afforded by a signal detection analysis of mating signals is that in a situation like that depicted in Figure 3.9, where the signals of two species overlap, the males successful in achieving matings will have a more extreme distribution of signal characteristics than the distribution in the population. That is to say, they will have exaggerated signals, and in fact this is often true (Ryan and Keddy-Hector 1992). As long as the male features that release female sexual behavior are at all similar between species living in a given area (*sympatric* species), the typical payoff matrix for this situation means that females should reject the conspecific males most similar to males of the other species. Therefore the average acceptable male will differ more from males of the other species (or from background noise of whatever sort) than from the average male of the species. If the male characteristics that elicit sexual responses in females are heritable, over generations this process will cause the average male to differ in a more and more extreme way from males of sympatric species and/or from the environmental background.

Exaggerated features elicit greater than normal responses in systems other than sexual behavior. Egg retrieving in the herring gull provides a classic example. An incubating herring gull that sees an egg placed just outside its nest uses its beak and neck to roll the egg into the nest. The Dutch ethologist Baerends and his colleagues (Baerends and Kruijt 1973) presented gulls with pairs of artificial eggs differing in size, color, or speckling and recorded which one of each pair the gulls chose. The preferred size and number of speckles were both greater than the values typical of the study population. The preferred values were combined in a giant, densely speckled egg to create a *supernormal releaser* of retrieval, an egg which the gulls preferred to a normal egg. Comparable effects of supernormality are found in other species of ground nesting birds (Figure 3.10). One might speculate that they appear when selection pressure works to sharpen a discrimination in only one direction. For example, presumably it is important not to retrieve a lot of noneggs. The activity wastes energy (beaks not being very efficient retrieval tools) and extra objects

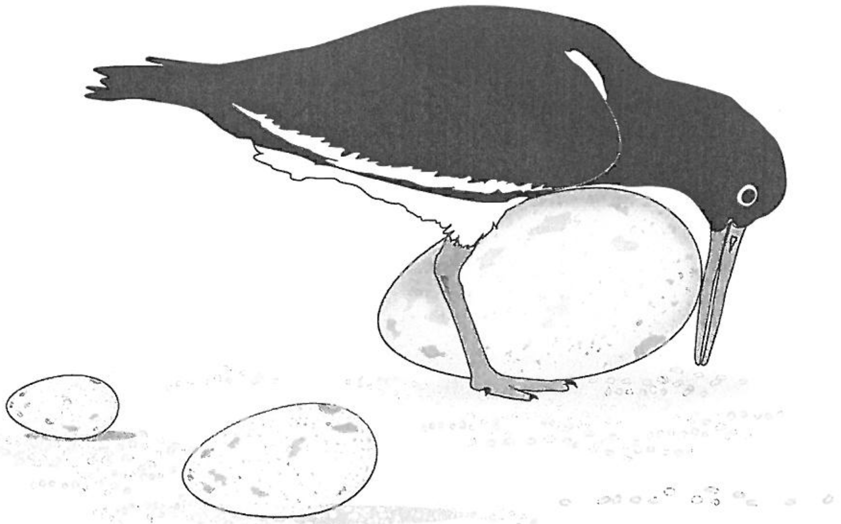
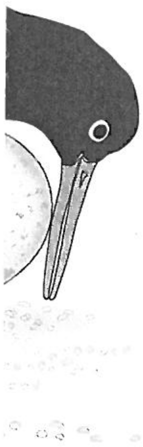


Figure 3.10. Oystercatcher attempting to incubate a supernormal egg. The egg on the left is a normal oystercatcher egg; the one to its right is a herring gull egg. After Tinbergen (1951) with permission.

f mating signals is that
of two species overlap,
xtreme distribution of
'hat is to say, they will
an and Keddy-Hector
ial behavior are at all
es), the typical payoff
onspecific males most
ptable male will differ
oise of whatever sort)
istics that elicit sexual
will cause the average
sympatric species and/

in systems other than
s a classic example.
its nest uses its beak
ist Baerends and his
airs of artificial eggs
of each pair the gulls
eater than the values
combined in a giant,
val, an egg which the
ormality are found in
it speculate that they
ion in only one direc-
a lot of noneggs. The
ols) and extra objects



g on the left is a normal
1951) with permission.

cluttering the nest mean less room for eggs and chicks. A discrimination in favor of supernormal eggs may indicate that over evolutionary time the typical nesting habitat contained more small, plain, dull than large, colorful, speckly noneggs, leading to a bias in favor of retrieving the largest, most speckly object in sight. An analogous phenomenon in discrimination learning is peak shift (see Chapter 6 and Ghirlanda and Enquist 2003).

3.5 Perception and evolution: Sensory ecology

Some of the most important sensory information animals have to process comes from other animals. Interactions between predators and prey, parents and offspring, males and females both shape and are shaped by the characteristics of sensory systems. Together with the features of the environment that determine the most effective channels for communication, the senses of their conspecifics and predators influence animals' behavior, appearance, and lifestyle. Unrelenting competition to detect the best habitat, food, and mates constantly selects for animals able to make sharp discriminations. The area of behavioral ecology that deals with these issues is sometimes called *sensory ecology*. Studies at the frontiers of sensory ecology combine physics, neuroscience, and molecular phylogeny with behavioral ecology to understand the evolution and present-day distribution of sensory abilities in terms of the stimuli animals are actually processing in nature (e.g., Bradbury and Vehrencamp 1998; Ghazanfar and Santos 2004; Endler and Mielke 2005; Endler et al. 2005; Fleishman, Leal, and Sheehan 2006). The rest of this section discusses two comparatively simple examples of the interrelationship between perception and the evolution of signals which illustrate how experimental and comparative methods, laboratory and field studies, sensory psychology and behavioral ecology can be integrated to shed light on the evolution and normal functioning of animal signaling systems.

3.5.1 Predators and prey

Most animals are subject to two conflicting selection pressures: be inconspicuous to predators but be conspicuous to selected conspecifics. One of the best illustrations of how the tradeoff between these pressures has influenced signals and behavior involves the color patterns and mating behavior of guppies (Endler 1991; Houde 1997). Guppies (*Poecilia reticulata*) are small South American fish that live in clear tropical streams. Mature males sport colored spots and patches that are used in courtship behavior. Male color pattern is heritable and varies in different populations. In experimental tests of the effectiveness of color patches, females are more likely to mate with males that have larger and brighter blue and orange, red, or yellow patches. Thus female choice creates sexual selection pressure for conspicuous coloration. In contrast, predators create selection pressure for cryptic coloration: duller, smaller, color patches, and patterns that match the background.

The effects of predation have been established in several ways. In the field, guppies are found in streams that have different numbers and kinds of visually hunting, diurnal predators, mostly other fish. Males from populations with more predators are more cryptically colored. Prawns are thought to see poorly in the red end of the spectrum. As might therefore be expected, guppies in areas with heavy predation by prawns have more orange than guppies subject to predators with better red-orange vision (Millar, Reznick, Kinnison et al. 2006). Predictions about the effects of predation have been tested directly by establishing guppies from a single genetic background and distribution of color patterns in laboratory "streams" and exposing them to different numbers and kinds of predators. In guppies' natural habitat of forest streams, the intensity and wavelength of light varies with the time of day (Figure 3.2). Visually hunting predators are most active in the middle of the day, but in both the laboratory and the field, guppies engage in more sexual display early and late in the day, that is, in relatively dim light. Taken all together, the transmission characteristics of tropical streams and the visual capabilities of guppies and their most common predators indicate that at the times of day when they are most likely to be courting, guppies' colors are relatively more conspicuous to other guppies than to guppy predators (Endler 1991; Millar et al. 2006).

The foregoing example illustrates how visual conspicuousness and crypticity are literally in the eyes of the beholder. Detailed sensory physiology may be needed to figure out whether color patterns that appear conspicuous or cryptic to us appear that way to the animals that normally view them (for examples see Endler and Mielke 2005; Fleishman, Leal, and Sheehan 2006). A particularly nice example involves camouflage of crab spiders (Thery et al. 2005). Crab spiders make their living sitting on flowers waiting to grab bees or other pollinators that happen by. But by resting in such an exposed position, the spiders make themselves conspicuous to insectivorous birds. Clearly, they should be colored so as to be inconspicuous to both birds and bees, but this is not easy because bees and birds have different color sensitivities (see Box 3.1). Thery and colleagues (2005) collected crab spiders (*Thomisus onustus*) from the yellow centers of white marguerite daisies and measured the relative intensities of wavelengths across the spectrum, including the ultraviolet, reflected by daisy petals and centers and by crab spiders. The daylight reflectance spectra were then related to the color sensitivities of birds (blue tits, typical predators in the French meadows where the spiders were collected) and honeybees. These computations showed that the spiders' color did not contrast sufficiently with the flower centers for them to be detected by either predator or prey. Their contrast with the petals was well above both birds' and bees' thresholds, which presumably selected for spiders to rest in the center. To make matters even more interesting, individuals of this species of crab spider also match their color to pink flowers, and they are similarly of low contrast to both birds and bees on this background as well (Thery and Casas 2002). To human eyes, Australian crab spiders (*T. spectabilis*) are cryptic on white daisies, but from a honeybees' point of view they are highly visible because they reflect much more UV than the daisy petals. Bees are actually attracted to flowers with these UV-reflecting spiders, apparently expressing a general preference for flowers with contrasting markings (Heiling, Herberstein, and Chittka 2003).

3.5.2 Sensory bias and sexual selection: Frog calls and fish tails

Darwin (1871) was the first to discuss an evolutionary puzzle that is still being debated today: why do males of some species have secondary sexual characters so large or conspicuous that they must be detrimental to survival? Natural selection would be expected to mitigate against cumbersome antlers and extraordinarily long brightly colored tails, so why do such exaggerated characters persist? Darwin's answer was that such ornaments evolve because females prefer them: the force of sexual selection outweighs the forces of natural selection. Roughly speaking, sexual selection occurs due to greater reproductive success of individuals preferred as mates by the opposite sex; in most cases females do the choosing, driving appearance and

rom a single genetic
reams" and exposing
tural habitat of forest
ie of day (Figure 3.2).
day, but in both the
early and late in the
ission characteristics
their most common
likely to be courting,
ppies than to guppy

ss and crypticity are
gy may be needed to
ptic to us appear that
e Endler and Mielke
ce example involves
ke their living sitting
by. But by resting in
ious to insectivorous
us to both birds and
nt color sensitivities
(*Thomisus onustus*)
ed the relative inten-
et, reflected by daisy
e spectra were then
dators in the French
These computations
h the flower centers
t with the petals was
elected for spiders to
uals of this species of
are similarly of low
ry and Casas 2002).
tic on white daisies,
se they reflect much
wers with these UV-
or flowers with con-

e that is still being
sexual characters so
l? Natural selection
xtraordinarily long
s persist? Darwin's
them: the force of
ly speaking, sexual
s preferred as mates
ing appearance and

---

behavior of males. A central question in this area is "What is the evolutionary cause of the observed patterns of female choice, in particular, females' preference in many species for exaggerated male characters?" There are several answers. As explained next, each may be correct for some situations (Andersson 1994; Maynard Smith and Harper 2003; Searcy and Nowicki 2005).

It is not particularly problematic why females may prefer male characters correlated with large size, good health, or—in species with biparental care—ability to help rear the young. For example, growing bright glossy feathers may be possible only if you can get enough of the right foods to eat and resist diseases and parasites. Such characters may signal that the male has "good genes" that allow him to be strong and healthy and/or provide resources for a female and her offspring. Genes for preferring males that are better fathers would spread because daughters of females with these genes would inherit preference for better fathers, sons would inherit the genes for being better fathers, and by definition better fathers have more offspring than poor ones. A preferred character of this sort might become exaggerated through evolution as discussed in Section 3.4.3, but it and the females' response to it are selected because it indicates male quality.

The "runaway" hypothesis of sexual signal evolution specifically accounts for signals that seem to have no intrinsic relationship to male quality. It is essentially Darwin's suggestion buttressed by mathematical modeling. Informally stated, if at some stage in evolution females by chance preferred an arbitrary male character, females with the preference and males with the character could come to dominate the gene pool, in a runaway positive feedback process. On this scenario, the female preference and the male character evolved together, and the preferred male character need not be correlated with male quality.

But what gets selection on such a character started in the first place? One prominent suggestion is that preexisting features of females' sensory systems or perceptual preferences make such characters especially attractive, a suggestion known as the sensory bias hypothesis (Ryan 1994; for discussion of the many different terms and ideas in this area see Endler and Basolo 1998). Some kind of arbitrary bias is needed to get runaway selection started, but the sensory bias theory has been thought to make at least two unique predictions (Fuller, Houle, and Travis 2005; Searcy and Nowicki 2005). First, female sexual preferences evolved before male characters. This possibility can be tested with comparative behavioral data and phylogenies. Second, a preference expressed in a sexual context may have a function in another context such as feeding or predator avoidance. For instance, male lizards of the species *Anolis auratus* start their sexual display with a rapid up and down motion of the head (Fleishman 1988). Sudden motion attracts attention in many contexts, and for good reason, as it could indicate a live prey item or an approaching predator. The sexual display of the male water mite *Neumania papillator* includes waving his appendages in a way that mimics the motion of prey items, and in fact hungry females are more likely than sated ones to respond to displaying males (Proctor 1992). The strong attraction of both male and female guppies to orange fruits suggests that the orange spots of male guppies similarly exploit a feeding preference (Rodd et al. 2002; but see Millar et al. 2006). By implication, in these cases responsiveness evolved first in the nonsexual context and males have been selected to exploit it in the sexual context. Cladistic analysis (Chapter 2) has supported this conclusion for water mites.

In all the foregoing examples the chief evidence that a more general preference is reflected in sexual signaling is the observation that all members of the species show it. For instance, whether breeding or not both male and female guppies are attracted to orange fruits (Rodd et al. 2002). When instead phylogenetic inference is the main support for a hypothesized preexisting bias, conclusions are very much dependent on the number of species used to collect behavioral data and to construct the phylogeny on which conclusions about signal evolution are based. This important point is illustrated very well by two of the original candidates for signals evolved through sensory bias. One is the swordlike extension on the tails of male swordtail fish (Ryan and Rand 1995; for another example see Garcia and Ramirez 2005). Female swordtails prefer long swords over short ones (Basolo 1990a; Basolo 1990b). Platyfish are a group of swordless species that share a common ancestor with swordtails (Figure 3.11), and females of a swordless platyfish species prefer males with swords as sensory bias predicts. Now the question for a phylogenetic analysis is whether the most recent common ancestor of swordtails and platyfish had a sword or not. The best phylogeny available when Basolo made her discovery (Figure 3.11top), indicates that swordlessness is ancestral, and therefore preference for swords must have evolved before swords. However, a later phylogeny based more heavily on similarities in DNA (Figure 3.11bottom) seems to indicate that swords were ancestral and have been gained and lost several times within the swordtail-platyfish group (Meyer, Morrissey, and Schartl 1994). But even newer behavioral data reveals that in a species

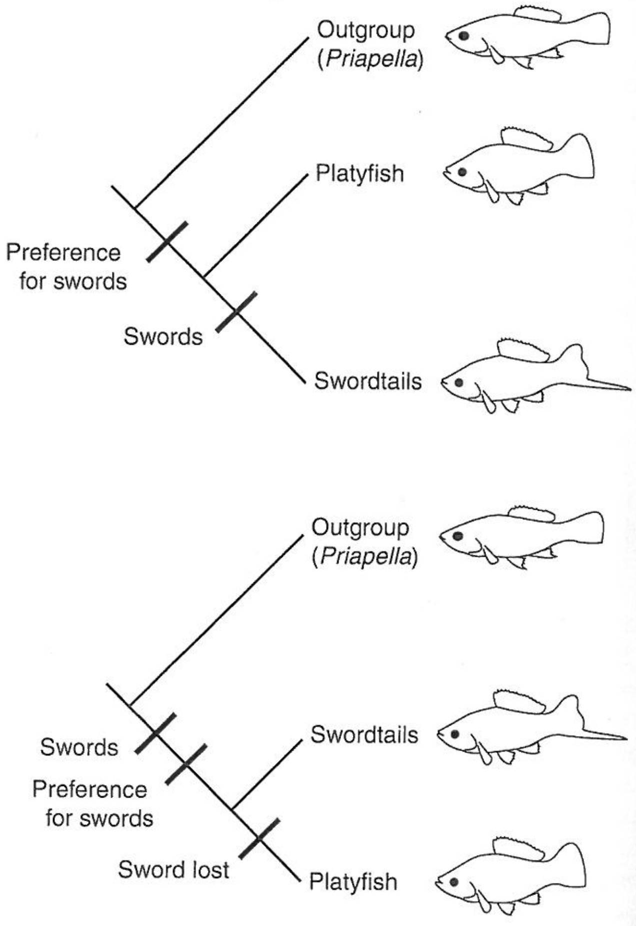
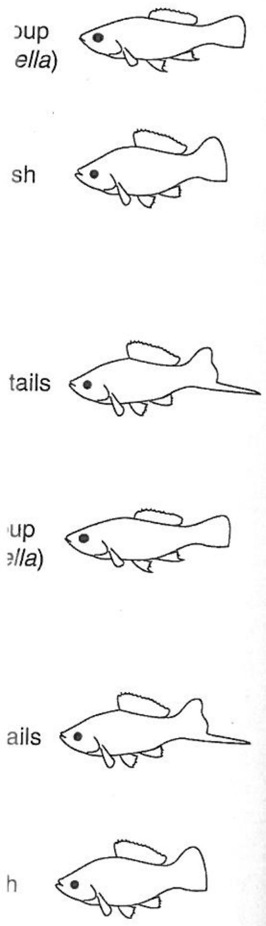


Figure 3.11. Possible alternative pathways for the evolution of swords and sword preference in swordtails and platyfish. The phylogenies are simplified, since each branch actually contains numerous species. Adapted from Basolo (1995a) with permission.

c inference is the main
ery much dependent on
onstruct the phylogeny
his important point is
ignals evolved through
le swordtail fish (Ryan
2005). Female sword-
1990b). Platyfish are a
estor with swordtails
efer males with swords
analysis is whether the
d a sword or not. The
ure 3.11top), indicates
or swords must have
e heavily on similarities
ere ancestral and have
atyfish group (Meyer,
reveals that in a species



in the outgroup for this phylogeny, that is, the closest relative of both swordtails and platyfish, females also prefer males with swords (Basolo 1995b; but see Basolo 2002), indicating that preference for swords predated any evolution of swords.

The call of the male túngara frog, *Physalaemus pustulosus,* is another male mating signal hypothesized to have evolved through exploiting the sensory bias of females (Ryan and Rand 1993). In this case tests of the sensory bias hypothesis have included physiological studies of the frogs' auditory system as well as behavior and phylogeny. The call of the male túngara frog contains a whine followed by a number of lower-pitched chucks. The whine is necessary and sufficient for mate recognition, but the addition of chucks enhances the attractiveness of the call to females in choice tests in the laboratory. Chucks contain predominantly the frequencies to which the female frog's inner ear is most sensitive, suggesting that chucks might be quite stimulating to females generally, even though males of closely related species do not add chucks to their calls. This proved to be the case with the first set of species studied. Females of the closely related species *P. coloradorum* responded more to *P. coloradorum* calls with added chucks than to unaltered calls. Thus they have a preference for calls with chucks, which they normally do not express because males of their species do not chuck. Phylogenetic analysis based on characters other than male mating calls initially indicated that the chucks are recently evolved, as the sensory bias hypothesis requires (Ryan and Rand 1993). Accordingly, the frog calls became a key example of signal evolution through sensory bias. However, when more species are included in both the phylogeny and the tests of auditory sensitivity and female preference, the pattern is inconsistent with preexisting sensory bias. Instead, female preference and male calls seem to have coevolved, implying that some degree of central decision making is involved in the females' choice (Ron 2008; see also Phelps, Rand, and Ryan 2006). Although this tale may not be all told yet, it illustrates very well the much more general principle that conclusions about the evolution of cognition and/or the role of cognition in evolution depend on testing plenty of species and having good information about the relationships among them. The latter, in particular, depends heavily on how many and which species are included in the analysis (see Ron 2008).

3.6 Search and attention

At any given moment, most of the surrounding environment is irrelevant for current behavior. For example, as you read this book, you may be drinking a cup of coffee and playing your stereo, but neither the taste of coffee nor the sound of music is relevant for the task at hand. For some species, like the *Bembyx* moth, the problem of selecting what parts of the world to respond to has been solved by the evolution of specialized sensory channels and stimulus coding mechanisms ensuring that the moth senses only the few things in the world that matter for survival and reproduction. But such reliable coding limits flexibility. Animals like birds, monkeys, and human beings that can perceive a wide range of stimuli from several sensory modalities need a way to ensure that, for example, they switch appropriately from looking for food at one moment to looking for a safe refuge at another. Attention is one process that does this selecting. Motivational processes may play a role too, for example by changing thresholds for responding to relevant stimuli with physiological state.

Concentrating on reading while doing other things illustrates how attention is used as a filter, deployed in this case in a top-down manner (i.e., through some internal decision process). But attention doesn't necessarily filter out all but one set of cues. A door slamming, or someone calling your name can grab attention (an example of a bottom-up or externally driven switch of attention). In these examples, attention has the beneficial effect of ensuring that the important things of the moment are processed best. But attention also has a cost: if we actually listen to the radio while reading, we'll get less out of the reading (and vice versa) than if we do one thing at a time. Why attention is limited is a much debated theoretical question. Obviously it sometimes solves the problem of animals not being able to do two physically incompatible things at once, such as search for food and watch for predators, but this does not explain why it should not be possible, for example, to search for two kinds of food as efficiently as for one or to read while listening to the radio. This property of attention may reflect basic limitations on the size of the brain due to the metabolic costs of neural tissue (Dukas 2004). Traditional psychological theorizing similarly assumed a limitation on perceptual processing resources or a bottleneck in more central processing, but contemporary theorizing has identified alternative possible mechanisms, some of them better specified (Luck and Vevera 2002). But rather than advancing any general theory, research on attention in nonhuman species has primarily aimed to establish effects similar to those found in people (Section 3.6) and show how attention plays a role in ecologically relevant behavior (Section 3.7).

3.6.1 Visual search: The basics

Much data and theory on attention in humans is based on research with visual stimuli (Luck and Vevera 2002). Comparable experiments with highly visual animals, primarily monkeys and birds, indicate that basic attentional processes are shared across species (reviews in Blough 2001; Zentall 2005b; Blough 2006). Clearly, however, the important things in life are sometimes defined by sound, smell, or other nonvisual stimuli. For example, a father penguin returning to the colony with food needs to be able to pick out his mate's or baby's calls from those of hundreds of others (Aubin and Jouventin 2002). Such *auditory scene analysis* has been extensively studied in the context of animal vocal communication (Hulse 2002). It is also important in understanding how bats distinguish prey-generated echoes from background noise (Moss and Surlykke 2001). However, because the most detailed analyses of animal attentional processes have addressed visual attention, that will be the focus here.

In visual search tasks (Schiffrin 1988; Treisman 1988) as the name implies, the subject searches for something by looking for it. The thing being searched for is referred to as the *target*. It is embedded among other items, the *distractors*. Figure 3.12a shows a typical example for a human subject, a target X among distracting Os, and one that might confront a visual granivorous predator, a black seed among white pebbles. No one reading this book would fail to find the X or the seed in Figure 3.12a, but suppose the figure had been flashed for a fraction of a second or the distractors were much more similar to the target, say Ys instead of Os surrounding the target X. Now the results would start to be interesting. Under these sorts of conditions, with limited viewing time or high similarity between target and distractors, subjects may make mistakes and/or take longer to find the target.

In Figure 3.12a, the target X seems to "pop out" from the background of Os. The same would be true if the target were a yellow X among red Xs or a moving dot among stationary ones. The pop out effect is evident in data from visual search tasks

ıe can grab attention
f attention). In these
that the important
so has a cost: if we
of the reading (and
is limited is a much
ves the problem of
things at once, such
not explain why it
nds of food as effi-
o. This property of
e brain due to the
psychological theo-
ssing resources or a
ıeorizing has identi-
specified (Luck and
, research on atten-
h effects similar to
ion plays a role in

research with visual
with highly visual
ttentional processes
05b; Blough 2006).
defined by sound,
uin returning to the
r baby's calls from
uch *auditory scene*
mal vocal commu-
g how bats distin-
nd Surlykke 2001).
tentional processes

e name implies, the
eing searched for is
ns, the *distractors.*
a target X among
ıs predator, a black
to find the X or the
fraction of a second
Ys instead of Os
esting. Under these
between target and
d the target.
ground of Os. The
s or a moving dot
visual search tasks

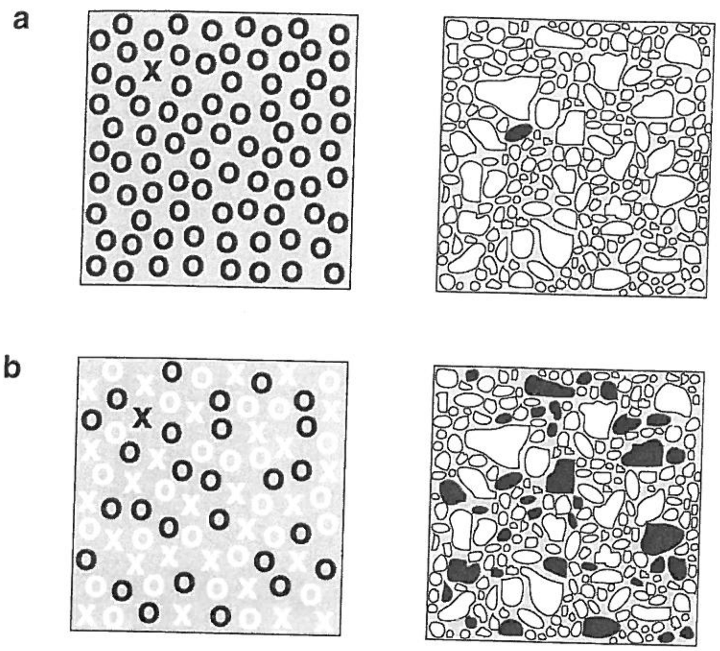


Figure 3.12. Typical stimuli for visual search experiments. a. Targets defined by a difference in one feature (shape or color) "pop out" from the background. b. Conjunctively defined targets, the black X and the black grain, take longer to find. Panels on the right adapted from Dawkins (1971) with permission.

in the fact that with such displays reaction time (latency to detect the target) increases only slightly with the number of distractors (Figure 3.13). In contrast, when the target is defined by the conjunction of two features, for example a black X or among black Os together with white Xs and Os (Figure 3.12b), reaction time increases sharply with the number of distractors. One interpretation of this pattern of data is that when target and distractors differ in just one feature, the objects in the display are processed in parallel, that is, all at the same time. When the target is defined by a conjunction of features, the items have to be processed serially, that is, one by one. With conjunctive targets, the times taken to decide "no, the target is not there" support this interpretation. Every item in the display must be mentally inspected in order to decide the target is absent. It will take twice as long on average to say (correctly) "No target" than to locate the target (Figure 3.13). The fact that the functions relating reaction time to number of distractors are straight lines indicates that processing each additional item takes a constant amount of time (Treisman and Gelade 1980).

3.6.2 Feature integration theory

Treisman's (1988, 1999) interpretation of results like those just described is that elementary features of objects such as shape, color, and motion are registered automatically without needing attention (preattentively). Identifying visual objects consisting of a conjunction of features requires that the object's location in space become the focus of attention and the features perceived there be integrated. Some of the evidence in support of Treisman's feature integration theory comes from experiments in which subjects are briefly shown a circular display of colored letters and asked to

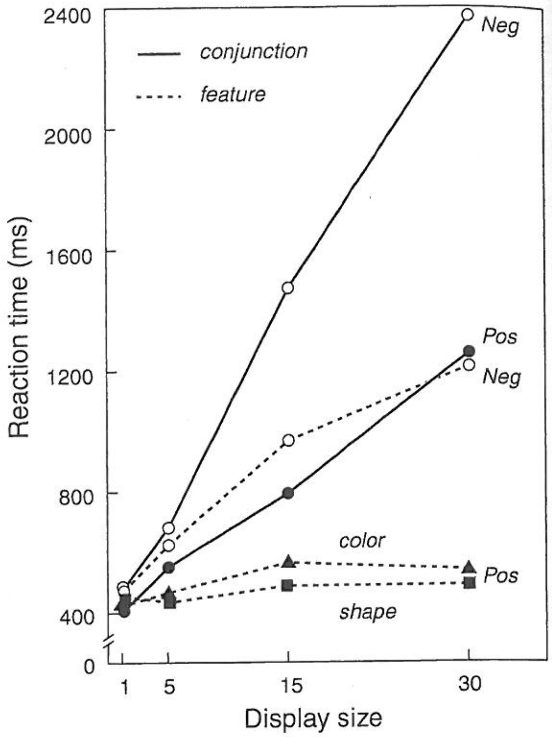
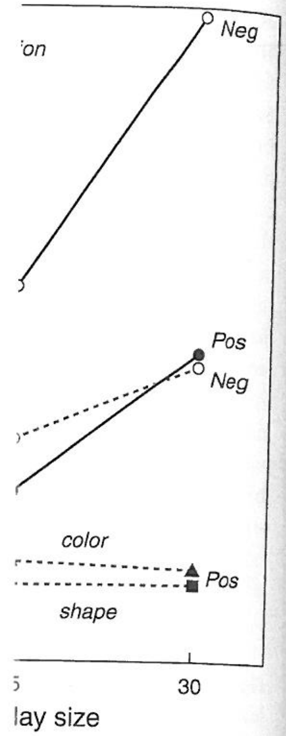


Figure 3.13. Human subjects' latencies to respond correctly in visual search experiments with a target defined by a single feature or a conjunction of features as a function of display size. On positive trials (Pos) the target was present; it was absent on negative (Neg) trials. Redrawn from Treisman and Gelade (1980) with permission.

report the color, the shape, or both the color and shape of the letter in one location. The probability of correctly reporting the conjunction of features is predicted almost perfectly by the probabilities of correctly reporting color and shape separately (Treisman 1988). This pattern of data is consistent with the notion that the object's features are first processed independently rather than as a unit. Moreover, identifying a conjunctive target is strongly associated with reporting its location correctly, as if objects are perceived as a spatial conjunction of independently processed features.

Another way to demonstrate the processes in feature integration is texture segregation. The idea behind texture segregation is that a cluster of identical objects is perceived as a distinct object in itself. As can be seen in Figure 3.14, the distinction between elemental and conjunctive targets is just as evident here as with individual targets: areas defined by a difference in one element, such as a cluster of white objects among black ones, pop out. Areas defined by a conjunction of elements, such as a cluster of white squares and black circles among white circles and black squares, take time to detect. Data from both humans and pigeons support this conclusion (Treisman and Gelade 1980; Cook 2001b).

In the experiments with pigeons (see Cook 2001b; Cook 1992a), birds were trained to peck at displays on a video monitor surrounded by an array of infrared emitters and detectors. This "touch frame" was positioned so that when the bird pecked at the TV screen its beak broke two infrared beams crossing the screen at right angles, and information about the location pecked was transmitted to the computer controlling the stimuli and reinforcers. The screen was covered with rows of small shapes, with one square about a quarter of the screen's area having different shapes from the rest



letter in one location.
features is predicted
ing color and shape
stent with the notion
rather than as a unit.
ciated with reporting
atial conjunction of

ation is texture segre-
of identical objects is
e 3.14, the distinction
ere as with individual
luster of white objects
of elements, such as a
nd black squares, take
port this conclusion

2a), birds were trained
f infrared emitters and
bird pecked at the TV
at right angles, and
computer controlling
of small shapes, with
shapes from the rest

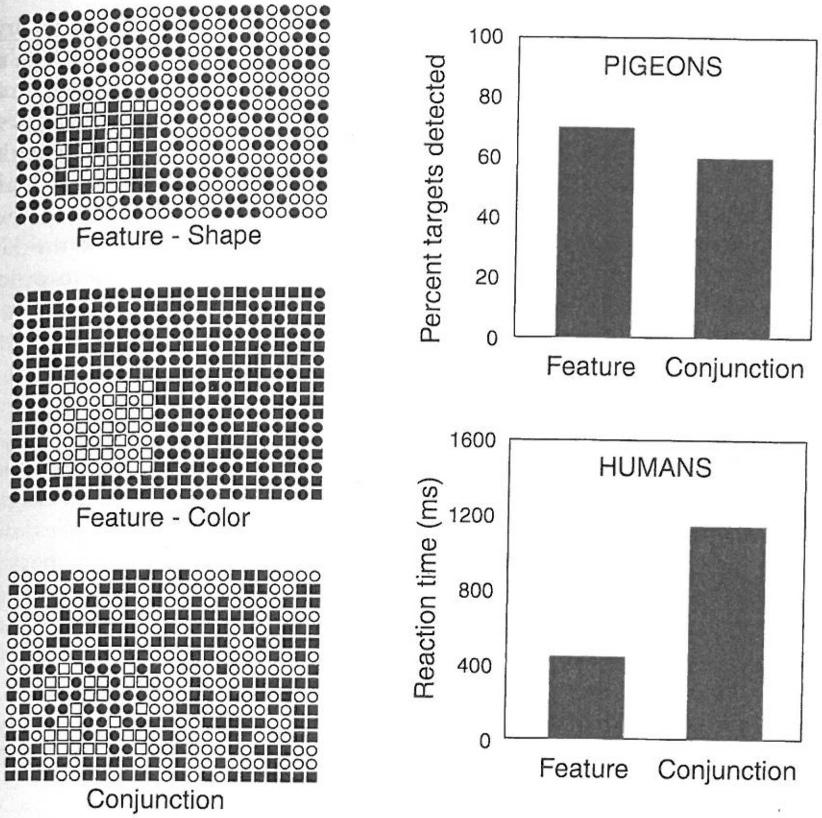


Figure 3.14. Stimuli used to study texture segregation by pigeons and humans and both species' performance with simple ("feature") and conjunctive targets. Data from Cook (1992b); stimuli reproduced from the same article with permission.

(Figure 3.14). The birds were reinforced with food for pecking five times anywhere on this rectangle; one peck elsewhere caused the screen to go dark and postponed the next trial. The pigeons were trained at first with a relatively small number of different small shapes and colors defining the target rectangle and just a few target positions, but they continued to perform well above chance when novel shapes, colors, and positions were introduced. These data alone suggest that, like humans, the pigeons perceived the cluster of distinctive items as "an object" and that they had learned "peck the object," not "peck the training items." Most importantly, targets defined by a difference in a single feature were consistently detected more accurately than targets defined by a conjunction of features. Cook (1992b) tested humans with the same displays as the pigeons. The pattern of results was the same, except that whereas the pigeons showed differences mainly in accuracy of detecting the target areas, people showed differences in reaction time (see Figure 3.14). Nevertheless, these data compellingly indicate that at least this one animal species, evolutionarily and neurologically very different from us, shares the same kind of elemental processing in the early stages of vision (review in Blough and Blough 1997; Blough 2001).

Feature integration can be contrasted with the Gestalt approach to perception, in which perception of the whole is primary and analysis into parts comes later. It also contrasts with the influential approach of J. J. Gibson (1979), which emphasizes the importance of ecologically relevant wholes. For instance, the spatial structure of the environment is immediately evident in the way objects move relative to each other when the observer moves: nearby objects move across the visual field faster than those farther away. The contrast between elemental and holistic approaches pervades theoretical debates about many cognitive processes. Feature integration theory assumes a modular organization of perception in that there is a separate module for processing each stimulus dimension. In evolution, modular organization would permit the ability to process additional dimensions to be added onto an initially simple perceptual system. Similarly, in a modular system the ability to process a feature of particular importance for a given species can be fine-tuned without affecting processing of other features.

3.6.3 Attention in visual search.

In experiments like those just described, visual search is used to test focused attention, that is, the subject searches for one thing at a time. The question being investigated is how the distractors in the visual display do just what their name implies, namely distract the subject from finding the target as rapidly and accurately as possible. If target and distractors are very different, the popout effect occurs and the number of distractors does not matter. But with increasing similarity between target and distractors, even when the subject searches for just one type of target reaction times increase (or accuracy decreases) as the number of distractors (the *display size*) or the similarity of the distractors to the target increases. The data from search for conjunctive targets in Figure 3.13 illustrate effects of display size in humans. Figure 3.15 illustrates comparable effects of similarity and display size for pigeons.

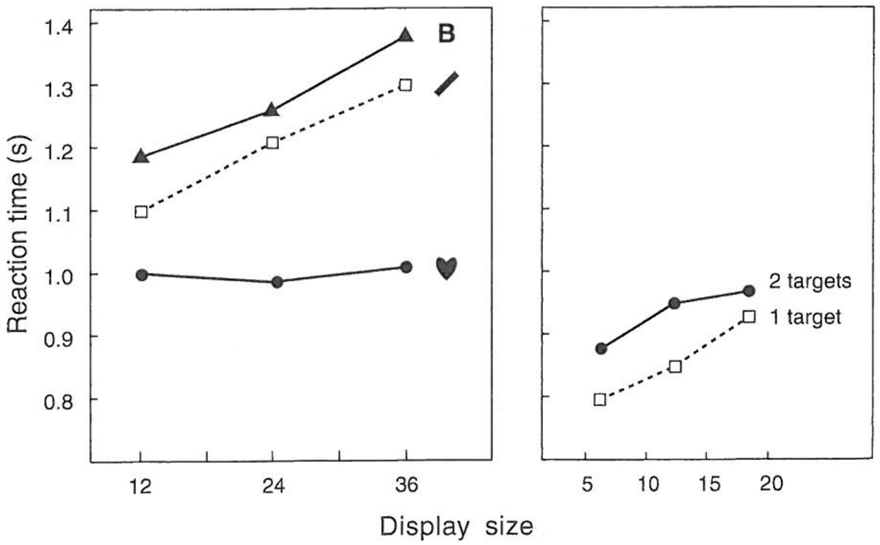
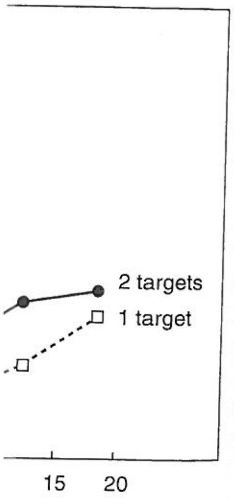


Figure 3.15. Effects of display size (number of items) and target-distractor similarity (left) or memory set size (right) on visual search in pigeons, as measured by time taken to locate the target (reaction time). Left panel redrawn from P. Blough (1992) with permission; the distractors were standard alphanumeric characters, hence the heart shape was the least similar and "popped out." Right panel, one pigeon's data from P. Blough (1989), redrawn with permission.

e spatial structure of the
ve relative to each other
ual field faster than those
ic approaches pervades
ture integration theory
is a separate module for
lar organization would
added onto an initially
the ability to process a
ne-tuned without affect-

to test focused attention,
ion being investigated is
r name implies, namely
ccurately as possible. If
curs and the number of
between target and dis-
of target reaction times
(the *display size*) or the
a from search for con-
in humans. Figure 3.15
r pigeons.



r similarity (left) or
aken to locate the target
n; the distractors were
nilar and "popped out."
ission.

Figure 3.15 also illustrates the effects of number of possible targets used in a series of trials, the memory set size. In human subjects, too, search slows as the number of potential targets increases. Subjects searching for just one sort of target are like specialist foragers, animals that eat only one kind of thing, whereas subjects for which targets are mixed unpredictably are like generalists, foragers that can eat several kinds of prey. The decrease in performance with a larger memory set size is a cost of being a generalist. If the targets were food items, the benefit to generalists of being able to eat more of what they encounter might have to be traded off against this cost. However, the detrimental effect of memory set size diminishes with extended practice. That is, search becomes automatized as if attention is automatically drawn to items that have frequently been attended to (Schiffrin 1988). With pigeons, too, the effect of display size on search accuracy disappears after extended training, but only with a comparatively small set of potential targets (Vreven and Blough 1998). These findings suggest that generalizing might not have a cost in the wild once animals are familiar with all available items.

The effect of memory set size means that a given target is found more quickly or accurately when it is the only one presented over a series of trials than when it is unpredictably mixed with one or more other targets. Finding one target of a given type *primes* attention to targets of that type. Priming is thought of as a transitory activation or facilitation of processing of the target's features. Priming can occur either sequentially as just described, or associatively. In associative priming, performance is facilitated by presenting a cue that has been associated with the target, either just before or during presentation of the target. For example, in a further part of the study whose results are displayed in Figure 3.15, distinctive borders were added to the stimulus displays. Black and white were paired with A and L, respectively; a striped border, paired equally often with A and L, served as an ambiguous cue (P. Blough 1989; D.Blough 1991). Performance with each letter was better when it was cued than otherwise. If each target is paired consistently with a particular distractor, the distractors themselves may serve as associative priming cues (Blough 1993a).

Priming seems not only to facilitate processing of the primed target, but to inhibit processing of unprimed targets. In P. Blough's (1989) experiments, performance on occasional test trials in which A appeared when L was cued or vice versa was worse than on trials with the ambiguous cue. Pigeons can also be primed to attend to particular areas of a display (Blough 1993b). These data on priming seem to suggest that if foraging is like visual search for prey scattered on a substrate of distractors, as Figure 3.12 was made to suggest, any sources of information about the identity of the prey aid search (Blough 1993a). These include what prey have been found recently (sequential priming), where they have been found (priming by locations), and what substrate they were found on (associative priming). It is not yet clear, however, whether these different sources of priming all work in the same way. When sequential and associative priming are combined, they do not always have the strictly additive effect that would be expected if both enhance the same attentional process (Kamil and Bond 2006).

For animals foraging in the wild, as we see in Chapter 11, what matters is not success or speed on any single trial but overall rate of food intake. A nice demonstration of how attentional priming translates into this currency was a study in which bluejays were trained to search on video displays for two simulated prey items, a brown horizontal bar and a white vertical ellipse in mixtures of different sized brown horizontal bars and white vertical ellipses (Dukas and Kamil 2001). The bird began a trial by pecking a "start" circle surrounding an image of one or both of the possible "prey." A single image reliably cued the item to be found in the upcoming display, presumably allowing the bird to focus its attention on items of the cued color, whereas a double image was an ambiguous cue to item type. As soon as a bird pecked a target once, it received half a mealworm and 3 seconds later the signal for the next trial, whereas pecking a distractor delayed the next trial for 15 seconds. This contingency meant that speed and accuracy at pecking the targets would increase the rate of food intake. Consistent with sequential and/or associative priming, the number of mealworms obtained per minute increased by about 50% when the upcoming prey image was signaled.

3.7 Attention and foraging: The behavioral ecology of attention

3.7.1 Search images

By comparing the kinds of insects birds brought to their young with the kinds available in the trees where the birds foraged, Luc Tinbergen (1960), brother of the more famous Niko referred to elsewhere in this book, discovered that insects are not preyed on when they first appear in the environment. Instead, a new prey type such as a freshly hatching species of caterpillar will suddenly begin to be taken when its abundance increases. This sudden increase in predation, Tinbergen suggested, occurs because predators adopt a specific searching image for that prey type after a few chance encounters. "The birds perform a highly selective sieving operation on the stimuli reaching the retina" (Tinbergen, 1960, 333). Described in this way, adopting a searching image (or *search image*) sounds like an attentional process. Recent experiments have supported this conclusion.

The idea that animals might search selectively, ignoring items that do not match a mental representation of desired prey, is appealing because it agrees so well with introspection. Most people have had the experience of not seeing what is right in front of their noses. Indeed, one of the earliest references to search images in animal behavior is von Uexküll's (1934/1957) description of looking for a familiar earthenware water jug and not seeing the glass one that had replaced it (Figure 3.16).

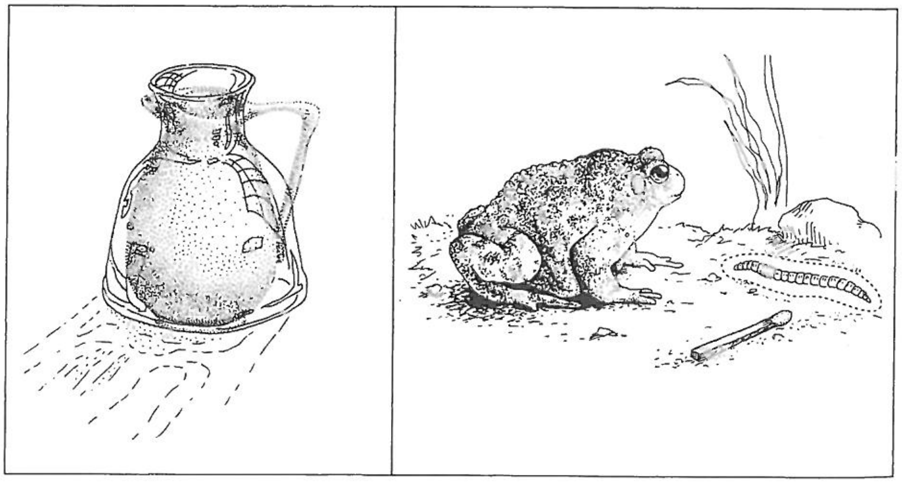


Figure 3.16. Von Uexküll's depiction of his own search image of an earthen water jug and of a frog's search image of a worm. After von Uexküll (1934/1957) with permission.

tems of the cued color,
As soon as a bird pecked
er the signal for the next
ır 15 seconds. This con-
s would increase the rate
priming, the number of
/hen the upcoming prey

ttention

young with the kinds
(1960), brother of the
red that insects are not
ı new prey type such as
to be taken when its
rgen suggested, occurs
prey type after a few
ving operation on the
n this way, adopting a
rocess. Recent experi-

ıs that do not match a
t agrees so well with
; what is right in front
ch images in animal
for a familiar earth-
ced it (Figure 3.16).

ter jug and of a frog's

Animals, too, von Uexkull suggested, could have a mental image of a prey item that enhances their ability to detect matching items and interferes with detecting others (Figure 3.16). It has generally been assumed that an animal can have only one search image at a time, that is, the search image enhances predation on one cryptic prey type while temporarily inhibiting detection of other types. Crypticity is important because search images are assumed to be useful only for prey that are difficult to find in the first place.

By themselves, Tinbergen's data can be explained in a number of ways. Runs of the same type of prey can be explained by the birds repeatedly visiting the same patch of habitat. If the birds were relatively young, they could have been learning that particular insects were suitable as prey or where or how to hunt for them (Dawkins 1971). Learning the characteristics of novel prey in the first place is not the same as selectively attending to a known prey type. Therefore, most recent experiments on search images have varied the abundance and/or crypticity of items that are familiar to the animals being tested. For example, Bond (1983; Langley et al. 1996) studied pigeons searching for two kinds of grains, black gram and wheat, scattered over multicolored gravel. Because the grains were the same color as some pieces of gravel, they were more difficult for the birds to detect on this background than on a plain gray one. After the birds were familiar with feeding on these grains on the gravel backgrounds, the relative proportions of black gram and wheat were varied randomly between 100% black gram and 100% wheat. The birds behaved as if adopting a search image for the more frequent type, taking proportionately more of it rather than matching the proportion taken to the proportion available (Figure 3.17). However, pigeons do match the proportion taken to the proportion available when the prey items are conspicuous, showing that crypticity is important, not just variations in relative proportion (Langley 1996).

One way to find more prey that are difficult to see is to search more slowly, spending longer scanning each section of the substrate (Gendron and Staddon 1983; Guilford and Dawkins 1987). A tradeoff between speed and accuracy in performing difficult discriminations is common to many species, including honeybees (Dyer and Chittka 2004). Reaction time is a good index of the amount of mental processing a task requires, even when it is performed very accurately (see Blough 2006). In the present example, there is an optimal speed-accuracy tradeoff for each

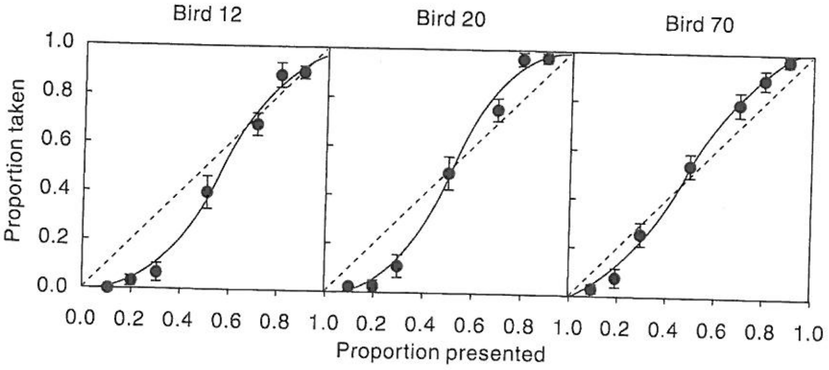


Figure 3.17. Proportion of cryptic grains of one type taken by each of three pigeons as a function of its proportion in a mixture of two types of cryptic grains in the study by Bond (1983). Redrawn with permission.

degree of crypticity that balances the potential benefit of encountering more prey by searching faster against the cost of missing cryptic items by searching too fast (Gendron and Staddon 1983).

The search rate hypothesis predicts that a predator searching slowly should detect all equally cryptic prey equally well. In contrast, an animal with a search image should take one type and ignore the other, even if both types are equally cryptic. Figure 3.17 shows that the two grains used were equally cryptic because when equal numbers were presented (proportion presented = 50%), equal numbers were taken. However, contrary to the search rate hypothesis, the proportion taken did not equal the proportion presented under all conditions. Disproportionate predation on the more abundant type implies that the birds were using a search image for the more frequently encountered grain. This does not mean, however, that animals faced with difficult discriminations in nature might not also search more slowly.

Allowing an animal to search freely for prey items as was done in these studies has some drawbacks as an experimental technique. The animal rather than the experimenter controls the rate and sequence of encounters, and the relative proportion of different items changes as the food depletes. To test the effect of recent experience on choice or detectability of prey it is necessary to present a standard test after differing experiences (Chapter 4). One way to do this is to present prey items one at a time. For example, Pietrewicz and Kamil (1981) tested blue jays (*Cyanocitta cristata*) in an operant task in which they pecked at slides showing two species of moths (blue jays' natural prey items) resting against tree trunks on which they were cryptic. The birds were rewarded with mealworms for indicating correctly that a moth was present. If no moth was present, pecking a central "moving on" key led to the next trial. These pecks generally had longer latencies than pecks to slides with a moth, as if the birds used exhaustive serial search to decide no moth was present. The critical data came from comparing performance in trials following runs of moths of the same type with performance in mixed trials with both species (Figure 3.18). Performance improved within runs as compared to mixed trials. Notably, the birds' accuracy at detecting the absence of a moth improved as well as their accuracy at detecting the presence of a moth, consistent with the notion that attention enhances detection of attended features. These data suggest that the bluejays had a search image for the moth species they had encountered most recently. Because the moths were depicted as they would appear in nature, one species on birch tree trunks and the other on oak trunks, associative priming may have been operating in addition to the sequential priming evident Figure 3.18.

When multiple kinds of prey items can be found on the same substrate, priming presumably occurs when several of the same type are found in succession by chance. Experiments in which pigeons search for grains among gravel have been used to analyze this situation (Reid and Shettleworth 1992; Langley 1996; Langley et al. 1996). Pamela Reid (Reid and Shettleworth 1992) used wheat dyed yellow, green, or brown on a background of green and brown gravel. A free search experiment similar to Bond's established that brown and green were equally cryptic whereas yellow grains were highly conspicuous to the pigeons. To control the birds' experience, Reid then used the apparatus shown in Figure 3.19. Small plaques of gravel, each holding one or two grains, were presented one at a time, and the birds were allowed a single peck at each one. In a run of green or brown after a run of conspicuous yellow grains, the birds' accuracy gradually increased, consistent with their forming a search image for the new cryptic type, just as when they searched freely for grains. However, after a switch from a run of one cryptic type to a run of the other, the birds performed just as

ountering more prey by
by searching too fast

ing slowly should detect
al with a search image
pes are equally cryptic.
ɔtic because when equal
al numbers were taken.
:ion taken did not equal
onate predation on the
rch image for the more
that animals faced with
e slowly.
lone in these studies has
rather than the experi-
e relative proportion of
of recent experience on
ıdard test after differing
items one at a time. For
'anocitta cristata) in an
:ies of moths (blue jays'
were cryptic. The birds
at a moth was present.
l to the next trial. These
ı a moth, as if the birds
. The critical data came
ıs of the same type with
Performance improved
ccuracy at detecting the
ecting the presence of a
detection of attended
age for the moth species
depicted as they would
e other on oak trunks,
the sequential priming

ame substrate, priming
n succession by chance.
avel have been used to
:y 1996; Langley et al.
t dyed yellow, green, or
ırch experiment similar
:ryptic whereas yellow
birds' experience, Reid
of gravel, each holding
s were allowed a single
spicuous yellow grains,
forming a search image
;rains. However, after a
birds performed just as

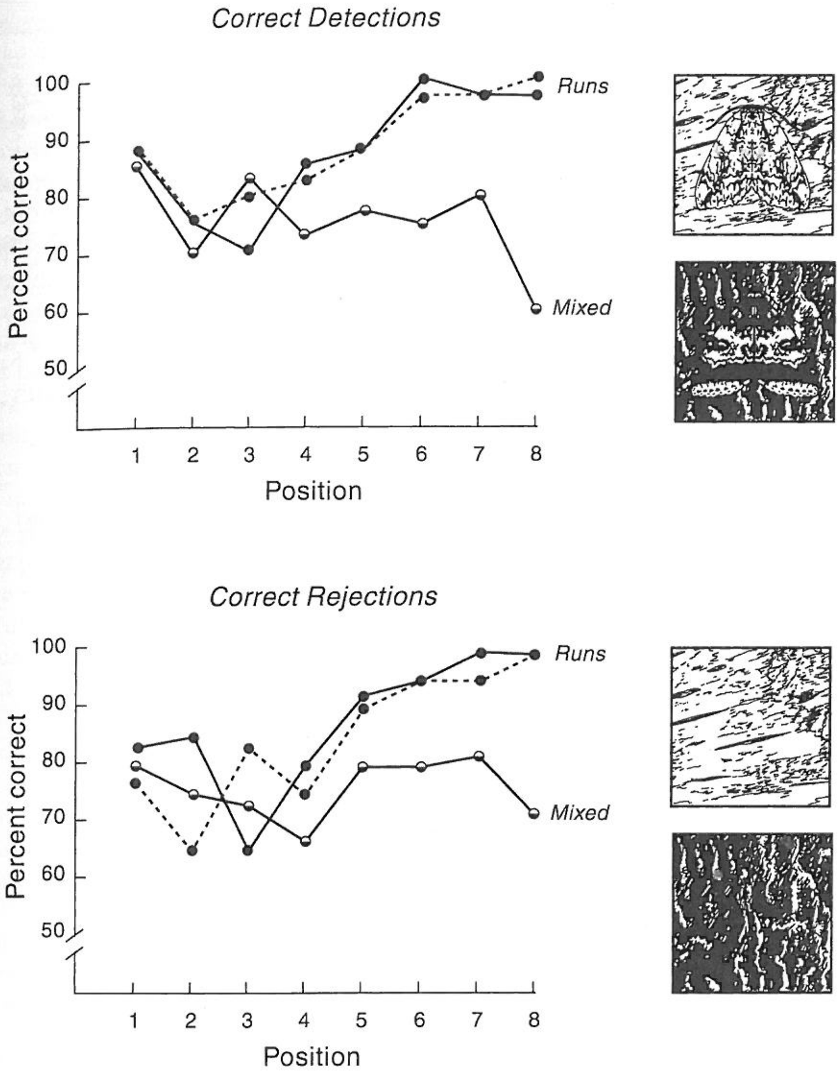


Figure 3.18. Performance of bluejays reinforced for reporting the presence (top panel) or absence (lower panel) of moths in slide images like those on the right in runs of the same moth species or trials with a mixture of two species. Adapted from Pietrewicz and Kamil (1981) with permission.

well as if they had a single cryptic type all along (Figure 3.19). This seems to mean that the birds' "search image" includes some feature distinguishing grains in general from gravel, perhaps shape or texture. Nevertheless, when Reid's pigeons had a choice between brown and green grains, the two cryptic types, after a run of one of them, they tended to choose the color they had just been having. This was not just a general preference for what they had been eating most recently, because the effect depended on the grains being cryptic. Thus the "search image" also seems to include information about the grain's color.

These results naturally lend themselves to interpretation in terms of feature detection and priming. Easy detection of the conspicuous yellow grains is an instance of the popout effect: the target (the grain) differs from the distractors (the bits of gravel) in a

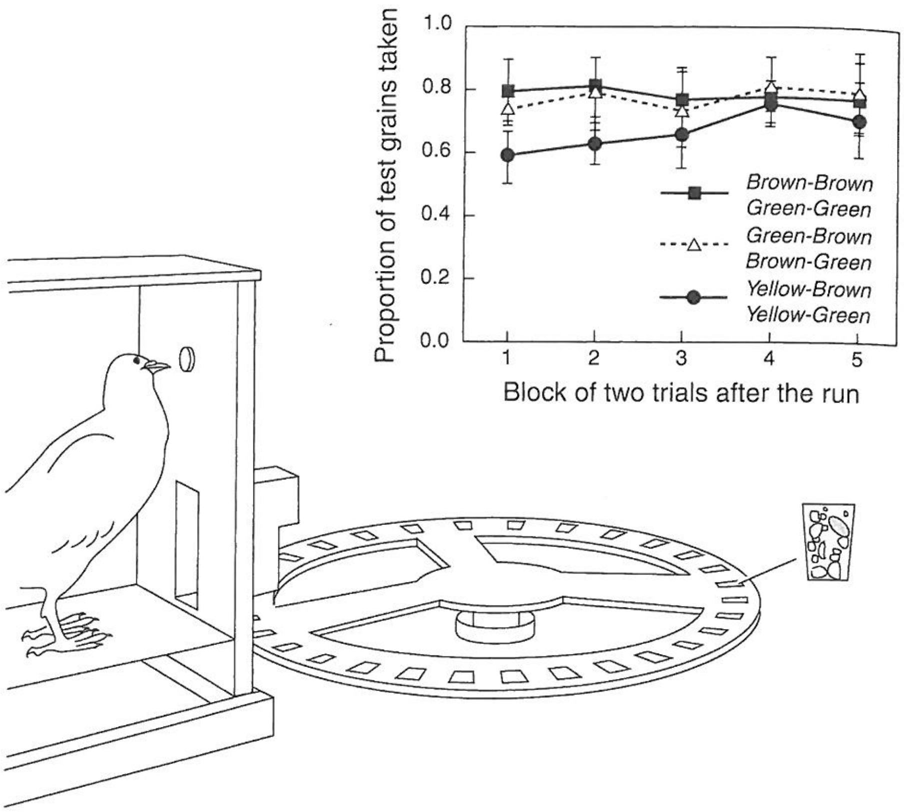
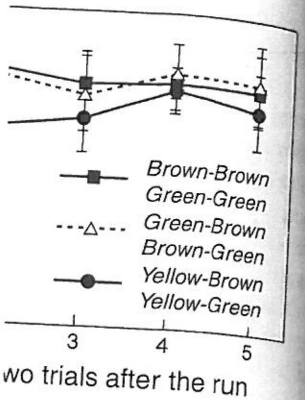
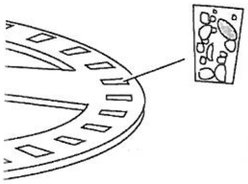


Figure 3.19. Search image effects in pigeons searching for cryptic brown or green or conspicuous yellow grains. Data from a test run of 10 grains after a run of the same or a different color, as indicated. Adapted from Reid and Shettleworth (1992) with permission.

single salient feature (color). The cryptic grains are difficult to detect because they resemble the distractors in color. Because the cryptic items were all grains of wheat, priming with grains dyed one color could enhance detection of other grains with the same shape, size, and texture. The effect on choice shows that the specific color was also primed to some extent. Such a priming effect occurs even if the priming grains are conspicuous, but it is detected only in a test with cryptic grains (Langley 1996). Thus, contrary to the fanciful depictions in Figure 3.16, the "search image" is a collection of independently primed features of the prey. This interpretation suggests that when, unlike the case in Reid's experiments, two cryptic items do not share features allowing them to be detected against their background, the search image/priming effect should be truly specific, with enhanced detection of one item accompanied by reduced detection of the other. Such an effect was observed in a study by Langley (1996) in which pigeons searched computer images of multicolored gravel for a bean or a grain of wheat. By manipulating features of the images, Langley also showed that the importance of color and shape differed for beans versus wheat (see also Plaisted and Mackintosh 1995).The type of background and the type of search task can also influence what features are attended to, as shown in an elegant study by Blough (2002) in which pigeons performed difficult detection and disambiguation tasks with a single set of striped disks. In summary, the "search image," that is, the





own or green or conspicuous
ne or a different color, as
on.

ult to detect because they
were all grains of wheat,
n of other grains with the
hat the specific color was
n if the priming grains are
ins (Langley 1996). Thus,
h image" is a collection of
tion suggests that when,
not share features allow-
ch image/priming effect
accompanied by reduced
dy by Langley (1996) in
ivel for a bean or a grain
y also showed that the
vheat (see also Plaisted
of search task can also
egant study by Blough
ambiguation tasks with
image," that is, the

representation or activation underlying sequential or associative priming, is rarely if ever an actual image of the item being searched for. Rather, what it consists of may vary from one situation and task to another depending on factors such as what distinguishes the item from the substrate and what features it shares with other concurrently available items.

The priming effects we have been discussing are by definition short-lived. Indeed, Bond (1983) suggested that sequential priming decays after a few seconds. But this raises a question about the interpretation of some findings reviewed in this section. For instance, consider that in Reid and Shettleworth's (1992) study two green grains were separated by twice as long on average in mixed green and brown trials as in green-only trials. When pigeons are detecting small black and white patterns against black and white checked backgrounds, a difference in presentation rate by itself can produce differences in discrimination accuracy (Plaisted, 1997). When items in runs were presented at the same rate as items of a single type were occurring in mixed trials, accuracy was no greater than in the matched mixed trials. Plaisted (1997) therefore proposed that search image effects reflect a short-lived priming of independent memory traces for recent items rather than priming of attention to particular item features. However, although this methodological feature should be to taken into account in studies of priming, so far there is no evidence that Plaisted's proposal accounts for results such as those discussed earlier in this section (Bond and Kamil 1999; Blough 2001; Blough 2006; Kamil and Bond 2006).

3.7.2 Search images and prey evolution

Attentional priming has implications for the evolution of species that are prey. For example cryptic prey of a single species should spread themselves out in the environment to reduce the chances of predators encountering them in runs. *Polymorphism,* that is, a tendency for different individuals of the same species to have markedly different colors or patterns, would have the same effect (Croze 1970; Bond 2007). But it is one thing to speculate on how predator psychology has selected for prey appearance and behavior, another thing to demonstrate that this could actually happen. Such a demonstration is provided by a series of studies with bluejays, using procedures similar to those of Pietrewicz and Kamil (1981) but with computer-generated "moths" (Figure 3.20) that "evolve" in response to predation (Kamil and Bond 2006). In the first experiment with this "virtual ecology" (Bond and Kamil 1998; Kamil and Bond 2001) the initial prey population consisted of three "species," digitized images of *Catocala* moths. They appeared on a background of random pixels that could vary from almost smooth grey on which the moths were very conspicuous to a mixture of patches similar to the patches on the moths. Bluejays that had been trained to detect the moths under very cryptic conditions then became the selective agents in the following way. Every day 240 moth images were used. In the first day of the experiment there were 80 of each species (Figure 3.20). At the end of each day, the moths detected by the jays were considered killed, and the remaining moths were allowed to reproduce (actually, here to clone themselves) to provide the population for the next day. In this way the least detectable moths became proportionately more numerous in the next virtual generation.

In three repetitions of this procedure with different initial conditions, the same moth (moth 1 in Figure 3.20)—evidently the most cryptic of the three—came to dominate. This was true even when it was in the minority to begin with, as in the

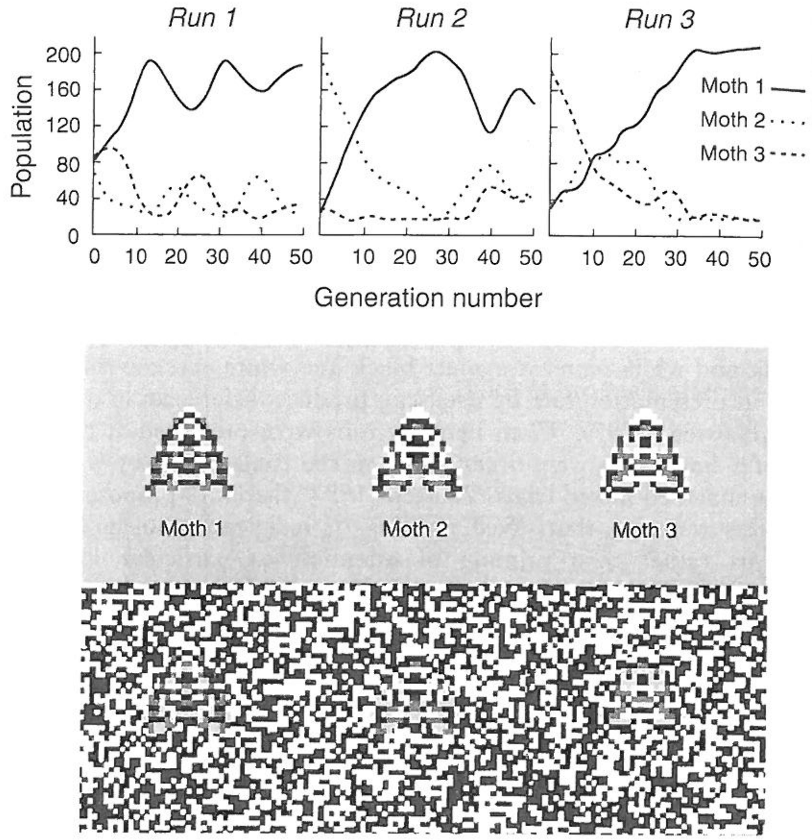


Figure 3.20. Lower panels: the three artificial moth species in Bond and Kamil's (1998) "virtual ecology" shown in both easy (gray background) and hard to discriminate conditions. Upper panel: changes in the virtual population over generations of predation by jays given different compositions of the initial population (Runs 1–3). After Bond and Kamil (1998) with permission.

second and third replications. The jays were showing the same kind of *frequency-dependent selection* evident in Bond's (1983) pigeons (Figure 3.17). A separate study (Bond and Kamil 1999) demonstrated that indeed jays show attentional priming effects with such digital moth displays. As the relatively conspicuous moths 2 and 3 were eliminated, individuals of moth 1 were found more often, priming detection. At the final abundances in each repetition, the intrinisically greater detectability of moths 2 and 3 was balanced by the primed detectability of moth 1.

The next step with this approach was to model evolution more realistically by modeling the genetics of wing patterns and letting the surviving virtual moths from a large and varied initial population "reproduce" via an algorithm that randomly recombined genes for different aspects of wing patterns (Bond and Kamil 2002; Bond and Kamil 2006). The populations that resulted from 100 generations of selection by jays were more cryptic and more diverse in appearance than control populations. Analysis of the sequences of events within sessions of the experiment showed that, just as would be expected, accuracy at detecting one of the more cryptic moths was better the more similar it was to the last moth detected. In summary, then, this approach shows that search image effects are still at work even in a dynamic

amil's (1998) "virtual
conditions. Upper panel:
en different compositions
rmission.

ne kind of *frequency-*
.17). A separate study
attentional priming
icuous moths 2 and 3
priming detection. At
ater detectability of
h 1.

more realistically by
virtual moths from a
ithm that randomly
d and Kamil 2002;
100 generations of
arance than control
s of the experiment
of the more cryptic
. In summary, then,
even in a dynamic

situation with multiple prey types, and that—just has been commonly hypothesized—they can have an important impact on prey evolution.

The results of all these studies with "virtual ecology" imply that the learning and attentional mechanisms of predators can help to maintain polymorphisms in populations of a single species by leading to *frequency dependent selection,* that is, as a type of prey becomes more frequent it is proportionately more preyed on (Bond 2007). The different prey types, which may be morphs of a single type, do not have to differ in crypticity. If one type is rare for any reason, it should have a survival advantage. Thus Figure 3.17 illustrates frequency-dependent predation when the "prey" are different kinds of grains. In a nice demonstration in the wild, male guppies with different tail color patterns were removed from isolated natural pools in Trinidad, recombined into experimental populations in which one tail color pattern or another was comparatively rare, and reintroduced. Males chosen to have a color pattern that was uncommon in their group were most likely to survive until the pool was resampled 2 to 3 weeks later (Olendorf et al. 2006).

3.7.3 Divided attention and vigilance

An animal that is foraging cannot wait until it is satiated to check for predators but should continuously divide attention between foraging and vigilance. The classic illustration of how hard it is for people to divide attention is the situation at a cocktail party: when many conversations are going on simultaneously, it is very difficult to follow more than one of them at a time. In tests of divided attention in the laboratory (see Luck and Vevera 2002), people are instructed to report on more than one source of information at once. In general, performance on a given task falls when attention must be shared between it and another task. The same is true in animals tested in common laboratory paradigms, most often short-term memory tasks (Chapter 7; Zentall 2005a). Just as in the tests of focused attention discussed up to now in this chapter, the detrimental effect of divided attention may diminish as practice leads to automatization (Schiffrin 1988), consistent with the idea that well-learned tasks demand fewer processing resources.

Birds that feed on the ground have been popular subjects for naturalistic studies of dividing visual attention between feeding and vigilance. Many such birds alternate short periods with their heads down, presumably attending to food-related cues, with short periods of head-up scanning, presumably attending to predator-related and/or social cues. For instance, members of a flock of starlings walking across a field probing the ground for leatherjackets raise their heads between pecks and scan the sky and bushes. The smaller the flock, the more time each individual spends scanning (Elgar 1989). More demanding foraging tasks leave less time for vigilance. For example, when blackbirds are foraging on cryptic baits they take longer between scans and spend a smaller proportion of the time scanning than when they are feeding on conspicuous baits (Lawrence 1984).

However, the assumption that head position defines the focus of attention is problematical. For one thing, as mentioned in Section 3.1, what an animal sees from different viewpoints depends on the structure of its visual system. Many birds have a wide field of view and an area of high density photoreceptors placed to detect things approaching from the side (Figure 3.3). As long as they have a clear field of view, with no low barriers, thick grass, or the like, birds may be able to spot a predator almost as well while feeding with head down as while scanning with head up (Lima and Bednekoff 1999; Fernandez-Juricic, Erichsen, and Kacelnik 2004). And in any case, most studies of divided attention in humans deal with a central filtering mechanism, not where the receptors are directed. Thus, although some animals do continually display brief bouts of vigilance while feeding, at the level of mechanism they may not be doing the same thing as person at a cocktail party who attends at one moment to Joe's voice and at the next to Pete's.

Fish have also been subjects in studies of the tradeoff between feeding and vigilance. Sticklebacks recently exposed to a model predator, a kingfisher, flying overhead, feed more slowly than fish not so exposed. It is not surprising that fear increases vigilance, that is, it redirects attention, just as any motivational state enhances the salience of relevant stimuli (Milinski and Heller 1978; Milinski 1984). Suppressing feeding when preparing to flee has a function in that flight responses direct blood flow and other physiological resources away from digestion and toward the muscles for escaping. Independently of such motivational conflicts, a high feeding rate may indicate that less attention is available for predators. This was nicely demonstrated in an experiment in which guppies feeding on water fleas (*Daphnia*) were exposed to predation by a cichlid fish (Figure 3.21, Godin and Smith 1988). The amount of attention devoted to foraging, as reflected in the speed of capturing prey, was manipulated by varying both the density of *Daphnia* and the guppies' hunger level. The faster the guppies were feeding (i.e., at shorter intercapture intervals in Figure 3.21), the more likely one was to be captured by the cichlid. Animals foraging in a group may also need to monitor social stimuli, experiencing a three-way conflict among feeding, watching for predators, and seeing what companions are doing. For instance, juvenile brown trout feeding with familiar companions fed faster and responded more quickly to a model heron than did trout with novel companions, who instead spent more time in aggressive interactions (Cresswell et al. 2003).

Dividing attention in all these naturalistic situations seems to have clear costs such as lower feeding rate or increased risk of being caught by a predator, but the most direct demonstration of such a cost is perhaps that by Dukas and Kamil (2000). Bluejays were trained to find cryptic items among distractors in a central area and two

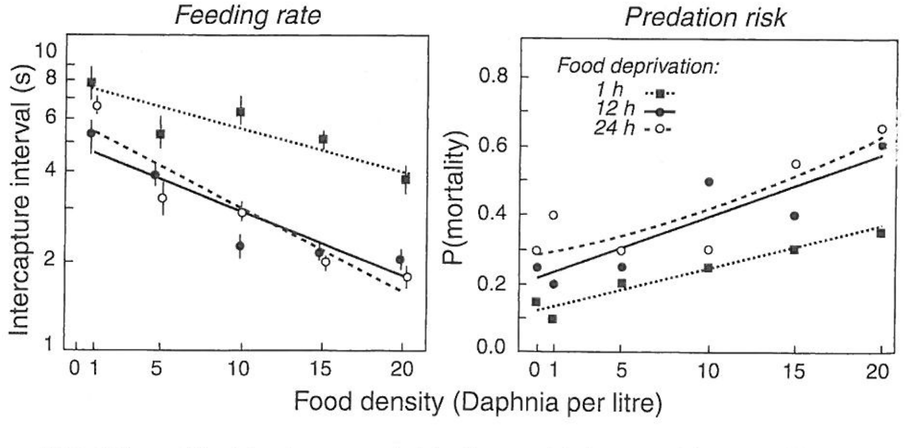
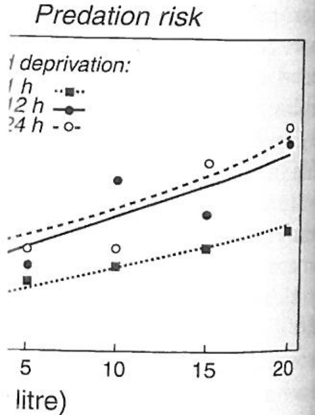


Figure 3.21. Effects of food density on guppies' feeding rate (the inverse of the interval between prey captures, left panel) and predation risk, the number of guppies caught by a predator. Redrawn from Godin and Smith (1988) with permission.

ans deal with a central filtering
ius, although some animals do
ding, at the level of mechanism
cktail party who attends at one

radeoff between feeding and
predator, a kingfisher, flying
sed. It is not surprising that
on, just as any motivational
(Milinski and Heller 1978;
ng to flee has a function in
physiological resources away
ping. Independently of such
idicate that less attention is
ed in an experiment in which
sed to predation by a cichlid
ount of attention devoted to
prey, was manipulated by
ies' hunger level. The faster
ire intervals in Figure 3.21),
chlid. Animals foraging in a
riencing a three-way conflict
what companions are doing.
niliar companions fed faster
than did trout with novel
ssive interactions (Cresswell

seems to have clear costs such
t by a predator, but the most
by Dukas and Kamil (2000).
ctors in a central area and two



verse of the interval between prey
ght by a predator. Redrawn from

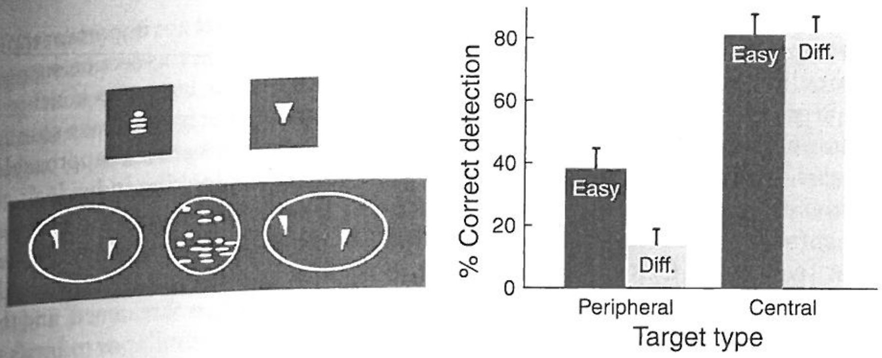


Figure 3.22. Procedure and results from Dukas and Kamil's (2000) demonstration of the cost of limited attention in bluejays. On the left, the two possible "prey items" are shown above a depiction of the video screen on a typical trial, with distracting elements present in the peripheral and central areas. Data, on the right, compare detection rate with prey in the central versus peripheral areas and when the task was relatively easy or difficult ("diff."). Adapted from Dukas and Kamil (2000) with permission.

peripheral areas on a video monitor (Figure 3.22). Birds pecked the center of the screen to cause the three prey-containing areas to appear for 500 milliseconds. They then had another 1000 milliseconds to peck the one area where a prey item had just appeared. Making the display brief and requiring the birds to peck the center of the screen ensured that they were always looking in the same place when the display appeared, much as people are required to look at a central fixation point in analogous tests. And by having competing foraging tasks Dukas and Kamil ensured that they were not measuring a change in vigilance associated with a motivational change, for example from hunger to fear. The jays were expected to devote most attention to the central part of the monitor because an item appeared there on 50% of the trials, whereas one appeared in each peripheral area on only 25% of trials. And indeed, as the central task was made more difficult by increasing the number of distractors, presumably thereby increasing its demands on attention, birds missed more of the peripheral prey (Figure 3.22).

The *confusion effect* may be another manifestation of divided attention in naturalistic situations. The confusion effect refers to the observation that many species of predators have more difficulty capturing prey when confronting a large school, swarm, or flock of similar individuals than when confronting one or a small group of individuals (Miller 1922; Krakauer 1995; Schradin 2000). The probability of an attack ending in prey capture once it has been initiated can decline dramatically with increases in the number of individuals in the group being attacked (Magurran 1990). The confusion effect has generally (cf. Krakauer 1995) been interpreted as caused by the predator dividing its attention among the prey rather than focusing on one until capturing it. The individual in a school of identical conspecifics is the limiting case of a cryptic prey item because it is identical to the "background" of surrounding individuals. On this view it is not surprising that odd individuals or stragglers in a group tend to be the ones captured. Just as in visual search (e.g., P. Blough 1979), the larger the group, the more detectable an odd individual seems to be (Milinski 1990). Notice that the predator confronted with a dense school of prey is assumed to be dividing attention among two or more spatial locations, perhaps because the motion it perceives at each one automatically attracts attention.

The evolutionary determinants of group living and group size are important topics in behavioral ecology (see Chapters 12 and 13). The material in this section suggests that the difficulty of effectively dividing attention confers at least two benefits of living in groups. One is that each individual in a group does not have to take so much attention away from foraging for vigilance because others can warn it of approaching predators. The other is that by being in a group of similar looking individuals the potential prey animal benefits from the ability of the swarm to confuse a predator. The confusion effect may account for several features of swarming or schooling species such as the fact that they tend not to show sexual dimorphism (i.e., males and females look the same), that they crowd together more when threatened, and that mixed species groups tend either to consist of species that look similar or to break up into same-species groups in the presence of a predator (Landeau and Terborgh 1986; Tegeder and Krause 1995).

3.8 Summary

Many universal principles of perception reflect the organization of the physical world (Shepard 1994). Paradoxically, some of the best support for such an adaptationist view of perception is diversity: general mechanisms have been tweaked by evolution in an adaptive way for each species. Animals differ dramatically in the sensory channels they use and in the patterns of sensitivity of those channels. Differences in sensory systems among species can be related to differences in their habitat and lifestyle. Nevertheless, all sensory systems that have been studied share some features, such as greater response to more intense stimuli, sensitivity to contrast, Weber's law, and a tendency to habituate.

Behavioral methods for discovering what animals perceive include testing natural behavior to the stimuli of interest and testing learned behavior using the methods of animal psychophysics. Signal detection theory is a general model of the discrimination of signals from background noise that applies to any situation where an animal has to make a difficult discrimination, and it has implications for the evolution of animal signals. In animal signaling systems, one animal provides a signal to which another animal, of the same or a different species, responds. Perception and the evolution of signals are therefore inextricably linked.

To understand how objects are perceived we have to go beyond sensitivities to individual stimulus modalities or features to ask how features are combined. One influential theory states that objects are perceived as the sum of individual primary features such as color and shape that co-occur at the same time and place. This feature integration theory is supported primarily by the performance of humans in visual search tasks, but some similar data have been reported from other species. To understand how behavior is controlled selectively by only some parts of the environment at any given time, it is necessary to understand attention. Characteristics of attention such as its susceptibility to priming have been studied in visual search tasks in humans and other animals. The apparent ability of foragers to form a search image, enabling them better to detect cryptic prey, may be explained by priming of attention to the features of the prey that best distinguish it from the background. Dividing attention between two or more tasks causes performance on each one to fall. The effects of divided attention can be seen in the tradeoff between foraging and vigilance and in the confusion effect, both of which create a selection pressure for animals to live in groups.

size are important topics
al in this section suggests
at least two benefits of
not have to take so much
n warn it of approaching
looking individuals the
n to confuse a predator.
swarming or schooling
dimorphism (i.e., males
hen threatened, and that
ok similar or to break up
eau and Terborgh 1986;

on of the physical world
r such an adaptationist
n tweaked by evolution
atically in the sensory
hannels. Differences in
es in their habitat and
ed share some features,
contrast, Weber's law,

include testing natural
r using the methods of
odel of the discrimina-
ation where an animal
ns for the evolution of
ides a signal to which
s. Perception and the

eyond sensitivities to
es are combined. One
of individual primary
nd place. This feature
of humans in visual
her species. To under-
of the environment at
cteristics of attention
earch tasks in humans
arch image, enabling
ng of attention to the
d. Dividing attention
o fall. The effects of
d vigilance and in the
r animals to live in

The story of research on search images is a good example of how hypotheses suggested by observations in the field were tested in the laboratory, using a whole range of approaches from the "naturalistic" to the "artificial," from tests in which animals search freely for familiar prey to those with controlled presentation of digital images. Some studies bridge the gap between tests of search image and those of visual search for abitrary targets like letters and shapes. And most recently, this research has come full circle in studies designed to to test hypotheses about how predators' attentional mechanisms drive the evolution of prey populations. Short-lived priming of feature detection is likely responsible for effects originally attributed to a search image for a prey item, but they do not mean that attentional priming is the only mechanism responsible for observations like Tinbergen's (1960). When animals first encounter novel prey items, they must learn to recognize them as prey and learn where to find them and how to capture and handle them, among other things. Each of these processes can be isolated and analyzed experimentally, as we will see in the next two chapters.

Further reading

This chapter has emphasized topics that connect perception with issues in behavioral ecology somewhat at the expense of the substantial work by comparative psychologists on more anthropocentric topics. More about such work can be found in the book edited by Wasserman and Zentall (2006b), the review by Spetch and Friedman (2006), and the online "cyberbook," *Avian Visual Cognition* (Cook 2001a). High-level introductions to basic topics in the psychological study of sensation and perception in humans, including attention, color vision, and signal detection theory, can be found in Volume 1 of *Stevens' Handbook of Experimental Psychology* (Yantis 2002).

Dusenbery's (1992) *Sensory Ecology* is an overview of the physical principles of information transmission, also covered in Bradbury and Vehrencamp's (1998) comprehensive text on the ecology and evolution of animal communication. The books by Maynard Smith and Harper (2003) and Searcy and Nowicki (2005) are both excellent briefer introductions to animal signaling, topics that we come back to in Chapter 14. Lythgoe's (1979) *The Ecology of Vision* is a classic, a rich source of information about adaptations in animal visual systems that has not been replaced. Kelber et al. (2003) is a comprehensive review of the mechanisms and distribution of animal color vision. A brief overview of methods in animal psychophysics is provided by Blough and Blough (1977). The two papers by Wiley (1994, 2006) are excellent introductions to signal detection theory and its implications for issues in animal communication.