

M. E. Nelson · M. A. MacIver

## Sensory acquisition in active sensing systems

Received: 23 November 2004 / Revised: 15 August 2005 / Accepted: 26 December 2005 / Published online: 28 January 2006  
© Springer-Verlag 2006

**Abstract** A defining feature of active sensing is the use of self-generated energy to probe the environment. Familiar biological examples include echolocation in bats and dolphins and active electrolocation in weakly electric fish. Organisms that utilize active sensing systems can potentially exert control over the characteristics of the probe energy, such as its intensity, direction, timing, and spectral characteristics. This is in contrast to passive sensing systems, which rely on extrinsic energy sources that are not directly controllable by the organism. The ability to control the probe energy adds a new dimension to the task of acquiring relevant information about the environment. Physical and ecological constraints confronted by active sensing systems include issues of signal propagation, attenuation, speed, energetics, and conspicuousness. These constraints influence the type of energy that organisms use to probe the environment, the amount of energy devoted to the process, and the way in which the nervous system integrates sensory and motor functions for optimizing sensory acquisition performance.

**Keywords** Active touch · Bioluminescence · Echolocation · Electrolocation · Sensory ecology

**Abbreviation** JAR: Jamming avoidance response

---

M. E. Nelson (✉)  
Department of Molecular and Integrative Physiology and The Beckman Institute for Advanced Science and Technology, University of Illinois at Urbana-Champaign, 405 N. Mathews Ave., Urbana, IL 61801, USA  
E-mail: m-nelson@uiuc.edu  
Tel.: +1-217-2441371  
Fax: +1-217-2445180

M. A. MacIver  
Department of Mechanical Engineering and Department of Biomedical Engineering, Northwestern University, Evanston, IL 60208-3111, USA

---

### Introduction

Sensory systems extract information by analyzing patterns of energy that are generated by or reflected from objects in the environment. In most cases, the energy originates from a source that is extrinsic to the sensing organism. For example, throughout evolutionary history, visual sensory systems have relied primarily on electromagnetic energy from the sun or other celestial sources. An alternative operating mode that has been adopted by some organisms is to use self-generated energy for probing the environment. The terms *passive* and *active* are often used as a convenient means of distinguishing between these two modes of sensing. The term “active sensing” originated in engineering to describe man-made systems that emit energy into the environment, such as radar and sonar (Bajcsy 1988). However, sensing systems can also be active in other ways, such as active control of eye movements in vision (Ballard 1991; Blake 1995). Here we restrict our use of *active sensing* to those systems that utilize self-generated energy. An interesting property of such systems is that they can potentially exert control over the properties of the energy source, such as its intensity, timing, directionality, or spectral characteristics. This review outlines the general physical and ecological constraints faced by active sensing systems and summarizes strategies that are used to control the energy source for the purpose of sensory acquisition.

The key properties of active sensing systems can be grouped into a few categories. These include the type of energy used to probe the environment (light, sound, etc.), the amount of energy devoted to the process (energetic costs and sensing range), where to emit the energy (directionality), when to emit the energy (timing), and finally how to coordinate and control both sensory and motor aspects to optimize performance (sensorimotor integration). Here we provide an overview of these issues and illustrate the main points with examples drawn from a variety of active sensing systems, including

echolocation in bats and dolphins (for reviews, see Au 1993; Thomas et al. 2004), active electrolocation in weakly electric fish (for reviews, see Bullock and Heiligenberg 1986; Moller 1995), active touch in the rodent whisker system (Brecht et al. 1997; Hartmann 2001) and insect antennal systems (Horseman et al. 1997; Dürr et al. 2001), and hydrodynamic imaging in blind cave fish (von Campenhausen et al. 1981; Hassan 1989; Montgomery et al. 2001). We first discuss important constraints on active sensing systems and explore why some forms of energy are more favorable than others for sensory acquisition. We then review strategies for controlling the spatial, temporal, and spectral properties of energy emission. Finally, we explore the implications for neural processing and sensorimotor integration.

### Physical and ecological constraints on active sensing

Many types of energy are available to animals for potential use in active sensing, including electromagnetic (light, infrared, ultraviolet, electrostatic fields), mechanical (touch, sound, vibration), heat, and chemical. These potential modes of active sensing are not equally prevalent in nature due to differences in signal dispersion, speed, attenuation, and conspicuousness of the probe energy. In some cases, active sensing involves propagation of energy through space, which allows detection of objects at a distance. In other cases, energy is transferred by direct contact with parts of the body, such as antennae or whiskers. We refer to these modes as “teleceptive” and “contact” active sensing, respectively. As discussed below, the constraints regarding energy propagation are different for these two modes.

#### Energy propagation

An important constraint on active sensing, particularly in the teleceptive mode, is that the return signal needs to be strong enough to activate sensory receptors at the receiver. Thus, it is important to consider how much of the energy flux from the source is returned to the receiver. If energy is emitted uniformly in all directions, the signal intensity falls with the square of the distance  $d$  because the flux is distributed over a sphere of increasing surface area  $4\pi d^2$  (Fig. 1a). This effect is referred to as geometric spreading. Even if the emitted signal is directional, such that it covers a limited angular extent, the decrease in intensity still follows an inverse-square relationship, but with a different scaling constant. The fraction of energy that impinges on a target is generally proportional to the ratio of the cross-sectional area of the target to the total surface area of the expanding sphere ( $\pi r_T^2/4\pi d^2$ ), where  $r_T$  is the target radius (Fig. 1a). For a single, small target ( $r_T \ll d$ ), the geometric spreading of the reflected energy from the target back to the receiver also tends to follow an inverse-square relationship. The amount of reflected energy that is

intercepted by the receiver (eye, ear, etc.) is proportional to  $(\pi r_R^2/4\pi d^2)$ , where  $r_R$  is the radius of the receiver (Fig. 1b). In teleceptive active sensing of small targets, geometric spreading costs are paid twice, once as energy is propagated from the emitter to the target and again as energy is returned from the target to the receiver. Thus, the fraction of the emitted energy that is returned to the receiver,  $f_{\text{return}}$ , falls off as a fourth power of the distance to the target (Dusenbery 1992):

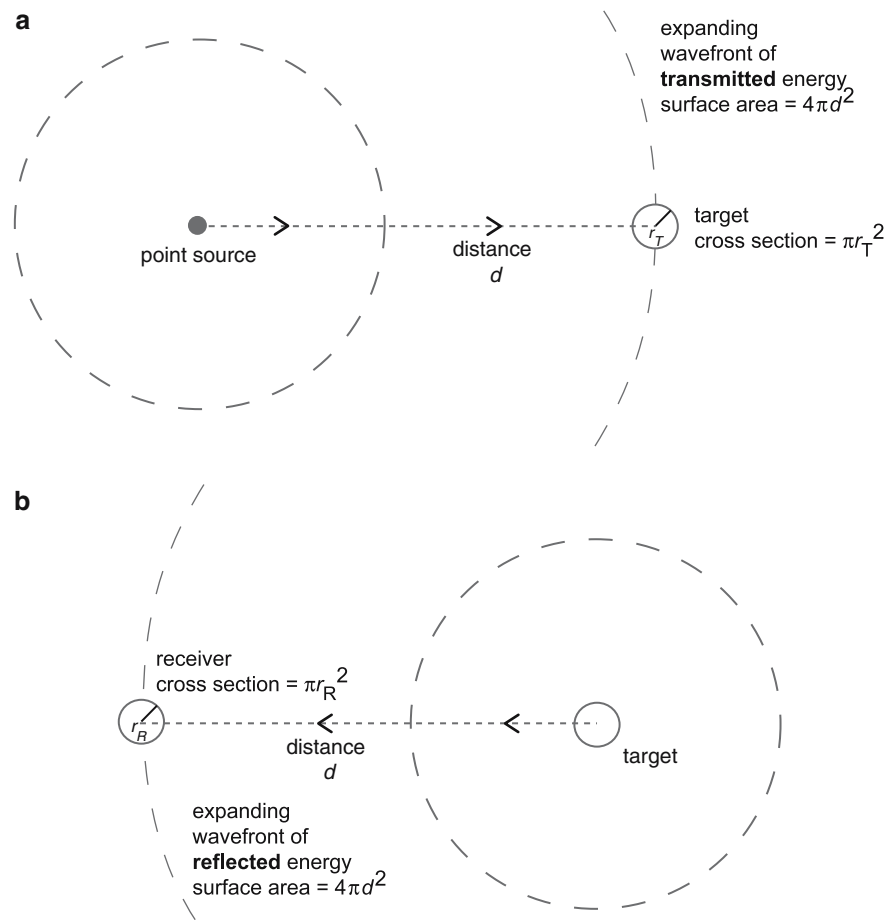
$$f_{\text{return}} \propto \left( \frac{\pi r_T^2}{4\pi d^2} \right) \left( \frac{\pi r_R^2}{4\pi d^2} \right) = \frac{r_T^2 r_R^2}{16d^4}. \quad (1)$$

In other words, doubling the target distance decreases the amount of energy returned to the receiver by a factor of 16. This analysis is for small targets; for a large, planar surface, such as a rocky wall scanned by an echolocating bat, the multiple return paths result only in one-way spherical spreading losses (Simmons et al. 1992; Holderied and von Helversen 2003).

Similar geometric spreading principles apply for the active electric sense in fish, even though the physical principles are somewhat different. In active electric sensing, the electric field used to probe the environment is generated from a dipole source (Knudsen 1975), rather than a point source. Also, the probe signal does not propagate away from the source as an electromagnetic wave, but rather is established almost instantaneously as a quasistatic electric field around the fish (Hopkins 1986). Similar to geometric spreading, the intensity of this electrostatic dipole field falls off with distance. When the probe field interacts with a target object, a second dipole is induced at the target location (Rasnow 1996). Thus, geometric spreading can be modeled using the electrostatic fields of two dipole sources. In the far field, the magnitude of the electric field from a dipole source falls off as the cube of the distance  $d$  (Knudsen 1975). Given that spreading costs must be paid twice, the signal intensity that is returned to the receiver would be expected to fall as the sixth power of distance. However, active electrolocation is most relevant for targets within about one body length of the fish. In this near-field region, the electric field intensity drops less rapidly with distance (Chen et al. 2005). Empirical measurements indicate that the return signal for the active electric sense falls off approximately as the fourth power of distance for small targets over the behaviorally relevant range of target distances (Chen et al. 2005), similar to geometric spreading effects in other systems.

The quartic power-law dependence of geometric spreading for teleceptive active sensing implies that the source intensity must generally be several orders of magnitude larger than the receiver threshold in order for the return signal to be strong enough to activate the receiver. For example, assume that an animal uses active sensing to detect an object one body length away, and that both the target radius and receiver radius (eye, ear, etc.) are approximately 10% of the body length. Equation 1 indicates that less than

**Fig. 1** Schematic diagram of geometric spreading effects in active sensing. **a** Transmission of energy from a point source to a target of radius  $r_T$ ; **b** reflected energy from the target back to a receiver of radius  $r_R$ . After Dusenbery (1992; p. 285)



0.001% of the emitted energy would be available to the receiver. Bats, dolphins, and weakly electric fish are capable of emitting energy into the environment with an intensity that is many orders of magnitude greater than the corresponding receptor threshold level. The requirement that the source intensity be much stronger than the receiver threshold rules out the use of radiant heat as a practical means for active sensing. In order to transfer sufficient heat energy to nearby objects to sense the resulting change in target temperature, the source temperature would need to be much higher than could be supported by biological tissue.

Geometric spreading is not an issue for contact forms of active sensing. Many organisms expend mechanical energy to probe the local environment with sensory appendages, such as antennae, vibrissae, legs, arms, and tentacles. Rats, for example, actively explore the space extending several centimeters to the sides and front of their head using their vibrissae (Carvell and Simons 1990; Hartmann 2001). The long macrovibrissae are actively swept back and forth at rates of 7–12 Hz using dedicated muscles (Berg and Kleinfeld 2003) that appear to be controlled by a central pattern generator (Gao et al. 2001). As nocturnal animals, rats rely heavily on their whisker system to provide information about their surroundings, including the position, size, shape,

orientation, and texture of objects (Brecht et al. 1997). Crickets and stick insects use their antennae to continually probe their environment during locomotion; the antennae perform rhythmic movements that are coupled to the stepping rhythm of the front legs (Horsemann et al. 1997; Dürr et al. 2001). For these sorts of contact active sensing systems, the steep power-law decay of returned energy associated with geometric spreading is not a constraint because mechanical energy is transferred to the environment via a compact, physical linkage (e.g. whisker, antenna) between the organism and the target. Thus, the maximum range is determined by the length of the associated tactile appendage (e.g., vibrissa or antenna). Even though these structures tend to be thin and light, the forces and torques required to counteract gravitational and inertial effects increase with probe length and are likely to place a significant constraint on sensing range.

#### Attenuation by scattering and absorption

In teleceptive systems, the effectiveness of the probe energy can also be reduced if energy is absorbed or scattered as it propagates through the intervening medium. For a parallel beam of energy (i.e. no geometric

spreading effects) in an attenuating medium, the decrease in intensity with distance can be described by an exponential decay (Dusenbery 1992). The attenuation length  $L$  is the distance at which the intensity drops to  $1/e$  ( $\approx 37\%$ ) of its initial value. The attenuation length is dependent on properties of the probe energy as well as properties of the medium. For example, the attenuation length for an acoustic signal varies with sound frequency (higher frequencies have shorter attenuation lengths). Attenuation costs, like geometric spreading costs, are paid twice for active sensing systems, once as energy is propagated from the emitter to the target and again as energy is returned from the target to the receiver. The effects of attenuation can exert considerable influence on the properties of sensory systems. For example, the sun emits a broad spectrum of electromagnetic radiation; most wavelengths are strongly attenuated in water, except for a narrow band in the “visible” part of the spectrum, which is where early photoreceptors of aquatic organisms evolved their sensitivity (Fernald 1997). Photoreceptors of terrestrial organisms retain their ancestral tuning to this narrow band of wavelengths, even though attenuation effects in air do not show such a sharp notch at visible wavelengths (Hudson 1969). Another part of the electromagnetic spectrum that exhibits relatively low attenuation in water is the low frequencies utilized by electric fish (Fernald 1997).

The attenuation length for light in air is on the order of kilometers, but it can be much shorter when the air contains scattering particles (e.g. rain, fog, smoke, dust). Under normal conditions, attenuation is not a limiting factor for terrestrial vision systems. Although propagation of light is extremely fast and usually not limited by attenuation, there are no obvious examples of terrestrial organisms using self-generated light as part of an active vision system. In general, terrestrial bioluminescence is rare (Dusenbery 1992); fireflies use bioluminescence for communication, and some species have been reported to increase their flashing frequency when landing (Buck 1978), but it is not clear whether this actually plays a role in illuminating the landing spot. Attenuation of light is more pronounced in underwater environments than in air. In clear water, the attenuation length for blue-green light (which has the longest attenuation length) is on the order of tens of meters. From the perspective of visual perception in a terrestrial environment, this is analogous to being in a heavy fog. In turbid waters, such as rivers and coastal waters, the attenuation length can drop to meters or less. Thus, light attenuation can pose a significant constraint on visual acquisition in underwater environments. This is particularly relevant for larger animals, such as marine mammals, which can cover several meters per second during high speed swimming (e.g. 2–5 m/s in bottlenose dolphins; Ridoux et al. 1997). Although aquatic bioluminescence is more common than terrestrial bioluminescence, there are very few instances of active visual systems that utilize self-generated bioluminescent energy. Two possible examples are reef-dwelling flashlight fish (Anomalopidae) and deep-sea

dragonfish (Malacosteidae). Dragonfish bioluminescence will be discussed in more detail in the section on conspicuousness. The anomalopid flashlight fish have a light organ underneath each eye that they can control by closing a lid or rotating the organ (Johnson and Rosenblatt 1988). The light organ is filled with bioluminescent bacteria (Haygood 1993). The fish are nocturnal and tend to emerge from their hiding places only on dark moonless nights. In addition to playing a role in communication, the light organ may also help the fish find food. The fact that bioluminescence-based active vision systems are rare may have more to do with issues of conspicuousness, as discussed below, than with limitations associated with signal propagation and attenuation.

In contrast to light, sound in underwater environments has a much greater attenuation length. In the range of human hearing, attenuation lengths can be on the order of hundreds of kilometers. Higher frequencies are attenuated more rapidly, but even in the ultrasonic range used by dolphins, attenuation lengths are on the order of a kilometer (Dusenbery 1992). Echolocation based on ultrasound is employed by most toothed whales (odontocetes), such as dolphins and porpoises. Odontocetes can detect prey-sized objects at distances on the order of 100 m (Au and Snyder 1980; Madsen et al. 2004), which is much further than they can see such objects, even under the best of lighting conditions. The attenuation length for sound in air is on the order of kilometers in the low frequency range of human hearing, but it drops to the order of meters in the high-frequency range of bat ultrasonic emissions (Dusenbery 1992). For bats, using high frequency emissions for echolocation has the benefit of allowing finer spatial resolution, but at the cost of decreased range due to attenuation effects (Jones 1999; Holderied and von Helversen 2003; Au 2004). For efficiency, aerial-feeding bats typically call once per wing beat period; attenuation effects are thought to be an important constraint on the bat’s ability to match its echolocation range to the flight distance covered during a single wingbeat period (Jones 1999; Holderied and von Helversen 2003).

### Propagation velocity

To provide timely information for guiding behavior, active sensing signals generally need to propagate much faster than the speed at which an organism moves through its environment. This condition is easily met for electromagnetic radiation, electrostatic fields, sound waves, and mechanical vibrations. Chemical signals, however, do not typically meet this criterion. If the intervening medium (air or water) is relatively still, then signal propagation takes place primarily by diffusion. But for spatial scales of centimeters or more, which are generally relevant for active sensing, diffusion is too slow to provide useful information for guiding behavior (Dusenbery 1992). Active chemical sensing can, in principle, be used for guiding slow movements of bio-



logical organisms at very short distance scales. The slime mold *Dictyostelium* appears to use ammonia as an active chemical probe to avoid obstacles during growth of the fruiting body. However, this form of active chemical sensing is only effective over distance scales of millimeters and time scales of minutes to hours (Bonner et al. 1986). Chemical signals can propagate at significantly higher velocities if the surrounding medium is in motion, as is often the case in the real world (e.g. wind, water currents). However, signal propagation in this case tends to be unidirectional; a flow that carries a chemical “probe” signal toward a target would not carry a “return” signal back toward the receiver. Thus, chemical sensing is not a generally useful mode for active sensory acquisition.

### Conspicuousness

Another constraint on the type of energy used for active sensing is related to its conspicuousness. Energy that is emitted into the environment for the purpose of active sensing can be detected by other organisms, including potential prey and potential predators. In some cases, conspicuousness can be advantageous if prey are naturally attracted to the energy source. This is the case for deep-sea anglerfish, which have a bioluminescent “lure” that extends above the head and can attract small prey (Munk 1999). If active sensing is used for prey detection, and the prey has similar receptor sensitivity, then the prey can potentially detect the presence of the probe at much greater distances than the probe can be used to detect the prey. This is because the energy flux of the active probe falls as  $d^{-2}$ , whereas the energy reflected back to the receiver from a small prey-sized target falls as  $d^{-4}$ . This effect is observed, for example, in the interactions between bats and insects that can detect ultrasonic echolocation probes (Miller and Surlykke 2001). The insect initiates an escape response based on early detection of the ultrasonic probe of an echolocating bat, before the bat is able to detect the insect (Miller and Surlykke 2001). In general, active sensing for the purpose of prey detection is most effective when the prey cannot detect the probe energy.

If the prey can detect the probe energy, one strategy to improve active sensing performance is to make the probe less conspicuous to the prey. For example, echolocating killer whales that feed on dolphins were found to produce more irregular, isolated single sonar clicks and fewer long duration trains than a sympatric population of killer whales that feed primarily on fish (Barrett-Lennard et al. 1996). Dolphins can detect the killer whale’s ultrasonic probe and take evasive action, whereas most fish cannot (a few species, such as the American shad, are able to detect ultrasound; Mann et al. 1998).

In addition to alerting prey, the emission of probe energy into the environment can make an active sensing organism more conspicuous to predators. The predator can take advantage of the emitted energy to detect and

track the source. For example, an organism that used a bioluminescent probe for active sensing at night would likely be easy prey for numerous predators with well-developed passive vision systems. Disrupting the tracking ability of potential predators may be one of the reasons why flashlight fish open and close a “lid” to expose their light organ briefly at unpredictable intervals, rather than leaving the light on continuously (McCosker 1977). The prevalence of passive vision systems may make it difficult for bioluminescence-based active photoreception to be a viable strategy in most ecological niches.

An interesting adaptation to make bioluminescence less conspicuous is found in the Malacosteid family of deep-sea dragonfish. These fish have two bioluminescent organs, one of which produces a near infrared wavelength of light that only they can see. The bioluminescent abilities and visual systems of most deep-sea organisms are tuned to the blue-green portion of the spectrum, because that wavelength has the longest attenuation length in water (Douglas and Partridge 1997). In general, deep-sea fish lack the visual pigments necessary to see yellow and red wavelengths. By producing a red light, the dragonfish can use active photoreception without alerting predators or prey. The biophysical mechanisms for producing and detecting these long wavelengths are fascinating but beyond the scope of this review (Widder et al. 1984; Partridge and Douglas 1995; Douglas et al. 1998).

Conspicuousness is also a factor in the interactions between electroreceptive fish. Strongly electric eels may utilize the discharges of the weakly electric fish to aid localization during predatory interactions (Westby 1988). Predatory interactions are thought to have had an important influence on the evolution of electric organ discharge waveforms used for active electrolocation (Stoddard 1999, 2002). Large catfish, which are one of the main predators of weakly electric fish, have the ability to detect low frequency electric fields via a passive electric sense. The ancestral electric organ discharge waveform for the active electrosensory system is thought to have been a monophasic pulse (Lissmann 1958). Such pulses have low-frequency spectral components and can thus be detected by predators with a passive electric sense. A biphasic waveform, with a second component of opposite polarity, has much less energy at low frequencies and is less detectable by electroreceptive predators (Stoddard 1999). Predation pressures may therefore have contributed to the evolution of higher frequency biphasic and multiphasic waveforms that are less conspicuous. In a typically less lethal form of conspicuousness, weakly electric fish can detect intruding conspecifics by following the current lines of the field being emitted by the conspecific at far greater distances than the active electrolocation system operates (Hopkins et al. 1997). This is an interesting use of their “active” electrosensory system to eavesdrop on the active signal emissions of nearby members of the same species.

Because of the potential conspicuousness of active sensing emissions to both predators and prey, the costs and benefits of active sensing are highly dependent on the ecological niche and sensory capabilities of sympatric organisms. Thus, simple cost–benefit analyses that examine the optimality of active sensing in terms of only one or two factors, such as energy costs or information rate, are not likely to capture the true complexity of the tradeoffs inherent in active sensing.

---

### What are the energetic costs of active sensing?

Generation and emission of energy into the environment for active sensing imposes a metabolic cost on the organism. Although much is known about the physiological mechanisms of active energy production, measurements and estimates of the metabolic load are scarce. Interestingly, for the cases that have been analyzed, the energetic cost of active sensing seems to be relatively low. In bats, coupling of the emission of echolocating pulses with expiration (which is in turn coupled to wing beating) during the search phase results in no incremental cost for echolocation during flight (Speakman and Racey 1991). This coupling does not exist during the terminal buzz phase, but whether this results in a change in energy expenditure is not known. Odontocetes cannot couple sound production with expiration because they do not breathe while they echolocate, but the energy in the echolocation signal is several orders of magnitude less as a fraction of body mass than for bats, so it is unlikely to pose a significant energetic load on the animal (Au 2004; Cranford and Amundin 2004).

In weakly electric fish, Hopkins (1999) estimates the metabolic load of signal generation in the pulse-type fish *Gnathonemus petersii* to be around 1%, based on earlier measurements by Bell et al. (1976). Oxygen consumption rates in weakly electric fish are about 50% lower than the expected value for teleost fishes of similar size, suggesting that electric field generation does not impose a high energetic cost (Julian et al. 2003). Blind cave fish detect objects in their environment by using their mechanosensory lateral line system to detect changes in the flow-field that is established by their own swimming movements (von Campenhausen et al. 1981; Weissert and von Campenhausen 1981). The fish is thought to use the resulting patterns of receptor activation to build up a representation of its environment, a process that has been called active hydrodynamic imaging (Hassan 1989). In novel environments, blind cave fish have been observed to increase their swimming velocity, presumably to increase the strength of the resulting mechanosensory cues (Teyke 1988). Otherwise, as is the case for bats in the search phase, the emission of active sensing energy is coupled to locomotion, and there may be little or no added cost during movement.

Overall, it seems that animals do not need to devote a large proportion of their energy budget to active sensing. In part this may reflect the fact that increasing energy output results in relatively modest gains in sensing range. As discussed earlier, the fraction of energy returned to the receiver in teleceptive active sensing generally falls as the fourth power of distance to the target (see Eq. 1). For a fixed receiver threshold, doubling the source power extends the detection range by only 19% ( $\sqrt[4]{2}$ ). Thus, large expenditures of sensing energy are not favored from a cost–benefit perspective. Another consideration is the level of habitat clutter, which can nullify any advantage of increasing the detection range much beyond the mean distance to environmental signal barriers.

---

### Variation and control of probe intensity

Variation and control of probe intensity can be observed across multiple biological time scales. On an evolutionary time scale, different species adjust their output levels to match the needs of a particular niche. For example, bats that glean their prey from surfaces in highly cluttered environments often produce weak echolocation calls and are sometimes referred to as whispering bats (Jones 1999; Schnitzler and Kalko 2001). Other bats that tend to forage in open areas produce echolocation calls that are 40–50 dB more intense. Changes in probe intensity can also take place over the lifetime of an individual organism. For example, it has been found that the strength of the electric field around gymnotiform weakly electric fish increases with fish length (Knudsen 1975). This may allow a growing fish to maintain a detection range that is scaled in proportion to its overall body length. This pattern is also found in passive sensing animals. As visually guided fish increase in size during growth, their visual detection range increases as well (Wanzenbock and Scheimer 1989). Daily changes in electric organ discharge amplitude and duration have been observed in some nocturnal weakly electric fish. Discharge intensity is lower during the day, perhaps to reduce energy expenditure and predation risk, and higher at night when the fish are active (Franchina and Stoddard 1998). Blind cave fish, when placed in unfamiliar surroundings, increase the intensity of their self-generated flow field by swimming at higher velocities for a period of time (Teyke 1988). Dolphins increase their probe intensity by 40 dB when echolocating in open pens (Au et al. 1974) versus concrete tanks (Evans 1973). Finally, probe intensity can be controlled over short time periods while interacting with individual target objects. For example, the emitted sonar pulse intensity is observed to decrease as dolphins approach a target, resulting in a nearly constant return amplitude (Au and Benoit-Bird 2003). This is an indirect effect of the way in which the clicks are produced by the phonic lips. As dolphins approach a target, they exert neural control to increase the pulse repetition rate. As the pulse rate increases, the pulse amplitude decreases

due to the biomechanics associated with pressurization of the nasal system (Au and Benoit-Bird 2003). There is evidence that the intensity of bat sonar pulses can also decrease during the terminal portion of the approach phase (Hartley 1992; Tian and Schnitzler 1997).

### When to emit the energy?

A principal tradeoff for active sensing systems in the time domain is the degree to which energy emissions are concentrated into brief periods of time (pulses) versus prolonged emissions (Fig. 2). Weakly electric fish provide a classic example of this. Some species emit brief electrical pulses separated by much longer interpulse intervals, whereas others generate continuous, quasi-sinusoidal oscillations (Bass 1986). These differences are used to classify weakly electric fish into two categories—pulse type and wave type—based on their electric organ discharge patterns. Pulse-type discharges have broadband frequency characteristics, whereas wave-type discharges have a tonal quality, with most of their energy in the fundamental and first few harmonics. A similar distinction exists in bat echolocation, although the temporal structure of bat echolocation calls is more varied. Some bats use brief, broadband, frequency modulated (FM) calls, and others emit more prolonged, constant frequency (CF) calls; some bats combine both CF and FM elements in their calls (for review, see Schnitzler et al. 2003). Dolphins produce brief ( $\approx 50 \mu\text{s}$ ) clicks for echolocation, two orders of magnitude shorter than a typical microchiropteran bat call, and they use longer, more tonal, whistles for communication (Au 1993). Interestingly, the one genus of megachiropteran bats that use echolocation also produce very brief ( $\approx 50 \mu\text{s}$ ) clicks, similar to those of dolphins (Holland et al. 2004).

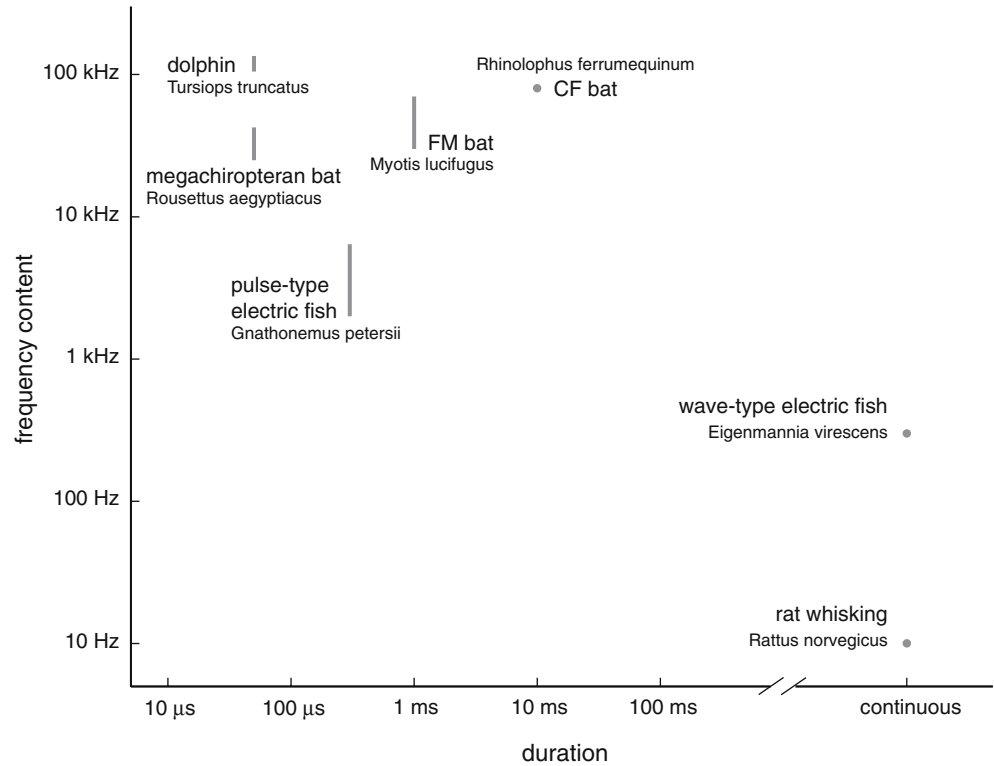
As noted above, rats mechanically probe their environment using vibrissae that are actively swept back and forth at rates of 7–12 Hz (Hartman 2001; Berg and Kleinfeld 2003). The active whisking system of rats, the active electrolocation systems of wave-type fish, and the hydrodynamic imaging of blind cave fish provide essentially continuous sampling of the environment, as is also the case for most forms of passive sensing. In contrast, pulse-type active electrolocation systems and all forms of echolocation provide a series of “snapshots” of the sensory world. This situation is analogous to passive vision in the dark with intermittent flashes of a strobe light to illuminate the scene. Upon each flash the system receives a snapshot of the environment and is functionally blind between flashes.

Many pulse-type electric fish have low, irregular discharge rates under resting conditions and exhibit increases in both rate and regularity when engaging in an active electrolocation task or in response to the detection of a novel electrolocation target (von der Emde and Ringer 1992; Moller 1995; Post and von der Emde 1999). Because transmission is essentially instantaneous for the

electric sense, changes in electric organ discharge rate are not due to echo-overlap constraints, as discussed below for bats and dolphins. Changes in discharge rate that are strongly correlated with target distance have not been reported. Rather, the increase in repetition rate in pulse-type electric fish likely reflects a general need to increase the rate at which sensory information is being acquired from the environment during electrolocation tasks. Wave-type weakly electric fish that have relatively high and temporally precise electric organ discharge frequencies (Moortgat et al. 1998) are typically found in fast-moving rivers and streams where electrosensory cues are changing rapidly (Julian et al. 2003). In general, if the rate of information transfer was the sole constraint on active sensing systems, one might expect evolution to have favored high, regular rates under all circumstances. Additional constraints such as energy demand, conspicuousness, and jamming-avoidance, have presumably led to a tradeoff that favors lower, irregular rates except under demanding or novel conditions.

Similar to the pulse-type electric fish, bats and dolphins modulate the intervals between echolocation pulses. Again, if information transfer was the primary constraint, one would expect high pulse rates to be favored. However, in addition to the other constraints already mentioned, echolocation systems must contend with propagation delays. Echolocation signals propagate at the speed of sound, approximately 340 m/s in air and 1,500 m/s in water. The delay between emission of an echolocation call and reception of the returned energy is proportional to target distance and is a principal cue for estimating target range (Au 1993; Portfors and Wenstrup 1999). For the normal working range of bat and dolphin echolocation, these delays can be on the order of tens of milliseconds for distant targets. Dolphins and bats adjust their call interval such that a new echolocation call is made only after receiving the echoes from the previous call (Jones 1999; Holderied and von Helversen 2003; Schotten et al. 2004). Otherwise there is an ambiguity in the assessment of echo delay due to multiple possible pairings between outgoing calls and returning echoes. For echolocating bats during the search phase, the source intensity is such that a detectable echo will be received before the next wing-beat/sonar call, and thus it varies according to the species-dependent hunting velocity and wingbeat interval. Because echo delay decreases with distance, bats and dolphins generally increase their call rate and reduce call amplitude as they approach a target. For bats and beaked whales, this is particularly apparent in the terminal “buzz” that is emitted just prior to prey capture (Schnitzler et al. 2003; Madsen et al. 2005). In addition to changing the interval between calls, most bats also shorten the duration and alter the frequency structure of individual calls within the sequence (Trappe and Schnitzler 1982; Ghose and Moss 2003; Schnitzler et al. 2003; Fenton 2004). In dolphins, the center frequency of the pulse spectrum varies with intensity—lower amplitude clicks have lower center frequencies—but dolphins

**Fig. 2** Representative duration and frequency content of a single active sensing emission for different types of active sensing systems. For broadband emissions, the indicated range reflects the estimated half-power bandwidth. A single call of a single individual is used to represent each emission type; the diagram does not illustrate differences between calls within an individual, differences between individuals, or differences across species within an operating mode. The representative species are: dolphin, *Tursiops truncatus*; megachiropteran bat, *Rousettus aegyptiacus*; CF bat, *Rhinolophus ferrumequinum*; FM bat, *Myotis lucifugus*; pulse-type electric fish, *Gnathonemus petersii*; wave-type electric fish, *Eigenmannia virescens*; and rat, *Rattus norvegicus*



do not seem to modulate frequency content as an independent variable (Madsen et al. 2004). Weakly electric fish do not appear to change the spectral content or duration of individual discharges when approaching a target.

### Where to emit the energy?

The principle tradeoff in the spatial domain is between concentrating the energy used in active sensing into either a narrowly focused beam (flashlight analogy) or a broadly distributed pattern (lantern analogy). Directing the energy in a narrow beam has two advantages. For a fixed energy expenditure, a focused beam concentrates the energy in one region of space and implicitly defines the return signal as originating from that direction. Provided that scattering or clutter is not a limiting factor, increasing the energy density in the beam increases the effective range of the probe. Because of the quartic power-law dependence of two-way geometric spreading, the range does not increase as rapidly as the decrease in angular coverage, so the total volume of space within which an object of a given size can be detected is decreased. However, by sequentially scanning the beam in different directions, an effectively larger volume of space can be covered. The main disadvantage of a narrow beam is that the system is temporarily “blind” in all other directions. This makes the task of finding and tracking targets more of a challenge. Distributing the energy more broadly in space facilitates rapid detection

of potential targets and makes it easier to maintain sensory contact with targets that are in motion. But these benefits generally come at the cost of a shorter working range.

Dolphins produce a relatively narrow echolocation beam (Fig. 3a). The beam width is approximately  $10^\circ$  in both the horizontal and vertical dimensions, as defined by the half-power point where the intensity is 3 dB below the peak (Au 1993). Beam formation is accomplished by the combined effects of cranial bones, which reflect backward-directed sound, and the melon, a fatty structure in the forehead region, which acts as an acoustic lens to focus the beam (Au 1993). By controlling their click amplitude, dolphins can influence the frequency content and, consequently, the spatial spread of the beam. It has been suggested that this provides a functionality similar to that of a flashlight with an adjustable beam width (Madsen et al. 2004). Head and body movements are used to scan the relatively narrow echolocation beam in both horizontal and vertical dimensions during the search phase of foraging behavior (Herzing 2004).

Bat echolocation emission patterns are significantly broader than those of dolphins (Fig. 3b), with a frequency-dependent half-pressure (6 dB down) beam width in *Eptesicus fuscus* that varies from about  $40^\circ$  at the higher frequency components of the call to  $110^\circ$  at the lower frequency components (Hartley and Suthers 1989). Bats, like dolphins, actively scan their environment while searching for prey. Field studies suggest that prey detection can occur in a cone of up to  $150^\circ$  ( $\pm 75^\circ$



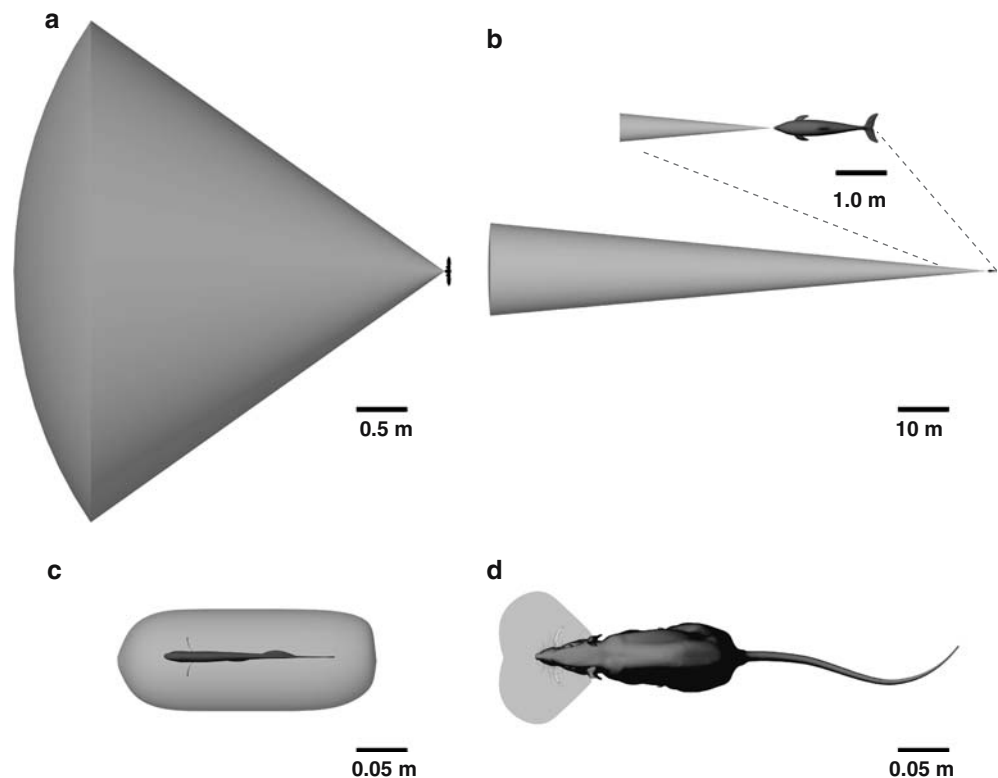
from midline), presumably due to pinnae and head movements during flight (Kalko 1995). Experimental studies in a flight chamber have documented head-scanning behavior in bats searching for a suspended mealworm (Ghose and Moss 2003). Because the echolocation beam is relatively wide, initial detection usually occurs when the target is at an off-axis position. The bat presumably combines delay, intensity, and spectral characteristics of the echo to estimate the likely target location (Erwin et al. 2001) and subsequently adjusts the head direction to precisely center the beam on the target (with a standard deviation of  $3^\circ$ ; Ghose and Moss 2003).

Contact active sensing systems, such as rat vibrissae (Hartmann 2001) and insect antennae (Dürr et al. 2001), tend to cover the region of space to either side of the head and directly in front of the animal. As illustrated in Fig. 3c, the rat macrovibrissae system provides coverage that typically extends up to 35% of a body length (Brecht et al. 1997) and has an angular coverage of approximately  $320^\circ$ , from directly in front of the rat to approximately  $\pm 160^\circ$  on either side (Carvell and Simons 1990; Brecht et al. 1997; Hartmann et al. 2003). As noted above, during walking, the antennae of stick insects and crickets perform continuous rhythmic movements that are coupled to the movement of the front legs. Biologically constrained kinematic models of antennal motion have been used to demonstrate how simple movement patterns can efficiently cover the 3D space in front of the animal (Krause and Dürr 2004).

Weakly electric fish emit dipolar electric field patterns that permit active sensing in virtually the entire  $360^\circ$

volume around the body (Heiligenberg 1975; Knudsen 1975; MacIver et al. 2001). The omnidirectional emission pattern (Fig. 3c) is complemented by an array of sensors that are broadly distributed over most parts of the body surface (Carr et al. 1982). The fish are thus able to detect targets located in almost any direction. However, the effective range of electrolocation is fairly short, generally less than the fish's body length. Walter Heiligenberg was one of the first researchers to realize that the near-field region of the field could not be adequately analyzed using models based on far-field dipole approximations. He was a pioneer in using computer modeling and simulation techniques to explore the spatial aspects of electrolocation in the behaviorally relevant range (Heiligenberg 1975). Although the emission pattern covers the entire region around the fish, the electric field can still be "aimed" to some extent by movements of the trunk and tail, which contains the electric organ. Some weakly electric fish commonly back up to approach novel objects and bend their tails back and forth during sensory acquisition. These tail "probing motor acts" have been investigated in African electric fish (Toerring and Moller 1984; von der Emde and Ringer 1992). The mormyrid *Gnathonemus petersii* has also been observed to manipulate a long, tapering sensory proboscis immediately ventral to the mouth, called the Schnauzenorgan, in a saccade-like fashion during food search (von der Emde 2006). In gymnotids, Heiligenberg (1975) modeled the tail-bending phenomenon and showed that it could enhance electric images on the trunk of the fish, a hypothesis supported by more

**Fig. 3** Schematic representation of different spatial patterns of emission for active sensing systems: **a** bat echolocation beam; the illustrated range is the estimated detection range for small prey (mosquitoes) averaged across several bat species (Holderied and von Helversen 2003; Kalko 1995); the spread corresponds to the half-power beam width of free-flying *Eptesicus fuscus* (Ghose and Moss 2003); **b** dolphin (*Tursiops truncatus*) echolocation beam; the illustrated range is for detecting a prey-sized, water-filled sphere (Au and Snyder 1980); **c** weakly electric fish (*Apteronotus albifrons*) envelope for electrosensory detection of *Daphnia magna* (MacIver et al. 2001); **d** rat (*Rattus norvegicus*) whisker system (Brecht et al. 1997)



recent reconstructions of electric images during exploratory movements (Assad et al. 1999). Controlling spatial aspects of the emission pattern thus seems to be a common strategy across all active sensing systems, whether they be narrow-beam, such as dolphin echolocation, or omnidirectional, such as fish electrolocation.

### Coordinating sensory and motor aspects of sensory acquisition

Optimizing sensory acquisition performance requires that sensory and motor aspects of active sensing be integrated and coordinated by the nervous system. In previous sections we have discussed motor actions involved in directing the energy in space (e.g. bat head movements, fish tail bends) and controlling its timing (e.g. range-dependent changes in echolocation pulse rate). This section reviews some other important aspects of sensorimotor integration, including matching of emitter and receiver characteristics, jamming avoidance behaviors, and the complementarity of the space in which prey can be sensed to the space that an animal is able to move to over short time periods.

#### Matching emitter and receiver characteristics

An important aspect of sensorimotor integration is the matching of tuning properties of sensory neurons to the emitter characteristics of the motor system. For example, peripheral electroreceptors in wave-type weakly electric fish are tuned to the fundamental frequency of the fish's electric organ discharge (Hopkins 1976). This allows the fish to emphasize signals related to its own discharge and filter out irrelevant electrical background noise at the receptor level. Sex steroid hormones are involved in coordinating the frequency tuning of the receptors with changes in the fish's discharge frequency (Zakon 1987). Behavioral thresholds in weakly electric fish exhibit a frequency dependence that is matched to the spectral composition of their discharge (Knudsen 1974). Similarly, bat auditory processing areas commonly exhibit an overrepresentation of the frequencies associated with harmonic components of the echolocation calls (Schuller and Pollak 1979; Wenstrup 1999). In the periphery, the pattern of auditory sensitivity complements the emission pattern to produce a net echolocation beam with higher radial symmetry and spectral contrast than the emission beam alone (Henze and O'Neill 1991; Fuzessery et al. 1992; Wotton et al. 1997). In dolphins, audiograms of sensitivity are matched to the peak frequency of the sonar click (Madsen et al. 2004). Dragonfish have special pigments in the retina that are dedicated to picking up the far-red bioluminescence of these fish (Partridge and Douglas 1995; Douglas and Partridge 1997).

Some active sensing systems maintain tight control over the frequency content of the signals of interest.

The electric organ discharge of wave-type weakly electric fish is one of the most accurate biological oscillators observed in nature (Moortgat et al. 1998). This frequency stability presumably facilitates rejection of noise in both the amplitude and phase processing pathways, and aids in the perception of capacitive properties of targets (von der Emde 1999). Rather than maintaining a constant emission frequency, certain bats use auditory feedback to maintain a constant echo frequency. This behavior, known as Doppler shift compensation, allows the bats to compensate for shifts in the frequency content of the signal that occur due to relative motion between the bat and its target (Schnitzler 1973; Metzner et al. 2002). A sensorimotor feedback loop maintains the frequency content of the returning signal within a narrow range of frequencies, termed the "auditory fovea." These particular frequencies are disproportionately represented in peripheral and central auditory pathways (Schuller and Pollak 1979), in a manner similar to the overrepresentation of the foveal region of space in the visual system. Doppler shift compensation is analogous to visual fixation and tracking behaviors, which maintain an object of interest in the high acuity region of the input space.

#### Jamming avoidance and eavesdropping

Establishing a close match between emitter and receiver characteristics allows an organism to emphasize components of sensory input that are related to its own emissions and suppress extraneous background noise from other sources in the environment. If there are conspecifics in the vicinity, the probe signals of these individuals can be close enough to the animal's own emitter characteristics so that the signals are not filtered out by receiver tuning properties. Thus conspecific signals can potentially interfere with the animal's own active sensing capabilities. Many active sensing systems have jamming avoidance behaviors that minimize the detrimental effects of conspecific signals. The best studied example is the jamming avoidance response (JAR) of the wave-type weakly electric fish, *Eigenmannia*, in which nearby fish reflexively shift their discharge frequencies away from one another to reduce low-frequency interference. Walter Heiligenberg and his collaborators systematically analyzed the anatomical, physiological, and computational principles of the JAR, making it one of the most completely understood examples of sensorimotor integration in any vertebrate sensory system. A detailed overview of more than two decades of research on the JAR and its broader implications for neural information processing can be found in Heiligenberg (1991), and recent progress is reviewed by Metzner (1999). Gymnotiform pulse-type electric fish, which discharge at rather regular rates, use a similar strategy to minimize temporal coincidence with neighboring fish by slightly modulating their pulse rates to avoid overlap (Heiligenberg et al. 1978). Mormyrid pulse-type fish tend to discharge irregularly and

therefore have a low probability of repeated coincidences with neighboring fish, although under some circumstances they exhibit a short-latency echo-response with respect to a neighbor's discharge that minimizes the chance of overlap (Russell et al. 1974). Jamming avoidance behaviors have also been described in bats (Surlykke and Moss 2000; Ulanovsky et al. 2004), but not in dolphins. Dolphin echolocation pulses are so brief that temporal coincidences with neighbors are rare. There is some evidence that dolphins can actually extract useful information by "eavesdropping" on echolocation signals from other dolphins (Xitco and Roitblat 1996).

### Collision avoidance

For animals that rely primarily on active sensing for navigation, the potential for colliding with objects in the environment establishes a need to coordinate sensing and locomotor actions. At the most fundamental level, the animal should be able to sense in the direction in which it is moving, consistent with the forward-biased sensing volumes of bats, dolphins, and rats, and with the omnidirectional sensing volumes of weakly electric fish, which are able to swim backwards, up (heave), and combine a roll with a heave to move laterally (MacIver et al. 2004). Dynamic considerations dictate that locomotor velocity and the sensing range should be controlled such that the animal can come to a halt or make an evasive maneuver to avoid collision with an obstacle detected at the edge of its sensing range. This is generally not an issue for odontocetes, which have a sensing range that far exceeds their stopping distance (Madsen et al. 2004). It is more of an issue for weakly electric fish because of their short electrolocation range (less than a body length; MacIver et al. 2001) and for bats because of their high flight velocities (up to 100 body lengths/s; Kalko 1995). However, both weakly electric knifefish (MacIver et al. 2001) and bats decelerate to a near halt from normal foraging velocities when capturing small prey (Kalko 1995), thus demonstrating that their locomotor abilities are well matched to their active sensing range.

### Complementarity of sensing volume geometry and locomotor abilities

The energy emission pattern and corresponding sensory properties determine a volume of space that an animal can effectively monitor via active sensing, which we refer to as the sensing volume. In general, the angular extent of this sensing volume is correlated with the animal's locomotor capabilities. This is perhaps most evident for the omnidirectional active sensing volume around apteronotid weakly electric fish (Fig. 3c), which is matched with a multidirectional locomotion system that allows the fish to quickly reach any point in the sensory volume (MacIver et al. 2001, 2004). The long undulating

ribbon fin along the bottom edge of the body confers a high degree of maneuverability to this fish, including the ability to swim backwards (Lannoo and Lannoo 1993). The long tapering body plan also allows for high roll angular velocities, which the fish uses to quickly reach points in the lateral portions of the omnidirectional sensing volume (MacIver et al. 2004). Rolls and rapid reversals are commonly observed in prey capture behavior (MacIver et al. 2001) and have been shown to be key components of maneuvers derived from optimal trajectory generation algorithms using idealized fluid mechanics and models of weakly electric fish bodies (MacIver et al. 2004).

Unlike weakly electric knifefish, most other active sensing organisms have a strong forward bias in their locomotor capabilities that is reflected by a forward bias in their active sensing emissions (Fig. 3a, b, d). With the exception of the nectar-feeding, hovering bats (Dudley and Winter 2002), bats are only able to fly in a forward direction, but because they are light (typically 5–60 g; Holderied and von Helversen 2003) the inertial constraints on the animal are slight, likely enabling the animal to make full use of its wide-angled sonar beam. The Reynolds number, a measure of the ratio of inertial to viscous forces, is approximately two orders of magnitude larger for an odontocete ( $\approx 10^6$ ; Weihs 2004) than for a bat ( $\approx 10^4$ ; Norberg 2002). A higher Reynolds number implies higher inertial constraints, consistent with echolocation beams of odontocetes covering a narrower angular extent than those of bats. The Reynolds number for weakly electric fish ( $\approx 10^3$ ; MacIver et al. 2004) is approximately an order of magnitude lower than that for bats, consistent with the fish possessing a sensing volume with broader angular coverage. Although the relationships discussed here have been based on an analysis of active sensing systems, the matching of sensing volume geometry and locomotor capabilities is an issue of broader importance for all types of sensory systems, both active and passive. Many of the issues surrounding active sensing systems that have been highlighted in this review have relevance for understanding all forms of sensory acquisition.

**Acknowledgements** This work was supported by a grant from the National Institute of Mental Health to M.E.N. (R01 MH49242); M.A.M. was supported in part by a grant from the Whitaker Foundation to Northwestern University. We thank Dr. Rüdiger Krahe for stimulating discussions and helpful feedback.

### References

- Assad C, Rasnow B, Stoddard PK (1999) Electric organ discharges and electric images during electrolocation. *J Exp Biol* 202:1185–1193
- Au WWL (1993) *The sonar of dolphins*. Springer, Berlin Heidelberg New York
- Au WWL (2004) A comparison of the sonar capabilities of bats and dolphins. In: Thomas JA, Moss CF, Vater M (eds) *Echolocation in bats and dolphins*. University of Chicago Press, Chicago, pp xiii–xxvii

- Au WWL, Benoit-Bird KJ (2003) Automatic gain control in the echolocation system of dolphins. *Nature* 423:861–863
- Au WWL, Snyder KJ (1980) Long-range target detection in open waters by an echolocating atlantic bottlenose dolphin (*Tursiops truncatus*). *J Acoust Soc Am* 68:1077–1084
- Au WWL, Floyd RW, Penner RH, Murchison AE (1974) Measurement of echolocation signals of the atlantic bottlenose dolphin, *Tursiops truncatus* Montagu, in open waters. *J Acoust Soc Am* 56:1280–1290
- Bajcsy R (1988) Active perception. *Proc IEEE* 76:996–1005
- Ballard DH (1991) Animate vision. *Artif Intell* 48:57–86
- Barrett-Lennard LG, Ford JKB, Heise KA (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Anim Behav* 51:553–565
- Bass AH (1986) Electric organs revisited. In: Bullock TH, Heiligenberg W (eds) *Electroreception*. Wiley, New York, pp 13–70
- Bell CC, Bradbury J, Russell CJ (1976) The electric organ of a mormyrid fish as a current and voltage source. *J Comp Physiol A* 110:65–88
- Berg RW, Kleinfeld D (2003) Rhythmic whisking by rat: retraction as well as protraction of the vibrissae is under active muscular control. *J Neurophysiol* 89:104–117
- Blake A (1995) Active vision. In: Arbib MA (ed) *The handbook of brain theory and neural networks*. MIT Press, Cambridge/Massachusetts, pp 61–63
- Bonner JT, Suthers HB, Odell GM (1986) Ammonia orients cell masses and speeds up aggregating cells of slime molds. *Nature* 323:630–632
- Brecht M, Preilowski B, Merzenich MM (1997) Functional architecture of the mystacial vibrissae. *Behav Brain Res* 84:81–97
- Buck JB (1978) Functions and evolutions of bioluminescence. In: Herring PJ (ed) *Bioluminescence in action*. Academic, New York, pp 419–460
- Bullock TH, Heiligenberg W (1986) *Electroreception*. Wiley, New York
- von Campenhausen C, Riess I, Weissert R (1981) Detection of stationary objects by the blind cave fish *Anoptichthys jordani* (Characidae). *J Comp Physiol A* 143:369–374
- Carr CE, Maler L, Sas E (1982) Peripheral organization and central projections of the electrosensory nerves in gymnotiform fish. *J Comp Neurol* 211:139–153
- Carvell GE, Simons DJ (1990) Biometric analyses of vibrissal tactile discrimination in the rat. *J Neurosci* 10:2638–2648
- Chen L, House JH, Krahe R, Nelson ME (2005) Modeling signal and background components of electrosensory scenes. *J Comp Physiol A* 168:331–345
- Cranford TW, Amundin M (2004) Biosonar pulse production in odontocetes: the state of our knowledge. In: Thomas JA, Moss CF, Vater M (eds) *Echolocation in bats and dolphins*. University of Chicago Press, Chicago, pp 27–35
- Douglas RH, Partridge JC (1997) On the visual pigments of deep-sea fish. *J Fish Biol* 50:68–85
- Douglas RH, Partridge JC, Dulai K, Hunt D, Mullineaux CW, Tauber A, Hynninen PH (1998) Dragon fish see using chlorophyll. *Nature* 393:423–424
- Dudley R, Winter Y (2002) Hovering flight mechanics of neotropical flower bats (Phyllostomidae: Glossophaginae) in normodense and hypodense gas mixtures. *J Exp Biol* 205:3669–3677
- Dürr V, König Y, Kittmann R (2001) The antennal motor system of the stick insect *Carausius morosus*: anatomy and antennal movement pattern during walking. *J Comp Physiol A* 187:131–144
- Dusenbery DB (1992) *Sensory ecology: how organisms acquire and respond to information*. WH Freeman, New York
- von der Emde G (1999) Active electrolocation of objects in weakly electric fish. *J Exp Biol* 202:1205–1215
- von der Emde G (2006) Non-visual environmental imaging and object detection through active electrolocation in weakly electric fish. *J Comp Physiol A* (in press)
- von der Emde G, Ringer T (1992) Electrolocation of capacitive objects in four species of pulse-type weakly electric fish. I. Discrimination performance. *Ethology* 91:326–338
- Erwin H, Wilson WW, Moss CF (2001) A computational model of sensorimotor integration in bat echolocation. *J Acoust Soc Am* 110:1176–1187
- Evans WE (1973) Echolocation by marine delphinids and one species of freshwater dolphin. *J Acoust Soc Am* 54:191–199
- Fenton MB (2004) Aerial-feeding bats: getting the most out of echolocation. In: Thomas JA, Moss CF, Vater M (eds) *Echolocation in bats and dolphins*. University of Chicago Press, Chicago, pp 350–355
- Fernald RD (1997) The evolution of eyes. *Brain Behav Evol* 50:253–259
- Franchina CR, Stoddard PK (1998) Plasticity of the electric organ discharge waveform of the electric fish *Brachyhypopomus pinnicaudatus*. I. Quantification of day–night changes. *J Comp Physiol A* 183:759–768
- Fuzessery ZM, Hartley DJ, Wenstrup JJ (1992) Spatial processing within the moustache bat echolocation system: possible mechanisms for optimization. *J Comp Physiol A* 170:57–71
- Gao P, Bermejo R, Zeigler HP (2001) Vibrissa deafferentation and rodent whisking patterns: behavioral evidence for a central pattern generator. *J Neurosci* 21:5374–5380
- Ghose K, Moss CF (2003) The sonar beam pattern of a flying bat as it tracks tethered insects. *J Acoust Soc Am* 114:1120–1131
- Hartley DJ (1992) Stabilization of perceived echo amplitudes in echolocating bats. I. Echo detection and automatic gain control in the big brown bat, *Eptesicus fuscus*, and the fishing bat, *Noctilio leporinus*. *J Acoust Soc Am* 91:1120–1132
- Hartley DJ, Suthers RA (1989) The sound emission pattern of the echolocating bat, *Eptesicus fuscus*. *J Acoust Soc Am* 85:1348–1351
- Hartmann MJ (2001) Active sensing capabilities of the rat whisker system. *Auton Robot* 11:249–254
- Hartmann MJ, Johnson NJ, Towal RB, Assad C (2003) Mechanical characteristics of rat vibrissae: resonant frequencies and damping in isolated whiskers and in the awake behaving animal. *J Neurosci* 23:6510–6519
- Hassan ES (1989) Hydrodynamic imaging of the surroundings by the lateral line of the blind cave fish *Anoptichthys jordani*. In: Coombs S, Peter G, Heinrich M (eds) *The mechanosensory lateral line: neurobiology and evolution*. Springer, Berlin Heidelberg New York, pp 217–227
- Haygood MG (1993) Light organ symbioses in fishes. *Crit Rev Microbiol* 19:191–216
- Heiligenberg W (1975) Theoretical and experimental approaches to spatial aspects of electrolocation. *J Comp Physiol A* 103:247–272
- Heiligenberg W (1991) *Neural nets in electric fish*. The MIT Press, Cambridge/Massachusetts
- Heiligenberg W, Baker C, Bastian J (1978) The jamming avoidance response in gymnotoid pulse species: a mechanism to minimize the probability of pulse train coincidence. *J Comp Physiol A* 124:211–224
- Henze D, O'Neill WE (1991) The emission pattern of vocalizations and directionality of the sonar system in the echolocating bat, *Pteronotus parnelli*. *J Acoust Soc Am* 89:2430–2434
- Herzing DL (2004) Social and nonsocial uses of echolocation in free-ranging *Stenella frontalis* and *Tursiops truncatus*. In: Thomas JA, Moss CF, Vater M (eds) *Echolocation in bats and dolphins*. University of Chicago Press, Chicago, pp 404–410
- Holdering MW, von Helversen O (2003) Echolocation range and wingbeat period match in aerial-hawking bats. *Proc R Soc Lond B* 270:2293–2299
- Holland RA, Waters DA, Rayner JMV (2004) Echolocation signal structure in the megachiropteran bat *Rousettus aegyptiacus* Geoffroy 1810. *J Exp Biol* 207:4361–4369
- Hopkins CD (1976) Stimulus filtering and electroreception: tubercular electroreceptors in three species of gymnotoid fish. *J Comp Physiol A* 111:171–207



- Hopkins CD (1986) Temporal structure of non-propagated electric communication. *Brain Behav Evol* 28:43–59
- Hopkins CD (1999) Design features for electric communication. *J Exp Biol* 202:1217–1228
- Hopkins CD, Shieh KT, McBride DW, Winslow M (1997) A quantitative analysis of passive electrolocation behavior in electric fish. *Brain Behav Evol* 50(suppl 1):32–59
- Horseman BG, Gebhardt M, Honegger HW (1997) Involvement of the suboesophageal and thoracic ganglia in the control of antennal movements in crickets. *J Comp Physiol A* 181:195–204
- Hudson RD (1969) *Infrared system engineering*. Wiley-Interscience, New York, p 144
- Johnson GD, Rosenblatt RH (1988) Mechanisms of light organ occlusion in flashlight fishes, family Anomalopidae (Teleostei, Beryciformes), and the evolution of the group. *Zool J Linn Soc* 94:65–96
- Jones G (1999) Scaling of echolocation call parameters in bats. *J Exp Biol* 202:3359–3367
- Julian D, Crampton WGR, Wolhgemuth SE, Albert JS (2003) Oxygen consumption in weakly electric neotropical fishes. *Oecologia* 137:502–511
- Kalko EK (1995) Insect pursuit, prey capture and echolocation in pipistrelle bats (Microchiroptera). *Anim Behav* 50:861–880
- Knudsen EI (1974) Behavioral thresholds to electric signals in high frequency electric fish. *J Comp Physiol A* 91:333–353
- Knudsen EI (1975) Spatial aspects of the electric fields generated by weakly electric fish. *J Comp Physiol A* 99:103–118
- Krause AF, Dürr V (2004) Tactile efficiency of insect antennae with two hinge joints. *Biol Cybern* 91:168–181
- Lannoo MJ, Lannoo SJ (1993) Why do electric fishes swim backwards? An hypothesis based on gymnotiform foraging behavior interpreted through sensory constraints. *Env Biol Fishes* 36:157–165
- Lissmann HW (1958) On the function and evolution of electric organs in fish. *J Exp Biol* 35:156–191
- MacIver MA, Sharabash NM, Nelson ME (2001) Prey-capture behavior in gymnotid electric fish: motion analysis and effects of water conductivity. *J Exp Biol* 204:543–557
- MacIver MA, Fontaine E, Burdick JW (2004) Designing future underwater vehicles: principles and mechanisms of the weakly electric fish. *IEEE J Oceanic Eng* 29:651–659
- Madsen PT, Kerr I, Payne R (2004) Echolocation clicks of two free-ranging, oceanic delphinids with different food preferences: false killer whales *Pseudorca crassidens* and Risso's dolphins *Grampus griseus*. *J Exp Biol* 207:1811–1823
- Madsen PT, Johnson M, de Soto NA, Zimmer WMX, Tyack P (2005) Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *J Exp Biol* 208:181–194
- Mann DA, Lu ZM, Hastings MC, Popper AN (1998) Detection of ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the American shad (*Alosa sapidissima*). *J Acoust Soc Am* 104:562–568
- McCosker JE (1977) Flashlight fishes. *Sci Am* 236(3):106–114
- Metzner W (1999) Neural circuitry for communication and jamming avoidance in gymnotiform electric fish. *J Exp Biol* 202:1365–1375
- Metzner W, Zhang SY, Smotherman M (2002) Doppler-shift compensation behavior in horseshoe bats revisited: auditory feedback controls both a decrease and an increase in call frequency. *J Exp Biol* 205:1607–1616
- Miller LA, Surlykke A (2001) How some insects detect and avoid being eaten by bats: tactics and countertactics of prey and predator. *Bioscience* 51:570–581
- Moller P (1995) *Electric fishes: history and behavior*. Chapman & Hall, London
- Montgomery JC, Coombs S, Baker CF (2001) The mechanosensory lateral line system of the hypogean form of *Astyanax fasciatus*. *Env Biol Fish* 62:87–96
- Moortgat KT, Keller CH, Bullock TH, Sejnowski TJ (1998) Sub-microsecond pacemaker precision is behaviorally modulated: the gymnotiform electromotor pathway. *Proc Natl Acad Sci USA* 95:4684–4689
- Munk O (1999) The escal photophore of ceratioids (Pisces; Ceratioidei): a review of structure and function. *Acta Zool* 80:265–284
- Norberg UML (2002) Structure, form, and function of flight in engineering and the living world. *J Morphol* 252:52–81
- Partridge JC, Douglas RH (1995) Far red sensitivity of dragon fish *Aristostomias titmani*. *Nature* 375:21–22
- Portfors CV, Wenstrup JJ (1999) Delay-tuned neurons in the inferior colliculus of the mustached bat: implications for analyses of target distance. *J Neurophysiol* 82:1326–1338
- Post N, von der Emde G (1999) The 'novelty response' in an electric fish: response properties and habituation. *Physiol Behav* 68:115–128
- Rasnow B (1996) The effects of simple objects on the electric field of *Apteronotus*. *J Comp Physiol A* 178:397–411
- Ridou V, Guinet C, Liret C, Creton P, Steenstrup R, Beauplet G (1997) A video sonar as a new tool to study marine mammals in the wild: measurements of dolphin swimming speed. *Mar Mammal Sci* 13:196–206
- Russell CJ, Myers JP, Bell CC (1974) The echo response in *Gnathonemus petersii* Mormyridae. *J Comp Physiol A* 92:181–200
- Schnitzler HU (1973) Control of Doppler shift compensation in the greater horseshoe bat, *Rhinolophus ferrumequinum*. *J Comp Physiol A* 82:79–92
- Schnitzler HU, Kalko EK (2001) Echolocation by insect-eating bats. *Bioscience* 51:557–569
- Schnitzler H, Moss CF, Denzinger A (2003) From spatial orientation to food acquisition in echolocating bats. *Trends Ecol Evol* 18:386–394
- Schotten M, Au WWL, Lammers MO, Aubauer R (2004) Echolocation recordings and localization of wild spinner dolphins (*Stenella longirostris*) and pantropical spotted dolphins (*S. attenuata*) using a four-hydrophone array. In: Thomas JA, Moss CF, Vater M (eds) *Echolocation in bats and dolphins*. University of Chicago Press, Chicago, pp 393–400
- Schuller G, Pollak G (1979) Disproportionate frequency representation in the inferior colliculus of Doppler-compensating greater horseshoe bats, *Rhinolophus ferrumequinum*. *J Comp Physiol A* 132:47–54
- Simmons JA, Moffat AJM, Masters WM (1992) Sonar gain control and echo detection thresholds in the echolocating bat, *Eptesicus fuscus*. *J Acoust Soc Am* 91:1150–1163
- Speakman JR, Racey PA (1991) No cost of echolocation for bats in flight. *Nature* 350:421–423
- Stoddard PK (1999) Predation enhances complexity in the evolution of electric fish signals. *Nature* 400:254–256
- Stoddard PK (2002) Electric signals: predation, sex, and environmental constraints. *Adv Stud Behav* 31:201–242
- Surlykke A, Moss CF (2000) Echolocation behavior of the big brown bat, *Eptesicus fuscus*, in the field and the laboratory. *J Acoust Soc Am* 108:2419–2429
- Teyke T (1988) Flow field, swimming velocity and boundary layer: parameters which affect the stimulus for the lateral line organ in blind fish. *J Comp Physiol A* 163:53–61
- Tian B, Schnitzler HU (1997) Echolocation signals of the greater horseshoe bat (*Rhinolophus ferrumequinum*) in transfer flight and during landing. *J Acoust Soc Am* 101:2347–2364
- Thomas JA, Moss CF, Vater M (2004) *Echolocation in bats and dolphins*. University of Chicago Press, Chicago
- Toerring MJ, Moller P (1984) Locomotor and electric displays associated with electrolocation during exploratory behavior in mormyrid fish. *Behav Brain Res* 12:291–306
- Trappe M, Schnitzler HU (1982) Doppler-shift compensation in insect-catching horseshoe bats. *Naturwissenschaften* 69:193–196
- Ulanovsky N, Fenton MB, Tsoar A, Korine C (2004) Dynamics of jamming avoidance in echolocating bats. *Proc R Soc Lond B* 271:1467–1475
- Wanzenböck J, Scheimer F (1989) Prey detection in cyprinids during early development. *Can J Fish Aquat Sci* 46:995–1001

- Weihls D (2004) The hydrodynamics of dolphin drafting. *J Biol* 3:801–816
- Weissert R, von Campenhausen C (1981) Discrimination between stationary objects by the blind cave fish *Anoptichthys jordani* (Characidae). *J Comp Physiol A* 143:375–381
- Wenstrup JJ (1999) Frequency organization and responses to complex sounds in the medial geniculate body of the mustached bat. *J Neurophysiol* 82:2528–2544
- Westby GWM (1988) The ecology, discharge diversity and predatory behavior of gymnotiform electric fish in the coastal streams of French Guiana. *Behav Ecol Soc* 22:341–354
- Widder EA, Latz MF, Herring PJ, Case JF (1984) Far-red bioluminescence from two deep-sea fishes. *Science* 225:512–514
- Wotton JM, Jenison RL, Hartley DJ (1997) The combination of echolocation emission and ear reception enhances directional spectral cues of the big brown bat, *Eptesicus fuscus*. *J Acoust Soc Am* 101:1723–1733
- Xitco MJ, Roitblat HL (1996) Object recognition through eavesdropping: passive echolocation in bottlenose dolphins. *Anim Learn Behav* 24:355–365
- Zakon HH (1987) Hormone-mediated plasticity in the electrosensory system of weakly electric fish. *Trends Neurosci* 10:416–421