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CHAPTER 26

Neuroethology

From Morphological Computation to Planning

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Introduction

Neuroethology is a field devoted to understanding the nervous system through the broader contexts of evolution, natural history, ecology, and everyday behavior; in other words, it is the study of situated nervous systems. Its focus is on how neural systems subserve behaviors that an animal performs in its natural habitat, such as capturing prey and evading predators, finding a mate, and navigating through its domain. Often the nervous system is examined in animals that exhibit extraordinary specializations in behavior, such as sonar-emitting bats and fish that hunt by detecting changes in a weak, self-generated electric field, because such specializations result in specialized neural circuitry, making neuron-level analvses more tractable. These experimentally tractable animals are sometimes referred to as "model systems." People generally prefer to work with an established model system so that they can build on a body of knowledge that has already been gathered about the system.

As a combination of the laboratory science of neurobiology and the field observation science of ethology, neuroethology has significant challenges, including determining how much of the ecological context of an animal is necessary or practical to import into the laboratory (for a review, see Pfluger & Menzel, 1999). Once the animal and its reduced environment are in the laboratory, another problem to be solved is how to extract, from its continuous and highly irregular activity, a particular behavior to focus on. One way that this issue has been dealt with historically (Pfluger & Menzel, 1999) is through avoidance of learned behaviors in favor of highly stereotyped innate behaviors. More recently, neuroethology has embraced model systems for studying limited forms of learning, such as the zebra finch (Marler, 1001), which learns its song from a tutor only during the first thirty-five days of life. After this period, the song is "crystallized" and does not vary.

With a behavior identified and characterized, the next step is to uncover its putative neural basis. Here a new set of issues

comes into play, centered on the technical difficulty of obtaining reliable recordings of the electrical activity of the animal's nervous system. Often this may not be feasible unless the animal is under anesthesia. Options include working on a "reduced prep," in which slices of brain, dissociated cells, or whole parts of the nervous system may be placed into a chamber where they can be perfused with oxygen, nutrients, or neuroactive drugs and stabilized for recording. A better approach, comparatively rare because of its technical difficulty, is implanting one or more permanent recording electrodes in the brain, mounted on a platform that is glued to the head with the signals sent out via cables or wirelessly; this technique is called "chronic recording." Such tools at best monitor the ongoing activity of one to hundreds of cells in networks that can consist of millions of cells (and only the electrical activity, at that). Larger-scale properties, spanning multiple networks, biomechanics, and behavior, are sometimes examined through the development of computer models of individual components that are then recombined in computo in simulation environments, an endeavor sometimes referred to as "computational neuroethology" (Chiel & Beer, 1997; Cliff, 1995). This then is the neuroethologist's modus operandi: find an animal offering certain experimental conveniences such as behavioral specializations, identify and quantify a behavior, and measure its neural correlates, if possible in the "awake, behaving animal," or if not, in some reduced preparation while delivering stimuli similar to those occurring during the identified behavior.

Neuroethology has several aspects that will be of interest to the situated cognition community. Because ethology is all about what goes on when an animal is embedded in its environment (consider the title of an important monograph of one of its founders: *The Animal in Its World* [Tinbergen, 1972]), and neurobiology is all about what goes on in the brain, often with only cursory attention to matters beyond the periphery of the head, how can the enterprise of neuroethology

work in the first instance? Even if you do not believe that the properties of interest in neuroethology relate to cognition, how the tension between the outside-the-body tendencies of ethology and the inside-the-head tendencies of neurophysiology plays out in neuroethology is alone instructive. That these aspects can be in tension needs further explanation; otherwise one might think that this is simply a matter of groups of scientists working on different parts of a big problem, where everyone recognizes that a division of labor is practical and necessary. Neurophysiological approaches often implicitly suggest that many, perhaps most, components of the nervous system can be understood without examining an animal's larger context, be it behavioral, biomechanical, or evolutionary. In contrast, neuroethologists believe that unless the larger context is understood - for example, by quantifying the profile of sensory signals that an animal is subject to in its habitat or by placing neural characters of related animals into phylogenetic trees ("neurocladistics") - many aspects of neural function will not be understood. Exemplifying this point, in several model systems neuroethologists have found that neural circuits involved in sensory processing exhibit very different response properties when they are subjected to naturalistic stimuli than to the nonnaturalistic stimuli more commonly used in neurobiology, because these are easier to generate and manipulate experimentally (see Sharpee et al., 2006, and references therein).

In view of these considerations, in the first part of the chapter I will discuss how the tension between the inward- and outwardlooking approaches of neuroethology may be resolved through excising bits of the world and encapsulating them into virtual reality apparatuses in the laboratory. In the second part of the chapter I will argue that results from neuroethology do, in fact, relate to cognition. Here I will first detail results from studies of morphological computation that expose the computational role of shape and structure in animal bodies in adaptive behavior, and then I will describe some recent results concerning the neuroethology of prey-capture behavior that may give insight into the origin of the paradigmatically cognitive faculty of planning. I will argue that the evolution of sensing systems that enable animals to perceive their environment far beyond the bounds of where they are immediately moving, possessing a *buena vista*, if you will, is key to the origin of planning. I call this the Buena Vista Sensing Club hypothesis. Through planning, members of the Buena Vista Sensing Club are able to make better use of this space in the guidance of their behavior than their more reactive *mala vista* brethren.

1. Internalism, Externalism, and Virtual Worlds in Neuroethology

The methodological and philosophical basis of neuroethology takes the situatedness of organisms as a basic fact and works forward from there. Both traditional cognitive science and much of neurobiology differ in emphasis, focusing on what goes on in the head (Clark, 1997; Hutchins, 1995; Noë, 2004; Rowlands, 1999; Wilson, 1995). This craniocentric approach often goes by the label of "internalism." What is variously called "situated cognition," "embodied cognition" (Ballard, Hayhoe, Pook, & Rao, 1997; Haugeland, 1998), "distributed cognition," "sensorimotor accounts of perception" (O'Regan & Noë, 2001), "active externalism" (Clark & Chalmers, 1998), "enactive externalism" (Noë, 2004), and "wide computationalism" (Wilson, 1994) all share the view that the properties of interest can depend on the head plus body plus environment. I will refer to these different approaches as "externalism."

Although situatedness is basic to neuroethology, as alluded to in the introduction, it is true that its two contributing disciplines pull in different directions: ethology to externalism and neurobiology to internalism. How is this tension resolved in neuroethology? Consider investigations into the sensory systems of two popular model systems in neuroethology, both nocturnal

animals that - like miners wearing headlamps - provide their own source of illumination for perceiving their dark environments: sonar-emitting bats and electric field-emitting fish (Figure 26.1a and 26.1c). For both model systems a substantial part of the sensory system exists in the interplay between generated signals and objects in the environment (Nelson & MacIver, 2006). Thus, a fundamental part of the literature is devoted to describing and analyzing how the self-generated signals propagate and interact with the environment - characterizing the sensory system as it operates outside of the body of these animals (on bats, see Boonman & Jones, 2002; Ghose & Moss, 2003; Hartley & Suthers, 1989; Miller & Surlykke, 2001; Parsons, Thorpe, & Dawson, 1997; Schnitzler, Moss, & Denzinger, 2003; on fish, see Assad, Rasnow, & Stoddard, 1999; Chen, House, Krahe, & Nelson, 2005; Rasnow, 1996; Rasnow & Bower, 1996). Recently, this work has been referred to as research into the sensory ecology of an animal (Barth & Schmid, 2001; Dusenbery, 1992). In these studies, the nervous system of the animal may hardly be mentioned.

Whereas the externalist tendencies of neuroethology have their most literal form in the context of this work on the activesensing model systems of bats and weakly electric fish, the focus on the relevant aspects of the external world in behavior is pervasive in the discipline, from characterization of odor plumes for studies of moths (Murlis, Willis, & Carde, 2000) to reconstruction of what a fly sees while it is buzzing around in an open field (van Hateren, Kern, Schwerdtfeger, & Egelhaaf, 2005). As pointed out by James J. Gibson (1979, p. 57), the pioneer of ecological approaches to perception, mechanical signals in the environment (stress, strain, pressure, inertia, gravity, friction, drag) are no less important in understanding behavior than are sensory signals in the environment. Neuroethologists therefore have an increasing stake in investigating mechanical factors with respect to both the animal and the environment (e.g., Chiel & Beer, 1997; Dickinson, 1996; Full & Tu, 1991; MacIver, Fontaine, & Burdick, 2004).

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Figure 26.1. Sensory volumes of different active sensing animals. a. Bat echolocation beam; the illustrated range is the estimated detection range for small prey (mosquitoes) averaged across several bat species. b. Dolphin; the illustrated range is the estimated detection range for a prey-sized, water-filled sphere. c. Weakly electric fish; the illustrated range is the estimated detection range for small prey (water fleas). d. Rat whisker system. Reproduced with permission from Nelson and MacIver (2006).

In parallel with sensory ecology, I refer to this as an animal's "mechanical ecology."

Those with internalist leanings should not fear, however. First, there is the safe refuge of the cognitive; to take this refuge, the internalist would argue that what we are considering here are not cognitive properties in the first instance, whereas only the notion that cognition depends on the brain was at issue. I will return to this point later. Aside from this defense from the irrelevance of neuroethology, recall that the modus operandi of the neuroethologist is to eventually relate natural behaviors to neuronal structures. This is done by recording neural activity either in awake, behaving animals or, more often, in fixed and anesthetized, or otherwise drastically reduced, forms (e.g., brain slices). "Aha!" our internalist interlocutor will exclaim, "Now we get to the important business: what you are really interested in is what goes on in the brain; you're not stuffing recording electrodes into the environment, are you?" There is some sense to the internalist's intuition in this

case. My argument is not that the important properties of interest depend on the brain alone, which internalism would insist on (at least for cognitive properties). Instead, often the properties very definitely do depend on the brain plus body plus environment, but the elements of the causal chain that are most resistant to being understood are largely in the brain and body alone, in part for mundane technical reasons such as accessibility to measurement. Evidence for this claim is that, in some cases, we have the capability to mimic the animal's world in such a way that the animal does not know any better. I will present three examples of virtual worlds used in neuroethological research that exemplify this point (Figure 26.2) for studies of insects, fish, and mammals. These virtual worlds pass the embodiment Turing test - animals situated in them happily converse with the proxy as if it were the real deal.

The first example is from work at the Max Planck Center for Biological Cybernetics, in Tübingen, Germany, in the late 1960s.



Figure 26.2. Three virtual worlds in neuroethology. a. Reichardt's closed-loop apparatus for the study of optomotor responses in house flies (Reichardt & Wenking, 1969). The fly is tethered on a rigid rod that senses the torques generated by the fly as it steers left or right and moves the surrounding visual panorama complementary to the motions that would naturally result from those torques. Modified from Reichardt and Poggio (1976). b. A closed-loop apparatus for the study of electromotor responses in weakly electric fish. The fish is held in the center of the tank either by mechanical constraint (not shown) or paralyzed by a drug and placed into a holder (not shown). Two graphite rods parallel to the fish deliver an electric field similar to what a nearby fish would emit. By bringing the frequency of the delivered field close to that of the fish in the tank (monitored via the vertical graphite rods), an electromotor behavior, the jamming-avoidance response, is triggered and sustained by following the fish's frequency changes. Similar to the apparatus in Watanabe and Takeda (1963). c. A closed-loop apparatus for studying the behavior of rats, based on Dahmen's (1080) similar device for insects and Götz and Gambke's (1968) servosphere. The ball is suspended by an air cushion. The animal walks while tethered to a force and torque sensor, whose signals are measured to alter the real time video projected onto the rat's visual surround. From Holscher et al. (2005) with permission.

During that time, Werner Reichardt used a preexisting system for recording the turning torque generated by flies that are flying while rigidly affixed to the end of a thin rod (Figure 26.2a). In his apparatus, the measured turning torque was transformed into a rotation of the surrounding visual panorama with an angular velocity proportional to the torque (Figure 26.2a; Reichardt & Poggio, 1976; Reichardt & Wenking, 1969), so that when the fly turned to the left or right, the surrounding visual scene changed appropriately. This approach has been heavily used in studies of fly behavior, from the neural basis of optomotor behaviors to learning and flight mechanics, as it enables precise

control of the stimulus and quantification of behavior.

The second example involves the elicitation of an interesting electromotor behavior in weakly electric fish. These fish discharge their weak electric field at a particular frequency that is both species specific and individual specific. When two fish happen across each other in their native habitat while discharging within a few hertz of each other, they will shift their discharge frequencies (via a motor nucleus in the brain) to avoid jamming their electrolocation systems. To study this behavior, a fish is placed in a tank and fixed in place either mechanically or by paralysis, using a drug (Figure 26.2b).

The fish's electric field is recorded, and a field that is slightly higher or lower in frequency than its field is introduced into the tank, eliciting the jamming-avoidance response (Watanabe & Takeda, 1963). The approach used here is again closed loop, because any changes in output frequency by the fish are monitored and used to adjust the frequency of the jamming stimulus so that the behavior can be continuously elicited. Using this method combined with neurophysiology, the jamming avoidance response became the first vertebrate behavior whose complete neural circuit from sensory input to motor output was understood (Heiligenberg, 1991).

The third example, also originally developed in the late 1960s at the Max Planck Center, is from studies by Karl Götz and others: an insect would walk on a sphere that counterrotates in such a way that the animal is always in one place, again greatly simplifying the measurement of behavior with video and the delivery of controlled stimuli. The original version, called a "servosphere," tracked the animal's location and fed the movement back to two motors that rotated the sphere so that the animal stayed roughly at the apex of the sphere (Götz & Gambke, 1968; Kramer, 1975; Varjú, 1975). A more recent variation (Figure 26.2c) does not use motors but instead has the animal tethered above the apex of a hollow sphere that is suspended by an air cushion and rotated by the animal's own movements (Dahmen, 1980; Holscher, Schnee, Dahmen, Setia, & Mallot, 2005). It comes as no surprise that two of these three examples stem from an institute devoted to cybernetics. For more details on this tradition see Eliasmith (this volume).

One response to these examples would be that this proves the internalist's point – the world does not matter; all one needs is to synthesize and input the right kind of signals. However, Alva Noë (2004, p. 224) makes a convincing case that far from being a triumph of internalism, the success of virtual reality scenarios is precisely what an externalist should hope for: it demonstrates that the elicited behavior depends on the brain plus the given part of the world. Nevertheless, the externalist may be given pause by considering the success of virtual-reality systems in neuroethology. These demonstrate that we understand the relevant couplings to the external world in select cases in a sufficient – not to say complete – way, whereas we have a long way to go to understand the internal goings-on of the brain and body.

2. Is Neuroethology Relevant to Situated Cognition?

I had mentioned that one way a cognitively inclined person might assert that neuroethology is not relevant to cognition is by arguing that the processes under consideration are not cognitive. That is, given that many cognitive scientists hold that the extension of cognition itself outside of the usual human case is controversial (Wilson & Clark, this volume), how can results on the zoo of small animals that neuroethology studies provide insight into situated cognition? The difficulty of bridging these two domains is exemplified by the mismatch between the cognitive capacities we attribute to humans with those attributes of nonhuman animals that are sanctioned by neuroethology. The attributions of neuroethologists have a distinctly mechanistic flavor, such as "encodes stimulus amplitude with neuron spike rate" or "rotates head to zero azimuth to target by comparing the intensity of sounds between the ears" or, on a behavioral level, "advertises fitness to a potential mate by the complexity of the song." Cognitive faculties, such as remembering, planning, and deliberating, have their clearest form in conscious, occurrent thought processes in humans, and their presence in nonhuman animals is not often broached by neuroethologists.

Nonetheless, an attraction of externalist approaches such as situated cognition is their ecumenical approach to all kinds of phenomena that have been previously barred from the tent of cognition. According to Adams and Aizawa (this volume), this more open approach is confused and results

from externalists (1) making the error of sliding from "x is causally coupled to a cognitive act" to "cognition is constituted by x," and (2) failing to clearly differentiate cognitive from noncognitive processes. An example they give of the first error is to make the jump from the fact that the reading of a thermostat is causally coupled to room temperature to the notion that the thermostat is constituted by the room-thermostat system. Similarly, they would argue, the fact that the cognitive act of long division with paper is causally coupled to the piece of paper is a fallacious basis for asserting that cognition is constituted by the human-paper system. However, unless one leaves cognition as an unanalyzed whole, it will have causally coupled subcomponents. Of these parts it would be correct, presumably, to make the move from causal coupling to constitution: in a case like this, the thermostat really would be constituted by the roomthermostat system. The key issue, therefore, is the proper characterization of what counts as cognition. Because this is poorly defined at present, I will take the strategy of considering causal proximity to cognition, in the hope that although we may not have a clear definition of cognition, we have some intuition about when we are closer to it or further away from it. We have clear intuition, for example, that the central processing unit in a computer is more proximal to a computation performed by the computer than is the table on which the computer is resting. Similarly, the most compelling examples of situated cognition are examples in which some bit of the world plays a central role: for example, the use of external objects such as maps during navigation (Hutchins, 1995). racks of letter tiles in Scrabble to remember words (Maglio, Matlock, Raphaely, Chernicky, & Kirsh, 1999), and paper and pen to manipulate numbers (Zhang & Wang, 2005). In these cases, one can reasonably argue that drawing the boundary of the cognitive at the skin is arbitrary (Clark & Chalmers, 1998).

With these considerations in mind (if not, perhaps, in the head), I will present results from neuroethology with a range of depen-

dencies on the external world and causal proximities to the cognitive. I should state at the outset that this is not meant to be a representative set of results; most of neuroethology consists of detailing the operation of neuronal circuits that support natural behaviors, and these will not be discussed. Even the preceding virtual-world examples are not representative of neuroethology as a whole because the discipline has a strong bias toward sensory systems and sensory acquisition, with only a few active systems for the study of motor function apart from the ones presented, such as research into the neural network responsible for chewing in crustaceans. This bias may be in part due to there being too few closed-loop apparatuses like those described previously, all of which require a considerable amount of engineering expertise. For a more representative sampling of neuroethology, I refer the reader to Web sites of neuroethology courses (Hopkins, 2005; MacIver & Nelson, 1996), surveys (Barth & Schmid, 2001; Carew, 2000; Hughes, 1999; Land & Nilsson, 2002; Zupanc, 2004), and conference proceedings of the International Society of Neuroethology.

Under the rubric of morphological computation, I will give the example of how the ears of bats perform a signal processing function by dint of their convoluted shape, and how the geometry of the fly compound eye may allow for the efficient extraction of self-motion from the optic-flow field. These two examples concern how the earlier mentioned sensory ecology of an animal, the ambient set of behaviorally relevant signals in an animal's habitat, is interwoven with preneuronal signal processing. I then briefly discuss bilateral symmetry, a ubiquitous feature of animal body plans, and the passive walker, a robotic model of human walking that consists of only rigid links and joints and yet is able to walk with a human gait. Both are examples of how the mechanical ecology of an animal (the ambient inertia, stiffness and compliance, drag or contact friction, and so on, of the animal and its coupling to the habitat) is interwoven with locomotion and control of position.

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Figure 26.3. A potpourri of bat pinnae. Ear-shape data and rendering courtesy of Rolf Müeller. The pinna is the outer ear; the tragus is the small pointed flap of tissue coming up from the base of the pinna.

These two examples of morphological computation highlight the importance of transneuronal processes in sophisticated signal processing and mechanical capabilities. However, the capabilities at issue are distant from more familiar examples of cognition. Following the section on morphological computation, I try to partially close the gap by exploring how recent work on the neuroethology of prey capture may give insight into one potential origin of the paradigmatically cognitive faculty of planning. On the basis of this work, I will argue that the sensory transcendence of the space of immediate movement provides a core basis of planning, an idea that I call the Buena Vista Sensing Club hypothesis. Given prior discussions of the relationship between planning and consciousness (Bridgeman, 1992, 2003), the Buena Vista Sensing Club hypothesis may also be a useful step in articulating an empirical approach to the evolution of consciousness.

2.1. Morphological Computation

2.1.1. BAT EARS

Bats have been a staple model system of neuroethology since Galambos and Griffin (1940) first elucidated the role of selfgenerated acoustic emissions in their nocturnal hunting behavior. In the intervening years, a host of laboratories have investigated how bats are able to perform their high-precision, high-speed prey-capture maneuvers in total darkness by using acoustic pulses, emitted from either the nose or mouth. The bat is a very successful example of an active-sensing system (eight hundred echolocating species worldwide), in which

an animal perceives the world via a selfgenerated signal source (Nelson & MacIver, 2006). From a signals perspective this is a remarkable feat, because all active-sensing animals must overcome spherical spreading (r^2) losses as a signal propagates away from them, as well as spherical spreading losses from the target back to the source, resulting in quartic attenuation of the signal with distance. Thus, to double their sensing range, active-sensing animals need to generate a signal at least sixteen times more powerful (Nelson & MacIver, 2006). As they hunt for prey, bats emit pulses of acoustic energy at frequencies of thirty kilohertz and above. The spectral composition of the signal varies greatly with species and habitat (Schnitzler et al., 2003). For example, bats that hunt in cluttered environments generate a call that has two components: a constant frequency (CF) portion followed by a downward frequency-modulated (FM) sweep. The CF portion of the call gives the bats better distance acuity, whereas the FM portion gives them multispectral cues concerning fine details of target shape and movement (Suga, 1990). During the final phase of a prey-capture sequence, called the "terminal buzz" phase, the bat rapidly increases the pulse rate (Ghose & Moss, 2003; Kalko, 1995) and switches exclusively to FM sweeps.

The bat is able to detect its horizontal angle (left-right bearing, or azimuth) to targets by analyzing both intensity and time differences in the sounds arriving at the two ears: if the target is to the left, the sound will arrive slightly earlier and with more intensity at the left ear than the right. However, an object's vertical position is not detectable in this manner. Instead, the intricate shapes of the bat's ear (pinnae) and tragi (Figure 26.3) provide cues to vertical elevation (Wotton, Haresign, & Simmons, 1995; Wotton & Simmons, 2000). Returning sonar cries follow different pathways through the pinna-tragus complex according to their angle of entry, inducing spectral cues that vary systematically with the elevation angle. The bat can then simply listen to these spectral cues to detect the elevation of the target. The conformation of skin and supporting tissue of the ear in the bat forms a computational device that solves a key problem in the localization of prey in three-dimensional space.

2.1.2 THE GEOMETRY OF THE FLY EYE

Movement through space creates a pattern of visual information called "optic flow." As you move forward through space, things to the side seem to move backward. The rate at which they move backward is a function of your distance to them, the horizontal angle, and your velocity: things looming directly ahead seem to hardly move at all. If you are rolling around the axis of forward motion, rather than translating (suppose you are flying in an ultralight airplane near the ground and a gust of wind hits so that one wing goes up and the other down), a different opticflow pattern occurs. Flies detect self-motion to help stabilize flight, and neuroethological evidence is emerging that the geometry and wiring of the photoreceptors on the eye of the fly make computing optic flow a trivial problem (Egelhaaf et al., 2002). A key finding has been that the orientations of the rows of photoreceptors along which the optic flow is computed, a function of the eye's geometry, coincide with the preferred directions of the neuron that those sensors connect to (Figure 26.4). A neuron dedicated to detecting a rolling motion of the fly connects to a row of sensors, ommatidia, that lie parallel to the optic-flow pattern that occurs on the eye when the fly rolls. Activation of that neuron would then be a reliable indicator that the corresponding optic flow, and thus rolling self-motion, is occurring.

The examples of bat ears and fly eyes show how the physical configuration of the body performs a sophisticated computational role in the life of these animals. Other examples include spectral filtering through pigmented oil drops in the eyes of birds (Varela, Palacios, & Goldsmith, 1993), distinct filtering •properties of ampullary versus tuberous electroreceptors in electric fish because of the presence of tightly packed skin cells in the lumen (Szabo, 1974), phonotaxis in crickets through resonance in their forelimbs (Michelsen, 1998;



Figure 26.4. Computing optic flow through eye geometry. a. Self-motion generates optic flow over the eyes. Arrows on the left plane represent the local motion vectors on the eye when the animal rolls around its longitudinal body axis. The local response properties of a neuronal tangential cell, the VS6 cell, are adapted to detect this particular self-rotation. It is assumed that with its large dendrite, this cell integrates signals from local input elements whose preferred directions (arrows on second-from-left plane) correspond to the direction of local motion vectors in roll-induced optic flow. b. Head of a female blowfly. White lines over the right eye indicate the course of ommatidial rows in the eye lattice. c. Organization of the receptive field of a VS6 cell. Orientation and length of arrows at different angular positions indicate the neuron's local preferred direction and motion sensitivity in the right visual hemisphere. o° azimuth and o° elevation corresponds to the point directly in front of the animal. Lines in the upper-left quadrant indicate the course of ommatidial rows, which are oriented vertically in the equatorial region of the eye (v-row). The direction of visual motion is thought to be analyzed mainly by interactions between ommatidia along the rows in the hexagonal eye lattice (cf. orientation of rows and arrows). In the dorsofrontal eye region, the course of the v-rows strongly shifts toward a horizontal orientation. This change in orientation is reflected by the change in local preferred directions of VS6 cells in corresponding regions of its receptive field. Text verbatim from Egelhaaf et al. (2002). Reproduced with permission.

Michelsen, Popov, & Lewis, 1994), and the role of cochlear micromechanics in hearing (Gummer, Hemmert, & Zenner, 1996; Russell & Kossl, 1999). In these cases, a significant amount of signal processing has been completed prior to entry of the signal into the nervous system. These examples show that key computations subserving adaptive behavior occur, in part, outside of the nervous system, a useful preliminary step toward the argument that cognition can depend on processes outside of the body. An important issue holding up acceptance of these points is how to relate the somewhat incommensurate form of analog computation apparent in these cases to the more mature notions of computation and algorithm complexity with digital representations (for an insightful discussion of the distinction between analog and digital, see Haugeland, 1981). This question, how computability over discrete spaces relates to computability over continuous spaces such as real numbers, has become a topic of interest over the past few years, and metrics such as the log of condition in the case of linear systems have been proposed (see reviews by Blum, 2004; Braverman & Cook, 2006).

2.1.3 BILATERAL SYMMETRY IN ANIMAL BODY PLANS

The bat and fly examples concern exploitation of structure in the sensory ecology of those animals. How do animals exploit structure in their mechanical ecology? A deep pattern connecting sensory processing and locomotion can be read in the bilateral symmetry of animals. All animals but sponges, jellyfish, comb jellies, and placozoans are bilaterally symmetrical. The bilaterian animal body plan, which appeared contemporaneously with the appearance of multicellular animals between 0.5 and 1.5 billion years ago, often includes high forward mobility along the midline axis (Grabowsky, 1994) and is closely coupled to cephalization, an adaptation that complements such mobility with a clustering of sensory organs around the anterior end of the organism. All vertebrates and most other highly mobile animals such as insects feature this neuromechanical complementarity. With this neuromechanical template (Full & Koditschek, 1999) came the active feeding behaviors and agile locomotion that correlate with the evolution of advanced nervous systems needed to control these behaviors (Conway, 1998; Dewel, 2000; Koob & Long, 2000; Northcutt, 2002; Paulin, 2005). I will return to these issues below when I discuss why the ability to sense objects distant from the body originated.

Consider what would happen during forward movement in a fluid were it not for symmetry around the midsagittal plane along which animals propel themselves: there would be an imbalance of drag forces

on the body, making the animal yaw (turn left or right) from the trajectory that is the shortest distance between two points. According to one theory of its origins, bilateral symmetry arose when a jellyfishlike ancestral form migrated from a midwater existence to crawling along the seafloor (Trochaea theory, Nielsen, 2001). Even when they are not moving on an aquatic or terrestrial surface, however, given their presence in volumes of water or air close to surfaces, all animals are more than two-dimensional creatures but not fully three-dimensional ones - even birds and fish typically move far less up and down than horizontally. As two-and-a-half-dimensional creatures, animals can exploit their bilaterally symmetrical sensory structures, such as ears, for control of horizontal bearing by simple comparisons between them, as in the bat (termed tropotaxis, and achieved by commissural fibers connecting bilaterally paired sensory nuclei in the brain; for more details, see Braitenberg, 1965, 1984; Hinde, 1970; MacIver et al., 2004). Thus, fundamental needs of efficient locomotion, and simple sensor-based control algorithms for the important decisions of leftward versus rightward movement via bilaterally paired sensory organs, appear to have been entrenched in the structure of animals since the dawn of their multicellular origins.

2.1.4 THE PASSIVE WALKER

Another observation concerning the importance of mechanical structure in subserving behavior comes from outside of neuroethology, in the field of robotics. Over the past several years, building on the work of McGeer (1992), Andy Ruina and others have been working on passive walkers. These robots, designed to be models of human bipedal walking, are able to walk with no energy other than the small amount imparted by an inclined plane, and nothing other than rigid links and joints. More recent versions use a very small amount of energy, similar to the amount used by humans, to walk on flat surfaces (Collins, Ruina, Tedrake, & Wisse, 2005). The implication of this work is that much of the efficiency



Figure 26.5. From reactivity with a mala vista to planning with a buena vista. Control and planning in prey-capture behavior as a function of the ratio between the sensory volume (SV) and the stopping motor volume (MV_{stop}) for two fictive animals: one (left) with the near unity ratio characteristic of many passive sensing animals that have poor acuity and active-sensing animals and another (right) with a large ratio to illustrate the rarer situation of long-range passive-sensing systems such as vision. a. With near-unity SV:MV_{stop} ratios, search proceeds in a raster-scan-like fashion through the environment. If a prey is close enough to be within one of these search tracks, it is detected and possibly captured. b. With large SV:MV_{stop} ratios, there is the possibility that multiple trajectories to a detected prey (dashed lines) can be assessed prior to action. After assessing multiple paths, one path is chosen (b1) that is longer than a path that may disclose the position of the predator to the prey too early (b2) or result in reaching an untraversable obstacle (b3).

of human movement may arise through having a skeletal structure and mass distribution that makes walking as energetically favorable to the body as swinging is to a pendulum. Such efficiency is enormously important: if we were as inefficient as the Honda bipedal robot Asimo, which requires at least ten times more energy per unit distance and weight (Collins et al., 2005), then with a full day's walking we would need to eat ten times more food than we typically eat. Further evidence of mechanical efficiency comes from computational studies using the technique of optimal control to find movements that minimize energy. These have

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derived commonly observed gaits in bipeds (Srinivasan & Ruina, 2006) and movements in fish (MacIver et al., 2004).

2.1.5 THE BONE-BRAIN CONTINUUM

A general pattern emerging from the work above is that regularities existing over disparate timescales in an animal's environment are absorbed by different systems of the body. The longest timescale regularities, such as the need for a balance of forces along the axis of travel to move in straight lines, are encapsulated at the level of structural tissues (bones, cartilage, chitin) in a bilaterally symmetrical body plan. The maintenance costs of these tissues are the lowest of any body material. The shortest timescale regularities, such as the current state of selfmotion, are encapsulated at both the structural level of sensor geometry and through energetically expensive neuronal processing, tissue which requires forty times more power per unit mass than bone (Martin & Fuhrman, 1955). The computations that an animal needs to move through space are spread across these systems. At this level of description, there is no basis for an invidious distinction between bone and brain.

2.2 The Buena Vista Sensing Club

The Buena Vista Sensing Club hypothesis suggests that the expansion of the range with which animals can monitor external space, relative to their usual velocity, has been one - perhaps the dominant - driving force for the evolution of the ability to plan. In most environments, distant goals cannot be effectively reached by single behaviors but instead require the sequencing of multiple behaviors. Although the sequencing could be purely reactive, it is clear that multiple approaches are possible when our perceptual world extends to a large expanse of heterogeneous space (Figure 26.5b); thus, at the very least, there is a basis for selection pressures that would lead to a capacity for evaluating multiple possible trajectories to a goal. The number of animals with the requisite sensory-mechanical balance conservatively includes cephalopods (squids, cuttlefish, octopus), raptors such as hawks and eagles, and many of the mammals. Before proceeding, I would like to address the question of why sensation jumped beyond the boundaries of animals in the first instance.

2.2.1 A BRIEF HISTORY OF TELECEPTIVE SENSATION

In his *Opticks*, Newton remarked, "Infinite space is the sensorium of the deity." In what ways is finite space the sensorium of lesser creatures? First, a bit of evolutionary background. Between 700 million years ago, the date of the earliest trace fossils of multicellu-

lar animals, and 1.6 billion years ago, the estimated time of the last common ancestor of plants and animals, all animals were unicellular and thus lacking a nervous system (Carroll, 2001; Meyerowitz, 2002). It seems likely that the nervous system is a solution to the problem of controlling the body when it is composed of more than a few cells (Nielsen, 2001), at which point diffusion breaks down as an effective communication system. Much of the nervous system is concerned with problems that arise from being mobile, and it appears that its evolution was greatly accelerated after animals discovered an appetite for eating other animals (Conway-Morris, 1998; Northcutt, 2002; Paulin, 2005). Consider the example of the tunicate, which has a mobile, bilaterally symmetrical larval stage, and a stationary (fixed to a substrate), asymmetrical adult phase: once it has reached its final resting spot, the tunicate digests much of its nervous system. Whether or not ignorance is bliss, for a sessile creature a brainless existence at least reduces the amount of grub it has to come by!

Let us consider the problem of sensorysignal-based movement guidance in some detail, because it appears central to the genesis of nervous systems. Our ancestors are unicellular animals for which, by dint of their small size, inertial forces on the body are dominated by drag forces (the ratio of these two is quantified by the Reynolds number). The simple consequence of this is that as soon as you stop generating forces to move, you will stop. Think of walking on normal ground versus skating on ice. In the former, as soon as you stop generating forces through your contact with the ground, you stop moving; in the latter, even after you stop pushing off the ice, you are still moving. In water, our ancestral environment, animals are in the viscous regime when they are below around a millimeter in size. As an animal grows larger, it enters the inertial regime, and now in the absence of active braking forces the animal will coast along through space for some time after cessation of force production. The relationship between control signals, such as those required to whip a flagellum to move

forward, and the point in space that the animal needs to reach, perhaps some tasty bacterium, is not straightforward in the inertial regime. This is because the animal cannot simply halt motion at the point of contact with the bacterium but needs to perform state estimation to predict how soon before the bacterium is reached it will need to shut off the generation of force as a function of its current dynamics (Paulin, 2005). Contact sensors such as mechanoreceptors are not sufficient: you need a teleceptive sensory system - one that can detect targets some distance away from your body without contact. There are several of these, most obviously the visual system, but also auditory, chemosensory, electrosensory, and the mechanosensory lateral line, which detects flow disturbances in water at a distance. For a given object, the maximal distance at which it can be detected using one of these teleceptive systems - as one moves the object in all directions around the body forms a surface we will refer to as the sensory volume (SV).

2.2.2 TELECEPTIVE SENSATION AND CONTROL

What determines how far away from the body, and in what directions, the sensory volume should extend to allow for effective control of the body in space? Consider the following scenario: you are driving along in the fog, able to only see a short distance in front of the car. Suddenly, a huge lumbering moose appears through the fog, standing in the roadway. You now have several options: step on the brakes, swerve, run into the moose, or some combination of these. Unfortunately, any action you take will be at least two hundred milliseconds after the moose-related sensory signals hit your retina, because of conduction and processing delays between the surface of your retina and the contraction of muscles in your lower or upper limbs. Now, if you see the moose three meters in front of the car, and you are going fifty kilometers per hour (fourteen meters per second), by the time you step on the brake, the moose is already going through your windshield. If we allow

about five hundred milliseconds for an evasive action such as braking or swerving to occur after you have initiated it (although actually it will be a function of, e.g., your velocity, mass, friction of the roadway-tire interface, braking power, speed of muscle contraction), that means you need to sense the moose around seven hundred milliseconds before contact, or ten or more meters away if you are going fifty kilometers per hour. In short, the neuromotor delay time plus the action time determine an effective horizon of reactivity; if you sense things inside of that horizon, you are powerless; if you sense things outside of the horizon, you will at least have time for the most basic of actions. This example gives a sense of the dynamic considerations involved in determining how far the sensory volume should extend in the direction of movement. As you extend your sensory volume beyond the horizon of reactivity, you allow for more than simple reactive control strategies, such as braking or swerving. With a buena vista, you can look far ahead and execute longduration plans such as multiple lane changes prior to an exit. However, note that these considerations only apply to less predictable features of the space - a situation where, as Haugeland (1998) nicely puts it, "perception is cheap, representation expensive" (p. 219). In less dynamic contexts, such as longrange navigation, and where perception is costly, guiding movement through internalized spatial maps may be more effective. If, for example, that moose on the road in front of you is actually stuffed, and has been inconveniently installed in the center of the road, you could eventually learn to avoid it early on, on the basis of your recognition, say, that it is just past the hairpin turn before Crazy Bob's Taxidermy and Pedicure. This represents the internalization of space in a form that, other than issues of changes in the space and the need to localize your position in the space, may be interchangeable with sensation. I will return to this point to discuss reports that active-sensing animals possess highly accurate spatial maps.

Whereas we have the concept of sensing range for discussing how the sensory volume

relates to control, there is no analogous concept for movement. In control theory, a discipline of engineering, where something can move over a given time span is called the "small-time reachable set," and I propose that this concept provides a usable motor system analogue to sensing range. To define it, we begin with a mechanical system characterized by a set of time-varying control inputs (e.g., for a car it could be rear-wheel rotational position and front-wheel steering angle). For this mechanical system one can estimate the small-time reachable set to be the region of space that the mechanical system can reach over a given time interval for all feasible control inputs (i.e., inputs that do not exceed the capacity of the system, such as a ninety-degree turning angle or acceleration beyond the power of the engine). The original work in this area concerns reachable sets of a kinematic car (e.g., Vendittelli, Laumond, & Nissoux, 1999), but more recent work treats the computation of reachable sets for continuous dynamical systems (Mitchell, Bayen, & Tomlin, 2005).

With the concept of the small-time reachable set, along with the notion of the sensory volume, I can address how the relative sizes of movement and sensing volumes relate to behavioral control. I will do this in the context of one popular model system for the study of sensory processing in animals, the weakly electric fish.

2.2.3 MOVEMENT AND SENSING SPACES IN WEAKLY ELECTRIC FISH

For studies of the weakly electric fish *Apteronotus albifrons*, the black-ghost knife fish, my colleagues and I have applied the concept of the small-time reachable set (hereafter termed the motor volume, MV) to determine the extent of the overlap between the motor volume and the sensory volume for detection and capture of prey (Snyder, Burdick, Nelson, & MacIver, 2007). As an object enters the weak electric field that the fish continually emits, distortions in the electric field are picked up by around fourteen thousand electroreceptors covering the entire body surface. These distortions

in the field are analyzed and used to direct subsequent behavior. Using the electric field and sensors as a teleceptive active-sensing system, the fish is able to hunt at night in the muddy rivers of the Amazon basin.

We quantified the three-dimensional shape and size of the electric fish's prey SV using a combination of behavioral and computational techniques that allowed us to estimate when the live prey could be detected (Snyder et al., 2007). The omnidirectional SV for prey is shown in Figure 26.6. The MV varies as a function of the time interval being examined, the fish's initial state, and the control inputs of the fish's musculoskeletal system over the time interval being considered. Because we do not have access to these control inputs, we estimated the MV empirically by analyzing motion capture data of these fish hunting for prey. The strategy we used was to look at all body displacements that occurred over a given time interval across multiple trials. We quantified the MV by placing a surface over the maximal displacements in all directions: thus, for each time interval. we obtained a particular MV. A fascinating and unexpected finding was that, similar to the SV, the MV is also omnidirectional, a testament to the remarkable morphology and maneuverability of these animals. Figure 26.6 shows the MV for three different time intervals, showing that it becomes larger and changes shape as the interval increases from over one hundred to seven hundred milliseconds.

We can now quantify how closely matched these two spaces are by coming up with a convenient measure of this match; we use the intersection of the two volumes divided by their union. When we examine this measure versus the time interval of movement, we find that the match is maximal at a time interval of about 432 milliseconds. The importance of this time interval is that it is close to the sum of the neuromotor delay and stopping times for the fish; it takes one hundred milliseconds for a detectable signal indicating prey to reach the brain and produce a behavioral reaction, and another two hundred milliseconds are required for



Figure 26.6. Sensory volume and motor volumes of a weakly electric fish. The prey SV (for a typical prey, the water flea *Daphnia magna*) and MVs of a weakly electric fish as a function of the indicated movement time. Adapted from Snyder et al., (2007).

the animal to come to a halt from standard hunting velocities and capture the prey. In other words, in an active-sensing animal, which has to invest metabolic energy to produce a sensing field, just enough energy is emitted for the animal to be able to detect the prey far enough out to stop. (Like many animals, these electric fish simplify the control problem of engulfing small prey by being nearly stationary at the point of ingestion.)

From an analysis of previously published data on bat prey capture we find evidence of a similar pattern: the echolocation SV (Figure 26.1a) is close to the MV at the sum of the neuromotor delay and the stopping time (Snyder et al., 2007). For convenience, I will refer to the particular MV associated with coming to a stop as an animal's stopping motor volume (MV_{stop}) .

When an animal needs to emit sixteen times more power to double its sensing range, we expect selection pressure against making the SV any larger than it needs to be. Here is where the great advantage of passivesensing systems, such as vision, becomes apparent: now the only cost associated with having a longer sensing range is having a larger eyeball and associated visual signal processing circuitry (Brooke, Hanley, & Laughlin, 1999; Land & Nilsson, 2002). With the resolution of our high-acuity visual systems, about one-sixtieth of a degree under ideal conditions, we can resolve a thirtycentimeter-long rabbit at one kilometer – a

distance that takes us more than ten minutes to walk at a good clip and about four minutes at a fast run. At night, and when our mechanical abilities are augmented by a vehicle, the relationship between our SV and MV_{stop} is not necessarily intuitive: we are strapping on a massive, fast mechanism that expands our MV_{stop}, while operating with low light levels, which shrinks our SV. The two factors combined with our considerable neuromotor latency result in surprisingly slow recommended night driving speeds from highway safety agencies (less than fifty kilometers per hour when using low-beam headlights; U.S. National Traffic Highway Safety Administration, 2004).

2.2.4 CONTROL AND PLANNING

How does this relate to control and planning? If the ratio of the SV to MV_{stop} is near one (Figure 26.5a), the set of behavioral options with respect to something just sensed is very small, limited to stopping, turning, and other behaviors that have simple relationships between sensory input and neuromotor output. We refer to these simple behaviors as "reactive" because there is only time for simple reflexive reactions. With simple mappings between inputs and movement, animals can embed control laws in parts of the nervous system like the spinal cord and hindbrain that feature minimal processing and conduction delays. As we increase the ratio of SV to MV_{stop}, an animal has the capacity to examine a larger space beyond that which it will immediately move several behavioral cycles into the future, where a behavioral cycle is the neuromotor delay time plus the time it takes to perform a simple action like stopping. The first consequence is that when targets of future behavior come into range, the animal has many options, and dynamics and neuromotor delays do not dominate potential response modes (Figure 26.5b). For example, an animal could sequence multiple behaviors to reach a goal, such as trotting over to a barrier, jumping over it, and then crouching under an obstruction. An animal with a

low SV:MV_{stop} ratio has little ability to evaluate different trajectories toward or away from the sensed object because of time and space constraints. With a large ratio, there will be multiple feasible trajectories to a distant goal. If these different trajectories vary in their likelihood of success, we would expect selection pressure to favor animals that are able to evaluate these different possibilities and then select the one most likely to lead to success.

Returning to the scene of Crazy Bob's Taxidermy and Pedicure, it is important to note that the preceding claims about control and planning are qualified by "with respect to something sensed." This is because we know that the ability to navigate through foraging areas far larger than the SV and return home is common among animals, whether they possess short- or long-range sensing systems. It appears that many animals develop a cognitive map of the larger territory over which they live, and they can index their position in this space either by using local landmarks or through path integration, where current position is estimated by updating some initially known position with each subsequent movement the animal makes (Hafting, Fyhn, Molden, Moser, & Moser, 2005). Provided that the features of interest in the space are not significantly altered between visits, it is quite conceivable that such animals could plan to revisit these features while relying only on path integration or on sensing of nearby landmarks.

In this way, a representation of space plus path integration or localization may be a good proxy for sensation. However, there are clear differences. Each unit of space contains potential harms and benefits for a typical animal. These fall into two categories: those items that are stable enough through time that their presence or absence can be internalized into an infrequently updated map of space, and those items that are not. In the former category are things such as environmental obstructions, the location of home, the level of the tide, where food has been cached for use during the winter, the location of flowering plants, and so forth.

Into the latter category is the present location of predators and prey and current weather conditions. Although there are clear advantages to being able to plan over stable features of the environment, planning over the SV is critical for predation and avoiding being preyed on. Because the shift to a mobile-predator lifestyle in the early Cambrian (more than five hundred million years ago) likely led to the innovation of the vertebrate head and related sensory structures from headless ancestors (Northcutt & Gans, 1983), any capacity that affects predatory ability has the potential to be a source of significant selection pressure on the nervous system of animals.

It is nonetheless interesting to consider some of the complex relationships among sensing range, rate at which the habitat changes over time, size of foraging area, animal speed, and accuracy of landmarkbased guidance systems. For example, bats appear to prefer linear landmark features between roost and foraging area (Schnitzler et al., 2003). This preference probably facilitates their observed reduced reliance on echolocation along bat flyways (preferred paths from roost to hunting grounds), as well as allowing a cruder spatial map (e.g., less frequent location updates) than would be necessitated if the bat were to follow a more fractal landmark structure at their high flying speed. Active sensing animals in general seem to have particularly accurate spatial maps (on electric fish, see Cain, 1995; Cain, Gerin, & Moller, 1994; on rodents, see Hafting et al., 2005; O'Keefe & Burgess, 2005; on bats, see Schnitzler et al., 2003). Clearly, however, there are many different ways that space can be internalized. For example, internalization could be as rudimentary as following a trail of chemical laid down by a fellow traveler, such as occurs with ants, or as complicated as the hippocampusdependent distributed spatial-cue binding found in mammals (Cohen & Eichenbaum, 1993).

A further difference between planning over sensed space and internalized space is that the latter may place significant demands

on structures such as the hippocampal formation that appears to be central to spatial cognition (Cohen & Eichenbaum, 1993; O'Keefe & Nadel, 1978; Hafting et al., 2005). An example of this is the seasonal expansion and shrinking of related brain structures in food-caching birds (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Sherry, Vaccarino, Buckenham, & Herz, 1989; Smulders, Sasson, & Devoogd, 1995). The shrinking and expansion of brain tissue with spatial memory load in these animals suggests that memory can be quite costly (Dukas, 1999). Quantification of this cost would allow us to assess the trade-off between maintaining a rapidly updated representation of space through sensation, with the associated costs of sensing (Laughlin, 2001), and a slowly updated representation that requires path integration or localization with the associated costs of spatial memory.

Ultimately, the tipping point between the effectiveness of single control laws versus planning (be it over internalized space or through sensing) may have to do with how densely occupied space is with behaviorally relevant contingencies, relative to movement speed and to the size of the MV_{stop}. This is similar to Levins's (1968) notion of environmental grain. Living in a very sparse environment and possessing long-range sensing systems, long reaction times, and a large amount of inertia (being massive and/or fast) is similar to living in a cluttered environment and having short-range sensing systems, short reaction times, and low inertia. The rain forest is not equivalent to a barren desert under equal sensory and movement conditions, but if the clutter of the rainforest contracts the SV or the desert increases speed, they could possess similar planning loads in this framework. In birds, it has been shown that flight speed increases with (body mass)^{0.167}, and visual resolution increases with (flight speed)1-33, so larger birds with more inertia resolve objects at longer times to contact than do smaller birds (Brooke et al., 1999). In bats, prey detection range is matched to the wingbeat interval, which in turn has a power law relationship

to body mass and flight speed (Holderied & von Helversen, 2003).

2.2.5 PUTTING BUENA VISTA TO THE TEST To test the Buena Vista Sensing Club hypothesis, ideally we would start with behavioral correlates of planning in a wide range of animals and relate them to their sensory and motor capacities. Unfortunately, adequate behavioral data on planning behavior are not available. Quantitative data on the motor and sensing spaces of a vast array of animals other than more modern vertebrates are also lacking. Cognitive neuroscientists, however, have been investigating the neural locus of planning in humans for some time. Thus, in lieu of the missing behavioral data, we will consider some of this evidence.

In humans, cognitive neuroscience has shown that the prefrontal cortex is important for planning (Damasio, 1985). Within primates, we know that humans have nearly doubled the volume of Brodmann's area 10, a prefrontal cortical area considered important for planning, over the closest nonhuman primate (Semendeferi, Armstrong, Schleicher, Zilles, & van Hoesen, 2001), whereas human visual acuity is not significantly better than that of other primates (Ross, 2000). This may be an exception to the Buena Vista Sensing Club hypothesis. However, the ability to plan without the help of symbolic methods such as language may have reached saturation in early primates. It is possible that with language and other symbol systems, hominids took planning to a new level. Although language is thought to be a more recent innovation than is compatible with increased frontal lobe volume, given recent evidence concerning the auditory capacity of early hominids, language use may be quite ancient (Martinez et al., 2004). Symbolic approaches can effectively extend a perceptual system to encompass an indefinite amount of space for planning through the reports from fellow symbol users; one example of this is the bee's waggle dance, which allows individual bees to communicate the location and richness of a foraging patch far beyond the SV of bees at the

hive. Given these considerations, comparing nonhuman primates, which as a group have larger eyes than other mammals (Ross, 2000), to other vertebrates may be more informative. Along these lines, it is known that mammals (which appear to make up the bulk of the members of the Buena Vista Sensing Club) have greatly increased the complexity of the forebrain over other vertebrates (Figure 26.7; Striedter, 2005).

One further point should be made to buttress the Buena Vista Sensing Club against complaints from members of the Mala Vista Sensing Club – all those animals with puny sensing ranges. They could argue that if anyone should have been pressured into having an ability to plan, it should have been them, because they would benefit even more from this ability than a Buena Vistite. There are three primary ways in which selection pressure to plan can be manifested. One is to evolve long-range sensing abilities, thus joining the Buena Vista Sensing Club. Another is through symbol use, such as language or waggle dances. The third is through an internal map plus path integration to determine where one is in that map, as discussed above. The first, joining the Buena Vista Sensing Club, is inapplicable, as we are addressing members of the Mala Vista Club. We will not consider the second, as symbolic approaches are rare. The third approach is possible, but we return to our previous point, that a capacity to plan over internalized space will not help with predation and avoiding being preyed on, both of which are significant sources of selection pressure on the nervous system. Whether other sources of selection pressure are sufficient to lead to planning is unclear. The presence of accurate spatial maps, and perhaps planning, in active-sensing animals would seem to suggest the answer is yes. However, two of the active-sensing modalities, echolocation and electrolocation, are in animals that have relatively recent, non-active-sensing ancestors. The ability to internalize large maps may be a holdover from long-range passive sensing habits and the exploitation of correspondingly large foraging areas - an echo of



Figure 26.7. Toward a comparative biology of planning. Phylogenetic tree depicting the relationships of major vertebrate groups. Numbers across the top indicate the number of cell groups experts have described in the forebrains of representative species. The symbols indicate approximately where forebrain complexity is likely to have increased (squares) or decreased (circles). Modified with permission from Striedter (2005).

an ancestral condition when perception was cheaper.

3. Conclusion

I began with a précis of how neuroethology navigates the sometimes contested realm of its own externalist and internalist leanings. In excising a piece of the world with an animal and coupling these together in closedloop apparatuses, neuroethology recognizes the unity of the external and internal in adaptive behavior. The virtual world examples also show that in some cases we understand the relevant external factors needed to elicit natural behaviors, whereas the neural and biomechanical underpinnings of these behaviors are still largely not understood; this in some measure supports an internalist bias in effort if not in philosophy.

As the first of two steps from neuroethology to situated cognition, I showed how present research on situated nervous systems within neuroethology is indicating the important computational role of nonneuronal sensory and mechanical structures in supporting adaptive behavior. Regularities in the world at multiple timescales

are encapsulated in the animal at a host of levels from structural tissues to neural responses, according to the temporal bandwidth of these regularities and associated energy trade-offs. For the second step, I elucidated how work on one model system in neuroethology, the weakly electric fish, may give insight into relationships among control, planning, and the ratio between the SV and MV_{stop}. I put forth the hypothesis that sensing beyond the MV_{stop} may be central to the evolution of planning. If true, the Buena Vista Sensing Club hypothesis naturalizes a formerly largely human faculty in a way that makes it approachable in more experimentally accessible animals.

Adams and Aizawa (this volume) raise the issue of the motivation for an externalist redefinition of cognition. As part of the effort to understand the intelligence of nonhuman animals, for neuroethologists the redefinition is driven by pragmatic needs. Craniocentrism simply does not work for understanding the kinds of quite sophisticated behaviors that neuroethologists are working on. As suggested by the three virtual-world examples, the instances of morphological computation, and the relationships among behavioral control, sensing, and mechanics I have discussed, they arise out of a tight interplay of body, brain, and environment, with deep ties to an animal's environment and evolutionary history.

I will end with some points about the implications of the Buena Vista Sensing Club hypothesis as it relates to extended mind issues and consciousness. In Clark and Chalmers's (1998) paper on the extended mind, they give the example of Otto the Alzheimer's patient and Inga - whose memory is unimpaired – determining the address of a museum. They argue that the address of the museum in Otto's address book, always with him, is functionally identical to Inga's (nonoccurrent) belief that the museum has some particular address. I would argue that the realm of readily interrogable space delivered by a long-range teleceptive sensory system can be equivalently thought of as an extended belief system; there as well, all potential subjects of perceptual fixation have the status of some type of belief in the extended cognitive system. The idea of the environment serving as an external memory story has been around since the 1970s, beginning with Dreyfus's work and later nicely encapsulated by Brooks in his "let the world be its own best model" (see Noë, 2004, p. 234, n14). Specific proposals as to how perceptual fixation via long-range sensing systems is important to cognition have been put forth by Dana Ballard and colleagues (Ballard et al., 1997). The need for members of the Buena Vista Sensing Club to manipulate this extended information space (LaValle, 2006) of beliefs to achieve distant goals would have gone quite beyond the capacity of reactive control strategies.

Bridgeman (1992) wrote, "Consciousness is the operation of the plan-executing mechanism, enabling behavior to be driven by plans rather than immediate environmental contingencies." Similar ideas were put forth by Humphrey (1992, p. 42). Consciousness, Prinz argues (this volume), is concerned with attention to intermediate-level representations that are useful for action. What I have presented here is a suggestion that planning, and perhaps therefore con-

sciousness, was only necessary once perceptual systems delivered choices at such a distance that reactive (nonconscious) control schemes for action were no longer advantageous. The lead-up to consciousness could therefore have been a gift of space wrought by passive teleceptive sensation in a niche where such acuity paid fitness dividends. The need to sequence behaviors over this space would then have given rise to executive control structures in the brain, including working memory and attention, for carrying out these sequences, in a case study of how "it is not the animal's brain that organizes its world, but the evolutionary ecology of the animal that organizes its brain" (Reed, 1996, p. 69).

Neuroethology, with its comparative approach and close attention to evolutionary, ecological, behavioral, and neural aspects of animal life, may at first seem an unlikely contributor to the field of situated cognition. However, as I hope the preceding examples have suggested, it is well poised to push forward our understanding of how simple and direct behavioral responses to sensory input can give way to abilities we more readily recognize as cognitive.

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