

The Senses as Signaling Systems

Abstract. A central goal of philosophy of perception is to uncover the nature of sensory capacities. Ideally, we would like an account that specifies what conditions need to be met in order for an organism to count as having the capacity to sense or perceive its environment. And on the assumption that sensory states are the kinds of things that can be accurate or inaccurate, a further goal of philosophy of perception is to identify the accuracy conditions for sensory states. In this paper I recommend a novel approach to these core issues, one that draws heavily on game-theoretic treatments of signaling in nature. A benefit of the approach is that it helps us to understand why biologists attribute sensory powers to such a diverse range of organisms, including plants, fungi, and algae.

1. The Need for a New Account

My leading question concerns the sensory capacities of biological organisms: What distinguishes these powers from other biological capacities organisms possess? My starting-point in addressing this question is Dretske's (1981: 56) brief characterization of the sensory: "think of an organism's sensory systems as channels for the receipt of information about their external environment." This characterization is echoed by Keeley (2002: 11): "think of the sensory modalities as 'avenues' into the organism for information about the physical state of the external world." The project here is to move beyond these slogans and offer a theory about what it takes to possess a sensory channel.

In line with the quotations from Dretske and Keeley, I am focusing on *exteroception*. I offer an account of what is required for an organism to sense its *external* (as opposed to *internal*) environment. The goal is to provide an account of exteroception that coheres with and illuminates practice in current biology. I want the account to be extensionally adequate in the

sense that it aligns with actual practice of attributing sensory powers in mainstream biology. Furthermore, I want the account to capture the underlying nature of biological sensory capacities, what makes them different from other biological features.

My project is continuous with Keeley's (2002) influential attempt to spell out the conditions an organism must satisfy in order to count as possessing a sense modality.¹ In the course of developing a view about how to differentiate the various sense modalities found in nature, Keeley offers an account of what it takes for an organism to possess a genuine sense. Keeley's discussion is especially relevant here because he shares the goal of articulating an account which can serve the purposes of biologists. Although his account has some nice features, it ultimately fails to satisfy this goal. It is extensionally inadequate.

Keeley (2002: 6) sums up his proposal as follows: "On my account, to possess a genuine sensory modality is to possess an appropriately wired-up sense organ that is historically dedicated to facilitating behavior with respect to an identifiable physical class of energy." According to Keeley, an organism with sensory powers must be endowed with a neural structure which evolved to be responsive to one of the fundamental forms of energy. Furthermore, this neural structure must be connected to the organism's central nervous system so as to allow the creature to respond behaviorally to the environmental stimulus.² In the interest of avoiding a lengthy digression on what counts as behavior, Keeley (2002: 15) cites Dretske's (1988: 2) gloss on behavior as *endogenously (i.e. internally) produced movement*. For my purposes it will be

¹ Keeley's discussion has had a significant influence on more recent philosophical investigations into the nature of sensory powers. See Picciuto & Carruthers 2014 and Matthen 2015. These more recent investigations have different aims from the one Keeley and I share. Keeley and I are attempting to articulate an account of the sensory that is useful for the biological sciences. Meanwhile, Picciuto & Carruthers are characterizing what they call 'a prototypical sense' and Matthen is discussing what he calls a 'traditional' notion of a sense.

² Cf. Burge (2010: 377): "The notion of a sensory system is a functional notion. A sensory system is a system of an entity capable of behavior."

useful to include this appeal to movement in my formulation of Keeley's account, even though Keeley falls short of endorsing this way of thinking about behavior.

Some features of this account are intended to confront real problems biologists face. Biologists will not wish to acknowledge a genuine capacity for electroreception in humans, even though we are able to discriminate live nine-volt batteries from dead ones by way of our tongues. Keeley's account handles this case by requiring *historically dedicated* neural structures. Further, biologists will not recognize genuine sensory powers when historically dedicated neural structures are no longer capable of servicing the animal's biological needs. Keeley hopes to confront the problem vestigial organs pose by requiring an ability to respond behaviorally to the relevant stimulus.

In spite of these strengths, Keeley's account is ultimately too narrow to serve the needs of practitioners of the life sciences. Biologists regularly attribute sensory powers to organisms which fail to meet the conditions specified. I will call attention to three problems along these lines.

First, biologists routinely attribute sensory capacities to organisms which lack neurons. Consider the single-celled *Paramecium*, which has no neurons and so cannot satisfy Keeley's conditions for possession of a genuine sense. Biologists assume that use of nerve cells is just one way for an organism to sense its environment. The *Paramecium* takes a more rudimentary path *via* receptors on the surface of an all-purpose cell. Greenspan (2007: 2) writes:

Senses go back a long way... Chemical sensing is almost certainly the original sense, given that life arose in the liquid environment of the sea and that even bacteria have a non-neuronal version of it. But with the arrival of multicellular animals, separate sense organs arose and with them the ability to see and hear as well as taste, smell, and touch. Sensory capacities evidently exist in the absence of distinct sense organs, and even in the absence of neurons altogether.

A second problem is that Keeley's account rules out the possibility of sensory processes disconnected from a creature's central nervous system. Biologists allow for the possibility of peripheral sensory systems, senses which can function independently of an organism's CNS. The octopus provides two illustrations of this point. First, octopus arms seem to be capable of controlling both voluntary and reflex responses to stimuli even when they have been denervated (Sumbre et al. 2001). In discussing a certain reflex response, Hague, Florini, and Andrews (2013: 103) write: "Overall, these observations provide indirect evidence that the arm has the sensory, integrative and motor elements capable of mediating a coordinated reflex withdrawal response to a potentially noxious stimulus." Second, in recent work on octopus camouflage Ramirez and Oakley (2015) argue that the octopus's ability to blend with surrounding colors depends on the ability of the octopus's skin to sense light. This study builds on previous work by Packard and Brancato (1993) which had shown that the skin's chromatic response to light can occur in dissociated or denervated skin.

A third worry about Keeley's account arises if we understand his behavioral constraint on sensory powers to require *movement* in response to a stimulus. This requirement straightforwardly conflicts with the pervasive practice among biologists of attributing sensory powers to sessile (immobile) organisms and to sessile stages of otherwise motile organisms. For example, there is widespread consensus among biologists that plants, algae, and fungi all possess sensory capacities.

For all of these reasons I think we would do well to make a fresh start on the problem of how to define biological sensory powers. But before I take up this challenge, I want to point out another shortcoming in attempts to develop Dretske's idea that sensory systems are channels for receipt of information. Dretske has advanced an influential approach to the question of how sensory error is possible. I will briefly indicate the need for a different approach.

Dretske's information-theoretic approach to the senses might appear to rule out the very possibility of sensory error. Dretske (1981: 45) insists that information is not the sort of thing that can be false. So the view that senses are channels for receipt of information would seem to exclude the possibility error. His strategy for accommodating sensory error appeals to the notion of biological malfunction. Sensory error occurs only when sensory systems fail to do what they were selected to do (Dretske 1986, 1988, 1995, Matthen 1988, Neander 1995, 2013). Natural standards of representational success and failure are present wherever organisms have structures devoted to relaying information about the environment. What these structures are *supposed* to do is fixed by their historical function, what they were selected to do. Talk of *error* is appropriate when information-conveying structures fail to do what they are supposed to do. All genuine cases of sensory error, then, are instances of malfunction, departure from normal sensory functioning for the species in question.

Elsewhere I have argued at length that Dretske's view of sensory error is problematic precisely because it ties error to departure from normal functioning for a species ([reference omitted for purposes of blind review], cf. McLaughlin 2016). Sensory systems in nature are routinely shaped by trade-offs which involve sacrificing accuracy for other ends like speed and energy efficiency. Acknowledging these failures of accuracy is central to understanding the adaptations of a species. Dretske's view is ill-equipped to accommodate sensory errors due to evolutionary trade-offs for the straightforward reason that they do not involve departure from normal functioning. They manifest themselves in the course of normal functioning.

I agree with Dretske that an information-theoretic approach to the senses needs to make room for the possibility of sensory error. After describing and defending my preferred account of the senses, I will return to the topic of error.

2. Senses as Signaling Systems

Consider again Dretske's preliminary characterization of a sensory system as a channel for receipt of information about the external environment. Typically a channel for information possesses a sender-receiver structure with signals conveyed from the sender to the receiver. Sender-receiver configurations are central posits of the mathematical theory of information and communication (Shannon 1948) and of game-theoretic treatments of signaling (Lewis 1969, Skyrms 1996, 2010a). A sender in a sender-receiver configuration (a signaling system) is something capable of receiving an external cue or stimulus as input and generating a signal as output,³ while a receiver is something capable of receiving the signal as input and generating an activity as output. For example, many animals susceptible to predation will send alarm calls when a predator is detected in the vicinity, and these calls incite heightened vigilance in those receiving them. Inter-organismal signaling systems like this one are composed of sender and receiver elements coordinated by mediating signals.

The central claim of this paper is a claim about the nature of biological sensory powers. The claim is that sensory systems are intra-organismal signaling systems with the same fundamental purpose and structure as inter-organismal signaling systems in nature. Like inter-organismal signaling systems, sensory systems exist because organisms face challenges which cannot be met effectively without information channeling. As Bowdan and Wyse (1996: 122) explain:

Organisms need information to solve at least three kinds of problems: (a) to maintain an appropriate environment, i.e., homeostasis; (b) to time activities (e.g., seasonal changes in behavior) or synchronize activities with those of conspecifics; and (c) to locate and

³ I have in mind signaling systems driven by *external* cues. Alarm calls by birds and other animals serve to illustrate signaling of this sort. Some signaling systems are instead driven by internal cues. For example, mating calls are typically triggered by internal (hormonal) states.

respond to resources or threats (e.g., by moving towards resources or evading or attacking threats).

Signaling is the central means by which organisms acquire the information they need. And whether the signaling occurs within an organism or between organisms, an evolutionarily stable signaling system includes senders and receivers coordinated in a way that allows organisms to make good use of the information conveyed by the mediating signals.

My view is that a biological sensory system must decompose into structurally distinct sender and receiver elements mediated by signals. At a minimum the sender component must include receptors (specifically, exteroceptors⁴) with the function of signaling, while the receiver component must be capable of generating discriminatory actions in response to the signals issued. A biological sensory system emerges once sender and receiver units arrive at an evolutionarily stable strategy. In the remainder of this section I spell out the details of this account of sensory powers, clarifying what I mean by ‘information,’ ‘receptor,’ ‘evolutionarily stable strategy,’ and ‘discriminatory action.’ In the following section I provide illustrations of coordinated sender and receiver units realizing sensory capacities.

The kind of information relevant in this context is what philosophers call *natural information*. The fruit’s bright coloration carries natural information about its ripeness, while the poisonous frog’s bright coloration carries natural information about its hazardousness. I endorse a version of Dretske’s influential account of natural information. Dretske (1981) takes natural information to be a relation holding between Kim-events (property instantiations). One event (the signal) carries natural information about another event (the signified) in virtue of the fact that the former changes⁵ the objective probability⁶ of the latter. Dretske maintains that the signal

⁴ When I speak of ‘receptors’ in what follows, I am talking specifically about *exteroceptors*. As I stated at the outset, I am following Dretske and Keeley and focusing on exteroception.

⁵ In biological signaling contexts, an event’s changing the probability of another event is more important than mere correlation between events. Animals tend to be good at internalizing probability-changing

must raise the probability of the signified to one. Like most theorists sympathetic with Dretske's general approach, I reject this specific requirement on the grounds that it is too demanding (Shea 2007, Skyrms 2010a, Scarantino & Piccinini 2010, Scarantino 2015, and Stegmann 2015). In biological contexts what generally matters is that the probabilistic correlation is strong enough for it to be productively exploited by organisms (cf. Millikan 2004: 44), but there is no harm in acknowledging natural information wherever the signal changes the probability of the signified—however slightly.⁷

We need the notion of information in order to understand the nature of receptors.⁸ Receptors are biological structures sensitive to a particular kind of energy, but this is hardly distinctive of receptors. Plants have a variety of photosensitive proteins which do not serve as photoreceptors, including proteins involved in photosynthesis (the process of converting electromagnetic energy into chemical energy to fuel an organism's activities) and photorepair (the process of utilizing blue light to repair DNA damage caused by exposure to UV rays). Photoreception is distinctive insofar as it exploits the stimulus (light) for *information* it carries about environmental conditions rather than for, say, *fuel*. Photoreceptors in plants are proteins specifically selected for the role of conveying information about environmental conditions (signaling), allowing a plant to coordinate its activities with environmental conditions in a manner that is biologically beneficial.

regularities and using them to guide future behavior. They are much less apt to make use of correlations between events which are not probability changing (Stegmann 2015).

⁶ I follow Skyrms (2010b: 157) in taking the relevant objective probabilities to be relative population frequencies.

⁷ It is one thing for a signal to carry natural information, another for a receiver to be in a position to exploit the signal for the information it carries. Natural information is supposed to be an objective commodity present in nature whether or not any creature is in a position to make use of it.

⁸ Some worry that the notion of information is too poorly understood to be fruitfully deployed in biological sciences like ecology (e.g. Owren et al. 2010 and Rendall et al. 2009). A more common perspective in ecology (e.g. Stevens 2013) acknowledges difficulties while insisting that the notion of information is nonetheless indispensable. My claim is that we cannot adequately distinguish sensory powers from other biological powers without invoking the concept of information (cf. Adams & Beighley 2013).

The receptors constituting the sender component of a sensory system have a biological function. Receptors are *for* something. They have a point or purpose that distinguishes them from other stimulus-sensitive items in an organism: they have the function of signaling. The notion of signaling, in turn, is a functional notion. Signaling has a point. It is for something further. This chain does not continue indefinitely. Nor does it run in circles. The terminus is an adaptive response to environmental conditions. If there were no such terminus, it would make no sense to speak of a function and so there would be no sense to speaking of receptors or signaling.

This functional dependence of receptors on adaptive responses makes them ideally suited to play the sender role in a sender-receiver arrangement. Within an evolutionarily stable signaling system, the sender has a role that defines it as a sender. Its role is to issue signals in response to environmental cues or stimuli. The signals, in turn, have the defining role of informing the activities of the receiver. What ultimately grounds the survival of a signaling system with its sender-receiver arrangement is the advantageous activity on the part of the receiver.

The idea of an evolutionarily stable strategy goes beyond the idea that members of the population do better vis-à-vis inclusive fitness *with* the signaling strategy than *without* conditioning their actions on signals; it also includes the idea that the signaling strategy is relatively impervious to mutations in the population. In principle we can acknowledge biological sensory powers when less robust forms of equilibrium are present,⁹ but I will focus on evolutionarily stable signaling strategies.¹⁰

⁹ We can even acknowledge sensory powers when they originally emerge through mutation—prior to their being favored by selective forces. What is crucial is that something is able to function as a receptor. For a notion of function that does not tie a trait's function to its evolutionary history, see Maley & Piccinini forthcoming.

¹⁰ Doing so is helpful in the context of discussing sensory content (§4).

Plant photoreception serves as a powerful illustration of a sender unit contributing to advantageous activity on the part of the receiver. In the following section I will discuss some examples of plant photoreception. In the meantime I need to say more about the receiver side of things. I noted above that the receiver element performs actions in response to signals received. In the first place I need to clarify when a response to a stimulus counts as *action* (as opposed to mere *reaction*).

When a plant is exposed to sunlight, some of its responses are mere reactions. For example, the plant may reflect green light¹¹ or its DNA may be damaged by UV rays. These reactions to sunlight contrast sharply with a plant's light-related activities like photosynthesis, photorepair, and photoprotection. The latter responses count as active because they are goal directed. Of course, plants do not have goals set by motivational states.¹² The relevant goal here is the biological goal of inclusive fitness. Since the larger project is to understand what biological sensory capacities are, it makes sense to focus on *biological* standards for action. And it is clear that photosynthesis, photorepair, and photoprotection count as active relative to the goal of inclusive fitness: in photosynthesis plants exploit incident light to fuel various activities crucial to a plant's biological success, in photorepair plants make use of blue light to repair DNA damage caused by exposure to UV rays, and in photoprotection plants confront excessive amounts of absorbed light by converting the surplus of energy into harmless thermal energy.

I have now specified what is required for the receiver unit's response to count as active. It must be goal directed. A further condition must be met in order for something to play the role of receiver in a signaling system. Not only must the organism's response to the stimulus be goal

¹¹ The green color of most plants is a consequence of the chlorophyll used in processes like photosynthesis. Being green itself does not appear to be *for* anything in plants.

¹² As a general rule, motivational states are explanatorily superfluous when it comes to making sense of reflex responses to stimuli. Think of the pupillary light reflex. My view is that motivational states first emerge in creatures capable of incentive-based learning, i.e. creatures susceptible to operant conditioning.

directed; the goal-directed activity must be caused in the normal way by receptor signaling dedicated to promoting that type of activity. Only then will the organism's response count as *discriminatory* action. Discriminatory action is a goal-directed response which exploits information carried by the stimulus.

One can give a partial characterization of receiver activity without mentioning the sender and its activity. One can say that it is an active (i.e. goal-directed) response to an environmental stimulus. But in order to specify its role *qua* receiver unit one has to talk about its place within a signaling system. While photosynthesis, photorepair, and photoprotection are clearly active responses to an environmental stimulus (light), they are not responses of sender-receiver configurations. They are not discriminatory actions. I turn next to some illustrations of discriminatory action.

3. Illustrations

One goal of the account of sensory powers introduced in §2 is to accommodate attributions of sensory powers in mainstream biology. The account is intended to include the cases Keeley's account rules out, so it allows for peripheral senses, for sensory capacities in creatures lacking neurons, and even for sensory powers in sessile creatures. A further goal of the account is to make these attributions intelligible by revealing the underlying nature of sensory capacities. In this section I show how the account sheds light on photoreception in plants.

I begin with the phenomenon of plant phototropism. Phototropic responses to light are manifestations of "a plant's ability to reorient organ growth toward (positive phototropism) or away from (negative phototropism) a directional light source" (Liscum et al. 2014). These changes in orientation have the function of optimizing light capture for purposes of photosynthesis. Accordingly, the way the plant's organs bend needs to be responsive to local

lighting conditions. In the early 1990s researchers discovered the class of photoreceptors at work in phototropism, namely, phototropins. Stimulation of phototropins by blue light initiates a signal in the form of redistribution of auxin, a plant hormone that stimulates growth. In positive phototropism auxin is transferred from the lit side of the plant to the shaded side, causing cell elongation in the latter (Briggs 2014). This alteration in growth pattern amounts to a bending of the organ towards the light.

There is general consensus among biologists that plant phototropism is a manifestation of sensory capacities. My sender-receiver model provides insight into this attribution of sensory powers. An adaptive response to environmental conditions (beneficial growth pattern) is traced back to receptor-driven signaling, where signaling is supposed to be a distinctive way of making use of a stimulus, exploiting the stimulus for information rather than, say, fuel. Photoreceptor signaling exemplifies the role of a sender unit in an evolutionarily stable strategy, while the advantageous growth pattern exemplifies activity of a receiver. Plant phototropism, then, encapsulates the basic components of a signaling system. Phototropic responses qualify as discriminatory actions, expressions of sensory powers.

In phototropism plants evidently exploit the stimulus for information it carries about the direction of the light source in the environment. Notice, though, that the very same stimulus (sunlight) can be exploited for information it carries about time of day. I offer two illustrations of this point, beginning with the phenomenon of photoentrainment. Plants use cryptochrome photoreceptors to discern external light and dark cycles in order to bring their circadian clock in line with day-night cycles, a process known as entrainment. Dodd et al. (2005: 630) have shown that “plants with a clock period matched to the environment contain more chlorophyll, fix more carbon, grow faster, and survive better than plants with circadian periods differing from their environment.”

We also find plants exploiting incident light for information it carries about time of day in the phenomenon of photoperiodism, the flowering response plants have to changes in the length of nights as seasons change. Some plants are referred to as “short day” plants because they flower only when nights are long, while others are referred to as “long day” plants because they flower only in response to short nights. The return of sunlight in the morning is detected by photoreceptors, including phytochrome, a receptor responsive to light in the red and far-red regions of the spectrum. Regulation of flowering by the photoperiod is crucial to the plant’s success: “Premature flowering limits vegetative growth and thus the accumulation of sufficient resources, while flowering too late puts the developing seeds at risk of harmful environmental conditions...” (Johansson and Staiger 2015)

One and the same stimulus is able to carry both temporal and spatial information in virtue of its changing probabilities. For example, light absorbed on the east side of a plant raises the probability of a source of light to the east, and the very same light absorbed after an extended period of darkness raises the probability of return of daylight. Of course, there is much more information here than any plant is in a position to exploit. There is information not just about return of daylight here and now, but information about return of daylight at many other locations and times. And this is just the tip of the iceberg.

Given the compresence of so much information in the stimulus, we have to look to the entire sender-receiver arrangement in order to determine which information carried by the stimulus is relevant to stabilization of the signaling system. We have to ask why conditioning behavior on signals is more advantageous than the best available strategy which does not do so. In the case of plant circadian rhythm, we have experimental evidence that plants do considerably less well when their cycles are not in sync with day-night cycles. Understanding why the strategy has stabilized goes hand-in-hand with understanding what type of discriminatory action the

stimulus is facilitating. In this example the cryptochrome photoreceptors are deployed for timing rather than, say, locating. The relevant information carried by the stimulus concerns time of day.

I have argued that my sender-receiver account of sensory powers provides insight into why biologists attribute sensory capacities to plants. On my view this attribution is ultimately grounded in the fact that plants possess evolutionarily stable, intra-organismal signaling systems which serve to coordinate plant activities with environmental circumstances. Although I have focused on plants, I could have made the same point by referencing research on fungi, algae, and even viruses.¹³ Biologists routinely invoke sensory powers to explain why organisms respond as they do to environmental stimuli. My account is intended to capture the underlying structure of this type of explanation. An adaptive response to external conditions is explained by appeal to receptor-driven signaling, where signaling is a process that exploits stimuli for information organisms need in order to confront problems of timing, locating, maintaining an appropriate environment...

4. Content in Signaling Systems

In §2 I introduced biological signaling as the fundamental means by which organisms gain the information they need to confront problems. Thinking of signals in information-theoretic terms has its advantages but also its limitations. There are contexts in which ecologists need to distinguish honest or true signals from dishonest or false ones. But if we think of signals in purely informational terms, it is difficult to see how error is possible. The informational content of a signal amounts to the way it changes probabilities.¹⁴ Informational content in this sense is not the

¹³ For the discovery of a receptor for communication between viruses, see Erez 2017.

¹⁴ A signal carries information in virtue of changing probabilities. For each type of event whose probability is affected by the signal, we can ask to what extent the posterior probability of the event has changed. We thereby arrive at one plausible way of capturing the informational content of a signal. Another option is simply to list the posterior probabilities for each of the events in question. These alternatives are distinguished by Godfrey-Smith (2012).

sort of thing that can misrepresent how things are in the world (Birch 2014, Shea et al. forthcoming). In this section I discuss a promising way of making room for error in inter-organismal signaling systems due to Nicholas Shea, Peter Godfrey-Smith, and Rosa Cao. I suggest that this strategy allows us to accommodate sensory error without invoking Dretske's problematic assimilation of error to malfunction (see §1).

Generally speaking, biological signaling systems are susceptible to deception. Mating calls are imitated to lure in prey, alarm calls are faked in order to distract an animal from food it has acquired, parasites mimic a colony's signature odor to gain admittance into the nest... The case I will focus on for illustrative purposes is a case of Batesian mimicry, deception in aposematic signaling (warning coloration). Bees and wasps have converged on a shared form of aposematic signaling. This type of convergence (referred to as *Müllerian mimicry*) has the advantage that different species share the costs associated with teaching naïve predators about their defenses (Stevens 2013: 46). There is experimental evidence that harmless hoverflies gain protection in virtue of possessing the same type of coloration (Dittrich et al. 1993, Stevens 2016). This feature of the hoverfly's appearance has no doubt been favored by selective forces because it affords protection.

Ecologists working on aposematism need a distinction between honest aposematic signaling and false signaling like that of the hoverfly. But this distinction eludes us if we think about the content of aposematic signals purely in informational terms. In order to accommodate the possibility of error in biological signaling systems, Shea et al. (forthcoming) have introduced the notion of *functional* content, which they contrast with *informational* content.

[W]e define functional content as follows. The messages in a sender-receiver system have functional content only if the system is at an equilibrium maintained by some selection process. If it is, then for each signal M , we ask whether there is a behavior...of the receiver

specific to M , in the sense that the receiver responds differently to M than it does to some other available signal... If so, we look at whether there is a specific state of the world that obtains on some occasions when the message is sent, where the relation between that state of the world and the behaviors produced by the message contributes to the stabilization of those sender and receiver behaviors. If so, that state is the content of M .

Acknowledging functional content allows us to make room for the possibility of error in aposematic signaling. Aposematism is a signaling strategy which encourages avoidance behavior. There is a specific type of event in the world that serves to stabilize aposematic signaling systems, namely, a prey's being unprofitable. An aposematic signal, then, means unprofitability at the signal's source. When harmless animals make use of aposematic signaling as a form of protection, the signals are false or inaccurate. Error occurs when the functional content of a signal does not match how things are in the world.

Notice that this approach to error in signaling systems does not assimilate error to biological malfunction. The hoverfly's aposematic signaling is not a product of malfunction or disorder—far from it! The hoverfly is engaged in a biologically adaptive form of deception. Nor is there anything statistically abnormal going on. Hoverflies routinely outnumber the model they are mimicking (Dittrich et al. 1993). Error depends on a discrepancy between the signal's functional content and how things are in the world, and functional content in turn depends on what type of event in the world serves to stabilize the signaling system. Error does not depend on biological malfunction.

Ecologists need to acknowledge error in the sensory realm as well. Doing so allows them to make sense of a variety of failures in goal-directed behavior (Kelley & Kelley 2014). Organisms routinely miss the mark because their senses deceive them. (Think, for example, of the sorts of task errors human and non-human subjects make when confronted with standard illusions in

experimental settings.) But if we follow Dretske and regard sensory systems as channels for the receipt of information, then we face a familiar problem. The informational content of a sensory signal is not the sort of thing that can be in error.

Fortunately, the notion of functional content introduced by Shea et al. is straightforwardly applicable to sensory systems as well if we think of these systems as signaling systems. Recall that photoperiodism is a strategy plants deploy in order to flower at the right time of year.

Photoperiodism involves two very different types of signal: (i) the signal (light) received by the plant's receptors and (ii) the subsequent signal issued by the receptors. The two signals are similar insofar as both raise the probability of return of daylight, and so carry information about return of daylight. They are, however, very different kinds of signals. Only the biological signal exists for the very purpose of signaling. When a signal exists thanks to its place in an evolutionarily stable strategy, it makes sense to speak of the signal's *functional content*, what it has the function of reporting about the world. Botanists tell us that what stabilizes the signaling system in question is return of daylight. So the plant's photoreceptor output signals return of daylight. Notice, though, that these signals can also be triggered by artificial light at night. In floriculture (cultivation of flowers) artificial lighting conditions are routinely deployed to induce out-of-season flowering. Here we have a discrepancy between functional content and how things are in the world. We have sensory error.

It is beyond the scope of this paper to develop a fully general account of sensory content.¹⁵ My goal in this section has been the modest one of indicating how an information-theoretic approach to the senses might allow for the possibility of error. As I stated in §1, I do not think that Dretske's influential approach to this issue is entirely successful. I have sketched an alternative that avoids Dretske's problematic assimilation of error to malfunction.

¹⁵ One question for future inquiry is how to capture the functional content of signaling systems in which the receiver is capable of a wide variety of actions in response to a given signal.

5. Conclusion

My primary goal in this paper has been to introduce and motivate a new account of biological sensory powers. At the heart of the account is the idea that senses are evolutionarily stable signaling strategies with the same underlying structure and purpose as inter-organismal signaling strategies in nature. Senses involve structurally distinct sender and receiver elements coordinated by mediating signals. These sender-receiver configurations are favored by selective forces because they allow a creature to acquire and exploit information needed to solve problems of locating, timing, maintaining an appropriate environment...

In my remarks on plant senses I have attempted to unearth the most basic conditions that have to be met in order for an organism to count as having the capacity to sense its environment. A sensory capacity requires structurally distinct, functionally defined units—sender and receiver—causally mediated by signals sent from the sender to the receiver. The sender unit must at the bare minimum include exteroceptors, items with the function of issuing signals in response to environmental stimuli. Meanwhile, the receiver unit must be capable of initiating an adaptive response to the signal issued.

I have highlighted two advantages of my sender-receiver account of sensory powers. First, it coheres with and illuminates actual practice of attributing sensory powers in mainstream biology. Second, it holds the promise of yielding an attractive approach to the accuracy conditions of sensory states.

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