**A role for representations in inflexible behavior**

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**Abstract**

Representationalists have routinely expressed skepticism about the idea that inflexible responses to stimuli (e.g. reflexive responses like the pupillary light reflex) are to be explained in representational terms. Representations are supposed to be more than just causal mediators in the chain of events stretching from stimulus to response, and it is difficult to see how the sensory states driving reflexes are doing more than playing the role of causal intermediaries. One popular strategy for distinguishing representations from mere causal mediators is to require that representations are decoupled from specific stimulus conditions. I believe this requirement on representation is mistaken and at odds with explanatory practices in sensory ecology. Even when sensory states have the job of coordinating a specific output with a specific input, we can still find them doing the work of representations, carrying information needed for organisms to respond successfully to environmental conditions. We can uncover information at work by intervening specifically on the information conveyed by sensory states, leaving their causal role undisturbed.

**Introduction**

According to representationalists, behavior is sometimes best explained on the assumption that organisms are guided by *internal representations* of their environment. Typically the notion of representation is analyzed in information-theoretic terms: representations are said to *carry information* about the environment. Information, in turn, is usually analyzed in terms of probability: one thing (the signal or representation) carries information about another (the signified) in virtue of the fact that the former *changes the probability* of the latter.[[1]](#footnote-1)

There is widespread agreement that carrying information in the sense of changing probabilities is not sufficient for representation. Two familiar issues have to do with the fact that representations serve as stand-ins for things in the organism’s environment. First, we can assess stand-ins for their faithfulness to the things for which they are serving as stand-ins. They can be assessed as accurate or inaccurate, for example. But information in the sense described is not the sort of thing that can be inaccurate or incorrect.[[2]](#footnote-2) Second, serving as a stand-in by carrying information about the environment goes beyond just playing a causal role in the chain of events extending from stimulus to response. In a typical case of animal behavior, every link in the causal chain stretching from stimulus to response will carry information about the environment. Representations are supposed to be more than just causal mediators which happen to carry information (e.g., Ramsey 2007, Orlandi 2014, Shea 2018). Representationalists need to distinguish cases where information is doing important explanatory work from cases where information is simply along for the ride.[[3]](#footnote-3) My focus here is on this second issue.

The need to distinguish internal representations from mere causal mediators is particularly salient when we consider so-called *receptor* or *detector* *representations* in biological organisms. We can offer a preliminary characterization of a receptor as something that has been set up to be set off by a stimulus. My focus in this paper is on *exteroceptors* in biological organisms, receptors set up to be set off by *external* stimuli.[[4]](#footnote-4) When an organism’s exteroceptors are set off by stimulus conditions, the receptors issue sensory signals with the job of coordinating an organism’s outputs with environmental conditions. Here is a relatively simple illustration: in the pupillary light reflex photoreceptor signals have the job of coordinating pupil size with external lighting conditions in order to optimize light capture. One possibility is that this coordination is achieved *via* representation: the sensory states have the function of conveying information about light intensity and the pupils constrict or dilate in accord with the information conveyed. Another possibility is that the sensory states coordinate inputs with outputs simply in virtue of their role as intermediaries in the causal chain stretching from stimulus to response. Whatever information the sensory states may carry is explanatorily idle *vis-à-vis* the triggered response.

How should we go about distinguishing representations from mere causal mediators? One popular strategy is to require that representations are decoupled from specific stimulus conditions (e.g. Cantwell-Smith 1996, Haugeland 1998, Sterelny 2003, Ramsey 2007, Chemero 2009, Orlandi 2014, Shea 2018). According to this approach, representational explanations of behavior presuppose a form of stimulus independence. A representation must be suited to explain performance independent of any specific stimulus condition (stimulus-free performance). On the assumption that a representation does not depend on any specific stimulus conditions to play its role in the production of behavior, it is something different from a go-between or mediator, a mere stage in the sequence of events reaching from stimulus to response. Information is free to do important explanatory work only when it is set apart from a rigid, stimulus-driven sequence of events.[[5]](#footnote-5)

Adopting language familiar from Sterelny (1996) and Artiga (2016), I refer to proponents of a de-coupleability requirement as *chauvinist* representationalists because they wish to *exclude* representations from the lowly status of causal mediators. More specifically, chauvinists insist that representational explanations of behavior are appropriate only when the behavioral response is independent of a specific stimulus condition. Meanwhile, *liberal* representationalists allow that something can be both a causal mediator dependent on a specific stimulus condition and a representation of the world.[[6]](#footnote-6) Liberals and chauvinists disagree about cases like the pupillary light reflex. Suppose a creature’s pupillary light reflex is relatively simple and triggered by just one factor, namely, intensity of light at the eyes. Chauvinists are committed to denying that information is at work here. The sensory states which bring about the activities of constricting and dilating are go-betweens or causal mediators dependent on a specific stimulus feature (light intensity); the information carried by these sensory states does not help to explain the changes in pupil size. Liberal representationalists, on the other hand, reject the exclusionary thinking of chauvinists and allow that the information carried by sensory states can be explanatorily significant even when it figures in reflexive responses like the pupillary light reflex.

What is at stake in the dispute between chauvinists and liberals? In this paper I emphasize the relevance of this debate to explanatory practices in ecology. Researchers in disciplines like behavioral ecology and sensory ecology routinely and deliberately appeal to information in making sense of behavior, and much of the behavior to be explained is reflexive in character. If chauvinists are right, biologists run the risk of overestimating the explanatory significance of information in animal lives by overlooking the importance of a de-coupleability requirement. In what follows I argue that we do not need a de-coupleability requirement in order to distinguish the representational or information-carrying role of sensory states from their causal role. Even in highly inflexible behavior we find sensory states doing the work of representations, carrying information needed for organisms to respond successfully to environmental conditions.

The two most powerful considerations in favor of chauvinism are due to Dretske (1988) and Ramsey (2007). I begin by describing Dretske’s argument for the claim that information is explanatorily idle in cases of inflexible behavior, and then go on to respond to the argument. Next I address Ramsey’s influential claim that so-called *receptor representations* fail to satisfy the job description associated with representations. I close by relating my claims to broader issues in teleosemantics and ecology.

**Hard cases for liberal representationalism**

Liberals and chauvinists agree that a representation’s contribution to behavior must go beyond the role of causal mediator. So what is it that sets representations apart from mere causal mediators? Here I adopt Dretske’s (1988) information-theoretic approach, which highlights the *information-carrying role* of representations. Dretske’s proposal is that representations of the world are internal states which have been recruited to influence behavior because of the information they carry. Representational explanations of behavior are appropriate when the organism’s output is dependent on or sensitive to the information carried by these recruited states. In this section I provide a brief overview of Dretske’s theory and explain why, on first glance, the view seems to favor chauvinist representationalism over liberal representationalism.

Dretske is thinking of representations as states internal to a system that serve to coordinate the system’s behavior with external conditions. Internal representations are supposed to be suited to this role of coordinating a system’s outputs with environmental conditions because they carry information about those conditions. Dretske analyzes information in probabilistic terms: one thing (the signal) carries information about another (the signified) in virtue of the fact that the former changes the probability of the latter. In order for something internal to a system to count as a representation, it needs to be recruited for a coordinating role precisely because it carries information about the system’s environment. Dretske illustrates the idea of recruitment with the example of a thermostat. The designer of the thermostat is the one who does the recruiting, assigning the job of turning the furnace on and off to, say, a bimetallic strip. The designer chooses the bimetallic strip for the job because the strip is suited to carry information about room temperature.

Recruitment occurs in nature as well as technology. Dretske distinguishes two forms of natural recruitment. I begin with recruitment through feedback-based learning. One of Dretske’s illustrations of recruitment through learning involves the phenomenon of aposematism, the use of bright coloration to warn predators of unprofitability. Suppose an insectivore has some unproductive encounters with bees and wasps, who share the same form of aposematic coloration. Suppose, further, that the predator has photoreceptors responsive to the distinctive coloration of the bees and wasps. The sensory signals issued by these photoreceptors raise the probability of and thereby carry information about unprofitability. With the help of negative reinforcement learning, these sensory signals can be recruited to bring about an avoidance response. They are recruited for this purpose precisely because they carry information about unprofitability.

The other form of recruitment in nature is recruitment through natural selection. Once again aposematism provides a nice illustration. Poisonous dart frogs can be so lethal that there is no opportunity for trial-and-error learning on the part of predators: their aversive response to the bright colors of the frogs needs to be hard-wired. As with recruitment through learning, sensory states get recruited to bring about an avoidance response. In this case, however, recruitment occurs *via* natural selection.

Dretske notes that information is sometimes explanatorily irrelevant to how an organism responds to a stimulus. Information is idle, he thinks, in cases where a sensory state has been recruited through natural selection to trigger a response. Consider the predators whose visual states have been recruited through natural selection to bring about an aversive response. Suppose the predators become geographically isolated from honest aposematic signals, and the only remaining signals of the kind in their local environment are dishonest (i.e. instances of Batesian mimicry). With this change in the environment, their visual states no longer carry information about or represent unprofitability. Since their avoidance behavior has been hard-wired through the process of natural selection, the predators will continue on with the behavior regardless of the loss in meaning.​ Dretske infers that meaning is irrelevant to their behavior on the grounds that the predators behave the way they do whether or not the relevant meaning is present. We might say that the behavior is *stimulus dependent* rather than *information dependent*.

Contrast this case with the case where the predator’s visual states have been recruited through learning. With behavior recruited through feedback in the form of rewards and punishments (operant conditioning), we can typically alter the behavior just by manipulating the information carried by the conditioned stimulus. By adjusting the predictive value of the stimulus, we thereby control whether or not the conditioned behaviors get reinforced. When conditioned behaviors are not sufficiently reinforced over time, we usually find that the conditioned responses get extinguished.[[7]](#footnote-7) Hence, the behavior is not dependent on the stimulus *per se*; rather, it is dependent on the information carried by the stimulus. Dretske (1988: 96) captures this important feature of operant conditioning in the following terms: “Only here do we find *information*, and not merely the structures that carry or embody information, being put to work in the production and control of behavior.”[[8]](#footnote-8)

Dretske has spelled out one way sensory states can transcend the role of mere causal mediator. Sometimes the behavior elicited by sensory states is sensitive to the information they carry. When responses are shaped by operant conditioning, interventions on the correlational information carried by sensory states routinely influence whether or not the conditioned response continues unabated. This dependence of the organism’s behavior on the information carried by sensory states suggests that the sensory states are doing more than just serving as causal mediators; they are playing the sort of information-carrying role we expect of representations.

At the same time Dretske has called our attention to some hard cases for liberal representationalism. The liberal representationalist thinks that sensory states can have an information-carrying role even when natural selection does the work of recruiting the sensory states to produce certain outputs. But in these cases it is difficult to discern an explanatory role for the information carried by the sensory states. The output occurs whether or not the information is present. The output appears to be stimulus dependent rather than information dependent. Accordingly, it is reasonable to wonder whether these sensory states are merely serving as intermediaries in the chain of events spanning from stimulus to response. The information they carry appears to be explanatorily idle.

**Information at work**

The hard cases for liberal representationalism are cases where natural selection has set up receptors to initiate a specific response to a specific stimulus. Generally speaking, these inflexible responses to stimuli are adaptive because they serve to coordinate an organism’s outputs with environmental conditions conducive to the biological success of those outputs. Consider a phenomenon like induced ovulation, which has the purpose of synchronizing ovulation with the presence of a potential mate. Suppose the receptors driving the ovulatory response are chemoreceptors responsive to pheromones produced by males of the species in question. The sensory states issued by the chemoreceptors raise the probability of and so carry information about the presence of a male. Nonetheless, it is hardly obvious that this information helps to explain the ovulatory response. A causal mediator can do the job of coordinating events, so the fact that the sensory states are playing this coordinating role is not enough to establish that they are genuinely functioning as representations of the world. We need some evidence that the information explains the coordination.

I am granting that sensory states have a causal role to play in the production of inflexible responses to stimuli. Under specific stimulus conditions receptors issue signals, and these sensory signals are indispensable links in the ordered sequence extending from the stimulus to the response. However, in the usual case the stimulus condition is not itself the environmental condition with which the creature’s output needs to coordinate. Rather, the receptors exploit the stimulus condition for information it carries about ecologically significant features of the environment. For example, the chemoreceptors dedicated to inducing ovulation exploit the stimulus for information it carries about something beyond the chemicals themselves, namely, the presence of a potential mate. Coordination with the environment is achieved thanks to something additional to the causal chain extending from stimulus to response, namely, a chain of information stretching from the world to the output. The sensory state is an indispensable link in this chain of information.[[9]](#footnote-9)

In addition to their causal role in the successful coordination of inflexible responses with favorable environmental conditions, sensory states have an information-conveying role. One way to isolate the information-conveying role of sensory states is to intervene on the information they carry. Intervening on the strength of the information carried by sensory states can affect the biological success of the behavior dependent on those sensory states. Consider the predator’s hard-wired avoidance response to aposematic signals. Suppose we measure success of avoidance responses in terms of the percentage of responses which are *hits* (potential target is unprofitable) as opposed to *false alarms* (potential target is profitable). All else equal, the percentage of hits should increase with an increase in the ratio of honest signalers to dishonest ones in the local environment of the predator. Likewise, by decreasing the ratio of honest signalers to dishonest ones we can decrease the percentage of hits. Information, then, is very much relevant to the ​biological success​ of the behavior. In the limiting case where correlational information is removed entirely and the sensory states no longer carry information about unprofitability, the behavior will no longer enjoy the kind of success it previously had. This change in the informational content of the visual states helps us to understand why the avoidance response is no longer biologically successful.

This example illustrates the point that an organism’s inflexible responses to a stimulus can exhibit an important kind of informational sensitivity. The biological success of the response can depend on the informational content of the sensory state. That is, the sensory state’s informational content can be explanatorily relevant to the success of the organism’s hard-wired response to the stimulus. So even in the absence of feedback-based learning, an organism’s behavior can exhibit a kind of informational dependence understood as something distinct from stimulus dependence. Informational dependence can be pried apart from stimulus dependence through manipulation of the information in question. Accordingly, we have evidence that the sensory states are functioning as more than mere causal mediators. By intervening on the information crucial to the success of inflexible behavior, we thereby disrupt the coordination between behavior and suitable environmental conditions. Furthermore, we interfere with the coordination without thereby altering the causal role of the sensory states. This disruption through intervention on correlational information serves as evidence that the success of the goal-directed behavior is explicable in informational terms. We have evidence that sensory states are playing an information-conveying role.

My strategy in responding to the hard cases for liberal representationalism has been to adjust the explanandum of representational explanations of behavior. Dretske denies that the hard cases involve information at work because the job he has in mind is “production and control of behavior.” Once information-carrying structures have been recruited *via* natural selection to produce behavior, the role of information seems to drop out of the picture. Receptor signaling continues to produce the behavior whether or not the information in question is present. I have suggested that we come to appreciate the explanatory role of information in the hard cases if we attend to successes and failures of the reflexive responses. This alternative suggestion is natural. We expect internal representations to help explain why organisms succeed and fail in their goal-directed behaviors (Shea 2018; Ganson 2018a).[[10]](#footnote-10) Acknowledging a predator’s sensory representation of unprofitability helps us to explain why the predator succeeds in avoiding unprofitable temptations in plain sight. A visual representation of unprofitability also helps us understand why, in cases of Batesian mimicry, predators sometimes forego what would in fact be a profitable venture. Positing sensory representations of unprofitability helps to explain the biological successes and failures of a predator’s responses to stimuli.

In this section I have been defending a liberal version of representationalism according to which even highly inflexible behavior can be explicable in representational terms. My strategy has been to identify an aspect of the behavior which is sensitive to the information carried by sensory states, namely, the biological success of the behavior. We have (defeasible) evidence that an organism’s sensory states are playing an information-carrying role when we can compromise the biological success of the organism’s behavior by intervening specifically on the information carried by the sensory states, leaving their causal role intact.[[11]](#footnote-11) The result of the intervention is a failure of coordination between the behavior and those environmental conditions favorable to the biological success of the behavior. This failure of coordination serves to highlight the information-carrying function of receptor representations.

To be clear, the goal of interventions of this sort is not to reveal historical facts about why sensory states were recruited in the first place. We are taking for granted that the sensory states driving inflexible behavior were recruited by natural selection because of the information they carry. Behavioral ecologists distinguish between a trait’s adaptive significance understood as a historical property and its current utility (Bateson & Laland 2013). The goal of the intervention is to reveal the current utility of the information carried by the sensory states. Intervention brings to light how information-carrying is crucial to *current* success in coordinating outputs with environmental conditions. We should not agree with Dretske that information becomes explanatorily idle once natural selection has done the work of recruiting sensory states for the information they carry.

**Ramsey’s job-description challenge**

According to Dretske, representations have a distinctive job to perform: they are recruited to coordinate outputs with states of the world. They are selected for the task because they change probabilities, and thereby carry information. Ramsey (2007: ch. 4) contends that this job description is not really distinctive of representations. Something can be recruited to coordinate events because it changes probabilities, and it can do so without playing a representational or information-conveying role. Suppose I plant a tree at a certain location to coordinate shade on my porch with sunny afternoons. I recruit the tree precisely because the presence of the tree raises the probability of shade on my porch in the afternoon. The tree is recruited because of the way it changes probabilities of other things, but it is not thereby serving to inform or playing an information-conveying role. Rather, the tree is playing a causal role in the production of a certain outcome (shade). So, Dretske has failed to capture what it takes to have the job of carrying information.

Ramsey formulates his objection as a worry specifically about so-called *receptor representations*. Recall that receptors are set up (recruited) to be set off by certain stimulus conditions. For example, some molluscs quickly close their shell in response to a sudden absence of light, a protective response known as *the shadow reflex*. The stimulus condition (sudden onset of darkness) triggers an excitatory response in dedicated photoreceptors (Wilkens 2008), and the photoreceptor signals bring about the protective response (closing of the shell). Ramsey asks how this sort of receptor-driven behavior differs from the behavior of a gun. A firing pin in a gun is set up to be set off by the pressing of the trigger. It is recruited to coordinate pressing of the trigger with firing of the bullet. The characteristic movement of the firing pin raises the probability that the trigger has been pressed and thereby carries information about the trigger, but the information carried by the pin “is not relevant to the job it performs” (2007: 136). The firing pin is doing nothing more than serving as a causal mediator in the production of a certain outcome, namely, the firing of the bullet.

My response to Ramsey falls in line with my response to the hard cases discussed above. Ramsey’s objection overlooks the crucial fact that the signals issued by receptors (sensory states) have a job beyond serving as causal mediators in the chain of events stretching from stimulus to response. Sensory states have the additional job of conveying information about environmental conditions. Recall my strategy for separating this information-conveying role of sensory states from their causal role. We do so by intervening on the correlational information conveyed by the states, leaving their causal role unchanged. This sort of intervention reveals the role of information in achieving biological success. The success of inflexible behavior typically requires coordination between the behavior and suitable environmental conditions, and coordination demands more than a causal chain extending from stimulus to response. It also depends on a chain of information stretching from the environmental conditions to the response. Sensory states play an indispensable role in bridging this informational gap.

The point I am making pertains to biological exteroceptors in general (Ganson 2018b). What sets these receptors apart from other stimulus-sensitive structures is their job of conveying information about environmental conditions. For example, what sets plant photoreceptors apart from other photosensitive proteins in plants is the fact that they specifically make use of information carried by the light. Plants have a variety of photosensitive proteins apart from 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 in so far as it exploits light for information it carries about environmental conditions, rather than for, say, fuel. We see photoreception at work in plant activities like phototropism (reorienting growth towards or away from a light source), photoentrainment (aligning the plant’s circadian clock with day-night cycles), and photoperiodism (synchronizing flowering with the appropriate season). Each of these sensory-driven activities aims to coordinate a plant’s outputs with environmental conditions favorable to the success of the outputs. 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.

Why think that photoreceptor signaling in plants has a job beyond its causal role of initiating a specific response to a specific stimulus condition? The intervention strategy is once again useful in isolating an information-carrying role for sensory states. Take the phenomenon of photoperiodism. Plants have phytochrome receptors responsive to the long-wavelength light of the morning sunrise, and they use the timing of the return of daylight (i.e. length of the night) as an indication of season. Successful coordination of flowering with the appropriate season involves exploiting the light for information it carries about the return of daylight. We can set this information-conveying role of phytochrome signaling apart from its causal role by intervening on the information carried by the sensory signals. For example, floriculturists systematically alter the information carried by the sensory states, using artificial lighting conditions to bring about flowering out of season. This manipulation undermines the evolutionary goal of coordinating flowering with a specific season, and it does so by intervening specifically on the correlational information carried by the sensory states. The floriculturists leave intact the causal role of phytochrome signaling, its job of being a causal intermediary between a specific stimulus (return of light) and a specific response (flowering).

We are now in a position to see why Ramsey’s gun example is not a suitable model for thinking about receptor representations in nature. Consider again the shadow reflex in molluscs. Within the mollusc’s natural habitat, the sudden absence of light raises the probability that a predator is present. The mollusc’s photoreceptors have the job of coordinating the protective response with an increase in the likelihood of attack, and they do so by issuing signals which raise the probability that a predator is present. The correlational information carried by these sensory states has an important explanatory role to play in the biological success of the protective response. Imagine that a population of molluscs invades a habitat devoid of relevant predators, and in this new environment sudden cessations of light no longer increase the likelihood of attack. This change in the information carried by the sensory states helps to explain the dramatic decline in the success of the protective response (i.e. the ubiquity of false alarms). Meanwhile, correlational information is irrelevant to whether a gun achieves its designed purpose. The movement of the firing pin in the gun is just a link in the causal chain of events extending from the stimulus (trigger press) to the response (bullet propulsion). It does not have the additional purpose of carrying information about environmental conditions.

I conclude that Ramsey’s worry about receptor representations is misplaced. The signals issued by biological receptors (sensory states) have a role in inflexible behavior beyond the part of serving as a causal link between stimulus and response. Sensory states also have the job of carrying information about environmental conditions. Indeed, this information-conveying assignment is plausibly regarded as the *defining role* of receptor signaling. Sensory states have the function of conveying information, securing an informational link between outputs and suitable environmental conditions. They do the work of representations.[[12]](#footnote-12)

**Successful signaling systems require information**

We have found that receptors are more than just triggers set up to be set off by proximal stimuli. By the same token, stimuli are more than just catalysts in the production of adaptive behavior. Stimuli routinely carry information vital to the biological success of inflexible behavior. They do so either as *signals* or *cues*. Stimuli serve as signals when, like sensory states, they have the biological function of conveying information. Think, for example, of sex pheromones which have evolved to carry information about the presence of a potential mate. Like signals, cues are important because they carry information about the environment. Unlike signals, however, cues have not evolved for the purpose of carrying information. For example, in the shadow reflex the stimuli (shadows cast upon the photoreceptors) serve as cues suggesting the presence of a predator.

In some cases stimuli do not appear to be serving as signals or cues. They are not important because they carry information about environmental conditions; they are important because they are themselves biologically significant aspects of the creature’s environment. Consider again our leading example of inflexible behavior, the pupillary light reflex. The important aspect of the stimulus is not the fact that it carries information. Light intensity at the eyes is itself the biologically important aspect of the environment with which output (pupil size) needs to coordinate. What is optically significant for the purpose of optimizing light capture is having pupil size adjusted to light intensity.

The acoustic reflex in humans offers a further illustration. The acoustic reflex serves to protect the inner ear from dangerously loud sounds. Receptors in the inner ear responsive to intense acoustic stimuli issue sensory signals to motor neurons in the middle ear, and the resulting contractions of the middle-ear muscles have the effect of reducing the intensity of the sound energy reaching the inner ear. Once again the stimulus is not important because it conveys information about something further. The reflex is supposed to coordinate the defensive response with an aspect of the stimulus itself.

It is easy to misunderstand the interest of these cases. The important point about the acoustic and pupillary light reflexes is not the fact that the sensory states have the function of coordinating behavior with proximal rather than distal conditions in the environment. Aplysia’s familiar withdrawal reflex also has the function of coordinating behavior with proximal conditions, but the stimulus condition (contact) is still being utilized for information it carries. Physical contact is not itself a threat demanding the protective measures of withdrawing gill and siphon; rather, contact serves as a cue by raising the probability of danger. The acoustic and pupillary light reflexes are distinctive because they do not exploit stimuli for information they carry.

Should we conclude that the receptors involved in the acoustic and pupillary light reflexes are mere triggers set up to be set off by proximal stimuli? I think we should resist this inference. Even when receptors are not exploiting stimuli for information they carry, it is still reasonable to suppose that receptor signaling has the function of conveying information. As we shall see, this supposition allows us to bring unity to a diverse range of biological phenomena.

Generally speaking, when inflexible behavior has been selected for, the behavior exhibits a sender-receiver structure. We find sensory states functioning as signals in a sender-receiver configuration (signaling system). Here I am working with an orthodox understanding of signaling systems in nature (e.g. Millikan 1989, Godfrey-Smith 2013, Artiga 2014). A sender in a signaling system is something capable of receiving an external stimulus or cue as input and of generating a signal as output, while a receiver is capable of receiving the signal as input and of generating an activity as output. Alarm calls in nature provide a nice illustration of a signaling system. Many animals susceptible to predation will send alarm calls when there are indications of a predator in the vicinity, and these calls incite heightened vigilance in those receiving them. Inter-organismal signaling systems like this are composed of sender and receiver elements brought in line by mediating signals. We find the same underlying structure present in inflexible behaviors like the acoustic reflex. The receptors in the inner ear responsive to high-intensity vibrations serve as senders, while the muscles in the middle ear play the role of receivers. The sensory states issued by the receptors serve to coordinate muscle contractions with the presence of threatening stimuli. The sensory states function as signals within an intra-organismal signaling system.[[13]](#footnote-13)

A further aspect of signaling systems in nature is their status as evolutionarily stable strategies. The idea of an evolutionarily stable strategy goes beyond the idea that members of the population do better *vis-a-vis* inclusive fitness *with* the signaling strategy than *without* conditioning their outputs on signals; it also includes the idea that the signaling strategy is relatively impervious to mutations in the population. But here I want to pause to reflect on the point that the strategy promotes biological success. Can we say something general about *why* conditioning behavior on signals is a biologically successful strategy? The answer generally favored is that simple signaling systems work because the mediating signals carry information about environmental conditions conducive to the biological success of the outputs generated by receivers (e.g Shea 2007, Skyrms 2010, Martinez 2013, Neander 2013). In this way simple signaling systems promote adaptive coordination between outputs and conditions favorable to the success of those outputs. Coordination is achieved by sensory signals which change the probabilities of fitting environmental conditions. It would otherwise be mysterious why conditioning behavior on signals is a successful strategy (Shea 2007).

The upshot is that acknowledging information at work allows us to bring unity to the diverse range of goal-directed inflexible behaviors in nature. What they have in common is a powerful strategy for coordinating outputs with suitable environmental conditions, a strategy that works precisely because the mediating sensory states change the probability of favorable environmental conditions. This information-carrying role of sensory states is integral to the strategy we find in goal-directed reflexes quite generally, including the pupillary light and acoustic reflexes.

**Information for ecology**

I have been working within Dretske’s information-theoretic framework for explaining behavior in representational terms. On this approach, representational explanation of behavior is appropriate just in case the behavior is dependent on (i.e. sensitive to) information carried by internal states recruited to carry the information in question. I depart from Dretske on the issue of whether inflexible behavior can satisfy this information-dependence requirement. My view is that inflexible behavior exhibits dependence on information when the *biological* *success* of the behavior is sensitive to the relevant information. When we are attentive to the biological success of goal-directed behavior, we can find information actively at work even in rigid forms of behavior recruited through natural selection.

In this section I highlight the continuity between this theoretical notion of *information at work* and explanatory practices in ecology. Since I have been defending a claim about the information-carrying role of *sensory states*, I focus specifically on *sensory* ecology. After some general remarks on sensory ecology, I suggest that sensory ecologists are relying on something like my liberal notion of information use. The more restricted notion recommended by chauvinists is not a good fit with how sensory ecologists go about explaining behavior.

Sensory ecology emerges as a distinct research program towards the end of the twentieth century, becoming widely recognized as a field of study in 1994 with the first international conference on the Ecology of Vision (Martin 2017: 16). A guiding assumption of this research program is the idea that organisms need information in order to address fundamental challenges like finding resources, avoiding threats, maintaining an appropriate environment, and synchronizing activities with aspects of the environment like seasonal change or the activities of conspecifics (Bowdan and Wyse 1996: 122). A central goal of sensory ecology is to determine “how animals gather and use information from their environment” (Stevens 2013: 17). This goal is explicit in the very title of Dusenbery’s (1992) classic text on the subject, *Sensory Ecology: How Organisms Acquire and Respond to Information*. In line with Dusenbery, Martin (2011: 239) offers the following definition of the discipline: “Sensory ecology investigates the information that underlies an animal’s interactions with its environment.”

In practice this definition is likely too broad because sensory ecologists are not typically concerned with animal-environment interactions common to plants like photoentrainment. For example, in their textbook on visual ecology, Cronin et al. (2014: 8) write: “For the purposes of this book, a visual sense must provide both spatial and temporal information at rates fast enough to enable complex behavior beyond such simple activities as photoperiodism or circadian timing.” While the authors admit that there is “no clear line” to be drawn between simple and complex activities, this distinction should not be confused with the distinction they draw later in the book between innate and learned behaviors (151-157).[[14]](#footnote-14) The authors point out that the informational demands of innate behaviors sometimes outstrip those of learned ones in terms of the number of receptor-types deployed.

A great deal of research in sensory ecology is premised on the assumption that animals make active use of information even in highly rigid responses to their environment. The widely investigated “sensory arms race” between moths and bats provides an illustration. In the interest of avoiding predation, moths have evolved a variety of hard-wired evasive strategies which depend on detecting the high-frequency echolocation calls of bats. One interesting strategy involves “sonar jamming” (Corcoran et al. 2009). When tiger moths detect the echolocating calls of bats, they issue ultrasonic clicks with the aim of scrambling the signals returning to the bats. Here we have an evolutionary arms race that is specifically concerned with information channels: the tiger moth has evolved an information channel (high-frequency auditory channel) specifically dedicated to facilitating a highly specific range of responses targeting another information channel (the auditory channel driving echolocation). This moth behavior is a prime example of *information use*, as sensory ecologists think about it.[[15]](#footnote-15)

My view about when information is at work aligns well with explanatory practices in sensory ecology. The biological success of the moth’s behavior is clearly dependent on the information carried by its auditory states. Suppose we were to intervene on the moth’s environment, introducing high-frequency noise and reducing the bat population or eliminating it altogether. We expect that this sort of intervention on the information carried by the moth’s auditory states would affect the success of its evasive behavior, reducing the percentage of hits. Accordingly, the information carried by the moth’s auditory states helps to explain the biological success of its hard-wired response. We are in agreement with sensory ecologists who regard the moth as making active use of the available auditory information.

Contrast this liberal understanding of information use with the more restricted understanding endorsed by chauvinists. Recall that chauvinists introduce a de-coupleability constraint on genuine representation in the interest of distinguishing representations from mere causal mediators. We expect the information carried by a representation to be explanatorily relevant to the behavior it produces. But when behavior is an inflexible response to a stimulus, the behavior occurs whether or not the information is present. The behavior appears to be *stimulus* dependent rather than *information* dependent. The sensory state driving the response carries information, but that information is not being put to use. It is simply along for the ride. We find information at work only when the information-carrying state is stimulus independent (i.e. decoupled from specific stimulus conditions). Accordingly, information is explanatorily idle in the moth case.

I conclude that the chauvinist’s more restricted understanding of information use is at odds with explanatory practices in sensory ecology. Of course, sensory ecologists have not been concerned to address the specific worry that information might be explanatorily idle in inflexible behavior, so it is unsurprising that their explanatory practices fail to comply with the chauvinist’s strictures. My deeper point in this paper is that the chauvinist’s de-coupleability requirement is *unnecessarily* *revisionary*. We do not need a de-coupleability requirement in order to make room for the possibility of information at work.[[16]](#footnote-16)

**Conclusion**

On Dretske’s influential theory of representation, the signals issued by exteroceptors are paradigm cases of representations. They are recruited to bring about behavior because they change the probabilities of other things and thereby have the job of carrying information. But even when something is a legitimate receptor representation recruited for the information it carries, we can worry that the information it carries is not explanatorily relevant to what the creature does. Suppose the behavior in question is an inflexible response recruited through natural selection—something like a mollusc’s shadow reflex. When the behavior is inflexible, Dretske worries that the information carried by the receptor representation is explanatorily idle. The behavioral output would occur even if the information carried by the representation were to change. The behavior is better described as *stimulus dependent* than *information dependent*.

Ramsey goes further, doubting whether these receptor-issued signals which trigger inflexible responses should even be regarded as representations. Representations are supposed to have the function of carrying information, but Dretske’s account of representation can be satisfied by things which are mere causal mediators. For example, I might plant a tree at a certain location because the presence of the tree raises the probability of shade on my porch in the afternoon. The tree is recruited because of the way it changes the probability of something else, but the tree’s job is not to carry information. Its job is to produce shade. Dretske’s account of representation is inadequate because it can be satisfied by things which are not playing an information-carrying role.

How should we accommodate the point emphasized by both Dretske and Ramsey that explanations of behavior in representational terms are fitting only where we find information at work? One common strategy is to concede the point that information is idle in rigid responses to specific stimulus conditions. Proponents of a de-coupleability requirement are in agreement that information is explanatorily superfluous when it figures in a rigid sequence of events extending from receptor stimulation to behavioral response. Information emerges as an explanatory force only when behavior is independent of a narrow range of triggering conditions. I believe this strategy is misguided. We do not need to impose a de-coupleability requirement to ensure that receptor representations are more than just causal mediators. The information carried by receptor representations helps to explain successful coordination between behavior and suitable environmental conditions, and it does so even when the behavior is an inflexible response to specific stimulus conditions. We can separate this information-carrying role of receptor representations from their causal role by intervening on the information the representations carry, disrupting the coordination without thereby altering the causal role of the representations.

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1. The canonical version of this approach is due to Skyrms (2010), who takes the informational content of a signal to be given by a list of the states of the world whose objective probability is changed by the signal and a vector indicating the extent and direction of the change in each case. [↑](#footnote-ref-1)
2. This issue is often referred to as *the problem of error*. The most popular strategy for addressing the problem is to understand error in terms of *malfunction*: error is possible only when information-carrying structures have the *function* of carrying information (e.g. Dretske 1986, Matthen 1988, Neander 1995). [↑](#footnote-ref-2)
3. Here I have in mind representationalists who endorse an information-theoretic approach to representation. Some representationalists, including Burge (2010) and Millikan (2004: ch. 5), reject the idea that representations are to be reductively analyzed in information-theoretic terms. [↑](#footnote-ref-3)
4. When I speak of *receptors* in what follows, I am talking specifically about exteroceptors. [↑](#footnote-ref-4)
5. My talk of representations being *decoupled* should be distinguished from Gärdenfors’s (1995) talk of *detached* representations. Detached representations in Gärdenfors’s sense “stand for objects or events that are neither present in the situation nor triggered by some recent situation.” They function “off-line,” so to speak. A representation can be decoupled without being detached. [↑](#footnote-ref-5)
6. For a recent defense of liberal representationalism, see Artiga 2016. For a response to Artiga, see Schulte 2019. [↑](#footnote-ref-6)
7. A common exception is habitual behavior: when a creature forms a habit, the conditioned response will continue without additional reinforcement. [↑](#footnote-ref-7)
8. For a recent critical discussion of Dretske’s views here, see Hofmann and Schulte 2014. [↑](#footnote-ref-8)
9. One might take issue with my characterization of the causal role of receptor signaling. I take receptor signaling to be an integral component of the ordered sequence running from the proximal stimulus to the response. One might think instead that receptor signaling figures in a larger causal chain extending from the ecologically significant feature of the environment to the reflexive response. Notice, though, that this alternative way of construing the causal role of receptor signaling is at odds with Dretske’s view about how signals succeed in carrying information. The signal does not need to be causally dependent on the ecologically significant feature of the world about which it carries information; the signal carries information about the signified in virtue of the fact that the signal changes the probability of the signified. In many cases a signal carries information about some ecologically significant feature of the world without the signal’s being causally dependent on the feature in question. The predator’s photoreceptors issue sensory signals carrying information about unprofitability, but these sensory states are not caused by unprofitability. They are caused by something that correlates with unprofitability, namely, bright coloration. Furthermore, the signal does not need to be causally dependent on the particular object or event about which it carries information. One event (signal) can carry correlational information about another (signified) when the correlation is due to a common cause. I discuss these points at length in forthcoming work. [↑](#footnote-ref-9)
10. I am assuming that selected-for inflexible behaviors are goal-directed. The relevant goal here is the biological goal of inclusive fitness. Even in a “reflex-like” organism such as a plant we should distinguish *actions* from mere *reactions*. When a plant’s DNA is damaged by exposure to sunlight, the plant is merely reacting to the stimulus. When a plant reorients its growth towards a light source (phototropism), the plant is engaged in a light-related activity. The ultimate goal of the activity is inclusive fitness. [↑](#footnote-ref-10)
11. Here I am drawing heavily on Shea’s (2018: 89-91) ‘evidential test’ for determining the role of information in successful performance of a task function. [↑](#footnote-ref-11)
12. Ramsey’s own positive suggestion about when receptor-issued signals function as representations is a slight tweak on Dretske’s view. Dretske asks when the information carried by a receptor representation is explanatorily relevant to the resulting behavior. His answer, of course, is that we find meaning or information at work when the representation is recruited to produce behavior through feedback-based learning. When a representation is recruited through feedback-based learning, the behavior is sensitive to the informational content of the representation. Following Dretske’s lead, Ramsey (2007: 27) suggests that a receptor-issued signal is functioning as a representation only when the information it carries is explanatorily relevant to the behavior it produces. The latter condition is met when the representation figures in learning or making inferences (2007: 141). [↑](#footnote-ref-12)
13. For further discussion of the idea that sensory systems are signaling systems, see Ganson 2018b. [↑](#footnote-ref-13)
14. While the distinction between innate and learned behaviors is relevant in some contexts, sensory ecologists tend not to worry about the ontogeny of behavior. They focus instead on the functional advantages of behavior and its underlying mechanisms (Stevens 2013: 8). [↑](#footnote-ref-14)
15. Skyrms (2010) attempts to capture the informational content of a signal *via* a list of the states of the world whose objective probability is changed by the signal and a vector indicating the extent and direction of the change in each case. Sensory ecologists are more often concerned with what Shea et al. (2018) call the *functional content* of a signal. In rough outline, we determine the functional content of a signal by identifying the state of the world causally responsible for the stabilization of the signaling system. For example, unprofitability is the state of the world that brings about the stabilization of aposematic signaling systems. So, the signals figuring in these systems have the function of carrying information about unprofitability. For further discussion see Ganson 2018b. [↑](#footnote-ref-15)
16. Burge (2010) does not endorse a de-coupleability requirement, so he does not fit the label “chauvinist” as we have defined it. However, he would agree with the chauvinist that the moth’s anti-predator behavior is not to be explained in representational terms. Burge concedes that the moth’s behavior is explicable in terms of functional registering of information, so he does not come into conflict with explanatory practices in sensory ecology. His point is just that we can account for the moth’s behavior without invoking distinctively representational notions like accuracy or veridicality conditions. An explanation in information-theoretic terms will suffice. For a compelling response to this line of argument, see Artiga (2016). Burge’s views on representation depend on the idea that perceptual psychology has a proprietary notion of representation. For criticisms of Burge’s claims about the role of representation in perceptual psychology, see Ganson et al. 2014. Burge also makes substantive assumptions about how explanations in perceptual psychology differ from explanations in biology. See Morgan 2018 for important criticisms of Burge on this issue. [↑](#footnote-ref-16)