Peer-reviewed version available at *Animals* **2018**, *8*, 50; doi:10.3390/ani8040050

*Review*

# A Consideration of the Relationship between Animals and Their Environment

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**Simple Summary:** An animal must harvest resources from its environment in order to survive, prosper and reproduce. How the animal interacts with its environment to achieve these outcomes remains a topic of ongoing enquiry. The long-held view that the environment exerts an instrumental influence over the animal is contested by theories that propose that a mutualism exists between the two. This paper provides a brief introduction to these latter so-called ecological models of the animal environment relationship. As a first step, the animal must sense the environment. The contemporary model that sensing and acting operate through a process of prediction and correction (termed active inference) complements the ecological models. As well as sensing the external environment, the animal needs to sense and control its internal physiological environment and also the environment of (immunological) molecular structures that it encounters in its internal and external worlds. The paper examines how the animal manages engagement with these physiological and immunological environments. Predicting and controlling its environments provides the animal with agency. The ability to exert agency can vary from encounter to encounter. The opportunity to foster agency in animals within our care is noted.

**Abstract:** The relationship of the animal with its environment has been of longstanding interest in philosophy and science. Here I provide a brief introduction to concepts that place an emphasis on mutualism as the basis of organism - environment interaction, in contrast to the long standing view that the environment exerts an instrumental role in shaping the organism. Two influential theories have been von Uexküll's theory of umwelt and Gibson's theory of affordances. The former envisioned the animal as immersed in its surroundings (umwelt) to form a functional unit. In a similar manner, the latter theory describes a unity between 1) environmental information that provides the animal with opportunities for action (affordances) and 2) the ability of the animal to perceive and engage with those affordances. These views have influenced more recent ecological models of the organism as the functional unit of biology and have also influenced models of immune function. In ecological models, agency is seen as the ability of the organism to predict and control its engagement with the environment in order to maintain its integrity. The predominant contemporary model of neural function in which perception and action are understood to operate through Bayes-like active inference complements the concept of agency as proposed by the mutualism models. However, it is suggested that rather than a constant mutualism, encounters between organism and environment range over a dynamic spectrum from dualism to mutualism. It is also suggested that along this spectrum, agency emerges when the balance of instrumentality shifts from the environment to the organism, and that the balance of this relationship can further progress towards a felicitous mutualism. Meaning emerges between environmental information and an agent as opportunity for action. Implications for opportunities to foster agency in animals within our care is noted.

**Keywords:** affordance; umwelt; agency; active inference; allostasis; immune cognition; situated Darwinism; information; entropy; free energy principle

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## 1. Introduction

To survive, thrive and reproduce an animal must harvest resources from its environment. How does the animal find the resources it needs? In fact, the animal is faced with two environments, one external and the other internal. This review provides a brief introduction to some historical accounts and contemporary views of how the animal senses and acts on its two environments to realise meaning in the entities it senses, and how the meaning that arises through actions confers agency on the animal that enables regulation of behavioural, physiological and immune functions. Commonalities are examined between von Uexküll's theory of umwelt, Gibson's theory of affordances, Patten's model of environs, Walsh's theory of situated Darwinism, the active inference model of neural function based on the free energy principle, and Tauber's concept of eco-immunology. It is hoped this outline will encourage readers to explore these concepts in more detail.

## 2. The animal's relationship with its external environment

In everyday life we think of the external environment as a concrete, structured, objective reality that we and other animals interact with continuously. This materialist conception of a mechanical environment was challenged in 1909 by the Estonian biologist von Uexküll who proposed that the animal is immersed in its surround world (umwelt) in a manner by which the animal and its environment constitute a functional interacting unit,, or function circle [1,2]. Uexküll proposed that for each species the umwelt is structured in signs or marks that the animal senses. In Uexküll's view the environment for each species is subjective and unique.

Without apparent knowledge of Uexküll's theory of the umwelt, in 1977, the American psychologist JJ Gibson introduced the concept of affordances to describe the resources available to the animal in its environment [3,4]. Gibson proposed that "[t]he affordances of the environment are what it offers the animal, what it *provides* or *furnishes*, either for good or ill [emphasis in original]" (p. 127). In Gibson's view, affordances are what the animal interacts with in its environment. Affordances can be surfaces to stand on, to lie on or to rub against, objects to chew, air to breathe, and so on. For a goat climbing on a cliff face to access plants and salt to eat, the crevices and ledges are affordances, but for cattle these same ledges may provide no affordance [5]. Affordances describe a relationship between the animal and its environment that can change as the animal develops through its life history [6]. Gibson considered that information in the environment, which he termed ecological information, has an objective character that provides a unique resource enabling the animal to acquire the substantive resources required for its existence [3,7]. On Gibson's view, affordances contain information that gains meaning or value through the action possibilities they offer an animal [7,8]. On this view of the environment from the perspective of ecological psychology, two species in one location may interact with differing sets of affordances that for each constitutes its own niche. In von Uexküll's terms, each has a different umwelt. Within a population, individuals may differ in the affordances they perceive [9].

Complementing JJ Gibson's ecological concept to affordances, EJ Gibson developed a theory of visual perception which proposed that the environment structures information, for instance by the way light bounces off surfaces. The structure provides the animal with opportunities to learn through perception, and through perception and action the animal learns the opportunities for engaging with affordances [10,11]. EJ Gibson suggests that learning these opportunities to engage positively with the environment develops the animal's agency. Thus, on EJ Gibson's view, the animal learns more meaning in its environment through action [10,11].

The interaction between the animal and entities of the environment in the utilisation of affordances is illustrated by tamarin monkeys amongst whom genetic variation confers trichromatic vision on some individuals and dichromatic vision on others. In foraging tests, trichromatic individuals identify ripe fruit more readily than dichromatic individuals, thus the affordance of ripe fruit differs with the visual ability of individuals [9]. Thus the information received from fruit and its meaning to the animal can differ between individuals.

Drawing on the von Uexküll's concept of umwelt and JJ Gibson's concept of affordance, Patten [12] proposed that the organism and the environment do not constitute a dualism bound together

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through transaction. Rather he proposed that the organism and its external environment combine to create an emergent property in nature as a complementary interactional unity. Patten suggested that, centred on the organism, is an afferent or input environ composed of affordances, and an efferent or output environ. Effectances generated by the organism in the output environ become new affordances with the potential to be part of the input environ of other organisms [12,13]. White [14] earlier used the term effectance to describe an inherent activity of the organism to engage with the environment as means to generate a psychological sense of competence. White's effectance has strong similarities to EJ Gibson's notion of agency through action. Patten's concepts of environs and effectances have been largely incorporated into the more comprehensive theory of niche construction [15].

More recently, Walsh [16] has extended Gisbon's concept of affordances to developed a theory of "Situated Darwinism" that proposes an organism-centric view of evolution, in contrast to the gene-centric view held by neo-Darwinism and the Modern Synthesis of Evolution. For Walsh[16],

> "The unit of greatest theoretical significance for evolution is not the gene, or for that matter even the organism *per se*. It is the organism situated in a system of affordances. Affordances are emergent entities; they are properties of a system, in this case, a system comprising an organism and its conditions of life. Affordances are constituted in large measure by the ways that organisms can exploit or ameliorate these conditions… An action, then, is a response initiated by the agent, to a set of affordances, in pursuit of her goals. The affordances are to a significant degree of the agent's making, and they evolve in concert with her actions and goals." (p209)

Thus for Walsh the organism's relationship with its environment is a dynamic mutualism rather than a reactive dualism in which environmental conditions are instrumental in shaping the phenotype of the individual and propelling genomic change through adaptation over time.

## 3. What is environmental information?

In his Information Theory, Claude Shannon [17] proposed that information is the reduction of uncertainty [18]. Information is a statistical concept in which low predictability has high entropy and absolute certainty has zero entropy. Following Shannon's work, considerable interest developed in "information" within biological sciences including neurobiology, genetics, behaviour, psychology, evolutionary biology and developmental biology [19]. In information theory and in biology, a distinction is drawn between the minimal requirements for coding and transmitting information (semiotics) and the meaning that information may convey (semantics) [20]. Maynard Smith [21] suggests that in the context of biology, semantic information is intentional or purposeful and that a test for intentionality is whether there is a valid concept of error whereby a change in the information (coding), such as a single nucleotide polymorphism, can lead to a change in the meaning [21]. In contrast, semiotic information has no valid concept of error. A change in semiotic information such as the distribution of a grass species in a sward may convey a change in meaning for a herbivore as to the value of the field as site to graze, but the change does not constitute an error in any operational sense. There is no necessary intentionality inherent within the particular distribution of the grass species to convey information to a grazing animal. (Further consideration of the concept of intentionality in biology is beyond the scope of this paper: for a detailed critique see [16]).

Jablonka [20] provides a broad definition of biological information in the following terms: "a source becomes an informational input when an interpreting receiver can react". This definition was developed further by Jablonka and Lamb [22] to specify that "a source becomes an informational input when an interpreting receiver can react to the form of the source (and variations in this form) in a functional manner." On this view, information is a biological notion that only exists through interpretation by living systems [22]. Thus information requires a living interpreter to gain meaning. This view aligns with the earlier concepts of umwelt and affordance whereby the information in the environment available to an organism differ in accord with the organism's ability to interact with those resources. Importantly, not only are living interpreters necessary to gain meaning from biological information, through their actions they become a source of new information. Here we see Patten's effectances becoming information for other entities. Cohen [23] captures this concept in the

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following terms: "… a living organism is a 'contrivance' for creating information, while paying its due to entropy".

## 4. Neurobiology of perception

Sensing the environment is a prerequisite for accessing information. The understanding that has emerged from neuro-behavioural studies is that perception is an inferential process that depends on *a priori* information derived from evolution, as well as during early developmental experience complemented by lifelong learning [24-26]. The brain, Sterling and Laughlin suggest, functions to reduce uncertainty [18]. Perception occurs in the brain, yet the brain faces a challenge. It is physically isolated from the external world yet requires information to regulate the engagement of the animal with its surrounds. Information about the external world is obtained via exteroceptors that sense light (sight), pressure (hearing, touch) and some types of chemical structures (taste, smell) as well as the position and motion of the body (proprioception). Exteroceptors send signals via afferent nervous tissue to the brain [27]. The brain can modify information impinging on the animal by sending efferent signals to muscles that initiate motor actions to change the animal's engagement with its environment. These sensorimotor actions can lead to a new set of stimuli invoking the next train of afferent sensory signals sent to the brain [26].

Recent models of neural function suggest that rather than operating as a stimulus response network, the brain generates internal models that draw meaning from sensory input via comparison of actual sensory input with input that is anticipated via inference from prior experience [28-31]. In the manner of Bayesian inference, predictions based on prior experience are updated by current information arriving from the sensory world. The important advance this model of brain function, termed active inference, has made over the wide range of other theories of perception and brain function is to provide a mechanistic link between on the one hand closely mapped neuroanatomical pathways of connectivity and neurophysiological activity within the brain [32,33], and on the other hand the phenomena of behaviour, perception and physiological regulation. In the active inference model, the brain acts predictively to minimise the discrepancy between the actual afferent signals received from sensors and the anticipated signals expected from prior experience. Thus for the external world, motor actions provide the bridge between expectation and received information. Updating predictions by incorporating new information (the error signal received via sensory pathways) into the brain's model reduces the cost to the animal of reconciling the discrepancy between unanticipated sensory input and expected input that occurs through exercising ongoing rectifying actions [26,33-36]. The operating process underpinning this model is termed the free energy principle [26].

Perception generated through active inference is not an internal representation of an invariant external structure but a prediction of the sensory stimuli that will arrive in the immediate future coupled to motor actions. Actions initiated to generate anticipated sensory input emerge as a property of neurophysiological activity operating within a neural architecture. Meaning in sensory information arises from similarity with past experience [29]. Thus in the active inference model, perception creates meaning of the information contained in the external environment through the effort of actions undertaken to match sensory input with expectations based on prior experience. Indeed, the reduction of unpredictability (surprise) in the environment through the updating of expectations by Bayes-like inference constitutes the transfer of information from the environment to the organism. Thus agency arises from the accretion of environmental information within the organism.

## 5. The internal environment

In addition to enabling the animal to engage with its external environment, a primary function of the brain is to maintain the internal environment of the animal in a physiological state conducive to surviving, thriving, and reproducing [28,37]. Sensory inputs from peripheral tissues relay information of fluctuations in physiological, vascular, metabolic, immune, neuroendocrine, autonomic and visceral functions to produce the sense termed interoception [27,38,39]. A growing

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body of evidence from maps of neural pathways and measures of neural activity indicates that, as with exteroception and sensori-motor actions, the brain regulates the internal environment through predictive and anticipatory actions based on inference, which in this internal domain is termed interoceptive inference [28-30,33,35]. Elucidation of these central mechanisms of predictive, anticipatory regulation of the internal state of the body is in accord with over a century of empirical evidence of the role of predictive, anticipatory actions of the animal in maintaining its homeostasis [40-42]. In 1988, Sterling and Eyer [43] termed this historically well recognised pattern of predictive homeostatic regulation allostasis. Their term draws attention to the anticipatory character of homeostatic regulation [44] and thus is in strong accord with the concepts of active inference and interoceptive inference. In some recent usage, homeostasis is used to describe the reflex arcs regulating physiological variables while allostasis is used to describe the process of higher level modulation of reflex arcs [33].

Functional pathway analysis in neural tissue indicates that networks regulating physiological functions are not modular but rather are interdependent [35]. Neurological linkages between interoceptive pathways and brain centres influencing psychological phenomena including emotion, decision making, pain and memory [35] are in accord with empirical evidence of links between physiological status and psychological functions [45]. Kleckner et al. [35] conclude that "… allostasis and interoception are fundamental features of the nervous system. Anatomical, physiological, and signal processing evidence suggests that a brain did not evolve for rationality, happiness, or accurate perception; rather, all brains accomplish the same core task: to efficiently ensure resources for physiological systems within an animal's body (i.e., its internal milieu) so that an animal can grow, survive, thrive, and reproduce. That is, the brain evolved to regulate *allostasis*. All psychological functions performed in the service of growing, surviving, thriving, and reproducing (such as remembering, emoting, paying attention, deciding, etc.) require the efficient regulation of metabolic and other biological resources [emphasis in original]."

An important feature of this neurological process for managing resources within the internal environment of the animal is the influence of interoception on the affective state of the animal. JJ Gibson noted that affordances in the environment can be for "good or ill" [3]. The term valence is used to describe the attractiveness or aversiveness of characteristics in the environment as well as the hedonic experience associated with them. Affect describes the dynamic core psychological state of the animal in terms of arousal and valence [46]. Perceptions arising from exteroception and interoception influence core affect which in turn modulates all behavioural, psychological and physiological functions of the animal [46-48]. More specifically, it has been proposed that the concordance and discordance between the anticipated and predicted perceptions arising from interoception and exteroception of the internal and external environments generates the valence and arousal of affect [32,48] and a sense of wellness [38].

For regulation of the interior milieu of the animal by interoceptive inference, actions initiated by neural efferent signals such as eating, changing heart rate, changing respiration rate, and releasing glucose can lead to changes in the stimuli impinging on the interoceptors lying at the interface between the brain and extraneural tissues. These stimuli such as ion concentration, oxygen tension, glucose concentration, hormone concentration, and immune cytokines within the internal environment of the animal provide the bridge across extraneural tissue that links expected (efferent) and actual (afferent) stimuli reporting the physiological status of the animal.

### 5.1 Do entities in the internal environment provide opportunities for agency?

Interoceptors sense two broad classes of stimuli: 1) physiological stimuli such as pH, temperature, metabolites, oxygen tension, organ and vessel distension, and; 2) molecular integrity of tissues via the immune system. Evidence in support of the proposition that agency can be exerted over the first class of stimuli is seen in anticipatory regulation of the physiological status of the body linked to cues sensed by interoceptors and exteroceptors. In addition to the well-recognised anticipatory physiological responses linked through exteroceptors to external cues such as a sound seen in classical conditioning paradigms described by Pavlov [49] and others, a large body of research

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has established the ability for interoceptive signals such as distension of the stomach to become predictive stimuli for interoceptive responses regulating physiology of the organism [39,40]. Thus physiological entities in the internal environment stimulating interoceptors can provide opportunities for actions that confer agency. Fotopoulou and Tsakiris [50] suggest that development of more accurate models of interoceptive inference during ontogeny in human infants accompanies development of the "felt self" as an entity engaging with the world. Furthermore, Stephan et al. [33] suggest that interoceptive perception of failure to regulate the internal environment diminishes self-efficacy.

In Fotopoulou and Tsakiris's model, the development of control over physiological functions though motor actions on the external world contributes to the development of agency and awareness of self, in part through establishing awareness of a boundary between the body and the external world [50]. From this perspective, agency describes the animal's ability to control its body in order to cause desired effects on both its external and internal environments [50]. Thus agency arises though actions initiated to modulate sensory inputs arising from exteroceptors or interocepetors. These actions reduce uncertainty through minimizing the error between prediction and actual sensation. In a similar manner, one can ask whether actions of the immune system confer agency on the animal.

There are at least four aspects to this question. Firstly, does sensory activity of the immune system provide information that contributes to the predictive control of behavioural and physiological actions? This question asks whether the immune system is a sensory organ enabling behavioural and physiological agency. Secondly, in a reciprocal manner, can non-immunological exteroceptor and interoceptor stimuli initiate immune actions? Thirdly, do activities of the immune system enable predictive control of the immune system's engagement with the molecular entities it senses? This is the core concept of immune agency. And fourthly, does the immune system, like the brain, operate by the free energy principle through Bayes like inference? This is a question about the operating principle of the immune system.

The immune system of vertebrates recognizes short sequences and conformations of molecules through two sets of receptors: a germ line encoded set that bind predominantly with molecular structures common amongst microorganisms that provide innate immunity, and a second set of receptors that are generated by somatic hypermutation of a small number of genes and provide adaptive immunity. These receptors of the adaptive immune system recognize short sections of molecules (epitopes derived from antigens) bound to major histocompatibility complex proteins of the host. A vast network of messengers produced within the immune system regulates its activity [23]. In addition, the brain has extensive afferent and efferent innervation of the immune system as well as bi-directional hormone and cytokine communication via blood [51,52]

The first proposition is very well supported. Immune activation by a wide variety of immune stimuli induce sickness behaviours that modify foraging and rest [53], and also induce alteration of metabolic activities [54,55]. These effects are understood to be predictive in that they can be initiated early in a disease setting before infection is well advanced and before pathological processes have been initiated by the infectious agent.

Evidence is support of the second question comes from studies of associative learning between immune stimuli and behavioural and physiological responses. When functions of the immune system have been examined in classical conditioning paradigms they have been found to be able to be entrained by conditioned stimuli such as a sucrose syrup in rats [52,56]. In this setting, rather than an immune stimulus being required for activation of an immune response, a non-immunological stimulus like sucrose syrup becomes the initiating stimulus. Activities of the immune system such a production of antibodies, activation of T lymphocytes, release of cytokines, and initiation of fever can all be initiated in an anticipatory manner in response to non-immunological cues.

The third question, does the immune system exercise immune agency, is more problematic. Here I follow Tauber's account of development of the concept of immune agency [57]. The concept grew out of Burnett's clonal selection theory, which is predicted on the notion that new antigen receptors generated by somatic mutation must be negatively selected to avoid reactivity against the tissues of

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the host as well as positively selected for affinity to foreign antigens. From this theory the concept emerged that the host has a fixed antigenic identity that is dictated by its genome and with which the immune system engages as defender and interrogator of that identity in a dualism that echoes the environment : genotype dualism of neo-Darwinism [57]. The growing realization that the vertebrate host is a holobiont comprised of a community of symbiotic organism that change during development of the host and over subsequent time periods [58] provides a conceptual challenge to the notion that the host animal possesses a unique immunological self. Recent studies on the transfer of proteins, RNA and DNA from environmental organisms into host cells and tissues via dietary exosomes [59] further erodes the concept that the host has a constant, bounded molecular identity. On this view, Tauber [57] and others have develop the concept that the immune system mediates a dialogue about molecular structures between the holobiont and its environment. It is interesting to note that Tauber's ecological concept of immune function (eco-immunology) has been influenced by JJ Gibson's ecological concept of affordances. On Tauber's view, the immune system does not respond in an on/off manner distinguishing molecular structures as self or non-self but responds to molecular structures in the context of disturbances to the resting state of the system. In language echoing Gibson's and Walsh's accounts of affordances, Tauber notes that "[i]n this mutualist setting, immune identity is dynamic and adjusts to the needs and opportunities offered by the environment" (p221). Thus the immune system does not operate to guard a defined immune self, rather "organismic identity emerges in dynamic encounters with the world (both within the body of the animal and beyond) in a world fraught with various friend and foe relationships" (p222). For Tauber, the function of the immune system as the mediator of a dialogue between the holobiont and molecular structures makes the question of agency (and immune self) redundant. One can take an alternative view however. Just as sensorimotor and visceromotor actions arising from active inference and interoceptive inference confer behavioural and physiological agency on the organism to manage engagement with its external and internal environments, we can characterise the actions of the immune system that arise from disturbances of immune perception as conferring agency on the holobiont to manage its dialogue with internal and external molecular structures in an active and predictive manner. Here immune agency is a character of the holobiont rather than the host.

The final question about the operating principle of the immune system is also problematic. Many models have been developed to describe the processes that provide the immune system with the ability to engage with molecular structures via responses that range on a spectrum from tolerance to rejection. A common metaphor describes the immune system as a cognitive entity that functions to reduce uncertainty in molecular signals of organismic integrity [23]. Thus the immune system is described with terms such as seeing antigens, deciding whether to respond, and recalling memory of past encounters. Cohen (and others) characterize the cognitive activities of the immune system in entropic terms [23]. In accord with Cohen's model, empirical evidence suggests that affinity maturation of the antibody specificity for antigens occurs via entropic principles [60]. In view of the power of the free energy model mentioned above to describe activity of that other cognitive system, the brain, it may be timely for a closer comparison of the entropic operating principles of the immune and neural systems. Indeed, in its general form, the free energy principle is a model of how biological systems maintain their state and form in the face of a changing environment and hence has intrinsic applicability to the immune system.

## 6. A relational spectrum between organism and environment

A commonality of the ecological models developed by von Uexküll, Gibson, Patten, Walsh, Cohen, Tauber and others is the mutualism of the relationship between the organism (holobiont) and its environment. An important question is whether mutualism adequately describes the spectrum of encounters the organism endures. That entities and events in the environment can be an impediment or threat to the organism is well recognized in these models, as is the concept that relationships range from embrace to rejection. Thus as mentioned above, Gibson notes that "[t]he affordances of the environment are what it offers the animal, what it provides or furnishes, either for good or ill", for Walsh affordances offer impediments or opportunities for fulfilment of goals and for Tauber the

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world is fraught with friend or foe relationships. The opportunity for the organism to engage and act to maintain its integrity during these encounters is not uniform. In the absence of an ability to predict and control these encounters the organism becomes an object of an instrumental environment. Here we see the relationship in terms of the dualism of neo-Darwinism. On the other hand, when the encounter becomes an affordance that provides opportunities for action, the organism gains agency to influence its engagement with the environment. Outcomes of this engagement (Patten's effectances, and the environmental changes induced by the organism in niche construction theory) can themselves be to the benefit or detriment of other organisms. Thus mutualism between the organism and its environment may be an extreme case, with encounters varying over time along a spectrum from dualism to mutualism. Agency, then, emerges at the point along this spectrum where the information perceived by the organism gains meaning through the opportunity for action. It arises from the transfer of unpredictability (information) from the environment to the organism. In this formulation, agency is a process that can vary in degree and change over time.

In metaphysical terms, this account sees agency and the ability to garner meaning from environmental information as a process rather than a thing, substance or attribute of the organism. Here agency has a "process" ontology rather than a "thing" (or substance) ontology [61]. This formulation accords with much prior writing on the dynamics of the engagement of the organism and its environment, including Fotopoulou and Tsakiris's model described above of the emergence of the ability of the neonate to distinguish it bodily boundaries and gain agency to control its physiological state through maturation of sensorimotor and visceromotor actions [50].

In practical terms, this account highlights the opportunity to provide animals in our care with an environment that fosters their ability to learn the opportunity for actions that confer agency over events and circumstances they experience [62]. An example of creating a unique affordance for each individual that improves its affective state is the use of call feeders in group housed sows [63,64]. In this system, each sow learns a personal auditory cue that signals a period of uncontested access to a communal feeder [65]. We have seen above that affordances are not only subjective but can differ between individuals in a population. A further opportunity then in the breeding of farm animals is to select animals with an enhanced ability to garner information from their environment through learning, and to also design environments that complement these skills [66,67].

## 7. Limitations

This paper provides only a very brief introduction to a wide range of concepts. For detailed accounts the reader is referred in the first instance to the comprehensive reviews cited in the paper. I have not attempted to address any evolutionary implications of the various models of the organism environment relationship described above with the exception of situated Darwinism. The focus, rather is on the extant organism as it navigates the course of its encounters with its environment. I have not attempted to adhere to a single definition of agency in view of the diversity of meanings the word has in the literature. I attempt however in the course of this paper to progress through a variety of more general usages to a narrower conception of agency in the conclusions below.

## 8. Conclusions

The relationship of the organism and its environment has been a topic of longstanding philosophical and scientific enquiry. Von Uexküll's concept of umwelt suggested that the relationship is subjective and relative and that the surrounds in which organisms are immersed differed between species. Von Uexküll's insight commenced a conceptual shift from a dualism between environment and organism towards one of mutualism. Following the development of Information Theory, descriptions of the environment have increasingly been in terms of information, in addition to materials and energy. Gibson's concept of affordances continued von Uexküll's theme of subjectivity and mutuality, and has been highly influential in shaping ideas in ecological immunology as well as Walsh's thesis of situated Darwinism. The concept that affordances provide an opportunity for action links together environment as a source of information with agency as the

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ability to control encounters between the organism and its surrounds. In short form, one can say that meaning emerges between information and an agent as opportunity for action.

The model of neural function termed the free energy principle provides a powerful descriptive account of the processes by which uncertainty (surprise) in sensory information received by exteroceptors and interoceptors is minimized through Bayes like inference. Through this process, sensorimotor and interoceptive actions are undertaken in order to reconcile discrepancies between prior expectations and actual sensory inputs. Active inference in sensorimotor actions is coupled with interceptive inference to provide predictive control of the animal's internal physiological environment. Activities of immune processes also confer ability on the animal to exhibit behavioural and physiological agency as well as confer immunological agency to the organism (as a holobiont) to manage its dialogue with molecular structures encountered in internal and external environments. The free energy principle is an entropic model of neural function that, at a high level of abstraction, bears strong similarities to Cohen's entropic model of immune cognition. A detailed reconciliation of these models may be propitious.

From analysis of these various viewpoints of the animal environment relationship it is suggested that for each organism a spectrum of encounters occurs between those with the character of a dualism wherein the environment is instrumental in influencing the organism, to those with the character of a mutualism wherein the organism and its surrounds comprise, in von Euxkull's term, a function circle. It is suggested that agency, as a process, emerges at that point on the spectrum where the balance of instrumentality shifts from the environment to the organism. Further progress along the spectrum towards mutualism represents a more felicitous interdependency between organism and environment. Nonetheless, the circumstances of existence remain in constant flux, thus encounters dynamically vary in their position along this spectrum. Actions of the organism create information that can be affordances, for good or ill, for other entities in the environment.

Within the framework of information theory, acquisition of agency is an entropic process that occurs through internalisation of unpredictability (surprise) from the environment into the animal. Emergence of a felicitous interdependent "function circle" between organism and environment is less probably again than organism as agent, and hence contains more entropy than an environment organism dualism.

If there is value in analysis of the organism environment relationship at this level of abstraction, it may lie in the understanding it provides of the integration within the animal of behavioural, physiological and immune functionalities, and the opportunities that flow from this understanding to better manage animals within our care.

**Acknowledgments:** The assistance of CSIRO library services is gratefully acknowledged. No grants supported this work.
**Conflict of interest:** The author declares no conflict of interest.

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