Biosemiotics (2024) 17:487–506
https://doi.org/10.1007/s12304-024-09579-6

RESEARCH

Animal Attention in the Context of Zoosemiotics

Siiri Tarrikas[1]

Received: 15 December 2023 / Accepted: 15 June 2024 / Published online: 25 June 2024

Abstract

Attention is viewed here as a complex of semiotic processes that leads to animals' choices and behavioral decisions. Besides the focusing role of attention, many other processes, such as prioritizing and binding perceptions to coherent reality, have historically been considered to be parts of attention. Semiotic tools can help to understand relations between perception and meaning-making and, therefore, to solve questions of attention's active or passive nature. Are animals actively shaping it, or is it something that happens to them? This article attempts to synthesize different theories of attention from the cognitive sciences and Uexküllian semiotics into a model that shows how meaning-making can be the basis for future attention. For this several different theories of attention belonging to different disciplines have been revisited and synthezised. Here, it is claimed that although it seems that something in the environment can capture attention without animals' active participation, attention is actually an active process that depends on meaning-making and interpretation. Attention is also viewed in the context of search behavior and connected with Jakob von Uexküll's terms of 'search image' and 'search tone', to which a a new term 'search schema' was added. Additionally, it is suggested that some animals can use qualisigns as category markers for attendance. The process of prioritizing attention depends on the construction of sense organs, which makes it species-specific and also from the individual experiences, meanings, and habits of the organism. Jakob von Uexküll imagined Umwelt as a "soap bubble" containing everything an animal can perceive. Attention limits perception in the current moment even more, being metaphorically speaking, a smaller dynamic bubble inside a big Umwelt bubble.

Keywords Animal attention · Umwelt · Zoosemiotics · Uexküll · Attention schema · Search schema

✉ Siiri Tarrikas
siiri.tarrikas@ut.ee

[1] Institute of Philosophy and Semiotics, Department of Semiotics, The University of Tartu, Tartu, Estonia

Introduction

Attention is an active process through which animals selectively focus on certain cues in the environment, therefore being able to make decisions and act in a meaningful way. Several disciplines used to state that attention is more or less belonging only to human consciousness, but now the growing body of evidence of different species sentience and cognition, even in non-vertebrates (Bivort & Swinderen, 2016; Klein & Barron, 2016; Nitayananda & Chittka, 2015), has set the scene and opened opportunities for more thorough research and discussion in the field of animal attention. Vertebrates, and at least some invertebrates, such as insects, arachnids, octopuses, and many others, have been shown to have selective and divided attention. This article looks at attention within the context of animal's perception and meaning-making in the framework of Uexküllian semiotics. We claim that even seemingly unconscious attention includes interpretative sign processes, although those may already be habitual and controlled by legisigns, called attention schemas (similarily to the *Attention Schema Theory* by Graziano & Kastner, 2011). Those attention schemas can be also interpreted as habits or rules of attending. Animals have diverse perceptual capacities and Umwelten, which influence how they attend. The study of attention in animals has traditionally been based on the limitation of perceptual and neural capacities (Cherry, 1953; Sperling, 1960), which limits attention either spatially (Wolfe, 1994) or because of limited action potentials (Zentall & Riley, 2000). Most attention studies deal either with conditions necessary for noticing incoming information (color, objects), viewing attention as a limited resource *Bottleneck Theory* (Broadbent, 1958), measuring animals' typical attention span, or identifying the neural correlates of the processes (Bivort & Swinderen, 2016:9). Some scientists even argue that there is no need for the term of 'attention' since psychogenesis[1] is able to cover all its processes. Psychogenesis begins to seek out structures even before sensing, and selection does not take place because there is nothing to choose from, as animals only encounter meaningless structures to which they must give meaning (Koenderink, 2019: 137). We propose that there is still need for the term of ''attention', and it is more easily comprehensible by examining it from the semiotic viewpoint. In semiotic research we see attention as a creative process, which is based on relations of animals with their environment, highlighting parts of Umwelt relevant at the moment. All this is based on meanings on the level of species and individual. Refining and tuning those processes are happening throughout the lifetime of the animal. Attention is also dependent from the construction of sense organs, which has evolutionary causes.

Through semiotic mechanisms, attention maintains a focus on the most relevant aspects of the environment for an animal, affecting how animals experience the world, with the precision that animals need it. Although animal' 's body plan and structure of sense organs determins a big part of species-specific attention, there are aspects that are determined by choises animals' make in everyday living and with relating to their environment. Attention unites perceptual information from vari-

[1] „Psychogenesis of visual awareness is "controlled hallucination". The hallucination is intentional, the control seeks to fit front-end neural activity. The visual front-end appears as a proxy of the Umwelt in "brain readable form"" (Koenderinck et al. 2015: 302).

ous senses with meanings, creating an integrated reality based on previous patterns of experience. Even the process of perception is guided by attention, a complex of selection processes based on previous knowledge patterns and experiences. As Jakob von Uexküll's *Umwelt theory* (1982) demonstrates, animals have species-specific Umwelten, their own subjective world, and, therefore, unique ways of attending to stimuli and making meanings. As attending to something inhibits the perception of everything else that is not in the focus at the moment, attention can be metaphorically seen as a more restrictive smaller bubble inside this large Umwelt bubble.

This work aims to look at attention as a semiotic process that mediates perception and meaning-making, investigates attention's role in the agency of animals in shaping their Umwelten, and seeks to answer the question of how the ways that animals attend to their environment shape the ways they experience it. Here, the complex relationship between attention and other semiotic processes is discussed, and the role of attention in animal sensory processing is examined. A model is proposed that unites meaning-making and attention schema theories, and shows that previously made meanings are important for attending.

Definition of Attention and its Subprocesses

Attention has many definitions, because several processes are traditionally grouped under the name of attention. Although attention is sometimes described only as "a physical process of interacting neurons and electrochemical signals" (Wilterson et al., 2020: 2) or as "the selective prioritization of the neural representations that are most relevant to one's current behavioral goals." (Buschman & Kastner, 2015), seeing it instead as a pattern of semiotic processes that helps select and focus on essential stimuli, can provide a new layer for understanding these processes.

Eco (2000: 14–15) sees attention as a presemiotic or even a protosemiotic phenomenon, as a primary indexicality, "It is not the primary act of attention that defines the something, it is the something that arouses the attention, indeed the attention lying in wait is already part (is evidence) of this something." (Eco, 2000: 15). He is, therefore, referring to the phenomenon inherent in attention, that it can be turned to objects in the environment by an animal, or that some objects seem to draw attention to them. This article attempts to clarify this phenomenon, so that attention remains within the range of agency of the individual animals.

Jennings defines the attention following its everyday use: Attention is a process of "mental selection that is within the control of the subject." (Jennings, 2012: 536). Most useful, for the purposes of this article, is a definition given by Tsotsos (2011: 51), who defines attention as a "set of mechanisms that help tune and control the search processes inherent in perception and cognition." Defining attention directly through search processes connects it to Uexküllian semiotics, especially with the concepts of 'search image' and 'search tone.' Search behavior is universal to most animals because they must fulfill their basic survival needs.

Search is an active process with the intention of finding the searchable by certain signs, which are markers of meaning categories and meaning patterns, where the searchable belongs to the individual animal. Searchable objects are dynamic objects

that can have different meanings for the animal, depending on the prevalent search tone that individual animals have at a precise moment. An individual's attention is not uniformly distributed across the perceptual field. Instead, it selectively focuses on the most promising parts of the environment. This process involves selective attention, which is the capacity of an animal to select some of the numerous available sensory inputs that are essential at a given moment, and actively ignore irrelevant signs.

The traditional approach shows that novelty, salience, and complexity can influence attention. Here, we consider instead the semiotic approach through meanings, which allows us to distinguish between meaning-based salience from salience, which is caused by the sensitivity of the sense organs and the size of the animal body, both of which have evolutionary origins. Novel or unexpected stimuli may capture animals' attention because they stand out from the familiar background, which means that this is meaning-based salience[2] because it is raised from the comparison of the know and unknown and anchored in meaning-making. In nature, novelty is often dangerous and, therefore, usually categorized as salient. However, this may not be the case for individual animals who are novelty seekers, i.e., neophiles. Physically salient stimuli, such as bright colors or loud sounds, may attract animals' attention even if they are irrelevant or not meaningful to a particular animal, but their sensory organs are sensitive to those signals. There is also the possibility that animal species have adapted to notice only the relevant colors and other features of the objects, since their attentional system (together with the perceptual system) is evolutionarily adapted to prioritize stimuli that are necessary for survival. Therefore, attention is mainly drawn to the more meaningful stimuli in Umwelten. One factor that influences attention is also the emotional significance of the signs. Emotionally charged signs, signifying threatening situations or rewarding outcomes, tend to capture attention more readily than neutral stimuli. For example, the cry of a bird's own offspring is usually more salient for the mother bird than the same communicative signs from other chicks.

Stages and Processes of Attention

Previous researchers have been dividing attention to several sub-processes (such as focused attention, selective attention, alternative, continuous, diffuse, divided attention and binding) and also observing different zones of attention, such as the object in focus, the conscious context, and the diffuse area surrounding it. For example, the two-stage process of perception proposed by *Feature Integration Theory* (Treisman & Gelade, 1980) involves a pre-attentive stage and a focused attention stage. During the pre-attentive stage, basic features are automatically extracted and stored in separate feature maps, while during the focused attention stage, these features are combined and used to identify objects. This theory also proposes that color, orientation, and intensity are features that can be searched for pre-attentively. (Treisman & Gelade, 1980) However, subsequent models have challenged and modified the *Feature Integration Theory*, such as *Guided Search Model 2.0*, which incorporates salience and bottom-up and top-down factors in a pre-attentive stage (Wolfe, 1994).

[2] The relative salience in the given context.

Another example is Duncan and Humphreys (1989), who proposed the *Attentional Engagement Theory*, emphasizing the role of perceptual organization and similarity in visual search. This enourmous diversity of theories made it difficult to understand how attention works. Therefore, we propose a more coherent and simultaneously working semiotic model (see Fig. 2 in Chap. 7) that combines different stages of attention into a coherent whole, and allows to see animals as active agents whose meaningful choises change the way they attend in the future.

Studies conducted on animals had their own challenges. They have mainly dealt with orienting, anticipation, stimulus discrimination (distinguishing the critical stimulus from the context), maintaining the focus, and parallel information processing (Bushnell, 1998). Researchers tend to concentrate on only one sense modality, mostly for practical reasons. Usual The easiest choise is usually the visual sense, which is not the dominant sense for all animals.

It has also been investigated whether animals find what they are looking for faster if they have an initial idea of it (Zentall 2005), similarly to Uexküll's search image. Uexküll also uses the concept of 'search tone' when there is a known function of the searchable, but no search image is currently available. An alternative explanation is that there are no search images or internal representations, but animals adjust their search to the noticeability of what is being sought (Gendron, 1986; Guilford & Dawkins, 1987); the more noticeable the sign, the quicker it will be found. In this article, we want to challenge this alternative explanation. We unite Uexküllian biosemiotics with some contemporary theories of attention to show the semiotic side of attentional processes.

The zoosemiotic perspective makes it possible to study the role of attention in sign processes and communication. Van Heusden sees memory as the basis of sign processes, which allows recognizing patterns and objects that stand out against the background of patterns (van Heusden, 2004: 9). However, one can only remember previously noticed phenomena, which shows that attention is the basis of both memory and sign processes.

Attention processes involve mediating and uniting processes. Cimatti (2018) shows that meaning is a relation that emerges through selection and that the whole semiosis can be creatively directed by attention.

> A living relation entails a selection, among all present things, of those that allow the formation of larger and more articulate assemblages. These things "mean" that a relation is possible. Natural meaning, then, is nothing but a thing's capacity to selectively establish links with other things—where selection means the capacity to pay attention to something rather than something else. Finally, biosemiosis means the ability to pay attention, i.e., to "select". There is no semiosis without this "control" of attention. (Cimatti, 2018: 83)

Attention can also be viewed as a semiotic process that shifts the focus between signs (sign processes) and meanings (Tarrikas, 2022). In this article, attention is seen as a semiotic process of cooperation between an organisms, the various parts (such as the neural system, senses, internal organs, and hormones), and the environment, during

which specific types and categories of signs and information received from perceptual organs are given priority because of the given situation, ignoring the rest.

We would like to emphasize that, although the brain plays a role in directing attention, the entire organism, at several levels, plays a role in attention as a whole. Attention is often studied as a cortical phenomenon, although it is not limited to the brain. The organism's states are mediated to their brains by various signs, which are also used to direct attention together with signs from the Umwelt. Various bodily feelings arise from cooperation of neural cells, hormones and other mediators. Sometimes attention can be finetuned even outside the body, for example, spiders can use their nets as attentional aids, which they can tune to various vibration frequencies, according to their needs. In animals, attention processes can work through different parts of the nervous system than in humans, especially in animals with simpler Umwelten, whose nervous system structures are differ tremendously from humans.

Attention as a Complex of Semiotic Processes

Attention has been studied in psychology, education, and neuroscience; however, the semiotics of attention (such as the relationship of attention with signs, perceptibility of signs, and what makes a sign an attention-capturing sign) remains mostly unexplored. Since animals have various perceptual capacities, ecological niches, and Umwelten, the signs and meanings[3] relevant to them differ significantly. Posner (2016), for example, showed that humans have several neural mechanisms for attention to work; some are connected with saccadic eye movements. However, frogs, for example, do not have saccadic eye movements; therefore, their attentional mechanisms differ from those of mammals. Neural tissues are plastic and adaptive, and there can be several ways for attentional mechanisms to function. The structure of animals' sensory organs significantly affects their attention and sign-recognition capacity. Also, context and meaning influence animals' attention. For example, in the case of emergency, animal's attention can work differently than in the case of usual foraging behavior. A famous example is Hess and Frisch's conflicting results regarding bee vision: Hess concluded that bees do not have color vision, and Frisch's experiments showed that they do. After intense discussion and new experiments, the results showed that, in the case of feeding, honeybees could discriminate between colors; however, when fleeing, they did not pay any attention to the colors and moved in the direction of the brightest light. (Dhein, 2021). Although bees can distinguish different colors with the same brightness, attention can inhibit this ability in the case of emergency. So, if there is not enough knowledge about how attention works in different contexts, it can lead to misinterpretations in science experiments. While attention determines which signs are perceived and interpreted, semiosis influences how the meanings of these signs are interpreted.

[3] For Uexküll, organisms have inner structures of representing the outer stimuli (similarily Kant's "schema"), through which organism establish which stimuli are meaningful to it and forms its umwelt. (von Uexküll, 1926: 94). The signs in the Umwelt are forming the mirrorworld or signworld.

The Umwelt of an organism is a constructed world filtered through their senses and interpreted through their own specific set of receptors and neural processes. This perspective allows us to view attention as directed semiosis specific to each species, guided by its Umwelt. Moreover, attention serves as a crucial set of processes that not only sustain the Umwelt in the present moment but also actively construct its future. In this way, attention becomes the interconnected link between an organism's past experiences and their present actions, while simultaneously shaping their future. Hoffmeyer (2008: 10) has shown that "experiences are holistic markers that direct the brain to focus its (our) attention on a single pathway in the spatiotemporal continuum. […] experience is the ultimate, immediate, and unconditional interpreter in the continuous biosemiosis of the organism at every moment." (Hoffmeyer, 2008: 10–11). Hoffmeyer's work emphasizes that experiences play a pivotal role in serving as powerful guides for attention and essential contributors to the construction of meanings.

At the same time, attention is needed as a mediating and guiding process in perception as "the brain's size in terms of memory, processing speed, and the number of processors is too small for the combinatorial nature of extracting and then appropriately reuniting the elements present in the input that human sense organs receive" (Tsotsos, 2011: 51). This is most likely also the case for other animals. The quantity of perceived information about the world, which comes from all senses, is enormous, and there is a need for selection and simplification that allows to act quickly and decisively. Attention is composed of semiotic mechanisms that select, change, and maintain focus on the information most meaningful and relevant to a behavior. Therefore, attention is a simplifying or filtering process that mediates and guides perception and meaning-making[4].

Attentional Processes and Perception (Binding)

Many neuroscience and psychology studies have focused on the information acquired through the visual sense, which is usually divided into spatial and feature-based attention (Davis & Palmer, 2004; Lindsay, 2019). Attention unites the perceptual information from senses with meanings and creates their reality, binding the signals from several senses into a single representation. It filters out information and determines which features (colors, shapes) should be bound together to represent the object. This means that without focused attention, there is no object identity available for the observer. (Tsotsos, 2011) When looking at attention from the viewpoint of Uexküllian semiotics, we see that objects (or their signs) belonging to some functional cycles[5] may be more noticeable or important than others, and sometimes animals have habits of noticing the cues of different functional cycles through different

[4] Jakob von Uexküll defines meaning as the subjective interpretation of sensory perceptions within an animal's umwelt, shaped by its relations with its living environment.

[5] In any action, the subject and object are linked by a closed chain of cause and effect. This chain starts from the objects' perceptual sign carriers, in the form of one or more stimuli that affect the animal's receptors. In the animal, the latter are connected in the perceptive network and then have an effect on the operative one. The operative network transmits to the effector organs a certain motor modality, which becomes part of the operative carriers of the object. The perceptive sign carriers are connected to the

senses. For example, von Uexküll (1926: 142) writes, "Among the Crustacea, the indications of prey-cycle seem to be of a purely chemical nature, while those from the enemy-cycle are optical." Therefore, we can consider the functional tone[6] as a category that unites objects that potentially have the same functional meaning for the animal, and for noticing purposes, animals are more sensitive to a concrete feature or combination of features that for them are indexical signs pointing to that category.

Perception is also an active process that needs attention. Dominating functional cycles and meanings in the Umwelten can change attention and, therefore, perception. Perception, learning, decision-making, and action require constant adjustment of the attentional systems. Brain studies in primates have shown that visual objects are encoded by their properties (DeYoe & van Essen, 1988). This theory is also supported by studies on pigeon pecking behavior, which have been studied using touchscreen technology, and showed that pigeons learn to track individual features that allow them to successfully solve complex categorization tasks (Wasserman & Castro, 2021). It is theorized that attending in a feature-based manner is older and more universal mechanism than attending iconic or indexical signs. We interpret those findings differently, considering that the features can only be signs[7] or markers that animals use to facilitate their attentional processes. Animals may assign a qualisign[8] as an indexical marker to a specific category for search purposes.

In visual search, orientation in landscape can play an important role for animals. Here, not only the objects but also the patterns are important. Koenderink also shows that the only detectable phenomena are patterns present across different scales of space and time and in a specific context (Koenderink, 2019: 173). This shows that, to interact with the environment, it is important to have a quick first impression of the surroundings. It is formed quickly, probably automatically, and unconsciously and is also thought to be feature-based. The elements in the environment need to be compared to concepts already in memory to aid in processing visual cues. According to Gibson (1979), grips of perception refer to patterns of activity in perceptual systems that are triggered by features of the environment, such as the texture or motion of an object. These grips guide attention as organisms explore and interact with their surroundings. This theory also supports our view that certain features can be markers of certain categories for animal, similarily to words in human language.

Perception, therefore, requires attention that binds reality to a coherent Umwelt. This may not be an easy task, because all those many ways of sensing require attentional processes that bind everything together for a coherent reality that allows animals to make decisions and act in the world in a species-specific and efficient way.

operative carriers by the counter-structure. This is how the cycle I defined as a 'functional cycle' is closed. (Uexküll 1921: 46)

[6] Functional tone for Uexküll is a new meaning that supplements the receptor image with the effector image of animals own actions (using the object about which animal has receptor image) (von Uexküll, 2010)

[7] From Peirce's system of signs.

[8] According to Peirce (EP 2:294) „a Qualisign is any quality in so far as it is a sign. Since a quality is whatever it is positively in itself, a quality can only denote an object by virtue of some common ingredient or similarity; so that a Qualisign is necessarily an Icon. Further, since a quality is a mere logical possibility, it can only be interpreted as a sign of essence, that is, as a Rheme.".

From Image Schemas to Search Images and Search Schemas

von Uexküll (1926: 94) showed that Kant compared the image schema of objects with stamps in the mind, which is necessary to unite signs from the senses into images. He concluded that this process is primarily unconscious. Kant said, "The imagination is a necessary ingredient of perception itself" (Kant [1781]1998: 120), claiming that imagination is involved in forming sense perceptions, helping us form representations of objects as images. Johnson (2017: 127), on the contrary, claims that the "image schema" is generated by body experiences, not by imagination. And Grady (2005: 44) sees image schemas as "mental representations of fundamental units of sensory experience." Rohrer (2005: 166) sees the image schema as "shared activation contours across perceptual modalities" that are "recurrent patterns of bodily experiences" in "image-like forms" (Rohrer, 2005: 173). Although differently expressed, each of those definitions can take us closer to the understanding of image schemas in animal cognition.

Animal cognition can most likely also be seen to work through images and image schemas, which arise from their bodily experiences and connect the mind, body, and the environment. However, another nuance is that an image schema is "simply a concise combination of its most important parts, and with a precision appropriate to the particular animal" (von Uexküll, 1926: 149). The schemas, therefore, are dependent on the animals' subjective experiences. Perceived features from several sense modalities can be organized into meaningful patterns through the use of image schemas. Here, we look at image schemas as being important for recognizing objects and cues, but attention schemas as necessary mediating factors for the noticing stage of attention.

Uexküll claims about the vision that "Qualities and schemata together compose the things of the outer world, as we see them displayed for us." (von Uexküll, 1926: 97), showing that the qualities of features are sometimes united to schemata, but can also be perceived separately. Uexküll stresses that "we do not by any means always search for a certain object with a unique perception image" (von Uexküll, 2010: 117). Far more often, we search "for an object that corresponds to a certain effect image" (von Uexküll, 2010: 117), which is related to the function objects may have, according to their functional tone.

Visual attention in search is also species-specific. For example, bumblebees are more easily distracted during their search behavior than honeybees. The search mechanism of honeybees is serial and, therefore, fast and inaccurate; bumblebees, on the contrary, have a parallel search mechanism and make decisions slowly but correctly. (Morawetz & Spaethe, 2012) In visual search, different species also have different strategies for attending the entire landscape; some prefer to attend to the bigger picture, and some start with finer details. Turner (1910:277) concluded that bees learn landmarks in the form of "memory pictures" when performing circling orientation flights above an object. Later, it was shown that honeybees first examine a wider scene using spatial configurations and relational rules, and only after that attend to a more detailed image of the scene, but the researchers also showed that this strategy could be changed with training, which shows their attentional plasticity. (Avarguès-Weber et al., 2015)

To be able to capture and hold attention, the visual, auditory, olfactory, or tactile signs should have a noticeable intensity, be novel or unexpected, and be meaningful or relevant to an animal. The context in which these signs appear is important in capturing and holding attention. Perceptual salience, which is the degree to which a sign stands out or captures attention compared to others in an environment, is a measure of how easily it can be detected and distinguished. Usually, feelings of hunger and thirst act as salient signs in Umwelten. This prioritization aligns with Maslow's pyramid, which emphasizes the fulfillment of basic needs before pursuing other goals. Therefore, search images emerging from the basic needs of animals can override attention and ensure survival when necessary. von Uexküll (1926: 142) points out that "it is not at all necessary that the indications of an animal should reach the same height in each of its function-cycles. As a rule, in the enemy-cycle a mere movement will serve, whereas in the prey-cycle even the outlines may have this value." We see the movement and outlines of the enemy as the features that work as signs attached to certain categories (such as 'enemies' or 'prey') to facilitate attending it; therefore, those signs can also be parts of the attention schemas - the rules for prioritizing certain abstractions or features over other perceptions.

Two types of perceptual salience, that are important for attention, can be distinguished. First, salience is caused by a strong sense stimulus, which is usually a feature of the object, such as loud noise for horses or dogs or the smell of the earthworm to the mole, which makes the object noticeable among others. Those features themselves could be noticed pre-attentively, but as shown later, only when they have established meanings as attention schemas can they be prioritized over other perceptions. On the other hand, meaning-based salience depends only on the meanings in the animals' Umwelten and individuals' subjective experiences. Salience can be influenced by various factors, including the physical characteristics of the stimulus (such as brightness, contrast, or color), novelty, personal relevance or interest, and the goals or needs of the animal, as well as contextual factors such as the background against which the stimulus is presented. For example, for a dog, a strong smell of food may be more salient and, therefore, capture more attention than other objects in the room. However, when dogs are in the woods, the smell of the food may be less salient than that of another animal.

As shown in Fig. 1, although something may capture attention because of its high perceptual salience, attention will move on if this object or sign does not have enough meaning-based salience.

In Uexküll's sense, the search image of an animal is a mental representation of the searchable object. If an animal does not have clear knowledge of the appearance of what it is searching for, it applies a search tone, the idea about the practical function of an object the animal is attempting to find (Tønnessen, 2018).

> A performance is always an action with a purpose; action without purpose does not reveal the function. /…/ Usable objects exist only for those who know their use. This clearly reveals how the mode of existence of objects depend on the observing subject./…/ Only when the parts and the properties of an object are clearly perceived as parts of a function, does the mixture of parts become a meaningful whole. (von Uexküll, 2010: 112).

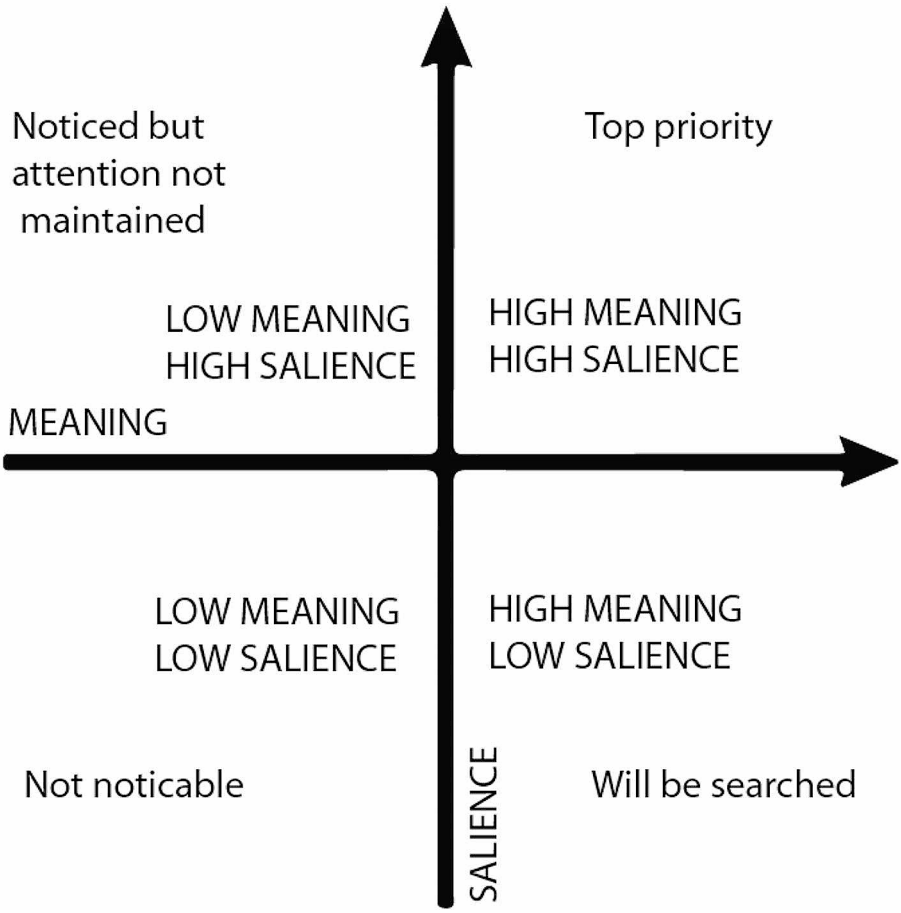

Fig. 1 Perceptual salience and meaning

Therefore, animals can start their search behavior when they have a search image, searchtone, or search schema. Search schema can be defined as "an iconic legisign[9] or image schema of the searchable. Such schema includes several features of the searchable, but gives an animal the possibility of choice since there could be several different objects which have such combination of features." (Tarrikas, 2023: 86). It is also different from Jakob von Uexküll's search tone because only the searchable function is known in the case of the search tone. Animals act when they have internal needs (hunger, pain, thirst, need for sleep or security, need to be at a comfortable temperature, etc.). In a search, the animal first notices or attends to the need with the help of bodily feelings as signs that help the animal find a meaningful search tone, search schema, or search image from memory, and then attention helps to focus the senses on finding objects, which can be associated with the search image, schema, or

[9] /./ Iconic Legisign is any general law or type, in so far as it requires each instance of it to embody a definite quality which renders it fit to call up in the mind the idea of a like Object. (EP2:294)

tone by some features. It may be suggested that at first, certain features are looked for as especially noticeable (easily attended) markers, and when a feature is found, attention will concentrate on this object, compare other features and meanings with it, and repeat those actions until the search is complete. Here, attention can be the process that connects those meaningful function features to the search tone and allows the focused search according to those meanings.

Jakob von Uexküll believes that the Umwelt of any mammal is species-specific, although sharing common mammalian traits. Here, we see that this also applies to attention. If two species share a territory, their views on the same things will have species-specific tones or shades for them, which also determines salience in terms of attention. Their search images will be different. Attention will be drawn in different ways and with different intensities to objects in their Umwelten, because of the different meanings attached to those objects by different species. Also, they have their own distractions and preferences in the environment. For horses, a new wheelbarrow can be a major distraction; however, for dogs, this is usually a neutral object. On the other hand, dogs can be distracted by a cat's smell, which is a neutral sign for horses.

Search images are simple mental representations of objects; therefore, we should presume that some category is already prespecified or primed, suitable representation is activated, and meaning is bound to it. Therefore, we can assume that the search images and meanings are construction stones for the attention schemas. Search images link the core Umwelt and mediated Umwelt (Tønnessen, 2018), assisting actual perception through expected or desired perceptual images.

Search images are important because image-based cognition is the most probable way in which animals can interact with the world. Kant (1998[1781]) observed that pictural cognition works through imagined images and image schemas. Therefore, we can distinguish between an image that is constructed at the time it is perceived, and the simpler abstract image of this perception image, which is called image schema. Neurosciences have shown, that the same parts of the brain work when we see something and when we imagine it, which supports Kant's theory. Kant's image schemas are, therefore, mental abstractions that lack finer details. Uexküll's search image is probably an image schema, in Kant's terms.

In animals' Umwelten, attention is the process of capturing and maintaining meaningful signals from the environment and comparing them with earlier sign patterns in memory; therefore, a meaningful relationship with the environment is possible. Bodily feelings are also signs for animals and usually very salient signs.

Attention Schemas and the Model of Attention

Attention Schema Theory (Graziano & Kastner, 2011) proposes that different brain regions work together to form a schematic metamodel of attention, or set of rules that guides its work. This representation, or the internal model, is the attention schema. We develop this theory further, showing that not only the brain, but also the organism as a whole is important in constructing attention schemas, and also stress that although some animals have differently constructed neural systems, they enable their attention to work with the precision that a specific animal needs. In constructing the

attention schema, the brain is not working alone but in relation to all parts of the nervous system and in meaningful relations with the environmental context where the animal is situated. Animals' attention can be seen as a directed agency of an animal, based on signs and their relations occurring in the context and environment. The attention schemas can be seen as habits of attending to certain patterns.

Figure 2 shows the manner in which attention can work. Attention has a noticing part and a meaning-making part. The meaning-making part combines the sensory signals into coherent images or reality, simplifies those images into image schemas and signs, and gives them meanings. It can recognize patterns and meanings by comparing new ones with those stored in memory. If anything is recognized as meaningful, then attention is maintained to it for longer. Meaningful signs can initiate functional cycles. Feedback is sent to the memory, especially to the attention schema, which is a set of rules on how attention will work.

An attention schema is, therefore, an internal representation or model of attentional rules which each organism constructs attention after receiving feedback from interaction with the environment, and it could also be partly inherited and species-specific. Attention mediates and guides perception and meaning-making, synthesizes perceptions, and binds different sensory modalities together. The meaning-making ability of animals helps them assess the environment, recognize whether there is anything new or even dangerous, and be creative, if necessary. Attention schemas maintain species-specific attention and, therefore, species-specific immediate reality, or Umwelt. Therefore, attention is a uniting factor that makes subjective phenomena possible and is the basis of the mechanisms for adaptive decision-making in natural environments. (In animals with simpler Umwelten, attention can work in much simpler ways.)

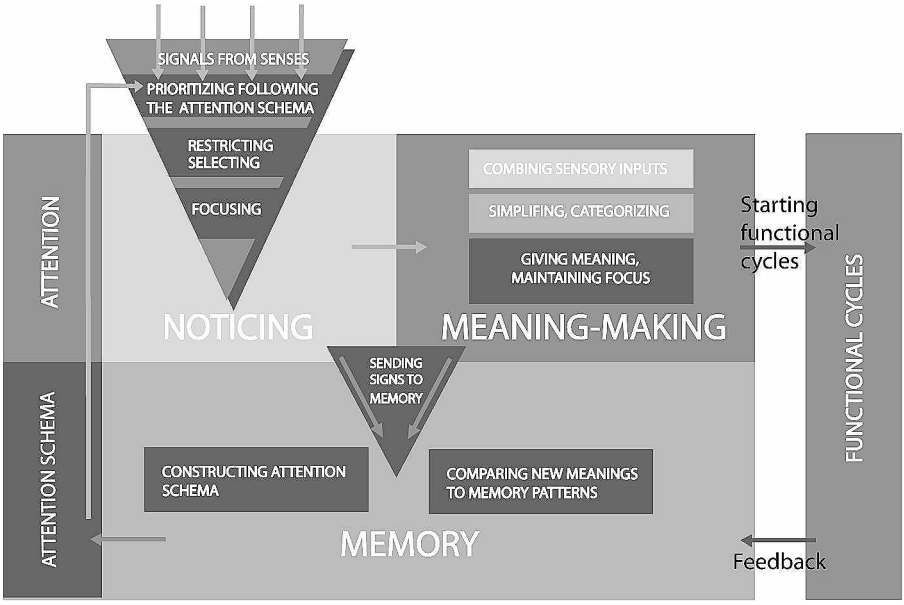

Fig. 2 Model of attention

As shown in Fig. 2, attention is a complex process involving several stages. The first part of the attentional process involves noticing. It starts with grabbing or drawing attention, which is the process of noticing something in the environment. It can work with salient features (as qualisigns of categories) and is guided by a previously developed attention schema that can work through indexical legisigns. Animals can use noticeable features as markers or signs of important objects, other animals, or something else in the environment.

The second stage involves uniting information from all the senses and forming an actual perception image of the object that has been noticed. This stage ends by focusing on a particular object, event, or situation and ignoring other stimuli that are not relevant.

The third stage combines perceptual signs with emerging bodily feelings. This stage involves comparing and integrating these feelings with the mental representation of the object or event, discovering the meanings of those new sensations (it also needs comparing meanings with meanings in memory systems). In this meaning-making stage, it is also determined how long attention will be maintained and when it is time to move on. In this stage, the relevant behaviors are chosen, and decisions are made about how and when to act. The functional cycles will be initiated, and the attentional processes will be cleared for new information.

All of these stages require the help of the attention schema, which will improve constantly because the objects in the environment and the animal's relations with the objects are dynamic. Attention is dynamic, therefore some processes can also work simultaneously.

As certain attention prioritization strategies are found to be efficient, they may become habitual, and this pattern of attention may turn into a habit (schema). Animals may have both innate species-specific attention schemas (or a tendency to acquire certain attentional habits) and prioritization rules acquired through learning. Therefore, attention schemas can be the basis of meaning-making, guiding attention through previously learned meanings and signs and helping an animal make predictions.

From the researcher's perspective, this model of attention helps to show the importance of meanings for attention and aids in understanding some of the rules underlying the attention of the species and the meanings that those are based on. This model can also help predict the attentional priorities and behaviors of animals. This model is a synthesis of previously existing ideas and theories meant to explicate how attention is closely interrelated with meaning-making and perception.

Animals develop their species-specific Umwelten through their own agency and attentional processes. Attentional processes, on the other hand, can change their Umwelt and initiate innovations, which are vital for the species. Lower-level semiotic processes affect higher-level semiosis and change the organism, its Umwelt, and its behavior. In addition, the environment can be a starting point for changes in Umwelt. All of these processes require mediation through attention.

Differently from Treisman's & Gelade's (1980) preattention stage that binds together different components (such as color, shape, and orientation) of representation, which have been maintained as separate units at the initial stages of object perception, we propose that it works with the help of attention schemas that allow

corporate meanings in this process. It can be a simultaneous process with other attentional processes, giving access to previous experiences and meanings through attention schemas. This shows that attention is caused by the agency of animals, and there is no need to divide it into top-down and bottom-up processes, or even into exogenous (reflexive) and endogenous (voluntary) attention (Weichselgartner & Sperling, 1987) because they are intertwined. Even seemingly unconscious attention is an interpretative sign process, although it is already habitual and controlled by legisigns called attention schemas.

Kant and Uexküll have schemas similar to those of Graziano. Kant (1998) talks about schema as something that mediates the world and internal mental structures, which alters experiences and itself gets changed by subjective experiences. Uexküll went a different way from the researchers who connected Kant's concept of an image schema with embodied cognition. von Uexküll and Kriszat (1956: 84) state that a schema organizes and synthesizes perceptual signs from different senses into a unified and identified perception image. The schema is not a passive receptacle for sensory input but an active system that structures and interprets sensory information in a meaningful and relevant way to the organism's Umwelt. Schema is constantly updated and refined based on an organism's experiences and interactions with its environment. Repeated exposure to particular stimuli causes an organism's schema to be more finely tuned and sensitive to relevant information, allowing it to respond more efficiently and effectively to the environment. Uexküll's concept of schema highlights the active and dynamic nature of perception, and the importance of pre-existing cognitive structures in organizing and synthesizing sensory information into a coherent and meaningful perception of the world.

The Attention Schema Theory (Graziano & Kastner, 2011; Wilterson & Graziano, 2021) has some problems from a semiotic perspective. The brain is not a control center separate from the body, which is why we propose in this work that attention management can take place through various cooperation and interaction mechanisms. At the lowest level, there is cooperation between neurons, and at the highest level, between the environment and organism. In *Attention Schema Theory* (Wilterson & Graziano 2021), attention schema or metamodel of attention, works through image schemas We look here from the viewpoint of semiotics and see attention working through legisigns. Therefore, the habits of noticing and directing attention form through the cooperation of internal signs received from the body, sense organs, are based on experiences and species-specific traits.

In different animals, different parts of the nervous system are responsible for semiotic processes related to attention, and apparently, there are also different mechanisms through which attention is directed, that is, different attention schemas (to use Graziano's term). There are also differences among members of the same animal species; some have more plastic neural systems than others. The strength of neural network connections determines the level of plasticity of the nervous system, and therefore, its readiness to change (Branchi, 2022:3). Attention is turned to new aspects of the environment more efficiently when connections are less rigid. Behavioral changes are not always beneficial but are sometimes inevitable in changing environments.

In addition to being the basis of meaning-making, guiding attention through previously learned meanings and signs, learning, teaching, and innovation in the popula-

tion also occurs with the help of attention. Agency[10], through attention, is as important as the building plan for animals to construct and maintain their Umwelten. Through it, adaptation to new situations and environmental changes takes place.

Species-specific Notability of Signs and Meanings

It is unclear how the mechanism of prioritizing attention varies across species and what factors contribute to this variation. The earliest forms of attending were probably automatic responses to environment, such as those observed in single-celled organisms. As organisms become more complex, attention has become more flexible and goal-directed. Krauzlis et al. (2018) have shown that although selective attention in mammals is associated with information processing in the neocortex, other animals, such as birds, reptiles, amphibians, and fishes, also possess the ability of selective attention. Although majority of animal species lack a neocortex, the other parts of their brains are responsible for the same functions. The presence of selective attention has been demonstrated in birds (Sridharan et al., 2014; Mysore et al., 2011), reptiles (Fleishman, 1986), and amphibians (Ewert, 1970). In frogs, the relationship between visual cues and behavior depends on novelty and motivation. When sensing the scent of earthworms, frogs snap at larger objects, which they ordinarily tend to avoid (Ewert, 1970), since the scent is an indexical sign of their presence, as it is possible to presume. When faced with a choice between two prey animals, toads usually choose the closest one, but their reaction time increases when they see both prey animals simultaneously (Ingle, 1973). Insect species also have different abilities to focus; for example, dragonflies can focus on only one fly within a swarm of flies (Wiederman & O'Carroll, 2013); honeybees can be more easily distracted from their search than bumblebees (Morawetz & Spaethe, 2012). Spiders are good at maintaining focus on salient objects such as prey animals (Bruce et al., 2021), and they can also use their webs as external attending aids. Jays (*Cyanocitta cristata*) do not notice peripheral objects (such as predators) when selectively attending to complicated central task (Dukas & Kamil, 2000).

The understanding of attention in non-mammalian species remains limited, and more research is needed to explore the nature of cognitive processes in animals with simpler Umwelten, such as earthworms or molluscs.

Meaning-making and Sustained Attention

There is a relationship between selective attention and meaning-making. Some objects are selected by attention and are found to be more useful by certain animals. Therefore, they acquire meanings in their Umwelten, and together with meaning-making, an appropriate attention schema is developed. Meanings are imprinted on previously meaningless objects when they are perceived and used by animals and

[10] Agency is the capacity of individual animals to engage in voluntary, self-generated, and goal-directed behavior that they are motivated to perform (Wemelsfelder, 1997).

are thereby transformed into subject-related meaning-carriers in their Umwelten (von Uexküll 1982[1940]). Sustained attention is a state in which attention is maintained on some things for some time, and this can be directly influenced by meanings because meaningful objects stay in focus longer. Sustained attention is important for learning. Maintaining attention long enough to learn some behavior so well that it turns into a habit can benefit neophilia, and therefore, innovation and adaption. When more behaviors are turned into habits, animals can free more neural capacity to attend to the novelty. It can also be assumed that animals whose environments are more stable and secure can be more neophilic. Which objects automatically attract an animal's attention is also connected to the meanings those objects have in the animals' Umwelten and also to the overall context or situation.

Habituation is an excellent example of attention and meaning making working together. von Uexküll (1928: 110) emphasizes the active role of living beings in searching for what captivates their interest in their surroundings and adjusting the existing conditions to suit their needs. The animal is, therefore, able to filter out irrelevant stimuli and learn to ignore previously relevant ones, leading to adaptation to the environment. Habituation occurs when the signal or action is repetitive, the response to novelty decreases, and an animal gives new meaning to this cue (considering it at least not dangerous) and learns to ignore it. This is the opposite of the attending process. However, when animals categorize repetitive signals as important ones, they will continue to attend to and respond to them. As we can see, feelings and reactions can only follow meaning-making. Attention is important for adaptation because novelty seeking and creativity are following something that captures attention, and that leads to adaptation.

Conclusion

Attention is essential for building and shaping animals' Umwelten and almost every aspect of their lives. In this article the concept of attention was viewed from the semiotic perspective in the context of the animal's perceptual experiences, and argued that attention is creatively shaped by the interpretive processes of the individual. We showed that attention is an umbrella term for several subprocesses, that has been here, after synthezising several previous theories, united for a model of attention, which helps visualize the different stages of attention and their relations. Proposed model unites *Attention Schema Theory* with Uexküllian semiotics and meaning-making and shows how animals are actively constructing the rules of attending through their previous meaning-making, and that meanings (result of previously happened semiosis) are shaping rules for attention to work in the future through feedback mechanisms. Noticing is considered here to be one part of attentional processes and therefore not equal to the term 'attention'. We showed that the interpretative sign processes may turn to habits which are controlled by attention schemas, which are continuously tuned by feedback mechanisms, and act as rules of attending in the future. There are rules of attention that are species-specific, but also those which have shaped in relation to the individual Umwelt. Attention, therefore, functions as a mediating mechanism in perception and meaning-making, and contributes to the dynamic process of

interpretation and meaning-making in an animal's interaction with its environment. We also analyzed how attention influences the interpretation and prioritization of environmental stimuli in different animal species and how the construction of animals' sense organs and acquired experiences shape their attention allocation.

Author Contributions Siiri Tarrikas is responsible for all the manuscript and the figures.

Funding This research was supported by the Estonian Research Council Grant "Meanings of endangered species in culture: ecology, semiotic modelling and reception" (PRG1504).

Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing Interests The authors declare no competing interests.

References

Avarguès-Weber, A., Dyer, A. G., Ferrah, N., & Giurfa, M. (2015). The forest or the trees: Preference for global over local image processing is reversed by prior experience in honeybees. *Proceedings of the Royal Society B: Biological Sciences*, 282(1799), 20142384. https://doi.org/10.1098/rspb.2014.2384.

Branchi, I. (2022). Plasticity in mental health: A network theory. *Neuroscience & Biobehavioral Reviews*, *138*, 104691. https://doi.org/10.1016/j.neubiorev.2022.104691.

Broadbent, D. E. (1958). *Perception and communication*. Pergamon.

Bruce, M., Daye, D., Long, M., Winsor, S., Menda, A. M., Hoy, G., & Jakob, R. R., E. M (2021). *Journal of Experimental Biology* 224 (8): jeb231035. https://doi.org/10.1242/jeb.231035.

Buschman, T. J., & Kastner, S. (2015). From behavior to neural dynamics: An integrated theory of attention. *Neuron*, *88*(1), 127–144. https://doi.org/10.1016/j.neuron.2015.09.017.

Bushnell, P. J. (1998). Behavioral approaches to the assessment of attention in animals. *Psychopharmacology (Berl)*, *138*, 231–259.

Cherry, E. C. (1953). Some experiments on the recognition of speech, with one and with two ears *The Journal of Acoustic Society of America* 25, 975–979. https://doi.org/10.1121/1.1907229.

Cimatti, F. (2018). *A biosemiotic ontology: The philosophy of Giorgio Prodi* (18(.). vol.). Springer.

Davis, E. T., & Palmer, J. (2004). Visual search and attention: An overview. *Spatial Vision*, *17*(4–5), 249–255. https://doi.org/10.1163/1568568041920168.

de Bivort, B. L., & van Swinderen, B. (2016). Evidence for selective attention in the insect brain. *Current Opinion in Insect Science*, *15*, 9–15. https://doi.org/10.1016/j.cois.2016.02.007.

DeYoe, E. A., & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neurosciences*, *11*(5), 219–226. https://doi.org/10.1016/0166-2236(88)90130-0.

Dhein, K. (2021). Karl Von Frisch and the Discipline of Ethology. *Journal of the History of Biology*, *54*, 739–767. https://doi.org/10.1007/s10739-021-09660-7. https://doi-org.ezproxy.utlib.ut.ee/.

doi: 10.1523/JNEUROSCI.4592-10.2011.

doi: 10.1007/BF00612043.

Dukas, R., & Kamil, A. C. (2000). The cost of limited attention in blue jays. *Behavioral Ecology*, *11*, 502–506. https://doi.org/10.1093/beheco/11.5.502.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*(3), 433–458. https://doi.org/10.1037/0033-295X.96.3.433.

Eco, U. (2000). *Kant and the Platypus: Essays on Language and Cognition* (1st Harvest). Harcourt.

Ewert, J. P. (1970). Neural mechanisms of prey-catching and avoidance behavior in the toad (Bufo bufo L). *Brain Behavior and Evolution*, *3*(1), 36–56. https://doi.org/10.1159/000125462.

Fleishman, L. J. (1986). Motion detection in the presence and absence of background motion in an Anolis lizard. *Journal of Comparative Physiology*, *159*(5), 711–720.

Gendron, R. P. (1986). Searching for cryptic prey: Evidence for optimal search rates and the formation of search images in quail. *Animal Behaviour*, *34*(3), 898–912. https://doi.org/10.1016/S0003-3472(86)80076-8.

Gibson, J. J. (1979). *The Ecological Approach to Visual Perception*. New Jersey. Erlbaum.

Grady, J. (2005). Image schemas and perception: Refining a definition. In B. Hampe (Ed.), *From perception to meaning: Image Schemas in Cognitive Linguistics* (pp. 35–56). De Gruyter Mouton. https://doi.org/10.1515/9783110197532.1.35.

Graziano, M. S., & Kastner, S. (2011). Human consciousness and its relationship to social neuroscience: A novel hypothesis. *Cognitive Neuroscience*, *2*(2), 98–113. https://doi.org/10.1080/17588928.2011.565121.

Guilford, T., & Dawkins, M. (1987). Search images not proven: A reappraisal of recent evidence. *Animal Behaviour*, *35*, 1838–1845. https://doi.org/10.1016/S0003-3472(87)80076-3.

Hoffmeyer, J. (2008). The Semiotic Niche. *Journal of Mediterranian Ecology*, *9*, 5–30.

Ingle, D. (1973). Two visual systems in the frog. Science 181, 4104, 1053–1055. https://doi.org/10.1126/science.181.4104.105.

Jennings, C. D. (2012). Subject of attention. *Synthese*, *189*, 535–554. https://doi.org/10.1007/s11229-012-0164-1.

Johnson, M. (2017). *Embodied mind, meaning, and reason: How our bodies give rise to understanding*. University of Chicago Press. https://doi.org/10.7208/chicago/9780226500393.001.0001.

Kant, I. (1998). [1781] *Critique of Pure Reason*. (Paul Guyer and Allen Wood Eds. andTrans.). Cambridge University Press. https://doi.org/10.1017/cbo9780511804649.

Klein, C., & Barron, A. B. (2016). Insects have the capacity for subjective experience. *Animal Sentience*, *9*(1). https://doi.org/10.51291/2377-7478.1113.

Koenderink, J. (2019). *Sentience*. De Clootcrans Press Utreht.

Koenderink, J., van Doorn, A., & Pinna, B. (2015). Psychogenesis of Gestalt. Gestalt Theory.

Krauzlis, R. J., Bogadhi, A. R., Herman, J. P., & Bollimunta, A. (2018). Selective attention without a neocortex. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *102*, 161–175. https://doi.org/10.1016/j.cortex.2017.08.026.

Lindsay, G. W. (2019). Attention in psychology, Neuroscience, and machine learning. *Frontiers in Computational Neuroscience*, 14–29. https://doi.org/10.3389/fncom.2020.00029.

Morawetz, L., & Spaethe, J. (2012). Visual attention in a complex search task differs between honeybees and bumblebees. *The Journal of Experimental Biology*, *215*, 2515–2523. https://doi.org/10.12688/f1000research.4799.2.

Mysore, S. P., Asadollahi, A., & Knudsen, E. I. (2011). Signaling of the strongest stimulus in the owl optic tectum. *Journal of Neuroscience*, *31*(14), 5186–5196.

Nityananda, V., & Chittka, L. (2015). Modality-specific attention in foraging bumblebees. *R Soc open sci*, 2150324150324. https://doi.org/10.1098/rsos.150324.

Posner, M. I. (2016). Orienting of attention: Then and now. *The Quarterly Journal of Experimental Psychology*, *69*(10), 1864–1875. https://doi.org/10.1080/17470218.2014.937446.

Rohrer, T. (2005). Image schemata in the brain. From perception to meaning: Image Schemas. *Cognitive Linguistics* (pp. 35–56). De Gruyter Mouton. https://doi.org/10.1515/9783110197532.1.35.

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, *74*(11), 1–29. https://doi.org/10.1037/h0093759.

Sridharan, D., Ramamurthy, D. L., Schwarz, J. S., & Knudsen, E. I. (2014). Visuospatial selective attention in chickens. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, *111*(19), E2056–E2065. https://doi.org/10.1073/pnas.1316824111.

Tarrikas, S. (2022). Modelling Animal Creativity from Uexküllian Approach—Attention, Search Image and Search Tone. *Biosemiotics* (2022) 15:531–553 https://doi.org/10.1007/s12304-022-09498-4.

Tarrikas, S. (2023). Otsingupildid kõverpeeglis. *Acta Semiotica Estica*, *XX*, 69–88.

Tønnessen, M. (2018). The search image as link between sensation, perception and action. *Biosystems*, *164*, 138–146. https://doi.org/10.1016/j.biosystems.2017.10.016.

Treisman, A., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*(1), 97–136. https://doi.org/10.1016/0010-0285(80)90005-5.

Tsotsos, J. K. (2011). A Computational Perspective on Visual Attention, MIT Press, ISBN 978-0-26-201541-7).

Turner, C. H. (1910). Experiments on Color-Vision of the Honey Bee. *Biological Bulletin*, *19*(5), 257–279. https://doi.org/10.2307/1536088.

van Heusden, B. P. (2004). In W. Wildgen (Ed.), *A Bandwidth Model of Semiotic Evolution*. B. P.

van Heusden, M. M. H., & Bax (Eds.). Semiotic evolution and the dynamics of Culture (3–33). P.I.E. - Peter Lang.
Vol. 37, No.3, 287–304.
von Uexküll, J. (1926). *Theoretical biology*. Harcourt, Brace & Co.
von Uexküll, J. (1928). Theoretische Biologie (2te ed.). Verlag von Julius Springer.
von Uexküll, J. (2010). *A foray into the worlds of animals and humans: With a theory of meaning. (J. O'Neil, Trans)*. University of Minnesota.
von Uexküll, J. (1982[1940). The theory of meaning. *Semiotica*, *42*(1), 25–82. https://doi.org/10.1515/semi.1982.42.1.25.
von Uexküll, J., & Kriszat, G. (1956). *Menschen Streifzüge Durch die Umwelten Von Tieren Und Menschen: Bedeutungslehre*. Rowohlt.
Wasserman, E. A., & Castro, L. (2021). Assessing attention in Category Learning by animals. *Current Directions in Psychological Science*, *30*(6), 495–502.
Weichselgartner, E., & Sperling, G. (1987). Dynamics of Automatic and controlled visual attention. *Science*, *238*(4828), 778–780. https://doi.org/10.1126/science.3672124.
Wemelsfelder, F. (1997). The scientific validity of subjective concepts in models of animal welfare. *Applied Animal Behaviour Science*, *53*, 75–88. https://doi.org/10.1016/S0168-1591(96)01152-5
Wiederman, S. D., & O'Carroll, D. C. (2013). Selective attention in an insect visual neuron. *Current Biology*, *23*, 156–161. https://doi.org/10.1016/j.cub.2012.11.048.
Wilterson, A. I., Kemper, C. M., Kim, N., Webb, T. W., Reblando, A. M. W., & Graziano, M. S. A. (2020). Attention control and the attention schema theory of consciousness. *Progress in Neurobiology*. https://doi.org/10.1016/J.PNEUROBIO.2020.101844.
Wilterson Andrew, I., & Graziano, M. S. (2021). The attention schema theory in a neural network agent: Controlling visuospatial attention using a descriptive model of attention. *Pnas*, *118*(33), e2102421118. https://doi.org/10.1073/pnas.2102421118.
Wolfe, J. M. (1994). Guided search 2.0 a revised model of visual search. *Psychonomic Bulletin & Review*, *1*, 202–238. https://doi.org/10.3758/BF03200774. https://doi-org.ezproxy.utlib.ut.ee/.
Zentall, T. R. (2005). Selective and divided attention in animals. *Behavioral Processes*, *29* 69(1), 1–15. https://doi.org/10.1016/j.beproc.2005.01.004.
Zentall, T. R., & Riley, D. A. (2000). Selective attention in animal discrimination learning. *Journal of General Psychology*, *127*(1), 45–66. https://doi.org/10.1080/00221300009598570.