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The *Umwelt* and Its Relevance to Animal Communication: Introduction to Special Issue

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This introduction applies J. von Uexküll's (1934/1957) concept of the *Umwelt* to the study of animal communication, particularly as it pertains to studies presented at a recent workshop on animal communication in the context of the environment. The environment is conceived broadly in the articles that follow, including the many physical and social environments in which an animal may find itself. The Umwelt concept is briefly expanded here to include also the personal microenvironment of the signaler in which the signal is embedded into the suite of concurrent nonsignaling behaviors of the individual. Other animals may even infer aspects of the signaler's own immediate Umwelt by noticing accompanying attentional cues such as the direction of eye gaze. In this way, part of the Umwelt can be accessible to companions, facilitating the communication process.

This special issue of the *Journal of Comparative Psychology* highlights research that was presented at an interdisciplinary workshop on animal behavior held at the University of California, Davis, in March 2000 entitled "Communication: The Animal in the Context of Its Environment." The workshop was designed to explore the role of auditory and vibrational communication signals of animals in relation to their physical and social environments, with special reference to the concepts of Von Uexküll (born in 1864, died in 1944). He was one of a distinguished group of zoologists who were active in Germany early in the last century, including Albrecht Bethe and Eric von Holst, who pioneered the study of the physiology of animal nervous systems in relation to their structure and behavior. Von Uexküll's research focused especially on invertebrates, including sea anemones, sipunculids, starfish, sea urchins, crabs, octopuses, and other mulluscs (see Bullock & Horridge, 1965). He is best known today for immortalizing the tick and its relationship to the mammalian hosts whose blood it feeds on and requires to reproduce. This example served to illustrate his concept of the *Umwelt*, which he described as the unique perceptual and effector worlds of each animal (Von Uexküll, 1934/1957). In reviews of his own and others' work, he emphasized the extreme phylogenetic contrasts that exist in the sensory worlds of different animal species. The concept is more complex than just sense organ physiology, embracing not only how animals sense and perceive their environments, both physical and social, but also what resources are proffered to the organism, how animals respond to their situation, and how those responses in turn modify both the environment and the organism's perceptions of the environment and of itself.

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There is much in common here with Gibson's concept of affordances (Gibson, 1986). Both Gibson and Von Uexküll strived to capture the extreme complexities of the relationships, both static and dynamic, between organisms and their environments. The immensity of this challenge requires efforts that may not always be convincing to other researchers. A degree of skepticism is evident in Lashley's (1957) comment about Von Uexküll, "although the descriptions of the animals' worlds give the reader a feeling for their experiences, this empathy is illusory and sometimes misleading" (1957, p. x). Nevertheless, in talking about Von Uexküll's work, Lashley concludes that "questions concerning the animal's mind are meaningful, and can be answered only in terms of the interaction of the animal with its environment" (Lashley, 1957, p. x). Nowhere is this more evident than in communicative behavior.

Although Von Uexküll's (1934/1957) concept of the Umwelt was not originally intended to explain animal communication, it has proven useful for this purpose. A signal produced by one animal changes the behavior of others, in turn modifying the signaler's own social environment. This change of circumstance often elicits yet another change in the individual's own behavior. This process can be illustrated by Von Uexküll's famous, somewhat mysterious "functional cycle" diagram (see Figure 1), which depicts perceptual and motor interactions of an animal with its environment. We might extend the functional cycle to include inputs from other companions whose interests and concerns may be different again. The social environment may include both active and passive participants, direct interactants and eavesdroppers, unidirectional and multidirectional exchanges, all with potential contributions to the social Umwelt. To highlight the contribution of social companions to the cyclical nature of communication, we have redrawn Von Uexküll's diagram as it might be applied to communication (see Figure 2).

Thus, each animal communicates in the context of its own personal Umwelt, surrounded by the particulars of its own life, which include individual conspecifics, heterospecifics, and the micro- and macrohabitats in which it lives. Each individual's

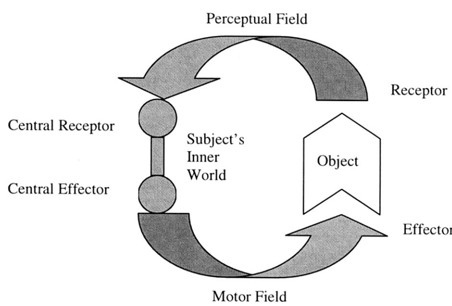

Figure 1. Von Uexküll's "functional cycle" (after Von Uexküll, 1934/1957; all labels are his original terms). The subject is drawn in gray and the object (or individual), with which the subject interacts, is drawn in white. From "A Stroll Through the Worlds of Animals and Men: A Picture Book of Invisible Worlds," by J. Von Uexküll, 1934, in *Instinctive Behavior: The Development of a Modern Concept* (p. 10), by C. H. Schiller (Ed.), New York: International Universities Press. Copyright 1957 by International Universities Press. Adapted with permission.

communicative ability, manifest in this environment, has consequences for its own reproductive success and influences the evolution of communication in the species as a whole. Important factors in this evolutionary process include the following aspects of an animal's Umwelt: the physical environment, the social environment, and what we would like to call the *personal environment*, including both the physical equipment for producing and sensing communication signals and the microenvironment of the signal in the context of the rest of the signaler's body. This last factor includes concurrent cues emanating from an animal during signal production, such as the body posture or chemical pheromones that may accompany an acoustic signal. The articles that follow address the physical environment (for overview, see Rundus & Hart, 2002), signal production and detection (see Randall & Crider, 2002), and the social environment, including both conspecifics (see Ruys & Schilling, 2002) and other species (Shier, 2002). Below, we also briefly address the personal environment of the signal in terms of concurrent behavioral cues, not addressed directly at the workshop.

The first two factors that influence the form of the signal, the production and detection mechanisms and the physical environment through which it is transmitted, are tightly associated with one another. Sound transmission can be helped or hindered by the physical environment; the structure of animal sounds is thought to have evolved in response to this constraint, which varies drastically according to where the animal lives (Ketten, 1997; Larom, 2002; Marten & Marler, 1977; Marten, Quine, & Marler, 1977; Morton, 1975; Rabin & Greene, 2002; Snowdon & de la Torre, 2002; Wiley & Richards, 1978, 1982). The transmission of substrate-borne vibrations can be even more profoundly facilitated or limited by the physical environment than airborne sounds (see Arnason, Hart, & O'Connell-Rodwell, 2002; Mason & Narins, 2002); the physical interface between air and water provides a particularly specialized conduit for propagating vibrational signals (Lema & Kelly, 2002).

The third factor is the social environment, which is clearly important for an animal's signaling behavior. Sensory proclivities of conspecifics influence signal design and usage. This includes the sensory and perceptual apparatus of the species and how it operates, influencing the evolution of signal structure (Ryan, 1998) and also the tendency of a responding individual to focus attention on a particular stimulus, which influences the immediate choice of signal usage by the signaler (West & King, 1988). King, West, and White (2002) have embarked on a new program to examine social influences on behavior and communication in group-living birds and have found that the effect of being a member of a social group has far-reaching consequences. Consistent with the Umwelt concept, King et al. have shown that the behavior of these birds both influences and is influenced by their social structure and spacing preferences. In addition, the reception and perceptual proclivities of other species, particularly those that prey on the signaling species or those that are preyed on by it, influence signal design on

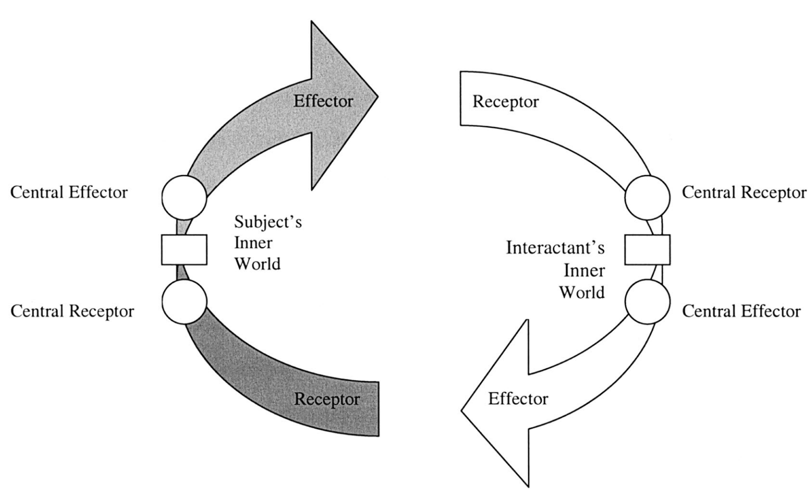

Figure 2. Reinterpretation of Von Uexküll's (1934/1957) functional cycle: social communication version. Here, we have expanded the role of the other interactant (right, in white) to match that of the subject (left, in gray). In this reinterpretation, we have deemphasized the central role of the subject, important in the original figure, in favor of an emphasis on the cyclical nature of each partner's effect on the other.

both the evolutionary and the proximate time scales (Owings, Rowe, & Rundus, 2002; Snowdon & de la Torre, 2002).

The final component of the environment of an animal's signal is the concurrent behavior of the individual signaler itself, which makes up the "personal microenvironment" of the signal. The signaler's behavior is sensed and perceived both by the signaler itself, contributing to its own self-perception, and by other animals, influencing the course of communication between them (Au, Lemonds, Vlachos, Nachtigal, & Roitblat, 2002). Von Uexküll wrote in 1934 that "we know nothing so far of the extent to which the subject's own body enters into his *Umwelt*" (1934/1957, p. 73); researchers are only now, many decades later, beginning to untangle these factors. An animal senses its own sounds and vibrations and smells its own scent (Mateo & Johnston, 2000). It may derive some idea of how it looks and sounds from how others respond to it (Hauber, Sherman, & Paprika, 2000). Other accompaniments to the production of a given signal are also sensed by the signaler itself, potentially contributing to its sense of a personal Umwelt.

When concurrent behaviors are perceptible to others, they may become an important part of the immediate environment of the communication signal. An acoustic signal, for example, can be seen as being set into the background of the animal's own behavior as a stone is set into a ring, a metaphor reminiscent of Von Uexküll's (1934/1957) original diagram (see Figure 1). Vocalizations may be accompanied by visual, chemical, and tactile signals as well as external and internal movement related to locomotion, physiology, or most important, sensory orientation, such as sniffing and movements of the eyes and ears. When nonsignaling behavior coincides with signaling behavior on a regular basis, observers may be able to take advantage of this coincidence and exploit the concomitants as information sources. This may lead to the formalization of the composite group of behaviors into a *multimodal signal* (being made of components perceived through different sensory channels).

Received by another animal, disparate components of a multimodal signal can be processed separately or in some cases by the same neuron, aptly labeled a *multimodal neuron* (e.g., Stein & Meredith, 1990). Because signals in different sensory modalities may have very different semantic content, one component can have a significant effect on the response to other components (see Massaro, 1998, for related discussion of the perception of signals with differing levels of ambiguity). As a consequence, multimodal combinations may have a profound impact on the efficacy and meaning of an animal's signal (Partan & Marler, 1999). An observer can, for example, infer referential information from a nonreferential call by assessing where the caller is looking. Such indexical cues provide information about an individual's current focus of attention and thus about the environmental cue that engenders interest, fear, or aggression in the signaler. Alternatively, emotional information can be gathered along with a referential vocalization by assessing concurrent visual cues such as facial expression (de Gelder & Vroomen, 2000; Marler, 1965). Many other examples of concurrent, multimodal signaling illustrate the importance of including the personal environment of the signal in an analysis of environmental influences on communication (e.g., see Cave, Guaitella, & Santi, 2001).

Although the Umwelt is usually treated as a species level concept, it is also heuristically useful in describing the perceptual worlds of individuals (as Von Uexküll, 1934/1957, originally pointed out). In fact, each individual voluntarily, and involuntarily, shapes its own immediate Umwelt, not only by registering and adjusting the posture and condition of its body and its physiological state but also by focusing attention selectively on certain aspects of its environment while neglecting others. The attentional focus is often indicated by gaze direction, as mentioned above, and also by head orientation and a variety of other visual cues depending on the species (crests in birds; ears in canids, equids, elephants, and other mammals; eyebrows and other eye markings in canids and primates, etc.). If other animals can read these attentional markers, it allows them a window into the signaler's personal Umwelt. Receivers in turn, by changes in their own gaze, head direction, and ear orientation, may sign reception of a signal and acknowledge its relevance to them (see Figure 2). Such exchanges can involve a third party, as when female vervet monkeys (*Cercopithecus aethiops*) look toward the mother of an infant whose distress call is heard (Cheney & Seyfarth, 1980), as though to say, "it's your problem." In such ways, the Umwelt of the individual becomes accessible to others, a fact that is potentially useful for conspecifics and heterospecifics alike.

The following articles revitalize Von Uexküll's (1934/1957) concept of the Umwelt and provide new analyses of the meaning of the term *environment*, particularly in the context of the physical and social circumstances in which an animal communicates. They are ambitious precisely because the concept of the environment of communication can be taken at so many levels, from the global ecosystem down to the individual. Although this collection is not intended to be comprehensive (its focus is mainly on acoustic and vibrational communication), it presents an important overview of the roles that the physical and social environments play in communication via air- and substrate-borne signals. The questions raised in these articles provide stimulating food for thought for students of animal communication in the coming years.

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