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**The Biological Substrate of Icons,
Indexes, and Symbols in Animal
Communication: A Neurosemiotic
Analysis of Vervet Monkey
Alarm Calls**

Introduction

According to C.S. Peirce, there are three fundamental kinds of signs underlying meaning processes—icons, indexes, symbols. The Peircean list of categories (Firstness, Secondness, Thirdness) constitutes an exhaustive system of exclusive and hierarchically organized classes of relations (monadic, dyadic, triadic) (Houser 1997: 14; Burch 1997; Brunning 1997). This system is the formal foundation of his architectonic philosophy (Parker 1998: 60) and of his classifications of signs (Kent 1997: 448). In this context, and relatively to the “most fundamental division of signs” (Peirce CP 2.275), these classes correspond to icons, indexes, and symbols that correspond to relations of similarity, contiguity, and law between S-O (sign-object) of the triad S-O-I (sign-object-interpretant). The properties associated with these modalities are: (1) S-O dependent of intrinsic properties of S (monadic), (2) S-O in spatio-temporal physical correlation (dyadic), and (3) S-O dependent of I mediation (triadic).

Icons are signs that stand for their objects through similarity or resemblance (Peirce CP 2.276), irrespective of any spatio-temporal



physical correlation that S has with existent O: “An Icon is a sign which refers to the Object that it denotes merely by virtue of characters of its own, and which it possesses, just the same, whether any such Object actually exists or not” (Peirce CP 2.247; see 8.335, 5.73). In contrast, if S is a sign of O by reason of a dyadic relation with O, then it is said to be an index of O. In that case, S is really determined by O in such a way that both must exist as events, S and O: “An Index is a sign which refers to the Object that it denotes by virtue of being really affected by that Object.... [Insofar] as the Index is affected by the Object, it necessarily has some Quality in common with the Object, and it is in respect to these that it refers to the Object. It does, therefore, involve a sort of Icon” (Peirce CP 2.248; see 2.304). Finally, if S is in a triadic relation with O, a third term, I, is required so that I stands for “O through S.” In this case, S is a symbol of O, and the determinative relation of S by O, a relation of law: “A Symbol is a law, or regularity of the indefinite future.... But a law necessarily governs, or ‘is embodied in’ individuals, and prescribes some of their qualities. Consequently, a constituent of a Symbol may be an Index, and a constituent may be an Icon” (Peirce CP 2. 293; see 2.299, 2.304, 2.249).¹

The Problem

What is the origin of the symbolic processes that underlie human vocal communication? Since animal communication is ultimately a product of neurobiological processes (see Lieberman 1984, 1998; Pinker and Bloom 1990; Bloom 1999), and all biological phenomena are presumed to be the product of gradual evolution (Darwin 1859), the solution to this problem cannot avoid a comparative study of meaning processes and their underlying neurobiological basis in non-human primates (Hauser 1996; Deacon 1997; Tomasello and Call 1997; Lieberman 1998). Whether these categories (icons, indexes, and symbols) apply to non-human animal communication is a matter of theoretical debate and controversy (Janik and Slater 2000), and no experimental evidence exists either against or in favor of such a scheme. There is, however, a great deal of descriptive knowledge about vocal communication in non-human primate species, the case of vervet monkeys being perhaps the best studied.

The Meaning of Alarm Calls in Vervet Monkeys

Vervet monkeys (figure 1) inhabit the African sub-Saharan plains and live in groups of up to 30 members. These primates possess a sophisticated repertoire of vocal signs that are used for intraspecific social interactions (confrontation, reconciliation, and alliance formation of different sorts) (Cheney and Seyfarth 1990; Hauser 1996), as well as for general alarm purposes regarding imminent predation on the group (Seyfarth et al. 1980). Field studies have revealed three main kinds of alarm calls used to warn about the presence of (1) terrestrial stalking predators such as leopards, (2) aerial raptors such as eagles, and (3) ground predators such as snakes (Strushaker 1967; Seyfarth et al. 1980). When a 'leopard' call is uttered, vervets escape to the top of nearby trees; 'eagle' calls cause vervets to hide under bushes, and 'snake' calls elicit rearing on the hindpaws and careful scrutiny of the surrounding terrain. Adults produce these calls only in reference to the presence of specific predators, and generate whole-group escape reactions. In contrast, infant vervets babble these calls in response to a variety of animals (predators and non-predators), as well as to inanimate objects such as falling leaves, and are paid little attention by adults. The progressive specificity of alarm-call production as vervets grow older indicates that a great deal of context learning is involved in the proper use of such calls (Cheney and Seyfarth 1990).

FIGURE 1 Vervet Monkey Vocalizing an Alarm Call

A Neurosemiotic Analysis of Vervet Monkey Alarm Calls

Consider two stimuli to which a vervet monkey reacts: the view of a predator and an alarm call played through a loudspeaker. The neural responses that code for the physical features of the visual image of the predator and the corresponding alarm call are iconic representations of their objects (Zaretsky and Konishi 1976; Tootell et al. 1988; Ribeiro et al. 1998), and exist within two independent modalities (visual and auditory) in a representational domain of the brain hereafter termed RD1 (see figure 2). The mere visualization of a predator must be, in principle, enough to generate an escape response via the motor system of the brain. In contrast, the physical properties of the acoustic alarm call (amplitude and frequency) do not stand for a specific predator in any intrinsic way.

In the absence of a previously established relationship between that call and the predator, the former will simply arouse the receiver's attention to any concomitant event of interest, generating a sensory scan response directed to the loudspeaker and its surroundings (Cheney and Seyfarth 1990). At least two things may happen then: if nothing of interest is found, the receiver should stay put, and therefore it can be said that the alarm call was not interpreted as anything other than an index of itself; if a predator is spotted stalking nearby, or if other vervet monkeys are observed fleeing to a neighboring refuge, the receiver should be prompted to flee. In these cases, the alarm call can be interpreted as an index either of the predator or of collective vervet monkey escape, with identical behavioral outcomes.

The experiment described above was performed by Cheney and Seyfarth (1990) in the field: predator-specific alarm calls were played from loudspeakers to groups of wild vervet monkeys, and their behaviors were carefully monitored. All individuals responded by looking around in search of a referent, and then fleeing to nearby refuges according to the specific type of call played ('leopard' calls evoked tree climbing, 'eagle' calls elicited bush hiding, etc.).

This simple but well designed experiment allows us to conclude that at least to one individual² in the vervet monkey group, alarm calls hold a previously established relationship to the predators they stand for, be it socially learned or genetically determined (Wilson 1975). If the alarm call operates in a sign-specific way in the absence of an external referent, then it is a symbol of a specific predator class. In other words, to say that an alarm call is

a symbol of a *type* of predator is equivalent to saying that this call evokes a brain representation (of any modality) that stands for the *class* of predators represented in a specific way. This symbolic relationship implies the association of at least two representations of a lower order (i.e., indexes or icons) in a higher-order representation domain, hereafter termed RD2 (figure 2), which should be able to command escape responses through connections with the motor systems of the brain.

Sensory stimuli present in the world are *iconically* represented in the brain within a first-order domain (RD1) according to specific modalities (visual or auditory, in our example). While the view of a predator represented in RD1 is sufficient to elicit an escape response through the brain's motor system, the representation of an alarm call alone in RD1 does not evoke any predator-specific meaning, and therefore fails to cause an escape response. Presented together, the two stimuli can be interpreted in RD1 as bearing an indexical relationship, i.e., the alarm is an index of the predator's presence, generating an escape response. The existence

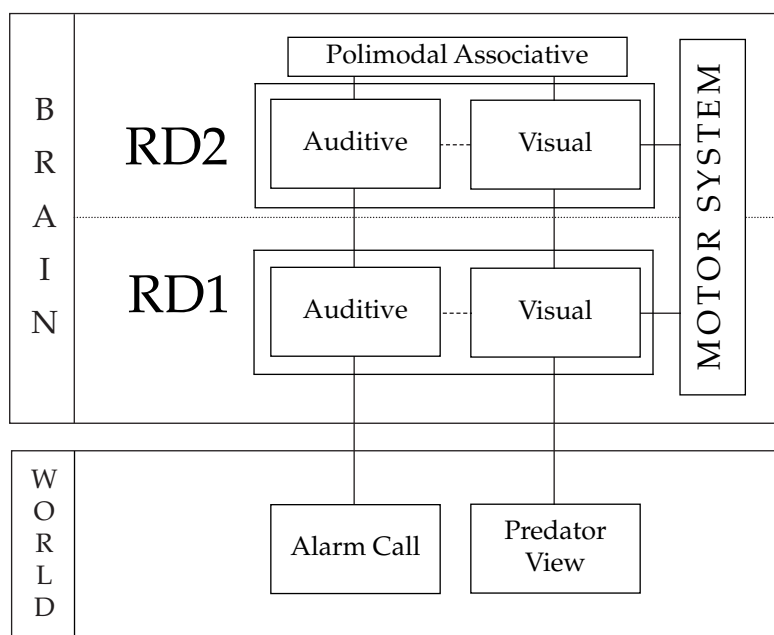


FIGURE 2 Schematic Diagram of World-Brain Interactions Involved in the Interpretation of Signs



of a higher-order domain of representation (RD2), which associates responses of both sensory modalities, enables the brain to interpret an alarm call presented alone as a *symbol* of its referent, i.e., the view of the predator, and an escape response ensues through the motor system.

In Search of the Neuroanatomical Substrates of Sign Interpretation

According to the hypothesis stated above, RD1 and RD2 should have different neuroanatomical substrates. Candidate regions to comprise RD1 are unimodal sensory ascending pathways spanning the mesencephalon, diencephalon, and early sensory neocortical areas. Candidate regions to integrate RD2 may be located in association areas in the parietal, temporal, and frontal neocortices, as well as the hippocampus, basal ganglia, and amygdala (Kandel et al. 1999).

We postulate that the identification of brain areas belonging to RD1 and RD2 is an empirical question that can be addressed by experiments comprising (a) specific neuroanatomical lesions of candidate regions, (b) presentation of auditory (alarm calls through a loudspeaker) and/or visual (predator view) stimuli to brain-lesioned vervet monkeys, and (c) recording of their behavioral responses so as to classify how the sensory signs were interpreted in each instance. Table 1 illustrates the behavioral analysis of one such *Gedanken* experiment.

Conclusions

Based on the available literature and on the Peircean fundamental classification of signs (icon, index, symbol), we have presented an analysis of meaning processes underlying the interpretation of alarm calls in vervet monkeys. We have identified putative neuroanatomical constraints for these processes, which postulate the existence of at least two distinct representational brain domains underlying the interpretation of alarm calls as either iconic/indexical or symbolical signs. Current knowledge in neurobiology suggests specific candidate regions to integrate these domains. We propose *Gedanken* brain-lesion ethological experiments, which should, in principle, allow for the identification of brain regions

TABLE 1 Behavioral Analysis of *Gedanken* Experiment

Site of neuro-anatomical lesion	Visual stimulus	Auditory stimulus	Post-stimulus sensory scan	Behavioral outcome	Sign interpretation
RD2	Yes	No	No	Escape	Predator icon
	No	Yes	Yes	Stay	Call index
	Yes	Yes	Yes	Escape	Predator index
RD1/Visual	Yes	No	No	Stay	No sign interpretation
	No	Yes	Yes	Escape	Predator symbol
RD1/Auditory	Yes	No	No	Escape	Predator icon
	No	Yes	No	Stay	No sign interpretation
RD2 and RD1/Visual	Yes	Yes	No	Escape	Predator icon
	Yes	No	No	Stay	No sign interpretation
	No	Yes	Yes	Stay	Call index
RD2 and RD1/Auditory	Yes	No	No	Escape	Predator icon
	No	Yes	No	Stay	No sign interpretation
	Yes	Yes	No	Escape	Predator icon

Note: RD1 and RD2 are generic terms for brain domains related to first-order (iconic/indexical) and second-order (symbolical) levels of representation, respectively. Depending on the relationship between stimulation and behavioral outcome, brain regions can be classified as belonging to RD1 or RD2.

involved in the different semiotic aspects of vervet monkey alarm call communication. Such experiments should also permit the mapping of hierarchical relations among the fundamental components of vocal signs in vervet monkeys. Finally, we suggest that certain specific behavior responses indicate the emergence of symbols in non-human primates. The transition from a sensory scan behavior after the alarm auditory perception to an escape reaction motivated solely by the call corresponds to the transition from indexical semiosis (reactive spatio-temporally) to symbolic semiosis. The object of the sign, in the latter case, is not an object but a class of objects, and therefore does not need to exist as a singular event. In other words, if there is a threshold $\text{index} > \text{symbol}$, then it should be possible to behaviorally identify the transition from 'object that is an event' to 'object that is a class of events', i.e., an

object that does not need to be present as an external particular object. An 'ethological symptom' of this would be the failure of an adult vervet presented with an alarm call to visually scan the environment before escaping in a predator-specific way.

The argument presented above generates many questions. For instance, does the learning of vervet monkey alarm calls involve an indexical (non-symbolical) phase? The late ontogenetic maturation of this process suggests its dependency on an indexical phase. If the Peircean hierarchical model is correct (icon > index > symbol), any damage to the neuroanatomical substrate required for the indexical phase must compromise the symbolic performance at later periods, while the contrary should not be true. The analytical framework applied here to the case of vervet monkey alarm calls should permit the profitable study of many different cases of animal communication, constituting a new research program that we suggest be called 'comparative neurosemiotics'.

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Notes

1. For an introduction to Peirce's theory of sign, see: Parker (1998), Liszka (1996), Santaella (1995), Fisch (1986), Queiroz (2001).
2. In the absence of further data we cannot exclude the possibility that only one individual recognized the alarm call as a sign of the predator, and all other monkeys followed the leader.

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