

## ***Semiotic modelling of biological processes: Non-human primate symbolic communication***

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**General abstract:** Here we introduce biosemiotics as a field of research that develops models of life processes focusing on their informational aspects. Peirce's general concept of semiosis can be used to analyze such processes, and provide a powerful basis for understanding the emergence of meaning in living systems, by contributing to the construction of a theory of biological information. Peirce's theory of sign action is introduced, and the relation between 'information processing' and sign processes is discussed, and, in fact, a semiotic definition of information is proposed. A biosemiotic model of genetic information processing in protein synthesis is developed.

### **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 nonhuman primate species, the case of vervet monkeys being perhaps the best studied.

### **2. African vervet monkeys alarm-call system**

Vervet monkeys inhabit the African sub-Saharan plains and live in groups of up to 30 members. These primates possess a sophisticated repertoire of vocal signs used for intra-specific alarm purposes regarding imminent predation on

the group. Field studies have revealed three main kinds of alarm-calls separately used to warn about the presence of (a) terrestrial stalking predators such as leopards, (b) aerial raptors such as eagles, and (c) ground predators such as snakes (Struhsaker 1967; Seyfarth, Cheney et al. 1980). Adult vervets produce these calls only in reference to the presence of predators. Such calls, when heard by other adults, motivate whole-group escape reactions that are specific to predator type. For instance, when a “terrestrial predator” call is uttered, vervets escape to the top of nearby trees; “aerial predator” calls cause vervets to hide under trees, and “ground predator” calls elicit rearing on the hindpaws and careful scrutiny of the surrounding terrain.

While adults share a code for predator reference, infant vervet monkeys babble these calls in response to a variety of animals (predators and non-predators), as well as to inanimate objects such as falling leaves etc. As a consequence, adults pay little attention to infant calls (Cheney and R. 1990; Seyfarth and Cheney 1997). The progressive specificity of alarm-call production as vervets grow older indicates that a great deal of learning is necessary before these calls can be used in the proper context (Seyfarth and Cheney 1980; Seyfarth and Cheney 1986). Indeed, field experiments in which predator-specific alarm-calls were played from loudspeakers to groups of wild vervet monkeys showed that adult individuals first responded to playbacks of alarm-calls by looking around in search of a referent (predator). Remarkably, even though this referent was always absent, adult animals consistently fled away to nearby refuges according to the specific type of alarm-call played. Infant monkeys, on the other hand, responded poorly to playbacks, and teenagers displayed intermediate behaviors (Seyfarth and Cheney 1980; Seyfarth and Cheney 1986; Cheney and R. 1990; Seyfarth and Cheney 1997). The assumption that the mapping between signs and objects can be learned is also supported by the observation that cross-fostered macaques, although unable to modify their call production, “did learn to recognize and respond to their adoptive mothers’ calls, and vice versa” (Cheney and Seyfarth 1998).

Taken together, these experiments indicate that the meaning of vervet monkey alarm-calls can be learned even in a highly noisy environment through social interactions with multiple tutors.

According to the Peircean classification of signs, if the alarm-call operates in a specific way even in the absence of the external referent, it must be interpreted as a symbol of a predator class. The transition from a sensory scan behavior after the alarm auditory perception to an escape reaction motivated solely by the alarm-call corresponds to the transition from indexical semiosis (interpretation by spatio-temporal coincidence) to symbolic semiosis (interpretation mediated by law or convention) (Figure 1). The object of the sign, in the latter case, is not an object-token but rather a class of objects, i.e., an object-type, and therefore does not need to exist as a singular event.

To say that an alarm-call is a symbol of a type of predator is equivalent to say that this call evokes a brain representation (of any modality) that stands for the class of predators represented in a law-like and specific way.

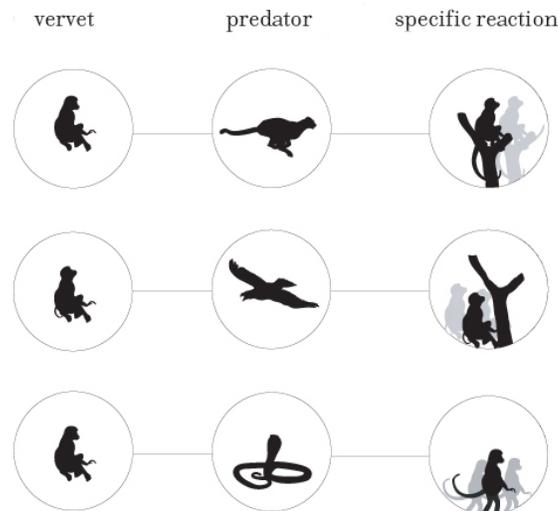


Figure 1: When a “leopard” call is uttered, vervets escape to the top of nearby trees; “eagle” calls cause vervets to hide under trees, and “snake” calls elicit rearing on the hindpaws and careful scrutiny of the surrounding terrain.

### 3. A neurosemiotic model of vervet monkey vocal communication

In order to gain insight into the mechanisms of vocal communication in vervet monkeys, we first modeled a “minimum” monkey brain so as to satisfy fundamental neurobiological and semiotical constraints (Ribeiro et al 2007; Queiroz and Ribeiro, 2002). Our model brain is composed of four interconnected representation domains (RD), in relationship with a perceptible world (figure 2):

- Two RD1: domains of primary sensory representation (eg. superior colliculus, lateral geniculate, visual and auditory primary cortices). These are the input layers of the system; for simplicity, we modeled only two modalities;
- One RD2: domain of secondary sensory association (eg. associative cortex, hippocampus, amygdala).
- One RD1: domain of primary motor representation (eg. M1 cortex, descending motor pathways, muscles); this is the output layer of the system.

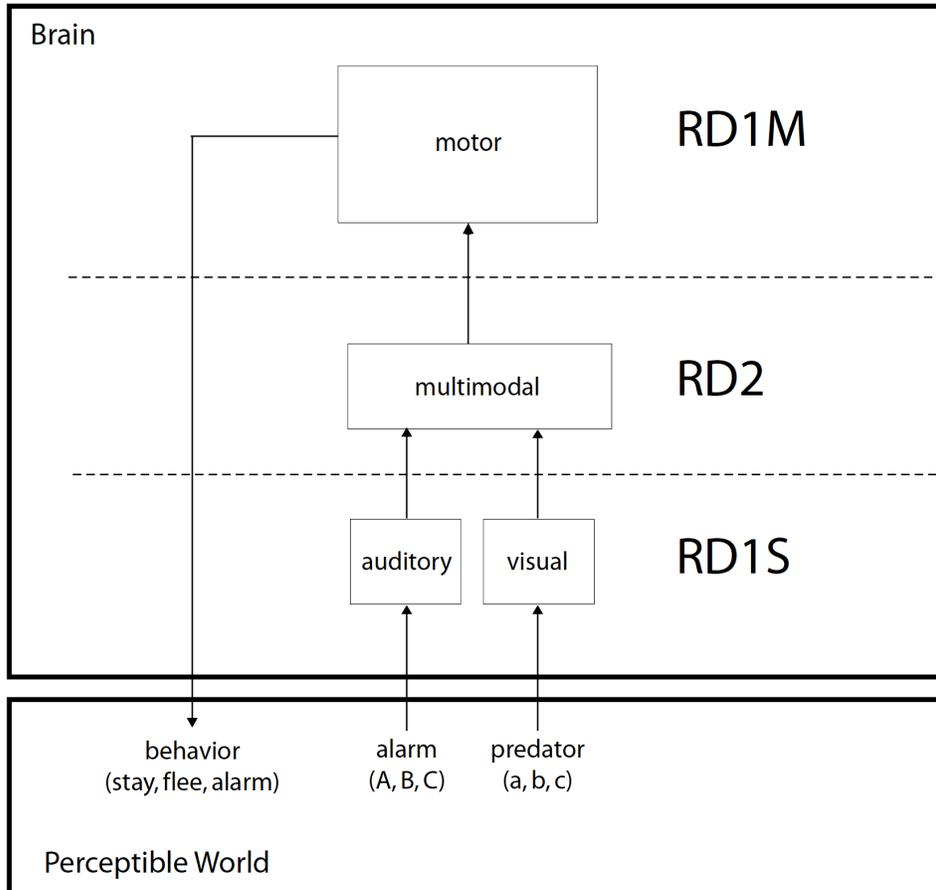


Figure 2: Schematic diagram of world-brain interactions involved in the interpretation of signs

Consider two stimuli available to a vervet monkey: the view of a predator and an alarm-call played through a loudspeaker (Cheney and Seyfarth, 1990). The neural responses that code for the physical features of the image of the predator and the corresponding sound of the 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 sensory modalities - visual and auditory - in primary representational domains of the brain (RD1; figure 2). The mere visualization of a predator must, in principle, be enough to generate an escape response via the motor system of the brain. In contrast, the physical properties of the acoustic alarm-call *per se* (e.g. amplitude and frequency) do not *stand for* the leopard in any intrinsic way. Thus, in the absence of a previously established relationship between that alarm-call and the predator, the former should only arouse the receiver's attention to any concomitant event of interest, generating a sensory scan response directed to the loudspeaker and its surroundings. If at that time a predator was spotted stalking nearby, or if other vervet monkeys were observed fleeing to a neighboring refuge, the receiver should be prompted to flee. In these cases the alarm-call would have been interpreted as an index either of the predator or of the collective vervet monkey escape, with

identical behavioral outcomes. However, if nothing of interest was to be found, the receiver should stay put, and therefore the alarm-call would have been interpreted simply as an index of itself.

The experiment described above was performed by Seyfarth and Cheney in the field. Predator-specific alarm-calls were played from loudspeakers to groups of wild vervets monkeys, and their behaviors were carefully monitored. All the adult individuals responded to playbacks of alarm-calls by looking around in search of a referent (predator). Remarkably, even though this referent was always absent, adult animals consistently fled away to nearby refuges according to the specific type of alarm-call played (“leopard” calls evoked tree-climbing, “eagle” calls elicited bush hiding etc). Infant monkeys, on the other hand, respond poorly to these playbacks, while teenagers display an intermediate behavior (Cheney and Seyfarth, 1990). This simple but well designed experiment allows us to conclude that, at least to one individual in the vervet monkey group, alarm-calls hold a previously established relationship to the predators they stand for. Furthermore, this relationship appears to be the product of social learning, since infant (naïve) vervet monkeys do not show signs of having it. Figure 3 depicts a semiotic graphic model of the “minimum” monkey brain discussed above.

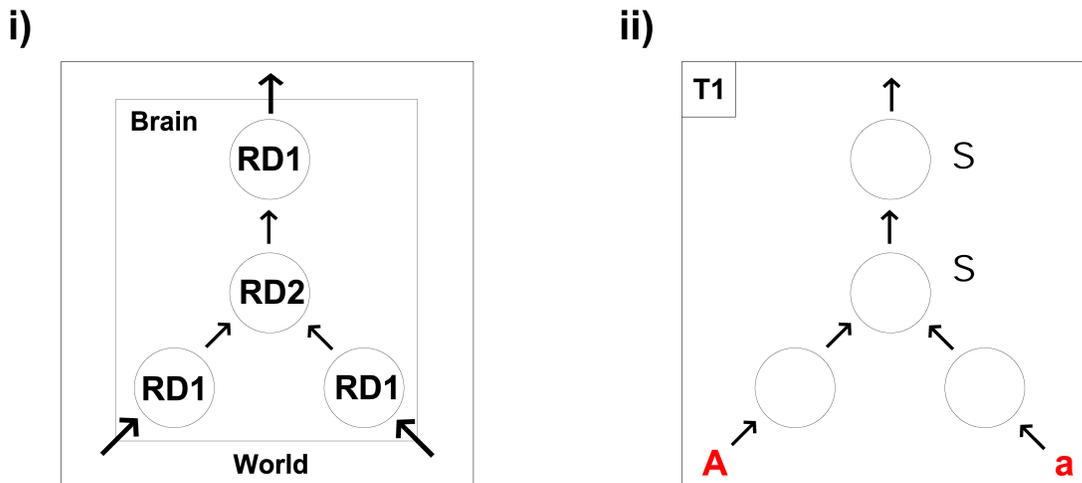


Figure 3: Modeling a “minimum” monkey brain. (i) Brain in relationship with the external world. Compare with diagram in figure 3. Arrows indicate information flow. (ii) Simplified version of the model in panel (i) The boundary between world and brain is omitted. Time is indicated in the upper left corner. The image represents an infant vervet monkey brain, assumed to have a “default” memory for the behavior “stay” (S) in response to a predator image (a) or a corresponding alarm-call (A).

A list of definitions follows:

- Circles stand for domains of representation in the monkey brain (RDs);

- Colors indicate the terms of the triadic relation - Red for Object; Green for Sign; Blue for Interpretant;

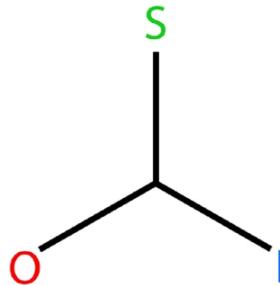


Figure 4: Semiotic triadic relation

- The white color designates a de-activated RD (circle) or the absence of an external object;
- Objects of the world are defined as elements with specific physical-temporal attributes.
- Objects presented to a monkey brain comprise predator images (a, b, c), corresponding alarm-calls vocalized by other monkeys (A, B, C), and reactive behaviors from neighboring monkeys that may be visible to other brains (F refers to "flee"; S refers to "stay");
- Information about object quality is represented by letters inside blue circles (interpretants);
- Black arrows indicate existing (latent but not necessarily active) channels of communication within the brain and between brain and world;
- Green arrows indicate instantiation of a communication channel, i.e. sign production;
- T1, T2, T3 etc represent time;
- Every sign must be interpreted as able to instantiate specific sign-events (sinsigns), by means of which can act as a sign;
- Memory of a representation (A) of the object (a) is defined as the probability of observing (A) given a certain context of object presentation that might or not include (a). Memory for a representation is indicated as letters outside the boundaries of circles;
- Every interpretation of a representation causes a slight increase in memory of that representation.
- In addition, objects may also carry the capacity to signify reward or punishment. This capacity (object value) is defined as positive and negative variables that can increase or decrease the memory of associated representations.
- -S refers to negative value imposed on brain representations associated with "stay";
- +F refers to positive value imposed on brain representations associated with "flee".

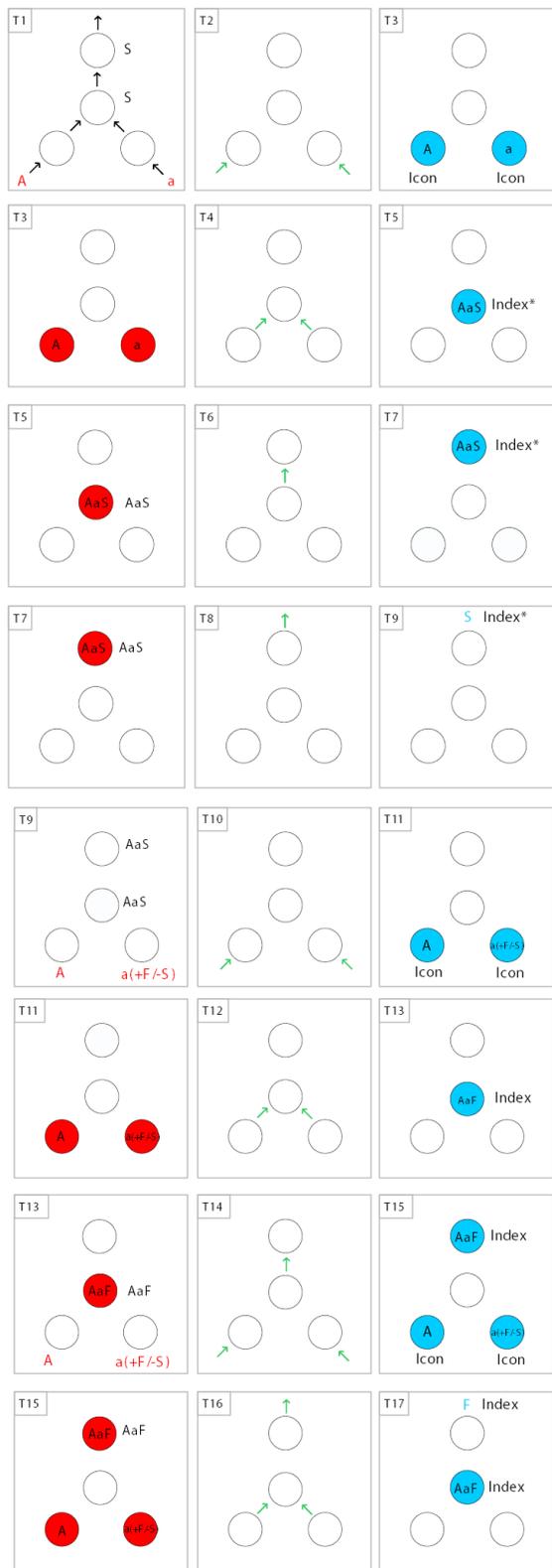
RDs can be modeled as neural networks in which particulars (*TOKENS*) correspond to the activation of specific trajectories within the RD, and generals (*TYPES*) correspond to the activation of many particulars grouped together by proximity in a metric space (e.g. shared synapses; see Edelman, 1995). By way of the amygdala, RD2 is the only domain able to evaluate the value of a given representation, so as to moderately increase or decrease the memory of that representation. Different magnitudes of value correspond to graded changes in memory. Once interpreted by RD2, value can affect downstream (motor) domains of the system.

#### 4. Behavioral simulations

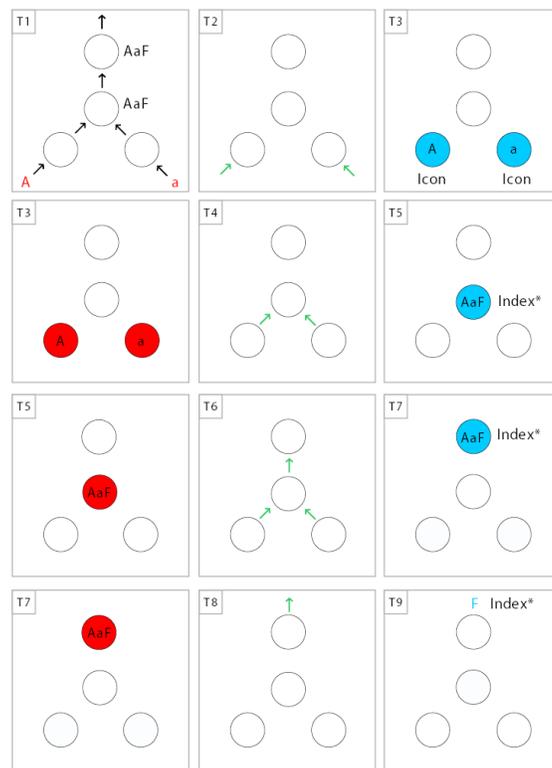
We evolved our model in time to explore the consequences of a single synchronous presentation of object(s) for the brain representation processes of adult (experienced) and infant (naïve) vervet monkeys. While infants are assumed to have no previous knowledge of the meaning of either alarm-calls or predator views (no “*a priori*” memory), adults are supposed to fully understand the vocal communication repertoire shared by the other adult members of the group.

We used our minimum model to implement a graphic simulation of vervet monkey intra-specific communication. Two extreme social categories were distinguished: infants were assumed to have no previous knowledge of the meaning of either alarm-calls or predator views. With no “*a priori*” memory in RD2 regarding these objects, infants initially react to any world scene with a default “stay” behavior. Adults, on the other hand, were considered to fully understand the meaning of predator images and of the vocal communication repertoire shared by other adult members of the group. This means that adults have memories in RD2 that associate the neural representations of predators and alarm-calls to “escape” reactions and further alarm calling. The consequences of a single synchronous presentation of both alarm call and predator view to an infant and an adult are shown in Figure 5. Infants are initially unresponsive to both alarm calls and predator views (S for “stay”), but exposure to the escape reaction of adult tutors leads to learning (Fig. 5a) As expected, adults escape much earlier than infants in this situation (Fig. 5b). In both cases, alarm calls (signs) are either interpreted as icons (eg. the topographic activation of visual and auditory RD1S by predator image or alarm-call, respectively) or as an index (the non-topographic, spatio-temporal conjunction of information from both modalities in RD2 and therefore in RD1M).

a



b



c

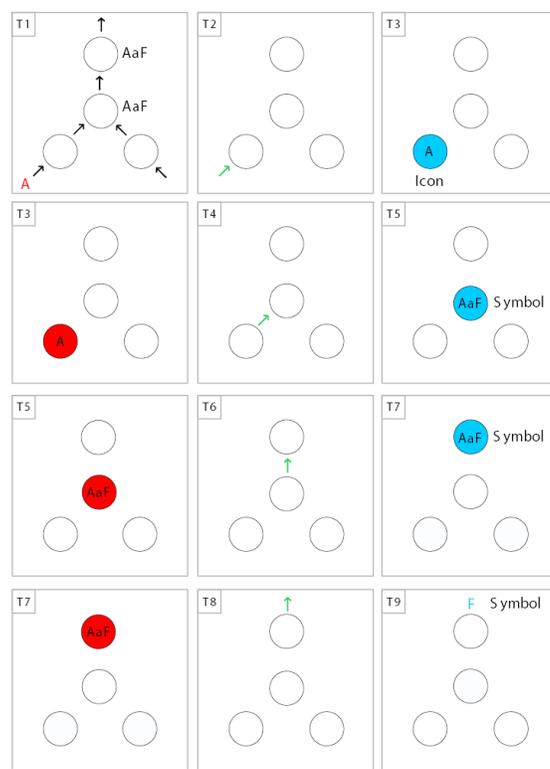


Figure 5: Storyboard of sign process of alarm call communication employing vervet monkeys' minimum brain architecture. Each frame is constituted of letters, arrows and circles. T1, T2, T3 etc represent instants in time. External objects presented to a monkey brain comprise predator images (a, b, c), corresponding alarm-calls vocalized by other monkeys (A, B, C), and reactive behaviors from neighboring monkeys that may be visible to other brains (F refers to "flee"; S refers to "stay"). Circles stand for domains of representation in the minimum brain (RDs). Circle colors indicate different types of neural representations according to their semiotic relationships - Red for object and Blue for interpretant. The white color designates a de-activated RD (circle) or the absence of an external object. Arrows represent signs, i.e. patterns of connectivity between brain areas, or between a brain area and the external world. Green arrows indicate instantiation of a connectivity pattern, i.e. the action of a sign translating from an object to an interpretant. Black arrows in T1 indicate latent (inactive) signs. Memory for a representation is indicated as letters outside the boundaries of circles in T1. Information about the particular identity of an external object is represented by outside letters in T1, T9 and T13 (arbitrary moments of occurrence); this information is preserved within the brain as indicated by letter inside circles thereafter. At T3, interpretants within RD1S become internal (neural) objects to be represented downstream, determining the repetition of T3 in the next frame, and so on. Every instantiation of a representation in RD2 causes a slight increase in memory of that representation. Every instantiation of a representation must be interpreted as either an Icon, or an Index, or a Symbol; Memory of a representation (A) of the object (a) is defined as the probability of observing (A) given a certain context of object presentation that might or not include (a). In addition, external objects may also carry the capacity to signify reward or punishment. This capacity (object value) is defined as positive and negative variables that can increase or decrease the memory of associated representations. -S refers to negative value imposed on brain representations associated with "stay"; +F refers to positive value imposed on brain representations associated with "flee". a) Infant simultaneously presented with predator image and alarm call. b), Adult simultaneously presented with predator image and alarm call. Once again an escape response is generated earlier (T9) than in infants (T17). This crucial symbolic step occurs in T5, when RD2 interprets the ascending iconic representation "A" as "AaF"). c) Adult presented with an alarm-call only.

Symbols emerged in our model when adults were presented with an alarm-call in the absence of a corresponding predator view, as in the playback experiment carried on by Seyfarth and Cheney (Seyfarth, Cheney et al. 1980). In this case, the lack of temporal pairing between alarm-call and predator image precludes interpretation of the alarm call as an index. According to the Peircean classification of signs, if the alarm-call operates in a specific way even in the absence of the external particular referent, then it must be interpreted as a symbol of a predator class and of a particular type of escape strategy (Queiroz & Ribeiro 2002). The transition from a sensory scan behavior after the alarm auditory perception to an escape reaction motivated solely by the alarm-call corresponds to the transition from an indexical (interpretation by spatio-temporal coincidence) to a symbolic process (interpretation mediated by law). 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. To say that an alarm-call is a symbol of a type of predator is equivalent to say that this call evokes a brain representation (of any sensory modality or combination of modalities) that stands for the class of predators represented in a lawful and specific way. This symbolic relationship implies the memorized association of at least two lower-order representations (i.e. indices or icons) in a higher-order representation domain (RD2). The neurosemiotic diagrams shown in Fig. 5 constitute an evidence that vervet monkeys, as much as described in the current literature (Struhsaker 1967; Seyfarth, Cheney et al. 1980; Seyfarth, Cheney 1986; Cheney, R. 1990; Seyfarth, Cheney 1997), employ symbols in their intra-specific communication.

## 5. Learning to associate predators with their respective alarm-calls

As noted above, the progressive specificity of alarm-call production as vervets approach adulthood has been observed (Cheney and Seyfarth, 1990). This opens the question of which mechanisms implement the learning of the responses to alarm-calls in vervets. This needs to be addressed with greater precision in the future but we note however that the model just described could easily support neuron-like reinforcement prediction operations, as defined for example by the Wagner-Rescorla rule (Rescorla and Wagner, 1972). Let  $u$  be a binary variable denoting the presence of a given stimulus (in our case a vervet alarm-call). Let  $v$  be a variable denoting the expected event or reinforcement, i.e. the prediction of the presence of a predator.  $v$  can be given by the expression

$$v = wu$$

where  $w$  is a “weight” which can be interpreted as the strength of the associative bond between the call and the presence of the predator. Changes in the weight value are defined by a learning rule known as the Rescorla-Wagner rule:

$$w \rightarrow w + \varepsilon \delta u$$

where  $\delta = r - v$ .  $r$  denotes the actual presence of the predator, so that  $\delta$  represents an error function of the prediction  $v$  with respect to  $r$  (i.e. the presence of the predator).  $\varepsilon$  is a learning rate (typically  $0 < \varepsilon < 1$ ). Learning in this case leads then to a minimization of the prediction error function and to an improvement in the ability to predict the presence of a predator following the emission of an alarm-call.

## 6. In search of the neuroanatomical substrates of sign interpretation

According to the hypothesis stated above, RD1 and RD2 should have different neuroanatomical substrates (Figure 3). 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.

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
	Yes	Yes	Yes	Escape	Predator symbol
RD1/Auditory	Yes	No	No	Escape	Predator icon
	No	Yes	No	Stay	No sign interpretation
	Yes	Yes	No	Escape	Predator icon
RD2 and RD1/Visual	Yes	No	No	Stay	No sign interpretation
	No	Yes	Yes	Stay	Call index
	Yes	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

Table 1: Lesion-playback *Gedanken* experiments in vervet monkeys: predicted behavioral outcomes and corresponding sign interpretation.

## 7. Symbols in non-human primates

Understanding how the vervet’s brain interprets an alarm-call leads us to the more general problem of defining which Peircean class of sign vervet calls belong to. The model developed so far argues that adult vervet monkeys are able, under specific circumstances, to interpret alarm-calls as dicent symbols of predators. This proposition is nevertheless controversial, because the use of symbols is usually associated to linguistic arbitrariness (Vauclair 1994, 1995: 100; Noble & Davidson 1996: 63) and semantic compositionality (Deacon 1997), which vervet monkeys presumably lack. In fact, the temporal pairing between an alarm-call and the sight of a predator would imply that a vervet call operates rather as an index. However, a large extent of the classical conditioning data provides evidence against simple associative rules. Indeed,

such rules can hardly explain phenomena such as time-scale invariance in autoshaping protocols, which is better accounted for by “information processing” theories (for a review, see Gallistel and Gibbon, 2000). Non-associative theories claim rather that conditioned responses should be seen as the result of symbolic manipulations in an information-processing system (Gallistel 2002). This later view would thus favor the assignment of symbolic properties to vervet monkey’s alarm-calls. Information processing theories, on the other hand, are less capable of telling us how alarm-calls can be learned. It is important to note that Peirce himself did not limit the concept of symbol to the notion of linguistic arbitrariness. The ideas of “habit”, that are “general rules to which the organism has become subjected” (CP 3.360), and “natural disposition” (CP 4.531), are more adequate to the issues discussed here. According to Peirce (CP 2.307; our emphasis), a symbol is “A Sign (q.v.) which is constituted a sign merely or mainly by the fact that it is used and understood as such, *whether the habit is natural or conventional*, and without regard to the motives which originally governed its selection.” In another passage Peirce defined a “Symbol as a sign which is determined by its dynamic object only in the sense that it will be so interpreted. It thus depends either upon a convention, a *habit*, or a *natural disposition* of its interpretant or of the field of its interpretant (that of which the interpretant is a determination)” (CP 8.335; our emphasis).

What kind of symbolic process are we describing? Peirce classified symbolic processes in a very original way. The dissociation from conventionality, and from intentional sign-user manipulation, permits to conceive natural legisigns, including natural symbols of different types. We suggest that a further exploration of the Peircean system for the 10 classes of signs will lead us to a formalism in which symbolic manipulation systems can implement learning, generate linguistic arbitrariness and semantic compositionality. In the Peircean extended system (EP 2: 289-299, 483-490; see Queiroz 2004, Farias & Queiroz 2004), symbols can be further analysed in 3 classes (Rhematic Symbol, Dicent Symbol, Argument), of which only the Argument would possess these properties -- “An Argument is a Sign which, for its Interpretant, is a Sign of law” (CP 2.252). It is a genuine sign: a sign interpreted as semiotically (not reactively or by similarity) standing for something general (TYPE). It possibly defines the condition of emergence of metarepresentational levels of semiosis and the capacity to manipulate signs in a very conceptual level (Noble & Davidson 1996: 61). The vervet allarm-call itself is a legisign, a general type that control the specific qualities associated to its instantiations, and depends of a sign using interpreter to *stands for* its object, this relations being interpreted as a spatio-temporal reaction. It is interpreted as a sign of a set of existent objects -- a Dicent Symbol.

## 7. 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 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? maturation of this process suggests its dependency on an indexical phase. If the Peircean hierarchical model is correct ( $\text{icon} > \text{index} > \text{symbol}$ ), 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.

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