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Linguistic Biases for Words Representing Threat?

Abstract

Popular theories in personality research argue for the existence of dimensions that underlie the behaviour, intentions and motives that comprise personality. A number of different research domains have implicated two of these dimensions to be of particular importance for gauging interpersonal aspects of personality. Cross-cultural research has shown that these two dimensions, Dominance / Passivity and Pro-Sociability / Anti-sociability, emerge through the analysis of natural language. The present study sought to investigate personality trait adjectives in relation to these two dimensions, arguing that adjectives that fall within a Dominant Anti-Social quadrant will have particular threat-related salience and cognitive biases. Three separate tests were conducted to assess the salience of threat to related personality adjectives with results indicating partial support for the hypothesis that natural language contains more words to describe threatening persons than positive or neutral persons.

Key words

Circumplex models, evolutionary psychology, linguistics, personality theory.

Linguistic Biases for Words Representing Threat?

Like most evolutionary psychologists, PINKER and BLOOM (1990) argue that the driving force behind the evolution of language was the advantage that it gave individuals in being able to communicate effectively with one another. In particular, language is extremely useful for conveying information about other individuals—including the ability to refer to specific others, and to describe and predict events in which they may be involved (DUNBAR 1996; MEALEY 1996; BARKOW 1996). Most importantly, it allows for an individual to be made aware of those aspects concerning another person that may directly impact on oneself.

Indeed, it has been argued that our concept of personality, along with the lexicon that is used to describe it, has developed in order to facilitate the organisation, explanation and understanding of interpersonal experience (JOHN/GOLDBERG/AGLEITNER 1984; BUSS 1997). The basis of the personality construct is the notion that individuals behave in a consistent, predictable manner toward one another. This consistency of behaviour or traits plays an important role in the algorithms that people use to evaluate their social experiences and interactions. People can be reliably distinguished by their interpersonal behaviour, and because these individual differences emerge as important features of social interactions, they thus become represented in natural language (GOLDBERG 1982; KENRICK/FUNDER 1988). It might be argued that the more important an individual difference in behavior is in terms of helping people to predict the conduct of others in their community, the more salient it will be (WOJCISZKE/BAZINSKA/JAWORSKI 1998). It follows that the more important a trait is, the more languages will have a term for it (GRAZIANO/EISENBERG 1997).

In their review of the personality literature, KENRICK and HOGAN (1991) argue that two dimensions of personality emerge as being most significant for distinguishing traits that impact upon interpersonal interactions. The first of these is social agreeableness; the second is power or dominance. Agreeableness and Dominance also emerge as the two most prominent dimensions of interpersonal interaction in many circumplex accounts of personality, although they are sometimes given different names, for example: Dominant–Submissive and Hostile–Affiliative (LORR/MCNAIR 1963); Association–Dissociation and Superordination–Subordination (HOGAN 1983); Solidarity/Conflict and Dominance/Submission (WHITE 1980). Researchers from a variety of other disciplines have also arrived at a

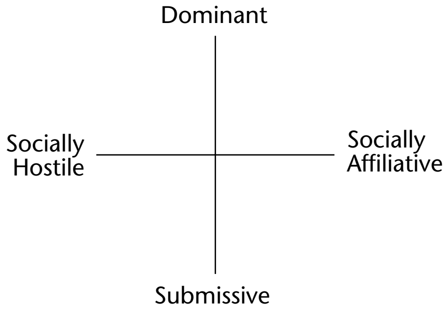

Figure 1: Dimensions of Universal Personality Schema.

two dimensional or circular representation of interpersonal behaviour. Besides personality psychology (BLOCK 1961; MYLLYNIEMI 1997), these include: developmental psychology (SCHAEFER/EDGERTON 1982); political psychology (BAILEY 1972); family psychology (SCHAEFER 1959); linguistics (MYLLYNIEMI 1997; ROSENBERG/NELSON/VEVEKENANTHAN 1968); kinesics (GIFFORD 1991); emotion psychology (MYLLYNIEMI 1997; RUSSEL 1997); social psychology (SCHAEFER 1961); and clinical psychology (BLASHFIELD 1986). (See Appendix A for a list of labels used by researchers in these disciplines).

The core idea emerging from these various domains of research is that there are two intersecting dimensions that underlie a universal conceptual scheme of human interaction. The first of these dimensions reflects dominance, status, power and surgency, whilst the second dimension reflects social affiliation, agreeableness and solidarity. These two dimensions are typically represented by perpendicular axes, shown in Figure 1, with the dominance dimension running in the North/South direction and the social affiliation dimension running East/West. Four quadrants are produced by this representation, depicting four categories of individuals in the social environment.

The ubiquity of these two dimensions suggests that dominance and agreeableness are among the most important traits that individuals use to evaluate others in the social community. Why should this be? Perhaps because although social living allows individuals to share resources such as food and shelter, there is also competition for these resources. This dynamic creates an elaborate and complex web of social interaction in which human beings engage in both prosocial, cooperative and antisocial, self-serving behaviour toward one another. In these circumstances it would be advantageous to be able to distinguish others who display dominant characteristics and who wield power over others. Similarly it would be advantageous to be able to determine the likelihood that another will be antisocial (BUSS 1997; COSMIDES/TOOBY 1996; MEALEY/DAOOD/KRAGE 1996).

As humans evolved their predisposition to interact in social groups, it is likely that they also evolved adaptations to help them overcome the threats potentially posed by others within the environment. Empirical research suggests that human beings have evolved adaptations to deal with threat at both specific and general levels of processing (DAVEY 1995; MEALEY 1996). For example, COSMIDES (1989) showed that instances of human rule breaking are much more readily identified than instances of logical rule breaking; HANSEN and HANSEN (1988) showed that angry faces are more readily identified in a crowd than are happy or neutral faces; MEALEY/DAOOD/KRAGE (1996) showed that faces of threatening individuals are preferentially remembered as compared to those of trustworthy or socially 'irrelevant' individuals. Based on these documented biases, NESSE (1997) postulated that there would be more words depicting negative (threatening) traits than words for positive or neutral traits. This study set out to test that hypothesis.

Method

There were three tests designed to test the hypothesis that there would be more words for threatening traits than positive or neutral traits.

Test 1: Adjective Categorisation Task

Materials. The first test involved a literal count of English-language personality adjectives. ALLPORT and ODBERT (1936) initiated a tradition of examining the lexical construction of personality terms by compiling a list of the 17000+ adjectives used in the English language. This compilation is organized according to four trait types: 1) neutral, non-evaluative personal terms such as 'active' and 'demure'; 2) terms denoting temporary moods such as 'appalled' and 'happy'; 3) social evaluative terms conveying judgments of personal conduct such as 'agreeable' and 'nasty' and 4) miscellaneous terms designating physical appearances, capabilities and developmental conditions such as 'stocky' and 'mousy'. Due to their social-evaluative nature, words listed in the third column of the ALLPORT and ODBERT adjective list are of particular interest for investigating interpersonal aspects of personality.

Procedure and analysis. A native speaker of English, blind to the hypothesis of the study, was paid to review the 5226 words listed column 3 of ALLPORT and ODBERT's (1936) list of personality trait names. This column comprised 29% of the entire list. Words in this column are specifically labeled as "Weighted Terms Conveying Social or Characterial Judgements of Personal Conduct, or Designating Influence on Others"; all describe social roles, relationships and personalities. The assessor was a female Australian nursing student for whom English was a first language. The assessor was asked to review the stimulus words and decide whether each word could be categorised into one of the four quadrants: Dominant Antisocial, Passive Antisocial, Dominant Prosocial, or Passive Prosocial. Any words that were unfamiliar to the assessor, or did not distinctly belong to one of the four quadrants were ignored and omitted from further analysis.

The number of words assigned to each quadrant was counted and a Chi square analysis was performed using a null model of all N being equal. The prediction was that there would be more adjectives assigned to the dominant antisocial quadrant than to any other quadrant.[1]

Test 2: Adjective Rating Task

Stimulus Words. The second test assessed raters' perceptions of the salience of various adjectives as measured by perceptions of frequency of word usage. A total of 306 words were rated, with each subject rating 153 words. All words were personality trait adjectives selected from lists compiled by ANDERSON (1968) and HAMPSON/GOLDBERG/JOHN (1987). The ANDERSON word list consisted of 555 "personality trait terms" which had been selected from ALLPORT and ODBERT list by updating with a modern dictionary, eliminating terms referring to physical, sexual and extreme characteristics, and selecting those words rated as more 'meaningful' by their sample of subjects. These terms were specifically selected to cover a broad range of "social desirability". The word list compiled by HAMPSON et al., was comprised of 573 "person-descriptive terms" selected to be representative of the five domains of personality described by the Five Factor Model. Half of these terms were considered to be 'desirable' and half were considered to be 'undesirable'. The stimulus words for the current study were chosen by selecting all words that appeared in both the ANDERSON and HAMPSON et al. word lists. These words, which were initially listed in alphabetical order, were run through a randomizing script such that they appeared in two lists of random order, with one half of the words in each list.

Rating Dimensions. Participants rated the stimulus words on three independent bipolar dimensions, using 7-point Likert scales for each dimension. The three dimensions were: 1) Passive–Dominant, 2) Prosocial–Antisocial, and 3) Infrequent–Frequent (with reference to common English usage). For each dimension, the value 4 signified a neutral position between the two poles, and the values 1 and 7 signified extreme values, with the value 1 corresponding to the first term in the title of the dimension, and the value 7 to the second term.

Two rating booklets were compiled, each containing half the stimulus words. Each booklet consisted of five sheets of A4 paper, with the front page giving instructions, and the remaining four pages listing the stimulus words and rating dimensions. The instruction sheet was identical for both stimulus sets, and consisted of an explanation of the task requirements, examples of how to use the rating dimensions, and a request not to turn over the page until instructed by the experimenter. The stimulus words and rating dimensions were presented vertically down the page, with one stimulus word and three Likert scales to a line. A maximum of forty words was presented on one page.

Procedure and analysis. 131 first year psychology students participated in the task in order to receive extra course credit. 28 participants were male, and 103 female; they had a mean age of 18.2 years. Participants received one of the two lists of stimulus words. After allowing five minutes for participants to read the instruction page and sign participation consent forms, the experimenter verbally repeated the instructions outlined on the first page of the rating booklets. The instructions directed participants to rate each stimulus word on the three dimensions by circling the appropriate number, from 1 to 7, that they felt was appropriate for each word. The instruction sheet specified that participants should not spend a long time thinking about each word, but to respond as quickly as possible to each rating. Participants were then given forty-five minutes to complete as many of the ratings as possible. The number of words to present per session had been chosen in the expectation that participants would manage to complete all of the ratings, as determined from a pilot test.

We assigned each adjective to a quadrant according to ratings on the first two dimensions: 91 words were assigned to the Dominant–Antisocial quadrant, 81 to the Dominant–Prosocial quadrant, 61 to the Passive–Antisocial quadrant, and 72 to the Passive–Prosocial quadrant. (One word fell exactly on the mid-point of Pro- and Antisocial, and so was not used in this analysis). We predicted that words perceived to be in the Dominant–Antisocial quadrant would be perceived as being used more frequently than other adjectives.[2]

Test 3: Synonym Count Task

Stimulus words. For the third test, representative words were selected from each quadrant (as determined in Test 2) and translated into 8 languages for which a thesaurus was available. Native speakers who were also fluent in English as a second language were recruited to translate the words from English into: German, Dutch, French, Russian, Spanish, Chinese, Hindi and Afrikaans. Fifteen words were selected from each of the four quadrants as determined by ratings in Test 2. The sixty words were selected on the basis of three criteria: (1) Frequency, i.e., the mean rating for word frequency in Test 2 was above 4 (measured on a 7-point Likert scale with 7 corresponding to 'most frequent'; (2) Quadrant Salience, i.e., the word was considered to be representative of the category to which it was assigned, determined by its mean rating on both the Passive/Dominant and Prosocial/Antisocial dimensions. Words assigned to the Dominant Antisocial quadrant were considered to be representative of that quadrant if the mean score on the Passive/Dominant dimension was greater than 5 (4 being neutral), and the mean score on the Prosocial/Antisocial dimension was less than 3 (4 being neutral). Words assigned to the Dominant Prosocial quadrant were considered representative if the mean scores on both the dimensions were greater than 5. Words assigned to the Passive Prosocial Quadrant were considered representative if the mean score on the Passive/Dominant dimension was less than 3, and the mean score on the Prosocial/Antisocial dimension was greater than 5. Words assigned to the Dominant Prosocial quadrant were considered representative if the mean scores on both the dimensions were less than 3; (3) words were selected to be equally salient on both dimensions. This was done by selecting only those words which had equally strong ratings on both dimensions, thus, falling into an X shape superimposed over the four quadrants (see Figure 2). This procedure excluded any words that were near neutral on any dimension and that were, therefore, basically unidimensional in terms of meaning.

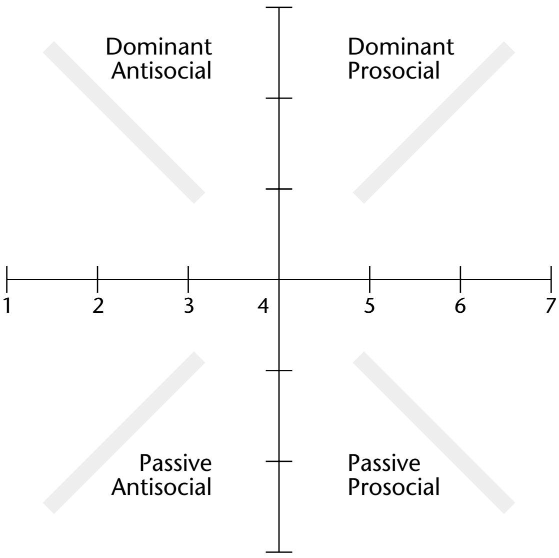

Figure 2: Position of Words Selected for Synonym Count Task.

The stimulus words were arranged into fifteen sets of four words with one word in each set coming from each of the four quadrants. Words in each set were matched for 'quadrant salience', based on the mean ratings of the Dominant/Passive and Prosocial/Antisocial scales (See Appendix B for the matched sets).

Thesauri / Synonym books. Two English Thesauri (LLOYD 1982; MCLEOD 1984) were used in order to order to obtain repeated measures for the English language. Thesauri or similarly constructed synonym books were also consulted for American English (LUTZ 1994); German (WEHRLE/EGGERS 1961); Dutch (VAN STERKENBURG 1991); French (DUPUIS 1975); Spanish (ESPASA-CALPE 1992), Afrikaans (EKSTEEN 1961), Chinese (WU 1979), Russian (EVGEN'EVA 1972) and Hindi (KUMAR/KUMAR 1996).

Procedure and analysis. Each of the stimulus words was translated into the each of languages mentioned above. (See Appendix C for a list of translations). For each language, the appropriate thesaurus was consulted by a native speaker who was asked to count the number of synonyms listed for each of the sixty words. The participants were blind to the nature of the study, but were instructed that if a word had one or more homonyms with meanings other than that of a personality trait, only the synonyms that were related to the personality trait were to be counted.

The mean synonym count for each quadrant was subject to a separate 2x2 ANOVA for each language, and a Chi Square and a 2x2 MANOVA were conducted on synonym counts across all languages. We predicted that within each language there would be, on average, a greater number of synonyms for words in the Dominant–Antisocial quadrant than for words in other quadrants. We also predicted that there would be a disproportionate number of languages for which the mean synonym count (across the fifteen words in each quadrant) was greatest in the Dominant–Antisocial quadrant.

Results

Preliminary analyses performed on all data showed no violations of analysis assumptions. Any missing values that occurred are mentioned below. The data were not transformed in any way for subsequent interpretation.

Test 1: Adjective Categorisation Task

The paid assessor assigned 2136 of the adjectives from Column 3 of ALLPORT and ODBERT's (1936) list of traits, to one of the four quadrants. The number of adjectives per quadrant were: 934 in the Dominant–Antisocial quadrant; 514 in the Dominant–Prosocial quadrant; 432 in the Passive–Antisocial quadrant; and 256 in the Passive–Prosocial quadrant.

Statistical analysis revealed that the number of adjectives per quadrant differed significantly and that more words were assigned to the Dominant Antisocial quadrant, as predicted.[3] (See Appendix C for statistical details).

Test 2: Adjective Rating Task

On the 7 point Likert scales, the overall mean rating of all adjectives was 4.19 (s.d = 1.08) for the Passive–Dominant dimension, and 3.99 (s.d = 1.26) for the Prosocial–Antisocial dimension. These were not significantly different from the center of the rating scale (4.00), confirming the representativeness of the adjectives selected for this test. Each adjective was assigned into one of four quadrants according to its mean value on both dimensions and the perceived frequency of usage was then compared across the quadrants.

The perceived frequency of use of Dominant–Antisocial adjectives was 4.49; of Dominant–Prosocial adjectives, 4.62; of Passive–Antisocial adjectives, 4.15; and of Passive–Prosocial adjectives, 4.73. Statistical analysis revealed a significant main effect of the Antisocial–Prosocial dimension with Antisocial adjectives being rated as less frequently used than Prosocial adjectives (see Appendix C). There was no significant main effect of Dominance/Passivity, however, a significant interaction emerged between the two dimensions such that among Dominant adjectives, Antisocial descriptors were rated as more frequently used than Prosocial descriptors, while among the Passive adjectives it was the reverse.[4]

Test 3: Synonym Count

The means and standard deviations for the number of synonyms counted for the fifteen stimulus words in each quadrant for the consulted thesauri are shown in Table 1. The number of words not listed in the thesaurus is also shown for each quadrant.

For each language, statistical analysis was performed on the number of synonyms for each stimulus word as categorized by quadrants (see Appendix C). No statistically significant results emerged from these analyses due to the unpredictably large variance in synonym counts for different words. There were, however, more synonyms for words in the Dominant–Antisocial category in two of the three English thesauri, as well as in the French, German, and Russian languages.

When analysis was undertaken to test the mean number of synonyms obtained for words in each quadrant across all eleven thesauri, a significant effect of quadrant was found such that more synonyms were listed, on average, for adjectives in the Dominant–Antisocial quadrant, as predicted. (In Table 1, the thesauri which had the highest mean number of synonyms in the Dominant–Antisocial quadrant are starred). The number of languages which had the highest mean synonym count were: for Dominant–Antisocial = 5; for Passive–Antisocial = 1; for Dominant–Prosocial = 1; for Passive–Prosocial = 4. Although these results are decidedly in the direction predicted, statistical analysis was not significant.

	Dominant Antisocial		Passive Antisocial		Dominant Prosocial		Passive Prosocial	
	Mean (m.val)	SD	Mean (m.val)	SD	Mean (m.val)	SD	Mean (m.val)	SD
***English (Collins)**	18.47 (0)	13.28	15.57 (1)	7.02	14.75 (3)	8.05	15.71 (1)	5.68
***English (Roget)**	60.53 (0)	32.56	44.08 (2)	19.87	42.60 (0)	31.43	47.27 (0)	31.43
American English	11.36 (1)	5.09	10.07 (1)	2.87	7.23 (2)	2.68	13.60 (0)	6.31
***French**	13.92 (3)	8.91	11.85 (2)	6.15	10.85 (2)	6.27	12.62 (2)	5.56
Dutch	3.06 (0)	2.24	3.50 (1)	1.70	3.67 (2)	1.95	4.33 (0)	2.80
***German**	44.00 (2)	33.96	41.93 (1)	22.78	34.92 (3)	15.54	33.93 (1)	32.78
Afrikaans	5.27 (0)	3.86	6.73 (0)	6.90	5.67 (0)	3.24	5.73 (0)	2.49
Spanish	9.21 (1)	5.49	7.08 (2)	2.39	13.75 (1)	2.78	8.20 (2)	2.39
Chinese	2.533 (0)	1.30	2.133 (0)	0.92	2.733 (0)	1.62	3.133 (0)	1.46
Hindi	14.33 (0)	9.12	19.67 (0)	11.90	19.47 (0)	15.15	23.43 (0)	14.00
***Russian**	7.57 (1)	4.85	6.39 (2)	3.66	6.00 (1)	3.06	4.14 (1)	2.47
OVERALL	17.30		15.36		14.69		15.64	

Table 1. Mean Synonym Counts in English and Foreign Language Thesauruses

Discussion

Three tests were conducted to test the hypothesis that there are more threat-related trait words in natural language than positive or neutral words.

The first hypothesis—that more English words would be identified at the Dominant and the Antisocial ends of the two basic personality dimensions—appears to have been confirmed, although further analysis of inter-personal differences in imputed word meaning are warranted. These results suggests that there has been a need to create terms describing threatening individuals more than there has been to describe non-threatening individuals. This inference is drawn from GOLDBERG's (1982) assertion that the more important an individual difference is, the more likely a term would have been created to describe it.

The second hypothesis, that words in the Dominant–Antisocial quadrant would be perceived to be more frequently used than words in other quadrants led to mixed results. The main effect of Antisociality went in the direction opposite to that predicted, with Antisocial adjectives being rated as *less* frequently used than Prosocial adjectives. On the other hand, there was a significant interaction effect such that among Dominant adjectives, Antisocial descriptors were perceived to be more frequently used than Prosocial descriptors, while among Passive adjectives, it was the reverse. It is perhaps the case that dominant antisocial terms are common because they describe people who represent threat, whereas passive prosocial terms are common because they describe people who are easy to manipulate; however, no particular interpretation is outstanding, and in fact, this interaction is the inverse of the interaction reported in a study of salience of faces representing the same four quadrants (MEALEY/DAOOD/KRAGE 1996).

The third hypothesis predicted that more synonyms would be listed for Dominant–Antisocial adjectives in English and foreign language thesauri than for adjectives from the other three quadrants. Three analyses were performed on the data. In the first analysis (a series of ANOVAs analyzing data from each thesaurus individually), no statistically significant results were obtained, although there were more synonyms for words in the Dominant–Antisocial quadrant in five of the eleven thesauri–including two of three English thesauri, as well as the French, the German, and the Russian thesauri. The results of a MANOVA comparing data across all languages/thesauri were statistically significant, with more synonyms, overall, listed for Dominant–Antisocial adjectives than for adjectives in other quadrants, as predicted. Finally, a Chi Square compared the number of languages which had the highest number of synonyms across each of the four quadrants. Whilst the sample size (11 thesauri) precluded a statistically significant result, in five of eleven thesauri, more synonyms were listed for Dominant–Antisocial adjectives than for others (see above). One unforeseen limitation of this task was the unavailability of foreign language thesauri; only eight languages other than English could be tested. If data were obtained for greater variety of languages, a statistically significant result may be achieved if the trend seen in the present study is continued.

In summary, this study has provided partial support for the hypothesis that natural language contains more words to describe threatening persons than positive or neutral persons. Although this is clearly true for the English language (as shown by the results of the first and the third test), it is erroneous to presume that this is true for all natural languages. Speculators might see the beginnings of an East–West pattern, in that the languages which emphasized Dominant Antisocial terms were all European (English, Russian, French and German), whereas the ones that did not included two Asian languages (Dutch, Afrikaans, Spanish, Chinese and Hindi). Further study of more languages might be able to uncover higher-order patterns relating the presence or absence of linguistic biases to attributes of social structure. In addition, investigation of individual differences in the assignment of words to quadrants and of the salience of words representing different quadrants, might shed more light on the intra- and interpersonal aspects of attention bias and personality ascription.

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Notes

1 The intent was to get a count from a typical English speaker. However, when an outside reader suggested that we get a count from a Professor of English, we did so. Also, in a subsequent effort to examine inter-personal variance in this assessment, we later obtained counts from three additional assessors. Similarities and differences in their ratings are addressed in a footnote in the Results section.

2 As with the word count, the intent was to assess perceptions of typical English speakers—thus, the ratings were obtained from a large sample of first-year University students. Once again, however, the same outside reader made a suggestion that we obtain actual word use frequencies from a published source. This analysis, however, is not appropriate for three reasons. Firstly, published counts assess actual word usage frequency, regardless of context or meaning. Thus, words that our raters assessed in the context of personality descriptors, appear in published lists with a single frequency indicator regardless of whether the word was used to describe a person or not. In fact, almost all of the 306 adjectives on our list could be used in one or more contexts other than as a personality descriptor: "bright" (Dominant–Prosocial) for example, could refer to a light or to a colour; "rash" (Dominant–Antisocial) could refer to a skin disorder or a policy decision; "unhealthy" (Passive–Antisocial) could refer to a diet or a lifestyle; and "sensitive" (Passive–Prosocial) could refer to a conversation topic or a body part (etc.). Secondly, published frequency counts do not differentiate situations when a word has been used by itself versus when it has been used with a qualifier or a negation, such as "he is not a very reliable person". It is likely that "positive" words are negated more often than "negative" words so as to avoid double negations (e.g., "not very smart" is probably more common than "not very stupid" and "not very reliable" is probably more common that "not very unreliable". Furthermore, it is unclear whether using the negation of a word is truly the same as using its antonym or whether "positive" and "negative" words are treated, cognitively, as separate natural categories (WHITMEYER 1997). Thirdly, word usage frequencies are representative only of the particular type of language samples that are assessed in the particular corpus. One word frequency index, for example, (DAHL 1979), uses samples of spoken language, and reports significant, large, and meaningful differences in tabulated word frequencies as compared to those obtained from samples of written language. For those interested, we did do an analysis of tabulated word frequencies from five different published lists. These are reported and discussed in a footnote in the results section.

3 The Professor of English apparently used more strict criteria for assigning words to quadrants, as he labeled far fewer words than did our paid assessor. The pattern, however, was exactly the same, with 101 words in the Dominant–Antisocial quadrant; 40 words in the Dominant–Prosocial quadrant; 27 words in the Passive–Antisocial quadrant; and 24 words in the Passive–Prosocial quadrant. As with our paid assessor, this, too, is statistically significant, with ($\chi^2_{(3)}$ = 79.47, $p < .001$). In none of the other three assessors, however, was this same pattern identified (although two of three reported more Dominant words than Passive words and two of three reported more Antisocial words than Prosocial words). Perhaps this non-replication relates to assessor recruitment (the last three were under duress to do the ratings to payback the second author for a prior favor)—or perhaps there is a personality difference among assessors that influences how they perceive and assign words. We are interested in pursuing this latter hypothesis in a further study, especially in regards to trait anxiety.

4 In a preliminary analysis of published word usage frequencies, we found that the three sources which utilized curricular materials for their text samples (THORNDIKE 1932; CARROLL/DAVIES/RICHMOND 1971, and BRELAND/JENKINS 1997) all reported higher frequencies of Prosocial terms

(both Dominant and Passive) than of Antisocial terms (both Dominant and Passive); the same was true for Francis/Kucera (1982), which uses a broader sample, but which remains confined to written text and specifically excludes written passages which reflect usage in speech, such as in drama and passages of dialogue from fiction texts. This was in stark contrast to the word frequencies reported by Dahl (1979), whose samples came from spoken dialogue. In these very personal conversations, Antisocial terms (both Dominant and Passive) were used with higher frequency than were Prosocial terms (both Dominant and Passive). Clearly the source of the linguistic samples is relevant. An interesting follow-up study could analyze and compare dialogue from different domains such as interpersonal settings and conversations (television, movies, and real gossip) versus instructional materials or other materials which are intended to educate and socialize their readers.

Appendix A

Examples of labels used from different research domains to represent axes of personality

Personality Psychology		
Leary (1957)	Dominance/Submission	Hostility/ Affiliation
Block (1961)	Dom+/Dom–	Lov–/Lov+
Developmental Psychology		
Schafer/Edgerton (1982)	Extraversion/ Introversion	Hostility/ Considerateness
Social Psychology		
Schaefer (1961)	Extraversion/ Introversion	Hostility/Love
Family Psychology		
Schaefer (1959)	Autonomy/ Control	Hostility/Love
Clinical Psychology		
Blashfield (1986)	Ambitious–Dominant/ Lazy–Submissive	Cold–Quarrelsome/ Warm–Agreeable
Emotion Psychology		
Russell (1997)	Arousal/ Sleepiness	Displeasure/ Pleasure
Myllyniemi (1997)	Dominance/ Submission	Defiance/ Affiliation
Linguistics		
Myllyniemi (1997)	Dominance Submission	Defiance/ Affiliation
Rosenberg (1968)	Hard/Soft	Bad/Good
Political Psychology		
Bailey (1972)	+Power/–Power	–Solidarity/ +Solidarity
Kinesics		
Gifford (1991)	Ambitious–Dominant/ Lazy–Submissive	Cold–Quarrelsome/ Warm–Agreeable

Appendix B

60 Stimulus Words for Synonym Count Task.

Dominant Antisocial	Dominant Prosocial	Passive Antisocial	Passive Prosocial
Rude	Bold	Weak	Calm
Argumentative	Outspoken	Silent	Relaxed
Cruel	Confident	Withdrawn	Sensitive
Insulting	Self-assured	Lonely	Sympathetic
Critical	Individualistic	Indecisive	Patient
Tactless	Decisive	Insecure	Sentimental
Irritable	Active	Lazy	Casual
Conceited	Self-disciplined	Worrying	Courteous
Superficial	Alert	Absent-minded	Thoughtful
Insincere	Brilliant	Forgetful	Neat
Suspicious	Efficient	Incompetent	Understanding
Cynical	Competent	Anxious	Respectful
Frustrated	Mature	Unhealthy	Rational
Skeptical	Intelligent	Preoccupied	Artistic
Immature	Punctual	Self-critical	Modest

Appendix C: Statistical Details of Results

Test 1: Adjective Categorisation Task

The number of adjectives per quadrant were: 934 in the Dominant–Antisocial quadrant; 514 in the Dominant–Prosocial quadrant; 432 in the Passive–Antisocial quadrant; and 256 in the Passive–Prosocial quadrant.

A Chi square analysis was performed, with the null hypothesis being that the number of words would be equal in the four quadrants. The results of the analysis showed that the number of adjectives per quadrant differed significantly ($\chi2$ (3) = 679.53, p < .001), and post-hoc analysis showed that more words were assigned to the Dominant Antisocial quadrant, as predicted.

Test 2: Adjective Rating Task

Perceived frequency ratings for the four categories were: Dominant–Antisocial adjectives: 4.49; Dominant–Prosocial adjectives: 4.62; Passive–Antisocial adjectives: 4.15; and Passive–Prosocial adjectives: 4.73. A 2x2 ANOVA revealed a significant main effect of the Antisocial–Prosocial dimension (F(1,305) = 9.19, p < .01), with Antisocial adjectives being rated as less frequently used than Prosocial adjectives. There was no significant main effect of Dominance/Passivity (F(1,305) = 1.92, ns), however, a significant interaction emerged between the two dimensions (F(1,305) = 6.87, p < .01) such that among Dominant adjectives, Antisocial descriptors were rated as more frequently used than Prosocial descriptors, while among the Passive adjectives it was the reverse.

Test 3: Synonym Count

For each language, a 2x2 ANOVA was performed on the number of synonyms for each stimulus word as categorized by quadrants. No statistically significant results emerged from these analyses due to the unpredictably large variance in synonym counts for different words. There were, however, more synonyms for words in the Dominant–Antisocial category in two of the three English thesauri, as well as in the French, German, and Russian languages.

A MANOVA was performed to test the mean number of synonyms obtained for words in each quadrant across all eleven thesauri, finding a significant effect of quadrant (F(3,32) = .10.50, p < .05). This indicated that over the eleven thesauri, more synonyms were listed, on average, for adjectives in the Dominant–Antisocial quadrant. The number of languages which had the highest mean synonym count were: for Dominant–Antisocial = 5; for Passive–Antisocial = 1; for Dominant–Prosocial = 1; for Passive–Prosocial = 4. Although these results are decidedly in the direction predicted, a Chi Square analysis for N = 11 was not statistically significant ($\chi^2_{(3)}$ = 4.79, p = 0.17).

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From Basic Adaptivity to Early Mind

The Origin and Evolution of Cognitive Capacities

Abstract

In this paper we try to understand cognition, as a specific phenomenon, that appears in motion-based multicellular organisms. This is due to the fact that when the size of the organism increases, adaptive sensorimotor coordination needs to be accomplished by an internal informational subsystem dynamically decoupled from general metabolic processes. Further increase in the complexity of this informational system (the NS) is also linked to size increase of animals. We will show that only vertebrate bauplan allows those body changes required for the emergence of new forms of cognitive phenomena such as emotions, leading to the appearance of an early form of mind.

Key words

Cognitive capacities, evolution, body plan, sensorimotor interaction, dynamical decoupling, autonomic nervous system, emotion.

1. Introduction: What Is Cognition?

The appearance and development of cognitive capacities represents probably the most important event in biological evolution because it implies a tremendous increase in complexity, both regarding internal organization of living beings and their ways of adaptive interactions. The phenomenon of cognition is obviously the result of evolution, but not all living beings achieve adaptation through cognitive mechanisms. Animals and plants, for instance, show very different types of lifetime adaptability, and generally speaking, we tend to associate cognitive phenomena with the kind of adaptive interactions of the former more than with the latter, because obviously they show resemblance to our own cognitive processes (especially in some of the animals more recently evolved). But the farther we look back in evolution, the more difficult it is to identify specific cognitive processes. At the same time, it is necessary to trace them back to the most ancient evolutionary stages in order to understand the origin of these peculiar processes. This leads us to the crucial question: Which are the sensible criteria for identifying specific cognitive phenomena, as opposed to the broad biological phenomena in which they are embedded?

Now, this question is loaded by a previous problem, namely, the disagreements about what do we mean by cognition. For example, whilst for some authors the motor adaptive behavior of bacteria is already a cognitive phenomenon (MATURANA/VARELA 1992; STEWART 1996) for others it is only possible to talk about cognition when we find at least some trace of consciousness or mind, which seems to happen at some stage of vertebrate evolution. In other words, we can take our own (either human or hominid) cognitive capacities as a model for identifying what is or is not cognitive. Or, alternatively, we could try to broaden the concept of cognition to include the most primitive ways of adaptive behavior. However, in neither case there is an objective justification for the chosen starting point. In the first case because, by leaving aside the whole evolutionary line that gives origin to those capacities, it is difficult to understand their functional origins or their relationship to the whole organism. In the second case because, by dissolving cognition in the broader biological phenomena, it is difficult to understand the nature and the function, even more, the evolutionary history of cognition as a specific phenomenon.

It is impossible to make a real progress in this discussion if we are not able to establish a common starting point. However, in our opinion there is one way of escaping from this dilemma: reformulating the question of the origin of cognition in radical evolutionary terms. Thus, instead of starting with such-and-such concept of cognition, based on purely intuitive criteria, we should try to understand what kind of adaptive mechanisms and under which conditions lead to more complex forms of adaptive interactions. Namely, we should ask questions like these: Which causes could explain the origin and development of bifurcations throughout the history of life in the degree of complexity within organisms and in their types of interactive adaptive capacities? What kind of (new) living organization could underlie it? And, what evolutionary implications would the development of cognitive capacities have?

If we were able to disentangle the basic milestones of the chain of causal events that lead from the most basic forms of adaptation to the first traces of mind and consciousness, we would be in a better position to substitute intuitive criteria with a more objective view of cognitive phenomena. Accordingly, in this paper we will try to sketch a genealogical explanation of cognitive phenomena. We will study the appearance and development of certain capacities, instead of from the point of view of the role they play in human cognition, focusing in what processes have brought them about, what structures have supported them and what functions they have served in the evolution of living beings. Thus, in this genealogical approach we would try to understand the different levels of cognition from a more encompassing (biological) perspective.

2. The Origin of Basic Cognition

2.1 Adaptivity and movement in unicellulars

Any individual living being is essentially an autonomous[1] system that interacts adaptively with its environment. Except some kinds of bacteria which live in very homogeneous and stable environments, all present day organisms posses the capacity to change in somatic time their forms of action according to different environmental conditions. Organisms have the capacity to detect those modifications in the environment that are relevant for the maintenance of their own organization and to trigger some internal and/or external processes contributing to their self-maintenance in each of these particular conditions. In order to do so, they choose one particular metabolic pathway among the repertoire available according to the particular state of the environment relevant to the functioning of the system.

The basis for adaptive action lies in the fact that organisms need to exert certain actions on their (changing) environments just to keep their metabolism going (Ruiz-Mirazo/Moreno 2000; Christensen/Bickhard 2002). These actions are accomplished through some functional modifications of its plastic metabolism, tuned to relevant environmental changes. In bacterial life adaptivity lies in the capacity of selectively controlling the expression of the genetic repertoire of the cell, thus enlarging its metabolic plasticity when certain external conditions occur. Despite its simplicity, this basic mechanism allows a great variety of forms of adaptive action.

Now, among the different forms of adaptive agency, motility is particularly interesting because its intrinsic relation with velocity and distance. Motility is the capacity to exert directional and *fast* movements according to *distal* conditions. Although the bacterium does not “detect” distant features, as it only “senses” the medium through certain contact proteins, its action as a whole can be interpreted as if directed by a distal goal. Bacteria such as E. Coli are equipped with mechanisms—flagella—that allow them to move following concentrations of sucrose (Neidhardt 1996). And this is accomplished even though it may mean a significant metabolic waste, i.e., to swim against a gradient force. This capacity would be the result of co-ordination between membrane receptors and motor mechanisms, mediated by metabolic paths in the inner cell (Losik/Kaiser 1997, Hoffmeyer 1998).

However, in the primitive forms of life motility is not substantially different from other forms of adaptability. For example, when the prokaryote *Caulobacter* lives in a very humid medium it persists fixed to the soil like a vegetal type, whereas, in dry periods, it reproduces and the new cells grow a flagellum capable of transporting them to a more humid environment. So, the interactive loops established by the most primitive organisms with their environment are always contrasted and evaluated according to the effects they have upon their basic capacity for self-construction (or self-maintenance), which is their main normative goal. In fact, in prokaryotic cells, body movement could be considered as just an extension of the set of mechanisms that are required for a minimal metabolism. So, capture of food by means of body movement (as opposed to exploitation of primary energy resources or fermentation processes) does not entail qualitatively important differences in adaptation mechanisms. At this level, the underlying organization of behavior and of morphological change is basically the same.

Now, this situation of indistinguishability begins to change as the size of organisms increases. Unlike other forms of adaptivity, at bigger sizes the organization of motility faces new problems raised by the need of fast internal coordination between detection and action. Accordingly, when eukaryotic cells appeared, motor responses had to be organized in a different manner than in small prokaryotes. Instead of organizing functional changes only by means of diffusion processes, eukaryotic cells are equipped with mechanisms allowing a precise and speedy distribution of substances. These—comparatively—big[2] cells are capable of rapid movement because they possess microtubules, which contribute not only to chemical channeling and plastic reorganization of selected parts of the internal structure of the cell, but also to external movement by means of undulipodia.[3] External eukaryotic organs for movement, like cillia or flagella, are much more complex structures than prokaryotic flagella, and adequate coordination between detection and motor tasks also requires more complex internal organization. But this new organization creates a conflict between simultaneous movement and regeneration (BUSS 1987; MAYNARD-SMITH/SZATHMARY 1995). This conflict is already pointing to an organization problem that will become more critical with the appearance of bigger organisms in evolution: the increasing difficulty in organisms of bigger sizes for the basic metabolic organization to efficiently support quick and versatile sensorimotor actions. As the size of the organism increases, the energetic and material costs for the metabolic organization to provide a rich and plastic enough system of internal patterns for supporting fast sensorimotor coordination tasks become incompatible with the accomplishment of the very function of self-maintenance.

2.2 The appearance of the neural organization as an autonomous level

The appearance of multicellular organisms was a critical point for the organization of motility. At this size it becomes impossible to organize, based on metabolism alone, quick and versatile sensorimotor actions.[4] There are two causes of this problem: the enlarged internal distance between parts of the body, which need to be connected with short delays (so that the organism can move fast); and the need to selectively modulate the organization of connections (to obtain adequate sensorimotor correlations). Hence, if metabolic network plasticity were the only mechanism for accomplishing adaptive interaction and self-maintenance, the behavioral repertoire would probably be very limited at the multicellular size.

The situation changed when in the development of some metazoans (the so called eumetazoans, which already developed tissues, mouth and digestive cavity) a new kind of cell—the neuron—started to differentiate. The neuron is a cell specialized in connecting sensorimotor surfaces in a plastic, fast, and (metabolically speaking) cheap way. Neurons differentiated as cells capable of forming branches, which may be interconnected through ion channels (controlled either by the electrical potential over the membrane or by ligand) in their membranes. These interconnected cells led to the establishment—about 600 mya—of a network able to manage an efficient coordination between sensor and motor/effector structures in multicellular organisms (LLINÁS 2001).

Since the very beginning of its evolution, this neural organization appeared as an extended network capable of producing a recurrent dynamics of specific patterns. Unlike chemical signals circulating within the body, which directly interact with metabolic processes, chemical or physical interchanges among neurons make recurrent interactions within the very Nervous System (hereafter, NS) possible, thus generating a new domain of patterns, specifically informational.[5]

What makes neural interconnections so special is that they create an incredibly rich and plastic internal world of patterns of fast connections, dynamically *decoupled* from the metabolic processes (MORENO/UMEREZ/IBANEZ 1997). As the phenomenon of decoupling is of fundamental importance for understanding the importance of the appearance of the NS, we will briefly introduce the concept of decoupling and next specify the way in which the NS is decoupled from the metabolic processes.

In a natural system, a phenomenon of decoupling appears when it gets organized in such a way that 1) a part of this system constitutes a new subsystem of interactions which operates according to a set of rules independent of the dynamics of the remaining system, so that each part appears as a relatively autonomous subsystem, though, 2) both are mutually dependent in their global interactions.

The relation between the NS and the metabolism is a particular form of decoupling (that we shall call *hierarchical decoupling*) because 1) the basic dynamics of the metabolism (M) produces a set of higher level variables (NS) so that, 2) NS specifies its own dynamics (i.e. NS is operationally closed or dynamically closed). Thus, the state of NS is undetermined by M. The kind of causation between M and NS is bottom-up, local and constructive, thus, NS is materially dependent on M; and 3) there is a global metaregulation between M and NS where causation is dynamic and global. Because they establish the global conditions of their respective maintenance/metastability: nor the higher, neither the lower level are fully autonomous, but only the global system.

Thus, the nervous interactions constitute a new, autonomous, level producing new phenomenology. However, the possibility of this autonomy[6] lies in the embodiment of the NS in a self-maintaining organization interacting in a given environment. Thus, the autonomy of the NS is both required and limited by its functional role. Ultimately, the logic of the activity of the NS depends on its participation in the logic of the global maintenance of the animal (its metabolism requires an adequate sensorimotor activity). And, in turn, metabolic organization supports NS´s construction, functioning and maintenance. Thus, NS and metabolism are connected in such a way that their respective maintenance (and therefore, existence) depend upon one another.

2.3 A new organization of the body

The rich plasticity of the NS allows for a qualitative increase in the complexity of the adaptive behavior of multicellular organisms. This plasticity is a consequence of the specific bio-chemical properties of neurons that permit stimulated dendritic branching on short timescales, entrained assembly depolarization, and a host of like basic properties. As a result, individual adaptability does not rely mainly on changes in body structure, but in the neural network. Thus, for these organisms—animals—behavior, understood as functional body movement, is the most important mode of adaptability: their metabolic self-maintenance is mainly produced through neurally controlled secretions and motor actions.

Now, in addition to allowing quick and efficient motility for organisms with body masses bigger than protozoans, the appearance of the NS opened up new, qualitatively different, modalities of adaptive interaction. Already at early stages of NS evolution, we can see some rudimentary learning, categorization and memory capacity (ARHEM/LILJENSTROM 1997). We tend to identify the main significance of the appearance of the NS in terms of the development of these capacities—and very soon new others, such as associative learning, communication and social cooperation—because they begin to appear as specifically cognitive[7] (insofar as these capacities apparently show increasing similarities with ours). However, from an evolutionary perspective, the importance of these new capacities lies mostly in the cascade of changes that they opened up. The appearance of the NS enabled new radical changes in body design, but its further development was only possible when new, very specific, body changes appeared.

Therefore, it would be an error to see the problem of evolution of cognitive capacities as a question concerning only the construction of increasingly complex and broad neural networks coupled to more complex sensorial and motor structures. Animals are much more than sophisticated robot-like systems, since their NSs, instead of controlling only sensorimotor organs (as in robots), are embedded in a biological (metabolic) organization. For example, the NS indirectly participates in the functioning of metabolism through the so-called neuroendocrine system.[8] And in turn, metabolism ensures the adequate maintenance of the NS (construction, repair, and adequate energetic supplies). This fact is not only important for their mutual maintenance, but for the constraints that each other imposes in their respective evolution. The organizational and structural consequences of the constraints that the evolution of each subsystem imposes on the other can account for many important aspects of cognitive phenomenology. Hence, the basis of cognitive phenomena does not lie ultimately only in a special subsystem—like the NS—but in the functional relationship between this system and the whole organization of the animal.

Accordingly, the potentialities of the NS cannot be developed independently of changes in the general organization of the body. On the contrary, as CHIEL and BEER (1997) have pointed out, the appearance and development of more complex kinds of adaptability is the result of interactions and constraints between the dynamics of the NS, the rest of the body, and the environment. In an animal, body organization is configured or shaped by the very evolution of the NS (and conversely), so that, to a high degree, both the NS and body organization are complementary. For example, not only has the muscular system been developed by evolution in a deep interrelation with increases in complexity of the NS, but so also have the organization of internal circulation, the system of fixation, and even the body shape.

Thus, basic potentialities of the NS to support complex forms of adaptive behavior cannot be unfolded only on the basis of more complex neural networks, if these are not accompanied by new ways of organization of body structure (bauplan). However, once fixed, a body plan becomes a constraining factor in the evolution of a given line of animals, since adaptations only take place inside the architectonic limits of the ancestral body plan (HICKMAN et al. 2001).

3. The Origin of Mind

3.1 Size, motility and body plans

By the early Cambrian, a rapid development of both NS and body plans took place (RAFF 1996), and a variety of relatively complex adaptive behaviors appeared. From the beginning, the evolution of the NS—as of other important features of the body plan—has taken two different paths. On the one hand, there is the line of protostomes, where the neural cells assemble themselves in a ventral nerve cord. The evolutionary trend of these NSs has tended towards accumulating neural cells into groups (ganglia) distributed along the body. On the other hand, there are the deuterostomes, whose NS has evolved into a process of first assembling neurons in a dorsal tube and later centralizing the bulk of these neurons in one mass, near the sensorial organs (encephalization). In fact the more complex development of the NS appears only in the second line (the deuterostomes), from which vertebrates have evolved.

This divergent line of evolution of the NS poses an important problem. The origin of phenomena such as emotions and awareness, tightly related to other cognitive capabilities such as complex self-directed learning (CHRISTENSEN/HOOKER 2000) and mental representations, is linked to the second aforementioned evolutionary line. Now, since relatively simple forms of the NS seem to be sufficient for allowing complex and diversified behavior patterns, what kind of role would a bigger neural development play? What kind of causes would explain the appearance and development of these new phenomena? And why did this development occur only in a particular evolutionary line (that of vertebrates)?

As we shall see, here again the answer is related to the issue of size. As happened before when multicellular organisms appeared, new increases in size posed serious problems to the organization of versatile and strong motility. In fact, in bigger animals control of movements gives rise to structural and organizational problems. Let us mention just three examples: first, movement of big body masses requires some surface for muscles to be inserted in. In invertebrates this is accomplished to some extent through the external skeleton, but for bigger body masses it would have to be too heavy, and body growth would also be constrained by this external rigid cover (STORER et al. 1979). Second, whereas small animals do not require special means in order to distribute nutrients and oxygen, or in order to collect their residual substances from catabolism, as all their cells are close to nutrient sources and environment, bigger animals need more complex and closed circulatory systems (NILSSON/HOLMGREN 1994). And third, the time needed for motor reaction increases. Whereas small animals can modify their movements very quickly (for instance, certain flies can change their flight within a few milliseconds (DOWNER 1988) animals with bigger body masses usually require much longer response times.

There are several reasons that explain why invertebrate bauplans preclude versatile motility at big corporal sizes.

Skeleton. Invertebrates lack an internal skeleton, which poses a problem (for big sized animals) since there is no adequate place for attaching muscles that have to realize quick and forceful movements. Vertebrates, on the contrary, possess an internal skeleton, allowing for more powerful attached muscles, which in turn allows for more efficient movement. An internal skeleton is also important for allowing a more complex and precise control of movement. From the evolutionary point of view, its origin seems to be related to a progressively predatory way of feeding—which requires strength in several muscles of the body—instead of feeding through substance filtering (PURNELL 2001). An internal skeleton also has more capacity to attain larger sizes than an external skeleton.

Circulatory system. Invertebrates usually have open circulatory systems: blood is pumped into a body cavity (hemocele) and then runs freely through tissues. This system is not very efficient for bigger animals, as there is not enough blood pressure that can move blood rapidly through tissues. As a consequence, this system cannot provide the energetic supplies needed in each particular part of the body quickly and efficiently. Though big invertebrates have closed circulatory systems, this is still far from a vertebrate´s circulatory system, in which blood circulates through a complicated pipe system that distributes it to every corner of the body at proper conditions of pressure and flow, which translates into speed and efficiency at the level of motor actions (STORER et al. 1979). What invertebrate closed circulatory systems lack is a fine tuned mechanism for controlling the conditions of the flow at each place and time. Efficient and versatile motor control at bigger sizes requires proper pressure and flow of nourishing blood, which in turn requires not only that the pipe-system is closed, but also a control system to regulate this pressure and flow depending on different internal and environmental circumstances. This is achieved by a system of receptors distributed along the blood vessels, which detect pressure of blood, oxygen concentration, and acid level (SHERWOOD 1997). These receptors are connected to the NS, but the link is through the so-called Autonomic Nervous System (ANS), that we will describe latter. The ANS can then modify pressure and flow of nourishing blood in different body areas and organs by means of a direct neural control of contraction or dilatation of vessel wall or of pump(heart) functioning. This kind of closed cardio-circulatory system allows for proper working of the muscles in a quicker and more efficient way, which improves animal movement. Therefore, only a circulatory system such as this allows the muscular system to mobilize a big body mass with speed and strength. This also implies fine control (through a highly efficient circulation of hormones, peptides and other regulatory substances) of the metabolism of other internal organs (viscera), so that there is fine modulation of different organs and their functions: digestion, respiration, sexual activity, immune defense.

Immunity. Invertebrates do have a primitive immune system that lacks capabilities for memory and specificity (BECK/HABICHT 1996). Such a system becomes inadequate as the complexity of the circulatory system increases. Vertebrate's circulatory system requires a new type of immune system. As the distribution of beneficial substances is facilitated, toxins and potentially harmful substances and organisms have more ease to enter into distant and vital parts of the organism. This is why a complex system of defense circulating along the vessels is needed, that is, the cellular immune defense system with its capacity for immune memory.

As a consequence, big size invertebrates (pogonophores, giant cephalopods and others now extinct[9]) are exceptional, and the ecological niches they occupy are also marginal. Even middle-size invertebrates, like octopuses, live at the limits of the functional capacities of their body plan. For instance, an octopus's circulatory system only allows them to perform short term muscular efforts. Lacking fine tuned control of blood circulation, they tire easily and their vascular system is forced to work close to its physiological limits (ABBOTT 1995).

So, in summary, radical changes in body organization were required to produce bigger animals, capable of motor versatility and efficiency. The appearance of animals whose body plan permitted these changes—the chordates—happened very early. From these animals evolved the primitive vertebrates, nearly 500 mya, and the basic structure of the vertebrate brain was established by 480 mya (MIKLOS/CAMPBELL/KANDEL 1994). Ultimately, however, all this was the result of the appearance, about 525 mya (that is, during the Cambrian radiation), of a new bauplan—that of chordates—whose latent potential became progressively unfolded through an evolutionary process of interplay between the appearance of some of the aforementioned features and subsequent evolutionary changes. As we will see in the next section, these body changes will both require and make possible critical changes in the NS organization and complexity. At the same time, these changes opened up a process of reorganization of the relations between body and NS, leading to the appearance of new forms of cognitive agency.

Next we are going to show the origin and consequences—both organizational and structural—of these changes.

3.2 Implications for the NS

One of the most significant aspects of the evolutionary history of vertebrates is the process of encephalization, namely, the increasing concentration of neurons in the head. This process was probably the result of a complex set of causes that operated in different evolutionary stages and on different kinds of vertebrates. Although a complete study of these causes is beyond the scope of this paper, we will try to understand here in terms of the body design, which factors have allowed a process of encephalization. Thus, from this perspective, the development of a new, fine tuned circulatory system was fundamental because it provides fine blood input regulation for the adequate functioning of big neural concentrations. In turn, these neural concentrations—through the ANS—allow for a fine control of the circulatory system. Thus, there is a kind of feedback between the evolution of the NS and the above mentioned changes in body organization. Vertebrate's ANS controls an adequate blood flow and pressure (through rhythm and strength of the heart and contraction/dilatation of the walls of the vessels) that maintains nutrient and oxygen intake in tissues far away from the external surfaces of the animal. This, again, requires more neural resources.

The increasing complexity of the NS in vertebrate evolution is also facilitated because it is embryogenically developed around the walls of a cylindrical cavity and is therefore favored by nourishment from the inside, as well as from the outside surface. In invertebrates neural concentrations are just accumulated one over the other with less room for nourishment structures. Even with a closed, efficient circulatory system, a fine energetic maintenance of these kind of increasingly big neural concentrations would be difficult (MONTALCINI 1999). Last, but not least, in vertebrates, the conduction of electrical impulses through axons is facilitated by myelinization, which is absent in invertebrates.

However, the key difference of the vertebrate's NS lies in its internal organization. Whilst the NS of invertebrates is fundamentally a distributed network of neural sets (ganglia) devoted to the organization and coordination of sensorimotor activity (besides an indirect control of metabolism-viscera through the neuroendocrine system), in vertebrates an important part of neural resources is devoted to control the metabolism (through direct neural modulation of the functioning of different viscera, like circulatory and respiratory systems), and this task becomes decoupled from sensorimotor control tasks.[10]

In invertebrates clusters of ganglia usually at the anterior end of the animal make up the brain. These ganglia exert control over the body segment ganglia. It is well known that in certain invertebrates the brain could reach a considerable development. Of special interest is the case of cephalopods, which constitute the most developed case of encephalization[11] in invertebrates. According with this development of their brain, certain cephalopods show remarkable learning capacities and other forms of complex behavior (for instance, in some cases they use their capacity to control changes of skin texture and color either for mimicking different fish appearances or for social communication; GRIEBEL et al. 2002). However, this seems to be the limit of neural complexity in invertebrates, since further evolution in their cognitive capacities would require a different bauplan (capable, for example, of supporting at the same time large body masses and a large variety and versatility of sensorimotor interactions in terrestrial environments). But this would require a radical change in the organization of the NS, including some structure capable of exerting a fine tuned neural control on the functioning of the viscera. So, eventual evolutionary increases in the size and complexity of invertebrate's brain could not be functionally recruited.[12]

Thus, the importance of the ANS for the evolution of vertebrate cognitive capacities lies in the fact that it is a key element in a new organization of the relation between the body and the NS. The ANS is a subsystem of the NS that receives information from all the viscera, integrates it by means of its own control centers, independently from the rest of the NS, and sends efferent instructions back to viscera so as to maintain adequate homeostasis. The rest of the NS—NS less ANS—is now increasingly specialized for control of sensorimotor activity independently of coordinating metabolism, and we shall refer to it hereafter as the Somatic Nervous System (SNS).[13]

Together with the SNS, there are the structures which provide a coordination mechanism between sensorimotor cognitive tasks brought about by the SNS, and internal organ control tasks brought about by the ANS. Coinciding with the appearance of reptiles (about 310 mya) appeared a specific structure in the brain, labeled the Limbic System, which is a system of interconnected nuclei that bridge the ANS and the SNS (GLOOR 1997). This system organizes the flow from the ANS to the SNS of both neural connectivity and secretion of peptides and other neuromodulator substances that can modify qualitative aspects (such as speed) in the operation of many brain circuits. The Limbic System organizes the flow back from the SNS to the ANS as well, by means of neural connectivity. In addition to that, the Limbic System also organizes secretion of hormonal substances in the blood stream that affect the functioning of viscera.

As EDELMAN (1992) points out, both the Autonomic and the Limbic Systems constitute "a system of the interior" as opposed to the "system of the exterior" that would be constituted by the SNS. According to this author, the system of the interior is composed of different structures that were selected during evolution to match the body, more than to match the large number of unanticipated signals from the outside world. These systems evolved to take care of body functions and are connected to body organs. On the other hand, the system of the exterior would have evolved to receive signals from

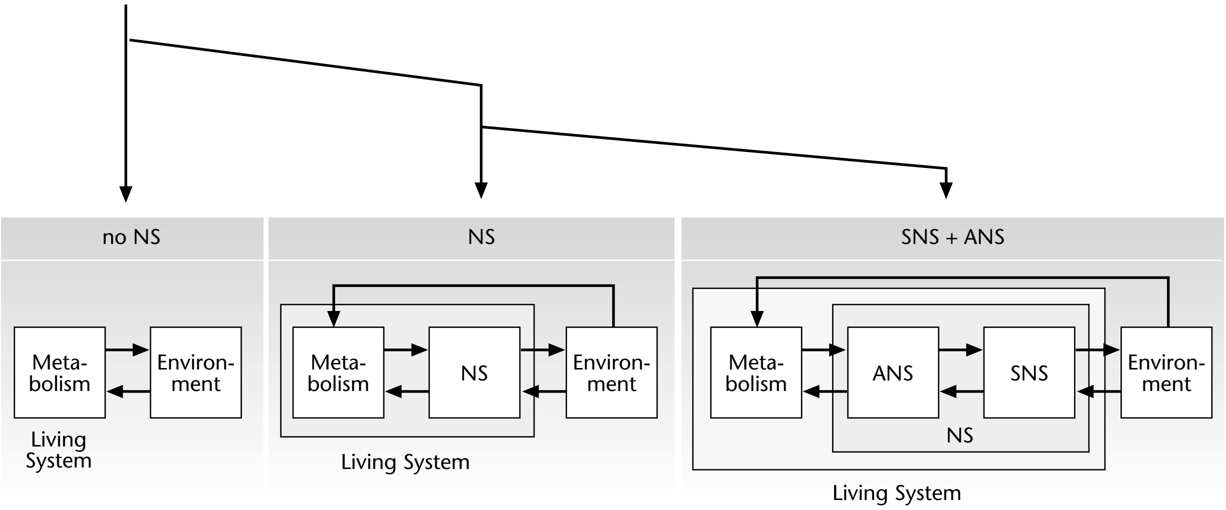

Figure 1: Major bifurcations on the evolution of adaptation.

sensory receptors and to give signals to voluntary muscles. It evolved to permit increasingly sophisticated motor behavior.

In summary, vertebrates have developed a complex visceral system, with its own fine-tuned control mechanisms, thanks to the aforementioned reorganization of their NS in two structurally and functionally separated parts. Although the origin of this separation remains unknown, a feedback between the organization of the body and that of the NS took place very soon in the evolution of vertebrates. This process was probably one of the crucial factors explaining the process of encephalization in vertebrate evolution[14]. It is tempting to suggest that the development of the ANS and the appearance of the Limbic System is related to the colonization of a terrestrial environment, since an aquatic environment seems less favorable for the evolution of cognitive capacities than a terrestrial one (terrestrial life faces a far more stressful range of environments than marine life (RAFF 1996)). This hypothesis is congruent with the fact that certain reptiles (i.e., crocodiles) show also a more evolved SNS (a first form of neocortex).

3.3 A new decoupling

Among all the changes that the appearance of vertebrate bauplans has conveyed, the reorganization of the NS in two separate parts was particularly crucial. As we have pointed out at the beginning of this part, the importance of this reorganization lies in the fact that it allowed a feedback between the development of more complex circulatory systems and an increase of neural concentrations in the brain. However, another no-less important consequence of this reorganization was the fact that the ANS has to be, to some extent, independent of environmental circumstances, and hence independent of sensorimotor activity, although coordinated with it. In that sense, whilst the SNS works according to complex decision-making processes, the ANS works according to relatively more simple thermostat-like reflexes, in order to maintain basic homeostasis in the organism (KANDEL 1995). This functional independence of the ANS is the fundamental element that will allow for a new line of evolution on the basis of a new body organization, since it frees the SNS from the increasingly complex tasks of controlling internal functions.

Thus, the ANS is dynamically decoupled[15] from the rest of the NS in the sense that it is a network whose components change independently of sensorimotor interactions. The ANS constrains the flow of neural information in such a way that the maintenance of the metabolism is ensured, together with a successful behavioral action. In turn, the SNS ensures, through the control of (sensorimotor) behavior, the recursive maintenance of the ANS[16]. Interestingly, the relation between these two decoupled neural systems is mediated through the metabolic organization (Figure 1).

But, actually, what is the reason for visceral control tasks to require the appearance of a functionally autonomous subsystem, instead of just a more complex centralized brain? When body organization became more complex, the NS had to take faster and finer tuned control over the organization of internal tasks. But since this system is implicated in the control of both movement and metabolism, as both tasks increased in complexity, the functioning became less and less efficient and increasingly unreliable. In fact, sheer coordinative burden reduction will require a new decoupling (this time within the NS) because it provides increased behavioral and thermodynamic efficiency. When a certain complexity threshold is reached, the only operative solution for controlling very different tasks requires a decoupling of the initial system into two different systems, whose respective dynamics each control a different kind of process (although this requires establishing a coordination system at another level).

The ANS, due to its relative autonomy from the external environment and due to certain physiological characteristics of its neurons and circuits (which are capable of becoming polarized and depolarized spontaneously) forms the basic drive from which initial activation of the NS is derived (Peters 2000). Now, this initial activation is necessary for the NS in order not to be completely driven by the environment. The organism needs to adapt to the environment, but sometimes it also needs to activate itself on its own.

An indirect consequence of this feature is a change in the functional relation of the NS with the body. As the ANS is sensitive to internal changes induced by stimulii originating in the viscera, it monitors need states that selectively control cognitive functions. This allows for a much more complex modulation of cognitive activities than in invertebrates. Thus, there is an indirect coordination between the ANS and the SNS through metabolism.

3.4 The functional role of emotions

Due to the fact that emotions arise at the level where this connection occurs, they play an essential role in reorganizing and selectively evaluating highly complex options of behavior. Therefore, emotions will play an important role in strictly cognitive tasks: they allow some kind of perception of hypothetical future consequences for the body according to different behavioral options. This means that the animal will be able to anticipate consequences of motor behavior on the visceral part of its body and general metabolism. This anticipation will also require the use of some kind of mental representation.[17] These representations or internal models are not directly connected to motor organs, but linked first to internal viscera by means of emotional phenomena. They will be fundamental for (the specification of) complex behavior and their role for behavior control seems to be in vertebrates much more complex and indirect than the role of neural configurations that control stereotyped behaviors in invertebrates. These representations will also require, in order to be translated into behavioral actions, some kind of higher order processing. Basically, it will be needed to evaluate possible consequences of internally anticipated behaviors, taking into account emotionally remembered or perceived experiences of the past. A similar idea has been pointed out by Bickhard (2000) who holds that emotions play a crucial role in handling uncertainty in highly complex environmental situations. According to this author, emotions would be a special kind of internal process, which consists of interactions with the animal's own internal uncertainty about how to proceed and to anticipate the interaction with the environment. Thus, in complex situations, the animal interacts with its own uncertainty, instead of directly interacting with the environment.

As we have already mentioned, the creation of two relatively independent structures in the NS requires new forms of coordination between them. Since the main control tasks of both Autonomic and Limbic Systems are related to the functioning of viscera, at least part of the relations between the SNS and the Limbic and Autonomic Systems is mediated by the viscera. Accordingly, the connection between the (nervous) system of the "interior" and of the "exterior" implies a constant feedback between (both structures of) the NS and the internal organs. As Damasio (1994) has pointed out, this coordination between the "cognitive" and the "visceral" NS implies an understanding of emotional phenomena as an ongoing feedback between the environment, the SNS, and the ANS, mediated by changes in visceral and metabolic states, so that the dynamics of each subsystem can be re-adjusted—with sufficient speed and precision—until a global viable interaction with the environment is reached, and so that these viable interactions become patterns to be remembered. Thus, according to this view, emotional processes happen not only in moments of stressful circumstances with high levels of arousal of the organism, but also at any time.

As Dennett claims (Dennett 1996), emotional mechanisms include simulating and rehearsing behavior trials not in the external environment, but in the internal environment of the animal, that is, in their own body. This process would generate emotional feedback signals to the brain which are used as evaluative mechanisms for those behaviors.

Thus, an emotional experience would typically start with the perception of an external stimulus (though can also be internal) by sensory regions of the brain (SNS). It is followed by some analysis by other SNS structures, regarding its stimulus qualities. From here signals are sent to limbic structures. These are relay structures from where other signals are sent through the ANS to the viscera of the body, such as the heart, stomach, etc. These signals have some pleasant or unpleasant consequences in the functioning of these viscera, which are signaled again to the brain. Here we have further analysis by SNS structures, and finally some kind of response to the original (external) stimulus (LEDOUX 1996).

Last, but not least important, external expression of emotions gives rise to the need of perceiving, interpreting and reacting to other organisms´ emotions (and hence, behaviors) thus contributing to a new mode of communicative and social behavior (SHEPHERD 1994). It will constitute the fundamental basis of nurturing behavior. It also plays an important role in predatory behavior as well, and in general in both competitive and collaborating aspects of social behavior. These kinds of behavior, at the same time, produce pressure for cognitive complexification. They are closely correlated with (and contribute to) the development of the vertebrate Limbic System (GLOOR 1997) and further in evolution, also to a special part of the ANS related to control of facial muscles (cranial or social autonomic nervous system (PORGES 1997)), which is very important for nonverbal communication (movement of lips, muzzles, scalp and external ear flaps, for example). This cranial or social component of ANS is developed in mammals.

3.5 Summary

Let us now summarize all these issues. We have intended to analyze how the decoupling within the NS itself enables a qualitative increase in the complexity of cognitive capacities in evolution. In the course of the evolution of vertebrates an increasing part of neural processing becomes decoupled from direct behavior control, because it is devoted to the internal visceral control tasks and to coordinate all this with a sensorimotor activity. Some time, probably when vertebrates were capable of complex and fast terrestrial movement and their brain attained a certain threshold of complexity[18], this neural activity devoted to the control of behavior through emotions became the basis of what will constitute the "mind", understood as a kind of slower, second-order neuro-somatic activity by means of which the animal is able to perceive a basic sense of self. This sense of self or basic awareness would be linked to new and more complex forms of coordination between the Limbic System and the SNS (EDELMAN 1992) or even involving the viscera (DAMASIO 1994 1999)[19]. Thus, instead of a fast, reactive, kind of adaptive agency, mind appears as a non reactive (anticipative) control of sensorimotor behavior, based on a kind of neural processing, which implies an ongoing feedback between the environment, the SNS and the ANS mediated by changes in visceral and metabolic states. This non-reactive kind of agency is probably a consequence of the fact that in the animal some neural configurations, instead of being directly used to control action, contribute to building internal models of reality (virtual interactions with the environment (COTTERILL 2001)). These internal models, assisted by emotional phenomena, allow for more complex modes of anticipatory behavior, like self-directed learning, and probably also for some form of awareness.

4. Concluding Remarks

In this paper we have attempted to travel from the most primitive forms of adaptive behavior until the earlier manifestations of the mind in animals, trying to understand from an evolutionary point of view the specific nature of cognition.

As we have argued, any form of life based on motility has to develop more complex forms of agency if, given sufficient time and conditions to evolve, its size increases significantly. But as a specific capacity, the origin of cognition is related with the functional organization of movement in multicellular organisms through NS, conceptualized as an internal subsystem supporting sensorimotor interactions, dynamically decoupled from metabolic processes. This decoupled system is necessary for the maintenance of these organisms through control of functional behaviors, but at the same time it is built, maintained and evaluated by the metabolic network. Cognition emerges then as a special kind of adaptability through macroscopic movement decoupled from metabolism (behavior). And this decoupled internal system, constituted by informational processes, is what supports the progressive emergence of a new kind of interactions: the cognitive interactions.

The entangled relation between the basic biological processes and the cognitive ones brings about a new, qualitatively different evolutionary process. Within this frame, the development of cognition appears as a strongly embodied process, where the potentialities and limitations of various basic body designs proved to be enabling or necessitating for further evolutionary development of new cognitive capacities, while others hit apparent ceilings. Cognition generates organisms whose maintenance is progressively more dependent upon their behavioral actions, which become, on their side, progressively complex. From this fundamental organization, increase in body size, among other factors, will lead to the development of new ways of decoupling affecting the NS itself, which imply different relationships with the rest of body organization. This new decoupling within the NS happens in vertebrate evolution, where a part of the NS, the Autonomic NS, controls viscera and indirectly controls metabolism, whilst the rest controls sensorimotor interactions. This second decoupling is going to be the fundamental element that has allowed for a new line of evolution on the basis of a body organization able to support versatile and rapid moving bigger organisms, and at the same time capable of allowing a self-sustaining process of encephalization producing the emergence of new levels of cognitive phenomena such as emotions and awareness. These complex forms of animal cognition, which can be labeled as Mind, require a globally integrated organization based on dynamically decoupled (informational) levels of organization.

We are still far from an understanding of the complexity of Human Mind. But we think that such a goal will require an understanding of the evolutionary processes leading to higher forms of cognition. We hope that this paper will contribute to this research.

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Notes

1 By autonomous here we understand a far-from-equilibrium system that constitutes and maintains itself establishing an organizational identity of its own, a functionally integrated (homeostatic and active) unit based on a set of endergonic–exergonic couplings between internal self-constructing processes, as well as with other processes of interaction with its environment (RUIZ-MIRAZO/PERETO/MORENO in press). Now, this concept of *basic* autonomy corresponds to an organism living in its environment, i.e., an agent. In this sense, only the whole organism is an autonomous system. However, besides this technical sense of the term, there is indeed a rather vague meaning of autonomy: autonomy as some degree of independence in the functioning of something with respect to another thing or process.

2 The size of eukaryotic cells is around 10.000 times bigger than that of prokaryotic cells.

3 In some cases, fast movement is accomplished thanks to symbiotic association with certain prokaryotes, like spirochaeta.

4 The case for plants with quick movement capacity is obviously a marginal case. Quick plant movements can be considered a consequence of coordination mechanisms that are not essentially decoupled from general metabolism. For example, in Dinee plants, rapid closing movements of the leaves involve changes in water pressure controlled by metabolic mechanisms (SIMONS 1981). As a consequence, this form of motility lacks flexibility and plasticity, and therefore there is no possibility of an evolutionary increase in the complexity of the motor response.

5 In a neural network certain physico–chemical events such as spikes and patterns of spikes can be described in informational terms for the following reasons: First, neural states can switch body states by configurational rather than energetic means (CARIANI 2001). And second, being dynamically decoupled from metabolic processes, these configurations can recursively operate on themselves, producing a kind of “formal processing”.

6 Henceforth we will use the term “autonomy” just in the sense of partial independence, in particular for naming some degree of functional independence of the Nervous System with respect to the metabolism. By no means we want to say that this (sub)system of an animal is autonomous in the same sense that the whole animal is.

7 These phenomena can be explained as the result of the development of the NS as a recursive network of informational patterns that control sensorimotor actions so as to achieve certain goals required for the survival of the organism. As has been shown in the last 20 years, simulations of the dynamics of interconnected idealized neurons (Neural Networks) can account for a variety of tasks considered as cognitive ones (such as categorization, memory, pattern recognition and associative learning). All these capacities are possible thanks to the almost unlimited potentiality for internal configuration processing that these neural networks possess.

8 In comparison with NS, the functioning of the neuroendocrine system is slower and more durable. As we will see in the next section, in certain animals, in addition to the neuroendocrine system, there is also a direct takeover by the NS of some body functions.

9 Other big invertebrates, such as the giant millipedes that existed during the mid Paleozoic, disappeared as soon as land predators appeared.

10 The basic way for the NS to control the functioning of the body is through the neuroendocrine system, which operates through highly specific substances (hormones) distributed by the circulatory system. Instead of the neuroendocrine system, which is based on diffusion and is largely distributed, a vertebrate's ANS is a centralized system which operates mainly through direct, fast neurally channelled control.

11 In certain big octopuses like the Red Octopus of the North Pacific, the brain can attain a considerably large size, containing more than 170 millions of neurons (WELLS 1978). However, the potential cognitive capacities of this increase in the size of brain are strongly restricted by the low conductivity due to the lack of myelin. Cephalopods compensate for this inconvenience by increasing the diameter of the axon, but this strategy precludes the development of more complex brains.

12 We cannot discard that something functionally similar to the ANS could have appeared in the evolutive history of invertebrates. However, the potential functional advantage of such invention would only be recruited if other changes in the organization of the body would occur simultaneously, so that a feedback between ANS and new, more complex bauplans were established.

13 Under the word Autonomic Nervous System some authors consider only the peripheral nerves that connect viscera and the central nervous system. However, we consider, following A. DAMASIO (1994) as well as SHEPHERD's (1994) ideas, the ANS as including the control nuclei for these peripheral nerves and we thus follow this critical functional division of the nervous system between the Autonomic (dedicated to homeostasis) and the Somatic, which is in fact the bulk of the NS and is more related to interaction with the environment by means of sensorial and motor phenomena. Some authors will even conceptualize both the Autonomic and the Limbic systems under one system.

14 However, this process was not an automatic result of the new bauplan, since it required the participation of many different causes (like, for example, the colonization of terrestrial niches). Thus, our point is that the new bauplan *permitted* the encephalization process, whereas the remaining ones, for different reasons, precluded this process.

15 Here again we can find a new form of dynamical decoupling because the two subsystems—ANS and SNS—can be distinguished by the asymmetry of the degree of connectivity and dynamic complexity within and between them, so that it is higher inside them than between; and 2) there are also distinctive differences on the rules governing their local dynamics (the neurons of ANS have the capacity of spontaneous polarization and depolarization).

16 Thus, along with the local decoupling already mentioned, at a global level there is an interaction between these two subsystems so that each one controls (directly or indirectly) the stability conditions of the other.

17 Though a serious analysis of the problem of representation is beyond the scope of this paper, the following is just a brief comment suggesting a direction for further exploration.

18 For reasons that are not yet well known, the mammalian line produced a significant increase in the neocortex. It has been suggested that during the long nocturnal period of mammalian evolution there was a growth in olfaction and a change in the thalamic pathway for visual processing, leading to a complexification of the neocortex (ABOITIZ 1992). This phylogenetic process was produced by exploiting the ontogenetic capacity of neurons for migration and formation of new pathways in the central NS (GERHART/KIRSCHNER 1997). Thus, according to these authors, it is possible that simply removing a constraint on growth may have been all that was necessary for neocortex evolution.

19 According to this author being aware of something (stimulus or own action) would be the process of linking the sense of self to that stimulus or action. That is, an animal is aware that its actions and perceptions are related to its own body. Thus, the animal needs a continuous feedback from viscera and other homeostatic detectors in order to have a sense of self, that is to be aware of the state of its own body, potential dangers to it, or its state of pleasure or need at any moment. So awareness means a bidirectional link, on the one hand towards the viscera and in general to the metabolic side of the body through emotional phenomena, and on the other hand to the environment through sernsorimotor coordination.

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Martin Brüne/Elaine Mulcahy

Exaptation, Co-optation, and the Evolution of Human Cognition

Abstract

The term 'exaptation' refers to the observation that adapted features or evolutionary by-products may be taken over or 'co-opted' in order to carry out new functions unrelated to the original ones, thereby increasing the organism's reproductive success. In this article, we question whether the concept of 'exaptation' is useful for evolutionary psychology and human cognition. While there are indeed examples of psychological mechanisms that may loosely be interpreted as 'exaptations', e.g., 'theory of mind' and language, we nevertheless propose not to use the concept of 'exaptation' in evolutionary psychology and to redefine 'co-optation' of evolved psychological mechanisms by culture-dependent novel cognitive skills. Furthermore, we suggest strengthening the association of evolutionary psychology with other neuroscientific fields such as neurobiology and brain imaging in order to gain further insight into the proximate and ultimate mechanisms involved in human cognition.

Key words

Exaptation, co-optation, recruitment, theory of mind, evolutionary psychology.

ROUGHLY 20 YEARS AGO the terms 'exaptation' and 'co-optation' were introduced into evolutionary biology and psychology primarily to explain the existence of characters in species that seemingly have not been a direct product of natural and sexual selection (GOULD/VRBA 1982). According to GOULD and VRBA's original account (1982) 'exaptations' represent present features of adaptive significance that took over or 'co-opted' either (1) adaptive characteristics that have evolved for other 'purposes', or (2) evolutionary by-products (so-called spandrels), in order to carry out new functions, thereby increasing the organism's reproductive success. The way they used the term 'exaptation' implied, however, that the structures in question have *not* necessarily undergone further modification after being 'co-opted'.

Birds' feathers, for instance, are widely acknowledged to provide a plausible example of the distinction between *ad*-apted and '*ex*-apted' functions, and are consequently the most re-iterated one in the literature. Feathers probably evolved in reptiles in the first place for insulation. They also might have served as sexual signals. (Note that 'evolved for' and 'purpose' are only shorthand and do, of course, not imply teleology.) Only much later were feathers used for flight. GOULD and VRBA (1982) suggested, therefore, that the 'co-optation' of an evolved characteristic for another function would better be termed 'ex-aptation'.

The term 'exaptation' has been accepted to be useful insofar as it replaces the old expression 'pre-adaptation'. The latter can be misleading because it can easily be mistakenly interpreted as suggesting that evolution can 'foresee' future functions that certain characters may take over.

In his book "Darwin's dangerous Idea", DENNETT (1995), however, criticises the entire concept of 'exaptation'. He argues that any evolved character might be labelled 'exapted', since every adaptive process is essentially linked to a change of the character's original function by natural and sexual selection at some point during its evolution. Oddly enough, he nevertheless inconsistently uses the term 'exaptation' throughout his book.

More recently, the 'exaptation' debate has re-emerged with respect to its useful application to human psychological mechanisms. GOULD (1991) has elaborated on the original 1982 paper, suggesting that the human brain may be regarded as 'the chief exemplar' of an exaptational organ and that human psychology critically depends on the brain's capacity to 'co-opt'. In his view, such diverse faculties as reading, writing, religion and fine arts could best be termed 'exaptations', which would imply a broadening of the concept of 'exaptation' to a variety of culturally evolved phenomena. In a similar vein, several scholars have recently proposed that, for instance, human language emerged via 'exaptation' of pre-existing neural structures in the brain (LIEBERMAN 1991; WILKINS/WAKEFIELD 1995) or of psychological mechanisms related to 'social calculus' (CALVIN/BICKERTON 2000).

Even more obfuscating, CUZZILLO (1991) has suggested that some psychopathological symptoms, e.g., neurotic mechanisms, may be explained in terms of a 'reversed exaptation'. For example, 'repetition compulsion', that is, an individual's urge to repeat certain types of behaviours that are clearly maladapted in a non-evolutionary (proximate) sense, may reflect the 'ex-aptation' of a novel capacity (symbolic representation) to carry out a phylogenetically old pattern of behaviour.

These accounts contradict the position of many evolutionary psychologists who instead propose that the brain consists of a set of evolved psychological mechanisms that carry out distinct evolved functions on a modular or domain-specific basis (e.g., COSMIDES/TOOBY 1992).

Following these lines, BUSS et al. (1998) have reasoned that GOULD's claim lacks consistency because his examples (1) fail to demonstrate a 'special design for the hypothesized function', (2) lack evidence for a 'later co-opted functionality', including the maintenance of the new function in the population, and (3) do not document a distinct original adaptive functionality.

Whereas BUSS et al. (1998) do not deny the existence of 'spandrels' or evolutionary by-products of adaptations in general, they argue that the 'co-optation' of an evolutionary by-product to serve an adaptive function *in the present* ('exaptation') deserves confirmation (1) of the adaptation from which the by-product emerged and (2) of the *secondary adaptational process* involved to alter a by-product into an 'exaptation'. Thus, according to BUSS et al. (1998), whilst 'exaptations' in human psychology are not considered impossible, their existence would be hard to prove if the rigorous criteria of scientific testing mentioned above were applied.

In this ongoing debate SKOYLES (1999) has tried to reconcile these divergent positions. He argues that neural plasticity could have evolved in humans as an adaptive function in fine tuning development and may consequently underlie, at least in part, the brain's capacity of 'exapting' evolved brain mechanisms. Blind persons for example, are able to make use of their visual cortex for tactile and auditory purposes, e.g., for Braille reading (PASCUAL-LEONE/TORRES 1993). That is, the original design of connecting the eye with the visual centres of the brain may be 'co-opted' by other perceptual modalities (O'LEARY/SCHLAGGAR/TUTTLE 1994). SKOYLES further reasoned that the acquisition of novel skills related to 'technology' (in a broader sense), such as reading, mathematics and computer programming might also fulfil BUSS et al.'s requirements of a genuine 'exaptation' through neural flexibility (SKOYLES 1999).

In this article, we (1) propose that many of the pros and cons of the claim that the concepts of 'exaptation' and 'co-optation' are useful tools to comprehend human psychology relate to insufficient definitional criteria of the terms. In particular, the distinctions between 'exaptation', 'co-optation' and the process of 'recruitment' appear to be vague and partly confused. (2) We provide evidence for the existence of human cognitive 'exaptations' and 'co-optations' – analogous to the one of birds' feathers – that fulfil BUSS et al.'s (1998) criteria. (3) At the same time we question, however, that the concept of 'exaptation' may significantly contribute to our understanding of how the human mind actually works and whether human psychological 'exaptations' in the strict sense do exist at all. We therefore conclude to refine the terminology in order to avoid further confusion.

'Theory of Mind': An Example of Psychological 'Exaptation'?

One of the hallmarks of human cognitive evolution is probably the emergence of metarepresentational abilities. The capacity to infer mental states in terms of own and other individuals' dispositions and intentions, commonly referred to as having a 'theory of mind' (PREMACK/WOODRUFF 1978), is essentially linked to the ability to represent a representation of another's mentality – metarepresentation (e.g., SUDDENDORF/WHITEN 2001). Many studies have dissected the cognitive architecture of a 'theory of mind module' (LESLIE 1987). They have revealed that 'theory of mind' emerged gradually in hominoid evolution, as indicated by the presence of basic theory of mind capacities in great apes (e.g., BYRNE 1995), and that the maturation of this cognitive capacity during child development follows distinct steps of acquisition of expertise in this domain (e.g., BARON-COHEN 1995).

There is broad consensus that 'theory of mind' probably emerged due to a need to be capable of coping with increasing complexities in the social environment (BROTHERS 1990). For example, this kind of social intelligence could have evolved as a response to the problem of reciprocal altruism, which may have induced an 'armsrace' of deception and cheating detection (but also co-operation, trust and empathy) in order to maximise an individual's social and eventually reproductive success (TRIVERS 1971; COSMIDES/TOOBY 1992). In other words, 'theory of mind' is certainly the product of natural and sexual selection.

Now, with respect to the 'exaptation' debate it is important that a number of studies point to the fact that the cognitive architecture of 'theory of mind' has evolved from a system for representing and attributing meaning to biological motion, i.e. 'intentions' (which does not necessarily involve awareness; FRITH/FRITH 1999). In an intriguing series of experiments CASTELLI et al. (2000) have shown that the brain areas involved in 'theory of mind', namely the medial prefrontal cortex, the superior temporal lobe and the temporal parietal junction, are specifically active in detecting goal-directed movements compared to random movements of objects. These findings could, therefore, be interpreted in a way that suggests that the cerebral representation of the cognitive capacity to impute mental states to others ('theory of mind') 'exapted' an evolved mechanism for monitoring the behaviour of other creatures and attributing 'intentionality'. In other words, the case of 'theory of mind' exactly parallels the well-known example of birds' feathers, hence representing an example of 'exaptation' that complies even with the rigorous standards proposed by BUSS et al. (1998). (Notably, this kind of research also establishes a critical and desirable link of evolutionary psychology with neuroscience by shedding light on the brain areas involved as revealed by functional brain imaging.)

Similarly, some aspects of the evolution of human language, in particular the syntactic qualities of language, have been interpreted in favour of a 'co-optation' of existing neural structures relating to motor control (LIEBERMAN 1991; WILKINS/WAKEFIELD 1995) or 'social calculus' relating to reciprocal altruism (CALVIN/BICKERTON 2000), although the explanatory power of 'exaptation' regarding language has been criticised as being 'ad-hoc' and 'arbitrary', lacking a concise definition of the concept (BOTHA 2002). As with 'theory of mind', human language may well be interpreted as 'exaptation' of a neural system that in the first place evolved as part of gestural communication in monkeys, where so-called 'mirror neurons' selectively fire when monkeys observe or imitate the behaviour of a con-specific (RIZZOLATTI/ARBIB 1998). This type of cells has also been found in the human ventral premotor cortex and in Broca's area, which is indicative for language having evolved from gestural communication (RIZZOLATTI/FOGASSI/GALLESE 2002).

GOULD and VRBA'S (1982) original account implied, however, that 'exapted' functions have *not* necessarily undergone further modification. Also, despite fulfilling BUSS et al.'s criteria, which allow for '*secondary* adaptation', the brain structure's involved in 'theory of mind' or human language almost certainly have undergone further modification. Therefore, they do not qualify as 'exaptations' in the original sense, and are actually better defined as ad-aptations. Due to the confusion in the literature as to what 'exaptation' and 'co-optation' really mean, we propose redefining the terms as follows:

Distinguishing Exaptation, Cultural 'Co-optation' and 'Recruitment'

'Exaptation' versus cultural 'co-optation'

If, for a moment, we acknowledge that 'exaptations' are evolutionary products that have been shaped by natural and/or sexual selection *after* having first co-opted an evolved function or by-product, then, as such, they would qualify as genuine *ad*-aptations and need not be specified as being different from adaptation. Moreover, since we claim that with respect to evolved psychological mechanisms, no 'exaptation' of an evolved feature exists that has not undergone further modification, the term becomes scientifically inadequate.

In contrast, reading, writing, religion and arts are clearly products of cultural evolution. However, although they have probably not induced changes in evolutionary design of the psychological mechanisms or brain structures involved, they do not meet the requirements of 'exaptations' in BUSS et al.'s terms, nor the stricter definitional criteria we have proposed. Thus, BUSS et al. (1998) rightly criticise that such evolutionarily novel abilities may at best be termed 'human co-optations'. We suggest that the term 'cultural co-optation' may more accurately describe these novel capacities. Cultural 'co-optations' are functions carried out in the present using adapted structures that evolved in the past. Or, as BUSS et al. (1998) put it, "adaptations exist in the present because their form was shaped in the past by selection for a particular function."

As the example of reading may illustrate, cultural co-optations do indeed make use of evolved cognitive mechanisms, e.g., eye tracking, gestalt perception, and so forth. Notably and most importantly, the *intact* functioning of the evolved mechanisms is indispensable for cultural 'co-optation' to take place. That is, if there are dysfunctions of evolved mechanisms as is the case in some forms of dyslexia, the 'co-optation' of a functional system for cultural purposes *per se* fails or is at least impaired. Interestingly, STEIN (2001) has recently argued that some people, who in a modern environment suffer from dyslexia, might have had selective disadvantages in the evolutionary past due to a failure of the underlying evolved function. That is, dysfunctions of a certain type of cells responsible for the fine attunement of eye movements and tracking of moving objects (found in some people with dyslexia) might also have compromised the detection of predators (STEIN 2001).

Cultural 'co-optation' versus 'recruitment'

For the sake of a clearer terminology, we briefly readdress here SKOYLES' (1999) argument of neural plasticity as 'exaptation'. Whereas we do not call into question that neural plasticity and behavioural flexibility do provide potent selection advantages and probably represent the biological basis of cultural evolution, the assertion that neural plasticity *per se* supports 'exaptation' does not hold. Whilst there certainly has been a general tendency in human evolution towards more openness of psychological mechanisms to learning and hence flexibility, the assumption of a specific 'multi purpose exaptational propensity', as we would call it, of a given (evolved) function (i.e. neural flexibility) is hard to test scientifically (or to refute), although neural flexibility may in a general sense be indispensable for all kinds of cultural '*co-optations*'. Rather, the example, given by SKOYLES, of the extension of the cerebral representation of hearing and Braille reading in blind individuals into the primary visual cortex (O'LEARY/SCHLAGGAR/TUTTLE 1994) may better be accounted for by 'recruitment'.

Recruitment is distinct from 'co-optation' because it represents the extension of a *pre-existing* function into *adjacent* neuronal fields or a summation effect of the function in question (as in muscle contraction), but not the take-over of a given function for a *qualitatively* distinct 'purpose'. Hence, if Braille readers extend the somatosensory field of their fingertips into brain areas that are typically used for vision, this would involve a change of sensory modality in the visual centres (feeling instead of seeing), which is not the case in cultural 'co-optation' as argued in the case of reading. Cultural 'co-optation' involves the emergence of a *new* function that uses pre-existing neuronal mechanisms.

Similar to cultural 'co-optation', however, the pervasiveness of 'recruitment' may partly depend on ongoing use of the recruited structures. In a functional brain imaging study, KARNI et al. (1995), for example, found that complex motor tasks practiced by adults over several weeks led to a two-phase pattern of increasing activation. In the first practicing phase (habituation), they observed that the size of the activated area of the motor cortex actually decreased, while in the second phase (enhancement) continuous practice induced a recruitment of additional motor units as revealed by fMRI. KARNI et al. (1995) concluded that this enlargement of cortical representation might be due to unmasking of pre-existing connections between populations of neurons. Moreover, even after stopping training this enlarged area of the motor cortex persisted in two of six individuals over a 21-week period. Although, over time, *in*activity would normally reduce the size of the cortical representation of a respective function, these experiments indicate that the retention of recruited patterns of neuronal activation may in fact be quite robust (KARNI et al. 1995).

Conclusions

In line with BUSS et al. (1998), the term 'exaptation' is of little use in human psychology and psychopathology, because 'exaptation' by no means would abandon the question of adaptation of the new function. Moreover, although we believe that 'theory of mind' and language do qualify as 'exaptations' of a pre-existing human psychological mechanism according to BUSS et al.'s (1998) criteria, like birds' feathers they, too, have undergone further modification. In fact, there is no case of an 'exaptation' on the molecular, physiological or psychological level where the originally 'co-opted' function has not undergone modification due to natural or sexual selection pressures. Therefore, we deem the term 'exaptation' superfluous in describing evolved psychological functions. Likewise, applying the term 'exaptation' to psychopathological symptoms and syndromes rather obscures our understanding of psychopathology in evolutionary terms. The various kinds of psychopathologies may better be accounted for as trade-offs, designflaws or dysfunctions of evolved psychological mechanisms (e.g., BRÜNE 2002) rather than as a reversal of adaptive processes via 'co-optation' of novel functions for phylogenetically older 'rigid' behaviours.

In conclusion, we suggest not to further use the highly problematic term 'exaptation' in evolutionary psychology. Besides its definitional shortcomings it, in the worst case, could also misleadingly suggest a discontinuity of human cognition and cognition in non-human primates and other animals and might therefore hamper progress in this emerging new field. The use of the term cultural 'co-optation' (as distinct from recruitment), in contrast, should be reserved for evolutionarily novel and culturally emerging capacities that make use of evolved psychological mechanisms, of which the fitness enhancing potential to the individual is currently unknown.'Co-optation', in contrast, may happen in the form of carrying out culturally evolved functions by using evolved psychological mechanisms. Whether such cultural 'co-optations' have adaptive significance in a way that they enhance the inclusive fitness of the individual is a question that cannot be answered in the present. In this respect, evolutionary psychology is a historical approach and cannot predict future consequences of current cognitive functions (BUSS et al. 1998).

Finally, the story of 'exaptation' may tell in addition that evolutionary psychology ought to be linked more tightly to other avenues of neuroscience, such as neurobiology and neuroimaging, in order to explore the actual representations of evolved psychological mechanisms in the human brain.

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Rupert Riedl

Systems Theory of Evolution[1]

Abstract

Contemporary theory of evolution is conceptually contradictory. Against morphology and palaentology, demonstrating directedness and internal coherence in evolutionary processes molecular genetics claims the role of chance and external selection as sufficient explanation.

The complexity of life leads to expect mutual or feedback causality. If the accidentally originated couplings of genes coding for phenes which are functionally dependent, consequently successful and stable, the functional relation within the system will be stepwise reproduced, leading to an imitative epigenotype.

This has two consequences: (1) Systems—even these with high complexity—remain adaptable, (2) The arising functional as well as genetic brudens (constraints) lead to a directed and ordered evolution of organisms.

Key words

Morphology, molecular genetics, Systems Theory, recursive causality.

What Do We Need From Systems Theory?

As student of Bertalanffy in the late forties, Systems Theory was understood as a part of 'theoretical biology'. The same position was taken by Paul Weiss, and we felt, that what is new in Systems Theory is to apply 'recursive' or 'recurrent' causality; that is to say, that every effect in living systems, in some way, feeds back to its own cause. An interwoven causality was the new perspective, in opposition to linear causality thinking, as supported by positivism. This was superseded by 'pragmatic reductionism', expecting to explain complex systems sufficiently from its constituents, as we expect to understand our every day life and our business world.

In the last fifty years Theoretical Biology gained different perspectives in different universities. Systems theory became commonplace, except that the necessity of adopting recursive causality did not attract much attention.

The metaphysical backgrounds became visible by comparing the two positions. If the 'big bang' made everything, including the earth, and the 'blue print', nothing but genetic instruction made men, than man is either planned by the creator, as Teilhard de Chardin derived from directed evolutionary pathways, or a senseless product of accidents, as Jacques Monod suggested, deriving it from complex functions put together by chance effects.

If recursive causality is adopted, evolution, putting it in short, seems neither to be of planned prestabilized harmony nor chaotic, without harmony. Evolutionary principles of self-organization allowed a post-stabilized harmony to develop, producing sense and purpose with its creatures, and allowing even god to be revealed or sensed as a necessary hope.

Reasons to Adopt the Systems Theory of Evolution

First: We are in many respects genetically well prepared to come along with our daily life. This is trivial. It is less trivial to state, that in others we are not: such as being confronted with large numbers and dimension, emergent processes, and complex systems. In problem-solving strategies the decision-making tree suggest us to expect and select regular, deterministic, indication-dependent, functional, and linear processes; while in complex systems many processes are irregular, indeterministic, independent from indications, and almost all of them not linear (Brehmer 1980). But the above simplification is itself biologically justified (Riedl 1992), because in many cases, particularly in our ancestors, quick decision was more important than to disentangle complexity.

The environmental problem is caused by a too simple, linear causality concept of profit maximization. After atmosphere, sea, forests, and soil have taken so many strikes from man, the biosphere starts to beat back by ozone holes, temperature and sea level rise, and deteriorated grounds. The way we see us in the universe depends much on how we grasp our Genesis. The theory of evolution must lay new grounds.

Second: The synthetic theory of neo-Darwinism, as it still provides the conceptual grounds of textbooks is not wrong, but not complete. I will elaborate on this.

The Gaps of Today's Perspectives

Many writers of modern texts avoid to discuss open questions. It seems as they take it necessary to furnish facts for exams. This may increase the edition, but obscures the view and does not encourage critical perspectives.

The process of evolution is taken linear. The center are the DNA strands, the 'blue print', suffering accidental mutative changes (true physical mistakes). By transcription and translation, including dominance, and interchange of alleles, gene pool size, and gene flow are the strands are producing proteins, and, in a way, forming organisms, by allopathic speciation new species, and by environmental and intraspecific selection the animal kingdom. This straightaway concept has somewhat softened by the metaphor of an 'epigenetic landscape', as Waddington (1957) has put it, and the growing knowledge of cascades of the action of regulatory genes. It however remained puzzling whether or not epigenetics may be still part of the above linearity.

Deviations of the old patterns have appeared: as first elaborated by Gould 1977, Alberch 1983, Raff/Kaufman 1983, but they did not change the mainstream.

First Set of Open Questions and Unexplained Phenomena

What allows complex systems to still be adaptable? May we expect an evolution of evolutionary processes, and if so, what may be the consequences?

General thoughts about complexity

The genome of a garden snail possesses about 10^8 base pairs, $3.3 \cdot 10^7$ triplets. They become translated into 21 amino acids, what compares much with our 24 letters. Such an amount of letters, for example, is held by the 20 volumes of 'Encyclopaedia Britannica' ($2.5 \cdot 10^7$). Assume a point mutation, changing one triplet, would improve the fitness. Should we then expect that the correction of a single letter in the 'Encyclopaedia' could improve its success on the market?

In addition, to find this very base pair or letter and change it to the right one by blind try and error, would need approximately 10^7 (ten million) new editions. Admit, that no comparison fully satisfies. But let us go only one step further to get to the point. Few words alter its meaning by changing one letter only. Assume a short word, such as 'and' should be changed in 'for'. No single change (such as: fnd, aod, anr) would improve the matter. Certainly the three changes could coincide (Simpson already in 1955, made us aware of this). But in our case this would need 10^{21} attempts. An impossibility both for the snail and the Encyclopaedia.

Adaptability of complex systems needs larger units; as we assemble letters most functionally to words and sentences. General thoughts about handling complexity do not indicate what form this lager unites may have. In principle they could have any form. A hierarchical pattern would be reasonable, because deposition and searching deposited information would go with the logarithm of two.

Although this insight does not describe a possibility but a necessity, not much has been gained. The first crucial point is to come.

Documents for lager gene units beyond neo-Darwinian explanation

Gene regulation from Lac-operon to homeobox genes underline the existence of such systems. But my point is, that morphological insights allows to foresee the principle behind. I put the documents in seven groups. None of them is a topic of the synthetic theory.

(1) *Synorganization* and *co-adaptation* makes us expect an intermodality of changing organs. If a mutation of a longer neck in giraffes is selected for, it can not be the backbone unless the spinal chord and all the rest elongates.

(2) Heteromophoses demonstrate that even in the case of a somatic mutation in an regeneration bud, a super-gene finds all the somatic genes, which are necessary to form a widely complete, complex organ on a wrong place: such as an antenna instead of an eye. This phenomenon is one among a group of facts which has led Darwin (1875), in his theory, to speculate on the existence of inner mechanisms, which are neither explained by Lamarcks theory of active adaptation nor by his own theory of selection.

(3) *Homeotic* or *System Mutants* demonstrate the same in gene mutants. In addition we see, that e.g. legs can be produced in different completeness and

on several places, but only with leg characters and on such places, where appendices (extremities) have been foreseen: *antenna, arista*, mouth parts. The super-gene must be switched on to reach more or less of the pertinent structures, but only those which belong to a leg, and the relation to former appendices must have to do with the phylogeny of the fly.

(4) *Cartesian transformation* (D'ARCY THOMPSON 1942) made evident that gradients of alteration must direct neighboring parts to change all, e.g. bones of a scull, to flatten, to elongate, or to shorten it harmoniously.

(5) *Regeneration*, such as rebuilding a limb in a salamander, a tail in a lizard, even to restore the layers of a wounded part of the skin, indicates that the necessary instructions open only in pertinent positions.

(6) *Phenocopies*, ontogenetic alterations by disturbances, tell us time and sequence in which master-switches act; namely in the sequence of phylogenetic innovations.

(7) The term *Homeosis* covers most phenomena listed in 1–6, we take it as indication for an inner order, built primarily on the basis of the construction and design of the organism and its history.

Summarizing, we may foresee specific structures in the development of the epigenetic system; their form will correspond to functional units of the phene system. I expect a mechanism (1–3) which makes, in an hierarchic pattern, such genes interdependent, which code for functionally interdependent penes, forming (4) gradients over (5) the sequence of the phylogenetic steps of innovation of the organism, depending primarily (6–7) on the design of the history of the organism itself, of passed, and less on present fitness conditions.

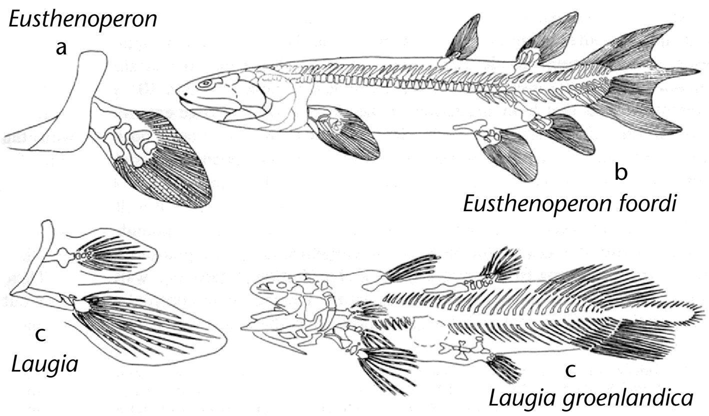

Figure 1: Early *crossopterygian* (*Sarcopterygii*, lobe-finned fishes). (a–b) Order *Osteolepiformes* (Middle Devonian to Lower Devonian). (c–d) Order *Coelacanthiformes* (Middle Devonian to Recent). Note the two pairs of articulated fins which nevertheless have dissimilar bony axes. In *Laugia* the second pair has moved far forward (from RIEDL 1978, p155)

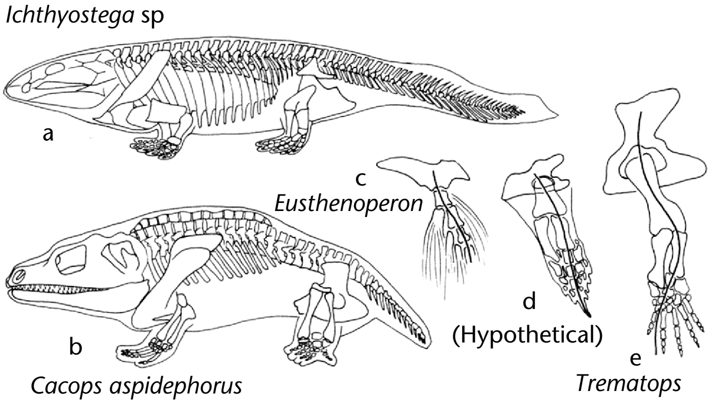

Figure 2: Early and primitive amphibians (*Labyrinthodonts*) and the theory of the evolution of limbs. (a) A representative of the *Ichthyostegalia* from the Upper Devonian. (b) A temnospondyl (Lower Carboniferous to Upper Trias). (c–e) Phylogenetic transition from the pelvic fin to the posterior *pentadactyl* limb. (c) Fin of an osteolepiform. (e) Posterior limb of a *temnospondyl*. The probably homologues bones of the limb axis are connected by a line. After GREGORY (1951) and MÜLLER (1966) (from RIEDL 1978, p156).

A model for linking genes coding for functionally linked phenes

Almost all features of an organism, that is all which are functionally adjoining, are interdependent. This interdependence develops with the new features and with approaching each other to form a new function. A very simple example can be given by the development of a joint.

Take a Devonian fish, such as an *Eusthenopteron* and a *Laugia* (Fig. 1), the *Stylopodium* of the front fins are very different in shape, compact in *Eusthenopteron*, slender and elongated in *Laugia*; and they do not really form movable joint with the *Zeugopodium*, with special muscles and ligaments, as we know from recent *Sarcopterygii*. They simply approach each other, making the fin both stiff and flexible.

In upper devon and lower carbon the joint is made, as in an *Ichthiostega* and a *Cacops*, and the usual theory (Fig. 2) lets us expect, that the new close contact between *Stylo* and *Zeugopodium* corresponds to the very precise operation joint of our elbow.

In *Eusthenopteron* and *Laugia* there is still much freedom in the form of the *Stylo* and *Zeugopodium*. Probably length and breadth of the approaching parts where independently coded by different genes. There is at least no need and no indication that they where under a common command.

The chances or speed of adaptability

Since we will soon run into very small numbers, let us be generous, take a high mutation rate of each feature (10^{-5}) and a high probability (10^{-1}) of changing a phene in the right sense; simply make a feature longer, shorter, more compact or more slender. Already a population of 10^6 individuals could expect one adequate change in each generation.

Now: what will happen if two front parts of bones approach each other forming the function of a demanding, precise working joint as in our elbow? If adaptation to new behavior requires to broaden the joint: this would work only if socket and head of the joint would change at the same time in the same way. We had this problem before. It is possible, but one has to wait remarkably longer. Under the given assumption the probability would decrease to about 10^{-12}; with other words our population of 10^6 specimens would have to wait 10^6 generations to expect this.

Today we know that many genes are related, e.g. put under the domain of an operator gene. The operator locks and opens by regulator molecules. We are also informed, that the number of such master gene systems has increased remarkably in the path of evolution; much more than the number of structural genes. No general model seems to be at hand to day to explain how such master genes develop and how they assemble the structural genes which they direct. But no doubt, they have developed, even in sub- and superimposed, maybe in a hierarchical order; but again under the blind condition of try and error.

It is however, in my question, of second importance how they develop. The question I raise is: which of them will be refuted by the production of a subvital or lethal mutant, and which will be successful and spread in the population. Those mutants which hinder necessary adaptation will slowly die out in a population; those which speed up adaptation will be preserved and spread within the population.

Take our example of forming a joint; and remember, that all the processes are meant to act by pure chance. If genes become linked which code for length and breadth of one of the two bones, this may do good for the bone. It could shrink or strengthen in proportion. But it weakens the joint. If however genes become linked which code for the shape of socket and head of the joint, the success would be remarkable. If we admit that the chance of this regulator gene to make the right change corresponds to other genes, than our population could expect the adaptation of the joint in each generation. It would not have to wait a million generations.

In an evolution that also competes for the speed of adaptation, the success would be as 10^{-12} to 10^{-6}, a millionfold. But even if the probability, that such a master gene develops may be a hundred thousand times less likely than that of a structural gene. The above sketched process would still be advantageous, selected for, and fostered in the population.

A feedback causality, or how to lose friends

Until this point of my story, some of my fellow biologists used to follow. They may have found this game of numbers not really necessary or enlightening, but the collection of morphological facts (Riedl 1975) was appreciated. A hundred reviews where mainly friendly, surprised to excited. My fellow evolutionists, later on, did not know what to do with it. Now, where is the problem?

Where the problem lies

Allow a personal remark to minimize the search of my possible error. Ernst Mayr, that time almost a fatherly friend, wrote me a flattering letter, stating in summary, that no further evolutionist will ever find it possible to bypass this contribution. In the following time, when he may have had a closer look, he himself never cited the book. At a personal conversation of feedback causality ten years later, Ernst, who could have afford this, become furious, and I had to learn: "There is the blueprint! And the blueprint makes everything!"

In a way, we come back to metaphysics. Particularly whether we can expect to explain even complex systems in a straight away linear causality, as in front of a box of children's bricks putting the tower up and then strip it carefully from the top.

What happens, when genes by chance are linked coding for phenes of opposite, or, in contrary, of interdependent functions? The first group will produce impediments, the other much success. What, by this way, happened to the genome? Something will be put and preserved in its structure which has to do with functional interdependencies of its products.

What kind of a feedback should this be?

In our example of a joint, a structure is put into the epigenetic system which corresponds or stands vicarious or representative for a specific phene; a joint. No epigenetic system coding for a joint was before in the genome, because there was also no joint in the phenes. Shall we say: the genome has 'learned' what a joint is? This is, maybe, saying to much. Nevertheless, if the model is accepted, we can expect, that assumable all or at least most of interdependencies of the phenes may have left their traces or marks in the epigenetic system.

How can we now label such a transport of information? The transformation from the phenes is obviously almost entirely chemically coded; from translation up to final most inductive processes. The feedback is obviously not. I have used the term 'by stochastic processes'. But this sounds rather vague. However, what label one may prefer, I have no doubts, that this feedback of information transfer exists, because it explains the puzzling seemingly different phenomena I listed above all together.

Lamarckism coming through the backdoor?

Fellow biologists who disliked this idea (RIEDL 1975, 1977) took it as an obscured or camouflaged lamarckism, sneaking environmental conditions into the genome. This has never been published but was laboratory gossip, good enough to put the complicate matter aside.

Of course, the last word about fitness is always spoken by the environment. But quite another question is which feature of the organization of an organism is free for adaptation to improve fitness. As soon e.g. an outer skeleton is optimized, there is no way to change it to an inner skeleton, although fitness, in many cases, would improve remarkably by such a change. And such patterns of fixations go deep into the whole organization. All mammals, with only two exceptions have seven collar bones, although giraffes would do better with more and dolphins with less; in the first case they are maximally stretched, in the later extremely compressed and widely fused.

After LAMARCKS conception the genome would actively 'learn' from the environment, keeping adaptability assumable extremely open, and dissolves patterns of order. In contrast, after my conception, the genome 'learns' only from its own products, keeps adaptability in complex systems for new characters, but reduces adaptability for old characters dramatically. It produces order in living organisms.

What can be explained?

Taken a hierarchy of *epigenetic unites,* corresponding widely to the hierarchic patterns of the phene system: If they are coding for large functional interdependencies of the organism, this explains (1) synorganization; coding hierarchically for a hierarchy of organs and organ parts, acting from somatic and germ cells as well, explains (2, 3) heteromorphoses and homeotic mutations; coding for subunits being balanced by superimposed units, this explains (4) Cartesian transformation; genes of somatic cells coding from large organ systems to small damages of tissues, explains (5) regeneration; being switched on in a sequence of developmental steps, explains (6) phenocopies; and if one takes all this actions forming 'inner order' in development together, this explains the overall principle of (7) homeosis in development.

Summing up: we expect all the pertinent functional principles of the phylogenetically passed fitness condition copied by feedback causality. The epigenetic system of each stem of organisms, WADDINGTONS 'Epigenotype' is an 'Imitatory Epigenotype' (RIEDL 1977).

Wagner's corridor model

A concept, symmetrical to mine, has been developed by Günther WAGNER. I started from morphological features deriving structures of the epigenetic system; WAGNER started from gene structures; namely from pleiotropies. Taken a corridor, along which the genome of a population is forced to climb a hill of fitness, much of the success will depend on the pleiotropic genes.

If the two, or more, phenes for which such a gene is coding, point in the upward direction of the corridor, then this gene will bring advantage to the increase of fitness and spread within the population; if the contrary is the case, one phene being changed in the right way, the other not, this gene will not have success in the population.

The result is similar to mine; those multifunctional genes which code for phenes, which need to change into the same direction to increase fitness, will be selected (see WAGNER e.g. 1983, 1988).

Confirmations of dependent origin's for our concepts are now coming mainly from the sides of molecular geneticists and developmental biologists; but this may not be the topic of this article.

Second Set of Discussed Problems and the Common Principle Behind

As the first side of the coin my theory had to develop a model by which it may come to find complex systems still adaptable. The second side of the coin holds basically also unexplained phenomena, or such, which do not share a common or overall explanation. They are the consequence of complex systems retaining their adaptability.

They have to do with four large groups phenomena (A–D): of 'old patterns', macro evolution, morphology, and systematics; in principal with directedness, order and predictability in evolution. To make clear, why the second set is a consequence of the first, I may add a metaphor.

The tale of the two blind gamblers

Two blind gamblers, a black and a white one, play dice in front of the king. Each has at he beginning two dice. One is red the other yellow. They are allowed to do with the dice what they want, except, of course, it has to be done blind. The king, at the beginning, will honor the 'double-6'; and he will tell the winner when this occurs.

The game stands for competition, each gambler for a gene pool, the dices eyes for mutation, the king for environmental selection, and the profit for fitness.

Both throw their dices, knowing, that, in the long run, they will have success within about 36 throws. As soon the white gambler learns about his success, he glues the dices together (Fig. 3). He will win from now on at least every 6th time. The black gambler will lie remarkably behind.

Now the king alters the role, honoring red-6 yellow-2. The black gambler (the unspecialized genome) will stay with his slow success. The white will not win anymore as long he does not get his two dice apart.

Assume the game gets more complex to four and eight dices honored is the 'quadruple-6' and the white player manages to get the four stepwise up, than he will still win every sixth time, while the black falls back from 1/36 to chances of 1/1296 to 1/1,679,616. But if the king changes the game again, also will the white come into troubles.

With growing complexity, the black will again fall back with his speed of adaptability, and under each condition of the environment, the white is all up, as long the conditions are not changed. The black will slowly assume to organize his dices, the white one will have to stay what he has, and rather search for a better environment. One can not cheat probability unless on pays back in reducing further ways of adaptability. This is the solution to the forthcoming problems of organized genomes.

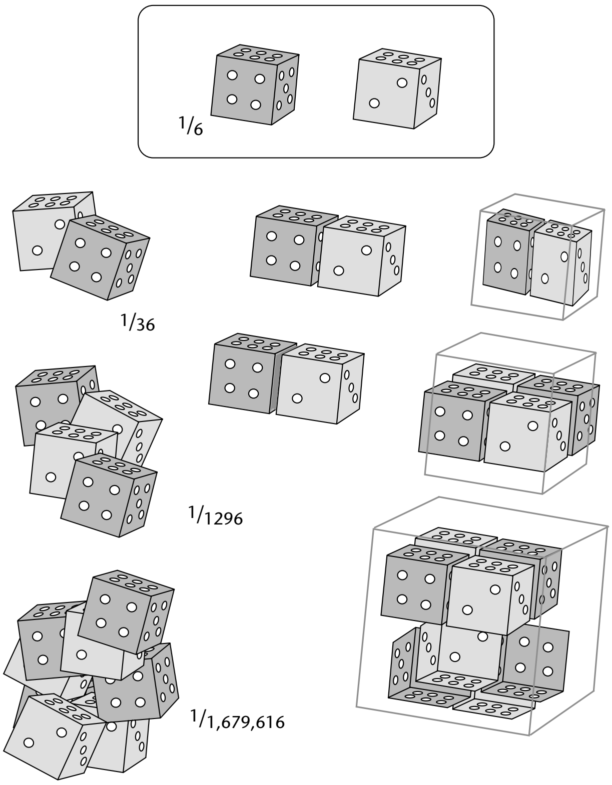

Figure 3

(A) Documents for old patters

The five groups of phenomena will demonstrate constraints in the form of old patterns within the developmental process. And if we adopt the insight of the genetic units as in the first set of questions, we will find them now in all levels which were of importance for fitness in the past phylogeny of the organisms.

(1) *Atavisms*, such as the appendix in man is puzzling, because without surgical interventions it lays under remarkable pressure of elimination. Why then does it still exist? It is assumed, that it has important functions for immunization in early development, left from times when it was a large organ.

(2) *Spontaneous atavisms* where again one of the phenomena which inspired DARWIN in his 'Pangenesis Theory' to assume 'inner mechanisms'. Referring to Geoffroy SAINT HILAIRE who already knew

such cases. "What", Darwin (1875, p368) states "can be more wonderful than that characters, which have disappeared during scores, or hundred, or eve thousands of generations, should suddenly reappear perfectly developed". He had pigeons and fowls in mind. Today we know numbers of cases; even in man: tailed children, surplus of nipples and alveoli, faces covered with hair, so-called 'dog-man', even cervical fistulae remnants of gill slits. It is now 150 to 200 years that the phenomenon is puzzling.

To make sure one estimates the strangeness of such phenomena, take a horse appearing with three hoofs, as the ancestors of horses had it. This is as astounding as if a motorcar with Bronze Age wheels would move out of the factory. We learn that a modern factory still has a Bronze Age and, assumable, a Middle Ages department kept and active; that produce all the wheels first, just having forgotten rolling the wheels to the middle age and further to last department, changing the products to modern fellows.

If we build a home, we do not start with a bower, rebuild it to a wooden cabin, to finally reform it to a brick home. We do not repeat our history materially, ontogeny does. We must assume, that the old units of instructions can not be overstepped, once they where indispensable for fitness, now they remained indispensable to carry on instructions for further changes. Biological systems have to stay with this; and no doubt, this restricts further possibilities of adaptation.

(3) *Induction*, in developmental biology 'the transfer of instruction'—and as I see it—from an phylogenetically older to a newer organ, which is building on it. Compared with my motorcar analogy, it corresponds to how the departments communicate with each other. Among a hundred of cases, let us take the dorsal cord as an example.

All Chordates, consequently all embryos of Vertebrates start with a dorsal chord. It tells the dorsal muscle-plate to divide in segments, the segments induces the spinal column where to put the vertebra, and the vertebra defines where the spinal-ganglia have to emerge, which organize the whole nervous system of the body. If one takes the dorsal chord out, e.g. of a frog embryo and puts it under ventral skin, the ventral muscle plates start to divide in segments; which it otherwise never does. If one takes the cord from an primitive fish an puts under a chickens skin, the chicken embryo still understands the message.

This remarkable insights tell us, that even the instruction to build up functional unites are preserved; corresponding to fitness conditions over the whole time of the species phylogenetical development: 450 million years. Since even sender 'language' and receiver are preserved over the whole phylogenetic time, one rightly speaks of 'Homodynamy', homologous messages. And, in spite of all mutative bombardment over the whole time, changes are causing lethal damage.

(4) In *Rudimentation* of complex organs, such as of eyes of cave dwelling fish and amphibians, I noticed, that the disintegration runs opposite to building up by induction. In the case of eyes first the vitreous body is reduced, then the bulbus, and lens, and longest remain traces of the *Nervus opticus*, which, as the 'eye-stalk' was first in embryonic development.

It seems as even in rudimentation the links of the chain must be opened from its end if not a great disturbance should occur.

(5) *Haeckel's phylogenetic law*, that fact, that ontogeny recapitulates phylogeny, found already in school books, became almost a commonplace. The more is it difficult to make it understood, that we have actually no explanation why this must be. But if one takes together what we have collected in this chapter, the explanation is at hand: the old departments and their information transfer turns out to be indispensable for every further development.

It has been argued, whether it is a law or just a rule. It is, as we now see, definitely a law; if one distinguishes between cenogenetic and palingenetic characters; the old versus the new. The first are adaptations to the larval or embryonic life. Such as floating devises of a starfish larva, or the umbilical cord of mammalian embryos. This is because every ontogeny had its phylogeny. The palingenetic ones are certainly recapitulations.

Summary: The genetic units which we uncovered within the 'first set of questions', corresponding to the hierarchy of pertinent functional unites reappear as 'old patterns' in the ontogenetic process. They can not be overstepped because being preserved as principles for further construction. And clearly they narrow further alternatives of adaptive radiation. This was in principle foreseen by Karl Ernst von Baer (1828).

(B) Documents from macro-evolution or cladogenesis

Most of the material of highest significance stems from paleontology. Important discoveries go back

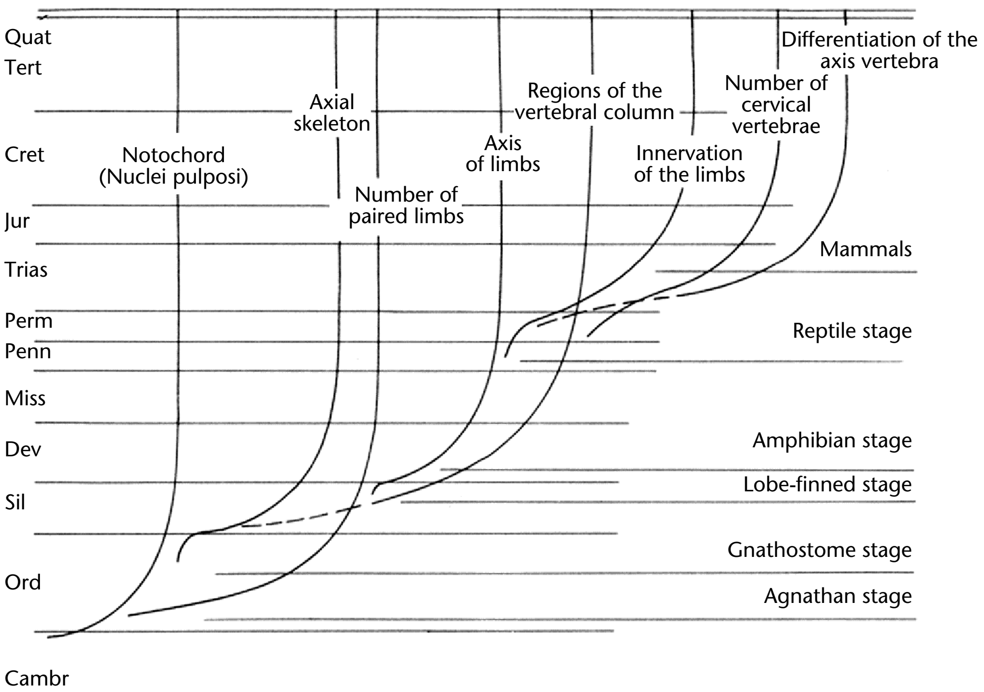

Figure 4: The building-up of typogenetic features upon typostatic ones, as shown by certain chracteristics of the axial skeleton and limbs in mammals and their ancestors. To the left the time intervals are shown and to the right the sequence of systematic groups (from Riedl 1978, p162; cf. also Figure 45 on p152).

to large parts of the 19. century. The field has been widely excluded in the 'Synthetic Theory of Evolution' concentrating of 'micro-evolution', ending where species turn into genera.

(1) *Parallel evolution* remained a puzzling phenomenon. The classical example are wolf and the bagwolf, a marsupial. The skeletons, skulls, and rows of teeth are much more similar, as the similar behaviors could explain. And if one considers that true mammals have separated from marsupials about hundred million years ago, then the phenomenon is surprising.

One may think that the ground plan of their ancestors was so stiff, that what ever carnivore developed from it hat to take exactly the same path. Committed, this is speculation; but the puzzle remains a problem of 'directed' evolution.

(2) *Trend* and *orthogenesis* are problems of a greater weight. Hundreds of sequences of fossils, from *Foraminifera* over snails to horses, just to name a few, are documented. And no doubt; if one plots the findings between the axes of time vertical and 'morphological distance', a measure of acquired structural difference, horizontal, than it becomes evident, that the upward trend with passing time straightens more and more. It was long discussed how 'ortho' (straight) an orthogenesis had to be a true orthogenesis. This was too academic. It is surprising enough that one finds trends everywhere doing almost no meandering despite enormous spans of time and deviation of the environmental characters.

We therefore must assume, that keeping the functional units is often more vital than to change them by adaptation. But why do trends straighten when time is passing?

(3) The term *'concave curves'* is not found in every biological dictionary, but often used by systematists. It may have been not luckily coined, but stands for a remarkable phenomenon. If trends have the tendency to straighten with time, then this indicates that structural changes reduce. The time-structure curve changes from a type producing to a type conserving stage, from a 'typogenetic' to a 'typostatic' phase. This has great influence on the patterns of the phylogenetic trees, in details as well as in the whole picture; all the branches tend to go steeper up, the higher it goes in the tree. We are accustomed to such pictures, but it remains a good question, why this must be so.

This phenomenon can be understood by an increase of optimization of functional and genetic unites and their interactions, making the probability of success of any alteration less likely. I spoke (RIEDL 1975) of functional burden. In the course of WAGNER's approach (1983, 1988) one could think of genetic burden.

In comparative anatomy, microscopically as well as in ultra-structures I become aware (RIEDL 1975), that these burdens follow four patterns: standard parts, hierarchical, interdependent, and traditive patterns, and their subforms, making the process of fixation sufficiently clear.

(4) The term *'Typostrophe'* means hat new types may repeatedly develop like stanza in a song. It faces the fact, that many phylogenetic pathways demonstrate, that, in the long, typostatic phases allow the offspring of a new typogenetic phase. This seems a contradiction of the former phenomena; yet it makes it the more transparent. Let us add a simple example:

Phylogeny has first largely experimented with the notochord in Chordates. It was either found only in the tail of the larva, remained only the tale of the adult, runs from the tail end to the tip of the nose, or reached only from tail to the head; but as soon it became the basis of the developing axial skeleton no change occurred any more (Fig. 4). The same happened first to the number, and than to the axis of paired limbs in Vertebrates, but as soon they became optimized, all Tetrapodes kept the same pattern in front and hindlimbs, regardless if in man, bats, horses or dolphins. But they also made the girdles necessary: and as soon the axial skeleton became burdened to carry shoulder and pelvis girdle, the regions of the vertebral column become differentiated and fixed.

Organ systems became increasingly burdened by new systems they have to carry. The chances of adaptive radiation reduces dramatically. But on the end of functional chains, new freedom opens the chance of success of evolutionary inventiveness. A puzzle for former evolutionist becomes now rather clear.

(5) *Additive Typogenesis* describes the same phenomenon from its other side. It questions why in evolution, some organ systems are free to changes, while others solidify. WIMSATT (1986) speaks of 'entrenchment'.

This, for us, is no problem anymore. We see now clearly why some organ system drift into fixation, and can predict which others gained freedom in adaptive radiation.

Summarizing we find, that optimized interdependency of organ systems lead to a reduction of adaptive freedom up to a hundred million years of canalization. The same with functional, and if the systems are copied, with genetic burden; while new unites, at the ends of functional interdependencies are free for adaptive innovation and evolutionary fantasy. And that the restrictions have nothing to do with a general lack of mutative impacts, but with elimination of mutants which do not fit to the 'interior requirements' of functional and genetic organization of our 'white gambler'.

(C) Justification of morphology and its mayor terms

After an investigation of the 'Academy-Controversy' between and Geoffroy SAINT HILAIRE, GOETHE (1795) coined the term 'Morphology', and Richard OWEN (1846) brought up the concept of 'Homology', separating it from 'Analogy', which before was generally used for similarity.

Morphology was thought to investigate the path of discovery, the principles which leads us to compare structures and form. Today I understand, that it is guided by inborn ways gestalt perception, itself an interaction between perception and theory forming based on experience and expectation. It is based on *'simul hoc'*, expecting coincidences of phenomena, comparable to David HUMES *'propter hoc'* expecting a succession of phenomena, the so called 'cause', which he took as a 'need of the soul' (RIEDL 2000); inspiring KANT to his critical investigations.

Later, this path of discovery become, in biology, confused with the path of explanation; it is now often, erroneously, felt, one could substitute the former with the latter. And 'morphology' as a term was not taken as the precondition for comparative anatomy, but for comparative anatomy itself. This had to do with blaming morphology as an outcome of 'German Idealistic Philosophy' (statement Ernst MAYR), but also with little interest in epistemology and with the fact, that gestalt perception works anyway. Consequently morphology was either distrusted or left further on to intuition. But intuition does not allow decisions in controversies.

(1) *Homology* is the central term. Homologies are essential or substantial similarities, having to do with the general organization of a group of organisms; in contrast to analogies as accidental similarities. But what is essential and what is accidental? Intuitionists take homologizing as an art, fostered by great experience, rationalists, due to temper, as

avoidable or nonsense, most biologists take it as an irritating or cumbersome puzzle.

Starting from synthesizing the homology criteria of REMANE (1971), I have, however, shown (RIEDL 1975 to 2000) that homologizing can be developed into a 'Probability Theorem'. The probability of taking two features as homologue depends on the number of unrefuted confirmations; confirmations of predictions in anatomically and systematically assumed further similarities. These homologues form hierarchies and pile up into hundreds and thousands of confirmations, making many homology expectations close to certainty.

For the topic of this article however, the explanation of the existence of homologues is simple: homologues are perceptible because of their partially resistance to adaptation; specifically with regard to either form or position, in 'homodynamy' also of function. Functional burden, and, if copied, genetic burden, makes understandable why homologues must exist. And they turn out to be the more conservative, the more burden they carry. They correspond exactly to all present and passed functional interdependencies for fitness conditions which where important both in phylogeny and ontogeny of the organism. We have no doubt, that also this structures have been permanently bombed by mutative alterations. But, with the exception of system mutations, the rest of this mutants must have been eliminated as subvital ore lethal forms.

If on splits the hierarchic pattern, such as the homology of the mammalian skeleton into backbone, backbone of the collar region, *Atlas* (first vertebra), its arc, they are all 'frame-homologues', holding further sub-homologues. If one dissects again e.g. the plate of the front joint of the arc, the lowest ore 'minimum homologue' of this specific file, one enters an other kind of homologies.

(2) *Homonomies* are homologues in mass production, identical unites spread over large parts of the body. In our example of dissecting a joints surface, we would find *'bone-trabeculae',* in them bone cells, than their mitochondria, and within mitochondria, again homonome structures, namely specific biomolecules. Symmetries, as in anemones, or metamers, as in earth worms articulation, are of a similar kind; namely identical, functional unites.

This makes the existence of both genetically coded and functional units evident, which can be reproduced up to remarkably large numbers; such as the little grey cells in our brain. This follows the principle of 'cheap order', organizing and linking much material with small information. We do the same with tiles or paving stones. This is the more remarkable, that, with the exception of the cilia, homonomes are all predisposed as mass products; such as identical muscle cells, hairs, teeth in sharks, or legs of arthropods, such as in millipedes. Only later in phylogeny they may gain individual characters; what we call differentiation.

(3) *Type* and *groundplan* are taken as the overall design of a related group of organisms. This was, what GOETHE had in mind, coining the term morphology as a new field of sciences. If one puts the homonomes together and piles on them the hierarchy of homologues, one ends up with a hierarchy of types; such as e.g. the type of butterflies having been specialized on the groundplan of the insects, the insects on the one of arthropods, and arthropods on the plan of articulates.

And as in the explanation of homologues and homonomies, we find now the complete set of conditions of burdens, and fixations of functional units. They repeat fitness conditions which have taken its rise from the time, when stepwise articulates, arthropods, insects and butterflies have developed. And it is the same sequence where fresh new characters with much freedom for adaptive radiation, have additionally burdened and fixed the grounds on which they had to built.

Summarizing we find the terms used in morphology justified, because they stand for phenomena, which not only are indispensable for the path of discovery, they also correspond to principles of the reduction of adaptability, as of our 'white gambler', along the path of explanation.

(D) The nature of systematics and of the natural system

More than two million species have, obviously by biologists, been arranged in half a million systematic categories; and the question can be raised has this large system been discovered or invented. Are the systematic categories a product of nature of our need to make order for description. And this, the more that neither the path of discovery nor the cause of fixations where really understood.

(1) With regard to *Systematic Categories* it has been asked what it actually means if one selects one special character to define a systematic unit. What, if one would take another character? The grouping would look different. And who could decide which of the two similar categories corresponds nature?

This hesitation is known as the *'weighting problem'*. It is based on a misunderstanding, which itself originates from an unawareness of the procedure of gestalt perception, the principle of morphology, leading the path of discovery. We think in 'fields of similarities' that is to say, that if one contemplates a gestalt this brings immediately all assumingly comparable cases out of our memory. In this process are always several to many characters involved. And for concept forming, along a path of optimization, the one solution is finally selected, which produces the smallest amount of contradictions or exceptions.

(2) *The Nature of the Natural System*. Rationalists among our fellow biologists have argued about the term 'natural system'. They took 'system' as a man made conception, and felt, that, if nature is in mind, than it would not follow a system, and if it is a system, than it is not anymore natural. For concepts of systematic units, they describe together the highest probability of the stepwise bifurcation of species and fixations of their characters along the paths of evolution.

This is also misleading. The nature of the natural system is actually most natural; widely designed by the laws of evolved evolutionary processes. This are the needs to adapt complex systems; gambling under competition for the speed of adaptation. The Natural System pictures not only the hierarchy of types and archetypes of penes, but, correspondingly, also a hierarchy of genotypes and archegenotypes.

Summary: The remarkable accomplishment, having reconstructed the paths of deployments of millions of fossil and recent organisms demonstrates two things. First, that our unconsciously working, inherited abilities of gestalt perception and thinking in similarity fields works surprisingly perfect. Secondly, that the uncovered patterns of similarities is the result of evolving the evolutionary mechanism, developed to keep increasingly complex mechanisms adaptable.

Looking back to this 'second side of the coin', the phenomena of old pattern, macro-evolution and cladogenesis, systematics and the natural system brought over a dozen large groups of phenomena, which all demonstrate restrictions of adaptive freedom, finding altogether a common explanation by this 'Systems Theory of Evolution'. The principle behind is the fact, that retaining adaptability of complex systems needs organization of the epigenetic system, corresponding to the hierarchy of functional interdependencies of the phenotypes, impose on probability. Keeping the adaptability of new organization, pays back to the 'accounts of probability' by reducing the adaptability of the basic organization.

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So what?

As I mentioned at the beginning of this article, the use of linear causality seems to me the main hurdle of adequately dealing with complex systems. Industries and business have fostered it too long. It is, besides possessivity, the main cause of the environmental problem. It is not yet fully seen, that complexity needs a more elaborated causality concept. Maybe this 'systems theory' contributes to understand, that we are not only handling querulous academic topics, but are close to metaphysical perspectives of how we are to see us in this world. But, again, this, in this article, is not my topic.

Note

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Christian Pázmándi

The Biological Type Concept

Abstract

Morphology provided the bulk of evidence for evolution at the times of Darwin, but its underpinning by an explicitly temporal component, that of phylogeny, is a later development which obscures its original foundations. Morphology was initially organized by types, which contain all observed forms in a concrete, picture-like manner. This original concept from Goethe was later overshadowed by the phylogenetic school of Haeckel, but two approaches continued along and transcended beyond Goethe's program: Rational systematics, based on rational morphology as outlined by Driesch and the type concepts of Riedl and Naef. Driesch tried to develop a morphology which would be enveloped in a totality of possible forms, with actual forms constituting a subset. The totality of possible forms should in his view be derived from an analysis of morphogenetic fields and their properties. Riedl coined his type concept in terms of adaptive constraint and opportunities. While both concepts are ambitious but very laborious, Naef tried to stay close to morphological practice and developed a comparatively simple concept. He substituted the central role of the "morphological instinct" of the researcher by a set of definitions and rules aimed at constructing natural types. This paper gives an overview over the concepts mentioned above, resulting in a biological type concept and illustrates it with an example from morphological research, delivering as well a distinction between three terms essential to morphological investigations: average, normal and typical.

Key words

Morphology, type, metamorphosis, pectoral fin.

It is an irony that the theory of evolution received most of its empirical support from morphology, but morphology itself faced a demise in the following decades. Conceptual groundwork within morphology became rare. The focus of attention shifted to phylogenetic research, as outlined by Haeckel, while the basic concepts of morphology itself had not even been elaborated fully. This article goes into the conceptual underpinnings of morphology by presenting the work of four scientists who devoted their efforts to such a task: Goethe, Driesch, Riedl, and Naef. They all share the belief that proper organization of organismic diversity in morphological research is at least partially mirrored in the generation of organismic diversity by the organisms themselves. I present their work and then a case study on shark fin variation which shows an application of the biological type concept.

Goethe

As a start, it seems appropriate to present a couple of quotes from Johann Wolfgang von Goethe, along with Georges Cuvier the founder of morphology, about central issues in morphology. While Cuvier was more concerned with practical issues, the erection of distinct "embranchements", or groups of taxa, Goethe set out to give a couple of principal statements.

I present them below, starting with a statement about the aim of morphology:

"Die Morphologie soll die Lehre von der Gestalt, der Bildung und Umbildung der organischen Körper enthalten" (Goethe 1977, p56)—"Morphology should contain the science of form, the formation and transformation of organic bodies" (my translation).

"Morphologie ruht auf der Überzeugung daß alles, was sei, sich auch andeuten und zeigen müsse" (Goethe 1977, p45)—"Morphology roots in the conviction that everything that exists must indicate itself and show itself as well" (my translation). If the type, to which I will come later in more detail, is a representative for the underlying diversity of the taxon it represents, and if the type is meant to be more than a mental construct, than the typical character state of a taxon is expected to match a realized character state in at least some instances.

"Die Gestalt ist ein Bewegliches, ein Werdendes, ein Vergehendes. Gestaltenlehre ist Verwandlungslehre. Die Lehre der Metamorphose ist der Schlüssel zu allen Zeichen der Natur" (Goethe 1977, p45)—"Form is changing. The science of form is a science of changes. The science of metamorphoses is the key to all signs of nature" (my translation). Form, the central issue of morphology, can only be understood fully by its transformations, not by a single instance. This leads the way to understand form as a totality:

"Der Deutsche hat für den Komplex des Daseins eines wirklichen Wesens den Begriff Gestalt." (GOETHE 1977, p48)—"Germans have for the complex of being of real creatures the term 'gestalt'" (my translation). "Gestalt" is not a directly observed shape but rather an integration from the actual shapes displayed by an organism.

The type should, in an abstract image, give a key to all gestalts of the group of organisms represented by the type. It is a norm by which organisms are described and judged. Their actual morphologies can be derived from it through transformations, called metamorphoses in this context.

For GOETHE, the type is like an immanent unchanging law which is evident in the particulars, which are changing. Close to this idea is the concept of a zootype manifested across animal phyla, or the concept of a phylotype within them (SLACK/HOLLAND/GRAHAM 1993). Those types are specific Hox-gene expression patterns at certain developmental stages, which characterize animals in the case of the zootype or particular animal phyla in the case of the phylotype. These types are not ideal, they can be observed and change over the course of evolution. Such a change might be small at the genotypic level but big at the phenotypic level, as it causes the origin of a new phylum with a distinct bauplan. Pending ongoing investigations of Hox-genes, macroevolution might be definable as a change of Hox-gene expression patterns which gives rise to new bauplans of new taxa.

Driesch

According to DARWINISM, the only relations between forms are material and historical—genealogical, in short. However, these genealogical relations are rarely observed, mostly inferred from morphology and systematics. Hans DRIESCH (1908) set out to develop a rational systematics and rational morphology, which ideally would be linked to a causal theory of morphogenesis. Rational morphology, as conceived by DRIESCH, tries to establish what is typical among the varieties of forms and how the type is realized in an individual, therefore recurring on a causal theory of morphogenesis. As such, it can serve as grounds for rational systematics, which not only tries to classify but also explains the diversity by means other than a historical narrative. Such an explanation is based on the knowledge of the laws of form. The type then is an irreducible order of parts. This minimalist arrangement serves as a template to organize observable diversity. Every form is typical as long as it is derived from the intrinsic nature of the organism and not imposed from the outside. This concept of the type is different from essentialist notions of the type, criticized by David HULL and Ernst MAYR.

Gerry WEBSTER writes about that: "From a realist perspective, the manifest properties of entities which are available to experience in material practice have to be understood as the realisation of dispositions which are grounded in the natures of things. Natures are determined by structures which are 'hidden' and, as such, not (immediately) accessible to experience; they have to be constructed by the speculative work of theoretical imagination." (WEBSTER 1996, p213). WEBSTER mentions the theory of morphogenetic fields as one leading up to a morphogenetic theory underlying rational systematics. If we understood morphogenetic fields, we could construct based on the rules of fields a rational system of forms and then check the path evolution actually took through this morphospace.

Or, to quote DRIESCH (1908, p264): Systematics "has to deal with the totality of the possible, not only the actual diversities.". DRIESCH is the father of the field concept, but did not elaborate it, as his view of the organism was that of a machine driven by an external force, entelechy. For Scott GILBERT et al. (1996), morphogenetic fields are the modules of the developing embryo. According to Brian GOODWIN (1996) fields are equations with genetic and environmental factors as values for their parameters. But this sets up an enormous workload, as one would have to experiment through all of the parameter space of the developing embryo in order to know the laws of the morphogenetic fields.

If we do not want to wait until development explains morphology, we have to stay within morphology and see if its central concept, the type concept, can be formulated so that types are no longer ideal but point to an underlying biological reality, like in the concept of the zootype.

Riedl

RIEDL (1975) goes back to the central aspect of the type first stated by GOETHE: he views the type as a rule of nature according to which organisms build themselves. Going beyond GOETHE, he then defines the type as a pattern of (adaptive) constraints and opportunities built by the set of characters of a particular taxon. The morphotype, then, is the pattern of the levels of fixation of the characters of a taxon. The higher the level of fixation, the smaller the freedom to vary. This variational freedom is mirrored in development in what RIEDL calls the "epigenotype" and caused by the epigenetic interdependencies of the developing organism and by the functional burden of its parts.

Rooting the type concept deep in a contemporary understanding of biology, RIEDL, however, sets up an enormous work program on how to construct the type, as one would have to explore all of the morphospace and its evolution in order to determine the pattern of constraints and opportunities. A type concept which is simpler to work with has been developed by Adolf NAEF.

Naef and the Biological Type Concept

Adolf NAEF, a mollusc systematist, set out to give morphology a conceptual basis in line with concurrent practice:

"Form (Struktur) ist das Lageverhältnis der Körperteile, soweit es im lebendigen Organismus durch den natürlichen Zusammenhang dieser Teile auch über den Verlauf vorübergehender (physiologischer) Verlagerungen hinweg behauptet wird" (NAEF 1935, p77)—"Form (structure) is an actively maintained topology of parts, as far as it is maintained in the living organism through the natural connection of those parts, also during transient (physiological) repositioning" (my translation). Later, he gives three definitions and an auxilliary definition, all regarding the type. I designate them as definitions 1–3 and as an auxilliary definition.

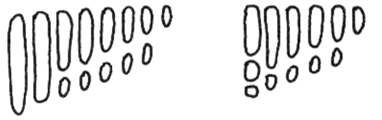
Definition 1: "Typen sind Normen in konkret bildhafter Fassung und als solche wesentlich mehr, als die mehr oder minder abstrakten Baupläne und Diagnosen. Während die letzteren nur das für die Vertreter je einer Gruppe Gemeinsame enthalten, umfassen die Typen alles für dieselbe Normale und in einem ganz allgemeinen, aber grundsätzlich rein formalen, ordnenden Sinne Primäre" (NAEF 1935, p94)—"Types are norms of a concrete, picture-like kind and as such much more than the more or less abstract bauplans and diagrams. While the latter contain only what is common for the members of a group, the types contain everything normal for them as well as primary, in a very general but in principle purely formal, ordering sense" (my translation).

Auxilliary definition: "In der Typologie tritt an die Stelle einfacher Begriffsabstufung der Begriff der Metamorphose, d.h. einer schrittweisen Variation oder 'Abwandlung' der beobachteten Formen in der Vorstellung. Durch Metamorphose wird das Besondere auf den allgemeinen Typus der betreffenden Gruppe 'zurückgeführt' oder von ihm 'hergeleitet'" (NAEF 1935, p96)—"In typology, simple gradation of terms is replaced by the term metamorphosis, that is a step-by-step mental variation or derivation of observed forms. Metamorphosis is the derivation of the special case from the general type of a group" (my translation).

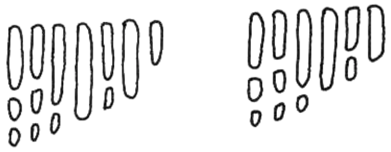
Definition 2: "Der Typus ist diejenige innerhalb einer Kategorie vorstellbare Naturform, mit der sich alle bekannten Formen dieser Katgorie durch die einfachste naturgemäße [...] Metamorphose verbunden denken lassen" (NAEF 1935, p96)—"The type is the imaginable natural form of a category from which the known forms of this category can be derived through the simplest natural metamorphosis" (my translation).

Definition 3: "Der Typus einer Gruppe ist also eine durchaus naturhaft (d.h. mit allen Eigenschaften eines Lebewesens) vorgestellte Organismenart, ebenso wie seine Metamorphose durchaus naturhaft aufgefaßte Übergangsformen umschließt. So ist er auch nicht nur ein Bau-, sondern vor allem ein Werdetypus, der eine Entwicklungsnorm zum Ausdruck bringt" (NAEF 1935, p99)—"The type is an imagined form which is natural (equipped with all properties of an organism) and imagined, like its metamorphoses, which contain transitional forms which are conceived as natural. Therefore, the type is not only a type with regards to construction but also, and most of all, a type with regards to becoming, expressesing a norm of development" (my translation).

I call this type concept biological because of its recourse on natural instead of ideal metamorphoses, as only those transformation are allowed which are at least potentially possible. Cases like Geoffrey St. HILAIRE's transformation of a lobster into a vertebrate, done by turning the lobster on its back (therefore, the lobster would be like a vertebrate having e.g its nervechord on the dorsal, not the ventral side), would not be included into since nothing close to that has ever been observed. It is interesting to note, as done by NAEF himself, that morphologists and systematists often work in a typological fashion without explicitly stating how they it. These are often well known scientists trusted by others in their judgement because of their expertise. Naef called this working by a "morphological instinct" and developed his rationale to overcome such prescientific conditions. For example, Victor Springer (1993), an eminent ichthyologist, admitted that he had difficulties reconstructing his modus operandi used in his work. Another interesting case in this aspect is delivered by the paleoichthyologist Rainer Zangerl (1981). He determined the morphotype of the pectoral fin of paleozoic Elasmobranchia as a series of of unsegmented, unbranched radials while noting that this condition is not observed in the sample. However, the diversity of elasmobranch pectoral fins could be organized in the most parsimonious way by comparing it to the unobserved morphotype.



average pattern pattern #18



pattern #11 typical pattern

Figure 1: Outlines of the caudal parts of four patterns of pectoral fin skeletons. The caudal edge points to the right, the proximal margin is on top.

A case study: Fin variation in *Squalus* (*Acanthias) vulgaris*

Erik Müller published a paper in 1909 about the pectoral fin of selachians—sharks—which includes a survey of pectoral fin variation in *Acanthias vulgaris*, nowadays called *Squalus vulgaris*. Based on this study, I will differentiate and define the usage of three terms: normal, average and typical. Twenty fin varieties are described by Müller, shown on his figures 1 to 3 and 10 to 29. There is considerable variation on the caudal margin of the fin: the radials, parallel rods of cartilage, differ in number and in the number of elements they consist of. The question arises on how to represent this variation. No relative frequencies of the individual patterns are given, so the most common pattern can not be taken, which would give one no clue about the other patterns anyway. All patterns are normal, that is, they are natural varieties brought about presumably by different environmental conditions. All are therefore, presumably, within the norm of reaction, which is defined as the set of phenotypic expressions of a genotype under different environmental conditions (Futuyma 1997). Note that a pattern can, in theory, be normal and rare at the same time. Abnormal are only those patterns which are not within the norm of reaction, which would be teratologies. As all patterns are normal, there is no clue as to the best representative of the variation of the sample. Below, the average and the typical pattern will be determined. It will also be determined which one of the two is the better representative of the sample.

As a first step, it is necessary to include some morphological information. The fin is composed of two kinds of skeletal elements: pterygia, which are solid elements extending more or less along the antero—posterior axis, and radials, long elements extending along the proximo—distal axis. The radials articulate proximally on the pterygia. I confined this survey to radials on the caudal side inserting on the metapterygial elements two to four, since the situation elsewhere is uniform, according to Müller. I calculated the average number of elements per radial, starting with the first radial on the second metapterygial element. The average pattern can be expressed in a formula of the kind (number of elements of the first radial)–(number of elements of the second radial)–…–(number of elements of the last radial). The formula of the average is: 1–1–2–2–2–2–2–1. This pattern (Figure 1) itself is not observed in the sample. The natural pattern (number eighteen) closest to the average pattern has the formula 0–0–3–2–2–2–2–1 (Figure 1). Closeness means in this context the number of transformations necessary to construct pattern number eighteen from the average pattern. Transformations are additions and deletions of radial elements. They are natural, because development shows that the primordial precartilagenous mesenchymal mass breaks up into radials which break up into elements (Balfour 1881; Goodrich 1906). Failure of an element to break off would show up as its deletion, a split as an addition of one element. Additions and deletions of single elements are also common also in tetrapod limb development (Shubin/Alberch 1986). It takes three transformations to go from pattern number eighteen to the average pattern. Counting all the transformations, from all observed patterns, renders a score, shown for the average pattern (A) in the first line of table 1 with a value of 155. Applying this calculation to all

	1	2	3	10	11	12	13	14	15	16	17	**18**	19	20	21	22	23	24	25	26	27	28	29	**Sum**
A	7	6	7	7	6	6	8	8	6	7	5	3	8	8	7	4	5	9	6	8	9	8	7	**155**
1		3	6	0	5	7	6	9	7	10	7	4	7	7	6	3	4	8	5	3	9	7	8	133
2			6	3	6	6	4	8	8	9	5	5	8	4	5	4	3	5	4	4	8	8	11	128
3				8	5	5	7	5	9	8	6	4	6	9	6	5	4	10	5	7	11	1	10	145
10					5	7	6	9	7	10	7	4	7	7	6	3	4	8	5	3	9	7	8	133
11						2	2	4	4	3	3	2	6	10	3	3	3	9	4	4	4	6	7	**100**
12							4	4	6	5	3	3	6	6	1	4	2	7	2	4	8	4	9	105
13								4	6	5	3	5	8	8	3	6	4	7	4	4	5	8	11	120
14									6	3	3	5	8	10	5	6	5	11	16	6	6	6	7	136
15										5	3	5	6	12	7	4	7	13	8	4	4	10	3	144
16											4	4	7	11	6	5	6	12	7	7	4	8	6	145
17												4	5	9	4	3	4	10	5	3	5	7	6	109
18													5	7	4	1	2	8	3	5	7	5	8	**100**
19														11	7	4	7	13	8	6	8	8	7	158
20															5	8	7	1	4	8	12	8	15	179
21																5	2	6	1	4	7	6	10	109
22																	3	9	6	4	6	6	7	107
23																		6	1	5	9	5	10	103
24																			5	9	14	9	16	195
25																				4	8	4	11	110
26																					4	8	7	113
27																						12	5	165
28																							12	155
29																								194
B	4	5	6	4	1	1	3	5	5	4	4	1	5	9	2	2	2	8	3	3	5	5	8	**95**

Table 1. Number of steps between patterns. A = average pattern, B = typical pattern.

pairwise comparisons within the dataset delivers a matrix (Table 1). On the right, there are the scores for each pattern. Patterns number eleven (0–3–3–2–1–2–1–1; Figure 1) and eighteen (0–0–3–2–2–2–2–1; Figure 1) have the lowest scores (100). This means that it takes the least number of transformational steps to construct all the other patterns if pattern number eleven or eighteen are chosen as candidates for a typical pattern. Note that the average pattern has a much higher score (155).

After determining these two patterns, I played around heuristically to see whether there is a pattern with an even lower score. The pattern with the lowest score (95) overall was Pattern B, with a strong resemblance to pattern eleven. It differs from it only by one element and has the formula 0–3–3–2–1–2–1–0. As it has the lowest score overall , it is the typical pattern for the observed variation. Note that pattern B is typical but not normal, not within the norm of reaction, as it is not among the observed patterns. But it is the typical pattern for two reasons: the observed variation can be derived with the least number of steps, and the derivations include only natural transformations, simple additions and deletions. Therefore, the observed variation can be derived from the typical pattern in a simpler manner than from the average pattern, which makes the typical pattern the one to be preferred.

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Theresa S. S. Schilhab

Out of Your Mind

Ontological and Epistemological Consciousness and the Question of Anthropomorphism

Abstract

Scientific attempts to demonstrate advanced cognitive abilities and consciousness in nonhumans are often met with charges of anthropomorphism. In this paper, I explore reasons for this inclination and make three assertions. First, there is a discrepancy between beliefs about consciousness (hereafter the ontological concept) and the way we operate on it, when attributing consciousness to others (the epistemological concept). Second, the epistemological concept is largely based on anthropocentric behavioural criteria. Third, substituting the epistemological for the ontological concept of consciousness explains why we confidently assign consciousness only to a limited number of animals such as humans and possibly great apes.

Key words

Consciousness, first-person perspective, third-person perspective, anthropomorphism, self-awareness.

Introduction

Though disagreeing on specific features the majority of philosophers, palaeoanthropologists, cognitive scientists, and like-minded scholars believe that the concept of consciousness applies meaningfully solely to humans (exceptions exist, see Griffin 1984, 2001, 2002; Sheets-Johnstone 1998). This anthropocentric conception is said to have originated most notably in the work of Descartes (e.g., Burwood/Gilbert/Lennon 1999; Jamieson 2002) and continues to influence the commonsense notion as well as scientific intuitions about consciousness.

Anthropocentric intuitions about consciousness exert themselves in criticism (so-called anthropomorphic charges) of research on nonhumans inviting to mentalistic interpretations (for instance Cheney/Seyfarth 1990; Parker/Mitchell 1994; Premack/Woodruff 1978; Whiten/Byrne 1988). Anthropomorphism is conceived of as the mistake of attributing human abilities to nonhumans (Fisher 1991, 1996; Kimble 1994; Mitchell/Thompson/Miles 1997). To some, anthropomorphism is inevitable emerging as a cognitive default resulting from human social cognition (Caporael/Heyes 1997; Kennedy 1992) or as an instantiation of an introspective modelling capacity (Eddy/Gallup/Povinelli 1993; Gallup/Marino/Eddy 1997). Some believe that research on nonhumans benefits from allusions to humans (Asquit 1984; De Waal 1991; Dennett 1983; Rivas/Burghardt 2002) and take anthropomorphism to be due to the mentalistic vocabulary inherited from folk psychology (for critical comments, see Heyes 1987; Kummer/Dasser/Hoyningen-Huene 1990). However, not everyone admits the charges of anthropomorphism in contemporary research. They seriously question the application of the concept to research in contemporary cognitive ethology (e.g., Brittan 2000; Fisher 1991, 1996; Rollin 1997, 1998). (For listing of different positions on anthropomorphism, see Bekoff/Allen 1997). Based on analysis of first- and third-person perspectives I adhere to this latter view.

In this paper I claim that charges of anthropomorphism result from discrepancy between beliefs about consciousness in the first-person sense (hereafter the ontological concept) and the way we operate on it, when attributing consciousness to others (the epistemological concept). Confounding of different approaches is hardly surprising, since the concept of consciousness has multiple characterizations (for a comprehensive review of aspects of consciousness, see Kim 1996, Velmans 1996). However, crucial to the question of anthropomorhism is the systematic substitution of one aspect of consciousness (the first-person sense) with another aspect (the third-person aspect). Indeed, I posit that charges of anthropomorphism result from mistaking the epistemological concept for the ontological. The confounding of the dual aspects of consciousness also explains the extremely limited range of animals we assign consciousness.

In the following I will briefly distinguish between consciousness in the first-person and third-person sense and introduce the notion of ontological and epistemological consciousness, respectively. Then I will discuss how the substitution of these aspects of consciousness leads to anthropomorphism thus arguing that the charge of anthropomorphism is a red herring in many pejorative discussions on the mental life of nonhumans.

Ontological Consciousness

Central to being conscious is having a subjective experience (e.g., GOLDMAN 2000; SEARLE 1992; VARELA 1996; VELMANS 1996).[1] That is, (DENNETT 1991, p45), "The things that stream by in our consciousness—you know: the pains and the aromas and daydreams and mental images and flashes of anger and lust". According to GOLDMAN (2000, p10), "consciousness is a phenomenon we initially understand (in large measure) from a first-person point of view".

Two points need to be stressed. First, the particular first-person feature of consciousness, shared with no other scientific subject, entails the process of introspection. Self-examination implies that any pain we experience will be the pain that is a manifestation of activity in our own body and brain. We will never experience pain that belongs to another person in the way we experience our own pain. This asymmetry peculiar to consciousness necessitates the distinction between first-person and third-person perspectives. Because of this asymmetry the first-person perspective is sometimes expounded as being primary to the third-person perspective. However, it is important to note that the alleged primacy does not follow from the asymmetry. Nevertheless, we tend to treat the first-person perspective as superior since opinions based on the first-person perspective are often better informed.

Second, biologically the intimacy of ones own sensations as opposed to that of others makes perfect sense. In this view the phenomenal sense originally developed as a means of judging the impact of environmental encounters in 'good'; those leading for instance to food - and 'bad'; those leading to lesions - as interactions to be pursued or shunned. Possessing such arrangements would raise the survival value of the organism, since it facilitates interactions positive to the organism and inhibits the harmful (for a discussion, see DENNETT 1996).

To most people, the phenomenal feel of consciousness is the genuine enigma and the reason why the phenomenon of consciousness is interesting in the first place (see for instance CHALMERS 1996; NAGEL 1974).[2] The enchanting effect is reinforced by the inadequacy of explanations on its origin such as the one offered by DENNETT (1996). Though operating with aptness, no rational explication can be given to why cognitive systems categorize encounters into good and bad qualities by way of 'what it feels like' (for a discussion on this see SCHILHAB 1998). If, as posited, the core function of 'what it feels like' is to sort stimuli with expediency, other devices could plausibly have been engineered. Contrivances, as scales with pointers in which deflection to the right or left mark the qualities of an experience could easily do the trick, without any accompanying feels.

In the following, I refer to the notion of first-person experiences by the term 'ontological consciousness'.[3] To claim that an organism possesses subjective experiences, irrespective of its validation to others, is to attribute ontological consciousness to it.

Epistemological Consciousness

If we want to address consciousness in other people or organisms, we have to approach from the third-person perspective; the interpersonal level at which everyone shares like admission requirements (for a critical discussion of this supposition, see VELMANS 1996). (For discussions on the third-person perspective, see ALLEN/BEKOFF 1997; SOBER 2000; WHITEN 1996).

With humans if someone states that he is in pain (is experiencing ontological consciousness), his verbal report is accepted to the extent in which the term 'pain' is applied in a proper way (for discussions on competent language users, see DUMMETT 1993). This does not imply that the 'expert', who is in pain, applies the term correctly, but since no one else has privileged access, the first-person view is authoritative in coining the subjective feeling. (If the first-person point of view implies 'privileged access' in the sense that the person in question has infallible knowledge compared with third party, this conjecture is not universally shared, see THOMPSON

1994).[4] I refer to this aspect of consciousness as epistemological consciousness. If an organism is ascribed epistemological consciousness, it is thought to comply with 'defined criteria'. In other words, the organism behaves adequately in certain contexts but need not actually to be conscious in any sense.

What exactly does this mean? Typically, with humans defined criteria means a mixture of verbal and non-verbal behaviours, which we acknowledge implicitly in daily life. For instance, in so-called self-recognition studies of children (e.g., AMSTERDAM 1972) verbal identification of self, such as personal pronouns or name (verbal behaviour) in response to the mirror image accompanied by certain behavioural sequences, are thought of as criterion of self-awareness (see especially BERTENTHAL/FISCHER 1978; BIGELOW 1981; MANS/CICCHETTI/SROUFE 1978; ROBINSON et al. 1990).

That focus is on epistemological consciousness in scientific and everyday contexts appears almost trivial, because of its inevitability. Thus, also attempts to develop a science of consciousness rest on verbal behaviours, when validating conscious states in others (GOLDMAN 2000; VARELA 1996; VELMANS 1996). As expressed by Max VELMANS, "S_1 to S_n might all report that a pin in the finger produces a pain in the finger, or a dose of aspirin reduces the pain. The fact that staring at a red spot produces a green after-image is similarly 'public', 'intersubjective' and 'repeatable'" (VELMANS 1996, p193). Here, the verbal report (behaviour) that a green after-image follows from the nonverbal act of staring at a red spot is used as indicative of a certain mental state. The methodology reflects the lack of alternatives to circumvent the asymmetry (for further discussion, see SCHILHAB 2002).

To summarise, one simply has to consent to the epistemological constraints and adopt assumptions of behavioural correlates if one is to address ontological consciousness in others. (In the next paragraph I will argue that the enterprise is doomed to fail). Of course, another position is that endorsed by behaviourists. It presumes that if consciousness in others is accessible from the third-person perspective only, it has no other form of existence, than the one it occupies in which it is accessible and thus acknowledgeable. The first-person perspective might just as well be a conceptual construct without reality (RORTY 1993). This presumption is however not widely accepted, since most people think consciousness is accessible particularly from the first-person perspective.

Substituting Epistemological Consciousness for Ontological Consciousness

Now, if first-person and third-person aspects of consciousness were different but still equal interpretations of the same phenomenon there would be no real problem. One would simply address the phenomenon from one of different alternative perspectives. However, what is generally believed is that a sacred relation between third- and first-person perspectives exists. The assumption is that the third-person perspective is an inferior imprint of the first-person perspective. By way of behavioural criteria one bridges the asymmetry and gets access (limited and error prone perhaps but nevertheless access) to the first-person perspective. In this understanding the puzzle is how to assess what behaviours (accessible from the third-person perspective) are criteria of what mental states (accessible from the first-person perspective only). We take epistemological consciousness to represent ontological consciousness. Ultimately, the substitution means that epistemological consciousness does not imply anything about mental states. However, I stress that a qualitative difference exists between ascriptions of epistemological and ontological consciousness. An organism being ascribed ontological consciousness is thought to have subjective experiences while an organism being ascribed epistemological consciousness simply complies with certain behavioural criteria. My claim is that in everyday and scientific life, this crucial difference is almost always neglected, and this is why charges of anthropomorphism at first sight seem reasonable.

The impact of this confusion is severe. Especially if as I assert, the criteria employed to attribute conscious states to organisms are species-specific to humans, that is anthropocentric, a theme I will return to in a short while. Solely those organisms sharing relevant behavioural features with humans are ever considered conscious in the ontological sense. Organisms not conforming to the behavioural criteria are discarded as non-conscious though basically, at best, we are agnostic with respect to their inner life. In practice, whether in laboratory settings or in everyday life, when we apply the term consciousness we do not differentiate between organisms that meet the criteria of consciousness (epistemological consciousness) and organisms that are conscious in the sense of first-person perspective (ontological consciousness). In practice, passing criteria of consciousness (the manifestation of certain behaviours) is indicative of being conscious (having phenomenal feels). The assumption that the third-person perspective is just the overt sign of the covert first-person perspective implies that the referent of the epistemological consciousness is confused with the referent of ontological consciousness. Implicitly equalising subjective experiences with contingent behavioural patterns entails that any difference between consciousness in the sense of ontology and epistemology is neglected.

Anthropomorphism

So far I have claimed that substitution of ontology with epistemology causes the continuous charges of anthropomorphism in cognitive ethology. To reiterate; anthropomorphism is the mistake of attributing human abilities to nonhumans. Ideally, if animals comply with those criteria stated by the epistemological concept, how can the results still be vulnerable to anthropomorphic charges? Only if results addressing mental life of nonhumans are taken to be measures of the ontological aspects of consciousness.

However, by now it should be clear that no approach exists by which we are capable of measuring ontological consciousness. The empirically applied methods by which to study consciousness are always directed at epistemological consciousness.To appreciate fully these assertions we have to explore in greater detail, what people actually do when they 'anthropomorphise' (for empirical studies, see EDDY/GALLUP/POVINELLI 1993; HERZOG/GALVIN 1997; RASMUSSEN/RAJECKI/CRAFT 1993). According to EDDY et al. (1993) when subjects were asked to rate the degree of similarity and cognitive abilities between themselves and a number of animals representing a so-called 'phylogenetic scale', the degree correlated to phylogenetic position. Thus, animals diverging early from the line leading to humans were considered less similar to humans than those diverging later. The only exceptions were cats and dogs, which were overrated compared with phylogenetic position. This suggests that people anthropomorphise according to "the degree of physical similarity between themselves and the species in question" as well as "the degree to which they have formed an attachment bond with a particular animal" (EDDY/GALLUP/POVINELLI et al. 1993).

Other studies (MITCHELL 1997; MITCHELL/HAMM 1997) suggest that inclinations to anthropomorphise depend on the consistency of the interpretation of various behaviours into a single coherent story. (For interpretations of the various behaviours into a single story even in obviously mindless things, see HEIDER/SIMMEL 1944).

To summarise, the empirical studies on anthropomorphism exemplify; 1) that by necessity measures of consciousness (here referred to as similarity in cognitive abilities) are always attached to the third-person perspective and could in theory be spelled out as behavioural and contextual criteria; 2) charges of anthropomorphism rely on substituting epistemological for ontological consciousness. At this point it is worth noting (MITCHELL 1997; MITCHELL/HAMM 1997) that criteria amounting to epistemological consciousness do not entail that animal behaviour and context must be very similar to what humans do, in terms of matching motor movements, similarity in physical form, and identity of context. An animal A might express anger by growling at and biting another animal B when B took (or tried to take) some food from it. Though humans rarely do the same thing in the same sort of context (possibly we refrain ourselves from doing so), we can still use 'anger' to describe the behaviour of both humans and animals. The chimpanzee's grimace looks like the human smile, but no one thinks they indicate the same mental state, even if the chimpanzee's grimace occurred during a birthday party for it. Same behaviour in same context need not equal same mental state attribution, and different behaviour in different context may very well lead to similar mental state attribution. However, if the chimpanzee grimaced consistently in situations where the human smile was appropriate, the interpretation would be like the human case. Thus, the important point is the consistency of the interpretation of various behaviours into a single coherent story (see also BENNETT 1991).

(For similar strategies on interpretation of human consciousness see DENNETT 1982, 1991).

Thus, the mistake of attributing human mental abilities (attribution of ontological consciousness) to nonhumans is invoked by behavioural and contextual resemblance to human settings (attribution of epistemological consciousness) (see also FISHER 1996). To anthropomorphise is in the end to mistake the referent of epistemological consciousness for the ontological referent.

Implications

The mix up of ontological and epistemological consciousness explains some of our intuitions about which animals should and which should not be assigned consciousness. Those nonhuman organisms living behaviourally and contextually comparable to humans are more likely to be attributed consciousness in the ontological sense, simply because of the focus on anthropocentric behaviours in epistemological consciousness. Species phylogenetically closer to humans are ceteris paribus more liable to be attributed consciousness than more distant species. Hence, chimpanzees sharing a more recent common ancestor with humans are more likely to meet the criteria than rhesus monkeys or lemurs, though all belong to the order of primates.

Frans DE WAAL develops a somewhat similar position named 'evolutionary parsimony'. This principle should come into play "especially when both humans and apes exhibit traits not seen in monkeys, and two explanations are proposed where one may do." (DE WAAL 1996, p65). (See also DE WAAL 1991). (MORGAN's canon—the idea, that one should prefer to attribute a lower rather than a higher psychological mechanism—a version of the principle of parsimony—strongly disapproves of that approach. However, one could argue that there is no reason to understand the canon in this way (see SOBER 1998).

A natural objection would be that attribution of consciousness due to familiarity of behaviour to for instance chimpanzees as opposed to lemurs reflects real-life familiarity, i.e., phylogenetic closeness, this I suppose is DE WAAL's position. Thus, attribution of consciousness to kin species is simply validated by psychological kinship, while organisms remote to humans do not partake in behavioural criteria of consciousness because of lack of psychological kinship. This argument seems persuasive, but it presupposes a connection between ontological (certain psychological traits) and epistemological consciousness (certain behavioural counterparts), that given the evidence presented in this paper cannot be defended. In so far great apes show same behaviour in same context, they are conveniently interpretable and thus the application of mental concepts is done to an exclusive group closely related to humans. Therefore, we should expect that attribution of consciousness is implausible to phylogenetically distant organisms like locusts and snails.

Thus, one consequence of the confusion of ontological and epistemological consciousness is adopting an anthropocentric stance with respect to consciousness in nonhumans. By inferring mental states from behaviours, we deny organisms behaving fundamentally differently from humans the possibility of being conscious. However, are there good reasons to pursue this tendency?

First, to some the whole notion of criteria of consciousness being anthropocentric, in the sense of being based on human concerns and coming from a human point of view, might seem unproblematic. They might hold that so do criteria for concepts in physics and mathematics. Thus, it is neither exceptional nor important to the discussions of consciousness. However, I strongly disagree. Granted that the concept of consciousness is highly controversial, adopting an anthropocentric stance impedes the understanding of the natural history and origin of the phenomenon. Furthermore, anthropocentrism eliminates the possibility of consciousness in organisms very different to humans. Thus, clarification of the impact of anthropocentrism in the approach to consciousness seems crucial if we are to progress in discussions on the topic.

Second, I believe that we ought to reconceptualise ideas about consciousness. We are mistaken if we expect ontological content to be uniquely determined by empirical observations. Neither decisive observations nor critical experiments will determine what an animal (or human) really experiences phenomenologically. (For a similar discussion on content of thought in animals JAMIESON 2002). Not because of the non-existence of subjective experiences in nonhumans but because of the indeterminacy in pinpointing mental states from third-person perspectives.

I believe that it takes an enormous effort to get divorced from the inclination to infer mental states from behaviour. Thus, also to question the alleged intuitions about consciousness in nonhumans. This is why competing theories such as addressing consciousness in terms of versatile adaptability of behaviour to changing circumstances and challenges (GRIFFIN 1984, 2001, 2002) are met with sceptical remarks (BLUMBERG/WASSERMAN 1995; WHITEN 1992). If there is no causal relation between ontological and epistemological consciousness, from where does the intuition come? I believe that the inclination to infer mental states from behaviours is pragmatically explainable. Employment of a theory of mind that endorses such causal connections seldom fails. By inferring certain mental states, human (and animal) behaviour is explainable (see DENNETT and his discussion on his 'intentional stance', DENNETT 1996). Thus, the inferred causal connection, implying that certain behaviours are always caused by specific mental states is a theoretical construct. As pointed out by DAVIS

(1997), behaviours are not always preceded by conscious thought, as demonstrated by a huge number of studies on implicit learning and memory (e.g., BERRY/DIENES 1993; REBER 1992, 1993; STADLER/FRENSCH 1998). We adopt theories implying causal connections between ontological and epistemological consciousness because of their explanatory power. It is not surprising then that scientific investigations offer similar explanations, since alternatives are not available.

One should be aware of the extent to which the limited applicability of mind related notions are imposed by the underlying anthropocentric premises resulting from a mix up of ontological and epistemological consciousness.

Conclusion

I have sketched how confusion of ontological and epistemological consciousness influences the assignment of consciousness to nonhumans as for instance the recurrent charges of anthropomorphism. In addition, I have claimed that employment of anthropocentric criteria explains why we intuitively accept consciousness in kin species but not remote groups of organisms. By explicating the implications of this anthropocentric stance, the range of its impact is clarified. Acknowledgment of anthropocentrism guiding our intuitions about consciousness is necessary if we want progress in controversies over consciousness.

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Notes

1 Descriptions of consciousness do not always focus one-sidedly on the first-person perspective. However, the centrality of the character usually goes unchallenged.

2 Theoreticians often claim that humans in contrast to nonhumans experience intricate phenomenological phenomena such as love and hate, which are incomparable to 'simple' phenomena such as pain or affect. In this context the difference, if any such exists, is of no importance. What counts is not content but exclusively whether or not 'it feels like anything' to the organism in question.

3 I am aware that the term 'ontological consciousness' connotes 'real' consciousness. This is not my intention. The term is chosen simply to point out the qualitative differences between consciousness in the sense of third-person and first-person perspective and because many theoreticians hold the first-person perspective to be real consciousness (e.g., GOLDMAN 2000; NAGEL 1974; SEARLE 1992; VELMANS 1996).

4 Some hold that the idea of privileged access is an illusion based mainly on the CARTESIAN idea of consciousness being transparent.

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Wolfgang M. Schleidt/Michael D. Shalter

Co-evolution of Humans and Canids

An Alternative View of Dog Domestication: Homo Homini Lupus?

Abstract

Dogs and wolves are part of the rich palette of predators and scavengers that co-evolved with herding ungulates about 10 Ma BP (million years before present). During the Ice Age, the gray wolf, Canis lupus*, became the top predator of Eurasia. Able to keep pace with herds of migratory ungulates wolves became the first mammalian "pastoralists".*

*Apes evolved as a small cluster of inconspicuous tree-dwelling and fruit-eating primates. Our own species separated from chimpanzee-like ancestors in Africa around 6 Ma BP and– apparently in the wider context of the global climate changes of the Ice Age–walked as true humans (*Homo erectus*) into the open savanna. Thus an agile tree climber transformed into a swift, cursorial running ape, with the potential for adopting the migratory life style that had become essential for the inhabitants of the savanna and steppe. In the absence of fruit trees, early humans turned into omnivorous gatherers and scavengers. They moved into the steppe of Eurasia and became skilled hunters.*

Sometime during the last Ice Age, our ancestors teamed up with pastoralist wolves. First, presumably, some humans adopted the wolves' life style as herd followers and herders of reindeer and other hoofed animals. Wolves and humans had found their match. We propose that first contacts between wolves and humans were truly mutual, and that the subsequent changes in both wolves and humans are understood best as co-evolution.

Key words

Chimpanzee, co-evolution, cooperation, dog, Eurasia, human, hunter, Ice Age, pastoralist, Pleistocene, social, pack, wolf.

Introduction

Why did our ancestors tame and domesticate wolves, of all creatures, and turn them into dogs to become man's best friend? Is man dog's best friend, as Mark DERR (DERR 1997) once dared to ask? Well, not according to Stephen BUDIANSKY's assertions in a new book, The Truth About Dogs (BUDIANSKY 2000). He claims that dogs are scavengers at heart "For all the myth and tales of dog's service to man, only a small fraction of dogs living off human society today earn their keep… the overwhelming majority of dogs were freeloaders" (p6), even though "in my role as brutally objective observer, I do love dogs" (p9). As scientists, we are skeptical about a successful journalist who claims to have found "the truth", especially in such a complex web of problems, connections, observations, opinions. And, his confession of his "love" for dogs has a strange contradictory ring.

Konrad LORENZ once stated: "*Of all creatures the one nearest to man in the fineness of its perceptions and in its capacity to render true friendship is a bitch.*" (LORENZ 1954, p85). Isn't it strange that, our being such an intelligent primate, we didn't domesticate chimpanzees as companions instead? Why did we choose wolves even though they are strong enough to maim or kill us? We do not claim to know "The Truth" but we offer in this paper a different view, with emphasis on companionship rather than human superiority.

Co-Evolution of Cooperation: An Alternative to Domestication?

The human species has refined sociality to a degree of complexity that remains unmatched in our world. The human capacity for cooperation starts at birth: even though a human mother is able to give birth and take care and full responsibility for the newborn, traditionally three women cooperate in the birth… the mother, the mother's mother and the midwife. Growing up is sheltered by complex helper systems, staffed by siblings, babysitters, and teachers far beyond puberty, and group living within the family is well supplemented by socialization among peers, from kindergarten, through school, kinship, work, and ending in funeral rites. But our communal life does not end there: We strive to join our ancestors in heaven, and meet our maker who made Adam in His likeness. Or, rather, humans created a god in their likeness who is their alter ego, and accepted by many as the ultimate judge of their moral behavior.

When we try looking back at the biological foundations of our moral behavior in a distant past, and, in the absence of any historical evidence turn to our closest relatives, the chimpanzees, we find ourselves in a strange conflict. The life of chimpanzees, especially their sociality, as revealed by the pioneering work of Jane GOODALL and others (GOODALL 1986; DE WAAL 1997) appears as a frightful caricature of human egoism. Even in their maternal behavior warmth and affection are apparently reduced to nursing and an occasional comforting hug; cooperation among group members is limited to occasional hunting episodes, or the persecution of a competitor, always aimed for one's own advantage and executed with MACHIAVELLIAN shrewdness. The first insight we get from chimpanzee society is: "We have come a long way". The high morality we claim as achievement of our species, however, is a very thin veneer on the old ape, and our newspapers are full of stories that reflect more chimpanzee than human ethics.

The closest approximation to human morality we can find in nature is that of the gray wolf, *Canis lupus*. This is especially odd in view of the bad reputation wolves have in our folklore, as expressed in the famous phrase, HOMO HOMINI LUPUS. In Thomas HOBBES' own words: „To speak impartially, both sayings are very true; That *Man to Man is a kind of God*; and that *Man to Man is an arrant Wolfe.* "(HOBBES 1651). Since HOBBES' time, however, our understanding of wolves has changed considerably, even though for a rancher who leaves his livestock unsupervised and unprotected by a good shepherd, an "arrant Wolfe" is to this day a formidable threat (MECH 1970; FOX 1975, 1980; MECH/BOITANI 2003). Wolves' ability to cooperate in a variety of situations, not only in well coordinated drives in the context of attacking prey, carrying items too heavy for any one individual, provisioning not only their own young but also other pack members, baby sitting, etc., is rivaled only by that of human societies. In addition, similar forms of cooperation are observed in two other closely related canids, the African Cape hunting dog and the Asian dhole. Therefore it is reasonable to assume that canid sociality and cooperativeness are old traits in terms of evolution, predating human sociality and cooperativeness by millions of years. Thus, we can give a new and very different meaning to HOMO HOMINI LUPUS: "*Man to Man is—or at least should be—a kind Wolfe.*"

This shift in our attitude toward wolves opens a new vista as to the origin of dogs. Instead of perpetuating our traditional attitude that our "domesticated animals" are intentional creations of human ingenuity, we propose that initial contacts between wolves and humans were truly mutual, and that various subsequent changes in both wolves and humans must be considered as a process of co-evolution. The impact of wolves' ethics on our own may well equal or even exceed that of our effect on wolves' changes in their becoming dogs in terms of their general appearance or specific behavioral traits.

The earliest suggestions that dogs do not fit the conventional paradigms of domestication, as proposed for hoofed animals and fowl, can be found in ZEUNER's pioneering work (ZEUNER 1963), but the gravity of the problem became apparent when the genetic relationship between wolves and dogs was elucidated by Robert WAYNE and Carles VILÀ (VILÀ et al. 1997), opening the possibility that the split between wolves and dogs may date back as far as 100 to 135 ka BP (135,000 years before present). Such a long common history of dogs and modern humans begs the question as to the dog's part in the endeavor of humans to take control of the world, and led to the formulation of a hypothetical "lupification" of human behavior, habits, and even ethics (SCHLEIDT 1998). Erhard OESER has pursued this lead and traced the contribution of dogs in the "humanization of the ape" in a wider context of human culture (OESER 2001, in press). Our own paper does not aspire to be a comprehensive review of the hypothetical co-evolution of cooperation between dogs and humans, but attempts merely to provide more details und pursue several collateral ideas emanating from the original proposal (SCHLEIDT 1998).

Primates and Canids: A Current View

Around 6 Ma BP humankind separated from chimpanzee-like tree dwelling and fruit-eating ancestors in Africa and moved as true human hunters and gatherers, *Homo sp.,* into the open savanna, conquered the plains of Eurasia, and became fierce hunters during the grueling conditions of the Ice Age.[1] There a new species emerged and dominated Europe and the Near East longer than any other

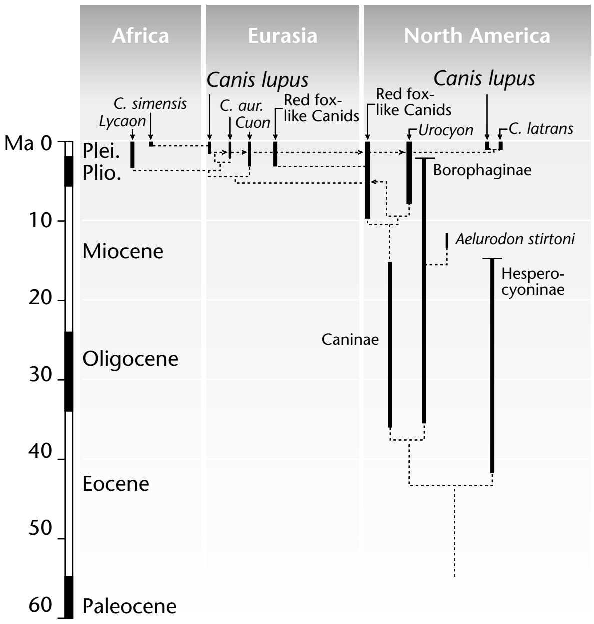

Figure 1: Cladogram indicating the phyletic relationship between *Canis lupus* and selected species and divisions of Canidae within their temporal and geographic ranges (after TEDFORD/TAYLOR/WANG 1995; MCKENNA/BELL 1997; WAYNE/VILÀ 2001, etc.).

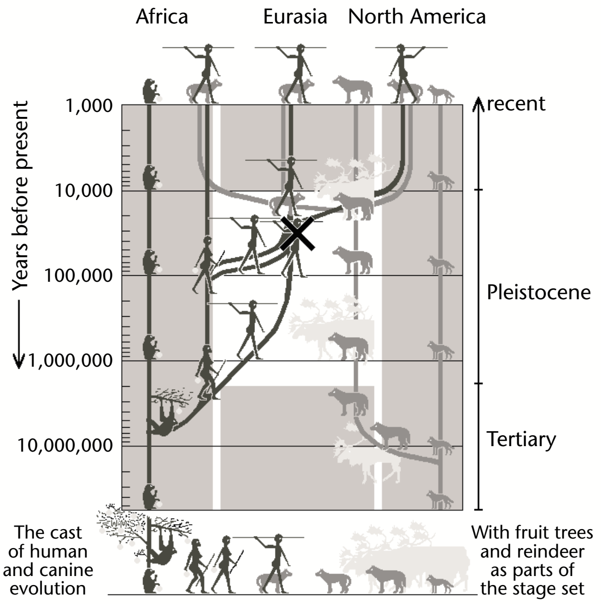

Figure 2: A schematic summary of the current teaching of human and canid evolution. Note the logarithmic time scale, and the simplistic view of Pleistocene as an epoch of inhospitable cold climate in circumpolar regions.

hominid: the clumsy, but successful Neanderthal man.[2] Meanwhile, around 150 ka BP—based on evidence from mtDNA—a superior woman, the legendary African Eve, had emerged. Her daughters moved into icy Europe and, thanks to their rich subcutaneous fat and superior intelligence, were able to outcompete Neanderthal women. Then, around 80 ka BP—based on evidence from nuclear DNA—the legendary African Adam emerged, the first man who really deserved the name "*Homo sapiens*". He took to the daughters of African Eve who flourished in icy Eurasia, killed all the reindeer, mammoths and Neanderthals, and did beautiful art-work in the caves of Spain and France. So the story goes.

Back to serious science: The canids, also known as (wild) "dogs", have their roots in North America.[3] They, too, emerged from the forest and were originally about the size of a fox when grasslands opened and herds of grazing ungulates, notably horses and antelopes, began to dominate the open plains. A multitude of swift canid predators evolved, and around 10 Ma BP, they started to cross into Asia, Europe, Africa, and back into North America. Thus, they became part of the rich palette of canid predators and scavengers, coexisting and competing with the big cats and hyenas: the wolves, jackals, coyotes (the latter all members of the genus *Canis*), and the aberrant "wild dogs"; the African Cape hunting dog, and the Asian dhole. The Genus *Canis* apparently evolved in Asia, and *Canis lupus*, the circumpolar big "wolf", as a species distinct from the various jackals, appeared about one million years BP.

At the end of the ice age, man tamed wolves, which were scavenging among the rich refuse of human camp sites, and by artificial selection created the multitude of dog breeds we know today. Or as an alternative hypothesis, scavenging wolves took the initiative and conned the affluent hunting and gathering humans into sharing their plenty, by pretending to be their obedient servants and hunting companions.

Primates and Canids: A Different View

There is something in the bond among wolves and between dogs and humans that goes beyond that between us and our closest primate relatives, the chimpanzees. Here *we are not talking about intelligence,* but about what we may poetically associate with *kindness of heart.* Jane GOODALL, invited to comment on K. LORENZ's statement quoted above, wrote in a letter to the first author:

"Dogs have been domesticated for a very long time. They have descended from wolves who were pack animals. They survive as a result of teamwork. They hunt together, den together, raise pups together. This ancient social order has been helpful in the domestication of the dog. Chimpanzees are individualists. They are boisterous and volatile in the wild. They are always on the lookout for opportunities to get the better of each other. They are not pack animals. If you watch wolves within a pack, nuzzling each other, wagging their tails in greeting, licking and protecting the pups, you see all the characteristics we love in dogs, including loyalty. If you watch wild chimps, you see the love between mother and offspring, and the bonds between siblings. Other relationships tend to be opportunistic. And even between family members, disputes often rise that may even lead to fights… even after hundreds of years of selective breeding, it would be hard if not impossible to produce a chimpanzee who could live with humans and have anything like such a good relationship as we have with our dogs. It is not related to intelligence, but the desire to help, to be obedient, to gain our approval." (GOODALL 1997).

Jane GOODALL's eloquent comparison is based not only on her own personal experience with dogs[4] and many years of living with chimpanzees (GOODALL 1986), but also less well known to the general public on her familiarity with and research on the wild dog, also called the Cape hunting dog (*Lycaon pictus*), the African brother of our gray wolf. We not only value a dog's intelligence, but its warm affection, playfulness, and loyalty. Several species of canids show these special traits, and several other really outstanding behavior patterns related to harmonious life in a pack. They do superb teamwork, not only during the hunt, but in denning together and raising pups together. Although the core of the pack is usually one extended family, pack members can also accept strangers. Equally, when a stranger or even a close kin fails to comply, it can be attacked, driven off, or even killed.

E Pluribus Unum

From many, one. Many people, many peoples, one nation. But also, if two or more persons can agree to cooperate, they are stronger than a single person. As a rule, the bigger the group, the easier it can subdue a single person or a few, or force them to comply. That is the basis of majority-ruled democracy. There is a catch, however: the members of the group must cooperate, communicate, and agree on a common goal.

That is not as easy as it sounds, even for intelligent human beings. The old primate trait of selfishness and MACHIAVELLIAN reasoning get in *the* way of *our* behaving communally. Let others take the risk and reap the gain for oneself and one's kin. Self interest first, and if there is a little surplus: practice nepotism. In theory, of course, we praise it as the highest expression of humaneness when, on rare occasion, a hero or saint can overcome temptations of selfishness. We preach love thy neighbor and ask our brave boys in uniform to be prepared to sacrifice their lives for the sake of their families, community, and nation; we admire the age-old saying, *Sweet it is to die for one's country.*

Strangely, there are indications that such humaneness, which many admire and hold, at least in theory, to be the highest achievement of humanity, was invented millions of years ago by early canids. It is practiced to this very day by some of their descendents and honed to perfection by members of the pack-hunting canid species: notably the gray wolf, but maybe even more so by the wild dog of Africa (*Lycaon pictus*), the dhole of India (*Cuon alpinus*) and, to a lesser extent, the bush dog of South America (*Spethos venaticus*). In fact, some of today's wolves may well be less social than their ancestors, as they have lost access to big herds of ungulates and now tend more toward a lifestyle similar to their "minor brothers:" coyotes, jackals, or even foxes.

The E PLURIBUS UNUM of the pack goes far beyond what makes UNUM, a unit , out of a herd or a gang of selfish fighters. As in the social insects (bees and ants), where the hive is only one of the units of selection (MORITZ 1993)[5], the pack became one of many systems upon which natural selection acts.

Humane Canids

Among all the canids one species became the most successful mammalian predator ever: *Canis lupus,* the gray wolf. It roamed over all the northern hemisphere north of 15°N (Fig. 3) (HARRINGTON/PAQUET 1982). In some areas the gray wolf coexisted with less social members of the genus, and in India it was sympatric with the dhole. The ubiquity of the gray wolf is apparently due to its rich behavioral repertoire and the ability to adapt its life style opportunistically to local and temporal conditions: most successfully as a pack hunter of midsize ungulates, but able to squeeze by on the diet and life style of a fox: hunting mice and picking berries.[6]

What is it that makes the ancient pack social system so successful? Well, it is not a single life history trait, anatomical feature, or type of physiology or

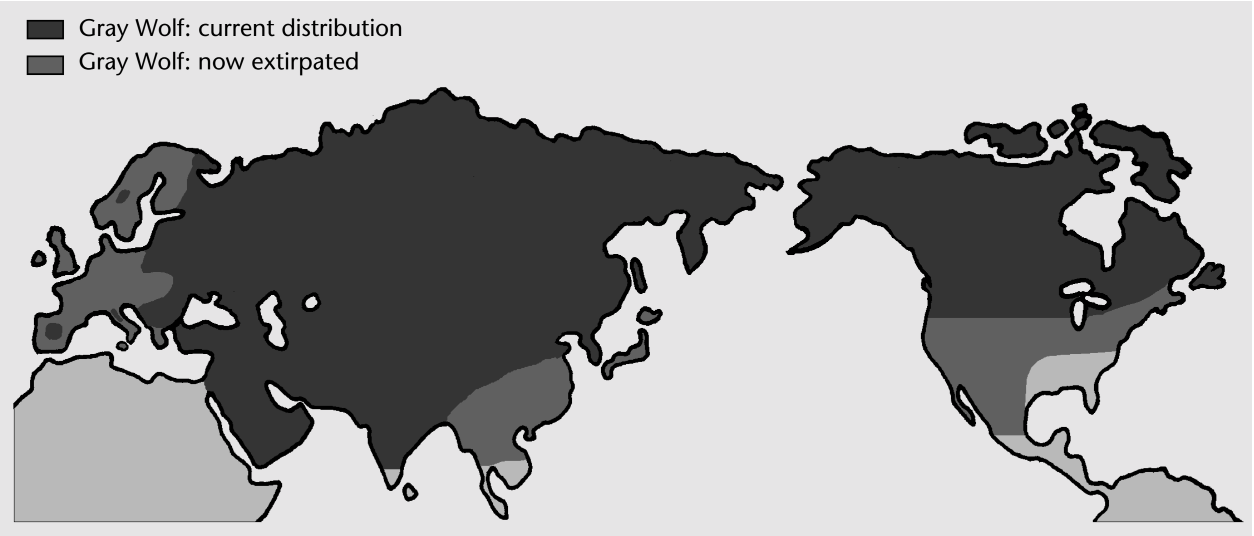

Figure 3: Grey wolf *(Canis lupus)* (after HARRINGTON/PAQUET 1982).

behavior. It is a whole array of specific adaptations which make communal life possible. Social pack-forming canids are essentially monogamous. Even though there may be several sexually mature adults in a pack, as a rule, only one pair breeds, but all members share food and parental care generously. Even siblings and friends share food and affection (unlike in chimps, lions, tigers, hyenas, where the strong tend to take from the meek).

The long-legged social canids are not only fast and long-distance runners, they are able to run as a single group, apparently well aware not only that another pack member is running where, but which individual. This awareness makes it possible for a team of dogs to pull a sled and run for hours without changing places, or for two dogs to race at full speed while holding onto a stick of wood.

Typically predators, when going for the kill, avoid the risk of disabling injury that would prevent them from hunting. The attacks on prey by lions, tigers, sharks, and the like conjure up images of bravery and fury. In reality, however, they are low-risk performances by smooth butchers. Only when they turn on each other, as, for example, in conspecific fighting over a limited resource (e.g. a female), do they incur high risk of getting seriously injured.

When canids hunt as a pack, they can, because of their focused attention and close cooperation, act much more as an integrated system than any group of chimps or lions, where the individual that makes the kill and can maintain possession of the carcass, or take it over by force, will get “the lion’s share”. In wolves each pack member can accept greater risks when attacking, because, when injured, the needy will be fed by the other pack members.[7] This cooperation and risk sharing not only among close relatives, but among individuals bonded as mated pairs or by lasting friendships among individuals of the same gender, is the central feature of canid pack living.

When wolves feed on a kill, there is growling and snarling, of course, and a low ranking pack member may have to wait, but compared to other predators there is little overt competition among pack members. All is tuned to swallow as much as possible as fast as possible (which is the basis for the story of Fenris-Wolf gulping down Odin, and for Grimm’s fairy tale bad wolf swallowing grandmother and Little Red Ridinghood).

Wolfing down prey is apparently an ancient canid trait: Around 11 Ma BP a wolf-type canid (*Strobodon stirtoni*) roamed Nebraska, and a skeleton of this species on display in the Museum of Natural History of the Smithsonian Institution in Washington, D.C.[8] reveals an amazing story: in the region of the ribcage one can see quantities of broken and etched bone representing at least two individuals of small antelope, leg bones articulated and neatly folded-up in the area where once the canid’s stomach had been.

Wolfing down prey is but the first phase of feeding, which allows pack members to make maximal use of each kill and to leave little for others. By the time jackals, hyenas, and vultures arrive, there is usually not much left.

The second phase of feeding starts when the wolves have reached a cozy place for a rest some distance from the kill, or when they get home to the den. They then regurgitate the large chunks, sharing with those that did not participate in the hunt, especially the pups and their babysitter, and carefully go over what they brought home in their stomach shopping bags. What had been carried communally, such as a leg of a prey, too large to swallow, is cut down to size, and pulled apart in a "tug of war", with "real growls", but actually quite playfully, and very different from the fighting over a kill, e.g., in hyenas. The pack at the den can process its loot in peace and spend time resting and digesting.

MACHIAVELLIANS, however, consider such doggish behavior—accommodating rather than fighting—as cowardly. Yet it is precisely what keeps canid pack members from incessant quarreling, as, for example, the way hyenas do, or from playing macho the way chimps or some humans cannot do without. The pack hunter's social awareness is equally amazing. Contrary to the popular belief that canids are specialized in sniffing and have limited eyesight, they constantly watch each other; each member of the pack knows not only who is who but also who is where and who is doing what. For example, in spite of all the generous sharing of food, if they prefer, they keep pieces for themselves; when an individual buries its leftovers, it can behave very secretively, and start to dig only when nobody is in sight. The same applies to smart dogs: do not believe that opening the fridge or reaching for a can opener triggers a mere Pavlovian conditioned reflex in your dog. If you watch it carefully, you will see its eyes move, depending on who is going where. And if you cannot see its eyes, the movement of the eyebrow (the light spot above a Doberman's eye or in the face mask of a husky) will tell you what it attends to, very much like you can determine what a dog listens to by observing its ears provided they are pointed like those of wild canids (SHALTER/FENTRESS/YOUNG 1977). If you question our claim and are hung up on your belief in Pavlovian conditioning, train your dog to bring specific items (toys you assign names to) and then give each to a different member of your family or deposit them at different locations. You will quickly realize that the conditioned reflex explanation for a dog's awareness is a gross simplification.

Like wolves, dogs are also very much aware of who is who, who is where, and who is doing what. This awareness is an essential feature of both: enabling dogs to fit so well into our human social fabric and enabling the pack-hunting wolves to lead a communal life: moving and hunting together, sharing, etc.

There are other behavioral features of importance for the canid pack algorithm, e.g. dealing with hierarchy with minimal bloodshed. Occasionally fights break out, and even close relatives can be killed, but only rarely does one observe strict rank orders and real macho behavior on the part of dominant pack members. Instead, enforcement of established rank can be a low-key affair, where serious threat by a high ranking member is rare compared to the gracious acceptance of a lower ranking individual's signs of compliance or even submission. This is what in dogs makes it easy for wolfish families to form mixed, multi-species packs: humans, dogs, cats, goats, sheep, horses living in harmony.

Finally, we may ask: What about wolves at very low population densities as in most of Europe, where, for the past several centuries, just about every wolf was shot on sight? What about the lone wolf? Human wolf eradication programs go for the conspicuous individuals, and a pack raiding a sheep shed or bringing down a cow in a pasture is much more conspicuous than a single wolf that is forced to adopt the lifestyle of a fox. Thus, the wolves surviving at very low densities may well have lost their social competence, both in their genetically endowed propensities and in their social pack-living skills. Their social skills are practiced only toward their mates and young. When hunting, it appears they use the basic bag of canid tricks that foxes are known for: wandering around low profile, looking, listening and sniffing, then stalking, jumping, and chasing down whatever one can grab: a frog, a mouse, a rabbit, a hare—prey up to about one's own body size—eating a few berries and a couple of mushrooms along the way. And, when two lone wolves meet, they can be so overwhelmed with joy that they bounce around and prance off together as if they were thinking: Let us prey!

Thus, the social systems of canids and their hunting strategies can be considered a continuum from fox to wolf, with the coyote and jackal somewhere in between. The African hunting dog and the dhole of India may be even a bit further out to the extreme of pack life, a life which only few, if any, of our wolves can indulge in today. But, the special success of the gray wolf may well be based on this species' potential to live well like a dhole and still survive when forced to live like a coyote.

Lupification of Canids

When we talk about our own primate descent, about the hominization of Australopithecines, we are easily led to believe that our ancestors had nothing better to do than to leave their beastly existence behind and let those not worthy of becoming "humans" die out (Neanderthals, bushmen, or the like). In spite of accepting the new creed of Darwinian natural selection , we find comfort in our cherished belief to *be fruitful, multiply, replenish the earth, and subdue it… to have dominion over the fish of the sea, and over the fowl of the air, and over every living thing that moveth upon the earth*. In other words, instead of seeing ourselves as part of the complex system of nature, we continue to pretend to be the very crown of creation.

If wolves could dig up the dens of their ancestors in Europe, Asia, and North America, sniffing at the old bones of their dead and the bones left of their meals, what would they find? How would wolves view the lupification of their canid ancestors?

As Africa is today considered to be the cradle of mankind, the origin of canids (as well as their old parasites, the fleas) is traceable to North America. When that continent became disconnected from the other land masses, some of its ancient predators specialized into fox-like carnivores, presumably living on small rodents, insectivores, and insects, with a degree of omnivorousness. When, possibly driven by changes in global climate, early horses and other ungulates changed from leaf eaters to grazers, grasses started to cover large areas of the earth, and an evolutionary arms race started between grazers and grasses. The predators latched onto this new and evolving ecosystem, preying on the smaller, slower grazers and especially on their young. As these herbivores responded by joining together in large herds, developing communal defense behaviors, and outgrowing their predators in size, the smart, fox-like early canids had to catch up with their prey. They grew larger and stronger, to the size of coyotes and larger. As a counter strategy to the herding of ungulates around 10 million BP, canids "invented" long legs for high speed running, the prerequisite for hunting in a fast moving pack.

When the land bridge united North America with the Asian continent in the area we call the Bering Strait, horses and canids poured into Asia. The horses, as fast runners, did exceedingly well in the open grassy plains of Asia and Africa, and the canids thrived on the native herbivores, which had adapted well to predation by felids, but were at the mercy of the new pack-hunting ancestors of wolves, hunting dogs, and dholes. Thus, when the pack hunters moved into Asia and Africa, they joined or even replaced the big cats at the top of the food pyramid. Not only did they compete for the resources formerly controlled by lions and tigers, but they even attacked them and, if they failed to kill them, at least they killed their cubs. Only during the last few thousand years did humans propel themselves in mass to the top of the food pyramid, displacing the canid pack hunters.

The Ice Age as the geological epoch and the "Mammoth Steppe" as the biogeographical substrate (GUTHRIE 1990, Fig. 4) are most important variables in the evolutionary puzzle of the genus Canis, and, more recently, the genus Homo as well. Our understanding of these variables has changed dramatically in our lifetime. We are still far from a consensus about the causation and dynamics of Pleistocene geology, climate and ecology, however, but it has become obvious that many, if not most, of previous teachings were wrong, especially the image of northern Eurasia and America being covered by one gigantic ice shield that only temporarily gave way to a little green during the interglacials. The last interglacial, the Ipswichian of England, about 135 ka BP until about 70 ka BP, had a climate in Europe warmer than today, with hippopotamus wallowing in the Thames and Mediterranean vegetation flourishing in the valleys of the Austrian Alps. On the other hand, the grueling cold of the last phase of the Wisconsin (in America; Weichsel in northern Europe and Würm in the European Alps) peaked only 18,000 years ago.

Canine Humans?

So, what is the difference between a beloved golden retriever bitch, as a member of our household, and a shewolf as a member of a wolf pack? Let us look, point by point, at what we said above, under the heading Humane Canids: what made the ancient pack social system so successful was not a single life history trait, anatomical feature, or matter of physiology or behavior, but a whole array of specific adaptations that make communal action possible.

Humans, at least in Western cultures, live more or less monogamously, roughly as monogamously as most members of wolf packs. We share parental care generously, even among siblings and friends. Many humans behave the canine way, others still behave like chimps or lions, not necessarily humanely. In the human species we find a very wide range of family structures and a great variety of even more complex ("non-family") social systems. Our spectrum includes the solitary existence of saintly hermits, family bands, villages to cities, nations, etc., with many niches for canine companions. A blind person may depend on a seeing-eye dog, a family dog

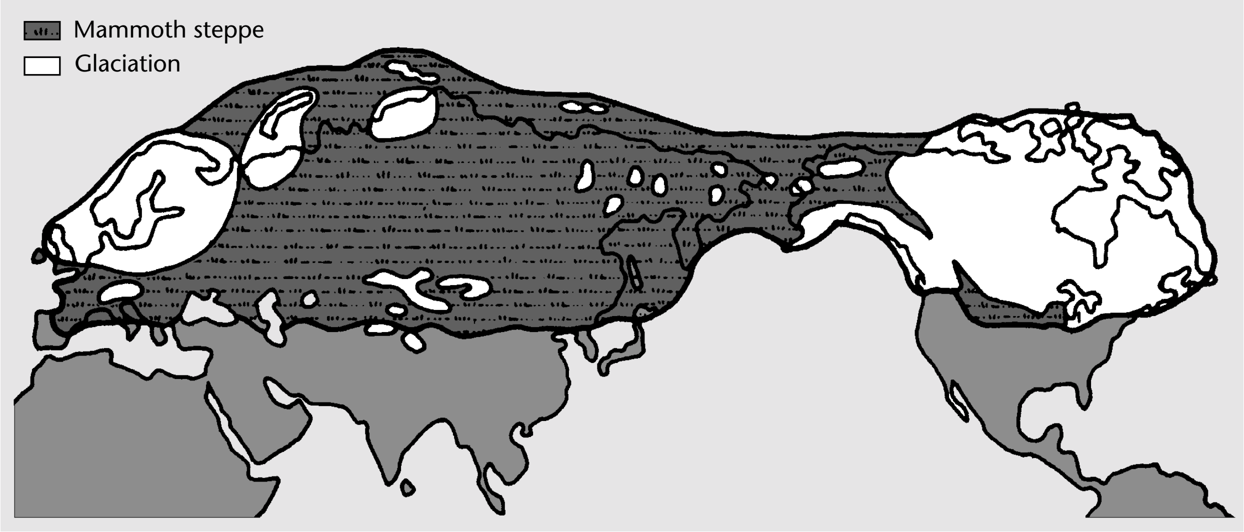

Figure 4: The "Mammoth Steppe" in the wider context of Pleistocene glaciation. The extent of the steppe varied over the last 2.5 million years and had been more extensive during glacial episodes and less so during interglacials, when varying parts of grassland were replaced by forests (after GUTHRIE 1990).

can be a great asset for a youngster, and a Dalmatian may not only serve as a fire department's helper in situations where humans are bound to fail, but also a beloved mascot.

Humans run neither as fast nor with as much endurance as wolves, but they walk their dog around the block several times a day, or take it along jogging, biking, or hiking. They let it sniff fire hydrants, trees, and the strange air when riding along in a car with its nose stuck out the window. On the other hand, most dogs' legs compared to those of wolves or working dogs are not suited for running and are even somewhat crippled. Not only dachshunds, bulldogs, Maltese, and Yorkshires act as if hobbled by their anatomy. Many a German shepherd champion is no match for a husky or greyhound on a long-distance run. Thus, many dogs prefer to lie on a windowsill and watch the world go by, having lost their wolfish striving for long-distance locomotion, as have most city dwellers, who no longer rely on their feet but on cars and elevators.

Joining dogs in communal hunting behavior was long reserved for pharaohs, royalty, and the upper class. Nowadays it is pretty much restricted to traditional Old English fox hunts with a pack of hounds, as sport for a few rich, to greyhound racing, as sport for the common man, and only exceptionally in the original, ancient mode: e.g., in the U.S., some still hunt with a pack of hounds—black bears and mountain lions, as well as squirrels. But today's stereotypes are the American hunter with rifle rack in his pickup truck and his retriever next to him, or the German forester with pipe and dachshund. But otherwise, hunting behavior by dogs is discouraged and subject to artificial selection: where local leash laws are not respected, strays are shot by game wardens or park police, or, at the very least, face an uncertain future in a pound. The only exceptions are a few breeds of so-called hunting dogs, (hounds, terriers), work/guard dogs (Dobermann, shepherds, St. Bernard, etc.), and the sporting group (beagles, fox terriers, golden retrievers, etc.), so long as they "work" under close human supervision.

Feeding on the kill? Well, what is in the food dish rarely involves much effort or opportunity to share or compete in a one-dog household. Although Fido still wolfs down his well-processed boneless meal, there is no need for him to regurgitate and look it over again. Once it's down, it stays down, thanks to the grinding action of the dogfood industry. To ensure our dogs' good teeth we buy special tartar-control treats, chewing toys, or a specially processed bone, piece of hide, dried pig's ear or ox penis!

The dog's social awareness is one of its greatest assets. Therefore, we remind you once again: contrary to the popular belief that canids are specialized in sniffing and have limited eyesight, they are constantly watching each other. A dog knows not only who is who but also who is where and who is doing what. This specific set of skills is a prerequisite for a dog's ability to know and recognize many different people. Ulysses returning home in rags after many years away and being recognized and greeted by his old dog has become the archetypical experience that repeats itself daily at many airports and train stations. And although dogs perform no obvious farewell ceremony, many show signs of sadness and depression after a beloved friend or any member of its family (its pack) has left.

A good family dog is well integrated into the social hierarchy and, provided there is a certain level of social competence among the human pack members, most dogs have no reason to even attempt to take over to become top dog and run the family.[9]

Domestication: Who Domesticated Whom?

The oldest remains of dogs, of a canid distinctly different from wolves, in the context of human activity are dated about 14,000 years BP, long before any trace of domesticated goats, sheep, and cattle (BENECKE 1995; SABLIN/KHLOPACHEV 2002). Thus, there is little argument that dogs are the oldest domesticated animal (ZEUNER 1963; SERPELL 1995). A word of caution, however; what do we mean by "domesticated"? In a most general sense: "no longer in its wild or natural state." But, were our own ancestors back then, long before they built permanent houses for themselves, less "wild" than the wolves they associated with? While canids are known to dig their own dens, and some of such dens may have been used by many generations, even over hundreds of years (THOMAS 1993), humans are apparently the only primates to make use of caves, and their association with dogs predates the construction of permanent houses by thousands of years. Is it not absurd to talk about the "domestication" of dogs by humans who had not yet any permanent domiciles ("domus")?

What are the signs of domestication in the archeological record? In mammals it is usually a reduction in overall size, a foreshortening and rounding of the skull, and faster sexual maturation. Once the ranges of variability of the assumed wild ancestors and those of the ancestors of our domesticated forms no longer overlap substantially, we assume that the exchange of genetic material between those two populations was reduced or interrupted by human interference and control.

Are such domesticated forms now members of a different new species? Let the professional taxonomists fight that out. It can get tricky, however, depending on whether you ask a morphologist, paleontologist, ethologist, or geneticist. The most common criterion for belonging to one species is interbreeding and having fertile offspring. But where do we draw the line between ancestral species? Could we interbreed with Neanderthals? In canids, we have a different problem: apparently, all species of the genus *Canis* can interbreed, e.g., the red wolf, *C. niger,* has revealed itself as a stable hybrid between the gray wolf, *C. lupus,* and the coyote, *C. latrans* (WAYNE/JENKS 1991).

In recent years, geneticists have developed a number of tests as measures for the degree of relatedness by comparing differences in the DNA of individuals and populations. Genetic differences between wild and domesticated forms can be estimated in various ways, and genetic distance can give us some idea of the elapsed time since two forms separated. Based on such studies in humans, for example, it has been assumed that the common ancestors of chimpanzees and early man split about 6 Ma BP. There is less agreement concerning the first *Homo sapiens*, the mother common to all modern humans; some scientists believe that this hypothetical Eve lived 160 ka BP in Africa, and our hypothetical Adam lived there 70 ka BP, but it will take a while before we come close to reconciling the many contradictory "facts"; that is, particular observations of the fossil and genetic evidence.[10]

New results, even more controversial, although supported by considerably larger data sets than many estimates of our own ancestry, indicate that the split between the ancestors of wolves and jackals occurred about 1 Ma BP. This study, based on the analysis of mtDNA (mitochondrial DNA) from various canids, was performed by Carles VILÀ et al. (1997, 1999) at the laboratory of Robert WAYNE at UCLA. mtDNA from 67 breeds of dog showed a high degree of similarity to that of wolves (as represented by 27 wolf populations from Europe, Asia, and North America), clearly supporting the hypothesis that dogs are descendent from wolves (not from the golden jackal or other canids, as Darwin, and many others had assumed previously).

But the most spectacular of WAYNE's results is that the first split between dogs and wolves dates back roughly 135 ka BP, nearly TEN times further back than indicated by any bones or any paleontological evidence found thus far! And, based on the same reasoning that traces our Eve and Adam back to Africa, WAYNE's data indicate that dogs are related closest to wolves found today between France and western Russia, and not to those in the Near East, where many of our domesticated animals and plants are assumed to have originated.

There is also indication of later influxes of wolf genes into dog populations, and this process is still going on in our time. It appears to us especially significant that the first dogs separated from wolves in an area and at a time when Neanderthals were the only hominids within the distribution range of wolves, even long before the time the hypothetical children of African Eve started to spread into Eurasia. Thus, the fate of dogs and humans has been intertwined for a very long time indeed.

Hominization and Canization

We now are confronted with this startling temporal and geographical coincidence between the emergence of mankind and dogkind, between hominization and canization. Reconsideration of past and current concepts of domestication has become inescapable. Even the term domestication has the wrong ring, since the meeting of wolves and modern humans predates, by far, anything that could be considered a human habitation in the form of a *domus* (Latin for house). Canids' use of dens dates back further. Consequently, instead of domestication, we should talk about "cubilication" (*cubile*, Latin for den[11]) as suggested earlier (SCHLEIDT 1998) and wonder who cubilicated whom.

From a biologist's vantage point, the intertwining process of hominization and canization makes sense only if viewed as coevolution. Whereas the evolution of man, our primate heritage, has attracted attention ever since the publication of Darwin's *The Descent of Man*, the evolution of wolves and dogs has remained a particular topic for paleontologists specialized in Pleistocene carnivores. *The descent of dogs,* to the best of our knowledge, has not been integrated into the descent of modern hominids. Consequently, we may ask: What was the state of affairs among our ancestors when some wolves separated from their conspecifics and became the immediate precursors of dogs?

At that time, Neanderthals were wandering around Europe, apparently having some success in killing mammoths, horses, and reindeer. Few animals can live on meat alone, however, so it has been proposed that Neanderthals similar to present-day gatherer-hunters also collected other foodstuffs (fruits, greens, tubers, etc.). In addition, they may have raided bee hives and underground grain stores of hamsters and other rodents. Unfortunately, there are many more artifacts attributed to Neanderthals than bodily remains, and much of what is being taught one day by one school of thought is challenged by another the next. Every new find seems to raise more questions than it answers.

Well, what about the state of wolfkind when Neanderthals roamed the "Mammoth Steppe", the Eurasian tundra and grass steppe ecosystems which reached from Spain to the far east of Siberia, and at times continued into the continent of North America? Although the mammoth must have been an impressive sight, it was not the species that constituted the greatest amount of biomass in that ecosystem. Mammoth bio-mass presumably could have been equaled by tasty rodents: lemmings, voles, squirrels, etc. and by the most abundant species of wolf food, the reindeer. Nowadays, Western culture's Santa's team, a few specimens in various zoos, and occasional images provided by National Geographic are all that is left of a species that was once part of one of the largest ecosystems on earth. Wolf packs, very likely, were an important part of that ecosystem.

Wolf: The Pastoralist

In fact, in Siberia, before it became a national sport to shoot wolves from helicopters, human pastoralists of reindeer, basically living off the herds they followed in their annual cycle of migration, not only tolerated wolf packs following their herds, but even considered those wolves to contribute to the breeding of better reindeer. Humans select only the best specimens for slaughter, whereas wolves take only what herd owners would never touch and would not even feed their own dogs: placentas on calving grounds, weaklings, the sick and the aged. So, in the ancient form of reindeer management, prior to governmental control, taxation, and special funding, and before bounty hunting and fur trade, wolves could have played a similar pastoral role: eliminating the unfit and keeping away the big cats, bears, and hyenas. Very much like today, in shepherd-controlled sheep herds, where the shepherd eliminates the unfit and dogs guard their herd from attacks by wolves.

Thus, among mammals, Eurasian wolves can be viewed as the first true pastoralists, ahead of human pastoralists by tens of thousands, hundreds of thousands of years. Wolves ability to hunt as packs, to share risk fairly among pack members, and to cooperate, unsurpassed by any of the big cats, moved them to the top of the food pyramid on the Eurasian plains.

It is noteworthy, however, that those wolves never became specialized big game hunters like the large cats of Africa. Wolves retained their full repertoire and zeal for hunting small rodents, taking birds and eggs, and in addition berries of various kinds, tending toward a degree of omnivorousness to which many human steak fans would pale in comparison.

Reindeer, traveling in ancient times, over hundreds of thousands, maybe millions of years, seasonally in vast herds in the realm between what is now Spain and eastern Siberia, and at times crossing the Bering strait into the North American continent, could well have coevolved with wolves in the sense that prey and predator became interdependent, symbiotic, as for example aphids and ants.

Some ants keep aphids throughout the winter in their nests, and, in the spring, when the first leaves appear, they take their aphids out to pasture in the trees. There, the aphids thrive and multiply under the close supervision and even protection of their ants, and, in exchange, they repay the ants service with aphid honey.

F. E. ZEUNER, reasoning about the domestication of dogs in his famous 1963 *History of Domesticated Animal*, after a careful comparison between herding behavior of wolves to single out potential prey and the herding behavior of sheep dogs, stated that "*the wolf and the pastoralists might be seen to have much in common.*"(ZEUNER 1963).

Man: The Reindeer Hunter

Could Neanderthals around 135 ka BP, having made it successfully through several ice age climate changes, presumably mainly by scavenging and occasionally killing big game, also have entered into the hypothetical ecosystem of the large herds of reindeer, protected by wolves? Had Neanderthals already ganged up with canids, even supplanting the wolves at the top of the food pyramid?

A single Neanderthal, even armed with fire, spear and stone weapons and with all his strength, would have been no match for a pack of wolves out to have him for a meal.

As a group, however, Neanderthals undoubtedly could keep a pack of wolves at bay, wound and even kill several members of the pack, convincing them that attempts to obtain human meat were not worth the risk (also still the best argument against human cannibalism as a stable strategy). Thus, we can assume that early Eurasian hominids, e.g., *Homo erectus,* armed with fire and spears (THIEME 1997), at least since around 400 ka PB, had the same mutual relationship with wolves as exists today in comparable cultures and situations. A single wolf may occasionally gulp down a little Red Ridinghood, but the hunter with his gun will surely get him. So, what would Neanderthals and wolves have gained from a cooperative coalition?

Since, at this moment, we lack evidence for the use of tamed wolves as hunting companions, let's look at other alternative uses. Pups could have been used as baby substitutes, hot water bottles, and toys or playmates for human children (GROVES 1999). Adult wolves, however, were probably a risky addition to a Neanderthal family. A single Neanderthal out alone would have been no match against his own wolf's jaws in a sudden flare-up dispute over rank, and it is hard to imagine that a man would take the risk of becoming outranked by his former companion much less his former servant. So, in the end, in the ensuing struggle, the bond between such a brave hunter and his wolf would have been broken: either the hunter loses his face, literally cut away by his former servant's fangs, or the wolf loses its skin.

In a fair comparison, Neanderthals were superior to wolves only in (1) having greater cognitive ability and foresight (reflected especially in their scouting and scavenging skills), (2) seeing better at longer distances (having an eye level twice that of wolves, able to cover four times an area in the steppe), and (3) being able to hit a distant target. The latter is especially significant in dealing with herds of ungulates, which tend not to run away from every little disturbance, but approach a serious predator with curiosity:

American Indians pulled over a wolves hide to get close to a herd of buffalos , and Bushman fooled African undulates using similar tricks. Even hiking on the Alpine high pastures with a dog can easily provoke such a mobbing response in cattle.

Another common behavior among herding ungulates is standing one's ground: When a single individual has been separated from its herd, it tends not to run from a small predator, apparently not to provoke pursuit. Standing still, however, it becomes an easy target for a skilled hunter's spear. Thus, a group of Neanderthals could have eased their way into the thriving business of wolf pastoralists, at first only as junior partners, and have shared the plenty of those large reindeer herds without raising the level of intra-pack social friction.[12]

How could all this have happened around 135 ka BP? The flow diagram at the very end of this paper (Fig. 6) stakes out the time–space continuum the past 60 Ma BP within three continents: North America, Africa, and Eurasia as centerfield where "Man meets dog" in a coevolutionary process. Glaciers had receded around the middle of the Riss glaciation, coniferous trees had reappeared, and after another advance of the glaciers and loess steppe, deciduous trees thrived in Europe's Riss-Würm interglacial period. All this must have resulted in major population changes, from the smallest plants and insects to the largest mammals. We are still far from understanding all the consequences of the dramatic changes of climate, and the interactions of even the most relevant biological variables in that complex ecosystem and its effect on evolution.

Especially our understanding of the climate of the past has dramatically changed during recent years, due to new insights into the effect of continental drift on ocean currents and air streams, and new records of the past climates from pollen analysis, and cores from drilling deep sea bottoms and ice caps. Thus, "Pleistocene" is not simply a past epoch of grueling freezes, subdivided by brief interstadial and interglacial warm spells; rather, "*we are*" in Pleistocene. What has been named "Holocene"—our current epoch in which humanity has begun to change the face of the earth—is just an interlude before the next cold phase (Fig. 5).

There are many more variables of fundamental importance for the evolutionary process: food plants: e.g., lichens and grasses, predators: notably the big cats, insect pests, infectious diseases, etc., not shown in this schema for reasons of clarity. But, at least, we constructed a basic framework for the coevolution of hominids and canids: depicting the global time–space continuum on a logarithmic time scale, coding basic climatic conditions and indicating the confines of the continental plates and narrow land bridges. Within this framework species can be added or deleted, as it best suits our needs to understand the weave of nature, where ultimately everything is connected to everything.

Unfortunately, the image of the ice age landscape as endless plains of inhospitable snow-covered permafrost, bordered by rolling blizzard swept steppe and glaciers is still deeply engrained in teaching and described in textbooks. Only slowly do we gain, by a more detailed, fine-grain analysis of local geography, climate, and vegetation, a more realistic picture of that important time span of human history. Yes, the winters, especially in areas covered by glaciers were long and hard, but in summer the temperature in the valleys and in the plains rose nearly as high as at present and supported vegetation similar to that of Central Europe today. And, in the interglacials, the temperatures were much higher than today, and areas now famous as European ski resorts supported Mediterranean vegetation.

One more point about climate is commonly not even mentioned, namely that the remarkable Pleistocene fluctuations did not roast and chill our ancestors and their dogs in a 100 000 year rhythm. As the trees, grasses and flowering plants did not die out, but moved gradually to stay within their preferred ranges of temperature and humidity, so did the animals, only faster, because they move with legs and not by seeds and their selective survival. Considering for how long *Homo erectus* type hominids were residents of Eurasia as far as China and for how long Neanderthals did very well for an amazingly long time, it is hard to believe that they disappeared without leaving a trace within the human genome. We personally favor the idea that we are not the descendents of an African elite, but a mixture of "the best of all our ancestors", wherever they were.

Another important aspect is that, by no stretch of the imagination, should we think that *all* wolves got attached to *all* reindeer, and that *all* Neanderthals lived off mammoths and cave bears at first and then suddenly switched to reindeer to become helpers to wolves. However, there was already some flint trade going on across Europe, and along such routes, tame wolves could have changed hands, or moved with humans, as human genes and customs spread from one group to the next.

Wolfkind Today

Once a few Neanderthals had learned to live with wolves and adopt the pack algorithm (going beyond the close ties of kinship, learning to cooperate closely, and sharing risks) many alternative ways to make a living became available. Within this process of coevolution, technology transfer and diversification began to thrive. Humans became better gatherers, better hunters, more successful fishermen, gardeners, astronauts, you name it. Wolves became hunting companions, guards, sled pulls, beasts of burden, baby substitutes, toys, food, human substitutes in experiments, and the first "astronauts" to circle our planet.

Today, man sits atop the food pyramid throughout the entire world. Reindeer are mostly out of sight, and of all the non-human mammalian species that roamed Eurasia 1 Ma BP, wolves were the most successful in increasing their numbers as dogs, that is, presumably followed by the aurochs

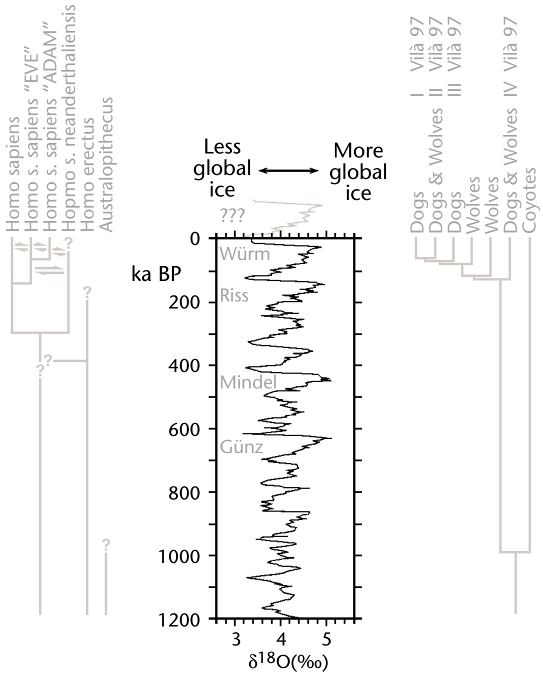

Figure 5: Climate and evolution of canids and hominids. In the center an estimate of global climate changes during the past 1.2 million years, effecting temperatures, ocean level, and subsequently, intercontinental faunal exchange (the extent of polar ice caps, based on oxygen isotope ratios in cores samples from the Ocean Drilling Program; van HUSEN 2000) Evolution of canids (left tree, estimates based on VILÀ et al. 1997) and of hominids.(right tree, based on various current sources). The labels Würm, Riss, Mindel and Gunz refer to the four major Alpine glaciations, where Würm corresponds to the North-west-European Weichsel and to the North-American Wisconsin glaciation. We could not resist extrapolating to the future glaciation (indicated by "???"), based on the familiar algorithm: "The sun will certainly rise tomorrow because it always did".

now represented by our cattle, or by sheep. In fact, wolves conquered Africa (e.g. as the Basenji infringed on the *Lycaon* range) and used humans as a vector to get to Australia (dingo), Polynesia, and Antarctica.

Wolves meeting humans in a phase of the latter's apprenticeship in wolf pastoralism and, in a subsequent process of coevolution, wolves becoming dogs and early humans becoming modern man, is a good alternative hypothesis to the current theories of domestication with man conquering beasts, including wolves, through cognitive superiority and to the bootstrapping theory of hominization with man domesticating himself (e.g., BUDIANSKY's idea that wolves weaseled their way into our hearts as scavengers).

Homo Homini Lupus?

"Man to Man is an arrant Wolfe" (HOBBES 1651). This pessimistic view that human nature is essentially brutish, antisocial and selfish led Thomas HOBBES (1588–1679) to recommend, in his treatise *Leviathan*, an all-powerful central government to impose order, ensure justice, and prevent men from destroying themselves in bestial fashion (HOBBES 1985). Homo homini lupus has been cited whenever humans turn on each other, attacking for no defendable reason, plundering, robbing, raping, or killing. Early accounts of our forefathers brutish behavior in the Bible and stories throughout history describe such atrocities, and have not ended today.

Are Wolves That Beastly?

The human is like a monkey to other humans. Is the wolf like a human to other humans? Well, there is some overlap, no doubt, and some dogs behave more humanely than some humans. Or, closer to the biological evidence, Homo homini Pithecus—Lupus homini Homo?

Final Remarks

This is not a POPPERIAN attempt to falsify any specific hypothesis concerning the evolution of humans or canids, but rather a proposal of an alternative that we find equally reasonable. We advocate the exploration of this alternative in the belief that within the complex process of co-evolution at different times and localities, a variety of interactions between humans and canids could have occurred that shaped their future interdependence.

The canids also known as (wild) "dogs" have their roots in North America. They were forest dwelling carnivores, originally about the size of a fox, with a leaning toward omnivorousness, akin to the feeding habits of the bears, their closest relatives. When grassland opened and herds of grazing ungulates, notably horses and antelopes began to dominate the open plains of North America, some early canids moved into this new habitat. A multitude of swift canid predators co-evolved with the herding ungulates, and around 10 Ma BP, they started to cross into Asia, Europe, Africa, and back into North America. Thus, the canids—the wolves, jackals, coyotes (all Members of the genus *Canis*), and the aberrant "wild dogs": the African Cape hunting dog, and the Asian dhole—became part of the rich palette of predators and scavengers, coexisting and competing with the cats, hyenas, bears and mustelids.

The advantage the canids had over their competitors was their special ability to deal with the herding strategies of the ungulates. While the big cats had become specialized for stalking and surprising their prey in a sudden, forceful attack, thus nipping away stragglers and individuals on the margins of a "selfish herd" (Hamilton 1971), the "wolf-type canids" were able to keep pace with the herds, move fast and enduringly, and make most efficient use of every single kill by their ability to "wolf down" a large part of the quarry before the scavengers had detected the kill. Today's "wolf-type canids" are considerably more social than any other predators; they generously share their loot with other pack members, a trait that dates back to around 5 Ma BP, to the common ancestor of the three social canids: wolf, cape hunting dog and dhole. The Genus *Canis* apparently evolved in Asia, and *Canis lupus*, the circumpolar big "wolf", as a species distinct from the coyote, appeared 1 Ma BP. Thus, it appears that the big cats' position on the very top of the food pyramid—with the lion as the "king" in the animal kingdom—had been relinquished to the social canids already several Ma BP. In fact, canids became herd followers, exploiting an ecological niche that anticipated early forms of pastoralism. And they never lost their omnivorous habits, their skills for hunting small prey, and at times of need their ability to survive by scavenging. With this wide range of abilities the social canids remained the dominant predator, until the invention of firearms propelled humankind to top of the food pyramid.

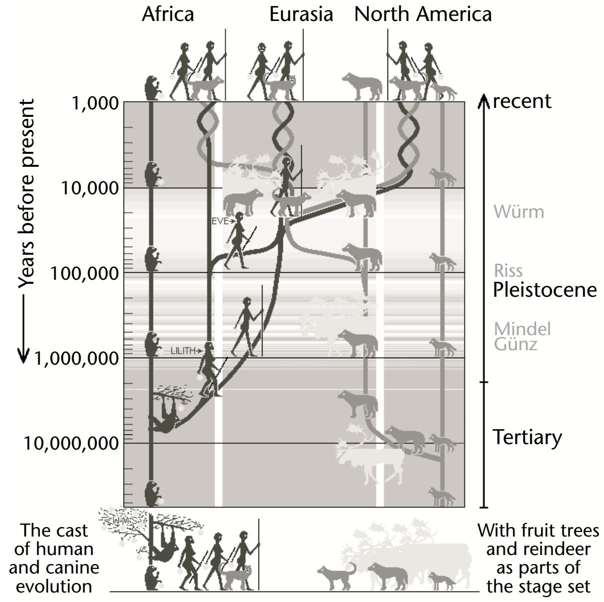

Figure 6: Graphic summary of the authors' reading of the current state of the evidence concerning canid and human coevolution.

As noted above, humankind separated from chimpanzee-like tree-dwelling and fruit-eating ancestors in Africa around 6 Ma BP and moved as true humans (Homo *erectus)* into the open savanna. In the absence of fruit trees, early humans turned into omnivorous gatherers and scavengers. Thanks to their superior brain power, they learned to discriminate among a multitude of resources, to avoid peril, e.g., by carrying a big stick and speaking softly (at least, at first) and to bluff the fierce predators into deserting their quarry. As cunning scavengers, they moved into the plains of Eurasia during the mild interglacials of the Ice Age, culminating in the successful Neanderthal of Europe and adjoining Asia. Meanwhile, around 150 ka BP the tribe of the legendary African Eve had emerged, and her daughters entered the Neanderthal domain. At this point, a strange coincidence occurred: at some time during the last ice age, our ancestors teamed up with pastoralist wolves (Figure 6). First, some humans adopted the wolves' life style as herd followers and herders of reindeer, horses, and other hoofed animals. Wolves and humans had found their match, and "dogs" diversified and moved into other human cultures. Of course, not all wolves had become pastoralists, and neither had all humans. In the fringes of their range, humans remained gatherers and scavengers, or specialized as fish–hunters, hunter–gatherers, hunter–gardeners and, ultimately, became agriculturists. And dogs complemented human skills and satisfied human needs in many ways beyond herding and hunting: as beasts-of-burden, guards, hot-water-bottles, diaper service, and as true trusted companions, e.g. as seeing-eye dogs.

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Notes

1 Because of the hypothetical, and sometimes highly speculative nature of the interpretation of the paleontological record of human evolution, exaggerated claims, and frequently changing emphasis, we restrict our review to a few essentials and abstain from citing specific references for specific statements.

2 Following the common practice of balancing the paucity of the archeological record by generous interpretations in plain language, we take the liberty of borrowing for our brief digest of human evolution a few of those popular terms.

3 The paleontological record of canid evolution is quite rich, compared to human remains. Our review is based mainly on JANIS/SCOTT/JACOBS (1998) and MUNTHE (1998).

4 Jane GOODALL im Interview: *„Ich hatte schon während meiner Kindheit einen wundervollen Lehrer: meinen Hund Rusty."* (BAUR 2001).

5 Sociobiologists have tried to convince us for nearly a quarter century that individual success is the one and only basis of evolution—ignoring the wisdom of beekeepers, who knew of multiple matings of the queen all along.

6 Of course, many different subspecies have been described, and we can well assume that in addition to pelage and skeleton behavioral traits vary as well. In the other extreme, we face the puzzling fact that all member of the genus Canis apparently can interbreed, and one may wonder whether the "genus" Canis should be considered a single species.

7 More generally stated: social predators should have more healed injuries than solitary predators. Of course, in close association with humans, tamed wolves and dogs also have the potential to be subject to abuse by humans (e.g., BIRD/BIRD 1937), but also the benefit of being nursed back to full strength, as observed in the archeological record (e.g., PUCHER 1986).

8 Catalogued as USNM (US National Museum, S.I., Washington, D.C.) 215320; further details in MUNTHE (1989).

9 Of course, we all know of cases where especially males dominate their family by force or where bitches rule by superior social competence!

10 A more detailed discussion of the "Out Of Africa" hypothesis does not appear feasible, considering the scarcity of early *Homo* fossils (compared to the fossil record of *Canis*). Thus, the readings of the human record are still highly diverse and personal. For example, the recent discovery of modern human fossils in Ethiopia dated 160 ka (CLARK et al. 2003; WHITE et al. 2003) only supports a presence in that region at that time, but does not falsify the multi regional hypothesis (e.g., WOLPOFF/CASPARI 1997).

11 Same root as in cubicle and concubine.

12 The association between humans and reindeer in Pleistocene Europe had early on led to speculation that reindeer herding is an ancient form of subsistence (JARMAN/BAILEY/JARMAN 1982). Even though this view has been contested (e.g., BENECKE 1995), in our considered opinion, this issue is far from resolved.

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Elina Vladimirova/John Mozgovoy

Sign Field Theory and Tracking Techniques Used in Studies of Small Carnivorous Mammals

Abstract

The article is devoted to the problems of animal behavior. The population stability bases on information, received by animal through their habitat characteristics without direct visual contacts with other animals. Behavioral reactions may have the numerical expression and can be calculated depending on the research tasks. Formalization of the animal activity implies simultaneous consideration of the following five parameters of the sign field: magnitude, anisotropy, intensity, the equivalent distance and the value of a given object. For a mammal, the equivalence of really different objects is established on the basis of equivalence of the animal's interactions with the objects.

Key words

Adaptation, sign field, footprints, information, environment.

Introduction

The first zoologist who use snow tracking for studying mammalian ecology and behavior was Alexander FORMOZOV from Moscow. Snow tracking is the most effective technique for determining animals' home range. The theory that we are about to illustrate provides an explanation for phenomena of intrapopulation and interspecific animal communication. We will discuss small predator mammals that live in the wild in the environs of Samara, Russia. The species under consideration include the red fox (*Vulpes vulpes*), the pine marten *(Martes martes)*, the ermine also known as short-tailed weasel *(Mustela erminea)*, and the least weasel (*Mustela nivalis)*. Studying the ways animals accumulate, store and pass on information brings us closer to the understanding of communication mechanisms for the above mentioned species. Our research focused on integration processes involving small predatory solitary mammals.

We were mainly interested in studying those cases of ethological information exchange where animals obtain information through their habitat characteristics without direct visual contact with other animals. The proposed theoretical statements are based on many field observations in which the authors used original techniques.

The semiotic status of the genetic code, interaction of animals by means of signs, and semiotic problems in general, were discussed in many serious works (SEBEOK 1972, 1976, 2001; KULL 1998, 2000; EMMECHE/HOFFMEYER 1991). The processes of encoding biological information on biochemical, biophysical, molecular-genetic and cellular levels are explained in semiotic context or through notions that, for the past few decades, have been used by semioticists and natural scientists likewise. For the branch of biosemiotics dealing with such processes Thomas A. SEBEOK suggested the term *endosemiotics* (SEBEOK 1976, pp149–188). The other branch deals with ethologic, ecological and communicational schemes developed in the context of semiotics. In SEBEOK's classification, this branch is called *exosemiotics* (SEBEOK 1976, p156).

SEBEOK came up with the idea of transforming endosemiotic codes into exosemiotic ones (SEBEOK 2001, p62). Although it seems unlikely that such transformation will be possible in the near future, current ethological, ecological and socio-biological researches can actually open 'the black box' of animal communication from the 'exit' side without addressing the genetic code in general or specific codes of instinctive responses (i.e., behavioral responses characteristic of given animal species). On the molecular-genetic level, we have nucleotide sequences that encode the synthesis of particular ferments. On the ethological level, we deal with 'genetically programmed' species-specific forms of environmental and behavioral perception. In other words, the issue of correlating species-specific genetic information with species-specific forms of behavior is never raised in ethological studies of real objects. Our experiments, however, were based on the assumption that such correlation exists, and in theoretical modelling we used the concept of *species behavior stereotype*.

In case of direct contacts, sign interaction between animals may take the form of a 'dialogue' or transfer of information to a specific addressee. Besides, animals of many species remain solitary for the most part of their life and interact through their informative environment. Through direct contacts, animals pass on significant information about their condition and environment; an animal may contact its partner deliberately and expect it to respond. More often, however, we witness a situation where information is passed on to animals inhabiting the same or adjacent territory without any communicative intention of the sender who changes its habitat in the course of its natural life. Later on the information is "read" by a recipient animal which, in its turn, makes some changes to the environment and leaves information on its own life activity for visitors to come. The information on animal life activity is, therefore, accumulated and stored in the environment for a long time. To an individual animal such information may characterize its habitat, other individuals or acts of communication between other individuals if there have been any. Our field research has demonstrated that, for any particular animal, traces of life activity left by the animal's conspecifics sharing the same habitat are more important than abiotic information.

A scientist that uses the technique described below for studying sign interaction between animals, does not deal with their habitat as such; rather, he or she deals with an informative sign field activated, in its perception process, by an animal's movement response. While a recipient animal is moving around in the sign field of its own or in that of a group, sign information is both read by the recipient, and produced to be read by other individuals that may visit the territory later. The sign field technique allows to split up the continuous information flow into "quanta" in which signifiers correlate with the signified. Therefore, this technique takes into account both the quantity and the physical form of sign information. It allows to measure sign behavior, mathematically process observation results, and model automatic regulation based on sign interaction of individuals. Buy using this technique one can simulate, in the form of field parameters, the real variety of elements comprising the information continuum. This is done, as much as possible, on the basis of perception of environmental sign information by its natural users.

Jakob von UEXKÜLL demonstrated the unique character of the perceptional world of an individual animal (UEXKÜLL 2001, p108). To describe the perceptional that is experienced by different species, he used the term *Umwelt*. We support UEXKÜLL's idea that animals' perception of reality is subjective. In our studies of this subjectivity we attempted to use calculations. This subjectivity accounts for the differences between sign fields of individual animals of the same species living in the same habitat. Parameters of biological sign fields are measurable. For a given animal, its sign field characteristics are also determined by the species it represents and the condition of its habitat. Communication process integrates the animal populations and, by doing so, balances the ecosystem structure.

Solitary mammals living in the wild often communicate by leaving unaddressed "messages" which are "recorded" in various objects and events of their environment. As a recipient animal moves around, any such message takes the shape of a succession of signs which is somewhat similar to a "text line". In the process of perception, the sign information is actualised by the recipient in the form of a chain of movements. Within the limits determined by the species and actual motivation of the recipient animal the message may be polysemic.

Inborn behavior mechanisms and specific experience acquired by an animal in ontogenesis ensure that the animal will, in some way, respond to environmental signals with its movements. To an extent, the boundaries of such experience are determined genetically, but they can vary a lot. It is the "learned" behavior component that accounts for a big difference that is sometimes observed between the inner worlds of two individual mammals. In the long run, behavioral polymorphism of individuals in a population of mammals provides for higher stability of ecosystems (MOZGOVOY 1976).

As we move on from studying inborn forms of animal behavior to studying learned behavior (i.e., behavior acquired in ontogenesis), it is important to remember that semiotic information should be distinguished from information in general. In information processing no new information is generated, the output being obtained from the input by carrying out pre-set operations. No new units of information with the meaning yet to be interpreted are created (FRUMKINA 1995, p103).

A number of issues of wild life ecology can be successfully addressed with a different approach which uses the concept of "message" without limiting the code boundaries for the information sender. This approach is supported by an Italian semioticist Umberto ECO who distinguishes between *information* and a *sign message*. According to ECO, a *sign message* has connotations emerging from the recipient's life experience, whereas *information* of any kind can be received by a properly tuned non-living mechanism. "A message that has no indications to the code used by the sender" can still be understood either on the basis of its "inner context" or from the "general communicative situation" (ECO 1998, p48, 70–73).

The theory of *biological sign field* has been confirmed by empirical evidence. The related techniques have been successfully tested. We believe that practical significance of the sign field theory goes beyond the scope of environmental science. The theory makes it possible to take into account both the physical form and the quantity of sign information in hierarchically structured semiotic systems.

1. The Biological Sign Field Theory As an Ecological Model Used in Studies of Mammals

According to N. P. NAUMOV, a biological sign field is "the total environmental impact of mammals that causes structural changes in their habitat" (NAUMOV 1977, p339). The authors of the related field research technique define a biological sign field as "a spatio-temporal continuum which is formed by a functioning ecosystem and, at the same time, determines the functioning of this ecosystem" (MOZGOVOY/ROSENBERG 1992, pp8–9). The function of a biological sign field is to inform animals of the environmental conditions, as well as the state of ecological systems. A sign field represents informative and communicative interaction between mammals and their environment. This interaction is studied from the sign information recipient's point of view (VLADIMIROVA 2002, p204). A specific sign field can be linked with an individual, a population, a specific group within a population (e.g., age or sex group), a co-adapted complex of environmentally close species, or a bioceonosis.

The formulation of the biological sign field theory in 1992 by J. P. MOZGOVOY was preceded by many years of his studies of mammalian behavior: MOZGOVOY had been collecting his data by tracking animals in winter since 1961. In wildlife ecology the method of collecting data by following footprints and marks that animals leave on the snow is known as FORMOZOV's and NASIMOVICH's technique. It can be used to study various parameters of mammalian life activity during the winter (NASIMOVICH 1955; FORMOZOV 1959; OSHMARIN/PIKUNOV 1990). This technique, however, fails to provide the means to cover a very important aspect of ecosystem functioning, namely the aspect of passing on information. This drawback may be eliminated by the use of "elementary" movements of animals as units that ensure consistency of results obtained by the snow tracking method. An elementary movement can be a response to the perception of sign field objects (external cues) or to inner stimuli determining the dominant motivation of an animal. Choosing elementary movements as units of field material is a distinctive feature of the research method described. Ability "to read" animal footprints is not, however, sufficient for studying animal behavior in the wild. The researcher must have clear-cut objectives and some kind of elementary structure units to measure animal behavior. A serious research needs a strong theoretical basis. The theory of a biological sign field of mammals may form such a basis (MOZGOVOY/ROSENBERG 1992, pp30–31).

The main challenge of applying this theory consists in maximizing the objectivity of studying movements of mammals in the subjectively significant environment. A researcher must not substitute his or her environmental perception for the animals' perception of the world. The objective interpretation of animal activity presents two methodological problems. The first one is the difficulty of "calibrating" environmental objects and events that provoke or may provoke animals' movement responses. It is difficult to determine the equality or inequality of signs for animals motivated in a certain way. Solving this problem would allow to take measurements. The second problem is the difficulty of determining the boundaries of the "quantum" of behavior which represents a movement response to a particular environmental cue (object or event). A researcher relates any such cue or sign perceived by an animal to an elementary movement response called a *drive*.

When collecting field material the researcher follows the footprints left by an animal and registers all environmental objects the animals orient themselves by and respond to with a movement. Learning to tell the species, age, sex, motivation and functional condition of an animal by looking at its footprints on the snow, or to decide how fresh the footprints are takes years of field observation practise. A good observer should be able to identify those elements in the environment that have provoked a particular movement response of an animal. Animals have certain species behavior stereotypes. The knowledge of these stereotypes allows an experienced researcher to relate the animal's movement activity in each particular situation to a particular kind of environmental signals and/or a particular sort of inner motivation. Wild predator mammals are quite "thrifty"—they mostly respond with a movement or some change of activity type to those environmental signals that carry a certain meaning to them. Thus, a good knowledge of wild life ecology is a prerequisite for the use of sign field technique. It will be of little or no use to a researcher lacking experience in field observation.

The sign field theory views animal behavior as a succession of discrete movement responses (drives) which are determined by two sets of factors, internal and external ones. The internal factors include the animal's species, the inborn power of its receptors, its genetic memory, individual characteristics (e.g., life experience, nervous system type, age and sex), its motivation and general behavior conditions in a particular situation. The external factors are environmental cues taken by the animal, which include the signs that indicate the population condition. The 'elementary' movement responses (drives) are chosen as key elements of analysis. A number of examples will be given later in the article.

Movements of a wild animal may be unguided by any visible landmarks. In such cases the string of footprints usually twists. Most of the time, however, animal movements *are* guided by some events or objects such as micro-relief elements (hummocks and hollows), shrubs, tufts of grass, patches of ice, other animals' paths, snow burrows, traces of conspecific animals' feeding, cleaning or relaxation, ski-tracks, traces of birds etc. Animals go straight to such objects. The same object may provoke different movement responses in the same animal. For example, a fox smelling or hearing a rodent under the snow, may respond to this smell or noise in four ways: it may stop and prick up its ears, it may also stalk, jump and try to catch the prey. Although each of the above mentioned drives can be viewed as a combination of even simpler elements or movements, counting elements consisting the drive is not relevant for a researcher, unlike counting drives—the movements which create certain behavior stereotypes in animals of a given species in situations similar to the one described. Very often the movements of an animal can be correlated with particular events in its environment.

We ignore the signified objects that cannot be related to particular footprints on the snow, which may be seen as a drawback of our method. We make a comparison between informational interactions of various individuals and/or groups with their environment. Therefore, we believe that we can leave out as unimportant those examples of animals' environmental perception which have not provoked any movement response, just as we reduce the numerator and denominator of a fraction in carrying out multiplication and division operations.

Snow tracking technique presents a challenge for those urban citizens who have no winter outdoor experience in the wilderness or cannot ski well. Most city people have a vague idea of animal life in the wild, especially, in winter. The expansion of suburbs into the country accompanied by the increasing use of snowmobiles in the woods makes the use of the sign field technique even more difficult. As a result, this technique, although being a very interesting method of animal ecology research, has not been widely accepted. The situation is further complicated by the necessity for a researcher specializing in ecology to master concepts of semiotics. However, from our experience we know that this task can be accomplished.

Species, sex, age and motivation of an animal can be identified by using the appropriate research techniques. The identification can only be successful if the researcher possesses good observation skills. When an animal's motivation, sex or age characteristics cannot be determined for certain, some extra observation may be necessary for collecting enough data to be able to choose between alternatives. FORMOZOV's tracking technique has become a standard practize of zoologist researchers studying wildlife in winter time. The method is quite sensitive and if applied with due care, can provide accurate quantitative data.

In the process of analysing animal behavior in a biological sign field a researcher collects data on the code, meaning and value of sign information perceived by animals as they move in their habitat. The environmental cues which guide animals as they move are associated with the sign information *code*. The search for specific external cues, as well as attempts to avoid them, is associated with the *meaning* of information. The intensity of movement responses to particular environmental cues indicate the *value* (significance) of information.

Patterns of objectively discrete elementary behavior acts are considered to be the main characteristics of the mammalian sign field. Movement elements, behavioral reactions of the same motivation, and parameters of the sign field which represents the animal's signal-information environment, may be expressed numerically and calculated according to the researcher's needs. It is important to remember that it is the individual whose information links are studied that serves as a "tool" or "device" to determine the field parameters. Information/sign interaction between animals and their environment can be studied not only on the level of individuals, but also on the level of populations, species or biocenosis.

The field material collected by using the snow tracking method can be organized in the following two ways:

1. formalization of certain traits of an individual interacting with the environment, with the emphasis on those environmental cues that provoked the movement response;
2. formalization of elementary movement acts and environmental cues, with the emphasis on the motivational type of the individual's behavior.

In the first case an individual's behavior is represented as a succession of drives and the researcher's attention is focused on the environmental cues as physical bearers of information that provoked movement responses, and on the quantitative assessment of these responses.

With this approach, the field parameters are not measured on an absolute spatio-temporal scale of physical or chemical states (in other words, this approach does not look at the reality detached from the perception of environmental cues by an animal); rather, they are measured on "informational" space and time scales that are characteristic of a living system.

Parameters of a sign field characterize its structure, i.e., the internal organization of a field as a sign-information system. This structure is determined by analysing interrelations between environmental objects—sign bearers—on one hand, and animals that perceive the signs as they move around, on the other.

In the second case drives are classified according to the dominant type of animal behavior (e.g., orienting towards objects, searching, exploration, relaxation and cleaning, defensive behavior). The data obtained characterize the animal's responses to particular signs in the process of their movement activity (MOZGOVOY/ROSENBERG 1992, pp27–28).

Formalization of the spatio-temporal information continuum of a sign field implies simultaneous consideration of the following five parameters of the field: magnitude, anisotropy, intensity, the equivalent distance and the value (significance) of a given object. The structure of a sign field, its functioning and main patterns of transformation can be determined by these characteristics:

1. the *magnitude* of a field is the number of *different kinds* of environmental objects and events involved in the information recipient's activity (two objects or events are considered to be of a different kind if animals of the given species with the given type of motivation respond to them by showing different behavior patterns). A characteristic of the subjectively significant part of the environment or the scope of environmental perception, the field magnitude shows the extent to which the state of animals' environment meets their expectations;
2. the *anisotropy* of a field is the total number of *all* environmental cues (objects and events) to which animals respond by some kind of movement. Anisotropy indicates the selectiveness of interaction between animals and their habitat;
3. the *intensity* of a field is the number of elementary movement responses to all environmental cues (the number of drives). It indicates the extent to which the information recipients' environmental expectations are met;
4. the equivalent distance is the distance (measured in meters) covered by a given animal or group of animals as they make 100 drives. It shows the impact of an individual or a group of animals on their habitat. The equivalent distance serves as a quantitative measure of the "information expansion" of the target object of studies. By reducing the above three field parameters to the equivalent distance one can obtain comparable numerical values of field parameters for animals with different body size and speed of biochemical reactions. For animals of different species any given equivalent distance used as a group field characteristic will correspond with the same number of drives and the same field intensity;
5. the value of a given sign (environmental cue) is the number of elementary movement responses it provoked in the animal or group under consideration.

For the mammals covered by our research all sign field parameters fall under the influence of both internal (inborn), and external (environmental) factors. However, all other things being equal, the magnitude of a sign field primarily indicates the variety of environmental cues that are new or present some interest to all representatives of a given species; in other words, it shows the character of information received. The field anisotropy primarily characterizes animal motivation, or the meaning of the information received. It is measured as the total number of the most preferable objects in the subjectively perceived landscape. Sign field intensity primarily characterizes an individual's willingness to respond to environmental cues; in other words, it shows the value of information received. The equivalent distance of a field is primarily associated with the species represented by the individual or group under consideration. This distance depends on how the individual or group perceive calendar time. In the theory of sign field time is seen as a measure of changes in the environment.

In biosemiotics the interaction between organisms and their environment is interpreted as a meaning of the lowest degree of semiosis (STEPANOV 1971, p28). For any particular organism its ability to recognize environmental objects closely correlates with the frequency and regularity of interaction between the organism and a given environment object. Signs primarily develop through the most regular interactions relevant to the life cycle.

In the language of humans trying to interprete the signs of interactions between mammals the same word may refer to a number of different objects or events. How can one tell, in trying to determine the magnitude of a sign field, whether two or more objects or events have the same meaning to an animal or a group of animals? For a mammal, the equivalence of really different objects is established on the basis of equivalence of the animal's interactions with the objects. We consider two different environmental cues as having equal meaning if animals of the same species, driven by the same type of motivator, respond to them in exactly the same way, i.e., by rather stereotyped behavior.

It should be noted that there are two different ways to calculate the magnitude, intensity and anisotropy of a biological sign field; the choice depends on the researcher's needs. In the first approach, these parameters are expressed in relation to the length of the string of footprints, measured in meters. In studying foxes' behavior, for example, it is convenient to calculate the field parameters for a string of footprints one thousand meters long. The second way of calculation is used to compare different animal species behavior or to calculate the parameters of a group sign field. In this second case the magnitude and anisotropy are calculated per unit of the equivalent distance. The field intensity divided by the equivalent distance always equals 100 drives, but the equivalent distance itself, expressed in meters, varies a lot. Of all techniques used in the statistical analysis of information field parameters variance analysis is the most convenient one.

Figure 1: These footprints belong to a red fox's (*Vulpes vulpes*). The sign field has the magnitude of 6 (i.e., the animal encounters 6 different kinds of objects, or environmental cues, to which it actively responds). The sign field anisotropy, i.e., the *total* number of environmental cues to which the animal responds, equals ten. The sign field intensity, i.e. the total number of "elementary" movement responses equals twelve.

Figures 1 and 2 illustrate the field material collection technique that takes into consideration sign field parameters. Fig. 1 shows footprints of a red fox *(Vulpes vulpes)*. The footprints were left while the animal was searching for food. The fox was moving from left to right. As it moved along, it was guided by the following succession of objects: (1) a ski-track, (2) a tree, (3) the same ski-track, (4) another tree, (5) the same ski-track once again, (6) footprints of an elk (*Alces alces*), (7) the same elk's footprints on the ski-track, (8) a stump, (9) a bush, (10) another stump (or, rather, a broken tree). In this case we are dealing with six different kinds of objects: (1) a ski-track, (2) a tree, (3) footprints of an elk, (4) the same elk's footprints on the ski-track, (5) a stump, and (6) a bush; thus, the magnitude of the sign field is 6. The total of ten objects provoked movement responses in the information recipient (the fox); thus, the field anisotropy equals ten. The field intensity on the given part of the animal's snow track equals twelve, which means that we can identify 12 elementary movements with which the animal responded to environmental cues. The following is the list of environmental cues with the number of responses to each cue in parentheses: the first encounter with a ski-track (1), a tree (1), the second encounter with the ski-track (1); another tree (1); the third encounter with the ski-track (1), an elk's footprints (1), the same elk's footprint on the ski-track (1); a stump (3 responses: approaching, territory marking, and reorientation—the animal turned around and paused), a bush (1)—the fox moved towards it,—and another stump (1). The question is whether we should consider an elk's footprints on a ski-track as a sign which is different from both a ski-track and an elk's footprints off a ski-track, or consider it to be a simple combination of the two objects that the animal came across earlier? Answering this kind of question will require a long animal observation practice. Our observation experience shows that the information that a fox derives from an elk's footprints on a ski-track is quite different to the one that it gets from a ski-track without footprints or from an elk's footprints off a ski-track. When they cross "dangerous" spots associated with human activities, animals often follow other animals, trying to imitate their behavior. The figure shows that, near the ski-track, the fox followed the elk's footprints precisely, trying to walk "in step" with the elk; but once it crossed the ski-track, it noticed a stump and moved towards it. Animals often follow other beasts' footprints, or the ones they left themselves earlier on.

Before collecting field material a researcher decides what length (in meters) of the string of footprints he or she is going to study. This enables him/her to compare the sign field parameters obtained for different animals. In the given example the fox's sign field parameters were calculated for a 1,000-meter-long string of footprints. This length was chosen experimentally. First, it was found that, on a stretch of about 1,000 meters, a fox comes across the entire variety of objects that can possibly arouse its interest. A researcher who follows footprints of a fox beyond the 1,000-meter point is unlikely to discover any objects meaningful to the animal, other than those that he or she has already seen. Second, the distance of 1,000 m is convenient for calculations: it is comparable to both the size of a hunting area that a red fox can cover within 24 hours, and the size of an area in the woods that a researcher tracking animal footprints in the snow can possibly cover during one field trip.

The string of footprints shown in Figure 2 belongs to a pine marten *(Martes martes)*. In this case the sign field has the magnitude of four—the animal came across four different objects that provoked its movement responses: (1) a large forked tree, (2) a bush, (3) a blade of grass, and (4) a stump. The anisotropy of the marten's sign field for the given section of its track of footprints (the total number of environmental cues/objects) also equals four, as all the objects are different. How did we decide that the large forked tree in the beginning of the studied section of the track and the stump with a branch sticking out meant different things to the marten? Once again, the researcher's decision was based on his long-term observation experience and professional intuition arising from his recollections of animals' responses to such kinds of objects. Animals of any particular species respond to environmental cues with a rather stereotyped set of movements which can be compared to a set "vocabulary". Martens searching for small rodents almost always jump on low stumps coming into sight unless they start seeing footprints of a fox quite often or for long periods of time, in which case they usually climb trees. The sight of foxes' footprints seems to put martens under stress. The intensity of the sign field of the marten whose track of footprints is shown in Figure 2 equals ten. (Such is the number of "elementary movements" with which the marten responded to the above mentioned four environmental cues). As for the forked tree, it provoked two responses in the animal: the marten approached it and leaned to it. As it moved

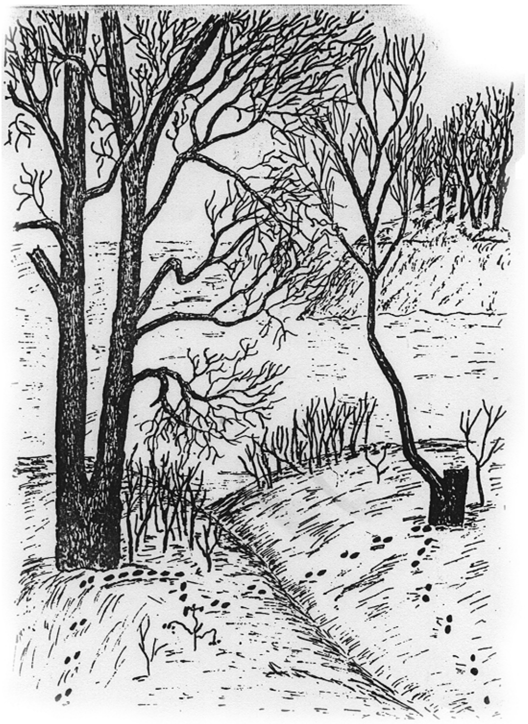

Figure 2: These footprints belong to a pine marten (*Martes martes*). The sign field has the magnitude of 4, the anisotropy in this case equals the magnitude, and the intensity equals 10.

further, the marten switched from galloping to a trot without any noticeable reason (unguided by any particular cue), which counts as one response; the bush and the blade of grass provoked one response each; the stump provoked three responses—the marten approached it, then jumped on it, and finally jumped off it; these responses were followed by another change of pace without any traceable cause (one other response); all in all, we have counted ten elementary movement responses. On its way the animal crossed a little hollow, but since this micro relief element did not provoke any response, it was not taken into consideration in the calculation the field magnitude. However, this landmark is worth being registered by a researcher, since it might have a meaning to an animal under different circumstances. Thus, a hollow has a different meaning to a fox than it does to a marten, since foxes, when they have a short rest during their hunting, sometimes lie down on a sunlit slope protected from the wind—"this way they can fully enjoy the heat of the sun by exposing one side to direct sun rays and the other side to the heat reflected from snow or a tree stump" (FORMOZOV 1959, p22).

Once the dominant motivation is known, assumptions can be made on the corresponding signified objects. The motivation provides the context of a message which an animal may receive from its habitat. Animals are motivated by their physiological needs such as hunger, thirst, the need to clean themselves, the need to rest, the need to reproduce, etc. Motivation of an animal can be increased by its emotional state. To the above-mentioned needs we should add the automatic stimulation phenomenon. As a result of this phenomenon a given type of behavior persists for some time after the physiological need that caused it was practically satisfied. Familiar environmental signals of low and medium intensity that provoke changes in the animal's behavior cannot change the animal's major (predominant) type of behavior. Such side signals may, however, cause temporary shifts in the animal's behavior. Activities to which the animal switches for short periods of time represent minor types of behavior. Long persistence of a particular type of behavior in an animal may cause nervous strain. Animals have a very short attention span; as a result, they alternate their major type of behavior with the minor types.

Since the proposed method of research requires the registration of animal movement responses, someone may have an impression that it is based on the theory of behaviorism. In fact, this impression is far from the truth. The main problem of zoosemioticians arises from the fact that they have no other way to determine the signified, but through the study of the signifier. Behaviorists have reduced this idea to absurdity by denying the very concept of the signified. The toughest challenge an animal tracker will face is splitting up the continuum of the animal's perception into units matching the animal's behavior patterns. In other words, we are dealing with a purely semiotic problem of attributing signifiers to the hypothetical objects they signify. In linking the signifiers with the signified it is important to know the traits of animals tracked as well as their sign system.

The authors of the mammalian sign field theory sought to provide researchers with tools to assess the informational contribution of different species and animals with different speed of biochemical reactions, to the alteration of their common habitat. By determining the magnitude, anisotropy and intensity of a sign field we can formalize communication processes in populations and co-adapted complexes of close mammal species, and compare adaptive behavior responses of different individuals, populations, species and representatives of different conspecific intra–population groups (e.g., groups of individuals of specific age or sex) (MOZGOVOY 1989, pp138–150).

The sign field theory provides the minimal set of parameters with which one can assess the population trends of small predatory mammals living across the Volga river from the city of Samara, Russia (MOZGOVOY 1987, pp3–9). According to the population self-regulation theory (SCHWARTZ 1980, pp126,164–166; GILIAROV 1990, p105), populations of mammals can maintain their number on the level appropriate for their habitat conditions. Apart from genetic mechanisms which predetermine the dominance of genotypes with a higher or lower fertility level, depending on the population size, there are other mechanisms that may cause changes of population; namely, stress mechanisms which change mammals' behavior and the size of their ecological niche (DAJOZ 1975, p245; GILLER 1988, p32). The hypothesis of the behavior regulation of predator mammals number puts forward the idea that social behavior depends on the population density at a certain moment of time; endocrine predator responses to a higher density change, first of all, territory and reproductive behavior responses through the increase of "individuals' aggression" (ROSENBERG/MOZGOVOY/GELASHVILLY 1999, p213).

	Fox	Marten	Ermine	Weasel
Number of animals observed	7	14	2	3
Total length of animal tracks (m)	37,823	82,162	1,325	1,000
Average field magnitude	23.4	18.5	17.0	11.0
Field magnitude range	18–33	12–32	15–18	5–17
Average anisotropy	44	107	234	197
Anisotropy range	42-67	99–200	–	–
Average intensity	111	289	468	695
Intensity range	97–150	240–456	–	–

Table 1: Sign field parameters for the red fox (*Vulpes vulpes*), the pine marten (*Martes martes*), the ermine (short-tailed weasel) (*Mustela erminea*) and the least weasel (*Mustela nivalis*). Field magnitude is calculated for the distance equivalent to 100 drives. Field intensity and anisotropy are calculated for sections of animal tracks 1,000 m long. The tracking was done in the woods of the Volga flood-lands across the river from the city of Samara, Russia in 1978–1982 (MOZGOVOY/ROSENBERG 1992)

The sign field theory and the related tracking technique helped solving a number of specific ecological problems. For example, we have compared responses of individuals and groups living under different degrees of anthropogenic pressure.

Table 1 shows sign field parameters for a fox *(Vulpes vulpes)*, a marten *(Martes martes)*, an ermine *(Mustela erminea)* and a weasel *(Mustela nivalis)*. The field magnitude was calculated for the distances equivalent to the same number of drives for all the animals. It shows the variety of environmental cues to which the animals responded. For the fox 100 elementary movement responses occurred on the section of its track 900 m long, for the marten the average distance equivalent to the same number of drives is 343 m, the equivalent distances for the ermine and the weasel are 220 m and 145 m respectively. The field intensity for the equivalent distance equals 100 elementary movements. The field anisotropy is determined as the total number of objects and events to which the animal responded while covering a fixed length of its track. Anisotropy may also be determined for the distance equivalent to 100 drives. In the example illustrated by the data in Table 1, anisotropy and intensity were calculated for 1,000 m of the animal's track of footprints. This was done to demonstrate the difference in the tempo of motion activity for different species. The research was carried out in the woods of flood-lands of the Volga valley in the Samara Oblast of Russia in 1978–1982.

As we see, some species respond to a greater variety of environmental cues than the other, due to more extensive environmental ties and better adaptability. The variety of an animal's ties with the environment can be measured as the number of environmental cues reflected in the animal's behavior. Among the predator mammals studied, the fox, whose sign field has a considerable magnitude, has the greatest ability to perceive, assimilate and transform environmental cues; therefore, it can be considered the dominant species in the co-adapted complex inhabiting woody flood-lands in the environs of Samara. Of the four species under consideration the fox has the lowest, and the weasel—the highest intensity of the sign field. The marten's sign field, for example, is 2.5–3.0 times more "intensive" than the fox's. One-way analysis of variance (ANOVA) has shown that the variance of intensity of an individual's sign field does not exceed the difference in field intensity between species, though for the marten the ratio of the highest to the lowest level of field intensity may be close to 2:1. The same is true about the variance of anisotropy within one species and between the species.

Let us now examine the sign field parameters of several individual foxes of different sex, age, and type of behavior. Each of these three factors somehow influences the sign field parameters. To estimate this influence analysis of variance was used. Fisher's criterion was applied to assess the reliability of the estimation. The data taken from the work of J. P. MOZGOVOY and I. V. YUDINA (1995) are shown in Table 2.

The material is divided into four parts according to the predominant type of motivation. Such division is necessary, since the sign field parameters depend on the type of behavior prevailing over a 24-hour period. Prevailing types of behaviour are easy to identify: they normally show themselves through, as long as the study of an animal's behaviour over a 24-hour period is complete. As animals change their activities going through the necessary stages between resting and hunting, all the sign field parameters increase.

Table 3 shows how the tempo of life (the speed of biochemical reactions) of the marten and the fox changes with age. The same animals were tracked during four winters while they were searching for food in the woods around the city of Samara, Russia. We can see that the tempo of life of any individual slows down with age. As it is known from various

Behavior type	The animal's sex and age group	Length of track (m)	Field magnitude	Field anisotropy	Field intensity	Distance equiv. to 100 drives
Escaping danger (passive defensive behavior)	Adult male	1,655	26	48	157	658
	Adult female	1,024	26	99	284	1,284
	Adult female	1,884	11	36	119	397
Foraging (searching for food)	Adult female	1,588	36	121	354	284
	Adult female	988	32	112	443	226
	Adult female	1,705	27	143	439	228
	Adult female	1,443	34	149	334	275
Change of feeding territory	Adult male	2,584	36	88	242	413
	Adult male	2,295	24	61	203	493
	Adult male	1,094	35	63	233	429
	Adult male	1,874	15	67	176	568
	Young male	2,358	21	47	98	1,020
	Young male	957	18	73	180	556
	Young male	1,060	21	53	174	575
	Adult female	1,478	23	76	254	394
Inspecting own territory	Adult female	1,114	42	89	408	245
	Adult male	1,541	46	106	434	230
	Adult male	1,549	44	139	373	268
	Young male	1,324	30	128	378	265

Table 2: The sign field parameters calculated for red foxes (*Vulpes vulpes*) with different behavior types. The magnitude, anisotropy and intensity were calculated for a 1000 m length of a track of footprints. Forests in the environs of Samara, Russia, 1994. (MOZGOVOY/YUDINA 1995).

Individual description	Sign field parameter	1980	1981	1982	1983
Adult female marten	Intensity	–	473	407	310
	Magnitude	–	38	34	32
Young male marten	Intensity	540	–	397	–
	Magnitude	41	–	27	–
Adult male fox	Intensity	–	–	276	195
	Magnitude	–	–	38	28

Table 3: Changes in sign field intensity and magnitude demonstrating the lowering tempo of life for two pine martens (*Martes martes*) and a red fox (*Vulpes vulpes*) as the animals advance in age. The parameters were calculated for a 1,000-meter-long section of a track of footprints. The tracking was done in the woods of the Volga flood-lands across the river from the city of Samara, Russia in 1980–1983. (MOZGOVOY/ROSENBERG 1992)

Animal species	Sign field magnitude	Average number of elementary movement responses to the footprints of a given species representative				
		human	fox	marten	ermine	weasel
Fox	26.4	18.6	31.4	0.8	–	–
Marten	20.5	16.0	4.0	18.8	–	–
Ermine	19.0	6.1	6.1	0.3	21.5	–
Weasel	12.0	4.6	20.2	0.5	–	2.9

Table 4: Information ties between the species of the same co-adapted complex. The field magnitude is calculated for the distance equivalent to 100 drives. The tracking was done in the environs of Samara, Russia, in 1992 (MOZGOVOY/ROSENBERG 1992).

Behavior type	Parameter	Bashkirsky Wildlife Reservation and Krasnosamarskoye Forestry		The Volga flood-lands across the river from the city of Samara	
		males	**females**	**males**	**females**
Food-searching	Number of individuals observed	1	3	4	4
	Covered length of track (m)	7,840	7,771	13,740	16,500
	Field intensity	224	291	368	510
Changing the feeding territory	Number of individuals observed	1	4	1	3
	Covered length of track (m)	4,860	4,960	1,722	12,494
	Field intensity	134	177	190	347

Table 5: Life tempo (movement activity) variations for the pine marten (*Martes martes*) expressed through the sign field intensity in areas with different degree of human impact on the environment. The tracking was done in the woods of the Volga flood-lands across the river from the city of Samara, Russia, in Krasnosamarskoye Forestry 100 km east of Samara, and in Bashkirsky Wildlife Reservation, in 1978-1985. (Mozgovoy/Rosenberg 1992).

scientific publications, this phenomenon is attributed to decreasing metabolism. Research of the same kind conducted during field seasons of 1993–2000 confirmed that there is correlation between animals' age and their tempo of life.

Let us now look at another example of how the sign field technique can be applied in animal ecology studies: this time we are going to examine the information links between the fox, the marten, the ermine and the weasel. Each of the four species of this complex reacts differently to the signs left by animals of the other species. This difference is clearly demonstrated in Table 4, which allows to build a hierarchy of informational dependence of the given species on the other species.

The analysis of the data presented in the table shows that, for any individual animal, traces left by animals of the same species have a much higher informational value than traces left by animals of any other species.

From the above we can draw the following conclusions. Animals of species with similar feeding habits that live in the same area, form the so-called co-adapted complex. (A co-adapted complex consists of populations representing several species with similar ecological requirements to their habitat (Mozgovoy/Rosenberg 1992, pp43–45). The niches occupied by the species represented in a co-adapted complex overlap. Animals within any given co-adapted complex exchange information on their habitat structure. The species of the same co-adapted complex respond to the same or similar environmental cues. Their sign fields consist of similar elements and do not differ a lot in magnitude. Animals respond to animals' footprints more actively than to landmarks. The intensity of contacts between individuals of the same species is higher than the intensity of interspecific contacts. The sign fields of males and females of the same species differ in magnitude. Compared to females, males respond more intensively to any unusual environmental cues including anthropogenic signs. The above conclusions based on the materials collected before 1992 were once again confirmed by our later research carried out in 1993–2000.

In the following example we compare the sign fields of animals living in similar environments which only differ in the degree of human impact on them. The data presented in Table 5 were collected during the winter months in 1978–1985. We studied the sign fields of 12 adult pine martens *(Martes martes)* living in the Volga flood-lands across the river from the city of Samara, in Krasnosamarskoye Preserve 100 km east of Samara, and in Bashkirsky Wildlife Reservation (Bashkortostan, the Southern Urals). The human impact on the animals' habitat increases as we go from Bashkirsky Reservation to Krasnosamarskoye Forestry to the environs of the city of Samara. The sign field intensity was calculated for 1,000-meter-long sections of animal tracks of footprints. This parameter characterizes the tempo of animal's life by showing how actively they move, and is determined as the total number of elementary movement responses per unit of distance.

As we can see, the pine marten shows a higher level of activity in the area with the stronger human impact on the environment. It results in the higher values of the sign field anisotropy and intensity. The anthropogenic factor causes a larger increase in the field

Animal	Factor (Category)	Sign field parameter	Factor influence rate, %	Weighted average (independent variables)	
				χ_1	χ_2
Fox (on a 500 m section of track)	Sex (adult individuals)			males	females
		Magnitude (number of objects)	–	18	19
		Anisotropy	–	36	39
		Intensity	8.7	89	133
Fox (on a 500 m section of track)	Age category (males)			adult	young
		Magnitude (number of objects)	2.2*	18	20
		Anisotropy	–	36	40
		Intensity	5.4	89	119
Marten (on a section with 26 different kinds of objects)	Age category (females)			adult	young
		Length of track covered by animal while it responded to 26 kinds of objects	–	440	395
		Anisotropy	–	83	82
		Intensity	2.0*	241	311

Table 6: Sign field parameters and results obtained using one-way analysis of variance (Mozgovoy/Rosenberg 1992). All the animal were tracked during food-searching in the woods of the Volga flood-lands across the river from the city of Samara, Russia, in 1990.
* The reliability rate for these values is estimated at 80% vs. 95% for other values in this column.

intensity of females compared to males. An increase in the anisotropy and intensity of biological sign fields may indicate that animals are put under stress.

The field parameters were processed using the one-way analysis of variance, the most effective statistical processing method. The results obtained are presented in Table 6.

2. The Sign Field As a Sign System of a Mammal

The sign field theory studies mammals living in the wild. For animals comprising a population or a co-adapted complex of close species, which respond to environmental cues, the following statements are true: (1) their information exchange with environment increases the adaptability of their population or co-adapted complex; (2) animals involved in the sign process have individual and group memory, as well as genetically fixed memory; hence, the memory of past experience is always present in a sign, producing connotations. A sign is a reference to a certain situation in the past, which was significant and therefore got registered in the animal's mind as a part of individual experience (either in the form of a movement response or in the form of a movement inhibition).

Mammals' behavior in their sign field is a process of 'reading' unaddressed messages about external objects, events and habitat conditions. In the theory of a biological sign field the external objects to which mammals respond by movements are considered as environmental cues, or signs. "When animals have direct contacts with each other, it is quite difficult to discern in their communication separate signs such as a movement, a pose, a sound etc.; hence, it is impossible to divide the interaction 'text' into elementary units. In case of indirect interaction through external objects and events which form a long-registered 'textual message', the recipient of the message responds to each sign by a movement or a series of movements, which form some kind of behavior pattern. This pattern can be understood from studying the traces of the animal's activity, and within it one can identify separate units—the "words" with which the animal answers to the 'message'" (Mozgovoy/Rosenberg/Vladimirova 1998, p17). It should be noted that the external objects themselves are not signs, but they are perceived as such by the animal-recipient.

One of the founders of zoosemiotics, Charles Morris, wrote in his book *Writings on the General the Theory of Signs*, "Men are the dominant sign-using animals. Animals other than man do, of course, respond to certain things as signs of something else, but such signs do not attain the complexity and elaboration which is found in human speech, writing, art, testing devices, medical diagnosis, and signaling instruments" (MORRIS 1971, p17). He went on, "The functioning of signs is, in general, a way in which certain existences take account of other existences through an intermediate class of existences" (MORRIS 1971, p23). In his other work, *Signification and Significance,* MORRIS introduced the basic semiotic concepts as follows: "Semiosis (or sign process) is regarded as a five-term relation—v, w, x, y, z—in which v sets up in w the disposition to react in a certain kind of way, x, to a certain kind of object, y (not then acting as a stimulus), under certain conditions, z. The v's, in the cases where this relation obtains, are signs, the w's are interpreters, the x's are interpretants, the y's are significations, and the z's are the contexts in which the signs occur" (MORRIS 1964, p2).

Once he introduced the key semiotic terms, MORRIS noted that he did it "for present purposes" (MORRIS 1964, p2). We fully support the semioticist when he wrote, "the formulation is not proposed as a definition of 'sign', for there may be things we shall want to call signs that do not meet the requirements of this formulation—I prefer to leave this an open question. The formulation simply gives the conditions for recognizing certain events as signs" (MORRIS 1964, p2).

It may seem that Charles MORRIS understands the idea of animals' sign behavior somewhat differently than the authors of the theory of a mammalian biological sign field, but a closer look at the problem will demonstrate that the differences arise from the use of two different approaches to modelling sign phenomena, one being static, the other dynamic. What the static approach calls "disposition to react in a certain way" (MORRIS 1964,p2), the dynamic approach refers to as "elementary movement responses to external objects and events" (MOZGOVOY/ROSENBERG 1992, p15) or "interpretants" (MORRIS 1964, p2). "Such a disposition can be interpreted in probabilistic terms, as the probability of reacting in a certain way under certain conditions because of the appearance of the sign. […] Or, as we shall see later, it can be interpreted as an intervening variable, postulated for theoretical purposes, and controllable by indirect empirical evidence" (MORRIS 1964, p3).

We are now going to define the concepts of 'semiosis' and 'sign' in such a way that, in our opinion, complies with our understanding of sign processes based on the theory of a biological sign field proposed by NAUMOV, MOZGOVOY and ROSENBERG. The analysis of these definitions helps better understand how the authors of the theory approach ecological and ethologic problems.

Given that zoosemiotics was founded to address ecological issues, the following definition of semiosis appears to be the most appropriate: semiosis is an energy consuming process, an adaptation mechanism that enables interaction of an individual or a larger living system with the environment. With this approach to the definition of semiosis the concept of 'sign' serves to demonstrate the relative character of linking the signifier primarily with the outer world and the signified—primarily with the inner world. In a specific research, this concept also helps consider the signifier and the signified as a unity, wherever possible. Semiosis is usually associated with energy consumption, and a 'sign' is viewed as a model of semiosis which is primarily oriented towards the environment. The term *Umwelt* introduced by UEXKÜLL, which denotes "the semiotic world of a living organism" and incorporates "all aspects of the world that are meaningful to a particular organism" (KULL 1998, p302), is used in the model that highlights in semiosis the features of a translation process (KULL 1988, p300). This semiosis model stresses that "an individual's ability to respond to environmental cues is limited" (DEWSBURY 1981, p21).

The interpretation of a sign as "a model carrying the most common functional properties of a given object or phenomenon", rather than "a real object or phenomenon" (LEONTYEV 1967, p37), in our opinion, does not contradict the above definitions, since psychic mechanisms construct adaptive—for a given level of functioning—simulations of reality, including scientific ones. Those who separate "reality" from "reality simulation" deny the fact that any scientific discourse implies simulating reality by means of language. We believe that the above interpretation of a sign is characteristic of MORRIS' and UEXKÜLL' works; it is also shared by modern biosemioticists, the authors of the sign field theory and many other researchers.

A. S. MELNICHUK wrote, "Solving researchers' disagreement [over the interpretation of the sign] comes down to solving one simple technical issue: which of the sign properties should we apply the term 'meaning' to?"(MELNICHUK 1968, p43). The tracking technique based on the theory of a mammalian biological sign field primarily associates 'meaning' with the field anisotropy. The authors of the theory agree with Claude LÉVI-STRAUSS who described meaning (signification) as "the operator of reorganization of the set being worked with" (LÉVI-STRAUSS 1999, p127, 129). The integrity of a 'text' (a set of objects perceived by the animal) is determined by the animal's biological motivation.

In zoosemiotics, as long as we distinguish between the notions of *sign*, *semiosis, meaning*, and *value*, semiosis can be described using parameters of a biological sign field: an individual's set of signs ('vocabulary') can be associated with the *field magnitude*; the notion of *field anisotropy* allows us to see what a given 'text' means to different individuals; *field intensity* can be used to measure the difference in the value of a given 'text' for different individuals. Correlating the notions of the sign field theory with linguistic notions has nothing to do with establishing contextual equivalence of notions by means of, say, the commutation test; rather, the notions are linked to emphasize—the way it is done with the natural human language—various aspects of the animal sign system which is less differentiated. In the pragmatically oriented theory of a sign field, the field magnitude, intensity and anisotropy respectively characterize the form, value and meaning of information (in other words, they function as "syntactic", "pragmatic" and "semantic" components of information) (ROSENBERG/MOZGOVOY/GELASHVILI 1999, p115). Once again, we should point out that these associations are made with the only purpose of stressing important aspects in the process of studying mammalian semiosis in its integrity.

I. F. VARDUL wrote, "In the information theory any amount of information is studied irrespective of its content. In linguistics (on a larger scale—in semiotics), the content of information is studied irrespective of its amount" (VARDUL 1967, p9). In our opinion, the sign field method is a tool which allows a researcher to analyse both the amount and content of information presented as a succession of signs.

Thus, in Zoosemiotics, the following definitions of the 'sign' are possible:

- a sign is something which, in some respect or capacity, stands for something to a motivated individual with some experience of interacting with the environment;
- a sign is a thing referring its user to some other thing;
- a sign is a thing associated with something that differs from the form being interpreted;
- a sign is a thing which provokes a movement response in the addressee when the signified correlates with the addressee's prevailing motivation;
- a sign is a transition from the perceived form (the signifier) to some contents (the signified) determined by its user's individual experience or the experience of the user's species;
- a sign is a thing that is likely to provoke in its user some kind of action related to the user's major motivation (intention)—the likelihood of this action should be less than 100%, otherwise we will be dealing with cause-and-effect rather than sign interaction.

In the sign field theory, an elementary movement act (a drive) is a unit within behavioral continuum, which is determined by correlating the signified with the signifier. There is still a chance that either the plane of expression or the plane of contents will be divided into units which have no correlation in their other plane, but such division of a continuous process of an animal's movement would be incorrect. For an animal the signified is a reminiscence of its previous experience and a reflection of what it seeks.

The problem of correlating signs of a biological field parallels a similar problem in linguistics. "The reduction of infinite variety of sign manifestations to a finite number of variants is based on Karl BÜHLER's principle of *abstract relevance* (BÜHLER 2000, p34), which states that of all the only relevant substantial abstract characteristics of a sign are the ones that have a semasiological function and—given that we speak of a sign system—can be determined by system oppositions" (T. V. BULYGINA 1967, pp8–9).

C. S. PIERCE writes about humans, "A sign, or representamen, is something which stands to somebody for something in some respect or capacity. It addresses somebody, that is, creates in the mind of that person an equivalent sign, or perhaps a more developed sign. That sign which it creates I call the interpretant of the first sign. The sign stands for something, its object. It stands for that object, not in all respects, but in reference to a sort of idea, which I have sometimes called the ground of the representamen". (PEIRCE 2000, p48). This definition seems suitable for a metalinguistic description of animal sign systems in studying mammalian sign fields.

Since objects and phenomena of the outer world may or may not meet the expectations of motivated animals, sign interaction between individuals and their environment can be viewed as a structured system of meanings, and the scientific discourse including the description of this interaction by a researcher can be viewed as a social phenomenon which depends on changes in its own structure.

For ecological purposes it is better to study semiosis from the perspective of the animal that receives

		Communication of mammals of the same or close species in the wild	**Human language**
Sign function (Bühler's classification)	**Symptom**	Characterizes the functional condition of the interaction process initiator (the message sender). Manifests itself in the sender's elementary movements.	Mainly characterizes the sender extralinguistically. May indicate the significance of the chosen information context for the sender, the sender's functional condition, ideology, the social censorship effects. In a number of cases may also indicate the sender's association with a particular social group or his/her marginal position, the sender's desire to win the addressee's empathy, his/her knowledge of the language code (vocabulary, dialect, preferable discourse etc.)
	Symbol	Characterizes correlation between the animal's motives and environmental phenomena.	Correlates with the things and situations mentioned in the utterance
	Signal	Controls the behavior and inner state of the second participant in communication process (the information recipient). Provokes a movement in response to the perception of a sign.	Links the subject of discourse and the situation in which communication takes place with the recipient's position. In case where the message makes sense to the recipient, the signal influences the recipient's behavior.

Table 7: Humans' vs. animals' sign functions.

information than from the perspective of the animal that sends a message and waits for response.

One reason why studying sign systems from a recipient's perspective is more relevant for ecological research is that signs are always vital for individual animals as environmental cues catching animals' attention. The closeness of attention may vary. On the one hand, the recipient is motivated to look for particular signs, relying on its individual and species experience; on the other hand, the sign is generated by the recipient's environment when environment matches the recipient's intentions and perception apparatus.

Which environmental cues attract individuals attention and affect their adaptive behavior? How can we determine the roles of the environment and the individual's functional condition in semiosis? To a researcher studying semiotics from the recipient's prospective, *anything* may look as a sign. Gestalt psychologists discerned figures and their background in the process of visual perception: figures, in their opinion, differ from their background in that they are rich in detals and have a structure. Since the actual semiosis has always a smaller scale than the potential one, in the real environment of an individual there are always objects and events that are not registered it its subjective (inner) world. The environment influence on an individual goes beyond its perceptive power. Since observation is the only way to "penetrate" animals' inner world, to obtain reliable and comparable objective results we should only register those environmental objects which provoke movement responses in animals.

Thus, the studies of semiosis based on the theory of a mammalian sign field mostly focus studying the process from the recipient's perspective. This approach is not shared by all semioticists. In general semiotics and, particularly, in zoosemiotics there are supporters of approaching the process from the sender's prospective. Indeed, animals often give a signal and wait for a response. We admit that, in studying ecology on the level of individuals, this approach may prove to be more productive than the one taken by the authors of the sign field theory—it all depends on the researcher's goals. Anyhow, the authors of the mammalian sign field theory admit the importance of studying the evolutional experience of various mammal species. The approach taken by their opponents is especially important in dealing with animals' intentional communication through signs.

The concepts of the theory bear a lot of resemblance to neo-behaviorists' ideas; the main difference being that the sign field theory created to solve specific ecological problems, studies both individuals and groups. Besides, unlike neo-behaviorist suppositions, the theory of a mammalian sign field deals with the whole 'text', rather than separate stimuli.

Semiotic studies centred around the sender of a sign message mainly focus on the sign function which by Karl Bühler called a 'symptom' (Bühler 2000, pp34–38). In Table 7 three different sign functions are compared for humans and other mammals. Those are the three functions identified by Bühler—symptomatic, symbolic and signalling; all of them are taken into account in the theory of a biological sign field.

Using sign field technique in the studies of mammals' communication allows us to describe two main operations used in the process of information exchange—selection and combination. Thus, once the number of signs of a certain kind, encountered by an individual, exceeds a certain limit, this causes a change in the individual's activity. The structure of a mammalian sign field parallels the structure of a text with its two aspects—paradigmatic and syntagmatic; in the sign field these two aspects correlate with the effect of self-stimulating behavior (when a certain type of behavior persists in spite of fulfilment of the physical need that caused it) and with "the shift in the predominant behavior type" accompanied by the appearance of a "minor activity" in line with the time division principle (MOZGOVOY/ROSENBERG/VLADIMIROVA 1998, p7).

Animals communicate with each other through their behavior both when they have direct contacts with each other, and when their adaptive behavior makes changes to their environment. With solitary animals, the main zoosemiotic problem is describing the structure of a non-intentional, unaddressed message 'recorded' in environmental objects and events and organised as a 'text' which an animal 'reads' as it moves around. The message is actualised as the animal moves in its own or group sign field. The researcher's task is to structure his or her process of reading sign messages so that it is very similar to the animal's process of receiving the messages.

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Todd K. Shackelford

Preventing, Correcting, and Anticipating Female Infidelity

Three Adaptive Problems of Sperm Competition

GEOFFREY PARKER INTRODUCED the idea of sperm competition in 1970. Based on his work on insects, PARKER defined sperm competition as the competition between the sperm of two or more males for the fertilization of one or more ova (PARKER 1970a, 1970b). In the decades since PARKER's groundbreaking work, sperm competition has been documented or inferred to exist in many species, including humans and birds (BAKER/BELLIS 1995; BIRKHEAD/MØLLER 1998; SHACKELFORD/LEBLANC 2001; SHACKELFORD et al. 2002; SMITH 1984). Sperm Competition Theory provides the framework for a body of work that examines the adaptations in males and in females that evolved to solve problems associated with sperm competition.

Abstract

Sperm competition occurs when the sperm of two or more males simultaneously occupy the reproductive tract of a female and thereby compete to fertilize an egg. Sperm competition has been documented or inferred to exist in many species, including humans and birds. Female infidelity creates the primary context for sperm competition. In animals that practice social monogamy and in which there is substantial paternal investment, males incur costs associated with a female partner's infidelity. A principle cost is investing resources in genetically unrelated offspring. Female sexual infidelity and the resulting sperm competition generated several adaptive problems for males over evolutionary history. In humans and in birds, these adaptive problems include preventing female infidelity, correcting female infidelity, and anticipating female infidelity. I review empirical work suggesting that males have evolved physiological and psychological mechanisms designed to solve these problems.

Key words

Female infidelity; sperm competition, evolutionary psychology, social monogamy.

In this article, I review work inspired by Sperm Competition Theory suggesting that male humans and paternally investing, socially monogamous male birds have a psychology that includes mechanisms designed to solve at least three specific adaptive problems of a female partner's infidelity. Over the evolutionary history of humans and paternally investing, socially monogamous birds, males faced the adaptive problems of (1) preventing a partner's infidelity, (2) correcting a partner's infidelity, and (3) anticipating a partner's infidelity. Although there are likely other adaptive problems concerning sperm competition, such as detecting infidelity or evaluating the timing of a female's infidelity, I limit the discussion to preventing, correcting, and anticipating female infidelity. The discussion of these specific adaptive problems highlights several directions for future work that may clarify our understanding of male psychology and behavior as it relates to female infidelity and sperm competition in birds, humans, and other socially monogamous, paternally investing species.

Overview

DALY and WILSON (1999) recently noted that the study of human evolutionary psychology shares much conceptually with the study of non-human animal behavior. Research on sperm competition in non-human animals—particularly birds—has clear implications for understanding human mating psychology and behavior. Because of the similarities in the mating systems of birds and humans, for example, research on sperm competition in birds (see

Adaptive problem	Evolved solution in birds	Evolved solution in humans
Preventing female infidelity	Mate guarding behaviors (Birkhead/Møller 1992)	Mate guarding behaviors (Flinn 1988)
Correcting female infidelity	Copulation immediately upon reunion (Hatchwell/Davies 1992) Forced copulation following extra-pair copulation (Birkhead et al. 1989)	Adjusted number of sperm inseminated (Baker/Bellis 1989) Increased sexual interest in partner (Shackelford et al. 2002) Increased perceived attractiveness of partner (Shackelford et al. 2002)
Anticipating female infidelity	Frequent copulation(Møller 1988)	Frequent copulation (Baker/Bellis 1995) Morbid jealousy (Daly/Wilson 1988; Turbott 1981)

Table 1. Three adaptive problems associated with sperm competition and proposed solutions

Birkhead/Møller 1992) provides a model for research on sperm competition in humans. Sperm competition has been studied in many animals, including several non-human primates (Birkhead/Møller 1998; Harvey/Harcourt 1984). I limit comparisons of human behavior and psychology primarily to various bird species, because of the similarities in mating systems between humans and birds (see below). In addition, comparing humans and birds provides a unique approach for evaluating the adaptive problems generated by sperm competition.

Like most species of birds, humans practice social monogamy (Baker/Bellis 1995; Birkhead/Møller 1992). In this mating system, males and females form long-term pair bonds. Males benefit through uncontested sexual access to their female partner, whereas females benefit through exclusive investment of a male in her and her offspring (Birkhead/Møller 1992; Trivers 1972). For both birds and humans, however, these pair bonds are not always sexually exclusive. Extra-pair copulation by males and by females of socially monogamous birds have been observed and documented by various methods, such as DNA fingerprinting tests of paternity (Birkhead/Møller 1992; Saino/Primmer/Ellegren/Møller 1997). Likewise, there is cross-cultural evidence of extra-pair copulation by male and female humans. Blood grouping studies of humans indicate a cross-cultural paternity discrepancy rate of about 10% (Smith 1984).

Birkhead and Møller (1992) argue that female infidelity creates the primary context for sperm competition in birds. Smith (1984) and Baker/Bellis (1995) provide parallel arguments for humans. For both birds and humans who practice social monogamy, female infidelity places a male at risk of cuckoldry, or investing in offspring to whom he is genetically unrelated. I propose that male humans and male birds faced similar adaptive problems within the domain of sperm competition. Specifically, I propose three sets of adaptive problems associated with sperm competition in birds and in humans. These are problems that deal with the prevention, correction, and anticipation of a female partner's infidelity. In the following sections, I describe the nature of these adaptive problems and identify behaviors that may be the output of evolved mechanisms designed to solve these problems. Table 1 provides a summary outline with relevant references.

Preventing Female Infidelity

A principle cost that males incur as a result of their partner's sexual infidelity is the risk of cuckoldry. There would have been tremendous selection pressures over evolutionary history for males to behave in ways that reduced the risk of investing in genetically unrelated offspring. These behaviors would prevent a partner from being sexually unfaithful or, barring that, prevent the rival male's sperm from reaching a partner's ovum or ova. The goal in this case, from the male's perspective, is to prevent insemination by a rival.

Male birds and male humans have a psychology that appears well designed to prevent or minimize sperm competition by reducing a partner's opportunity for extra-pair copulation. Birkhead and Møller (1992) describe several behaviors in birds that function to prevent rival insemination. Mate guarding behaviors, for example, include the vigilant watch that male birds keep over their partner. The mate guarding behaviors documented in birds parallel some of the mate guarding behaviors documented in humans. These behaviors range from vigilance over a partner's whereabouts to rifling through a partner's personal mail (Buss 1988; Buss/Shackel-

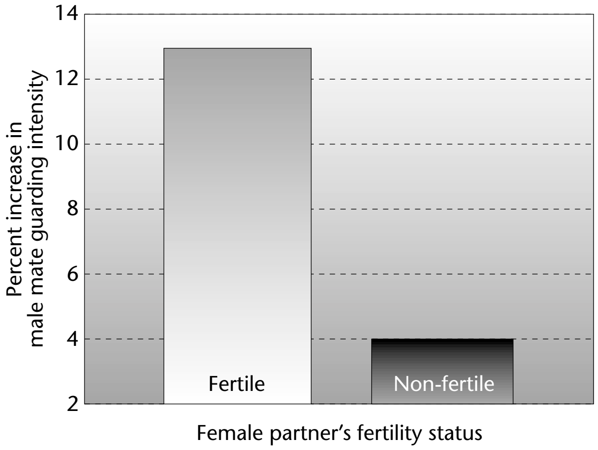

Figure 1: Percent increase in mate guarding intensity in male swallows following experimental detainment from female partner as a function of partner's fertility status. Data from MØLLER (1987). Adapted from BIRKHEAD/MØLLER (1992), Figure 9.7, p130.

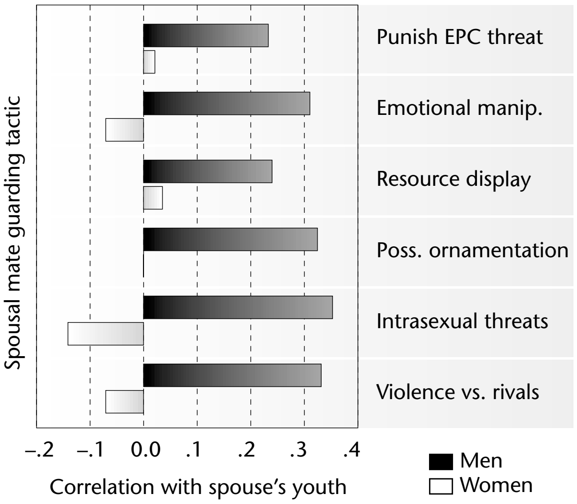

Figure 2: Partial correlations between human spousal mate guarding and partner's age, controlling for own age and length of relationship. All spousal mate-guarding tactics (punishment of extra-pair copulation (EPC) threat, emotional manipulation, resource display, possessive ornamentation, intrasexual threats, and violence against rivals) are significantly correlated with wife's age, but not husband's age ($p \leq .05$). Following are example behaviors included in each mate-guarding tactic. Punishment of EPC threat includes behaviors such as, "Hit spouse when he/she caught spouse flirting with someone else". Emotional manipulation includes behaviors such as, "Threatened to harm self if spouse ever left him/her". Resource display includes behaviors such as, "Spent a lot of money on spouse". Possessive ornamentation includes behaviors such as, "Gave spouse jewelry to signify that he/she was taken". Intrasexual threats include behaviors such as, "Threatened to hit the person who was making moves on spouse". Violence against rivals includes behaviors such as, "Got friends to beat up the person who had made a pass at spouse". Adapted from BUSS/SHACKELFORD (1997), Table 3, p351.

FORD 1997; FLINN 1988). Additionally, in many species of birds and in humans, male mate guarding behaviors are more frequent and more intense with a more reproductively valuable partner (BIRKHEAD/MØLLER 1992; BUSS/SHACKELFORD 1997; FLINN 1988). MØLLER (1987) showed that, following experimental detainment from their partner, male swallows increase the intensity of mate guarding more for fertile than for non-fertile partners (see Figure 1). Likewise, BUSS and SHACKELFORD (1997; see also FLINN 1988) documented that a man's mate guarding is positively correlated with his wife's reproductive value, as indexed by her age, even after controlling for the man's age and the length of the relationship. A woman's mate guarding, however, is not correlated with her husband's age after the woman's age and the length of the relationship are controlled statistically (see Figure 2). These behavioral similarities suggest psychological similarities in male birds and male humans.

Preventing sperm competition is one solution to the adaptive problem of female sexual infidelity. Acts of mate guarding have costs, however. Male birds engaged in mate guarding expend time and energy that could be used to locate food or acquire additional mates, for example. Significant weight loss has been documented in male ducks that spend more time mate guarding and, consequently, less time feeding (ASHCROFT 1976). In humans, a man may be unable to maintain a successful career if too much time and effort is spent watching his partner's every move. Furthermore, despite the best mate guarding efforts, neither a male bird nor a male human can be certain of his partner's fidelity.

Given that preventative measures are not foolproof, males may be equipped with another set of mechanisms designed to "correct" a female partner's infidelity. These mechanisms might generate behaviors that allow a male to compete for paternity if his partner has been unfaithful.

Correcting Female Infidelity

In the case of preventing infidelity, the goal, from the male's perspective, is to avoid sperm competition. When a female partner's infidelity is detected or suspected, however, the chance to compete is desired. Biologists and psychologists studying humans and birds have identified factors linked with the risk of female infidelity (BAKER/BELLIS 1995; BIRKHEAD/

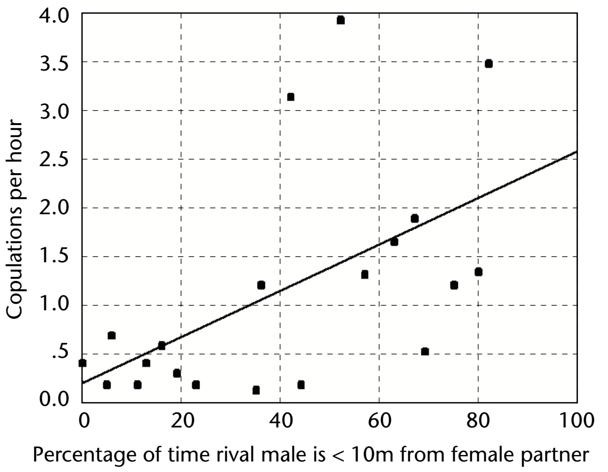

Figure 3: In-pair copulation rate as a function of the proportion of time female dunnocks spent within 10 m of a rival male. Males initiated significantly more copulations as their partner spent more time near rivals ($p < .05$) Adapted from Davies (1983), Figure 3, p336.

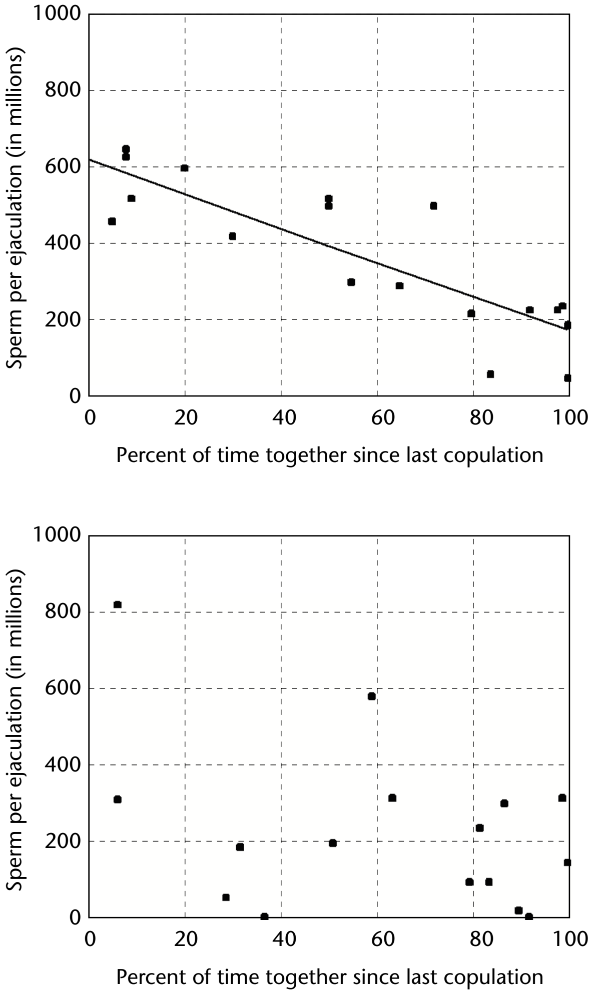

Figure 4: *Top:* Number of sperm ejaculated at human couple's next copulation as a function of the percent of time couple spent together since their last copulation. Correlation is significant ($p < .001$). Adapted from Baker/Bellis (1989), Figure 1, p868. *Bottom:* Number of sperm ejaculated at next masturbation as a function of the percent of time human couple spent together since their last copulation. Correlation is not significant ($p > .05$). Adapted from Baker/Bellis (1989), Figure 1, p868.

Møller 1992; Shackelford/Buss 1997). One of these factors is the percentage of time a pair or a couple has spent together since their last copulation. As the percentage of time that a couple has spent together since their last copulation decreases, the risk that a female has copulated with a rival male increases (Baker/Bellis 1995; Birkhead/Møller 1992).

Males who suspect or detect a partner's infidelity can address this adaptive problem in at least two ways. The first is to copulate with their partner. Without copulation, there is no chance for sperm competition and, therefore, no chance for the in-pair male to sire his partner's offspring. The second is to increase the number of sperm inseminated during copulation. The psychology and physiology of male humans appear to be designed to gauge the risk of infidelity and to take appropriate corrective action by adjusting the number of sperm inseminated into their partner (Baker/Bellis 1995; Shackelford et al. 2002). Although this sperm number adjustment is not yet documented in birds, some birds might be equipped with an alternative mechanism for correcting a partner's infidelity. Davies (1983) showed that male dunnocks increase the rate at which they copulate with their partners as a function of the percent of time that a rival spends in close proximity to her (see Figure 3). Male dunnocks also have been shown to copulate immediately upon reunion with their partners as a way of correcting possible infidelity (Hatchwell/Davies 1992). Additionally, forced copulation following extra-pair copulation may serve the function of correcting infidelity. Forced copulation following extra-pair copulation has been documented in zebra finches (Birkhead/Hunter/Pellat 1989), carrion rooks (Goodwin 1955), and in many species of waterfowl (see, e.g., McKinney/Derrickson/Mineau 1983).

Biologists studying humans have documented a negative correlation between the percentage of time a couple has spent together since their last copulation and the number of sperm a male inseminates at the couple's next copulation (Baker/Bellis 1989, 1995). This adjustment occurs only at the couple's

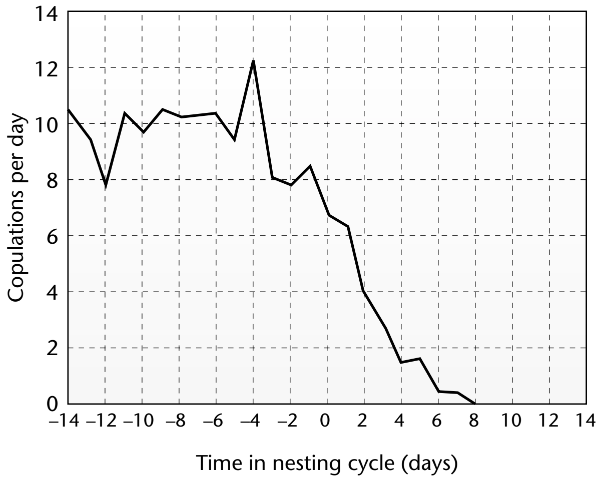

Figure 5: Number of osprey copulations per day as a function of time in nesting cycle. Day 0 is the day that the first egg was laid. Female fertility peaks in the days just before the first egg is laid and rapidly declines to zero following the onset of egg laying. Data from BIRKHEAD/LESSELS (1988). Adapted from BIRKHEAD/MØLLER (1988), Figure 1, p1674.

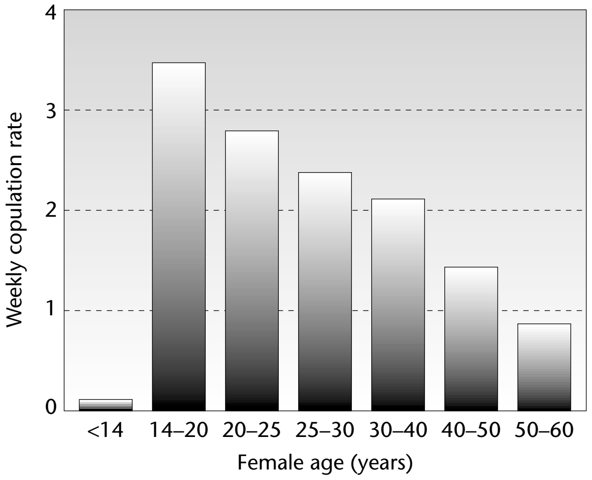

Figure 6: Weekly human copulation rate as a function female age. Adapted from BAKER/BELLIS (1995, Box 4.8, p63).

next copulation (see Figure 4 top), and not at the male's next masturbation (see Figure 4 bottom). The effectiveness of this adjustment decreases with the time that passes after a suspected extra-pair copulation, however. Males who were motivated to copulate as soon as possible following a suspected infidelity would have benefited reproductively (BAKER/BELLIS 1995; BIRKHEAD/MØLLER 1992). Recent research on humans documents that the percentage of time that a couple has spent *apart* since their last copulation (in which the risk of sperm competition and subsequent cuckoldry is higher), and not the total amount of time since their last copulation, predicts men's ratings of their partner's attractiveness (SHACKELFORD et al. 2002). Men's interest in copulating with their partner also is predicted by the percentage of time the couple has spent apart since their last copulation (SHACKELFORD et al. 2002). Copulatory interest and ejaculate competitiveness, both sensitive to the risk of a female partner's infidelity, may be outputs of evolved mechanisms designed to solve the adaptive problem of correcting a female partner's infidelity.

Anticipating Female Infidelity

Anticipating infidelity is another problem that male humans and paternally investing, socially monogamous male birds may have faced recurrently over evolutionary history. Implicit in the act of preventing a partner's infidelity is anticipating that infidelity. Anticipating infidelity, however, is not equivalent to preventing infidelity. A male might anticipate an infidelity, but he may be unable to prevent it. The costs of mate guarding may be too high, for example (BIRKHEAD/MØLLER 1992; KEMPENAERS/VERHEYEN/DHONDT 1995). But a male can do better than standing by and waiting until the infidelity has happened before taking action. BIRKHEAD and LESSELLS (1988) showed that although a male osprey must *decrease* his mate guarding intensity in order to forage for food for his partner during her fertile phase, he *increases* the rate at which he copulates with her during this period (see Figure 5). BAKER and BELLIS (1995) documented an analogous pattern in humans. Figure 6 shows that men mated to younger, more reproductively valuable women copulate more frequently with their partners than do men mated to older, less reproductively valuable women. This work on birds and on humans suggests that frequent copulation and insemination might maintain a male's competitive status in his partner's reproductive tract during the time that he cannot account for her behavior (BAKER/BELLIS 1995; MØLLER 1988).

In birds and in humans, past female infidelity and sexual promiscuity are good predictors of future female infidelity (BAKER/BELLIS 1995; BIRKHEAD/MØLLER 1992). Male humans and male birds may use information about a female partner's previous infidelities to predict her future infidelity, and then adjust their preventative and anticipatory behaviors accordingly. I hypothesize, for example, that male humans and male birds that anticipate a partner's infidelity in the near future will initiate more frequent copulation with their partners, especially nearer to the time of the anticipated, but unpreventable, infidelity. A prediction derived from this hypothesis is that males who anticipate a future infidelity, and who are about to spend time apart from their partner, will pursue copulation immediately prior to their separation. The closer this copulation is to separation, the greater the chances that a later ejaculate of a rival will meet competitive sperm in the female's reproductive tract. As another example, I hypothesize a relationship between anticipated sperm competition and "morbid jealousy" in human males (DALY/WILSON 1988; TURBOTT 1981): Men who display intense, frequent, and often violent jealousy toward their partner may be reacting to real or imagined cues to their partner's future infidelity.

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Summary and Concluding Remarks

Male humans and paternally investing, socially monogamous male birds may have a psychology and physiology that includes mechanisms designed to solve at least three adaptive problems of a female partner's infidelity and subsequent sperm competition. These three adaptive problems are preventing a partner's infidelity, correcting a partner's infidelity, and anticipating a partner's infidelity. Although I focused on humans and birds in this review, these adaptive problems are likely to have been recurrently confronted by ancestral males of other socially monogamous, paternally investing species. The males of these species, like male humans and male birds, may have evolved psychological and physiological mechanisms designed to solve these adaptive problems. Future work can profitably test these hypotheses, in addition to other hypotheses presented in this review, all of which are inspired by modern Sperm Competition Theory.

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Zusammenfassungen der Artikel in deutscher Sprache

Anneliese Spinks/Linda Mealey

Linguistische Einflüsse auf Worte im Zusammenhang mit Bedrohung?

Die zentrale Triebkraft, welche die Evolution der Sprache bedingte war der Vorteil effizienter interpersonaler Kommunikation. Die Fähigkeit Informationen über Artgenossen zu erhalten, die deren Verhalten erklären und Vorhersagen ermöglichen erweisen sich dabei als besonders wichtig.

Der größte Teil der vorliegenden Persönlichkeitskonzepte sieht dabei die zentralen Eigenschaften von Persönlichkeit im interpersonalen Bereich. Diesen Konzeptionen liegt die Annahme zugrunde, dass sich Individuen im sozialen Bereich konsistent und voraussagbar verhalten, wobei die interindividuellen Unterschiede auch in der natürlichen Sprache ersichtlich werden. Zwei Persönlichkeitsdimensionen erweisen sich dabei als zentral und werden auch in der vorliegenden Untersuchung näher analysiert: soziale Übereinstimmung und Macht/Dominanz.

Da sich die Evolution des Menschen überwiegend innerhalb sozialer Kleingruppen vollzog, war es zweifellos von Vorteil Mechanismen zu entwickeln, welche anzeigen inwiefern eine bedrohliche soziale Situation vorliegt. Ausgangspunkt dieser Studie ist dabei die Hypothese, dass die natürliche Sprache über mehr Worte zur Beschreibung bedrohlicher Personen verfügt als zur Beschreibung neutraler bzw. positiver Personen.

Alvaro Moreno/Asier Lasa

Von elementaren Adaptationen zu frühen Formen des Geistes: Über Ursprung und Evolution kognitiver Kapazitäten

In diesem Artikel wird der Versuch unternommen die Besonderheiten kognitiver Prozesse – ausgehend von einfachsten Formen adaptiven Verhaltens bis zu komplexeren Formen – aus einer evolutionären Perspektive darzustellen.

Die Ursprünge von Kognition liegen dabei in der funktionellen Organisation der Bewegungen bei vielzelligen Organismen, welche durch das Nervensystem bewerkstelligt wird. Das Nervensystem wird dabei als ein internes Subsystem interpretiert, welches sensomotorische Interaktionen bedingt, die von metabolischen Vorgängen dynamisch entkoppelt sind. Kognition entsteht dabei als eine besondere Form der Anpassung durch makroskopische Bewegungen welche in weiterer Folge zu kognitiven Interaktionen führen.

Weitere Komplexitätszunahme innerhalb des Nervensystems steht dabei in Verbindung mit Größenzunahme. Dabei ist es vor allem der Wirbeltierbauplan, welcher diese Veränderungen und damit das Entstehen neuer Formen kognitiver Prozesse (wie beispielsweise Emotionen und frühe Formen des Bewusstseins) ermöglicht.

Martin Brüne/Elaine Mulcahy

Exaptation, Ko-optation und kognitive Evolution des Menschen

Der Ausdruck „Ex-aptation", geprägt von GOULD und VRBA (1982), bezieht sich auf die Beobachtung, dass stammesgeschichtlich entstandene Eigenschaften von Organismen oder sogenannte evolutionäre „Nebenprodukte" scheinbar neue Funktionen ausüben und somit Anpassungsvorteile für den Organismus bieten können. Als Paradebeispiel gilt die Evolution des Federkleides. Federn entstanden wohl ursprünglich bei Reptilien zur besseren Wärmeisolierung und möglicherweise auch als sexuelle Signalgeber. Erst später wurden sie zum Fliegen „benutzt" bzw. „ko-optiert" (die hier verwendeten Termini sind nicht im teleologischen Sinne zu deuten, sondern dienen lediglich der sprachlichen Vereinfachung!). Der Ausdruck Exaptation sollte ursprünglich den der „Prä-adaptation" ersetzen, gerade deshalb, weil letzterer einen „teleologischen Beigeschmack" hat. Der Begriff Exaptation ist aber deshalb problematisch, weil er impliziert, dass derartige neue Funktionen auch ohne weitere strukturelle Modifikationen übernommen werden können. In einer späteren Arbeit hat GOULD (1991) argumentiert, dass „Exaptation“ sogar auf zahlreiche menschliche psychische Eigenschaften, wie etwa Sprachvermögen, Lesen, Schreiben, Ausüben von Religion, künstlerisches Schaffen etc. zuträfe; das menschliche Gehirn geradezu zur Exaptation prädestiniert sei. Derartige evolutionäre Errungenschaften des Menschen seien nicht durch natürliche oder sexuelle Selektion zu erklären.

Im vorliegenden Beitrag werden unter Bezugnahme auf BUSS et al. (1998) geäußerten Kritik die Schwächen dieser Begrifflichkeiten an Hand des Beispiels der Evolution von Metarepräsentanzen (Wissen über Wissen) diskutiert.

Die Fähigkeit zur Perspektivübernahme kann durchaus – analog des viel zitierten Federn-Beispiels – als Exaptation interpretiert werden. Wie neuere Untersuchungen mittels funktioneller Bildgebung nahe legen, entwickelte sich diese aus der Fähigkeit, zielgerichtete Bewegungen belebter Objekte wahrnehmen zu können. In ähnlicher Weise kann für die Entstehung menschlicher Sprache die Exaptation bestehender Mechanismen der gestischen Kommunikation postuliert werden. Es muss aber bezweifelt werden, ob dies ohne weitere strukturelle adaptive Modifikation möglich war. Unserer Auffassung zufolge ist die Unterscheidung von *Ad*-aptation somit hinfällig, der Begriff Exaptation, zumindest in der evolutionären Psychologie, überflüssig. Andere Ausdrücke wie derjenige der Ko-optation müssen definitorisch klarer gefasst und etwa von „Recruitment“ abgegrenzt werden. Wir schlagen vor, den Terminus Ko-optation der Ausübung kulturell entstandener Fähigkeiten durch stammesgeschichtlich entstandene psychische Mechanismen vorzubehalten. Die stärkere Verschränkung von evolutionärer Psychologie mit anderen Neurowissenschaften, etwa funktioneller Bildgebung, ist wünschenswert und notwendig.

Rupert Riedl
Systemtheorie der Evolution

Die Evolutionstheorie von heute ist wissenschaftstheoretisch widersprüchlich. Denn die molekulargenetischen Lösungen und jene aus Morphologie und Paläontologie ignorieren wechselseitig die aufgedeckten Phänomene. Letztere weisen Richtungshaftigkeit der Evolutions-Bahnen und innere Abstimmungen nach, erstere setzen auf Zufallsänderungen und Auslese durch das Milieu.

Die Komplexität des Lebendigen setzt die Wahrnehmung von Wechselkausalität (mutual causality) voraus. Wenn jene zufällig entstandenen Genkoppelungen Erfolg haben und erhalten bleiben die für funktionsabhängige Gene kodieren, dann wird der Funktionszusammenhang im System kopiert, es entsteht ein „imitatorischer Epigenotypus“.

Das hat zwei Konsequenzen. Erstens bleiben auch Systeme beliebig hoher Komplexität noch adaptierbar. Zweitens folgen funktionelle wie genetische Bürden (constraints), die zu einer gebahnten, geordneten Evolution des Organismenreichs führen.

Christian Pázmándi
Das biologische Typenkonzept

Die Morphologie lieferte zur Zeit DARWINS den Hauptteil an Belegen für die Evolution, aber ihre Unterfütterung mit einer ausdrücklich zeitlichen Komponente, der der Phylogenie, ist eine spätere Entwicklung, die die ursprüngliche Grundlagen verschleiert. Die Morphologie war ursprünglich über Typen organisiert, die die beobachteten Formen in konkreter, bildhafter Fassung enthalten. Diese ursprüngliche Konzept von Goethe wurde später von der phylogenetischen Schule HAECKELS überschattet, aber drei Ansätze folgen GOETHES Programm und gehen darüber hinaus: das der rationalen Systematik, basierend auf rationaler Morphologie, wie von DRIESCH entworfen, das Typenkonzept von RIEDL und NAEF. Driesch versuchte eine Morphologie zu entwickeln die eingehüllt ist in die Totalität möglicher Formen, von der die verwirklichten Formen eine Teilmenge darstellen. Die Totalität möglicher Formen sollte seiner Ansicht nach abgeleitet werden aus einer Analyse morphogenetischer Felder und ihrer Eigenschaften. RIEDL formulierte den Typus als ein Muster von adaptiven Zwängen und Möglichkeiten. Während beide Konzepte ehrgeizig aber sehr weitreichend sind, versuchte Naef ein simples Typenkonzept zu entwickeln, nahe bei morphologischer Praxis. Er ersetzte die zentrale Rolle des „morphologischen Instinkts“ des Forschers durch einen Satz von Definitionen und Regeln, mit dem Blick in Richtung einer Konstruktion natürlicher Typen. Der vorliegende Artikel gibt einen Überblick über die erwähnten Konzepte, resultierend in einem biologischen Typenkonzept, welches veranschaulicht wird durch ein Beispiel aus der morphologischen Forschung, wobei drei für morphologische Forschung wesentliche Begriffe unterschieden werden: durchschnittlich, normal und typisch.

Theresa S. S. Schilhab

Ontologisches sowie epistemologisches Bewusstsein und die Frage des Anthropomorphismus

Wissenschaftliche Ansätze, welche den Versuch unternehmen höhere kognitive Fähigkeiten und Bewusstsein auch in nicht menschlichen Lebewesen nachzuweisen stehen oft im Verdacht des Anthropomorphismus. In diesem Artikel versuche ich auf der Grundlage von drei Überlegungen die Gründe für dieses Argument darzustellen:

1. Es besteht ein Unterschied zwischen den Vermutungen bzw. dem Glauben an Bewusstsein (das ontologische Konzept) und der Art und Weise wie gehandelt wird, wenn wir einem Anderen Bewusstsein zusprechen (das epistemologische Konzept)
2. Das epistemologische Konzept beruht weitestgehend auf anthropozentrischen verhaltensmäßigen Kriterien
3. Indem das epistemologische durch das ontologische Konzept des Bewusstseins ersetzt wird, wird deutlich warum wir Bewusstsein nur einer begrenzten Anzahl von Tieren – wie beispielsweise Menschen und möglicherweise manchen höheren Primaten zusprechen.

Indem wir einem Organismus ontologisches Bewusstsein zusprechen gehen wir davon aus, dass dieser über subjektive Erfahrung verfügt. Die Zuschreibung epistemologischen Bewusstseins beinhaltet jedoch vielfach nur bestimmte verhaltensmäßige Kennzeichen. Dieser Unterschied wird im Alltagsleben, wie auch in wissenschaftlichen Bereichen vernachlässigt, was zu beträchtlichen Verwirrungen führen kann.

Wolfgang M. Schleidt/Michael D. Shalter

Co-Evolution von Menschen und Wölfen

Hunde und Wölfe sind Mitglieder einer vielfältigen Gruppe von Raubtieren und Aasfressern, welche vor etwa 10 Millionen Jahren in Koevolution mit herdenbildenden Huftieren entstanden sind. Während der Eiszeit wurde der Wolf, *Canis lupus,* das beherrschende Raubtier Eurasiens. Durch seine Fähigkeit, mit den wandernden Huftieren Schritt zu halten, wurde der Wolf der erste „Hirte“ unter den Säugetieren.

Menschenaffen entstanden zunächst als kleine Gruppe unauffälliger, kletternder, fruchtfressende Primaten. Im Umfeld globaler Klimaänderungen der Eiszeit trennten sich die Vorfahren unserer eigenen Art von schimpansenartigen Primaten, verließen den Wald und gingen als echte Menschen (*Homo erectus*) aufrecht in die offene Graslandschaft. Aus dem agile Baumbewohner wurde ein schneller, herumschweifender „Laufaffe“ mit dem Potential, den Lebensstil eines Wanderers anzunehmen, der für die Bewohner der eiszeitlichen Savannen und Steppen so wichtig geworden war. Mangels früchtetragender Bäume wurden die frühen Hominiden zu Allesfressern, insbesondere Sammler und Aasfresser. Diese Hominiden stießen in die Steppen Eurasiens vor und wurden mit der Erfindung des Speeres erfolgreiche Jäger.

Während der letzten Eiszeit schlossen sich unsere Vorfahren an herdenfolgende „Hirtenwölfe“ an: Einzelne Familien wählten den Lebensstil der Herdenfolger, und wanderten zuerst wohl mit den riesigen Rentier-Herden. Wölfe und Menschen entdeckten die Möglichkeit der Zusammenarbeit. Wir vertreten hier die Ansicht, dass schon die frühen Kontakte zwischen Wölfen und Menschen auf Gegenseitigkeit beruhten, und auch die weiteren Veränderungen – unsere moralische Hominisation ebenso wie die Entstehung der Haushunde – am besten als Koevolution zu erklären sind.

Elina Vladimirova/John Mozgovoy

Die Theorie des Zeichenfeldes und ihre Anwendung bei der Interpretation von Spurbildern von kleinen Raubtieren im Schnee

Kleine Raubtiere, z.B. Fuchs, Marder, Hermelin, Wiesel leben überwiegend solitär und treten selten in direkten Kontakt miteinander. Indem diese Tiere jedoch innerhalb eines gemeinsamen Habitats leben sind sie gleichartigen Umweltbedingungen unterworfen.

Im sog. Zeichenfeld werden die Interaktionen zwischen den Organismen und ihrer Umgebung ersichtlich. Laut der Theorie des Zeichenfeldes kann tierisches Verhalten als eine Folge von abgegrenzten Bewegungsmustern interpretiert werden, die durch innere und äußere Faktoren bedingt sind. Als konkretes Forschungsmaterial werden Spuren und andere Zeichen welche die Tiere im Schnee hinterlassen untersucht. Dank dieser Spuren kann man die Zahl der elementaren Bewegungen, welche die Tiere bei der Wahrnehmung bestimmter Gegenstände bzw. in bestimmten Situationen machen genau quantifizieren.

Für die Theorie des Zeichenfeldes sind die drei folgenden Faktoren zentral: Größe, Anisotropie und Spannung des Zeichenfeldes.

Die Größe des Zeichenfeldes bezieht sich auf die Zahl verschiedener Gegenstände und Erscheinungen der Umwelt, auf deren Wahrnehmung die Tiere einer bestimmten Art reagieren.

Die Anisotropie des Zeichenfeldes bezeichnet alle Gegenstände und Erscheinungen der Umwelt, auf welche die Tiere mit bestimmten Verhaltensmustern reagieren, wobei eine bestimmte Distanz von zentraler Bedeutung ist.

Die Spannung bzw. Intensität des Zeichenfeldes bezieht sich auf die Bereitschaft des Organismus auf bestimmte Umgebungsbedingungen zu reagieren.

Die Begriffe, die für die Modellierung und Beschreibung der Besonderheiten von Informations – und Zeichenprozessen von Säugetieren verwendet werden, stammen aus der Biosemiotik.

Der Vergleich einzelner Faktoren im Zeichenfeld bringt verschiedene ökologische Probleme einer Lösung näher, wie etwas die Frage inwieweit männliche und weibliche Organismen unterschiedlich auf Gegenstände der anthropogenen Umwelt reagieren.

Todd K. Shackelford

Über das Verhindern, die Korrektur und die Voraussicht weiblicher Untreue: Drei adaptive Probleme der Sperminenkonkurrenz

Spermienkonkurrenz tritt dann auf, wenn sich Spermien von zwei oder mehreren unterschiedlichen Männchen in den Reproduktionsorganen des Weibchens befinden und hinsichtlich der Befruchtung des Eis konkurrieren. Es ist vor allem weibliche Untreue, welche den primären Hintergrund der Spermienkonkurrenz darstellt. Männchen sind davon insofern betroffen, als sie – im Falle weiblicher Untreue, beträchtliche Ressourcen in genetisch nicht verwandte Nachkommen investieren.

In dieser Arbeit wird unter Rückgriff auf vorliegende empirische Untersuchungen aufgezeigt, welche physiologischen und psychischen Mechanismen sich bei männlichen Organismen (vor allem Vögel und Menschen) entwickelt haben um diese Probleme zu lösen. Diese Mechanismen beziehen sich dabei vor allem darauf weibliche Untreue überhaupt zu verhindern, sie – wenn nötig – zu korrigieren und sie zu antizipieren.