ANTHROPOLOGIE • XXXIII/1-2 • pp. 83-98 • 1995

BERTRAND L. DEPUTTE

SOCIAL ONTOGENY IN PRIMATES: SEMANTICS, CONCEPTS, FACTS AND PROCESSES

ABSTRACT: Ontogeny is one of the most complex issues in biology, as it includes every process which leads to a living, reproducing individual. When the individual is a primate, because of the dramatic importance of experience (learning and memory processes), and the influence of the social group in which he is born, he becomes a unique being. Social ontogeny refers to the ontogenetic processes through which a newborn develops into a social individual. Social ontogeny is a subset of behavioral ontogeny, which is itself a subset of ontogeny. All these terms are first defined to avoid emptying "Ontogeny" of its fundamental and essential meaning. It should be remembered that ontogeny refers only to an individual. The issue of social ontogeny is addressed using the general framework developed by Hailman (1982). This framework used a "Phenotype Approach" to ontogeny. The different methods used to describe the social development were briefly presented. It is emphasized that these methods are inadequate to address the question of the "Social Ontogeny" which results from complex, highly interactive processes. Multivariate techniques were described as useful tools for analyzing social ontogenetic processes. The behavioral differentiation and the two main socializing processes, the acquisition of a behavioral repertoire and the development of relationships, were analyzed. Studies of the ontogeny of grey-cheeked mangabeys and rhesus monkeys served as examples. In the former species the influence of the variety of social environments was investigated, while in the latter one the behavioral sex differentiation was questioned. With regard to this question, the term "Diposotism" was proposed to specifically refer to differences in frequency of homologous behaviors between females and males, whereas "Behavioral Dimorphism" would be restricted to differences in motor patterns between female or male behaviors. The results of these studies emphasized the importance of interactions on the development of a social individual and the importance of the variety of the social environments infants are born in. Finally, a modification to Hailman's ontogenetic function was proposed. This modification is intended to account for the specificity of the primate ontogeny, namely its social, hence interactive, nature.

KEY WORDS: Social ontogeny – Methodology – Multivariate analyses – Non-human primates

INTRODUCTION

Semantic issue and definitions

From fecundation to death through reproductive capacities, an organism is subjected to changes in all the dimensions of its biological complexity. Among these changes, those associated with developmental and maturational processes are irreversible. Development infers a dynamic of changes, processing from undifferentiated states to organized, specialized or mature ones (Bogin 1988). Development implies changes, but it does not imply that these changes should stop at a certain stage. On the contrary, maturity implies a finite, precisely defined state reached by an organ or a system. An individual has a certain internal anatomy, a certain morphology, a certain physiology. In addition, it can acquire a certain experience, processes information in a certain way and displays certain behaviors. All of these dimensions, from anatomy to behavior, and possibly other ones, are subjected to development and some of them to maturation. All these processes that lead to an individual are included in the process called ONTOGENY, meaning **"the genesis of an individual"** (from the Greek ontos - the being, the person and genesis - creation, origin). In "The American

Heritage Dictionary", ontogeny is defined as "the course of development of *an individual organism*" (my underlining). Consequently the term ONTOGENY encompasses a large diversity of developmental processes, from embryogeny to sexual maturation and to certain behavioral capacities. (With reference to the definition given above for maturity, it would be incorrect to talk about "behavioral maturity" as, to a large extent, behaviors are constantly subjected to changes through experience after the brain has reached its organizational maturity - a given number of neurons and a certain level of connection). Although ontogeny refers to development, it should not be used as a synonym of "development", since ontogeny specifically refers to the development of one individual, considered as a whole organism, and not to the development of the diversity of dimensions that compose it, or to the development of a phenomenon. Therefore, it is correct to say "physiological ontogeny", "behavioral ontogeny" (Bekoff and Byers 1981), "social ontogeny", "prenatal ontogeny" (as a possible, but unnecessary, synonym of embryogeny), ontogeny of *Pipistrellus pipistrellus*, ontogeny of primates, ontogeny of carnivores (primate ontogeny or carnivore ontogeny are even better terms), vertebrate ontogeny (Bekoff and Byers 1981), etc... All of these are correct terms, but it is incorrect to say "ontogeny of behavior", "ontogeny of vocalizations", "ontogeny of locomotion", "ontogeny of play", etc.; in all these cases, very often encountered in the literature ever since 1932, the term ontogeny should be replaced by development. Ontogeny and development could both refer to an individual, but while development could also refer to phenomena, ontogeny should not. Ontogeny should only refer to individuals, taken as a whole, the Ontos. Ontogeny is an ontological term. One possible explanation of the widespread misuse of "Ontogeny" could be the deserved success of Tinbergen's works and his reformulation of the 4 principal questions in biology. Tinbergen (1963) added "ontogeny" to Huxley's 3 questions about biological phenomena - causation, function and evolution . Causation of behavior, function of behavior and evolution of behavior are all correct expressions. Consequently, without further etymological care and/or use of a dictionary, ontogeny could also have been improperly considered to refer to phenomena.

Conceptual issues and additional definitions

Fussiness about etymology and semantics is not just a matter of fussiness *per se*, since semantic thoughtlessness leads to emptying concepts of their original meanings, to creating unnecessary synonyms, and to overlooking the related issues of the concepts concerned. Progressively, the sad consequence of considering a global concept like ontogeny to be a mere, or fashionable, synonym of development, is that ontogeny is now emptied of its unique meaning and has become an overlooked phenomenon. When someone says "Internet", he means "Internet". When someone says "Ontogeny", it is not sure, at all, that he actually means "ontogeny". It is not clear that he is dealing with the intrinsic complexity of the development of an individual, rather than the much greater simplicity of a given, isolated phenomenon (sometimes complex enough anyway). It is valid, for analytical purposes, to separate an individual into his large number of components. But ontogeny precisely refers to the way all these components interact and are arranged to produce a developing individual. Those who use the term "ontogeny" in place of "development of this and that", are indeed referring to ontogenetic processes, but not to Ontogeny (some ontogenetic processes could be used in synonymy with developmental processes).

Considering its actual definition, ontogeny consequently implies several related issues:

– Wholeness: Ontogeny always deals with one indivisible individual. However, for analytical convenience, the global process of ontogeny may be subdivided into particular dimensions or developmental stages, such as embryogeny ("prenatal ontogeny"), or "behavioral ontogeny".

– Individuality and Uniqueness: As a consequence of sexual reproduction, an individual is a unique being, since he is the product of the mixing of the genetic potentialities of 2 different individuals. The individual character of a primate is even enhanced through his long period of immaturity. In addition, the development within a social group and the subsequent complexity of individual experience add *uniqueness* to individuality (cf Mason 1976).

– Longitudinal approach: This is a specific methodological constraint arising from the actual definition of ontogeny; as ontogeny deals with the development of an individual, the data should be collected longitudinally on the same individual, along his development.

– Complexity: As a consequence of wholeness, ontogeny refers to several phenomena interrelated either simultaneously or sequentially.

– Interactions between developmental processes: this is a second consequence of wholeness: the social development, for example, is dependent upon the development of the sensory-motor and locomotor apparatus.

– Time and irreversibility: As any developmental process, ontogeny implies a temporal dimension and irreversibility, as ontogeny is also related to the aging process. Once adult, an individual cannot go back to the earlier stages (at least without the requirements of magic or artifacts - Faust, Peter Pan).

Hailman's framework for the study of ontogeny

Hailman (1982) proposed that "Ontogeny is the transition of one phenotypic control pattern to another, mediated by environmental contingencies". He first defined the phenotypic control function (C):

$$C:(M_j, S_k) \mapsto B_{jk}$$

which for each combination of a motivational state (M_j) and a defined external stimulus input (S_k) determines a behavioral distribution (B_{jk}). Hailman emphasized the uniqueness of the phenotype in assuming that "the Phenotypic Control Function determines a particular distribution of output probabilities". Then he set an ontogenetic function (O):

$$O:(P_{t-1}, G, E) \mapsto P_t$$

which maps the ontogenetic changes of one phenotype, its genotype G and the present environment E to a new phenotype, during "some conveniently small increment of time" (from t-1 to t). He proposed considering the process of an individual's ontogeny as one set of changes of control of his behavior during his life. Therefore the Ontogenetic Function includes the Phenotypic Control Function.

SOCIAL ONTOGENY: THE "PRIMATE" PARADIGM

Defining social ontogeny

Keeping in mind the Hailman's thoughtful framework for ontogeny, one can draw a schematic representation of Ontogeny and its subsets *(Figure 1)*.

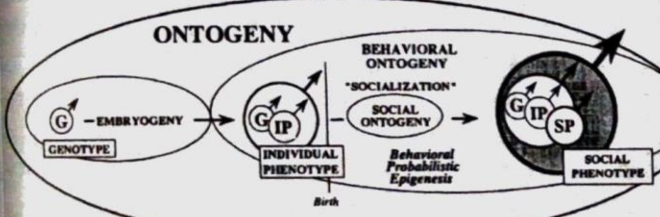

FIGURE 1. Schematic representation of a male primate ontogeny and its components: Prior to birth, a male genotype builds a male "individual phenotype", through the ontogenetic process of "embryogeny". During the last stages of the gestation a second fundamental ontogenetic process, the "behavioral ontogeny", starts with the development of the nervous and motor systems. After birth, the rest of a primate ontogeny occurs within a social group. The influence of the social group refers to a non-genetic process of development. The behavioral ontogeny becomes mainly a "social ontogeny" that also includes the development of some specific features of the primate social life. Consequently a "social phenotype" is built up, including the "individual phenotype" plus the individual social network, which includes some individual social specificities (modified from Deputte 1995).

Embryogeny is determined by the genotype and leads to an "individual phenotype". In primates, the newborn starts his life within a social milieu. Most of his development is influenced by, and during early stages dependent on, interactions with other group members (cf Hinde 1987). Consequently, the behavioral ontogeny is mainly an epigenetic process, and could be called a "Behavioral Probabilistic epigenesis", to use the terms coined by Gottlieb (1970). The "social ontogeny", itself a subset of behavioral ontogeny, is an epigenetic

$$\text{ONTOGENY} \subset \begin{array}{c}\text{behavioral}\\ \text{ontogeny}\end{array} \subset \begin{array}{c}\text{social}\\ \text{ontogeny}\end{array}$$

process, since social ontogeny is characterized by the interactions between a developing individual phenotype and social environmental variables (Mason, 1976; Bernstein & Williams, 1986; Fig.1). Therefore "Dialectics" is a new key word for social ontogeny. Hinde (1987) considered that dialectics also occur between the different levels of social complexity.

In the issue of primate social ontogeny, it is important to spell out what E includes in Hailman's ontogenetic function formula. It includes the social group, es, in which the young primate is born. This social group is itself a component of the primate population, e_p, and both are embedded in an animal community, C, including predators, competitors and other sympatric primate species. In addition, the environment of the social group includes the food resources, F, and is influenced by abiotic factors, A. Consequently E, in the ontogenetic function formula, becomes a function E:

$$E:(e_s, e_p, C, F, A)$$

A social group is here defined by some of its essential features: temporal stability, spatial cohesiveness, coordination of activities of members by means of communicative events, individual recognition between group members and discrimination of non-members (Bernstein and Williams, 1986). A social group has both a structure and an organization; the former refers here only to the demographic structure of a group, especially the number of adult males and females (van Schaik & van Hooff, 1983; Rowell, 1972; Fedigan, 1982), the latter refers to the nature of the relationships, especially between the adults, and to other features resulting from social interactions, such as segregation of sex classes or age-sex classes or the dominance hierarchy.

Since a social group has a certain permanence and stability, interactions between group members are highly recurrent. Therefore, as Hinde (1976b) proposed, there are different levels of complexity within a social group: the observable interactions, the social relationships, inferred from the patterning, and the content of the interactions and the social organization (called "social structure" by Hinde) which results from the interplay of all the relationships. Each individual has his own way of distributing his interactions among various group members; this constitutes a "social network" (Berman 1982) within which "relationships affect relationships" (Hinde 1979). Consequently, a member of a social group has two essential features - his individuality *and* his social network - and a social group becomes an integrated sum of all these networks, yielding an high level of complexity.

A "social phenotype" could be defined as the "individual phenotype" (a genotypic resultant), in addition to, and interacting with, the associated individual social network (an epigenetic component). Therefore "Social ontogeny", which could also be partly referred to as "socialization", establishes a new phenotype, a social phenotype S_p *(Figure 1)*.

As mentioned before, "social ontogeny" is only a component of behavioral ontogeny. Consequently, social ontogeny is dependent on some fundamental features of primate development: the degree of immaturity of a newborn primate, which implies a great deal of parental or parental-like care, and the slow rate of maturation (e.g. motor coordination and, to a much greater extent, sexual maturation).

Returning to Hailman's formula, social ontogeny could be considered as the process which transforms an individual phenotype into a social phenotype *(Figure 2)*. The Social Ontogenetic function, O_s, maps the ontogenetic changes of an individual phenotype at birth, IP_{t0}, its genotype and the environment, into a "social phenotype", SP, within a group of already-established social phenotypes (both males and females).

So it could be hypothesized that the social ontogeny is dependent on the nature of social interactions between the developing individual and the rest of the group composed of several unique social phenotypes (E, in the "social ontogenetic" function; *Figure 2*).

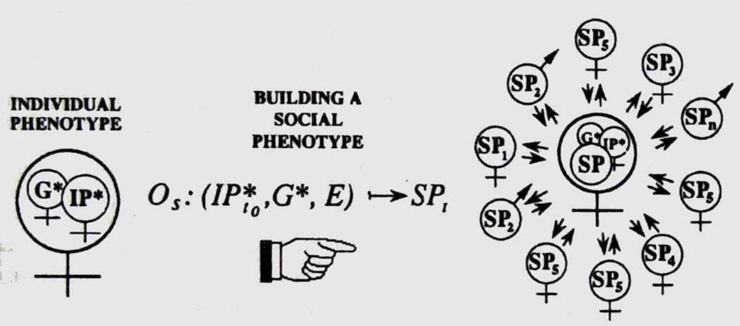

FIGURE 2. Schematic representation of the "Social Ontogeny": The Social Ontogenetic function, O_s, maps the changes of an individual phenotype at birth, IP_{t0}, into a "social phenotype", SP, through interactions with already established social phenotypes (both males and females).

Defining social ontogenetic processes

Throughout ontogeny, and in relation to his behavioral development, a primate infant will discover the different features of the social phenotypes he is living with. Three different phenotypes could be distinguished, each of them having specific features available to the infant through different modalities *(Figures 3 & 4)*. Based on their morphology, "individual phenotype", each group member is unique *(Figure 3)*. However, based on certain common morphological features, and because they share some behavioral sets, individuals can be grouped into classes *(Figure 3)*. Actually, a social phenotype is both unique along one dimension and class-specific along another *(Figure 3)*.

Partner	Phenotype	
	Kind	Feature
f1	Individual	Morphology
Adult female	Class Individual	Morphology Behavior
Adult female-f1	Social	Behavior

FIGURE 3. The phenotypic components of a social partner: Each group member, here an adult female, is actually composed of different kinds of phenotypes which are progressively available to an infant as his cognitive and behavioral capabilities develop. Only individual and social phenotypes have unique features which are discovered by an infant at different stages of his ontogeny.

The characteristics of the social phenotypes an infant is exposed to are available through different processes involving different cognitive abilities *(Figure 4)*. As vision and memory develop, an infant will first discriminate and, later, individually recognize the "individual phenotypes" surrounding him. An infant will then learn the social dispositions of his partners and how to deal with them in the course of interactions. By doing so, he will develop a social repertoire which will progressively fit most, if not all, the social situations he is involved in. At the same time he will learn that all individuals do not behave the same way towards him. This differentiation is the consequence of class phenotypes, that is, of the age-sex classes. The awareness of "class individual phenotypes" implies both perceptual-cognitive and behavioral-motor mechanisms. Being aware of the "class individual phenotypes" through interactions also means the development of a social-behavioral repertoire and partner differentiation *(Figure 4)*. The recurrence of interactions within a group leads to establishing relationships and a social network, possibly requiring individual recognition (or a somehow similar capacity; *Figure 4*).

Defining a behavioral repertoire

Any behavior observed during a social interaction and performed towards a partner could be called social behavior. Because a social group is spatially cohesive and temporally stable, social interactions are recurrent between group members. Individuals become skilled at interpreting every move, every gesture of a companion. Therefore a social behavioral repertoire is actually a very large one, and only certain specific communicative behaviors, such as facial mimics, vocalizations, special postures, have a particular meaning within a given social group of a given species. The social character of other behaviors are inferred from the response, or lack of it, of the partners of interactions. The behaviors an individual could perform depend on his motor capacities. Consequently, describing social ontogeny involves describing the development of behaviors which are used in interactions. In addition, as an infant interacts with many different "social phenotypes", he will have to adjust to this variety, and then display a large array of behaviors. Building a social behavioral repertoire is one fundamental process of social ontogeny. A second fundamental process is to establish a network of social relationships. This means that an infant progressively differentiates his social behavior in relation with more and more individualized partners.

A

PARTNER	BEHAVIOR	PROCESS 1	PROCESS 2	OUTPUT
f1	observation	perceptual	discrimination	Individual recognition
f1 to Adult female	interaction	learning memory (perceptual)	developing a social repertoire (behavioral)	Socialization 1- Social behavioral repertoire Partner differentiation
Adult female to Adult female f1	relationship Patterning of interactions	learning and updating memory (perceptual)	differentiating a social repertoire building a social network (behavioral)	Socialization 2- Social relationship Social network Identification

B

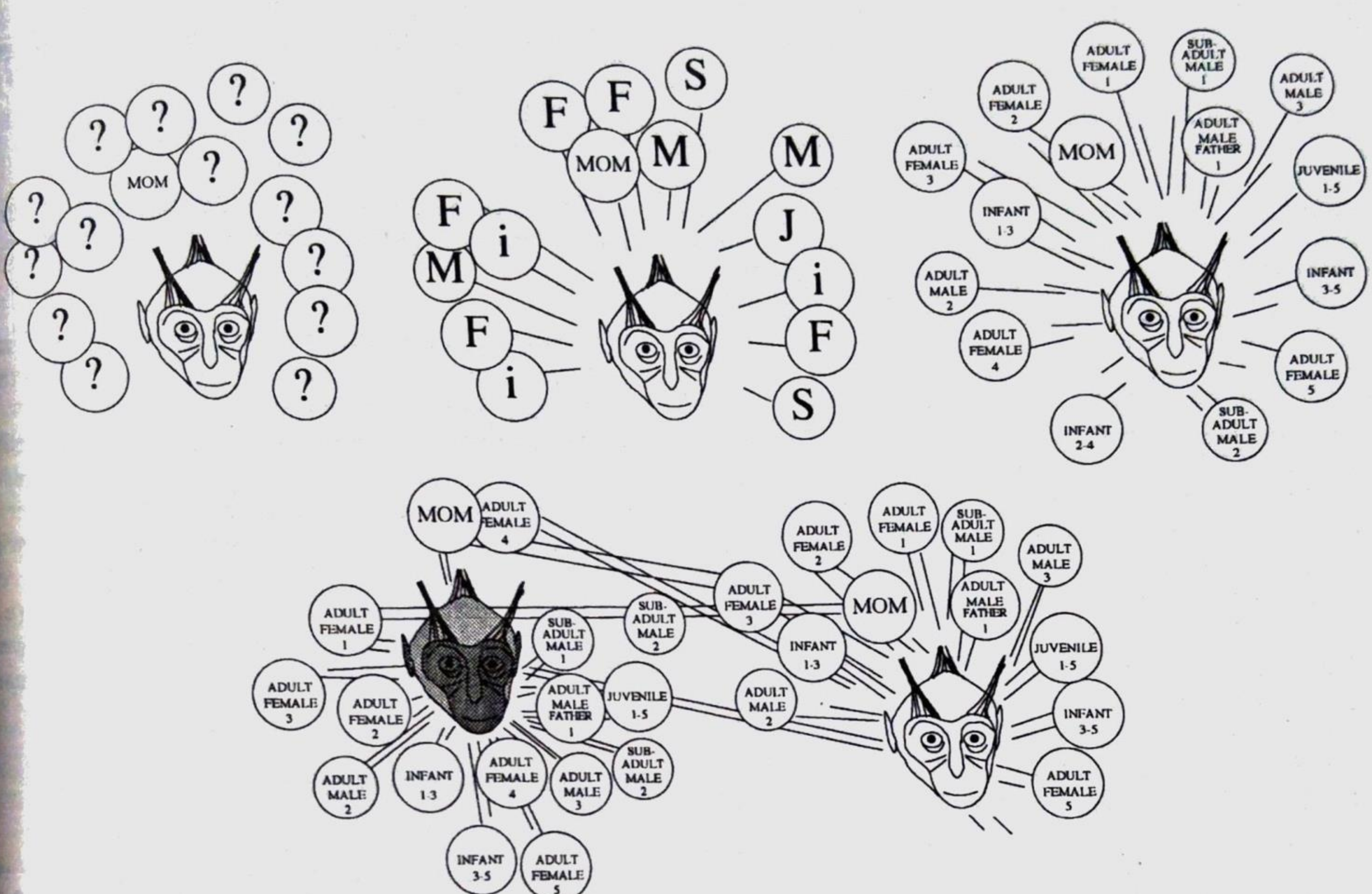

FIGURE 4. A. Social ontogenetic processes associated with the different phenotypic dimensions of a group partner that infants are subjected to during their ontogeny: Here an infant progressively discovers the several features of an adult female. Through recurrent observations, he first discriminates her from other partners, using her unique morphological features. Then, while interacting with this adult female and other group members, the infant will become aware of certain similarities within the adult female class. This leads to a new kind of partner differentiation. Through interactions the infant will develop his social/behavioral repertoire. As the social organization imposes different constraints on each member, the multidimensional social phenotypes the infant is interacting with are unique. This will lead to a further differentiation of the infant's social repertoire, and to the setting-up of a unique social network.
B. Socialization processes illustrated in the social ontogeny of a grey-cheeked mangabey infant. Top row: from left to right, discrimination of partners, class of partners, and of individuals. Bottom row: Building of a network of social relationships.

In the following sections, examples will be drawn from ontogenetic studies of grey-cheeked mangabeys and rhesus macaques (Deputte 1983, 1985, 1986a, 1986b, Deputte & Quris 1996, and Deputte & Goy 1991 and in prep, respectively).

FACTS AND METHODOLOGICAL ISSUES

Only longitudinal studies are relevant to the issue of social ontogeny. The same individuals should be observed from periods of time ranging from a few months to a few years. When the sampling method uses a cross-sectional approach, the studies do not concern the issue of social ontogeny but that of social ontogenetic processes or social development.

Description of social development

There is quite a large literature on primate infant development, both in the field and in the lab. Most of these studies address the behavioral development issue. The classical way of describing primate social development has been, and still is, to plot the frequency of several selected behaviors against time. Each selected behavior is considered as representative of a set of ontogenetic processes. The behaviors are selected to illustrate the development of perceptual capabilities (e.g. Deputte1985, 1986a; *Figure 5*) or motor, gestural and/or locomotor capabilities.

In grey-cheeked mangabeys, observed longitudinally from 6 to 54 months, the development of social looking behavior showed 3 main periods. The first one, lasting

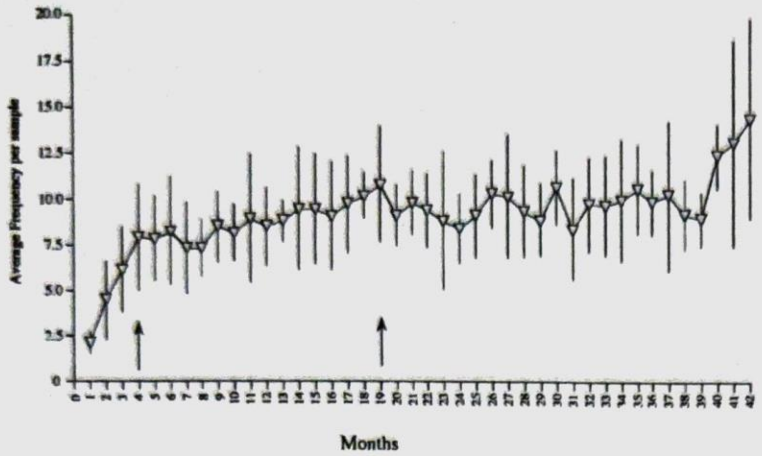

FIGURE 5. Development of social looking behavior in grey-cheeked mangabey infants (social looking behavior = looking behavior addressed to group members). Arrows indicate the end of the first two periods, from 0 to 4 months and from 4 to 19 months (see text).

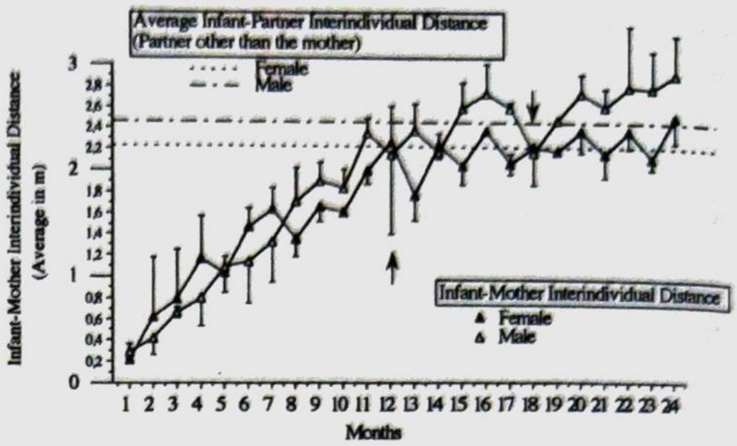

FIGURE 6. Changes in infant-mother distances during the first 2 years in male and female grey-cheeked mangabey infants.

from birth until month 4, was characterized by a sharp increase, and the second one, from 4 to month 19, by a plateau of frequency of looking behaviors, followed by a fluctuating high level of visual social awareness *(Figure 5)*. It is likely that these two phases characterized the neurophysiological development of vision; the initial phase corresponding to the rapid development of perceptual capabilities, such as visual acuity and contrast sensitivity. The second phase likely corresponded to the later slow development of the neocortical structures involved in the cognitive processing of information. When focusing on mother-infant interactions, the locomotor capabilities were mainly used to describe the important process of the infant's increasing independence from the mother.

In such cases, most often, the outcomes of locomotion, i.e. infant-mother distances, are analyzed, rather than locomotor abilities *per se*. At 3 months, captive infant mangabeys and pig-tailed macaques are out of reach of their mother most of the time(Deputte 1986a and Jensen, Bobbit and Gordon 1968, respectively; cf *Figure 6*) and, in the wild, infant baboons are at least 5 meters from their mother at 5 months of age (Altmann, 1978).

The gestural development could also be used to illustrate this increasing independence from the mother or decreasing need of exclusive contact with the mother. In grey-cheeked mangabeys, as in other cercopithecids, infants progressively established less and less ventro-ventral contact with their mothers or other partners (e.g. Deputte 1986a; *Figure 7*). At the same time, they were carried less and less often by the partners they were used to huddle with.

Processes in social development

The Index Approach

Other plots could be provided for a large array of behaviors. All these plots yield a patchwork picture of primate social ontogeny. However, these rather descriptive results fail to indicate HOW this happens and WHAT processes are involved. Assuming the paramount impor-

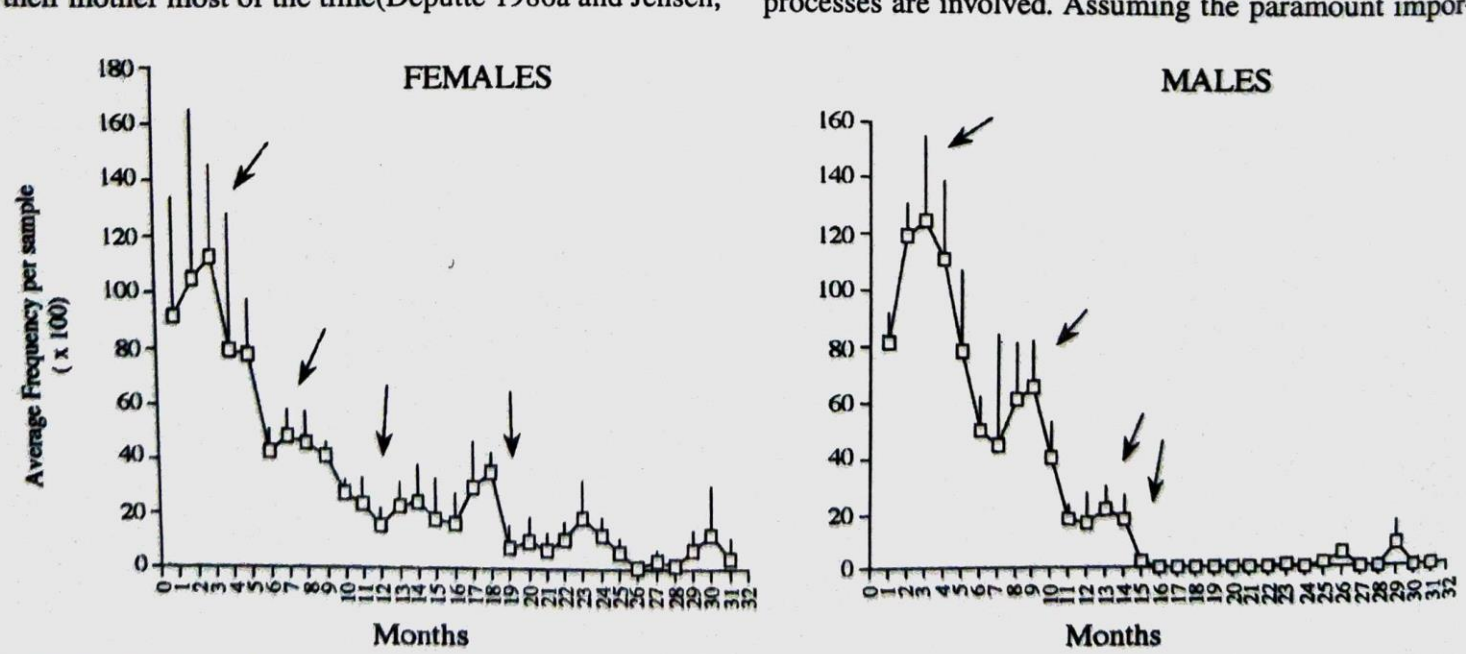

FIGURE 7. Changes in huddling behavior in male and female grey-cheeked mangabey infants during the first 2 and half years. Arrows indicate either peaks or changes in huddling frequency. The changes are more or less synchronous between males and females, but huddling disappears in males after month 15.

tance of interactive processes in primate development, Hinde and his collaborators attempted to move a step further from the classical frequency-time plots, to deal with the HOW. Focusing on mother-infant relationships, they devised some techniques to assess the respective roles of the mother and her infant in the dynamic of their relationships. They then defined two indices, the Approach-Leave Index (Hinde & Atkinson, 1970) and the Making-Breaking Contact Index (Hinde & White, 1974). These two indices helped determine which one - the mother or her infant - is responsible for maintaining proximity, on the one hand, and ventro-ventral contact, on the other hand. This index approach clearly indicated that more or less independent variables were not satisfactory to describe primate social ontogeny. It was a definite step towards integrated variables to deal with interactive processes. However, the fact that two indices have to be defined to account for two related sets of phenomena proved that only a first level of integration had been reached.

SOCIAL INVESTMENT INDEX (S.I.I.)

A - Computation of the S.I.I.

$$S.I.I. = \frac{(G\% - R\%)}{2}$$

$$\text{with } G\% = \frac{G^+ - G^-}{G^+ + G^-} \text{ and } R\% = \frac{R^+ - R^-}{R^+ + R^-}$$

G^+, R^+ = affiliative ("positive") behaviors and G^-, R^- = agonistic ("negative") behaviors where $G^- = (G^-_{ag} + G^-_{av})$ and $R^- = (R^-_{ag} + R^-_{av})$ with G^-_{ag}, R^-_{ag} = "negative"-aggressive behaviors and G^-_{av}, R^-_{av} = "negative"-avoidance behaviors.

B - Interpretations of the values of S.I.I.

S.I.I.	Conditions	
+100 to +50	G% > 0 and R% < 0	Subject's Responsibility
+50 to 0	G% > 0 and R% > 0 with G%>R% or G% < 0 and R% < 0 with G%<R%	Subject's Responsibility
0 to -50	R% > 0 and G% > 0 with R%>G% or R% < 0 and G% < 0 with R%<G%	Partner's Responsibility
-50 to -100	R% > 0 and G% < 0	Partner's Responsibility

C - Types of Relationships related to the different components of the S.I.I.

SUBJECT (G)		PARTNER (R)	+	+	+	-	-	-
		0	A	AE	E	A	AE	E
	0	0+/0+	0+/A+	0+/AE+	0+/E+	0+/A-	0+/AE-	0+/E-
+	A	A+/0+	A+/A+	A+/AE+	A+/E+	A+/A-	A+/AE-	A+/E-
+	AE	AE+/0+	AE+/A+	AE+/AE+	AE+/E+	AE+/A-	AE+/AE-	AE+/E-
+	E	E+/0+	E+/A+	E+/AE+	E+/E+	E+/A-	E+/AE-	E+/E-
-	A	A-/0+	A-/A+	A-/AE+	A-/E+	*A-/A-*	A-/AE-	A-/E-
-	AE	AE-/0+	AE-/A+	AE-/AE+	AE-/E+	AE-/A-	AE-/AE-	AE-/E-
-	E	E-/0+	E-/A+	E-/AE+	E-/E+	E-/A-	E-/AE-	*E-/E-*

FIGURE 8. Social Investment Index (S.I.I.): (A) computation , (B) interpretation of values and (C) related types of relationships . In C, + and - mean that G+ > G - and G+< G -, respectively (same for R). 0, A, AE, E feature the nature of the agonistic components of the S.I.I., G - and R -. 0; ag=ev=0 (G- and/or R- =0), A; ag>av, AE; ag=av, E; av>ag. The shaded cells represent the types of relationships symmetrical to those in the other half of the table. The types in italics are the most unstable ones.
An "A+/E+" relationship means that both partners are displaying mainly affiliative behaviors to each other (+): when a conflict occurs, one individual, the subject, displays mainly aggressive behavior (A) and his partner mainly avoidance behavior (E). This "A+/E+" relationship could be qualified as positive and complementary. It represents what is generally referred as a stable dominance-submission relationship. In contrast, an "A-/E-" relationship represents an unstable dominance-submission relationship. In an "A-/A-" relationship, interactions between the two partners primarily consist of aggressive conflicts in which none of the partners yields any ground or in which each partner alternately wins. This relationship is likely to be unstable.

To proceed a step further, along the line of Hinde's indices, I proposed a more integrated index, the Social Investment Index – S.I.I., which aims to assess the role of each partner of a dyad in setting the nature of the relationship (Deputte, 1983). Following Hinde's suggestion, this index helped in making inferences from interactions to relationships. The Social Investment Index is the difference between the relative, positive or negative, amount of affiliative behaviors given by a focus-subject and the same ratio from the given partner *(Figure 8)*.

In contrast with Hinde's indices, a fairly large number of different behaviors (69 behaviors) are used in the computation of the S.I.I., as it is intended to provide an integrated picture of a relationship (Deputte, 1983). Using a large number of behaviors actually stressed the multidimensionality of the social behavior, many different behaviors having possibly the same meaning in terms of the nature of a relationship.

The display of negative, agonistic, behaviors results in an increase in distance between the partners of a dyad. However, this increase could result from two different but complementary behaviors: some relate to aggression, a partner intending to make his partner move away, others to "spontaneous" avoidance (not preceded by aggressive behaviors). The S.I.I. ranged from +100% to –100% *(Figure 8)*. Within the 0 to 50% range, the two partners invested positively in the relationship, with the focus-subject initiating more positive interactions than his partner *(Figure 8)*. The 50% to 100% range could be called the "overinvestment range" as the subject kept on giving positive behaviors while receiving a majority of negative behaviors, either aggressive or avoidance ones, from his partner *(Figure 8)*. The Social Investment Index yielded a single numeric value, but some additional information associated with this value are needed to provide a complete and accurate interpretation *(Figures 8A & B)*. One important piece of information is the balance between aggressive and avoidance behaviors for each member of the dyad *(Figure 8A)*. This balance, plus the sign of G% and R%, yields 28 different types of social relationships *(Figure 8C)*.

The three dimensions of an integrating index, such as the S.I.I. (numeric value, sign, nature of agonistic component), exemplifies the difficulty of dealing with an interactive process with only one number – or only one behavior.

However, the changes in S.I.I. during ontogeny clearly indicate, at a first glance, the changes in the nature of infant-partner relationships *(Figure 9)*. In grey-cheeked

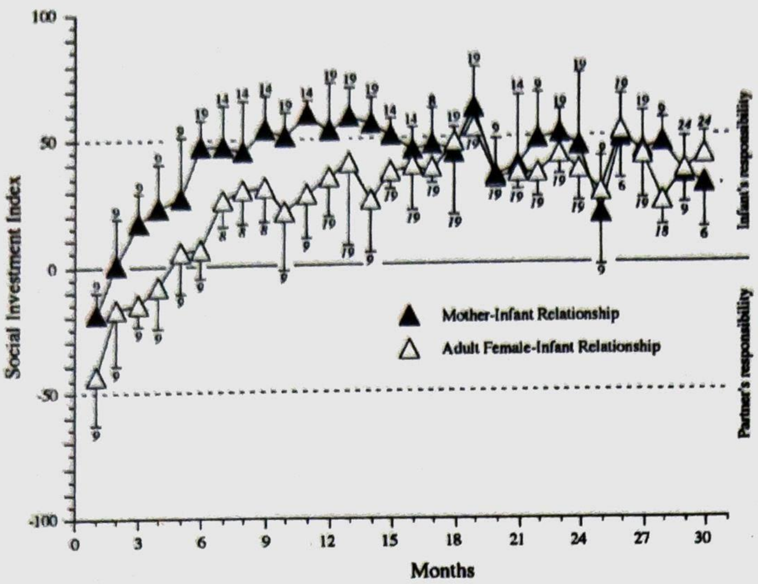

FIGURE 9. Changes in Social Investment Index (S.I.I.) in two types of dyads, infant-mother and infant-adult female, in grey-cheeked mangabeys: The standard deviations are associated to the value of the means. N = 9 but it varied between 7 to 5 depending on infant's age. The numbers above or below the standard deviations indicate the nature of the relationships (infant-adult females = numbers in italics): 6 = AE+/AE+, 8 = E+/A+, 9 = E+/AE+, 14 = E+/A-, 18 = AE+/AE-, 19 = E+/AE-, 24 = AE+/E- (cf text and *Figure 8*).

mangabeys, infants "overinvest" in their relationships with their mothers, while they never do this in their relationships with adult females *(Figure 9)*. As early as the second month, infants are responsible for the positive nature of the relationship with their mother *(Figure 9)*. Around month six, and up to month 15, the relationship changed, as the mother becomes more rejecting. Beyond 2 years of age, the relationship changes because the infant changes his behavior towards his mother *(Figure 9)*. During the first 5 months, the infant-mother and infant-adult female relationships are quite similar, although the adult females take the main role in setting a positive relationship, in contrast with the mothers *(Figure 9)*. During the first 30 months, the nature of infant-mother relationships changed more often than that of the infant-adult female relationships (17 changes in infant-mother relationships vs. 5 changes in infant-adult female relationships; *Figure 9*). The greatest differentiation between these two relationships occurred beyond 2 years of age *(Figure 9)*.

The Multivariate Approach

Although Hinde's indices and the S.I.I. give more information about processes and a more integrated picture of the social ontogeny, they still fail to deal with the complexity of the development of the social behavioral repertoire and of that of the intertwined social networks. In an attempt to offer a comprehensive picture of social behavioral development or socialization, repeated ANOVAs are sometimes used. However repeated ANOVAs or even MANOVAs, more relevant and statistically more acceptable techniques, are not yet satisfactory for dealing with the complexity of social ontogeny, since these techniques cannot picture at once all the relationships between highly related variables.

In an attempt to provide such pictures, we tried another "Multifactorial" approach dealing with "Behavioral profiles", large sets of behaviors, instead of being concerned with one behavior or a small set of related behaviors. The "Behavioral profiles" referred to the differential diversity of social behaviors expressed during dyadic interactions between individuals and classes of partners, or between classes of partners. As a consequence, sets of behaviors became characteristic of interactions between classes of individuals. Therefore, by extension, "Behavioral profiles" could mean "behavioral profiles of dyadic interactions" or, for example, "behavioral profiles of mother->infant interactions" or "behavioral profiles of infant->mother interactions". "Behavioral profiles" are quite similar to "Activity Profiles" (Bernstein, 1971), but "Activity Profiles" applied to both social and non-social behaviors, and are more specifically related to the "Time-Budgets" approach (Bernstein, 1971 and also cf. Deputte, 1979). In addition, whereas "Activity profiles" corresponded to a molar level of behavioral analysis, "Behavioral profiles" corresponded to a molecular, and even lower (fine-grain), level of behavioral description. The "Role concept", developed by Bernstein (Bernstein & Sharpe, 1966) and later exemplified in different primate species (Fedigan, 1972, 1976; Bramblett, 1973; Fairbanks et al., 1978, etc.), is a special example of a "behavioral profile". Harlow, when defining the different affectional systems (Harlow & Harlow, 1965) and especially Hinde, when he described the partner's influences on infant development (Hinde & Spencer-Booth, 1967; Hinde, 1969; Hinde, 1971) assumed, more or less explicitly, a behavioral differentiation in infant-partner interactions (cf Deputte, 1986b). In other words, they assumed that there were specific behavioral profiles in interactions between infants and their partners, mother, adult females – "aunts", adult males and peers.

In the "Behavioral profile" approach, a behavioral repertoire is defined *a priori*, and the determination of behavioral sets characteristic of different periods of ontogeny and of different classes of partners is investigated. In this approach, the behavioral repertoire is generally quite large, as it is intended to cover the behavioral expression of adults and infants along their development. It includes, for example, 156 and 160 mutually exclusive behavioral units in the studies of behavioral ontogeny in grey-cheeked mangabeys and in rhesus macaques, respectively (Deputte 1986a, Deputte & Goy 1991). In previous studies, interactions between infants and the different age-sex classes of partners were considered separately. In our approach, we attempted to move a step further in dealing simultaneously with the multidimensionality of social behavior (a large behavioral repertoire) and a social group (different "unique" individual partners belonging to different age-sex classes). This approach was exemplified with two studies, one of social ontogeny of grey-cheeked mangabeys, completed on 9 subjects born in 3 different groups, and another one on the development of behavioral sex differences in 20 rhesus macaque infants belonging to

4 different groups. Two different multivariate techniques have been used: one, the Correspondence Factorial Analysis -CFA, basically provides a description of the latent structure underlying the data set (Benzecri et al., 1973; ter Braak, 1987); the other one, the Principal Component Analysis with Instrumental Variables -PCAIV, is basically analytic, and, as a MANOVA, yields information about the influence of selected independent variables on the variability of the dependent variables under consideration.

The Multivariate Descriptive Approach

In the basic matrix set for the Correspondence Factorial Analysis (CFA) multivariate analysis, the behavioral units are represented by the columns, and the infant-partner

	BEHAVIORAL UNITS										
INFANT-PARTNERS Interactions (+ Age)	B.U.1	B.U.2	B.U.3	B.U.4	B.U.5	B.U.j	..	..	..	B.U.156	ΣR
1- Inf1-M-P1	F/s 1,1	F/s 1,2				F/s 1,j					Σ1,.
2- Inf1-F-P1											
....											
4- Inf1-A. F.-P1											
....											
6- Inf2-M-P1											
....											
i- Inf1-M-P6	F/s i,1		F/s i,3			F/s i,j					Σ i,.
....											
....											
170- Inf10-Im-P7										F/s 170,156	
Σ C (B.U.)	Σ .,1	Σ ., 2				Σ .,j				Σ ., 156	

FIGURE 10. Behaviors x Partners Matrix: Contingency Table for Correspondence Factorial Analysis and other Multivariate Techniques. Row Identification: e.g. Inf1-M-P1= Interaction between Infant 1 with his mother (M) during the first period of ontogeny, P1 (P1 to P7). AF= Adult Female, F=Father, Im=Immature sibling. F/s = Frequency per sample.

dyads by the rows *(Figure 10)*. The frequency per 5-minute-focal sample was computed for each behavior over periods of one month, or longer. Each row actually represents the interactions between a given infant with an age-sex class of partners over a certain period of the infant's ontogeny. Each cell then contains the frequency per unit of time of a given behavior observed during the dyadic interactions *(Figure 10)*. The Correspondence Factorial Analysis explored, in a descriptive way, the contingencies between the two sets of variables: behaviors, on the one hand, and subject-partner-age, on the other hand. These contingencies are computed in a multidimensional space, and several factors explaining the variable underlying structure are determined (the first factors of the analysis are determined in order to maximize the variance extracted from the set of data; more details are available in Deputte & Goy, 1991 and Deputte & Quris, 1996). This kind of analysis yielded a graphic representation of the results. In this representation, the factors are the axes of the plot and the relationships between and within the two sets of variables are visible simultaneously.

As an example, a behavioral differentiation is clear in ontogeny of rhesus macaque infants between 1 to 7 months *(Figure 11)*. When rhesus infants initiated interactions with their partners (mother, adult females or other male and

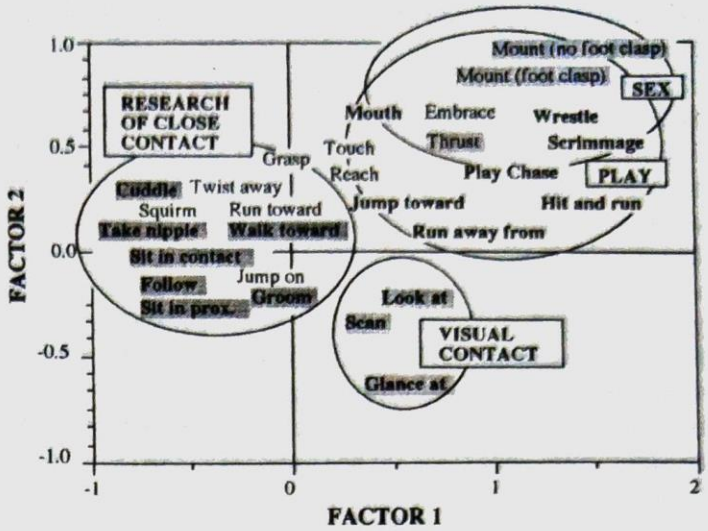

FIGURE 11. Behavioral profiles of infant-to-partners interactions in rhesus macaques (20 infant-mother pairs). Graphical representation of the results of a Correspondence Factorial Analysis. Projection on the plane of the first 2 factors: the 4 principal clusters are included in ellipses and the principal behaviors are differentially shaded (modified from Deputte & Goy 1991).

female infants) four main clusters could be discriminated along the two principal axes.

The first factor (horizontal axis) could be called "Duration of social interactions", contrasting long-lasting contacts represented by the cluster "Research of close contact" with brief and repetitive contacts, including visual contacts and sex and play interactions *(Figure 11)*. The second factor is the "Intensity of social contacts", opposing absence of physical contact (visual contact) to extensive manipulations of the partner's body (sex and play interactions; *Figure 11*). Other behaviors, not represented on the graph, participated less in this differentiation, although they might be associated with one of the clusters mentioned. In this example, only the behaviors, the columns of the matrix, are represented. However the infant-partner interactions, the rows of the matrix, could be represented on the same graph. In that case, the proximity of the points featuring the infant-partner interactions, the rows, and those featuring the behaviors, the columns, indicates a correlation between these two sets. Consequently, behavioral clusters could be associated with certain dyadic interactions. The social ontogeny of 9 grey-cheeked mangabey infants, from birth to 2 and a half years, serves as another example. In this analysis, it can be assumed that the behavioral differentiation is actually a consequence of the nature of the partner who is interacting with an infant *(Figure 12)*. In addition, the behavioral profiles of partner-to-infant interactions change with time *(Figure 12)*.

The two main factors of the C.F.A. were, on the first horizontal axis, "Locomotor activity during interactions", opposing static (protective behaviors, grooming, reaching out, sitting in proximity, etc.) to dynamic (running towards, wrestling, chasing, etc.) interactions along this axis and, on the second, vertical axis, "Regulation of social contact" opposing attraction (searching contact behaviors) to repulsion (aggressive behaviors; *Figure 12*). However, it became apparent that the behavioral clusters characterized the different Partner-> Infant dyads at different periods of the infants' ontogeny (Deputte, 1986a, 1986b; *Figure 12*). However, Mother->Infant and Adult Female->Infant behavioral profiles were very different until the infants were 8 months old *(Figure 12).* Up to this age, mothers are mostly protective, while adult females mainly seek to contact infants, as mothers more or less prevent adult females from having access to their infants. From 8 months on, the Adult Female-> and Mother->Infant behavioral profiles became quite similar, including breaking contact and aggressive behavior on the one hand, and grooming behavior on the other hand *(Figure 12).* Quite similarly, Adult Male and Father interactions included the same sets of behavior until the infants are 8 months old *(Figure 12).*

Then Fathers became progressively more and more aggressive towards infants (now juveniles, Deputte, 1992), whereas Adult Males became more and more cautious in their attempts to interact with the infants *(Figure 12).* Finally, up to the time when the infants are 3 months old, immature partners, like adult females, were attracted by infants, and attempted to interact with them. As the infants' independence increased, Immature-Infant interactions developed into playful interactions *(Figure 12).* The same Behavior-Partner differentiation has been demonstrated in the study of rhesus social development. The Behavior-Partner differentiation, demonstrated through these analyses, confirms and illustrates i) the social role concept, ii) the importance of social organization, which imposes constraints on the individual's social network and, consequently, on his behavioral expression in his interactions with other partners in general and with infants especially, and iii) the differential role each group member plays in infants' social development through interactions. In addition, this Behavior-Partner differentiation confirms the usefulness of the "Social Phenotype Approach" when social ontogeny is studied: in the course of his social ontogeny, an infant becomes progressively aware both of partners' morphological characteristics and associated social behavioral ones. In so doing, an infant goes through a so-called process of "Social Identification" *(Figure 4).*

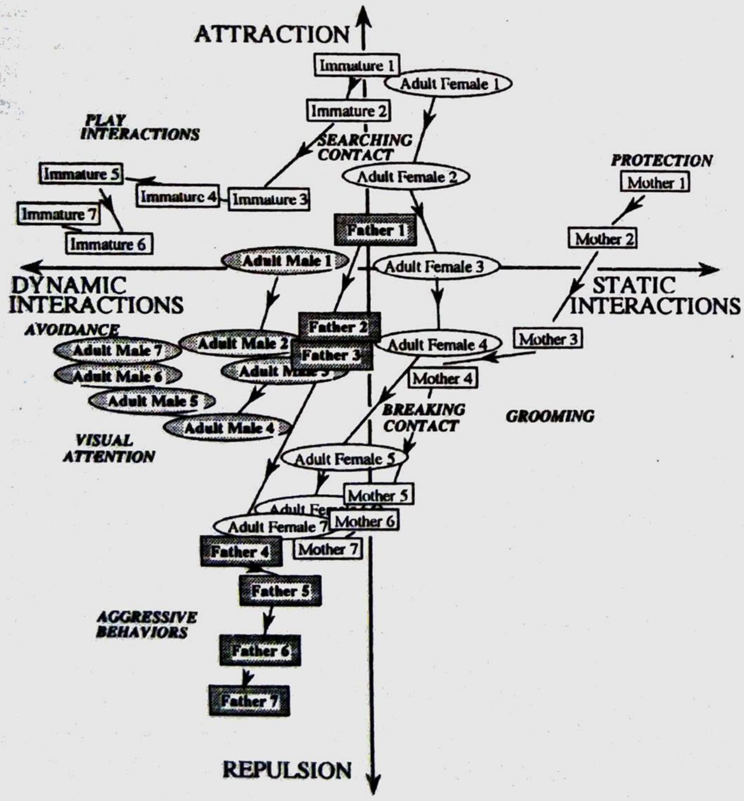

FIGURE 12. Changes in behavioral profiles of partners-to-infant interactions in grey-cheeked mangabeys during ontogeny of 9 infant subjects. Graphical representation of the results of a Correspondence Factorial Analysis. Projection on the plane of the first two factors: the principal clusters are given in capitalized italics. The different age-sex classes of partner are included within boxes or ellipses. The numbers associated with the classes of partner correspond to the period of the infant's ontogeny: 1 = 0 to 1 month, 2 = 2 to 3 months, 3= 4 to 8 months, 4= 8 to 12 months, 5= 12 to 18 months, 6= 18 to 24 months, 7= 24 to 30 months. The arrows connect the same partner-infant dyads for successive periods of ontogeny.

The Multivariate Analytic Approach

From the previous descriptive analysis, two major socialization processes emerged: the acquisition of a behavioral repertoire and the establishment of a network of social relationships. As the previous analysis suggested, these two processes are inter- dependent, as both result from social interactions. This interactive feature has to be investigated, as well as the influence that different independent variables might have on these processes. A similar, but more analytical, multivariate approach than that described previously was used in the study of social ontogeny in grey-cheeked mangabeys.

a) *Influence of the social environment on socialization processes*

The hypothesis assumed here is that if the infants' partners, the social phenotypes, have an influence on the socialization processes, then different social environments should yield different outputs or, at least, a different developmental timing for the processes under consideration. In a given species, it can be hypothesized that large and complex groups would provide their young with greater chances to acquire a large behavioral repertoire rapidly, or, possibly, a larger one than young in smaller and less diverse groups. However, an infant will acquire a greater and/or more complex repertoire only if he actually interacts with a large variety of partners having different behavioral profiles. Thus the 8 grey-cheeked mangabey infants were born within three groups representing different social environments (one UniMale/UniFemale, UM/UF, one UniMale/MultiFemale, UM/MF, and one MultiMale/MultiFemale, MM/MF, as per the classification of Fedigan, 1982). These social environments differed in many ways – their size, their demographic structure, their social organization and the "personal history" of each group member. Referring to Altmann's approach to behavioral diversity (Altmann, 1965), a rich

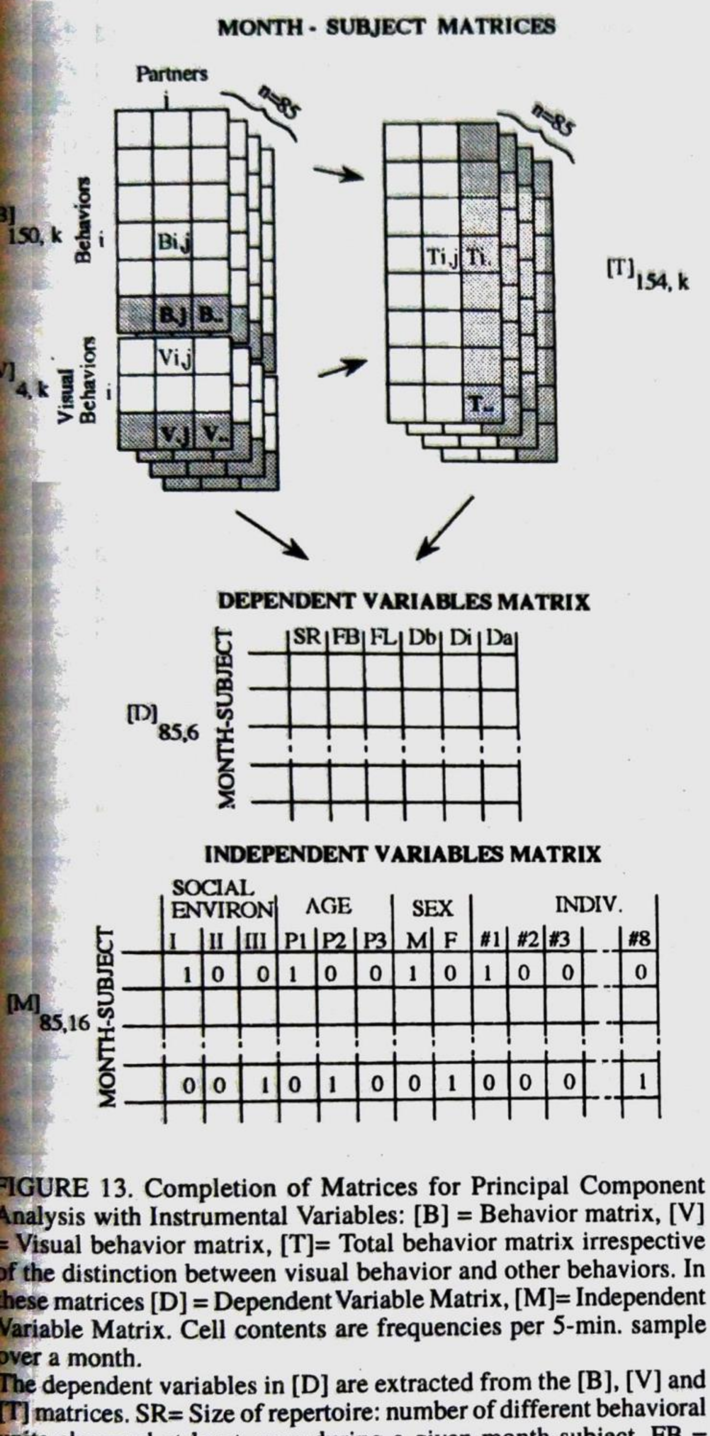

FIGURE 13. Completion of Matrices for Principal Component Analysis with Instrumental Variables: [B] = Behavior matrix, [V] = Visual behavior matrix, [T]= Total behavior matrix irrespective of the distinction between visual behavior and other behaviors. In these matrices [D] = Dependent Variable Matrix, [M]= Independent Variable Matrix. Cell contents are frequencies per 5-min. sample over a month.

The dependent variables in [D] are extracted from the [B], [V] and [T] matrices. SR= Size of repertoire: number of different behavioral units observed at least once during a given month-subject. FB = Total frequency of behaviors: B.., from the [B] matrix. FL= Total frequency of looks, V.., from the [V] matrix. Db= Diversity of behaviors:

$$D_b = -\sum_{i=1}^{m} (Ti./T..)(\log(Ti./T..))$$ where m = 154; Ti. and T.. are respectively the sum of the ith row and the grand total ([T] matrix).

D_i = Diversity of interactions: $$D_i = -\sum_{j=1}^{k} (B._j / B..)(\log(B._j) / B..))$$

where $B._j$ the total of the jth column in the [B] matrix and k varying from 3 to 8 depending on the group size. Da= Diversity of attention:

$$D_a = -\sum_{j=1}^{k} (V._j/V..)(\log(V._j/V..))$$ where $V._j$ the total of the jth column in the [V] matrix and k varying from 3 to 8 depending on the group size (modified from Deputte & Quris 1996).

and complex individual repertoire would include most if not all *a priori* defined behavioral units, *and* a high proportion of units would be observed with a comparably high frequency. In contrast, a rich but simple repertoire would include the same number of units as previously, but only a few units would be observed most often. The complexity of interaction patterns can be assessed in the same way: a complex network of interactions will be the consequence of a balanced level of interactions with all available partners. In contrast, a simple network will be assessed if an individual interacts most of the time with only one or a few partners. These behavioral or interaction complexities were illustrated by the frequency distribution of behavioral patterns, and represented with synthetic parameters such as diversity or uncertainty indices, derived from Shannon's information theory (Altmann, 1965). As before, Behavior-Partner matrices were set for each month and each subject (85 months-subjects; *Figure 13*).

Six dependent, variables (to be explained) are extracted from each month-subject matrix *(Figure 13)*. 1 – The Size of the Social Repertoire: the number of different behavioral units observed at least once during a given month-subject, which reflects the overall variety of the infant's behavioral expression (or the variety of the social stimulation received by an infant; Deputte et Quris 1996), 2 – The Total Frequency of Behavior, an expression of the intensity of social interactions, 3 – The Diversity of Behavior, referring to the structure of the observed behavioral repertoire – this describes whether the behavioral expression, e.g. given by the young subject, is dominated by only a few, often recurring behaviors (low diversity) or is balanced between a large number of behaviors (high diversity; Deputte & Quris, 1996), 4 – The Total Frequency of Looks, 5 – The Diversity of Interaction, which shows whether a subject initiates interactions with or is contacted by very few partners very often (low diversity), or distributes his interactions evenly between or is contacted evenly by a large number of partners (high diversity; Deputte & Quris, 1996), 6 – The Diversity of Attention, which is like the diversity of interaction, but is computed only with reference to social looking behavior.

The first three variables describe more specifically the acquisition of a social behavioral repertoire, the last three the development of a social network. Three developmental periods were considered: from 1 to 6 months, from 7 to 12 and from 13 to 18 months.

The Principal Component Analysis with Instrumental Variables, P.C.A.I.V. (ter Braak, 1987; Sabatier et al., 1989; Lebreton et al., 1991; and cf Deputte & Quris, 1996) was used here. This Multivariate technique allowed consideration of several variables simultaneously, measurement of the correlations between the dependent variables, and evaluation of an underlying structure of the data, combining the properties of a Multiple Analysis of Variance and a Principal Component Analysis. The principle of this multivariate analysis consists in computing the expected values of the matrix [D] in relation to the model as expressed in the columns of the [M] matrix (*Figure 13;* and cf Deputte & Quris, 1996). The [M] matrix is therefore that of the independent variables, the Social Environment, Infants' Age, Infants' Sex and the Infants' Individuality (*Figure 12;* for further details see Deputte &

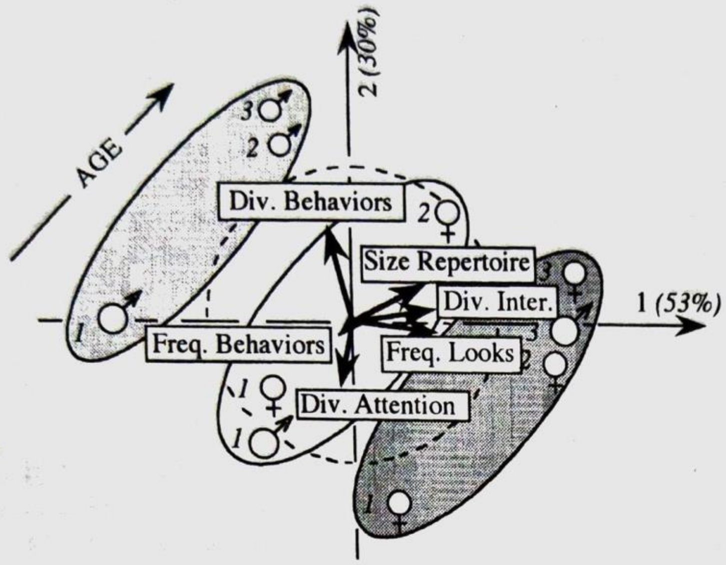

FIGURE 14. Influence of social environments in socializing processes in grey-cheeked mangabey infants' ontogeny.
Graphical display of the results of the 3-variable Principle Components Analysis with Instrumental Variables (P.C.A.I.V.). Infants as initiators. Representation of the projections on the plane of the first 2 factors of the P.C.A.I.V., of the 6 dependent variables, shown as vectors, and of the centers of gravity of the clusters of points featuring the individuals grouped following the model variables (these centers of gravity are represented by a female or male symbol preceded by a number in italics, indicating the age-period: *1* = 0 to 6 , *2* = 7 to 12 and *3* = 13 to 18 months). The centers of gravity for individuals belonging to the same social structure are enclosed in an ellipse (dark grey = MM/MF, light grey = UM/MF, white = UM/UF; see text for definitions of the social structures). The dashed circle features the "correlation circle" (radius=1). Within this circle, the length of the vectors features how much a dependent variable is explained by the model. On each axis the percentage of extracted variance is indicated. The Age-arrow on the left of the figure indicates the influence of the Age variable. When points are in the direction of a vector (the length of which being close to 1), this means that these points or this cluster of points are positively correlated with this vector-variable (e.g. age with size of the repertoire and diversity of behaviors with the UM/UF social environment). The correlations between the dependent variables are represented by the cosine of the angle formed by the corresponding vectors: the acuter the angle, the more the dependent variables are positively correlated (e.g. the size of the repertoire, diversity of interactions, frequency of looks).

Quris, 1996). Additionally, in the P.C.A.I.V. technique a *multivariate* Fisher's F (explained variance/non-explained variance) can be computed, and the value of this Multivariate F can be tested using a Monte Carlo technique (Ter Braak, 1992).

When infants initiated interactions, the size of the repertoire, the diversity of interactions and the frequency of looks were highly positively correlated *(Figure 14).* The earliest stage of social ontogeny was clearly different from later stages, and was characterized by an initially small size of the repertoire, social interactions and behavioral expression, which started to differentiate only after 6 months. More importantly for the purpose of the hypothesis, the 3 social environments were clearly differentiated *(Figure 14).* Each social structure had a specific effect on socialization processes, whatever the age of the infants, the greatest variety of social stimulations being found in the UniMale/MultiFemale structure (Deputte & Quris, 1996). These influences of social environment illustrate the social constraints imposed on individuals attempting to contact infants. Although a large MultiMale/MultiFemale environment potentially provides infants with a large diversity of social phenotypes, all this diversity would be available to infants only if the social structure of the group allowed partners to contact any infant equally. If this is not the case, infants would be exposed to "individual phenotypes", or a partner diversity not different from that of UM/MF or even UM/UF groups. Therefore the influences of Age, Social Structure and Sex, to a much lesser extent, significantly affected more the two socialization processes under consideration - acquiring a social behavioral repertoire and building-up a network of relationships - than individual characteristics.

b) Influence of infant's sex in social ontogeny

– Definitions, Dimorphism and Diposotism, and general issue

Sex is determined by the genome, and the infants are born within a group including individuals of the two genders. The individual phenotypes were either male or female. Many behavioral differences between male and female adult primates have been described (e.g. cf Fedigan, 1982; Deputte, 1995). These differences are often referred to as *sex behavioral dimorphism*, with regard to sexual dimorphism applied to weight, size, color or other physical features. However, when behavior is concerned, two sets of phenomena may be observed: the homologous behaviors displayed by females are different in their patterns from those of the males, vocal behavior being a good example of this. In this case the term, and the concept, sex dimorphism is appropriate, especially in reference to "sonograms" (e.g. Deputte & Leclerc-Cassan, 1981). Conversely, many other differences between females and males are related to consistent differences in frequencies of behavior, the best example being grooming behavior, much more frequently performed by females than by males. However, in this case the behavior has the same form, only its frequency is dependent upon the sex of the performer.

Thus, in order to make the nature of the differences more precise, it will be more appropriate to use the term "*DIPOSOTISM*" from the Greek "Posos", which means in what quantity, and "Di", two. Diposotism then refers specifically to differences in frequencies of behaviors homologous, or having the same "shape", in males and females.

During ontogeny. the genome determines a hormonal environment, yielding a sexed individual phenotype. After birth, however, the principal factor influencing the social ontogeny is the social environment. Then the question arises: "Is the social phenotype sexed?" or, in other words, "Does the sexual behavioral diposotism fit the sexual dimorphism?". The alternative hypothesis is that, in contrast to the morphological phenotype, the social phenotype is non-sexed, since the social behavior develops through interactions with partners of both sexes; the social phenotype would have a bi-potentiality (cf Deputte, 1995). This would partly explain the dominance of a reversible, context-dependent, diposotism over a fixed behavioral dimorphism.

– Origin of behavioral sex differentiation in rhesus macaque infants

The development of a possible behavioral sex differentiation has been tested in rhesus monkey infants (Deputte & Goy, 1991). The prenatal influences of hormones on later behavioral development has been demonstrated through different studies (Goldfoot et al., 1984; Goy & Phoenix, 1972; Goy & Resko, 1972; Goy & Robinson, 1982; Goy et al., 1988). For example, it has been demonstrated that virilized females display some behaviors, such as play and mounting, with the same frequency as normal males or, at least, much more (high diposotism) than males castrated at birth and normal females. Isosexual rearing studies have emphasized the importance of an adequate companion for the development of some "diposotic" behaviors (Goldfoot et al., 1984): females reared in an isosexual environment mounted more and presented less than females reared in an environment including peers of both sexes, whereas, symmetrically, "isosexual" males mounted less and presented more than males reared with both females and males (Goldfoot et al., 1984).

A study investigating the influence of group partners (mothers, adult females and peers of both sexes) on the development of behavioral sex differentiation was completed on 20 rhesus infants – 8 females, 8 males and 4 DES-virilized females – whose mothers has been injected with 100 mg of Diethylstilbestrol from day 115 to day 139 of gestation, hence a rather low total dose of this virilizing hormone. The infants lived in 4 groups. Each group was composed of 5 infant-mother dyads, 2 male infants, 2 female infants and 1 DES female infant-mother dyad. The development of infants was followed from month 1 until month 6. The behavioral repertoire includes 160 behavioral units. Partner-Behavior matrices were set (see *Figure 10*). The Partners, the rows of the matrix, were actually a combination of the individual infant, his age, his sex and the partner he is interacting with (Deputte & Goy, 1991; Deputte et al., in press). The multivariate analysis was a Correspondence Factorial Analysis with Instrumental Variables, C.F.A.I.V., which is similar to the C.P.A.I.V. but computed on a contingency matrix. The dependent variables were the behaviors of the repertoire. Five independent variables were considered, Infant's Sex, Partner of the Interaction, Mother's Rank, Age, and Social Group. The behavioral sex differentiation was investigated by asking the question: Are the behavioral profiles discriminated according to the infants' sex?

Again, a clear behavioral and partner-differentiation emerged from this study *(Figure 15);* Infants used significantly different sets of behaviors when interacting with their mother or with adult females (mothers of other infants) or with other infants (Multivariate $F(34,1008)=8.18$, $p<0.001$). Interactions with the mother are characterized by research of close contact behaviors, those with adult females by visual contact only, and those with other infants by sex and play behaviors *(Figures 11 and 15)*. However, the sex of the infant had a rather weak effect on this differentiation *(Figure 15)*. This result seems to contradict previous results on the effects of hormones on infant behavioral development, which show a clear differentiation between male and female infants (e.g. Goy & Resko, 1972; Goy & Robinson, 1982; Goy et al., 1988). However, the former study is concerned with the whole behavioral repertoire, whereas the latter was concerned only with a rather discrete subset of behaviors. The apparent difference does not exist if the CFAIV technique is

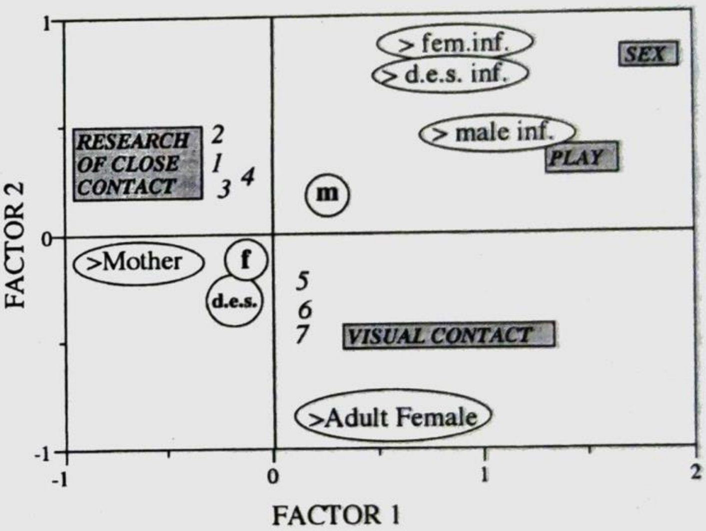

FIGURE 15. Influence of sex in the development of social behavior in rhesus macaque infants' ontogeny.
Graphical display of the results of the 3-variable Correspondence Factorial Analysis with Instrumental Variables (C.F.A.I.V.). Infants as initiators. Representation of the projections on the plane of the first 2 factors of the C.F.A.I.V., of the 3 independent variables (sex, partner and age) and of the centers of gravity of the behavioral clusters (dependent variables). For sake of clarity, only the four principal clusters have been represented *(see Fig. 11)*. The "Partner" variable is indicated within ellipses; > means that infants initiate interactions with the different partners (see text). The different modalities of the "Age" variable, months, are indicated with numbers in italics. The "Sex" variable is indicated with bold letters within circles (females: f and d.e.s. ; males: m).
The closer the independent variables from the center of the graph, the weaker the influence of the variable; the "Partner" variable has the strongest influence on the infant's behavioral differentiation. The first 4 months differ from the 3 last ones. The closer a dependent variable to an independent one, the stronger the association between them: e.g. The "research of close contact" behavioral cluster characterizes the infant to mother interactions (">Mother") during the first 4 months (*1, 2, 3, 4*). Male infants to male infants are characterized by play, and male infants to female infants by sex. Females, both normal and treated, interact more with adult females (both their mothers and the other infants' mothers); f and d.e.s. are closer to ">Mother" and to ">Adult female". This occurs more likely when infants are over 4 months old.

applied to the same set of behaviors as those used in Goy and coll's studies. When only infant-infant interactions are considered, and when tactile, mounting and play behaviors (12 exclusive behavioral units) are the dependent variables and age, partner and infant's sex are the independent variables, the infant's sex becomes the most important differentiating factor (57% of the overall explained variation).

CONCLUSIONS

The complexity of social ontogeny can be addressed with appropriate multivariate techniques, from MANOVAs to more geometrically oriented techniques, CPAIV and CFAIV. Social environment has a powerful influence on the development of social behavior, as this development is dependent upon social interactions. Within a social group, the dyad is the basic subsystem. However, it should be remembered that a dyad is actually an interface of two social networks. The timing of the acquisition of a social behavioral repertoire is a function of the nature of the interactions and, consequently, a function of the partners involved in them. The social network develops through an identification process of the social phenotypes.

Returning to Hailman's formula, it should be pointed out that the e_s component of E (1) is fundamentally dynamic

$$E:(e_S, e_p, C, F, A) \qquad (1)$$

This dynamic feature could be formalized in defining a "Systemic function" S (2), representing the dynamic interactions between all the social phenotypes in a group (through their social networks):

$$S:(e_{s_{t-2}}, SP_1, SP_2, SP_3, \ldots, SP_n, E^I) \mapsto e_{s_{t-1}} \qquad (2)$$

where the function S controls the changes of the social environment es, during a time span from t-2 to t-1, under the influence of the social phenotypes which composed the group and the rest of the environmental variables E'. All the different studies presented in this paper stress the integrated influence of the social phenotypes on the development of the new ones, through the existence of social networks and interactions. Then Hailman's original formula could be modified to account for the multi-level dialectic feature of primate social ontogeny. The outputs of the "Systemic function" (2) could be introduced within the Ontogenetic function, which can be renamed as a "Social Ontogenetic function":

$$O:(SP_{0_{t-1}}, G, e_{s_{t-1}}, E') \mapsto SP_{0_t} \qquad (3)$$

which maps the ontogenetic changes of one social phenotype, SP_0, its genotype G, the initial social environment and other environmental components E' to a new social phenotype, during an increment of time (from t-1 to t). In the same way the social group, social networks, and, consequently, social systemic function are influenced by the presence and the development of a new phenotype. To account for this, the "Social systemic function" could be modified: SP0 is the new social phenotype and n has consequently increased.

$$S:(e_{s_{t-1}}, SP_0, SP_1, SP_2, SP_3, \ldots, SP_n, E') \mapsto e_{s_t} \qquad (4)$$

The Social systemic function could be viewed as a composition of ontogenetic functions. It is worth recalling that the ontogenetic function acts during the whole life of an individual. Hence the social phenotypes SP in the formula (4) are not fixed but dynamic entities of the social systemic function. As Mason (1976) asserted, "Individuals are both the products and the producers of societies".

REFERENCES

ALTMANN J., 1978: Infant independence in yellow baboons. In: G.M. Burghardt & M. Bekoff (Eds.): *The development of behavior: comparative and evolutionary aspects*. Pp. 253-277. Garland STPM Press, New York.

BEKOFF M., BYERS J.A., 1981: A critical reanalysis of the ontogeny and phylogeny of mammalian social and locomotor play: an ethological Hornet's nest. In: K. Immelmann, G.W. Barlow, L. Petrinovitch & M. Main, (Eds.): *Behavioral development - The Bielefeld Interdisciplinary Project*. Pp. 296–337. Cambridge University Press, Cambridge.

BENZECRI J. P. et Coll., 1973: *L'analyse des donnés II: L'analyse des correspondances*. Dunod, Paris.

BERMAN C. M., 1982: The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys. I. Social networks and differentiation. *Anim. Behav*. XXX: 149–162.

BERNSTEIN I. S., 1971: Activity profiles of primate groups. In: A.M. Schrier and F. Stollnitz, (Eds.): *Behavior of nonhuman primates: modern trends*. Vol.3. Pp. 69-104. Academic Press, New York.

BERSTEIN I. S., SHARPE L. G., 1966: Social roles in a rhesus monkey group. *Behaviour*. XXVI: 91–104.

BERNSTEIN I. S., WILLIAMS L. E., 1986: The study of social organization. In: G. Mitchell & J. Erwin, (Eds.): *Comparative Primate Biology, Vol. 2A: Behavior, Conservation & Ecology*. Pp. 195–213. Alan R Liss, New York.

BOGIN B., 1988: *Patterns of human growth* . Cambridge University Press, Cambridge, U. K.,. 267 p.

BRAMBLETT C. A., 1973: Social organization as an expression of role behavior among Old World monkeys. *Primates*. XIV: 101-112.

DEPUTTE B. L., 1979: Etude des "budget-temps" d'un groupe captif de macaques de Java (*Macaca fascicularis*): mise en évidence de la synchronisation des activités. La Terre et la Vie, XXXIII: 241–252.

DEPUTTE B. L., 1983: Ontogenetic development of dyadic social relationships: assessing individual roles. *American Journal of Primatology*. IV: 309–318.

DEPUTTE B. L., 1985: Développement du comportement visuel social chez une jeune femelle cercocèbe (*Cercocebus albigena albigena*): étude préliminaire sur un groupe captif. *Biology of Behaviour*. X: 113–150.

DEPUTTE B. L., 1986a: *Ontogenèse du cercocèbe à joues blanches (Lophocebus albigena albigena) en captivité: développement des comportements de communication et des relations sociales*. Unpubl. Doctoral Dissertation. Université, de Rennes I.

DEPUTTE B. L., 1986b: Parner's roles in the socialization of young captive mangabeys (*Lophocebus albigena albigena*). In: L. Passera & J. P. Lachaud (Eds.): *The individual and society*. Pp. 109–117. I. E. C. Privat, Toulouse.

DEPUTTE B. L., 1992: Life-History of captive grey-cheeked mangabeys:physical and sexual development. *International Journal of Primatology*. XIII: 509–531.

DEPUTTE B. L., 1995 : Structuration des comportements en fonction du sexe chez les primates. In A. Ducros & M. Panoff, (Eds.): *La Frontiere des sexes*. Pp. 29–71, P.U.F., Paris.

DEPUTTE B. L., LECLERC-CASSAN M., 1981: Sex determination and age estimation in the white-cheeked gibbon (*Hylobates concolor leucogenys*): anatomical and behavioural features. *International Zoo Yearbook*. XXI: 187–193.

DEPUTTE B. L., QURIS R., 1996: Socialization processes in primates: use of multivariate analyses. I. Application to social development of captive mangabeys. *Behavioural Processes*. XXXVI: 135–149..

DEPUTTE B. L., GOY R. W., 1991: Development of behavioral sexual differences: experimental study of prenatal Diethylstilbestrol (D.E.S.) female rhesus macaque infants. In: A. Ehara, T. Kimura, O. Takenaka, M. Iwamoto, (Eds.): *Primatology today*. Pp. 465-468. Elsevier, Amsterdam.

FAIRBANKS L. A., McGUIRE M. T., PAGE N., 1978: Social roles in captive vervet monkeys (*Cercopithecus aethiops sabaeus*). *Behavioural Processes*. III: 335–352.

FEDIGAN L. M., 1972: Roles and activities of male geladas (*Theropithecus gelada*). *Behaviour*. XLI: 82–90.

FEDIGAN L. M., 1976: *A study of roles in the Arashiyama West troop of Japanese macaques (Macaca fuscata)*. Contrib. Primat. 9, Karger, Basel.

FEDIGAN L. M., 1982: *Primate paradigms: sex roles and social bonds*. Eden Press, Montreal.

GOLDFOOT D. A., WALLEN K., NEFF D. A., McBRAIR, M. C. & GOY, R. W., 1984: Social influences on the display of sexually dimorphic behavior in rhesus monkeys: isosexual rearing . *Arch. Sex. Behav.* XIII: 395–412.

GOTTLIEB G., 1970: Conceptions of prenatal behavior. In: L.R. Aronson, D.S. Lehrman, J.S. Rosenblatt, E. Tobach, (Eds.): *Development and evolution of behavior – essays in memory of T. C. Schneirla*. Pp. 111–137. W.H. Freeman & Co., San Francisco.

GOY R. W. , PHOENIX C. H., 1972: The effects of testosterone propionate administered before birth on the development of behavior in genetic female rhesus monkeys.; In C. Sawyer & R.Gorski ,(Eds.): *Steroid hormones and Brain functions*. Pp. 193–201. Univ. of California Press, Berkeley,.

GOY R. W., RESKO J. A., 1972: Gonadal hormones and behavior of normal and pseudohermaphroditic nonhuman female primates. *Rec. Prog. Hormone Res.* XXVIII: 707–733.

GOY R.W., ROBINSON J.A., 1982: Prenatal exposure of rhesus monkeys to patent androgens: morphological, behavioral and physiological consequences. *Banbury Report*. XI : 355–378.

GOY R. W., BERCOVITCH F. B., McBRAIR M. C., 1988: Behavioral masculinization is independent of genital masculinization in prenatally androgenized female rhesus macaques. *Hormones and Behavior* . XXII: 552-571.

HARLOW H. F. & HARLOW M. K., 1965: The affectional systems. In: A. M. Schrier, H. F. Harlow & F. Stollnitz, (Eds.): *Behavior of nonhuman primates: modern trends*. Vol.1. Pp. 287–334. Academic Press, New York.

HINDE R. A., 1969: Influence of social companions and temporary separation on mother-infant relations in rhesus monkeys. In: B. M. Foss, (Ed.): *Determinants of infant behaviour*. Vol. 4. Pp. 37–40. Methuen, London.

HINDE R. A., 1971: Development of social behavior. In: A.M. Schrier & F. Stollnitz, (Eds.): *Behavior of nonhuman primates: modern trends*. Vol. 3. Pp. 1–60. Academic Press, New York.

HINDE R. A., 1976a: On describing relationships. *J. Child. Psychol. Psychiatry*. XVII: 1–19.

HINDE R. A., 1976b: Interactions, relationships and social structure. *Man*. XI: 1–17.

HINDE R. A., 1979: *Towards understanding relationships*. Academic Press, London.

HINDE R. A., 1987: *Individuals, relationships and culture: Links between Ethology and the Social Sciences*. Cambridge University Press, Cambridge.

HINDE R. A., ATKINSON S., 1970. Assessing the roles of social partners in maintaining social proximity as exemplified by mother-infant relations in rhesus monkeys. *Anim. Behav*. XVIII: 169-176.

HINDE R. A., SPENCER-BOOTH Y., 1969: The effects of social companions on mother-infant relations in rhesus monkeys. In: D. Morris, (Ed.): *Primate ethology*. Pp. 267–286. Weidenfeld & Nicolson, London.

HINDE R. A., WHITE L., 1974. The dynamics of a relationship: rhesus monkey ventro-ventral contact. *J. comp. physiol. Psychol.* LXXXVI: 8–23.

JENSEN G. D., BOBBITT R. A., GORDON B. N., 1968: Sex differences in the development of independence of infant monkeys. *Behaviour* XXX: 1–14.

LEBRETON J. D., SABATIER R, BANCO J. L., BACOU A. M., 1991: Principal Component and Correspondence Analysis with respect to instrumental variables: an overview of their role in studies of structure – activity and species – environment relationships. In: J. Devillers, W. Karcher, (Eds.): *Applied Multivariate Analysis in S.A.R. and Environmental Studies*. Pp. 85–114. ECSC, EEC, EAEC, Brussels.

MASON W. A., 1976: Primate social behavior: pattern and process. In: R. B. Masterton et al., (Eds.): *Evolution of brain and behavior in vertebrates*. Pp. 425–455. Lawrence Erlbaum Associates, Hillsdale, New Jersey.

SABATIER R., LEBRETON J. D., CHESSEL D., 1989. Principal Component Analysis with instumental variables as a tool for modelling composition data. In: R. Coppi, S. Bolasco, (Eds.): *Multiway Data Analysis*. Pp. 341–352; Elsevier Science Publishers, B.V. North Holland, Amsterdam.

SCHAIK van, C. P., van HOOFF J. A.R. A. M., 1983. On the ultimate causes of primate social systems. *Behaviour*. LXXXV: 91–117.

TER BRAAK C. J. F., 1987: Ordination. In R. H. G. Jongman, C. J. F. ter Braak, O. F. R. van Tongeren, (Eds.): *Data analysis in community and landscape ecology*. Pp. 91–173. PUDOC, Wageningen, The Netherlands.

TER BRAAK C. J. F., 1992: Permutation versus bootstrap signifiance tests in multiple regression and ANOVA. In K.-H. Jöckel, G. Rothe and W. Sendler (Eds.), *Bootstraping and related techniques*, Pp. 79–86. Springer Verlag, Berlin.

THOMAN E. B., ACEBO C., DREYER C. A., BECKER P. T., FREESE M. P., 1979: Individuality in the interactive process. In: E. B. Thoman (Ed.): *Origins of the infant's social responsiveness*. Pp. 305–338. Lawrence Erlbaum Associates Publ., Hillsdale, New Jersey.

TINBERGEN N., 1963: On aims and methods of ethology. *Z. Tierpsychol.* XX: 410–429.

Bertrand L. Deputte
CNRS/URA 373
Laboratoire de Primatologie-Biologie évolutive
Station Biologique
35380 Paimpont
France