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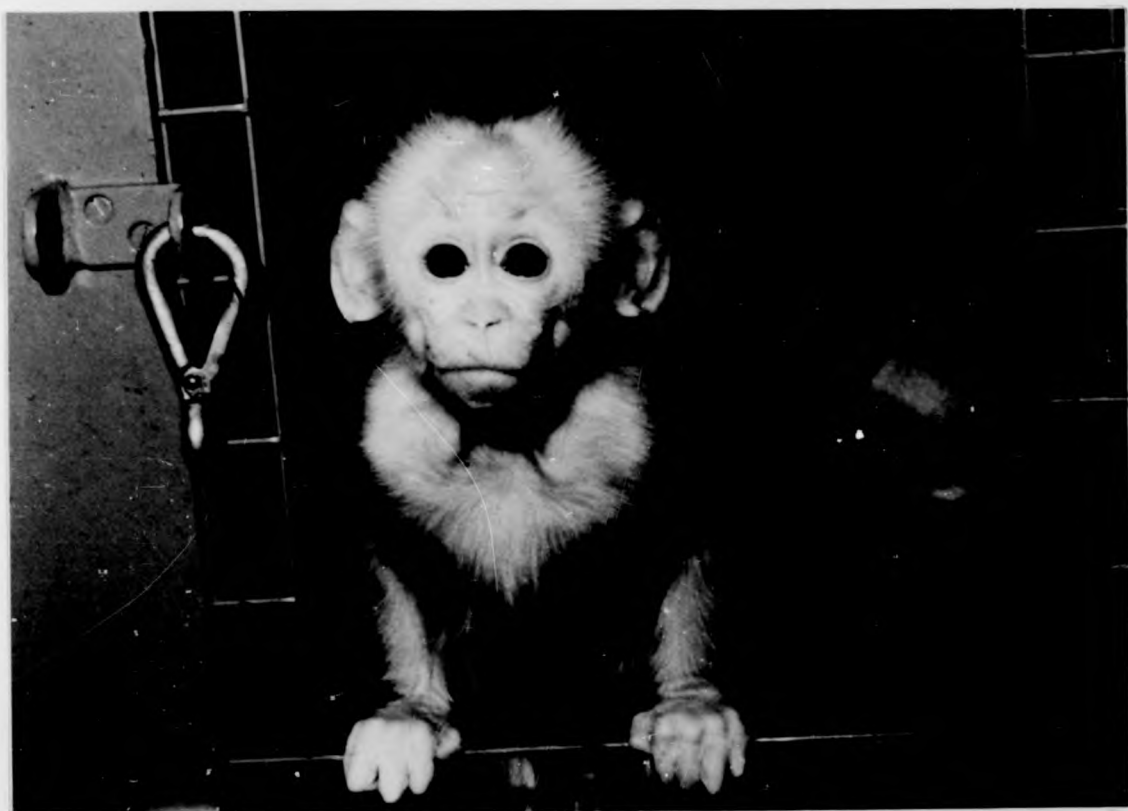
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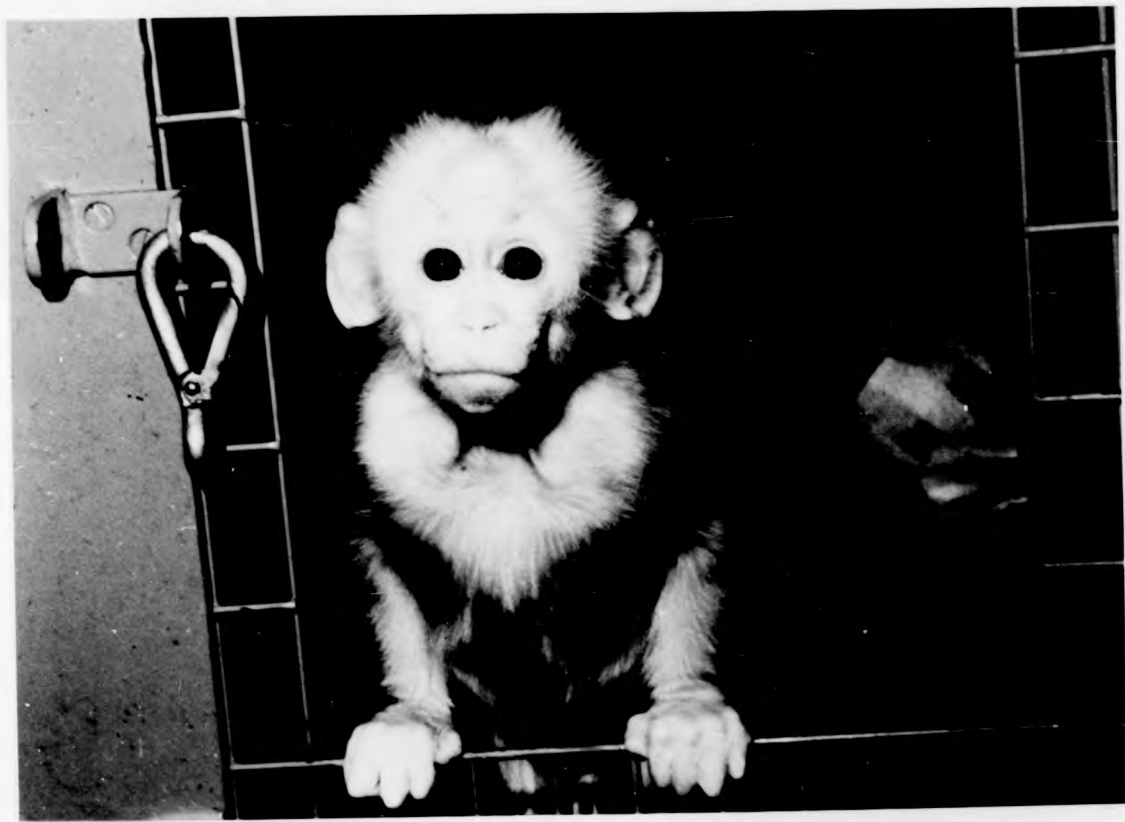
JUNE WALKER LEONARD

PERSONALITY, DOMINANCE EXPERIENCE, AND THE
DEVELOPMENT OF SOCIAL BEHAVIOUR IN
LABORATORY STUMPTAIL MACAQUES
(*MACACA ARCTOIDES*)

Submitted for the degree of Ph.D.

May 1980





Frontispiece An infant stumptail macaque
(photo by A.S. Chamove).

ACKNOWLEDGEMENTS

I am grateful to the SRC for financial support of this project, and also to the Psychology Department, University of Stirling, for provision of facilities for research.

I am also very grateful to A.S. Chamove, who supervised my research, and generously provided advice and encouragement at all stages of the project.

I am grateful to the technicians of the Psychology Department for all their excellent technical help; especially help with audio recording, with the DTU, with cage modifications, and also help in socializing infants and in carrying out slides tests.

I would like to acknowledge the help of G. Cameron who provided programmes for the preliminary sorting of paper tape data and for its storage on computer disc. I am grateful also for his provision of photographs.

I am also grateful to T.J. Leonard who provided programmes for measures of central tendency and variability for DTU data, and programmes for various statistical tests of significance. I would also like to acknowledge his help in analyzing data in social test one and stimulus animal tests.

I would like to express my gratitude to Dr C.J. Henty and Dr W.C. McGrew, University of Stirling, and Dr D.A. Goldfoot and Dr G.R. Stephenson, Wisconsin Regional Primate Research Center, for advice and criticism when asked.

I am especially grateful to Dr D.A. Goldfoot for his encouragement in the later stages of the project.

Finally, I would like to acknowledge the library of the Entomology Division, DSIR (NZ), for generous provision of reference material.

Preface

The major aim of this study was to test some aspects of a preliminary theoretical model for the causal explanation of primate social behaviour. At the outset, and throughout the study, the fundamental question asked was "How do individual monkeys come to behave the way they do in their social groups?"

Review of the primate literature had indicated that while there was an abundance of data on various aspects of social behaviour and its development in several primate species, there was a noticeable lack of theory formulation (Hinde 1974; 1976), and little systematic examination of causal mechanisms (Suomi 1976). This study was designed in an attempt to contribute towards the process of filling these gaps.

Preliminary observation (Walker Leonard pers. obs. 1974) of laboratory groups of *Macaca arctoides* had suggested that at least three potentially useful causal factors may be involved in determining the individual's behaviour in social situations. These three factors consisted of the dominance rank, personality characteristics, and genetic sex of the individual.

At the beginning of the study, 1974, there existed a large and growing body of research into the causal mechanisms involved in sexually-differentiated

behaviour (Goy and Goldfoot 1974), however, the explanatory utility of the dominance concept was controversial (Garltan 1968; Rowell 1974), and the utility of the concept of personality was barely contemplated (Chamove 1972). Consequently, the major focus was on the latter two concepts with the sex factor having minor emphasis.

One major objective was to formulate a theoretical model incorporating these proposed causal factors in such a way as to explain variability in the development of primate social behaviour. A second major objective was to enquire whether the concepts *per se* were in fact empirically meaningful. A third major objective was to experimentally investigate some of the causal hypotheses deduced from the theoretical model.

The ordering of the chapters in this thesis reflects this ordering of objectives.

Thus chapter one reviews the recent nonhuman primate literature in order to describe and evaluate current causal models of social behaviour.

Chapter two outlines the transactional model tested in this study. Essentially, this model views the development of social behaviour in the individual as a process involving the constant interplay between

conceptually distinct sources of variability in behaviour. In this study, the factors of interest included the personality dispositions and specific dominance experiences of individual monkeys.

Chapters three and four examine the descriptive and explanatory utility of the dominance concept; chapter five examines the utility of Eysenck's theory of personality for the study of primate social behaviour.

Chapter seven investigates the communicative abilities of socially-deprived stumptail macaques.

Chapter eight examines methods for characterizing personality in infant stumptail macaques and investigates whether personality characteristics assessed at an early age are predictive of personality characteristics at a later age.

Chapter nine looks at the interaction between the personality characteristics of the individual and its specific dominance experiences throughout development.

Finally, chapter ten reviews the main experimental findings in order to evaluate the underlying theoretical model.

ABSTRACT

The utility of the concepts of personality and social dominance for the explanation of the development of social behaviour in laboratory stumptail macaques was examined.

A peer-rearing paradigm was used. Infants were separated from their mothers at eight days of age, reared in social isolation until three months of age, then given experimentally-controlled dominance experience with peers until fifteen months of age.

It was found that socially-isolated infant stumptails were capable of exhibiting all of the communication signals examined in this study; they exhibited them in appropriate affective contexts; and they appeared capable of recognizing specific stumptail communication signals. In addition, they seemed capable of combining the units of communication into meaningful higher-order behaviour patterns, e.g., to enlist help in multi-animal agonistic interactions.

It was found that individual stumptail macaques could be reliably ordered on each of Eysenck's three dimensions of personality, i.e., neuroticism, extraversion, and psychoticism; and that knowledge about these personality characteristics may enable the prediction of certain of the individual's behavioural characteristics.

Furthermore, it was found that the personality characteristics of the individual at four months of age may be useful in predicting its personality characteristics at fifteen months of age, and also its future dominance status.

It was found that if experimentally-manipulated dominance experience thwarted the attainment of this "predicted" dominance status, this led to specific changes in the personality characteristics of the individual in novel situations; if experimentally-manipulated dominance experience supported the attainment of "predicted" status, then the personality characteristics of individuals in novel situations did not change.

Finally, dominance experience was found to affect the frequency with which dominance strategy behaviour was exhibited in newly-formed triads; but it was not found to affect the probability of dominance, submission, play, sex, or affiliation, in novel situations.

It was concluded that the data supported a transactional model of causation.

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CHAPTER ONE

How do individuals come to behave the way they do? A review of research into the ontogenetic determinants of social behaviour in nonhuman primates.

On reviewing the primate literature, one is impressed by the large and constantly growing body of data on social behaviour and its development in the individual (Hinde 1976).

However, one is perhaps equally impressed at the relative lack of formal theory development. As Hinde (1974) points out, at present there does not seem to be a widely accepted theory of the development of social behaviour in primates integrating the empirical data into an ordered scheme. Bower (1979) makes a similar comment with respect to human development.

Yet facts alone do not make a science (Eysenck 1970). A theory is necessary for giving structure to the data, for attempting to explain phenomena, and for generating new and meaningful research questions.

The absence of formalized theory development does not, however, imply the absence of underlying theoretical models: it is unlikely (and probably impossible) that any scientific investigator gathers data without some kind of theory in mind (Gewirtz 1968).

The premises and deductions of this theory, however, may be rather informal, or inarticulated, at the preliminary stages of the investigation.

In this chapter, the primate experimental literature on the CAUSAL determinants of social behaviour is reviewed in order to critically examine some of the informal models that have been used for the explanation of primate social behaviour.

The aim of this review is not to provide an exhaustive critique of the relevant literature, but rather to highlight some of the important theoretical considerations which should be taken into account when formalized theory development takes place.

In this way, it is hoped to provide both a skeleton outline of the empirical and theoretical contexts for the present study, and a preliminary discussion of the particular model examined in this thesis.

MODELS OF CAUSATION

An interest in the causation of the individual's behaviour leads the investigator directly to a consideration of the nature-nurture issue.

As Lerner (1978 p 1) states: "sufficient explanations of behaviour must necessarily include

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MODELS OF CAUSATION

An interest in the causation of the individual's behaviour leads the investigator directly to a consideration of the nature-nurture issue.

As Lerner (1978 p 1) states: "sufficient explanations of behaviour must necessarily include

reference to the confluence of the inner biological/physiological components of an organism, its immediate physical/environmental and social/experiential mileus, and the historical/cultural contexts within which these organismic and experiential processes are embedded."

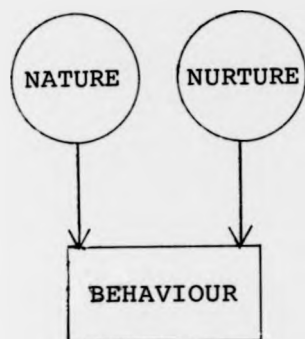
The traditional approaches to the question of causation in behaviour have been recently summarized in the human literature (e.g., Brofenbrenner 1977; Kuhn 1978; Lerner 1978; Sameroff 1975). They have typically involved either a "main effects" model (nature vs. nurture) or an "interactionist" model (nature x nurture).

Recently, however, a third model has begun to be formulated. Sameroff (1975) has called it a "transactional" model; Lerner (1978) refers to it as a "dynamic interactionism" model; and Riegel (1975) has called it a "dialectical" model. Despite these different labels, the authors have described a model that is essentially similar in its basic aspects.

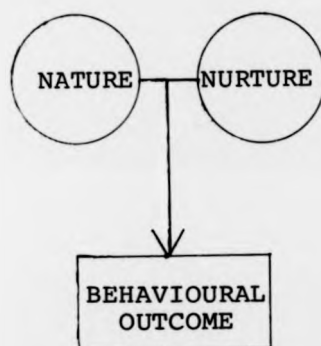
1. The main effects model

In the main effects model, figure 1a, either nature or nurture is considered to be the main contributor to the development of a particular behaviour.

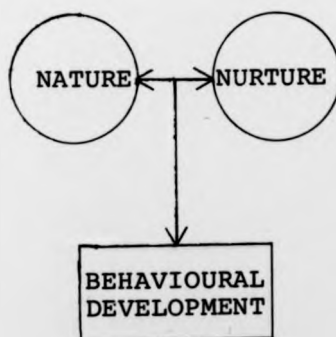
The work of Lorenz (1965) is representative



a) the main effects model



b) the interactionist model



c) the transactional model

Figure 1. Causal models in the explanation of behavioural development.

of the main effects nature perspective; the work of Skinner (1974) representative of the nurture perspective.

2. The interactionist model.

The interactionist model, on the other hand, figure 1b, stresses the importance of the interaction between nature and nurture variables in the determination of behaviour.

Adoption of this model may lead the investigator to set up tables in which each combination of nature is assigned a development consequence. For example, a table might be set up which states that "Children with good constitutions raised in good environments will have the best outcomes. Children with poor constitutions raised in inadequate environments will have the worst outcomes. Children with good constitutions raised in poor environments, will have intermediate outcomes" (Sameroff 1975 p 66).

The interactionist model certainly appears to have more predictive efficiency than the main effects model. But it still leaves much unexplained variance at both the theoretical and practical levels (Sameroff 1975): it is concerned only with the outcomes of development; it views each variable as a static determinant of behaviour (i.e., neither source of variability is held

to be capable of affecting the other); and it makes no attempt to encompass the process aspects of development.

3. The transactional model.

The transactional model, however, attempts to encompass what both the main effects and interactionist models leave out. And in a sense, it may be thought of as a superordinate model.

It asserts that although nature and nurture are conceptually different, they are totally interdependent; their relationship being one of dynamic as opposed to static interactionism.

Thus the variables and processes of each source of variability, while being qualitatively disparate, are dependent on the variables and processes of the alternative source as contributors to its own constitution. Contact between the organism and the environment is thus seen as a transaction in which each is capable of being altered by the other throughout the development.

For example, an extremely sensitive infant may tend to detect minute changes in environmental stimulation and may react adversely to vigorous stimulation compared to a fairly insensitive infant. Such differences are

likely to evoke differences in the quality and/or quantity of a given partner's behaviour toward the different individuals. Thus the mother of a sensitive infant may tend to provide this infant with less vigorous stimulation than she would provide for a less sensitive infant.

In effect, the individual's reaction tendencies may be instrumental in shaping his/her environment. Such reaction tendencies, or predispositions, may, however, in turn be affected by the environment in which the infant finds itself.

Thus a primarily friendly, contact-comfort oriented infant may tend to be contact oriented in later life only if the early environment supports this tendency.

The transactional model tends to focus attention on the details of the process of behavioural development in the individual. And, as a result, investigators adopting this model are better placed to investigate the mechanisms involved in the development of behaviour than those adopting the static interactionist model.

In the primate experimental literature, examples of all three models can be found.

THE MAIN EFFECTS MODEL IN THE PRIMATE LITERATURE

The first major series of experiments on primate social behaviour were carried out at the Wisconsin primate laboratories.

The early research at Wisconsin tended to operate within the so-called "deprivation paradigm"; focusing on the role of various environmental variables in the development of social behaviour in the rhesus monkey, *Macaca mulatta*.

In these studies, a major objective was to describe differences in social behaviour that might be attributable to variations in factors like mothering, interaction with agemates, inanimate object stimulation, and so on. Extensive reviews of this literature may be found in Harlow and Harlow (1965), Hinde (1971), Jensen and Bobbitt (1968), and Sackett and Rupenthal (1973).

The classic experimental rearing conditions consisted of the following: (a) total isolation; (b) surrogate mothering; (c) partial isolation, or wire-cage rearing; (d) peer rearing; (e) mother-peer; (f) semi-natural conditions. Several other variations have also been examined.

In conditions (a) to (d), infants are separated from their mothers at birth or shortly after. Early total isolates are put in enclosed cages, permitting no visual, auditory or tactual contact with other living beings, except for early minimal contact with a technician in order to teach the infant to self-feed.

Late total isolates, partial isolates, and peer-reared infants all spend the first few weeks of life in a nursery until they can self-feed. They are exposed to their rearing condition at various experimentally-determined ages.

In the mother-peer condition, mothers and their infants may be housed in either a gang cage situation, which permits physical interaction between all members of the social group, or a playpen situation, where mother-infant dyads live in wire cages and only the infants have access to a communal play area.

Comparison of the behaviour of these differentially reared groups in a variety of test situations has pointed to both unlearned and experiential factors that should be taken into account in any theory of primate social behaviour. And, as will be shown in the following discussion, it has also enabled the identification of processes and mechanisms likely to be involved in the development of primate social behaviour, although most of these have not yet been studied

empirically.

1. Unlearned factors.

Examination of the behaviour of socially isolated neonates has shown that infant rhesus monkeys have various reflex responses in their behavioural repertoire at birth. These include rooting, orienting, startle response and grasping. Most of these function in the natural environment to ensure and maintain close contact of the infant with its mother, i.e., they mediate interaction with the social environment.

In addition to these unlearned reflex responses, it appears that more complex aspects of behaviour may also rest on innate mechanisms, rather than on acquisition through social learning.

Sackett (1966) examined the behavioural responses of total isolates, during their first 4 months of life, to slides and motion pictures of monkeys, humans and inanimate objects. He found that, after the infants had reached 1 month of age, pictures of monkeys elicited more exploration and play responses than did pictures of other objects. Furthermore, pictures of infant and threatening monkeys produced the highest frequency of all recorded responses. (Responses recorded at this age included vocalization, disturbance, play, explore and activity).

No fear responses were recorded in response to any of the stimuli until the infants had reached a mean of 80 days. From 80 to 120 days, fear, withdrawal, and disturbance were displayed frequently whenever a picture of a threatening monkey was shown, even although these pictures had not previously elicited these responses.

It was concluded that at least two kinds of socially meaningful visual stimuli, i.e., pictures of monkeys threatening and pictures of infants, appear to have unlearned, prepotent activating properties for socially naive monkeys. The visual stimuli involved in monkey threat behaviour appear to function as an *innate releasing mechanism* (IRM) for fearful behaviour and this IRM appears to be maturational in nature.

Unfortunately, this study has several drawbacks: some of them associated with the general deprivation technique; some unique to this particular study.

The general drawbacks of the deprivation technique have been well documented in the literature, e.g., Mason, Davenport and Menzel (1968); the particular drawbacks of this study include:

a) the technique of repeated presentation of the same visual stimuli throughout the 4 month test period. This

may have resulted in habituation to some of the test stimuli before the development of an appropriate discriminatory response.

b) lack of detailed description of the communicative responses of the infants.

c) no systematic examination of the response of the infants to different rhesus communicative expressions (visual and vocal).

Despite these drawbacks, it is possible to make the general statement that at least certain aspects of social communication in monkeys may lie in IRM's rather than in acquisition through social learning mechanisms (Sackett 1966).

Social preference studies by Sackett, Suomi and Grady (1970) and Suomi, Sackett and Harlow (1970) point to further IRM's which may operate in monkey social behaviour.

Sackett *et al* (1970), for example, examined the preferences of partial isolates and adult feral monkeys for 3 different stimulus animals: a rhesus, pigtail and stump-tail adult female. They found that both the feral monkeys and the partial isolates of under ten months preferred the rhesus stimulus animal.

They concluded that the appearance, vocalization, or some other response of the adult rhesus, must elicit approach in the absence of any specific previous learning.

However, partial isolates are reared in conditions where they can see and hear other infant rhesus monkeys. Thus it is not possible to reject the hypothesis that preferences for adults of the same species may be conditioned by early exposure to infants of the species.

Suomi *et al* (1970) tested preferences of partial isolates for a male versus a female adult rhesus monkey. They found that partial isolates under 10 months preferred the female; while those over 10 months preferred the stimulus of their own sex.

Such findings *suggest* the existence of unlearned response biases in young rhesus monkeys.

Unlearned factors are also suggested by the finding of sex differences in the levels at which certain behaviours are exhibited: male monkeys, for example, tend to exhibit more rough and tumble play than female monkeys (Harlow and Lauerdsdorf 1974). And many of the sexually dimorphic behaviours studied in the laboratory have been related to prenatal hormonal conditions (Goy and Phoenix 1971). However, as

Goldfoot (1976, pers. comm.) points out, subsequent social conditions may be sufficient to alter the degree and even the direction of the sexual dimorphism in any particular behaviour. Thus the finding of a sex difference itself is not sufficient to attribute it to biological factors. It must be replicable under a variety of conditions.

If it is indeed found that IRM's appear to be implicated in the development of a particular aspect of primate social behaviour, detailed investigation of the processes involved and the cues used must then be made.

2. Environmental factors.

The mere existence of unlearned responses does not ensure adequate development, however. Total social isolation from soon after birth to around 1 year of age produces individuals with both abnormal behaviours (the 'deprivation syndrome') and abnormal responses in social situations (Harlow and Harlow 1962). The severity of these effects depends on both the duration of the isolation and the age at which it begins (Sackett and Rupenthal 1973).

In order to produce behaviourally adaptable monkeys, physical interactions with either the mother or agemates are necessary (Jensen and Bobbit 1968). Perhaps not unexpectedly, interactions with both the mother and peers

turns out to be the best condition for the development of adaptable social behaviour in monkeys.

Until recently, it was thought that the effects of total social isolation were fixed (Harlow and Suomi 1971; Sackett and Tripp 1968). Now, however, it would appear that these abnormalities can be remedied by specific therapeutic procedures (Novak 1979).

The effects of a number of other environmental variables have also been investigated, including: the quality of the nonsocial environment (Jensen and Bobbitt 1968; Singh 1969); parity of the mother (Seay 1966); the species of monkey tested (Rosenblum 1972; Sackett *et al* 1976); and most have been found to result in differences in individual social behaviour in a variety of test situations. Environmental factors, then, appear to play a significant role in the development of social behaviour in primates.

In discussing the role of environmental influences on social behaviour, various learning mechanisms are usually invoked to account for the development of social responses. Hinde and Stevenson-Hinde (1976) examine the possible roles of exposure learning, classical conditioning and operant conditioning in the development of social behaviour.

To date, however, there have been no studies which specifically examine the sequential and temporal details of inter-individual interaction chains in order to discover which learning mechanisms are involved, at which points in development.

In addition to the involvement of various learning mechanisms, and associated information processing mechanisms, *emotionality* has been implicated as a mediating variable in the development of social behaviour. For example, Harlow and Harlow (1965) postulate that several of the effects of social deprivation may be due to interference with the development of the emotional systems. Goy, Wallen and Goldfoot (1974), in discussing the sexual behaviour of peer vs. mother-infant reared male rhesus monkeys, suggest that the absence of a positive emotional atmosphere may be causally related to the observed deficiencies in the sexual behaviour of peer-reared males.

Again, there has been no direct investigation of these proposed roles of emotionality in the development of the individual primate's social behaviour.

As Jensen and Bobbitt (1968) conclude, the deprivation paradigm has generated much fruitful research, pointing to both hereditary and experiential factors which should be taken into account in any theory of the

development of primate social behaviour, and pointing to mechanisms which may be involved in this development. However, it has not yet given us any details of the processes involved in development, or any detailed examination of how the likely mechanisms might have their effects.

Suomi (1976) argues that the 'observational' nature of much of the primate 'experimental' studies is responsible for this situation. Thus he argues (Suomi 1976 p 226) that "at best, environmental manipulations have been indirect in these studies; there have been no direct attempts to control the specific behaviours of one or the other dyad member, no attempts to control the nature of social stimulation from other individuals in the environment, and no attempts to influence internal variables of either dyad member, such as manipulating hormone levels artificially in the mother or manipulating the infant's overall levels of activity with procedures such as chronic administration of amphetamine or chlorpromazine."

As Chamove (1979, pers. comm.) points out, there have actually been some attempts to control the nature of the social stimuli presented to infants. Thus he cites the motherless-mother experiments (Arling and Harlow 1967) as a case in point.

In these experiments the nature of the stimuli coming from motherless-mothers is measurably different from that coming from feral mothers, i.e., motherless-mothers abuse their infants more. It would appear that the infants of such mothers show no defects in their later social behaviour compared to controls (Sackett and Rupenthal 1973).

To return to Suomi's (1976) argument, however, it can be seen that, basically, he is saying 2 things. Firstly, he states explicitly that no progress will be made in studying the mechanisms underlying social development until a 'truly experimental' approach is taken. Secondly, he is implicitly advocating a shift from studying rather gross summary variables (Gewirtz 1968), like category of companion, to looking at variables on a different level of analysis.

Such a shift indicates that a change is taking place in his underlying conceptions of the phenomena involved in the development of primate social behaviour. Presumably this change is taking place because of limitations in the heuristic utility of former models.

It could be argued, therefore, that rather than attributing the present lack of information on mechanisms in development to the lack of 'truly experimental' studies, it should instead be attributed to limitations in the underlying theoretical conceptions of

the classic primate deprivation studies.

In the following section, the underlying theoretical conceptions of the deprivation studies will be examined in an attempt to determine the heuristic utility of their approach and to show why the advocated shift is necessary.

Underlying theoretical conceptions of the deprivation studies

In examining the theoretical framework of any approach, Gewirtz (1968) has pointed out that it is important to ask the following interrelated questions:

1. Is the theory internally consistent?
i.e., a) are the variables at the same level of analysis?

b) are the empirical constructs related to the theoretical constructs?

c) do they measure what they purport to measure?
2. Is the theory consistent with and efficient for the researchers purpose?
i.e., are the levels of analysis appropriate for the purpose?
3. Is the theory compatible with accruing empirical data?

Perhaps the most fundamental question is "are we measuring what we purport to measure?". In the history of psychology, there has been a tendency for empirical constructs to bear little resemblance to theoretical constructs. For example, in discussing personality research, Block (1977 p 40) states "Psychologists have been extraordinarily casual and even irresponsible in developing measures to represent concepts".

In the primate social deprivation literature, it is assumed that studies working within this paradigm are addressing the problem of the development of social behaviour. One of the most fundamental aspects of social behaviour is that it involves a behavioural interaction between at least 2 different individuals. Yet none of the early deprivation studies measure the interactional aspect of social behaviour directly. Rather, the behaviour of the individual is studied unilaterally.

Whether social interactions can be understood by studying the elements in isolation, or whether the interaction process should be measured directly, is a debatable issue. It could be argued, as Lewis and Rosenblum (1974 p XIX) point out, that "this strategy of looking at elements unilaterally may be useful if we are able ultimately to incorporate these characteristics within an interactional framework".

In the primate deprivation literature, this integrating step does not appear to have been taken. Thus while the deprivation studies appear to be concerned with inter-individual phenomena, i.e., social behaviour, they actually measure intra-individual phenomena, i.e., the individual's repertoire of social responses.

As yet, no attempt has been made by investigators working within this paradigm, to resynthesize the behaviour of individuals in an interactive process. In any case, this resynthesis step is impossible for most of the deprivation studies, for they tend to measure the mean frequency or duration of a particular behaviour shown by an individual in a particular test, and tend to ignore the sequential and interactive patterning of the individual(s) behaviour.

However, as long as it is made explicit that the deprivation literature is concerned with intra-individual phenomena and not inter-individual interactions, then this may not be a problem. Of course, it does have serious implications for what we might have thought was the state of our knowledge about causal factors in the development of social interaction phenomena.

A second question which must be asked is whether the

variables examined by the deprivation approach have been conceptualized at the same level of analysis. In order to answer this question, we must have an idea of possible explanatory levels in the study of primate social behaviour.

Hinde and Hinde (1976) recently proposed that social behaviour may be profitably examined on three different conceptual levels - interactions, relationships and social structure. In their scheme, those levels are contained each within the next, in a nested arrangement of structures.

A social interaction may be said to occur whenever 2 or more individuals engage in an interpersonal communicative sequence of behaviour. Social relationships, on the other hand, possess qualities emergent from the patterning of the constituent interactions and refer to the course of interactions between particular individuals. Social structure emerges out of the content, quality and patterning of constituent relationships.

If we examine the deprivation literature with this hierarchic conception of levels in mind, it can be seen that dependent variables have tended to be operationalized at the level of individual interactions (while ignoring the interactional dimension). Thus the most common measures consist of scoring the frequency

and/or duration of play, aggression, fear etc., in response to either social or nonsocial stimuli.

None of the independent variables reported in this literature, however, have been operationalized at this level. Some have been operationalized above this level, e.g., species differences, category of companion. Others have not been social variables at all, e.g., environmental richness vs. privation.

As Gewirtz (1968) argues, examining relationships between variables at the same level of analysis is likely to account most efficiently for the variance in the data. By contrast, when variables are selected at different levels of analysis, an increase in residual unexplained variance is often found: mainly because a variable at one level may have more than one correlate at other levels.

For example, although mothers and peers separately, may both be effective in producing normal social development in the infant (Jensen and Bobbitt 1968), this may be due to:

- a) mothers increasing their play with infants, when peers and other adults are absent,

or

b) peers increasing their affiliative responses to
agemates, when mothers are not available,

and so on (Hinde 1972).

In other words, the social development of the
infant (dependent variable) may have more than one
correlate at the level of class of companion
(independent variable). A more efficient explanation
of this particular data may therefore be achieved by
looking at the relationship between variables which are
both selected at the behavioural level of analysis.

The finding of disparity in the levels of analysis
among variables investigated in the deprivation
literature emphasizes the need for careful
consideration of the choice of both independent and
dependent variables in the search for efficient
explanations of the data. The appropriateness of a
given level should, of course, be determined by the
purposes of the researcher, and probably no one level of
abstraction should be conceived as more fundamental or
adequate than another.

Suomi's advocated shift to looking at independent
variables on the interactional level of analysis,
indicates that variables at previously chosen levels
have accounted rather poorly for observed variance in the

data. There now appears to be a movement towards examining variables on similar level of analysis.

A third question which must be asked concerns the compatibility of the underlying model with the accruing empirical findings.

Examination of the deprivation literature indicates that the early studies tended to operate on the basis of the main effects model. Thus nature and nurture were conceptualized as contributing to behavioural variability in a mechanistic fashion (Sameroff 1975).

Later research has, however, shown that the main effects model should be discarded in favour of some kind of interactional model. Sackett (1974), for example, has shown that the effects of social deprivation vary with the genetic sex of the deprived animal. Thus, although female total isolates were markedly affected by their rearing experience, they were less affected than their male counterparts.

Whether or not the main effects model should best be replaced by a static interactional or a transactional model will be discussed later in this chapter.

From this brief discussion, it can be seen that the underlying theory of the early deprivation studies may

be criticized on several grounds. Thus, while the deprivation literature talks about the development of social behaviour, it tends to measure the individual's repertoire of social responses and neglects the interactional dimension of the individual's social behaviour. Furthermore, in the early literature, independent and dependent variables tended to be selected at different levels of analysis, with independent variables tending to be chosen at gross levels. Finally, it would appear that the theoretical model of causation assumed in these early studies is too simplistic to account for the actual processes involved in behavioural development.

Given these drawbacks, it was inevitable that a shift in theoretical emphasis, such as that advocated by Suomi (1976), would take place. This shift has been advocated by other workers in the field of primate social development, e.g., Hinde and his co-workers at Cambridge, Jensen, Bobbitt and co-workers at Washington. See, for example, Hinde (1969) and Bobbitt, Gourevitch, Miller and Jensen (1969).

THE TRANSACTIONAL MODEL IN THE PRIMATE LITERATURE

Both of these groups have, from the outset, been interested in the developmental details of the interaction process. Thus they have attempted to

measure the interaction process directly: Hinde *et al* by examining the roles of partners in the observed changes over time in the nature of a given social relationship; Jensen, Bobbitt, *et al* by examining the patterns and sequences of behaviour which seem to characterize an interaction.

The way in which these two groups measure the interaction process is, however, considerably different. Jensen's group, for example, collects detailed descriptive data on the behaviours of individuals involved in a particular interaction. The sequential patterning of these behaviours within a given interactive bout, and the sequential patterning of the bouts themselves, are preserved for analysis.

In event, this method provides a running commentary on the behaviour of individuals in an interaction. From this raw data, several kinds of higher-order measures can be abstracted, e.g., relative frequencies, patterns of simultaneously occurring behaviours, etc.

This method, as Bobbitt *et al* (1969) point out, is most useful for generating hypotheses about social interactions. These may then be subsequently tested in experimental conditions.

Hinde's group tends to ignore the specific details of the sequential patterning of behaviour. Their measures consist of calculations of the relative proportion of time spent on/off the mother; accepted/rejected by the mother; approaching/leaving the mother etc. (Hinde 1969).

Their studies to date have looked at various questions, including: the nature of age changes in the behavioural measures; whether the changes are due to changes in the mother or the infant; individual differences in the mother-infant relationship; the effect of a period of maternal deprivation on the measures, and so on.

Their general method involves postulating a small number of basic changes in one or other individual and predicting the effect of these hypothetical changes on the behavioural measures. If one or more of these basic changes are adequate to account for actual observed changes in the measures, certain pairs of measures should be highly correlated with each other (Hinde and White 1974). In this way, it is possible to identify who plays which part in the observed changes in behavioural measures over time.

From inspection of the nature of the hypotheses examined, and the methods used, it can be seen that both

of these groups have tended to operate from an underlying transactional, or dynamic interactional, model of causation. Thus the behaviour of both partners in a dyadic interaction is assessed for its possible contribution to the relationship between the two.

In comparison with the Wisconsin studies, the underlying theoretical conceptions of these studies have tended to be internally consistent. Thus they have tended to measure variables on the same level of analysis, i.e., the interactional level. Furthermore, in theory, these studies are better placed to investigate the mechanisms involved in the development of social behaviour since they look at the actual details of the development process.

However, as Suomi (1976) points out, even this approach has not yet provided details of the mechanisms or principles involved in the determination of the individual's social behaviour.

THE INTERACTIONIST MODEL IN THE PRIMATE LITERATURE

The interactionist model is primarily represented by sex differences studies in the primate literature. Thus investigators interested in sex differences in behaviour, and operating within an interactionist framework, tend to look at the contribution of specific

environmental variables as well as the contribution of genetic sex to the development of particular social behaviours.

Goldfoot and Wallen (1978), for example, examined the effects of both the dominance rank and genetic sex of the individual on the demonstration of particular behaviours in infant rhesus monkeys.

Previous research had shown that

- a) the higher positions in the dominance hierarchy are occupied primarily by males; the lower by females,
- b) high ranking animals display mounting behaviour more frequently than low ranking animals; low ranking animals tend to show presenting behaviour most frequently.

From such findings, it was impossible to label either behaviour as sexually dimorphic until the effects of dominance rank and genetic sex had been experimentally separated.

Goldfoot and Wallen's (1978) technique involved looking at the behaviour of males and females reared in same-sex groups, i.e., all female or all male groups. This ensured the production of some low ranking males and some high ranking females.

They found that in female isosexual groups, high ranking individuals showed more mounting than low ranking individuals; and in male isosexual groups, low ranking individuals showed more presenting behaviour than high ranking individuals.

As Goldfoot (1977 pers. comm.) points out, however, there is a disturbing circularity inherent in the findings. Thus it is not known whether high dominance rank leads to mounting, or whether mounting somehow leads to the establishment or maintenance of being dominant.

Thus while studies such as Goldfoot and Wallen's (1978) are in advance over studies which examine the effects of only 1 variable at a time (main effects model), they have certain drawbacks compared with the transactional approach: they do not encompass the process aspects of development, nor do they admit the possibility that nature and nurture variables might continuously interact and be capable of altering each other throughout development.

For instance, in Goldfoot and Wallen's study, their findings could suggest that mounting and presenting behaviours are in fact an expression of some other aspect of individuality which may at the outset be highly correlated with genetic sex, but which is capable of

being altered through interaction with environmental (i.e. dominance) experience, such that the original correlation with genetic sex may be obscured.

CONCLUSION

As can be seen from the previous discussion, all 3 causal models, as presently used in the primate literature, have certain advantages and drawbacks. And none of them, so far, has been successful in providing details of the causal mechanisms involved in the development of the individual's social behaviour.

However, they do suggest guidelines for future study in this field. Thus they lead to the conclusion that

- a) an experimental approach should be taken, with direct control of independent variables
- b) independent variables should be chosen at similar levels of analysis to the dependent variables of interest
- c) both genetic and environmental variables should be represented
- d) the actual details of the developmental process should be examined.

In summary, a transactional model of causation, examined in a rigorously controlled experimental situation, would appear to be indicated by the literature.

Such an approach has also been advocated by Lerner (1978) in his discussion of the causal analysis of human social behaviour. However, it is somewhat more difficult to effect in human research given the many ethical limitations on direct experimentation.

In the nonhuman primates, direct control of variables is more feasible (Suomi 1976). And it is likely, since monkeys and man are probably influenced by similar genetic and experiential variables governing the development of behaviour (Goy and Goldfoot 1973), that studies on monkeys or apes, working within this advocated approach, may contribute substantially to the general study of the development of social behaviour. This contribution is likely to be either methodological or theoretical or both.

In advocating the experimental approach, it must of course be remembered that there are limitations in the extent to which relationships between variables established in a controlled situation can be generalized to the complex naturalistic setting. In environments in which there are many variables in complex interaction,

the significance of any given variable, or limited set of variables, may be radically altered by the larger context.

The recognition of this limitation is a timely reminder that progressive analysis of specific problems should be followed up by a resynthesis process which assesses the relationship between variables and assesses the adequacy of the initial analysis (Hinde 1971). This requires a continual awareness of the multifactorial determination of behavioural development and a knowledge of the normative social milieu of the species.

CHAPTER TWO

A transactional model for explaining the development of social behaviour in primates.

In order to explain the development of social behaviour in the individual, it is not enough to describe what A does to B (and B to A), how they do it, and how these interactions are patterned over time; it is also necessary to seek principles which might account for the development of the individual's specific characteristics of interacting (Hinde 1976).

As discussed in chapter 1, causal principles for the explanation of behaviour may be of two theoretically distinct types: organismic (nature) variables, or environmental (nurture) variables. In a transactional model, both types must be represented for the explanation of any phenomenon.

In this chapter, the potential utility of two possible explanatory principles is examined: the first, the concept of dominance, may be thought of as an environmental variable; the second, the concept of personality, may be thought of as an organismic variable. In addition, a transactional model of causation, incorporating these explanatory principles, is outlined.

DOMINANCE AND PERSONALITY IN THE PRIMATE LITERATURE

The concept of dominance has received a great deal of attention, both theoretical and empirical, in the primate literature.

In the past, it was accorded the status of a basic structuring mechanism in primate social organization (Gouzoules 1975; Rowell 1974). Recently, however, there has been considerable controversy over its potential explanatory utility (see chapter 3).

The concept of personality has been relatively neglected in the study of primate social behaviour. However, it has long been acknowledged as a potentially important principle. For example, Maslow (1940) hypothesized that social behaviour and group organization, in both human and nonhuman primate groups, is based in part on individual personality.

Despite the lipservice paid to the importance of personality in the primate literature (see Van Hoof 1967; Van Lawick-Goodall 1968), there has been little systematic research into characterizing dimensions of personality in monkeys and apes, and virtually no attempt to incorporate personality into an explanatory theory of primate social behaviour.

THE CONCEPT OF SOCIAL DOMINANCE

Dominance refers to a pattern of imbalance, or complementarity, in interactions between individuals (Hinde 1978).

In the primate literature, dominance typically refers to complementarity in agonistic interactions. Thus an animal whose behaviour is not limited by the others is called "dominant", i.e., it can chastise the other with impunity (Hausfater 1975), and it may be able to lay claim to preferred food, resting places, etc. (Bernstein 1976). An animal whose behaviour is limited and who also shows submission is called "subordinate" (Deag 1977).

In established primate social groups, the outcome of aggressive interactions between particular individuals tends to be relatively stable over time and we talk of the individuals as having a particular dominance relationship. Furthermore, the patterning of these dominance relationships within any particular group may conform to a fairly stable structure or dominance hierarchy.

In the primate literature, dominance has tended to be studied at both the relationship and structural levels, although, as Hinde (1978) argues, there has been a

tendency to confuse the relationship and structural definitions of this concept. This may have partly given rise to the current controversy over the utility of the dominance concept, and this issue is examined in detail in chapter 3.

In the present study, the aim was to locate explanatory variables at the interactional level of analysis, thus a third possible use of the dominance concept was introduced, namely, that of dominance experience.

This refers to the individual's experience throughout development as either a "pecker" (sender of dominance behaviour; receiver of submissive behaviour) or one who is "pecked at" (receiver of dominance behaviour; sender of submissive behaviour) in his/her interactions with individuals in the social group.

Several investigators have pointed out that as soon as the infant is capable of moving around independently, then he/she is likely to be involved in dominance interactions, both as a receiver of maternal protection (de Waal 1977) and as a receiver of mild aggression from other members of the group (Gouzoules 1975).

Deag and Crook (1971), for example, point out that in the Barbary macaque (*Macaca sylvanus*), adult males

may involve infants as young as one week old in their dominance interactions. Ransom and Ransom (1971) suggest that the use of infants by adult males in baboon (*Papio anubis*) dominance interactions, may lead to the infant taking the initiative and attempting to elicit help from adult males in future agonistic encounters.

Personal observation (Walker Leonard pers. obs. 1976) of laboratory groups of stumptail macaques (*Macaca arctoides*) indicated that by 2-3 months of age, infants were being used as "agonistic buffers" (Deag and Crook 1971) in subadult male agonistic interactions, and that by 6 months of age, one female infant (Sabrina) was eliciting help, and joining in to help out others, in agonistic interactions involving subadult and adult members of the group.

It would appear, therefore, that in baboon (Ransom and Ransom 1971), macaque (Deag and Crook 1971) and chimpanzee (De Waal 1977) groups, at least, dominance experience is an empirically meaningful environmental influence which may affect the development of the individual's social behaviour.

POSSIBLE EFFECTS OF DOMINANCE EXPERIENCE ON SOCIAL BEHAVIOUR

In theory, dominance experience may affect the development of social behaviour in either a direct or an

indirect manner.

Direct effects would consist of influencing the occurrence, frequency, duration and patterning of particular social behaviours. For example, Chevalier-Skolnikoff (1973) has suggested that the particular threat expression a monkey will make in a particular situation may depend on his/her dominance rank relative to the other individuals in the interaction. Thus, in stumptails, an alpha individual might display an open mouth threat gesture; while in a similar situation, a lower ranking individual will display a scream threat expression.

Indirect effects may occur via the effect of dominance experience on the social confidence or emotionality of the individual. De Vore (1963), for example, has suggested that in baboons, infants of dominant mothers are subject to less insecurity and frustration than infants of subordinate mothers. Thus infants of dominant mothers tend to develop in a social environment conducive to confidence and emotional stability, and they tend to achieve high dominance status. Whether or not dominance makes the individual confident or whether only confident individuals become dominant is, of course, an empirical question.

Conversely, it may be hypothesized that infants of subordinate mothers who repeatedly experience

frustration and failure in agonistic interactions may develop what Seligman (1975) has termed "learned helplessness".

The idea that social experience may have some of its effects on behaviour via emotionality has also been promoted by Goy *et al* (1974) (see chapter 1).

To date, no studies have been reported, which attempt to experimentally examine the effects of specific dominance experiences on the development of the infant primate's social behaviour and/or emotionality characteristics. However, a few studies have been reported which give some support to these hypothesized effects of dominance experience.

1. The hypothesis of direct effects

Chamove and Bowman (1976) and Marsden (1968) examined the effect of manipulating dominance rank on the social behaviour of juvenile and adult rhesus macaques.

In the Marsden (1968) study, an attempt was made to induce changes in the agonistic dominance rank of individuals living in a stable social group by removing and/or adding specific individuals.

In the Chamove and Bowman (1976) study, juvenile rhesus monkeys were grouped together in newly formed tetrads in such a way that each individual could theoretically be observed in each of the four possible dominance positions within the group.

Both studies report that when occupying different dominance positions, individuals show a concomitant change in their behavioural characteristics.

Thus Marsden (1968) states that one could apply the designation "dominance set" when referring to individuals during their periods of alpha status. Similarly, Chamove and Bowman (1976) state that there was a tendency for behaviours that make up the dominant category (i.e., aggression, threat, directed approach and non directed strutting) to be intercorrelated, and that this tendency was greatest for monkeys when occupying the alpha position in their groups, compared with when they were either intermediate or subordinate in rank.

The effects of dominance experience on social behaviour, however, were found to be modified by individual differences in the subjects observed.

Thus both Chamove and Bowman (1976) and Marsden (1968) point out that there was considerable individual variation in, what might loosely be called,

the "style" with which animals interacted when in similar dominance positions.

Chamove and Bowman (1976), for example, contrast individuals who were highly aggressive when occupying the alpha position, with individuals who appeared relaxed and self-confident, and were relatively unaggressive, as alpha animals.

Such individual differences among the animals appeared to be an important determinant of the number of different dominance positions in which an animal was able to be observed in the Chamove and Bowman study. One very striking example is that of the individual S1, who was only ever able to be observed as an alpha animal.

Attempts by Chamove (pers. comm. 1974) to manipulate dominance status in adult feral stump-tail macaques resulted in similar findings. Thus it was found that for some individuals it was impossible to obtain groupings of animals where they would be alpha, and that for others, it was extremely difficult to obtain groupings where they would be anything but alpha.

It may be concluded, therefore, that although a specific change in dominance position may be associated with specific changes in social behaviour, constraints

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It may be concluded, therefore, that although a specific change in dominance position may be associated with specific changes in social behaviour, constraints

appear to operate such that only certain individuals may be found to occupy certain dominance positions.

2. The hypothesis of indirect effects

There have been several studies on the relationship between dominance rank and those physiological measures which might be taken as indicators of emotional reactivity (e.g. heart rate: Candland, Bryan, Nazar, Kopf and Sendor 1970), or indicators of stress (e.g. adrenocortical activity: Chamove and Bowman 1976; 1978).

These studies have tended to support the general hypothesis that the stress response system is overreactive in subordinate compared with dominant monkeys (see Deag 1977; Rowell 1974).

Thus Candland *et al* (1970) reported a J-shaped relationship between heart rate and dominance, with the subordinate animal having the highest rate of responding.

In that study, adult male squirrel monkeys (*Saimiri sciureus*) were paired together, and it was found that when animals changed in dominance, their heart rates changed accordingly. Such findings tend to support the hypothesis that the observed correlation was due to the

effects of dominance on heart rate, rather than due to the effects of some other factor.

However, Candland *et al* (1970) also found that individual differences modified the effects of dominance. Thus they found that one of the animals was consistently dominant in all his pairings, and that two others were consistently subordinate.

In conclusion, although the evidence is suggestive only, it would appear that dominance experience may have at least temporary effects on both social behaviour (Chamove and Bowman 1976; Marsden 1968) and emotionality (Candland *et al* 1970; Chamove and Bowman 1976; 1978).

Furthermore, there appears to be an interaction between dominance experience and some aspect of individual differences in the determination of social behaviour in nonhuman primates.

In the next section, we will examine one potentially useful dimension of individual difference, namely, the concept of personality.

THE CONCEPT OF PERSONALITY

From a theoretical point of view, the concept of personality may be useful in at least two ways.

The first consists of its use as an intervening variable to provide economy in the description of the data. This economy in description may amount to a first stage in explanation (Hinde 1978).

For example, if on examining the personality characteristics of individuals. It is found that there are basically two or three different "types" of alpha animal (e.g., aggressively over-reactive alphas; calm affiliative alphas; unsociable alphas) and that each type acts in consistent and predictable ways, then this would increase our understanding of both personality and dominance.

The second way in which personality might function in a theoretical framework is as a causal determinant of social behaviour.

Thus several authors, including Eysenck (1967) and Thomas, Chess and Birch (1970), have suggested that there is an inherited biological basis to personality which predisposes individuals to react in one way versus another.

It is conceivable, for instance, that only those individuals predisposed to being emotionally unreactive individuals will develop into animals of alpha status; whereas individuals predisposed to being emotionally

reactive will tend to become subordinate animals.
(These hypotheses are phrased simplistically in order to merely illustrate the possibility of causal effects).

In theory, then, the concept of personality may be a potentially important explanatory principle. In order to introduce it specifically into the study of the development of primate social behaviour, however, it is necessary to discover which personality variables are like to be most useful in this case.

Review of the primate literature on personality

One of the first studies explicitly directed towards the characterization of potentially important personality variables in a primate species was reported by Chamove, Eysenck and Harlow (1972).

In that study, the social behaviour of juvenile rhesus monkeys in various laboratory test situations was observed. The resulting data were analyzed by a principle components analysis, rotated to oblique simple structure.

Analysis of the data from tests in which the subjects were observed in their familiar social group situation revealed three clear factors having little intercorrelation. These were labelled fear, play and aggression-hostility.

Analysis of data from test situations in which the subject was introduced either alone, or with a familiar peer, to a strange stimulus monkey did not yield such a clear picture.

In their discussion, Chamove *et al* (1972) tentatively suggest that these three factors, namely fear, play, and aggression-hostility, may be similar to the dimensions of neuroticism, extraversion and psychoticism deduced from factor analytic studies of human data. They go on to say that such dimensions of personality might be expected to be similar in monkeys and man, if we are correct in assuming that the physiological, neurological and anatomical substrata which might be thought to underlie personality, are similar in monkeys and man.

This is an interesting argument, and it would indeed be convenient for the development of a general theory of personality and social behaviour if heuristically useful dimensions of personality were similar in both human and nonhuman primates: a point which will be discussed in later chapters.

A rather different approach to the study of primate personality has been taken by Biurski and his co-workers (Biurski, Kellerman, Plutchik and Weininger 1973; Biurski, Plutchik and Kellerman 1978). In these studies, the behaviour of baboons and chimps in the wild was observed. Observers were asked to rate

individual animals on a forced-choice rating scale, the Emotions Profile Index (EPI).

This scale yields measures on eight emotion dimensions derived from Plutchik's (1962) theory of emotionality-personality for humans. Raters choose one trait from each of 45 pairs according to which appears to be most applicable to the individual they are observing.

The 4 basic scoring categories of the EPI include a) trust vs. distrust, b) timidity vs. aggression, c) gregariousness vs. depression, d) control vs. dyscontrol. Personality profiles can be computed from the individual's scores on each of these emotional categories.

They report that the average personality profiles of humans, chimps and baboons, according to these criteria, are similar and suggest that there may actually be a similar 'normal' personality pattern in all the higher primates.

In addition, they report that for chimps and baboons, the personality profiles, constructed from this method, reflect known sex and status difference in these species.

A third study of primate personality has been reported by Stevenson-Hinde and Zunz (1978). Like Biurski *et al* (1973; 1978). they also use a rating technique to assess individual differences, and like Chamove *et al* (1972), they have looked at the laboratory social behaviour of rhesus monkeys.

In their study, observers were asked to rate individuals using a list of behaviourally defined adjectives, e.g., *sociable*: seeks companionship of others; *insecure*: hesitates to act alone, seeks reassurance from others.

The ratings, made on a 7 point scale, were then structured by means of principle component analysis without rotation. Three principle components emerged.

The first was positively correlated with confident, effective (or dominant), aggressive and strong; and negatively correlated with insecure, subordinate, apprehensive, fearful.

The second had positive loadings for active, excitable, curious and eccentric; and negative loadings for equable (relaxed) and slow.

The third component ranged from sociable to solitary.

This approach also yields a personal profile

for each animal. Thus individuals may be precisely quantified on each component and comparisons of individual profiles can then be made.

From this brief descriptive review, it can be seen that these three studies of primate personality have each reported a different methodology and different empirical constructs. In addition, they each appear to have rather different underlying conceptions about the organization of personality in primates. Contrast, for example, the use of Eysenck's theory vs. Plutchik's theory of personality.

Presumably, any future studies might report yet different methods and constructs. How then, might we evaluate the various theories and decide which is likely to be the most useful?

Higher vs. Lower-order factors

If we look again at the above three studies, it can be seen that Chamove *et al* (1972) and Stevenson-Hinde and Zunz (1978) are interested in empirical factors at a similar level of analysis, i.e., higher-order factors. Biurski *et al* (1973; 1978), on the other hand, are interested in lower level factors.

Such a difference is reminiscent of the trait/type controversy in the human personality literature, with

Cattell (1967) being representative of the trait level of analysis (lower-order factors), and Eysenck (1967) being a major proponent of the type level of analysis (higher-order factors).

Both Cattell and Eysenck are apparently aware of the descriptive value of traits, like sociability, as well as the existence of type factors, like neuroticism (Eysenck and Eysenck 1969). And it has been shown that correlations between Cattell's trait factors produces higher-order constructs equivalent to Eysenck's factors (Eysenck and Eysenck 1969; Royce 1973). What appears to be in dispute in the human literature is the utility of the higher-order type factors versus the lower-order trait factors.

Probably no one level should be thought of as fundamentally more useful than another, however. Instead, the utility of a particular level should be assessed from the investigators purposes and interests. Thus, while the lower order factors (e.g., Cattell's traits; Biurski's emotional categories) may be most useful where the investigator is interested in the descriptive details of emotionality-personality; for other purposes, higher-order factors (e.g., Eysenck's types) may be more useful.

In this study, the higher-order level of analysis was chosen.

At first glance, this level of analysis appeared to be the more promising for the beginning study of primate personality. For instance, it makes good sense, when the area of interest has not yet been mapped out, to progress from the general to the specific level of analysis.

Furthermore, personal observation (Walker Leonard 1974 pers. obs.) of the laboratory behaviour of *Macaca arctoides* had suggested that emotional reactivity was a most pertinent dimension of individual differences among the animals observed. Review of the animal behaviour literature suggested that my conception of this dimension was similar to Eysenck's conception of the dimension of neuroticism (see Savage and Eysenck 1964). Eysenck had in fact cited the animal breeding experiments (e.g., Tyron 1940) as evidence for the biological basis of the dimension of neuroticism.

Having discovered this isomorphism, it was decided to begin with Eysenck's (Eysenck and Eysenck 1969) theory of personality, and adapt it, where necessary, for the specific study of primate personality.

A further reason for selecting Eysenck's theory, as opposed to Cattell's or Plutchik's, for example, was that Eysenck's theory not only describes the structure of personality, it also provides an explanatory account

of the development of personality (see next section). Thus, rather than merely prescribing an inventory of personality, it presents an interpretative theory of personality and social behaviour (Royce 1973).

It was thus potentially both more fertile and more heuristically useful for the explanation of the development of social behaviour in the individual. This, together with the demonstration (Chamove *et al* 1972) that Eysenck's dimensions may be potentially useful for at least one nonhuman primate species, (*M. Mulatta*), led to the selection of Eysenck's theory in preference to others.

Eysenck's theory of personality

The reader is referred to Eysenck (1967) and Eysenck and Eysenck (1969) for a comprehensive exposition of Eysenck's theory of personality: only a general description of the explanatory framework will be outlined here. However, detailed description and discussion of his theory, particularly as it relates to the explanation of primate social behaviour, will be given in chapters 5 and 8.

Eysenck's theory describes 3 potentially useful and more or less independent dimensions of personality, namely, neuroticism, extraversion and psychoticism. Its

basic premise is that it is possible to order individuals from high to low on each personality dimension; a fairly complete description of the individual's personality being given by a combination of his/her scores on all 3 dimensions.

Neuroticism, or emotionality, may be thought of as persistent over reaction to environmental stimulation (Eysenck and Eysenck 1969; Gray 1973; Plutchik 1962). It therefore refers to the overall tenor of a person's emotional reaction, (Royce 1973) rather than distinguishable modes of emotional reaction. The latter level of analysis is exemplified by Plutchik's theory (1962).

Thus, if compared to others, an individual tends to show excessive emotional response in novel situations, then that individual may be rated as relatively neurotic or emotionally reactive.

Extraversion, on the other hand, is reflected in differences in arousal and inhibition (Eysenck 1967). Thus extraverts are characterized by low levels of cortical arousal and strong reactive inhibition; whilst introverts are characterized by high arousal and weak inhibition. As a result, individuals that are relatively extravert tend to seek strong sensory stimuli and are rather changeable in their behaviour compared to relatively introverted individuals.

Psychoticism is the least investigated dimension in this theory. However, it is proposed that psychoticism is reflected in solitary, hostile and inappropriate social behaviour.

In Eysenck's theory, personality differences are explained, in part, by assuming that underlying these dimensions are specific neurological and anatomical substrata, and that inherited differences in these biological bases of personality predispose the individual to react in one way vs. another.

The dimension of neuroticism has been linked to the autonomic system (visceral brain) and the dimension of extraversion to the brain stem arousal system (reticular formation). The biological basis of psychoticism has not been extensively dealt with, but it has been suggested that this dimension may be linked to the neurophysiological systems underlying male sexuality (Chamove *et al* 1972; Gray 1973).

Thus personality itself is not thought of as being inherited, rather it is the biological substratum underlying personality that is inherited. Personality itself is thought of as developing out of the ongoing interaction between biological predispositions and environmental input (Eysenck 1970).

It is therefore conceivable that while an individual may be thought of as predisposed to being emotionally reactive, the environmental input may be such that he/she becomes relatively calm in specific social situations.

Eysenck's theory, then, appears to adopt a transactional model of the causal determination of personality. As such, it is compatible with the theoretical approach taken in this study.

A TRANSACTIONAL MODEL FOR THE EXPLANATION OF THE
DEVELOPMENT OF PRIMATE SOCIAL BEHAVIOUR

Figure 2 summarizes the possible causal relationships among personality, dominance experience, and the development of the individual's social behaviour which have been discussed in this chapter. This diagram also includes the effects of heredity on social behaviour discussed in chapter 1 (unlearned reflexes; IRM's; etc.).

In presenting this model, it is not suggested that the principles of dominance experience or personality are the only possible explanatory principles, or indeed even the most useful principles, in the study of primate social development.

Similarly, it is not suggested that the causal

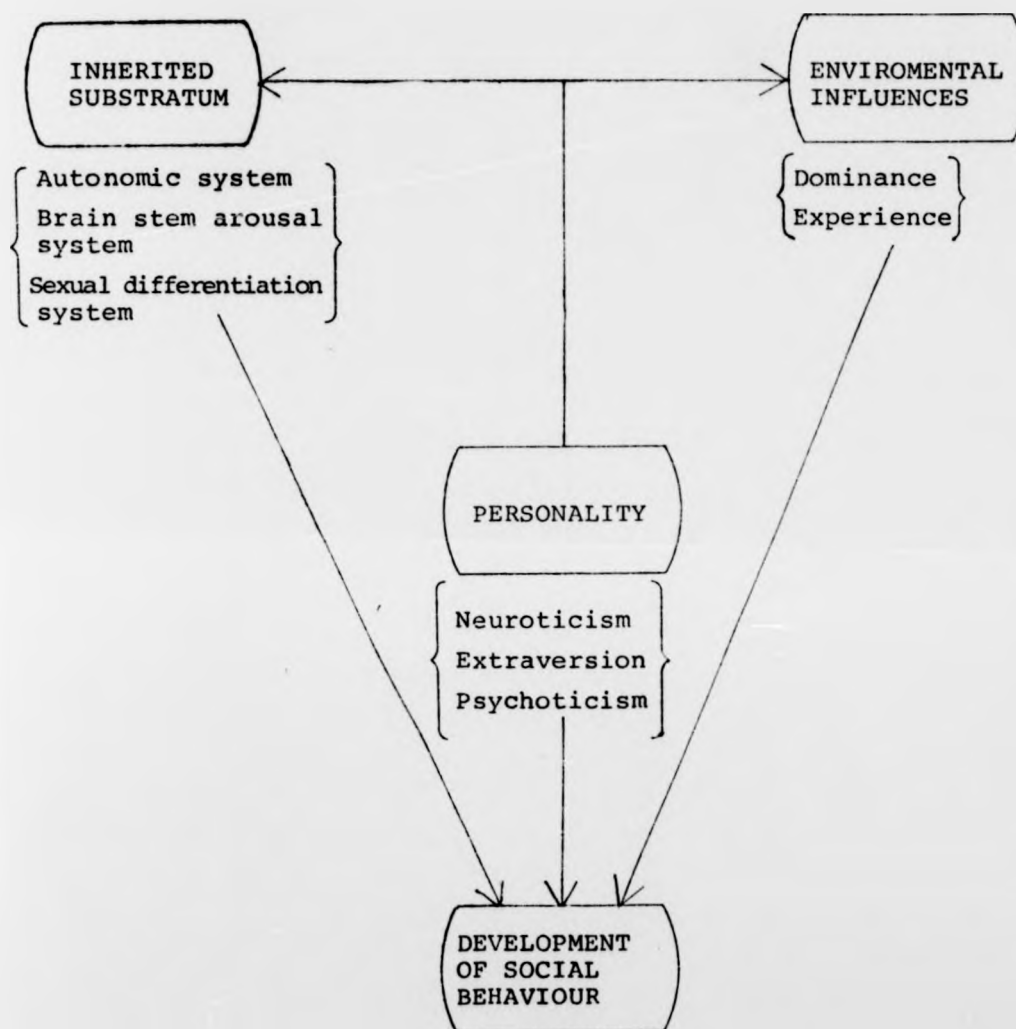


Figure 2. A transactional model for the explanation of some aspects of the development of primate social behaviour.

relations outlined in this model are the only possible relationships among the variables of interest.

One can in fact see various problems with the model as it now stands. For instance, it is conceivable that each of the proposed principles may have its effects at two different levels.

Thus, while dominance experience may interact with inherited predispositions to produce personality differences; dominance experience may also be thought of as interacting with the developing personality to produce specific effects on social behaviour.

Similarly, while personality itself may be seen as developing out of the interaction between inherited predispositions and environmental influences; personality may also be thought of as a contributor to social development.

These points serve to emphasize the arbitrariness of our conceptual distinction between organismic and experiential variables.

The model presented in figure 2, then, should be thought of as the simplest version of the potential causal relations pertaining among these variables. As such, it is only a preliminary theoretical model:

empirical findings will no doubt suggest elaborations and revisions of this basic framework.

This theoretical model was used in the present investigation to guide the experimental analysis of the development of social behaviour in infant stumptail macaques. The experimental aims and design of the main development study, based on this transactional model, are presented in chapter 6.

CHAPTER THREE

The dominance controversy in the primate literature.

In the recent primate literature (e.g., Deag 1977; Gartlan 1968; Hinde 1978; Rowell 1974), there has been a growing debate on the explanatory utility of the concept of social dominance, and several authors have advocated abandoning this concept in favour of the role concept in the study of primate social behaviour.

The argument rests on at least three separate criticisms of the dominance concept.

The first is that the concept is not adequately defined. Thus Rowell (1974) has stated that authors have disagreed, not only on an operational definition, but also on almost every aspect of behaviour which dominance has been said to govern. Gartlan (1964) collected from the primate literature, a list of diametrically opposed pairs of statements about the effect of dominance and the behaviour of dominant animals.

The second critique of the dominance concept states that dominance hierarchies are mainly a phenomenon of captivity. Thus Gartlan (1968) and Rowell (1971) have argued that in truly wild primates, hierarchies are tenuous or absent, compared to their omnipresence in captive primate groups.

The final criticism is that the dominance concept has no predictive or explanatory value. This argument is based on the observation that rank orders based on aggression are not necessarily correlated with rank orders based on other aspects of social behaviour.

Such criticisms have been instrumental in recent attempts (Deag 1977; Hinde 1978; Richards 1974; Walker Leonard 1979) to vindicate the concept of dominance, both as a useful descriptive concept and as a useful explanatory concept in the study of primate social behaviour.

In this chapter, and the next, the main theoretical and empirical definitions of dominance in the primate literature will be discussed: the aim being to examine some of the limits of the usefulness of this concept.

DEFINITIONS OF DOMINANCE

Hinde (1978) has pointed out that in the past the dominance concept has been used in a rather global fashion, covering all aspects of dominance, when in fact one can discern several different meanings, depending on the context in which the concept is used.

This confounding of definitions may have partly contributed to the present controversy. If so,

separating out the different meanings of dominance may help determine if the concept has any explanatory use.

Hinde (1978) suggests at least a two-fold distinction: the use of dominance as a concept at the relationship level; the use of dominance as a concept at the structural level. To this we might add two further distinctions, i.e., the use of dominance as a concept at the interactional level (see previous chapter); and the use of dominance as a concept at the process level of explanation (see next chapter).

In the following discussion, the definition and measurement of dominance at the relationship and structural levels will be examined.

DOMINANCE AT THE RELATIONSHIP LEVEL

Basically, the concept of dominance refers to a pattern of imbalance, or complementarity, in behavioural interactions between individuals. In such complementary relationships, one individual "bosses" the other (Hinde 1978): the term "bosses" being used in a general sense at this stage.

At the relationship level, the interest is predominantly in dominance as a pattern of imbalance between particular individuals. Thus it need not refer

to the structure of the dominance relationships within the social group as a whole.

If we assess any particular dominance relationship in terms of 1 dependent variable only, then dominance is merely an alternative label for that behaviour. In order for the concept to be useful in the explanation, as well as the description, of behaviour, then the following conditions must be met (Hinde 1978 p 28):

- "(1) we are concerned with a number of different dyads (A and B, C and D, etc);
- (2) each dyad has a multiplex relationship involving comparable complementary interactions in which one bosses the other;
- (3) the pattern of imbalance in those interactions is similar in the different dyads."

For example, "suppose that A hits B more than B hits A, and C hits D more than D hits C; that A has feeding precedence over B and C over D; and that B grooms A more than A grooms B, and D grooms C more than C grooms D; and similarly with other dyads. We can simplify our description by using dominance/subordination as an "intervening variable" (MacCorquodale and Meehl 1954) that predicts the direction of hitting, food preference

and grooming : in brief, A is dominant to B, and C to D."

This use of the dominance concept at the relationship level has only recently begun to be discussed (see Hinde 1978), hence its empirical utility has not yet been assessed.

DOMINANCE AT THE STRUCTURAL LEVEL

At the structural level, interest is specifically in the patterning of dominance relationships within the total social group.

Thus, a structural definition of dominance refers to the ranking of individuals within the social group in terms of who "bosses" whom (Hinde 1978). The resulting picture is of a "peck order" (Schjelderup-Ebbe 1922), rank order, or dominance hierarchy.

These orders may be linear, in which case the alpha individual is dominant to all others, beta is dominant to all except alpha, and so on down to omega, the lowest ranking in the group. On the other hand, peck orders may be complicated by triangular relationships, where individual A bosses B, and B bosses C, but C bosses A. Or they may be telescoped, as when one individual bosses all the others, but the subordinates do not boss each other. (Good discussion of the possible types of hierarchy is given in Dawkins 1976) .

Measurement of the dominance hierarchy in primate groups

In the primate literature, the most generally accepted structural definition of dominance is based on the direction and relative frequency of particular social behaviours within the group (Deag 1977; Keverne, Leonard, Scruton and Young 1978).

Studies which report total frequencies of behaviours, and rank animals according to this criterion, would not therefore be considered as giving a correct indication of the dominance hierarchy as defined here (see Rayor and Chiszar 1978 for a comparison of different measures of dominance hierarchies).

Thus the most aggressive animal would not necessarily be the most dominant. The most dominant animal would be the one who attacks all other animals in the group more than they attack him/her, and this could be one of the least aggressive individuals in the social group, according to total frequency of attacks.

In addition to attack behaviour, various other behaviours have been measured in studies of primate social hierarchies, e.g., mounting, threat, attack, submission, grooming, priority of access etc. As Deag (1977) points out, all of these behaviours, in one study or another, have been *uncritically* associated with dominance, and this situation has partly contributed to

the recently voiced dissatisfaction with the dominance concept (Gartlan 1968; Rowell 1974).

In order to introduce some conceptual clarity into the area, Deag (1977) has argued that the actual label for the hierarchy being discussed should reflect the particular behaviour being measured.

For example, if the emphasis is on submissive behaviour, we should talk about "subordinacy hierarchies"; if the emphasis is on threat and avoidance, we should talk about "agonistic hierarchies"; and only if the emphasis is actually on aggression, should we talk about dominance hierarchies.

Deag's (1977) argument represents a return to the original conception of peck order, based on the distribution of agonistic behaviour, but it incorporates Rowell's (1974) recent argument for the separation of subordinance hierarchies from dominance hierarchies.

Since it is debatable whether hierarchies based on different social behaviours are correlated (Hinde 1978), and unknown whether dominance and subordinance hierarchies are based on similar mechanisms, or operate according to similar principles, then Deag's (1977) argument to "split" rather than "lump" conceptual categories appears to make good sense at this stage.

Thus dominance hierarchies should be restricted in the first place to rank orderings based on the relative frequency and direction of aggressive behaviours among members of a social group. Empirical studies of a particular group or species should then determine whether it will be possible to include other behaviours.

In the literature, some studies have reported dominance hierarchies calculated from pairing individuals who were otherwise separately housed (Clark and Dillon 1973). This is often a useful procedure for examining particular questions, but as Deag (1977) points out, the "hierarchies" obtained from this technique should not be confused with the hierarchies observed in socially living groups of primates.

Indeed, the hierarchies deduced from pairings often bear no resemblance to the hierarchy that evolves when the same individuals are placed together in a group (Hinde 1978). This discrepancy between the different "hierarchies" probably reflects the discrepancy between *basic rank*, based on individual attributes, and *dependent rank*, based on alliances between animals (see Kawai 1958).

In the past, behaviour used to assess dominance hierarchies has tended to be measured at the dyadic level, i.e., interactions between pairwise combinations of animals, at the expense of higher-order multi-animal

interactions (Walker Leonard 1979), i.e., coalitions, alliances. Deag (1977 p 466), for example, states that "to avoid the confounding effects of coalitions, dyadic interactions are preferred."

This neglect of alliance behaviour has probably contributed directly to the present lack of knowledge about the processes by which individuals attain and maintain their position in a particular dominance hierarchy: a point which will be discussed in chapter 4.

linear dominance hierarchies

The structural definition of dominance starts to take on special significance if, in any particular social group, it is found that the pattern of dominance relationships conforms to a linear dominance hierarchy.

In a linear hierarchy, individuals can be thought of as occupying specific positions in the peck order, i.e., alpha (A), beta (B), and so on; and dominance rank becomes "a useful unifying concept against which to assess the pattern of direction of agonistic interactions in a group." (Hinde 1978 p 30).

The linear hierarchy should not, however, be thought of as a static concept. Thus while at any given point in time, the dominance hierarchy of a particular group may always conform to a linear pattern, it may be

found that the specific positions individuals occupy in this hierarchy may change over time (Boelkins 1967; Koyama 1970), or indeed that a change may be induced (Marsden 1968). Investigators now appear to be turning their attention towards this mobility within the hierarchy (Stephenson, 1977, pers. comm.).

In addition to changes in positions, the hierarchy itself may change its form. Thus at certain points in time it may comprise triangular relationships of the form B bosses C, C bosses D, but D bosses B.

It is likely that such triangular relationships signify a change is taking place in the specific positions individuals hold within the hierarchy. In the theoretical example above, it might be hypothesized that D's relationships signify a process of upward mobility, and B's, downward mobility.

In the primate literature, linear hierarchies have been reported for many species, despite the fact that such straight line hierarchies are improbable in terms of the initial properties of individuals (Chase 1974; Hinde 1978). And contrary to Rowell (1974) and Gartlan's (1968) criticism, those hierarchies have been found not only in laboratory groups (Keverne *et al* 1978; Rayor and Chiszar 1978; Richards 1974), but also in wild primate groups (Deag 1977; Hausfater 1975; Struhsaker 1967).

All of these recent studies have based their assessment of the dominance hierarchy on the relative frequency and direction of behaviour. It would appear, therefore, that this particular conception of dominance is likely to be of use in the study of primate social behaviour.

However, in order to discover whether the concept of dominance hierarchy will be useful in an explanatory or predictive way, then further conditions must be met.

The explanatory utility of dominance hierarchy

Hinde (1978) has pointed out that if it can be demonstrated that several different measures of aggressive dominance are intercorrelated, then the concept of dominance rank begins to take on a preliminary explanatory role by serving as an intervening variable linking together several dependent variables.

Furthermore, if it is found that the aggressive rank order is correlated with other types of rank order (e.g., grooming rank order), then the dominance concept will begin to take on an even greater explanatory role. In this case, position in the hierarchy may have explanatory value by referring to an attribute directly or indirectly responsible for all the intercorrelated

facets of behaviour (Hinde 1974).

At present, it has been found that various measures of aggressive dominance are correlated in some primate groups (Deag 1977; Richards 1974; Simpson 1973), however, the search for intercorrelations between various types of rank orders have been rather varied in success. Thus, although for captive rhesus, Richards (1974) reported significant correlations between measures based on various criteria, Bernstein (1970) found rather low correlations between different types of rank order.

The discovery of poor correlations calls into question the predictive value of dominance rank from one social situation to another and leads to the argument that there is no evidence for any "quality of dominance" either inherent or acquired by animals which could influence the way in which rank relationships become structured (Rowell 1974).

But, perhaps, just as we were too ready to accept the concept of dominance as universally useful for the understanding of primate social behaviour, we should beware of just as hasty a rejection of this concept.

Instead, the precise limits of its usefulness should be empirically examined (Hinde 1978). This should entail not only the examination of the utility of the

concept of dominance rank (based on the relative frequency and direction of behaviour) for each group/species of interest, but also a search for alternative conceptions and measures of dominance which may prove to be useful for the understanding of primate social behaviour and social structure.

In this thesis, both routes are explored. The search for alternative conceptions is discussed in the next chapter. In the following section, the utility of the concept of dominance rank for the study of the social behaviour of laboratory stumptail macaques is examined.

INTERCORRELATIONS OF VARIOUS MEASURES OF DOMINANCE
IN LABORATORY STUMPTAIL MACAQUES

METHOD

Six groups of stumptail macaques were observed. Details of the age/sex composition, and early rearing experience of the groups is given in table 1.

Group 6 was a group of wild-born adults used for breeding purposes in the main primate colony. Groups 1 to 5 were groups of juveniles which had been involved in a study by Chamove (unpub. data) on the effects of early rearing experience on later social behaviour.

Table 1. Age/sex composition, and early rearing experience of the sample.

Group number	Group name	Rearing experience	Animal number/ name	Sex	Age
1	Dark	Animals individually housed, but given daily social experience for a period of one hour withagemates in total darkness	1	F	lyr 8m
			2	F	
			3	M	
			4	F	
2	Peer	Animals individually housed and given daily social experience for a period of one hour withagemates in normal light	5	M	lyr 8m
			6	F	
			7	F	
			8	F	
3	Isolate	Animals individually housed and received no social experience	10	F	lyr 6m
			11	F	
			12	M	
			13	F	
4	Adult-peer	Animals individually housed and given daily social experience for a period of one hour with both age-mates and wild-born adults in a group	14	M	lyr 5m
			15	M	
			16	F	
			17	F	
5	Social	Animals were housed in a group cage with their mothers and the other members of their social group	18	M	lyr 5m
			19	F	
			22	F	
			23	F	

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			16	F	
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			19	F	
			22	F	
			23	F	

Table 1 contd

Group number	Group name	Rearing experience	Animal number/ name	Sex	Age
6	Feral	Wild caught as adults and transported to Stirling primate unit for breeding purposes	Angus Bangla John Russell Paint Kid Hana	M F F F F F	Adult

Individuals in group 5 (social group) had been reared together with their mothers and an adult male, in the main colony. They were separated from the adults at approximately 14 months of age and housed together as a group.

Individuals in groups 1 to 4 were separated from their mothers at around 10 days of age. They were then housed in individual cages in the primate nursery. These cages permitted visual and auditory access to the laboratory environment, but no visual or tactual access to other monkeys. Social experience for groups 1, 2 and 4 was superimposed on this basic isolation paradigm.

At 15 months of age, the individuals were grouped together in tetrads of like-reared animals. At the beginning of this study, the subjects had been living continuously in these groups for at least 3 months.

Table 2 summarizes the test situations used and the dates of testing the various groups.

All groups were tested in their group home cage between 1400 and 1500 hours on week days. The observer sat in full view of the animals, all of which had been fully habituated to the presence of a passive observer.

Data were collected by means of a handwritten symbol system encoding the occurrence of specific behaviour

Table 2. Test situations employed in a study of personality and dominance in stump-tail macaques

Test name	Situation	Groups tested	Date (all 1975)	Duration of test
General social	Free social interaction in the group of like-reared animals	Groups 1-5	July	30 mins
		Group 6	January	40 mins
Milk test (4 tests)	Group deprived of milk for one day prior to testing. On testing, the animals are given access to a single source of milk	Groups 1-5	May	10 mins
			(3 tests)	
		Group 6	July	30 mins
			February	40 mins
Orange juice test	Group presented with a single source of orange juice	Group 6	February	40 mins
			(1 test)	
Novel object	Unfamiliar object placed in the home cage of the group	Groups 1-4	June	10 mins
Toy test	Familiar play object placed in the home cage of the group	Groups 1-4	June	10 mins

patterns onto data sheets. Details of this system are given in Appendix 1. Behaviour patterns consisted of the normative communication signals for *Macaca arctoides* (Bertrand 1969; Chevalier - Skolnikoff 1973).

The data collection method gave a record of the frequency and sequential patterning of behaviour, the identity of the subject and the object of his/her behaviour. Behaviour was sampled using a shifting focal animal technique, with switches in focal animal occurring once every 15 seconds. Sample data sheets given in Appendix 2.

Only data from the individual's focal sample was included in the analysis (Shapiro and Altham 1978).

Dominance relationships were measured by 3 different methods:

Method 1: This consisted of a simple linear arrangement of individuals within the group according to total frequency of dominance displays.

Method 2: Here the relative frequency and direction of behaviour was taken into account. This method consisted of computing matrices of the distribution of behaviours between pairwise combinations of individuals within the group. Rows in the matrix denoted senders of specific gestures; columns denoted

receivers. By comparing the relative frequency of behaviour sent and received by individuals in the group, it was possible to determine if a linear arrangement of individuals on any particular behaviour was applicable, and also to ascertain the positions of individuals within linear hierarchies.

Method 3: This consisted of a priority of access measure. In other words, the order in which individuals within the group had access to the test object was scored. In the competitive food tests, novel object tests and toy tests, access was scored when an individual first contacted the object; in the milk and orange juice tests, control of the bottle for 30 seconds was taken as the criterion for access.

Table 3 lists the behaviour patterns scored in the different methods of assessing dominance rank.

In addition, the relative percentage of 5 different motivational types of behaviour, i.e., play, sex, affiliation, dominance and submission, shown by the individual in the test situation was assessed.

Classification of behaviour according to presumed underlying motivation is given in appendix 3.

Table 3. Behavioural measures of social dominance in groups of stump-tail macaques

Measure	Behaviour	Definition
<u>Method 1</u>		
Frequency of dominance displays	dominance display	animal grabs hold of object and bounces vigorously up and down, with rigid body posture and tense facial expression
<u>Method 2</u>		
Direction of aggression	brow threat	intense visual fixation, brows alternately raised and lowered
	open-mouth threat	as for brow threat, but mouth open and accompanied by low pitched vocalization. "Huh" sound
	scream threat	intense visual fixation with grimace and screeching vocalization
	teeth-chatter threat	intense visual fixation accompanied by teeth-chattering and a characteristic vocalization. "Eh-eh" sound
	chase) grab) bite))))

Table 3 contd

Measure	Behaviour	Definition
<u>Method 2 contd</u>		
Direction of submission	teeth chatter	rapid opening and closing of mouth. Lips fully vertically retracted baring the teeth which chatter audibly
	grimace	mouth corners drawn back, lips vertically retracted baring teeth. Often accompanied by a shrieking vocalization
	withdraw	movement away from an acknowledged stimulus
	flee	rapid movement away from an acknowledged stimulus
	freeze	tense, rigid posture with limbs and face protectively held close to body
	scream	characteristic high pitched noisy vocalization
Direction of mount	mount	individual clasps pelvis of a presenting animal with its hands and makes thrusting movements towards

Table 3 contd

Measure	Behaviour	Definition
<u>Method 2 contd</u>		
		the perineum of the presenting animal
Direction of present	present	animal orients perineum towards a partner
Direction of groom	groom	searching and picking with fingers or mouth through the fur of a partner
Direction of visual monitoring	visual explore	looking at a specific object
<u>Method 3</u>		
Order of access to food, novel object, toy	hand, mouth or foot contact	as implied
Control of milk or orange juice bottle	sucking bottle nozzle for 30 secs	as implied

RESULTS

1. Intercorrelation of dominance measures

Table 4 presents the rankings obtained from the different measures of dominance for groups 1 to 6.

Method 2 measures, i.e., directionality scores, were only computed for milk tests, since the behaviours of interest occurred too infrequently in other situations to be of use. Only one rank ordering is reported for milk tests because rank orders were identical in each of these tests.

It was found that there was significant correlation at the 0.01 level (Kendall's coefficient of concordance) amongst all measures of dominance computed for groups 2, 5 and 6; and significant correlation amongst 4 measures for groups 1 and 3.

Group 4 (Adult-peer) was the only group showing no significant intercorrelation among dominance measures. This group also showed lack of linearity on the direction of aggression measure. All other groups showed linear hierarchies for all dominance measures.

Groom, mount and present were shown too infrequently in the juvenile groups, except 'present' in the social group, to be of any use in ranking individuals. These

Table 4. Intercorrelation of rankings obtained from different measures of social dominance in 6 groups of stump-tail macaques

Group 1 (Dark)	Method 3				Method 2				Method 1			Value of Kendall's coefficient of concordance (W)
	Priority access milk	Priority access novel object	Priority access toy	Direction aggression	Direction submission	Direction visual monitor	Direction groom	Direction present	Direction mount	Total frequency dominance display		
1	2	1	1	2	2	2	2			0	0.96	
2	4	3.5	4	4	3.5	4			0			
3	1	2	3	1	1	1			2			
4	3	3.5	2	3	3.5	3			0			
	*			*	*	*						
Group 2 (Peer)	5	3	3.5	3	3	3				0	0.72	
6	4	4	3.5	4	4	2			0			
7	2	1.5	2	2	2	4			0			
8	1	1.5	1	1	1	1			0			
	*		*	*	*	*						

not a useful measure here

not a useful measure here

not a useful measure here

Table 4 contd

	Priority access	Priority access novel object	Priority access toy	Direction aggression	Direction submission	Direction visual monitor	Direction groom	Direction present mount	Direction Total frequency dominance display of concordance (w)	Value of Kendall's coefficient of concordance (w)
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Group 3 (Isolate)

Inconclusive

10	1.5	1.5	1.5	2	2	2			0	0.96
11	4	4	3	4	4	4			0	
12	1.5	1.5	1.5	1	1	1			0	
13	3	3	4	3	3	3			0	

Group 4 (Adult-peer)

14	3	2	4		3	4			0	not a useful measure here
15	1	4	1	not linear	1.5	1			0	
16	4	3	2		4	2			0	
17	2	1	3	not linear	1.5	3			0	

not a useful measure here

not a useful measure here

not a useful measure here

Table 4 contd

	Priority access milk	Priority access novel object	Priority access toy	Priority aggression	Priority submission	Priority visual monitor	Priority groom	Priority present mount	Priority Direction Total	Value of frequency Kendall's dominance coefficient of display concordance (W)
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Group 5
(Mother-infant)

18				1	1	1		1	1	0.94
19				2	2	2		2	0	
22			no data	4	4	4		3	0	
23			no data	3	3	3		4	0	
*			no data	*	*	*		*		

Group 6 **
(Feral)

A	1	no data		1.5	1		1	1.5	1.5	1	0.96
B	2			1.5	2		2	1.5	1.5	0	
J-R	3			3	3		3.5	3	3	0	
P	4			4	4	no data here	3.5	4	4	0	
K	5			5	5	no data here	5	5.5	5	0	
H	6			6	6	no data here	6	5.5	6	0	
*	*			*	*	*	*	*	*		

* indicates those measures which significantly correlate at the 0.01 level (Kendall's coefficient of concordance (W)).

** Group 6 showed identical rank order for priority of access in both milk and orange juice tests.

behaviours were, however, useful for assessing dominance in the feral adult group.

Dominance displays were also infrequent and exhibited only by alpha males in groups 1 (Dark), 5 (Social) and 6 (adult-feral).

2. Motivational disposition and dominance rank

Table 5 gives details of the observed and expected \bar{X} relative frequency of dominance, submission, play, and affiliation according to dominance rank for those juvenile groups exhibiting a stable linear dominance hierarchy.

From this table, it can be seen that in the milk test situation, both the alphas and the animals ranking second in groups of 4 tend to have a higher probability of dominance and a lower probability of submission than expected. The omegas and the animals ranking third in groups of 4 tend, on the other hand, tend to have a lower probability of dominance and a higher probability of submission than expected.

DISCUSSION

The finding of significant intercorrelation between most of the different measures used, in 5 of the 6 groups of different early experience and age/sex

Table 5. Observed (O) and expected (E) mean relative frequency of dominance, submission, play and affiliation in milk test situations for 4 groups of differentially-reared juvenile stumptail macaques.

a) DARK GROUP

rank	dominance	motivational type			
		dominance	submission	play	affiliation
1	O	66.7	0.0	33.3	0.0
	E	29.5	10.4	41.1	19.0
2	O	25.5	5.6	36.5	32.5
	E	29.5	10.4	41.1	19.0
3	O	17.7	22.6	29.0	30.8
	E	29.6	10.4	41.1	19.0
4	O	7.8	13.4	65.0	12.4
	E	29.1	10.3	40.5	18.7

Contingency coefficient (c) = 0.53;

df = 9; $\chi^2 = 153.95$;

significant at 0.001 level

Table 5 contd

b) PEER GROUP

rank	dominance	motivational type			
		dominance	submission	play	affiliation
1	O	59.7	4.2	13.9	22.2
	E	37.9	25.5	6.8	29.8
2	O	56.7	4.2	1.6	37.4
	E	37.9	25.4	6.8	29.8
3	O	32.1	40.1	11.1	16.7
	E	37.9	25.5	6.8	29.8
4	O	0.0	51.2	0.0	40.5
	E	34.8	25.3	6.8	27.4

$C = 0.55$; $df = 9$; $X^2 = 171$;

significant at 0.001 level

Table 5 contd

c) ISOLATE GROUP

rank	dominance	motivational type			
		dominance	submission	play	affiliation
1	O	85.5	0.0	5.6	8.9
	E	37.4	26.5	15.8	20.2
2	O	28.7	32.3	20.4	18.6
	E	37.4	26.5	15.8	20.2
3	O	21.9	46.3	3.0	28.8
	E	37.4	26.5	15.8	20.2
4	O	13.6	27.6	34.2	24.7
	E	37.5	26.6	15.8	20.3

$C = 0.55$; $df = 9$; $\chi^2 = 178.7$;

significant at 0.001 level

Table 5 contd

d) SOCIAL GROUP*

rank		motivational type		
		dominance	dominance	submission
1	O	38.9	0.0	60.6
	E	24.6	20.4	54.5
2	O	38.5	4.5	53.4
	E	23.8	19.8	52.8
3	O	18.7	29.2	52.1
	E	24.7	20.5	54.8
4	O	1.8	47.5	50.8
	E	24.7	20.5	54.8

$C = 0.47$; $df = 6$; $\chi^2 = 112.53$;

significant at 0.001 level

*play not observed in milk test situation for this group

composition, suggests that for laboratory stumptail macaques, dominance is an important aspect of social behaviour.

Only one group (Adult-peer) showed no intercorrelation between measures, and this group was later found to have been in the process of changing its dominance relationships at the time of this study.

For laboratory stumptail macaques, then, position in the hierarchy would appear to have potential explanatory utility.

It may encompass not only the relative frequency and direction of aggressive behaviour, but also the relative frequency and direction of submissive behaviour, visual monitoring, presenting, mounting (feral adults only), grooming (feral adults only), and the priority of access to a source of milk or orange juice. It may also affect the relative occurrence of different types of behaviour.

It may, therefore, be thought of as referring to an attribute directly or indirectly responsible for all those facets of behaviour (Hinde 1974).

It would appear that for these animals, there may indeed be a "quality of dominance" which influences the way in which rank relationships become structured

(Rowell 1974). The next logical task would be to discover what such a quality may consist of, and this is discussed in the next chapter and chapter 9.

ASSESSING THE EXPLANATORY UTILITY OF THE CONCEPT OF
DOMINANCE

If, in any study, poor correlations among different measures of dominance are found, rather than uncritically assuming that the concept of dominance rank has little explanatory utility for the group in question, perhaps such negative findings should instead lead us to question our basic assumptions about assessing the explanatory utility of the concept.

Hinde (1978), for example, has argued that in order to discover whether aggressive rank order and other aspects of social behaviour are related, it may be necessary to look for more complicated relations than just surface correlations between different types of rankings.

In justifying this argument, he discusses Seyfarth's (1976) study of 8 female baboons. This group showed a stable rank order over a 15 month study period.

Seyfarth (1976) found that the females gave their most frequent grooming responses per grooming solicitation to the highest ranking individual in the group, next most

frequent to the second highest, and so on.

However, he also found that the amount of grooming in absolute terms was usually greatest with individuals of comparable rank. Thus individuals of high rank groomed others of high rank most frequently, those of middle rank groomed others of middle rank, and so on. As a result, the rank ordering of individuals according to relative frequency and direction of grooming responses did not correlate with the aggressive rank ordering of individuals.

Hinde (1978) points out that these findings can be understood in terms of principles concerning greater attractiveness but lower availability of high ranking individuals, i.e., each female is thwarted from grooming high ranking individuals by others to an extent related to her own rank.

Thus, in Seyfarth's (1976) study, while dominance rank order is not correlated with the surface structure (i.e., the actual observed distribution) of grooming interactions, and thus cannot directly explain it, it is useful in association with principles that refer to behavioural propensities and how they interact.

If, therefore, the explanatory role of the concept of dominance rank is limited to surface correlations

between rank orders, then the potential explanatory utility of this concept may be prematurely restricted.

It could be argued, then, that poor surface correlations between rank orders should not necessarily lead to the conclusion that dominance rank has no explanatory utility. Instead, we should attempt to link the dominance concept with other explanatory principles in order to account for particular aspects of primate social behaviour (Hinde 1978; Keverne *et al* 1978).

ALTERNATIVE LEVELS OF ANALYSIS

In the recent primate literature, examination of agonistic interactions involving more than two individuals has suggested an alternative conception of dominance. This entails switching from looking at dominance hierarchies as static structures, to looking at them as basically dynamic structures (refer to section on linear hierarchies above).

This involves thinking of the individual as potentially being a dominance strategy user, and looking at his/her methods of attaining/maintaining a given rank position in the dominance hierarchy (Walker leonard 1979).

It has been suggested (Walker Leonard 1979) that this conception enables the postulation of a "quality of dominance" which may influence the way in which rank relationships become structured, and which may also partly determine and predict change in affiliative relationships in the social group.

In the next chapter, the underlying conceptions of this "strategy approach" to the study of primate social behaviour are examined.

CHAPTER FOUR

A strategy approach to the study of primate dominance.

Personal observation (Walker Leonard pers. obs. 1974) of laboratory groups of stump-tail macaques indicated that many of the fights which occurred tended to involve more than two individuals. For example, many fights appeared to start with one individual threatening a second while "seeking support" from a third.

Review of the primate literature at the time showed that this multi-animal involvement in agonistic interactions appeared to be a fairly widespread phenomenon (Deag and Crook 1971; Kawai 1958; Koyama 1970; Kummer 1967; Marsden 1968; Ransom and Ransom 1971; Varley and Symes 1966); and descriptive accounts had pointed to a set of behavioural "techniques" commonly observed in such interactions.

Kummer (1967), for example, had shown that in hamadryas baboons (*Papio hamadryas*), an adult female is able to establish a triadic interaction with herself in the role of *protégé* and the leader male in the role of *protector*.

The most simple form of becoming the *protégé* is to

arrive first at the male's side. More complex forms involve the protégé in threatening her opponent, and staying as much as possible between the male and her opponent, while presenting to the male. Such behaviour indicates that the protégé is responding not only to the male and to the opponent, but also to the opponent's status relative to the male (Anderson and Mason 1974).

In the recent literature, these techniques have tended to be referred to as "social skills" (Bernstein 1976); and in Walker Leonard (1979), a preliminary conceptual framework for the study of this behaviour was outlined.

A CONCEPTUAL FRAMEWORK FOR THE STUDY OF SOCIAL SKILLS IN PRIMATES

In this scheme, social skills are assumed to operate in various contexts with various different results. Their use is thought of as involving the selection of a particular goal-directed sequence of behaviour from a set of possible sequences of behaviour: "goal" is held to be synonymous with "stopping condition" (Dawkins 1976).

Pursuit of such goals is thought of as involving the individual in the selection of a particular "strategy"

of behaviour, which is adapted to a particular end-state. Each strategy may be achieved by various alternative techniques, or tactics, the terminal units being the observable behaviours themselves.



These hierarchical relations are not just descriptive; they are assumed to reflect the organization of the competence underlying skilled behaviour.

Thus, just as manual skills involve the manipulation of objects, social skills are thought of as involving the manipulation of social relationships: they are held to rest on the ability of the individual to use information about existing relationships within the social group in order to manipulate these to his/her own advantage.

This entails the ability to switch from one tactic to another depending on the social context, in pursuit of a given goal. It also entails the ability to switch from goal to goal.

Social skills, then, are thought of as complex

behaviours which point to the involvement of cognition in the regulation of social relationships. And, certainly, primates are intelligent enough to be capable of this level of cognition (Humphreys 1976, Jarrard 1971).

STRATEGY USE IN PRIMATE AGONISTIC INTERACTIONS

If we take the specific case of agonistic interactions, then it can be argued that skilled behaviour, here, involves the recognition by a given individual of the dominance relations between at least 2 other animals, and between each of them and itself. Thus, in Kummer's (1967) example, the protégé was responding not only to the male and the opponent, but also to the opponent's status relative to the male.

A possible goal of such skilled behaviour in agonistic interactions may be to avoid becoming the most subordinate, or scapegoat, individual in a particular agonistic interaction. In order to achieve this goal, individuals may be thought of as employing alternative "dominance" (or "avoiding subordination") strategies.

In agonistic interactions involving three individuals it is theoretically possible to differentiate two such alternative dominance strategies. These include

- (a) making sure one is not the subordinate *and* trying to become the most dominant of the three individuals ("*monopolizing strategy*"), and
- (b) making sure one is not the most subordinate *but not* trying to become the most dominant of the three individuals ("*intermediate strategy*").

Empirical studies (Walker Leonard unpub. data; Walker Leonard 1979) indicate that a third class of strategy should also be included, namely, "*presumptive and ambiguous strategies*", where the specific goal of the individual is not recognizable from its immediate tactics.

It is possible to classify the various agonistic techniques (or dominance tactics) recently described in the primate literature, according to this scheme.

Mason (1978), for example, described two dominance tactics observed in groups of rhesus monkeys during a water bottle competition test.

The first tactic involves a behavioural pattern which had previously been termed "enlistment" (Hall and De Vore 1965). In Mason's (1978) water bottle tests, this may occur when a monkey waiting for access to the bottle, and lower in status to the monkey currently in contact with the bottle, threatens the occupant of the

bottle while directing appeasement behaviour at a monkey of higher status than the one currently occupying the bottle.

This pattern may result in the displacement of the occupant from the bottle. And, as Mason (1978) comments, it can be argued that this tactic may prove to be most useful for changing the dominance relationships between the three animals concerned.

In terms of the monopolizing-intermediate-ambiguous strategy classification, this tactic would be subsumed under intermediate strategy use, since in terms of the rank relationships denoted by the deployment of agonistic behaviours, the strategy user is placing itself intermediate in rank between the other two, i.e., it threatens one while appeasing the other in some way.

A second tactic described by Mason (1978) has been termed "redirection of aggression". Here an individual when threatened by a more dominant animal will quickly turn to threaten an individual lower in status than itself. This often results in the more dominant animal joining in to threaten the lower status animal. By the same criterion as above, this tactic would also classify as an intermediate strategy.

De Waal (1978a) has described two quite different

tactics. The first of these he calls reactor alliances. Here, one animal intervenes in an agonistic interaction between two other animals by attacking the aggressive party. This tactic would classify as a monopolizing tactic since the intervening animal, by attacking the aggressor of the dyad, is indicating his dominance over the other two.

The second tactic described by de Waal (1978) is termed an actor alliance. In this alliance, the intervening animal joins in an agonistic interaction in order to support the aggressive party. In the present classification system, this tactic would be classified as an ambiguous tactic since it does not indicate the rank relationship between the intervening animal and the aggressive party of the dyad. As such, it could be used by animals seeking to become dominant, or by those seeking only to avoid becoming subordinate in a particular interaction. De Waal's (1978) data reflect this ambiguity; since he states that the most likely function of actor alliances is to regulate *unstable* relations between the alliance partners.

In walker Leonard (1979) the tactics characteristically observed in triadic agonistic interactions of newly formed groups of juvenile stump-tail macaques were described. The classification of these tactics according to the monopolizing-intermediate-ambiguous strategy scheme is

given in figure 3. Table 6 presents a description of the behaviours involved in each tactic. Figure 4 shows three animals involved in a triadic agonistic interaction.

The merits of this particular classification scheme, and its underlying theoretical conceptions, will of course depend on its empirical utility.

EMPIRICAL UTILITY OF THE PROPOSED THEORETICAL FRAMEWORK

Basically, the approach assumes that the individual primate actively constructs rank relationships to his/her maximum benefit in the course of his/her agonistic interactions within the group. This hypothesis has also been suggested by Cheney (1977) and De Waal (1978).

If it can be shown that this is a meaningful approach to primate agonistic behaviour, then it could be argued that a quality of dominance, namely "dominance strategy use" may be postulated which influences the structuring of rank relationships within social groups.

In Walker Leonard (1979) preliminary evidence in support of this approach was presented. The data suggested that the resulting rank positions within newly formed triads of juvenile stump-tail macaques may be predicted by the strategy behaviour of the individuals

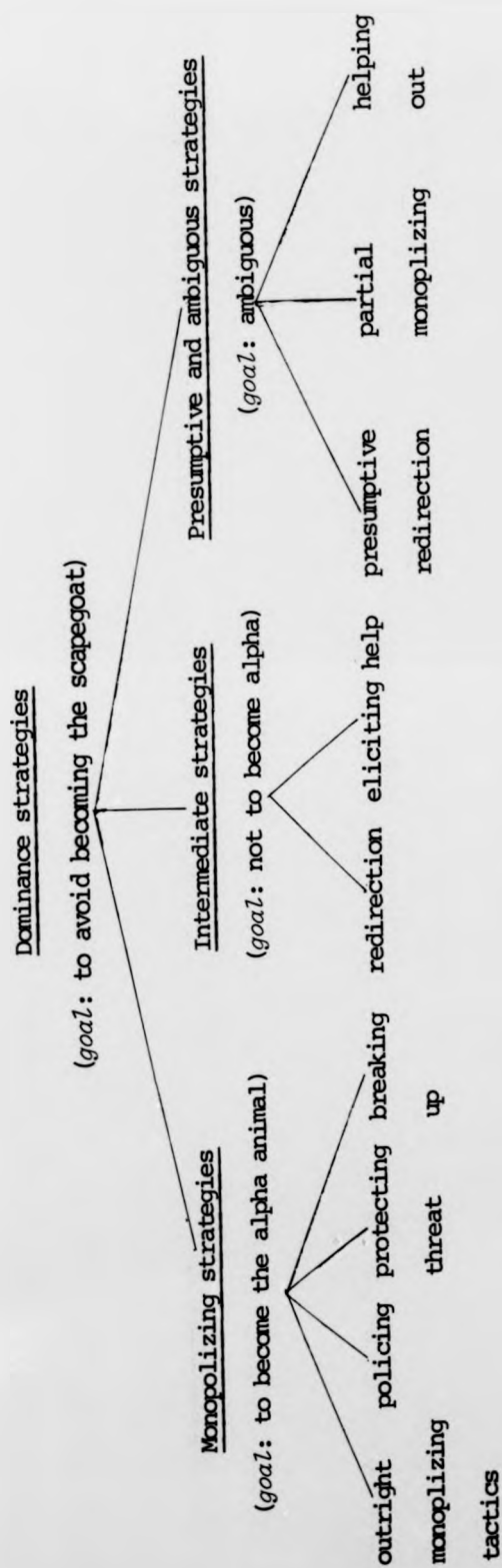


Figure 3. Classification of dominance strategies in juvenile stumptail macaques.

Table 6. Description of dominance tactics in juvenile stumptail macaques.

Dominance strategy	Tactics	Behavioural description	Examples
Monopolizing	Outright monopolizing	S directs dominance behaviours either simultaneously or in sequential fashion towards 2 animals.	In juvenile stumptails this might consist of the monopolizing individual grabbing hold of one animal and vigorously bouncing up and down on him with tense body posture and facial expression, and then immediately threatening or chasing a third participant.
	Policing	S directs dominance towards either the aggressor in an agonistic dyad or the dominant in a status interaction.	The policing individual might intervene in a dyad by threatening or attacking the individual who is displaying dominance over the third animal.
	Protecting threat	S directs dominance-sexual behaviours towards the aggressor in a dyad.	The animal displaying protecting threat behaviour will mount an individual who is threatening or attacking a third.
	Breaking-up	S directs aggressive behaviour to 1 or 2 animals in a non-aggressive, non-status dyad.	The animal may break up a grooming dyad by grabbing one of the grooming pair.

Table 6 contd

Dominance strategy	Tactics	Behavioural description	Examples
Intermediate	Redirection	S directs appeasement behaviour to one animal whilst directing dominance behaviour to the other.	The protégé in the Hamadryas example cited in the text, was eliciting help from her protector by presenting to him and threatening her opponent. This might result in the protector joining in to help out his protégé, on the other hand it might also result in his demonstrating policing tactics.
Ambiguous	Partial monopolizing	S directs dominance behaviour to one animal and some other response (but not appeasement) to the second.	S might direct an open mouth threat to one individual, then visually fixate and approach the third.
	Helping-out	S directs aggressive behaviour towards the object of aggression in an agonistic dyad.	Essentially, the helping-out individual joins in with the aggressor to help attack the third animal.
	Presumptive redirection	S directs aggressive behaviour to a third animal in response to non-aggressive behaviour directed to itself by the first animal.	If an individual approaches and contacts S, he will respond by threatening or attacking a third animal.



Figure 4. A triadic agonistic interaction in juvenile stump-tail macaques. Animals from left to right are numbers 30, 26, 33. 33 has just threatened and attacked 30 who is screaming; 26 joined in to help out 33 by threatening and attacking 30.



Figure 4. A triadic agonistic interaction in juvenile stump-tail macaques. Animals from left to right are numbers 30, 26, 33. 33 has just threatened and attacked 30 who is screaming; 26 joined in to *help out* 33 by threatening and attacking 30.

prior to settlement on a stable rank order.

Thus, only those animals who became alpha, and those who became midranking, in newly formed groups of three, were observed to exhibit dominance strategies. Animals who became subordinate in the new triads were never observed to exhibit any dominance strategies throughout the test period.

Although the data were too preliminary to be statistically significant, the results did give tentative support to the hypotheses:

- (a) that the individual showing the most monopolizing strategies becomes the alpha animal in newly formed triads ($p = 0.05$, Mann Whitney U).
- (b) that the individual showing the most intermediate strategies becomes the midranking animal in newly formed triads ($p = 0.443$, Mann Whitney U).

It was concluded in that paper that eventual rank positions in these newly formed hierarchies of juvenile stumptail macaques resulted from the tactics used (or not used) by the individuals concerned.

Furthermore, since individuals were found to display dominance tactics within the first 6 minutes ($\bar{X} = 2\text{min } 48\text{sec}$) of the animals first sighting each other, it was

suggested that the correlation between strategy use and resulting rank was due to the immediate efforts of individuals to set up rank relationships to their own benefit.

These preliminary findings, then, give some support to the idea that dominance strategy use may be a useful concept in the study of primate agonistic behaviour.

It may even be useful in an explanatory or predictive manner. Thus it has been suggested (Walker Leonard 1979), that the concept of strategy use may be useful in predicting change in affiliative relationships in the social group.

For example, personal observation (Walker Leonard 1977) of laboratory groups of adult stumptail macaques, indicated that low-ranking individuals, who have successfully joined in a series of agonistic interactions to help out a high-ranking individual, show a subsequent increase in friendly interactions (grooming, huddling, etc.,) with the individual they have helped out.

It has also been suggested (Walker Leonard 1979) that future strategy use itself may be predicted by the quality of affiliative relationships among individual animals.

Thus in stumptails, it is found that only those juveniles with a particularly friendly relationship with a given adult will attempt to elicit that adult's help in an agonistic interaction.

Similar hypotheses have also been suggested by Cheney (1977) and de Waal (1978).

If future research concludes that the concept of dominance strategy use is *not* useful for the explanation of behaviour, it will, however, retain its utility as a descriptive concept.

Thus, by recording the dominance tactics of individuals within any particular group, it should be possible to chart, in a behaviourally meaningful way, the rise and fall of particular individuals within the dominance hierarchy.

Examination of the raw data record in Walker Leonard (1979), for example, showed that the long term goals of individuals may be achieved by a series of short term objectives.

Thus, in a newly-formed triad, ambiguous tactics may precede settling on a particular monopolizing or intermediate tactic, and an intermediate tactic may precede the eventual achievement of alpha status by

monopolizing tactics. Such switches presumably depend on contextual considerations as well as individual motivation and skill.

The concept of strategy use would therefore appear to be a promising alternative conception of dominance; and before the concept of social dominance is summarily dismissed (see Garltan 1968; Rowell 1974), the utility of this alternative conception should be further investigated.

HOW DO INDIVIDUALS COME TO USE PARTICULAR TACTICS IN PARTICULAR SITUATIONS?

A start has recently been made to examine the ontogenetic determinants of strategy use.

Thus Anderson and Mason (1974; 1978) have shown that in rhesus this ability appears to be dependent on adequate early socialization.

In their studies, groups of socially isolated monkeys (surrogate-reared) did not exhibit any dominance tactics; while groups of relatively experienced monkeys (mother-reared until 6 months, then peer-reared) showed a variety of such behaviours.

In a recent study (Chamove and Walker Leonard, unpub. data), I compared the dominance strategy

behaviour of differentially reared groups of juvenile stumptail macaques, but came to a rather different conclusion about the importance of social experience.

In this study, it was found that isolation-reared stumptail macaques were capable of displaying all of the dominance tactics typical of juvenile animals. One of the isolation-reared animals actually showed the highest recorded frequency of monopolizing tactics in the sample studied (20 animals). He even showed more, in a shorter time span, than any of the animals observed in Walker Leonard (1979) (12 animals). He subsequently became the alpha animal in his triad.

It was therefore concluded that social experience is not necessarily as important for the development of these behaviours as Anderson and Mason (1974; 1978) have suggested.

This conclusion was supported by the finding that 3 month-old socially isolated stumptails displayed dominance tactics in their first-ever triadic interaction with peers (unpub. data from DIMS study, see chapter 6 for details of procedure. Also see Walker Leonard 1978).

The discrepancy between Anderson and Mason's (1974; 1978) findings and the findings of the Chamove and Walker Leonard (unpub. data) study may have resulted from a

number of factors. Thus it might be attributable to species differences, different early rearing conditions, or different testing conditions.

Take, for example, the testing conditions of the two studies. Anderson and Mason (1978) looked at the behaviour of individuals in an established social group during a water competition test; whereas we looked at the behaviour of individuals in newly-formed triads (procedure reported in Walker Leonard 1979).

It is likely that the newly-formed group situation actually enhances the occurrence of strategy behaviour, since individuals are unfamiliar, and therefore endeavour to work out their dominance relationships as quickly as possible. The water competition situation, on the other hand, may differentially affect the occurrence of strategy behaviour in animals of different early experience.

Thus, in relatively normally-reared individuals, this situation may not adversely affect the occurrence of opportunistic behaviour; it may actually enhance it; whereas in relatively deprived individuals, this kind of situation may actually depress the occurrence of such behaviour.

Before a conclusion about the role of early

experience may be reached, therefore, more detailed investigations must be carried out.

Early experience is not likely to be the only factor involved. Thus it has been suggested that sex differences (De Waal 1978; Walker Leonard 1979), or personality differences (Walker Leonard 1979), may also be important in the development of differential strategy use.

The role of these factors, however, has not yet been experimentally examined. Investigation of the role of personality, for instance, must await definitive studies on the characterization and importance of personality differences in primate species.

In the next chapter, the potential utility of one particular theory of personality, i.e., Eysenck's theory of personality, for the study of primate social behaviour is examined.

CHAPTER FIVE

Eysenck's theory of personality: a pilot study of its utility in the study of primate social behaviour.

Most primate researchers would agree that there is considerable individual variation in primate social behaviour. Even monkeys who have been reared in essentially the same experimental conditions will display a wide range of individual differences in response to standard stimuli (Sackett 1974).

Given this diversity, it could be argued that by lumping individuals together and talking of them as a homogeneous group, e.g., "isolates", we may limit our understanding of the development of social behaviour in primates (Hinde 1972). What is needed is some method of reducing the observed variance in such a way as to yield a more meaningful understanding of the development of behaviour, as well as insight into the causation and functions of behaviour.

One way of reducing this variance is to introduce variables which parcel out the effects to meaningful constructs. Thus individual differences in behaviour may be reduced and explained by dividing the sample into age/sex/dominance rank classes. In this chapter, it will be argued that the introduction of personality variables

into the study of primate social behaviour may also lead to a reduction in variance and a greater, richer understanding of why individuals behave the way they do.

The idea that primates have definite personalities is widespread in the literature (see for example, Van Hoof 1967; Van Lawick-Goodall 1968), but it has been paid lipservice only, until recently, when at least three investigations have directed attention to the study of primate personality, i.e., Biurski *et al* 1968; Chamove *et al* 1972; Stevenson-Hinde and Zunz 1978.

As discussed in chapter 2, each of these studies had as their major aim the characterization of the structure of primate personality. However, each of them, while contributing greatly to the beginning study of primate personality, has certain limitations and drawbacks. For example, Biurski *et al* (1968) and Stevenson-Hinde and Zunz (1978) use rather subjective measures which rely on the observer's interpretation of behaviour.

Chamove *et al* (1972), on the other hand, attempt to report more objective measures of behaviour, but they mix categories of behaviour selected according to different criteria. Thus, in some of their categories, the behaviour of the partner is taken into account in the determination of the subject's behaviour (e.g., inappropriate withdrawal), whereas in other categories it

is not (e.g., social play). In addition, their behavioural categories are defined at a rather gross level of analysis, and it could be argued that a better understanding of personality may be achieved from a more detailed categorization of behaviour.

In this chapter, two pilot studies will be reported. The first was originally designed to look specifically at the intercorrelation between different measures of social dominance in laboratory stumptail macaques (see chapter 3); the second was designed to look at the communicative abilities of differentially reared juvenile stumptail macaques (see chapter 7). However, the nature of the data collection methods enabled two exploratory studies of primate personality to be carried out.

In these exploratory studies, the main aim was to examine methods of measuring personality which rely on the direct observation of ongoing behaviour at a fairly detailed level of analysis. This involved:

- a) the deduction of potentially useful measures
- b) assessing the reliability of such measures across similar and across different test situations
- c) attempting to assess the validity of the measures used.

Secondary aims included:

1. to investigate whether there was any correlation between personality and dominance rank in laboratory groups of juvenile stumptail macaques.
2. to investigate whether dominance rank could be predicted from personality attributes assessed in non social test situations prior to social experience in a stable group.

Eysenck's (1969) theory of personality was taken as the starting point and guide in the search for relevant personality variables. As discussed in chapter 2, Eysenck's theory postulates 3 potentially useful measures of personality, namely neuroticism, extraversion and psychoticism. Its basic premise is that it is possible to order individuals from high to low on each personality dimension; a fairly complete description of the individual's personality being given by a combination of high/low scores on all three dimensions.

One of the advantages of choosing Eysenck's theory as a guide in the beginning study of primate personality is that this theory, by making specific assumptions about the biological bases of these dimensions of personality, tells us which aspects of behaviour are likely to be related to each specific dimension, i.e., it structures the search for possible behavioural measures of personality.

An alternative approach would be to collect data on the social behaviour of individuals in a variety of situations and then factor analyze to arrive at inherent structure.

This latter approach is useful for uncovering structure in a previously uncharted area. However, the factor analysis technique itself, is only as good as the measures on which it operates, and unless the measures are chosen with some underlying theory in mind, one might discover factors that are either uninterpretable, or which may be mistakenly interpreted to be personality factors.

Fruitful research, however, as Magnusson and Endler (1977) point out, does not presuppose the use of only one method of data collection, nor one method of data treatment, nor one research strategy, nor one class of variables. Instead many approaches and many new and creative strategies are needed. One must of course suit the method, strategy and constructs to the problem chosen.

In this study, the main aim was to develop useful measuring procedures, thus it was argued that by making the underlying theory explicit - a theory of personality which appeared to be of potential use for the study of primate social behaviour (Chamove *et al* 1972) - then it was likely that a meaningful set of measuring procedures

would be arrived at more economically than by the use of the factor analysis technique.

GENERAL METHOD

A sample of 20 juvenile stumptail macaques was observed. This sample was divided into 5 groups, each comprising 4 animals. These groups had been involved in a study by Chamove (unpublished data) on the effects of early rearing experience on the development of social behaviour.

Details of the sex and early rearing experience of the animals are given in table 1, chapter 3.

Behavioural measures of personality in primates

NEUROTICISM

Neuroticism, or emotionality, may be thought of as persistent overreaction to environmental stimulation (Eysenck and Eysenck 1969; Plutchik 1962). In primate species, visual and vocal expressions are thought of as indicating underlying emotions (Chevalier - Skolnikoff 1973). Therefore useful behavioural measures of neuroticism in primates are likely to be derived from measures of the intensity, frequency and/or duration of visual and vocal expressions of emotionality.

In primate species, then, the more neurotic individuals should show greater frequency/duration of high intensity expressive behaviour in response to standard stimuli.

This hypothesis rests on the assumption that intensity of expression can be measured. Achieving an objective measure of intensity may be problematical. If, however, neuroticism is based on autonomic activity, the latter being indicated by various physiological measures, e.g., heart rate, muscular tonus, etc., then it will be possible to use physiological indices of intensity in expressive behaviour.

In the present study, subjective assessment of muscular tonus (relatively tense vs. relatively relaxed) provided the basis for judging the intensity of specific expressive behaviours in the communication repertoire of stump-tail macaques.

The gradation of behaviours from low to high intensity is given in table 7. Definition of these behaviours is given in appendix IV.

In this study, neuroticism was measured by determining the frequency of high intensity expressive behaviours exhibited by the individual in the test situation.

Table 7. Gradation of emotionally expressive behaviours of stumptail macaques, according to judged muscular tension.

Behaviour-type	low intensity	high intensity
submission	still; present withdraw	teeth-chatter; grimace; freeze; jerk; scream; bitey
play	all play behaviours	
dominance	mount; yawn; teeth chomp; brow threat; open mouth threat; chase; grab;bite	bounce; teeth chatter threat; scream threat;
sex	anogenital inspect; mount	masturbation
affiliation	all affiliation behaviours	
others	approach; open mouth; self huddle	self aggression

Within each group, the individual showing the greatest frequency of these behaviours was considered to be the most neurotic and was given a rank of 4. The individual showing the least was considered to be the least neurotic and was given a rank of 1.

Neuroticism was also assessed by an interpretative technique. Thus the animals were rated according to judged emotional overreaction. This was based on their response in a variety of test situations. Again individuals within each group were ranked from 1 (relatively calm) to 4 (relatively neurotic).

EXTRAVERSION

According to Eysenck's (1967) theory, extraversion results from differential activity of the reticular formation. This is reflected in differences in arousal and inhibition. Extraverts are characterized by low levels of cortical arousal and strong reactive inhibition; while introverts are characterized by high arousal and weak inhibition. These differences in brain function lead to associated differences in behaviour. Thus extraverts tend to be arousal seeking and changeable in their behaviour, while introverts show stimulus aversion and less distractability from tasks in hand.

It was reasoned that since cortical arousal is a

component of the orienting reflex, then visual orienting behaviour may be a useful index of extraversion - introversion in primates: the more introverted, or highly aroused, individuals may be expected to exhibit more visual orienting behaviour than the more extravert, or less aroused, individuals.

In these studies, extraversion - introversion was measured by determining, for a standard time period, the frequency of switches in the object of attention by the individual in the test situation. The greater the frequency of switches then the more introvert the individual was considered to be.

Individuals within the group were ranked from 1 to 4 depending on their scores. Thus the animal showing the most switches in attention in a particular group on a particular test was given the rank of 1, indicating relatively low extraversion or high introversion. The animal showing the least was given the rank of 4 to indicate relatively high extraversion or low introversion.

PSYCHOTICISM

This dimension has not been intensively studied in the literature, however, it has been suggested that it is reflected in solitary, hostile and inappropriate social behaviour (Eysenck 1967).

In these studies, the utility of 1 potentially useful measure of psychoticism was examined. This consisted of scoring the frequency of socially directed aggression and the frequency of solitary behaviour exhibited by the individual in the test situation.

Individuals were ranked in order of psychoticism depending on their combined solitary and aggression scores.

For example, if in social tests, the scores were as follows (actual data):

Group 5: Milk test 1

Animal	frequency solitary	frequency aggression
18	3	2
19	8	6
22	9	0
23	8	2

then the animals would be ranked 19, 23, 18, 22 from high (rank 4) to low (rank 1) on psychoticism.

Aggressive behaviours included all those listed under "method 2: direction of aggression", in table 3, chapter 3. Solitary behaviour was scored whenever an animal sat on its own, at least 1 metre away from the nearest animal,

displaying either self-directed huddling, stereotyped behaviours, or exhibiting no obvious behaviour pattern.

STUDY 1 : PERSONALITY CHARACTERISTICS OF JUVENILE
STUMPTAIL MACAQUES AS ASSESSED IN SOCIAL
SITUATIONS

METHOD

Each of the 5 juvenile groups was observed in 4 milk test situations, where animals had to compete within their social group for access to a single source of milk, and also in 1 general social situation, where animals were observed as they freely interacted in their normal social group.

Details of these test situations is given in table 2, chapter 3.

Data were collected by means of a handwritten symbol system (appendix I) encoding the occurrence of specific behaviour patterns onto data sheets (appendix II). The behaviour patterns consisted of the normative communication signals for *Macaca arctoides* (Bertrand 1969; Chevalier-Skolnikoff 1973).

This method gives a record of the frequency and sequential patterning of behaviour, the identity of the subject, and the object of the behaviour.

Behaviour was sampled using a shifting focal animal technique, with switches in focal animal occurring once every 15 seconds. Only data from the individual's focal sample was included in the analysis (Shapiro and Altham 1978).

Extraversion was scored in the general social situation and 1 of the 4 milk test situations. Neuroticism was assessed from 3 of the 4 milk test situations and from subjective judgements based on the observer's knowledge of the animals in a variety of situations. Psychoticism was assessed from 3 of the 4 milk test situations.

RESULTS

1. Reliability of measures of personality

The rank orderings on extraversion, neuroticism and psychoticism for individuals within their social group are presented in table 8.

In this table, a rank of 4 indicates high extraversion, neuroticism or psychoticism; a rank of 1 indicates low extraversion, neuroticism or psychoticism.

For extraversion, the Spearman rank correlation (r_s) between measures assessed in 2 situations was 0.8 (not

Table 8. Extraversion, psychoticism and emotionality in groups of juvenile stump-tail macaques.

Group	EXTRAVERSION				PSYCHOTICISM				EMOTIONALITY				
	Individual social test	General social test	Milk test 4	Correlation between extraversion measures (r_s)	Milk test 1	Milk test 2	Milk test 3	Correlation between psychoticism measures (W)	Observer ratings	Milk test 1	Milk test 2	Milk test 3	Correlation between emotionality measures (W)
Dark	1	3	4		4	2	3		2	1.5	2	2	
	2	4	3	0.8 n.s.	2	2	2.5	0.4	4	3.5	2	3.5	0.6*
	3	2	2		3	4	4		1	1.5	2	1	
	4	1	1		1	2	2.5		3	3.5	4	3.5	
Peer	5	4	4		4	4	4		3	3.5	4	4	
	6	1	3	0.4 n.s.	1.5	1	1	0.9	4	1	3	3	0.5
	7	2	1		1.5	2	2		2	3.5	1.5	1	
	8	3	2		3	3	3		1	2	1.5	2	
Isolate	10	3	4		1	1	1		1.5	4	2.5	3.5	
	11	4	3	0.8 n.s.	2	2	3	0.7	4	2	4	3.5	0.6*
	12	1	1		3	3	4		1.5	1	1	1.5	
	13	2	2		4	4	2		3	3	2.5	1.5	
Adult-peer	14	3	4		3	3	4		4	3	4	4	
	15	4	3	0.8 n.s.	1	1.5	2	0.2	1	4	3	3	0.5
	16	2	2		4	1.5	2		3	1.5	1	1.5	
	17	1	1		2	4	2		2	1.5	2	1.5	
Social	18	4	4		2	2	2		1	3	1	1	
	19	1	3	0.4 n.s.	4	4	4	1.0	2	1.5	3	2	0.7*
	22	2	1		1	1	1		3	4	4	4	
	23	3	2		3	3	3		3	1.5	2	3	

*significant at 0.05 level

significant) in 3 of the 5 groups and 0.4 (not significant) in the other 2 groups.

For neuroticism, Kendall's coefficient of concordance (W) was significant at the 0.05 level for the dark, isolate and social groups. It was not significant for the peer or adult-peer groups.

For psychoticism, the significance of W for $N = 4$, $K = 3$, was not listed in Seigel (1956). However, it can be seen that the intercorrelation of rankings on psychoticism was perfect for the social group ($W = 1.0$) and almost perfect for the peer group ($W = 0.9$).

2. Personality and dominance rank

Table 9 presents the rankings on neuroticism and psychoticism with respect to dominance rank for those groups where a) the measures of neuroticism/or psychoticism were significantly reliable, and b) the groups showed a stable linear dominance hierarchy.

For psychoticism, there was no significant correlation with dominance rank (Spearman $r_s = 0.4$ n.s.)

For neuroticism, Kendall's W was 0.87, indicating that this dimension was correlated with dominance rank. Significance of W could not however be tested for $N = 4$, $K = 3$.

Table 9. Personality and dominance rank in juvenile
stumptail macaques.

a) PSYCHOTICISM

Dominance rank	Group		$r_s = 0.4$ n.s.
	Peer	Social	
1	3	2	
2	2	4	
3	4	3	
4	1	1	

b) NEUROTICISM

Dominance rank	Group			$w = 0.8$
	Dark	Isolate	Social	
1	1	1	1	
2	2	2.5	2.5	
3	3.5	2.5	2.5	
4	3.5	4	4	

STUDY 2 : PERSONALITY CHARACTERISTICS OF JUVENILE
STUMPTAIL MACAQUES, ASSESSED IN NON-SOCIAL
SITUATIONS

METHOD

Animals were placed individually in a test cage (cuboid : height 121.3cm; breadth 71.7cm; depth 85.7cm) and presented with coloured slides of monkeys and humans, and a tape recording of monkey calls.

There were 3 test conditions:

1. Slides Alone (SA) - In this condition, 9 slides (1 human and 8 stumptail monkeys) were presented in a fixed order. Details of the slide stimuli are given in table 10(a). Each slide was presented for 60 seconds after which it was removed and the next presented (condition designed by Chamove 1974).

2. Calls Alone (CA) - In this condition, a tape recording of 10 common stumptail calls was played. The calls had been recorded in the laboratory, and the natural intensity of the call was preserved.

Details of the nature of the call stimuli are given in table 10(b). Description of the composition of the tape is presented in figure 5.

Table 10. Description of stimuli presented in slides/
calls tests.

c) SLIDES AND CALLS

Stimulus number	a) SLIDES ALONE	b) CALLS ALONE	matched slide stimuli
1	human neutral expression	soft grunts	mother cradling infant
2	infant visual explore	cheeps	infant visual explore
3	infant grimace	woo calls	female visual explore
4	female visual explore	affiliation rattle	male cradling infant
5	mother with infant on nipple	threat grunts	female brow threat
6	female grimace	teeth chatter threat call	juvenile teeth chatter threat
7	male open mouth threat	scream	infant grimace
8	male yawn	teeth chomp	male masturbation
9	female rear view	sex rattle	male teeth chatter invite
10	—	ejaculatory growl	male ejaculatory face

3. Slides and calls (S and C) - In this condition, 10 slide stimuli were interspersed with the 10 monkey calls presented in the CA condition.

Details of the slide and call stimuli are given in table 10(c), and figure 5.

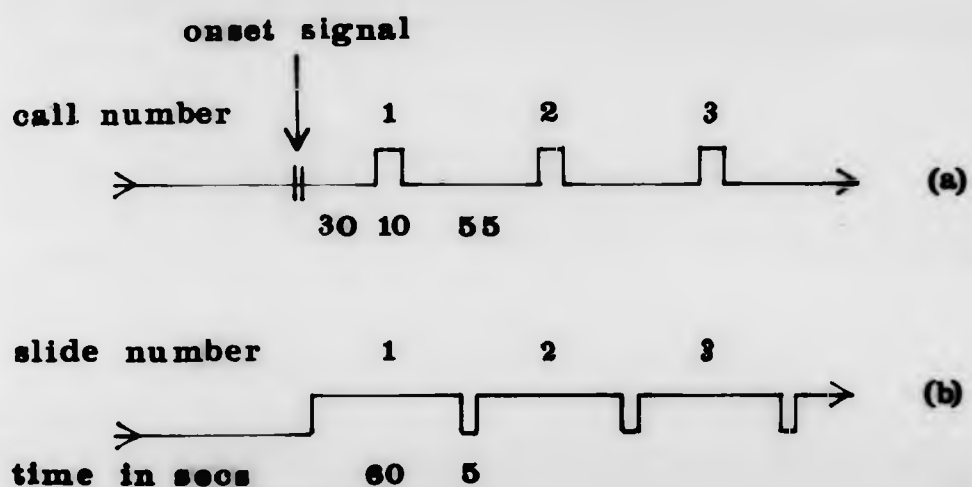


Figure 5. Composition of audio tape (a), and matched presentation of slide stimuli (b), for slides/calls tests.

Each individual received all 3 conditions in the order SA, CA, then S and C.

All tests took place between 14.30 and 15.30 hrs when the individuals were approximately 15 months of age. Dates of testing ranged from November 1974 (Dark group) to April 1975 (Social group).

All individuals had been previously adapted to the test cage by being individually housed there for a period of one week prior to testing.

Data were collected by means of a handwritten symbol notation method (appendix I) which gave details of the true frequency and sequential patterning of the behaviour of individuals as they responded to the test stimuli. Sample data sheet is given in Appendix V.

RESULTS

1. Reliability of measures of personality

The rank orderings on extraversion, neuroticism and psychoticism for S/C tests are presented in table 11.

Since $N = 4$, $K = 3$ for all groups, the significance of the W values could not be tested. However, it can be seen that for extraversion, the rankings on the 3 S/C tests for the adult peer group were highly correlated ($W = 0.9$). The rankings for the isolate group were also fairly highly correlated ($W = 0.6$).

For neuroticism, the rankings on the 3 S/C tests were highly correlated for both the adult peer and the social group ($W = 0.9$).

Table 11. Rankings on extraversion, neuroticism and psychoticism for juvenile stump-tail macaques in slides/calls tests.

Group	Individual	EXTRAVERSION				NEUROTICISM				PSYCHOTICISM			
		SA	CA	S+C	(W)	SA	CA	S+C	(W)	SA	CA	S+C	(W)
Dark	1	4	1	4	(0.3)	1	3	1	(0.4)	*	*	*	
	2	2	4	1		3	4	3					
	3	1	2	2		4	1	4					
	4	3	3	3		2	2	2					
Peer	5	2	2	2	(0.4)	1.5		2					
	6	3	1	3		3.5	*	1	$r_s =$	*	*	*	
	7	4	3	4		1.5		4	0.3				
	8	1	4	1		3.5		3					
Isolate	10	3	4	3	(0.6)	3		2.5		*	*	*	
	11	1	3	2		2		1					
	12	2	1	1		1	*	4	$r_s =$	*	*	*	
	13	4	2	4		4		2.5	0.3				
Adult-peer	14	3	4	3.5	(0.9)	4	2	4	(0.9)	*	*	*	
	15	1	1	1		2	3	3					
	16	2	2	2		1	1	1					
	17	4	3	3.5		3	4	2					
Social	18	3	3	3	(0.1)	3	3	2	(0.9)	3.5	3.5	3.5	(0.3)
	19	2	1	4		1	1	1		1	1	3.5	
	22	1	4	1		2	4	4		2	3.5	1	
	23	4	2	2		4	2	3		3.5	2	2	

* measure did not permit ranking of individuals

The psychoticism measure (i.e., compound aggression and solitary score) did not yield a useful ranking of individuals in the S/C tests; mainly because aggression was not readily elicited by these tests.

2. Personality and dominance rank

As was seen from table 11, rankings were highly correlated across tests for the adult peer and isolate groups on extraversion, and for the adult peer and social groups on neuroticism.

Since the adult peer group did not show a consistent linear dominance hierarchy (see chapter 3) it was excluded from analysis.

For S/C tests therefore, the resulting relationships between dimensions of personality and dominance rank were as follows:

a) Extraversion : isolate group

dominance rank	extraversion rank
1	1
2	3.5
3	3.5
4	2

b) Neuroticism : social group

dominance rank	neuroticism rank
1	1
2	3
3	2
4	4

COMPARISON OF MILK TEST AND S/S TEST RESULTS1. Personality dimensions

Neuroticism was the only dimension which yielded significantly intercorrelated rank orderings of individuals in both milk test and S/C test situations.

For the milk test situations, the rank orderings of individuals were significantly intercorrelated in the dark, isolate and social groups. For the S/C situation, the rank orderings of individuals were significantly intercorrelated for the adult peer and social groups.

The rank orderings for individuals in the social group, measured in milk test situations, S/C tests, and also assessed subjectively from a variety of situations, were found to be significantly intercorrelated ($W = 0.36$; significant at 0.05 level of significance).

The rank orderings for this group in these various test situations are given below:

Social group : rank orderings on neuroticism

Individual	milk tests			observer's rating	S/C tests		
	1	2	3		SA	CA	S + C
18	3	1	1	1	2	2	2
19	1.5	3	2	2	3	4	1
22	4	4	4	4	4	1	4
23	1.5	2	3	3	1	3	3

2. Personality and dominance rank

Neuroticism was the only dimension which was significantly correlated with dominance rank in both the milk and S/C test situations.

In the milk test situation, neuroticism was negatively correlated with dominance rank (animals high on neuroticism were low in dominance) for the dark, isolate and social groups.

In the S/C tests, it was negatively correlated with dominance for the social group.

DISCUSSION AND CONCLUSIONS

The main aim of these studies was to examine in a preliminary way, the utility of specific methods for measuring Eysenck's dimensions of personality in a primate species.

This involved firstly, the deduction of potentially useful measures, and secondly, the assessment of the validity and reliability of such measures.

1. Selection of measures, and validity

Eysenck's (1967) theory itself provides a useful guide to the selection of appropriate measures. Thus it makes specific assumptions about the biological bases of the dimensions of extraversion, neuroticism and psychoticism, and, in this way, tells us which aspects of behaviour are likely to be related to each specific dimension.

These hypotheses about the biological bases of the 3 personality dimensions have been experimentally examined for both humans and some animal species (see Eysenck 1967 and also Royce 1973). Although there is some debate over the exact nature of the relationship pertaining amongst the 3 dimensions (Gray 1973), it would appear that the relation of the individual dimensions to specific neuro-physiological substrata is at least provisionally accepted (Royce 1973).

The measures of extraversion, neuroticism and psychoticism developed in this study were directly deducted from Eysenck's (1967) theory of the biological bases of personality, and thus, it could be argued that they appear to have considerable face validity.

Criterion validity was not systematically assessed in this particular study. However, there was found to be a significant correlation between judged emotional reactivity and emotionality based on the frequency of high intensity expressive behaviours, which gives some support to the validity of the neuroticism dimension, at least.

In addition, this dimension was found to be correlated with dominance rank in a manner similar to that already indicated in the primate literature (see chapter 2). Thus, individuals high on emotionality were low in dominance rank; individuals low on emotionality were high in dominance rank. This finding gives further support to the validity of this dimension.

2. Reliability

Reliability of the methods varied according to the dimension measured and the test situation used.

Thus while rank orderings on extraversion were not

significantly intercorrelated in the social situations; they were highly correlated for 2 of the 5 groups in the non-social situations. For neuroticism, there was significant intercorrelation between rank orderings in both social and non-social situations. For psychoticism, rank orderings were highly correlated for 2 of the 5 groups in the social situation.

Lack of intercorrelation among rank orderings for a specific dimension may have been due to a variety of factors. For example, the method used to measure a particular dimension may not be the most suitable, or perhaps the dimension itself is not the most useful for characterizing primate personality. On the other hand, the lack of intercorrelation may be the result of small sample size ($N = 4$ in each group), or the result of situation effects masking or interfering with personality characteristics.

These possibilities indicate that there is a need to look at these same measures, and perhaps additional measures, in a larger sample under a wider range of situations. This is done in chapter 8.

A secondary aim in this study was to look at the relationship between personality and dominance rank.

Thus it was found that neuroticism was significantly correlated with dominance rank for the dark, isolate and social groups in social situations; and for the social group only, in non-social situations. The nature of this relationship was such that the most dominant animal tended to be the most calm, while the most subordinate animal tended to be the most neurotic.

The other 2 dimensions were not found to be correlated with dominance rank.

From this study alone, there is no way of discovering whether dominance rank affects personality or personality affects the attainment of dominance rank. However, if the isolate group had produced reliable rank orderings on neuroticism in the non-social situations, as they did in the social situation, we may have gained some indication of cause and effect. For this group were tested in the non-social situations *before* they had any experience of living in a social group.

In conclusion, we have seen that the measures of personality examined in this study appear to be promising methods for characterizing the personality characteristics of juvenile stumptail macaques. Thus they have considerable face validity with Eysenck's dimensions of personality, and may produce reliable rank orderings of individuals in certain circumstances.

However, there is a need for a more intensive investigation of the utility of these dimensions of personality in the study of primate social behaviour.

A more detailed investigation of personality was undertaken in the major study reported in this thesis. Details of its aims and experimental design are given in the next chapter.

CHAPTER SIX

Aims and Experimental Design.

Review of the primate literature (chapter 1) had indicated the need for studies which experimentally examine the ontogenetic determinants of social behaviour, and which describe the actual details of behavioural development, as well as the long term behavioural outcomes of any specific manipulation.

The aim of such studies should be firstly, to identify the sources of behavioural differences among individuals, and secondly, to examine how these factors produce the observed differences in behaviour (Hinde 1968).

In the remaining chapters of this thesis, several studies are reported which were undertaken with these general aims in mind.

In these studies, a transactional model of causation, diagrammatically, represented in figure 6, was selected for examination. The most general hypothesis of this model is that in primate species, both the inherited dispositions (i.e., both personality attributes and behavioural abilities) of the individual, and the individual's specific dominance experiences, interact

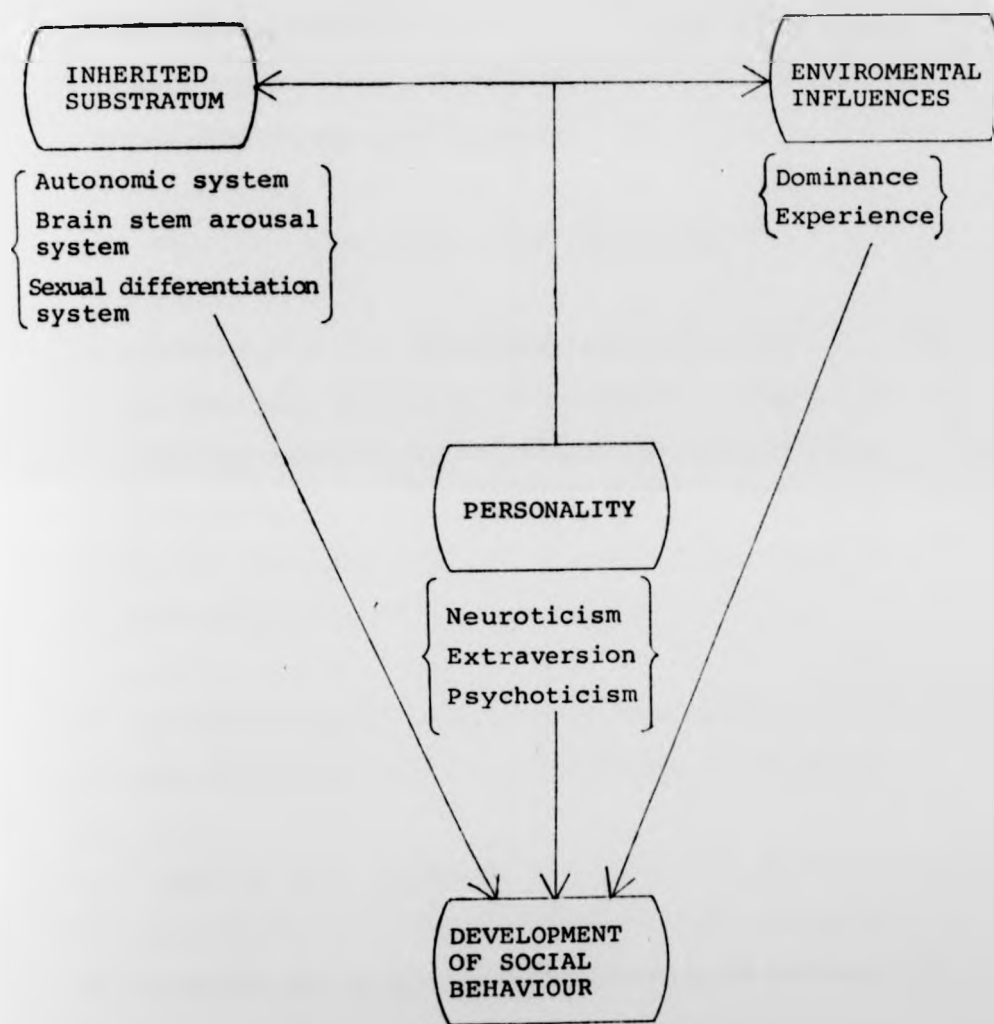


Figure 6. A transactional model for the explanation of some aspects of the development of primate social behaviour.

throughout development to influence certain aspects of the individual's social behaviour.

On inspection of figure 6, it can be seen that in any experimental examination of this model, certain minimum conditions must be met.

Thus the experimental design must permit:

- 1) assessment of the individual's dispositions (personality attributes and behavioural abilities) *prior* to experimental manipulation of experience,
- 2) maximum control over the dominance experiences of the individual throughout development, and
- 3) assessment of the individual's personality and social behaviour characteristics throughout development.

This in turn presumes:

- 1) selection and measurement of appropriate personality and behavioural variables
- 2) selection and manipulation of appropriate dominance experience variables

POSSIBLE APPROACHES

One possible approach for the examination of this model might involve cross-fostering infants on mothers of different dominance status (Chamove, pers. comm. 1974). Thus one could assess the infant's personality and behavioural dispositions while with its natural mother; assign the infant to a foster mother of specific dominance rank; then assess the infant's personality and social behaviour characteristics throughout development.

This cross-fostering approach has been used in studies of rat behaviour (Denenberg, Grotta and Zarrow 1963).

But although monkey mothers will accept and care for adopted infants (Chamove, pers. comm. 1974), there are several drawbacks to this approach.

Firstly, this approach would not yield an unbiased estimate of the infant's personality characteristics: the measures would always reflect the influence of, to a greater or lesser degree, the mother's and the foster-mother's behaviour. Thus while it would be possible to assess *change* in personality characteristics associated with specific experience, it would not be possible to examine any hypotheses about the individual's inherited predispositions.

Secondly, since adult monkeys may switch in dominance rank (see chapter 3), there is no guarantee that a given mother will retain her specific dominance rank for the duration of the infant's development. Changes in rank would add further factors for consideration which would not really be desirable.

An alternative approach to cross-fostering would be to alter the behavioural characteristics of the mother or the infant by either hormone manipulation or chronic drug administration.

Thus the mother's dominance rank might be altered by administration of testosterone or the infant's activity altered by administration of chlorpromazine or amphetamines (Suomi 1976).

In this type of approach, however, there are complications of unknown behavioural side-effects, unknown sites of action of many of the behaviour-altering drugs, and unknown mechanisms whereby these drugs produce their effects.

It can be seen that neither of the suggested approaches is satisfactory. What is needed at this stage of our knowledge is an approach which is as free from as many as possible of likely contaminating influences. In other words, we need an approach where

the variables of interest are isolated and examined in a maximally controlled situation. Then a core of knowledge about the specific effects of particular variables in the development of social behaviour may be obtained.

There are, of course, limitations in the extent to which relationships between variables established in strictly controlled situations can be generalized to the complex naturalistic situation. However, if the analysis of specific problems is followed up by a resynthesis process which assesses the relationship between the variables, and the adequacy of the initial analysis, then it is likely that this approach will be of value (see chapter 1).

As Hinde (1971) has argued, in the study of primate social development, no 1 method - naturalistic; controlled; field; laboratory - should be thought of as superior to the others. All can contribute; and the complex problems of social development can only be solved with the use, not only of these methods, but also many others which may be developed - for the different methods should illuminate each other.

In the present series of studies, the controlled experimental approach was used to examine the development of social behaviour in laboratory born and reared stumptail macaques.

VARIABLES OF INTEREST

1. Personality

Eysenck's (1967) theory of personality guided the selection and measurement of personality variables in the studies to be reported in chapters 6 to 9.

Thus the dimensions of interest included neuroticism, extraversion and psychoticism. These were measured by methods investigated in the pilot studies reported in chapter 5, and also by additional methods developed during these studies.

2. Dominance experience

It was decided to investigate the effects of 4 different kinds of dominance experience throughout development:

- a) *dominant only* - where the individual interacts only with those over whom he/she is dominant,
- b) *subordinate only* - where the individual interacts only as the lowest ranking animal in any particular group,
- c) *intermediate* - where the individual interacts only as

a mid-ranking animal,

- d) *mixed* - where the individual interacts alternatively as a dominant and as a subordinate animal.

These four conditions were suggested by Chamove (pers. comm. 1975).

The first 3 conditions represent the simplest classification of dominance experience types within any social group. The fourth was chosen for comparison purposes (see chapter 9).

3. Social behaviour

The dependent variable of interest was the social communication behaviour of individuals.

This resulted in a focus on molecular units of behaviour, e.g., teeth chatter, open mouth threat face etc. Details of the classificatory scheme used are given in appendix IV.

A major advantage of this scheme is that it is based on an objective classification of behaviour, rather than on a more interpretative classification.

The data record consisted of the frequency and

sequential patterning of communicative behaviours in non social tests; for social tests, the duration of behaviour was also recorded.

Preservation of the sequential patterning of behaviour meant that various higher-order measures, e.g., dominance strategies, could be computed.

GENERAL APPROACH

The general design involved separating a sample of 13 stump-tail infants from their mothers at 8 days of age, rearing them in social isolation until 3 months of age, then giving them social experience with peers in such a way that each infant received a specific experimentally-controlled dominance experience, i.e., either dominant only (D), intermediate (I), mixed (M) or subordinate (S).

As a result of the dominance experience conditions investigated by this study, it is referred to as the DIMS study.

One advantage of the approach is that it permits assessment of the individual's personality and communicative abilities both prior to (i.e., social isolation phase) and during specific dominance experience (i.e. peer experience phase). Thus it permits

hypotheses about the individual's predispositions (both personality and communicative abilities) to be examined.

It may be objected that this advantage is offset by the possibility that the period of early social isolation may have deleterious consequences for the development of social behaviour.

At the time of this study, however, it had been shown that rhesus infants, isolated for the first 3 months, and then exposed to social interactions, appear to develop almost normal social behaviour (Griffin and Harlow 1966). In addition, in the present series of experiments, every effort was made to ensure that the socially deprived period did not also mean sensory deprivation.

Thus, throughout this 3 month period, the infants could hear other monkeys, although they could not see them; they could see and hear what was going on in the laboratory environment (mainly the comings and goings of technicians and researchers); they were handled daily (for weighing); they had access to various objects for manipulation (see figure 7), including pieces of terry-towelling for contact comfort; and they were given access to a variety of different test cages.

It was expected that the above procedures would lessen



Figure 7: Infant stump-tailed macaque exploring a novel object (photo by G. Cameron).



Figure 7: Infant stump-tail macaque exploring a novel object (photo by G. Cameron).

any probable effects of social isolation.

Social experience was first given at 3 months in accordance with standard laboratory procedure at Stirling primate unit: 3 months being the age at which infant macaques show an increase in exploratory and play behaviour; leaving their mothers and seeking out their peers.

A peer-rearing paradigm, where infants had social experience with peers for 1-2 hours daily (depending on age), was chosen because this enabled maximum control of dominance experience. The next section gives details of the manipulation of dominance experience.

The Wisconsin studies of the time had shown that peer contact alone is sufficient to produce normal social behaviour (Chamove 1966; Harlow and Harlow 1965). Recent research, however, has argued that this is not really the case.

Thus Goy and Goldfoot (1974) point out what peer-reared rhesus infants tend to be deficient in sexual behaviour and also that peer groups of rhesus have a near "lord of the flies" aspect about them (Goldfoot 1977) compared to more normally reared infants. Thus displays of threat, aggression and submission are frequent daily occurrences and are exaggerated compared

to the levels shown by infants in mother-infant groups.

Studies on the motivational disposition of differentially-reared stump-tail juveniles (see table 27, chapter 7) would seem to support this finding. Thus in milk test situations (see chapter 5), peer-reared juveniles showed a significantly (χ^2 , significant at 0.001 level) higher frequency of dominance and submission than expected.

It would appear, then, that the emotional environment of peer-reared infants is excessively antagonistic compared with more normally reared infants. This aspect is borne in mind when examining the results of the DIMS study.

In retrospect, however, it can be said that the excessive concern of peer-reared infants with agonistic interactions proved to be a positive advantage in the DIMS study, since this study focused on manipulating agonistic dominance.

EXPERIMENTAL DESIGN

As previously mentioned, the overall design consisted of 3 distinct phases.

- 1) *social isolation phase* (8 days - 3.25 months)

2) *peer experience phase* (3.25 months - 14.5 months)

3) *group living phase* (14.5 months - 3 years)

1. Social isolation phase

In this phase, the infants were separated from their mothers at 8 days of age and placed in an incubator for 1 day. During this time, they were hand fed by a technician wearing a face mask to prevent facial signalling. They were also encouraged by the technician to self feed from a milk bottle.

At 9 days of age, the infants were moved from the incubator to individual wire cages in the nursery. They lived individually in these cages until they reached 14.5 months of age.

These "home" cages permitted visual and auditory access to the laboratory environment; but no visual or tactual access to any other monkey. Details of cage and incubator dimensions are given in table 12.

In both the incubator and home cage, milk was available *ad lib* throughout the day and overnight. The infants were given pieces of terry towelling (called "diapers" in these studies) for contact comfort (see figure 8) and were handled daily for weighing until 6 months of age.



Figure 8: Infant stumptail macaque with diaper
(photo by A. Chamove).



Figure 8: Infant stump-tail macaque with diaper
(photo by A. Chamove).

Table 12. Descriptive details of cages used in DIMS study (all measurements given in cms).

Cage	Dimensions	Description	Test situations
incubator	radius = 29.21	hemispherical; perspex	separation; prior move 1
nursery home cages			
A) white	h* = 68.58 b* = 53.34 c* = 60.96	cuboid wire cage) with removable) opaque perspex) sides)	all isolation-phase tests, except slides/calls
B) galvanized	h = 69.85 b = 67.31 d = 59.69	cuboid wire cage)))	slides/calls
blue test cage	h = 121.29 b = 71.76 d = 85.73	cuboid wire cage with removable perspex sides	slides/calls; stimulus animal tests
black test cage	see fig. 9	trapezoid	all tests with peers

*h = height; b = breadth; d = depth

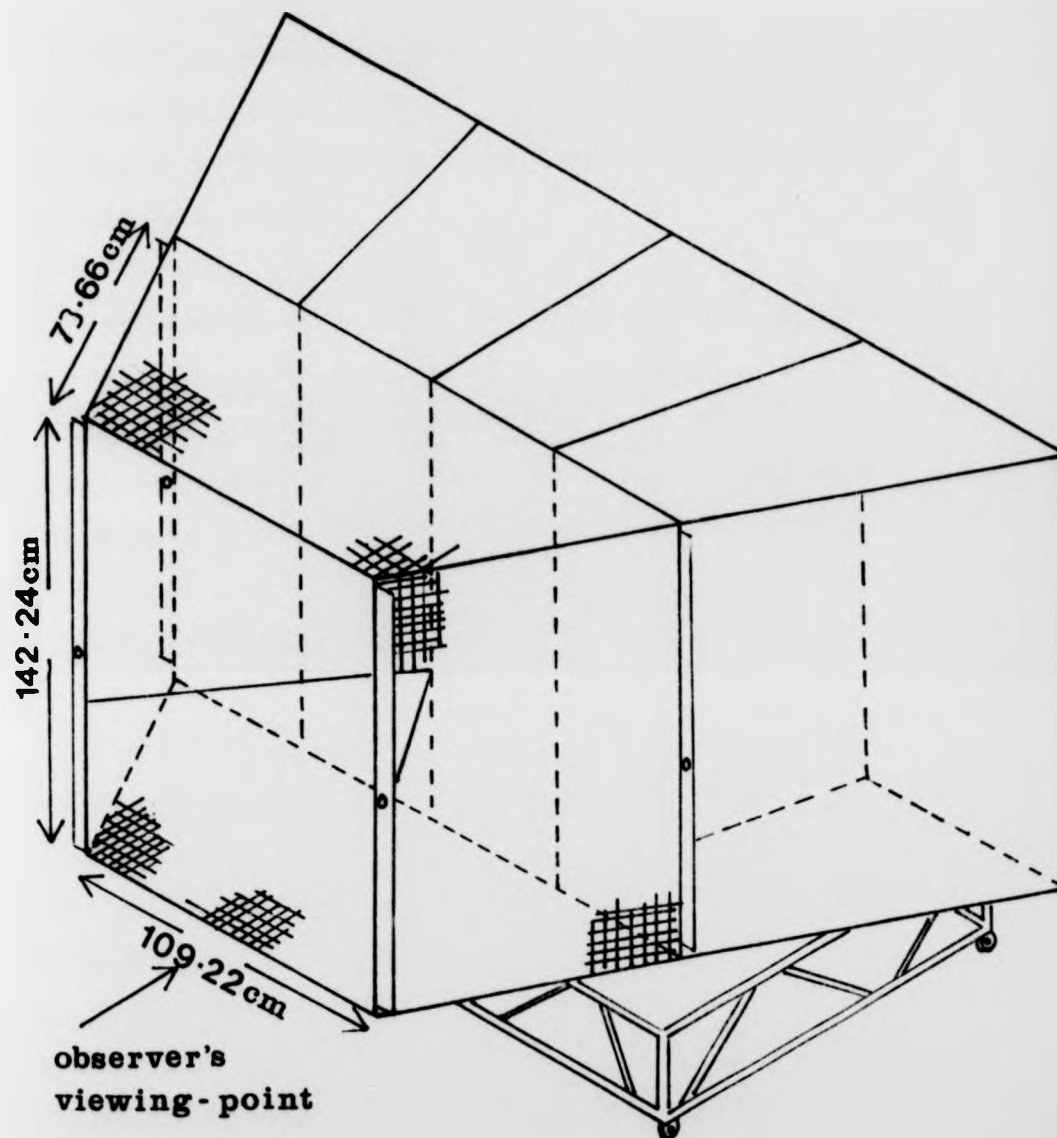


Figure 9. The black test cage. Only the front section was used for social tests (drawn by J. Russell).

Every effort was made to ensure that the infants were not unduly stressed in their home environment. Strangers/visitors to the laboratory were not permitted to enter the nursery.

Throughout this phase, the personality dispositions and the communicative abilities of the infants were measured in a variety of non social test situations. Details of the test situations are given in chapter 7, and details of the testing schedule in appendix VI.

2. Peer experience phase

At 3.25 months of age, each infant was given daily social experience in dyads or triads with its peers.

This daily peer experience was given either in the infants' nursery cages (modified by removing opaque partitions separating the individual cages), or in one of a variety of test cages, depending on the experimental schedule. Figure 9 and table 12 give details of cages.

The period of peer interaction was 1 hour per day for infants under 6 months of age, and 2 hours per day for those over 6 months. Diapers were always present in the cages with the infants: 3 diapers for dyads; 4 for triads.

Daily peer experience was experimentally controlled

so that each individual received only 1 type of dominance experience (Dominant, Intermediate, Mixed or Subordinate) from 3.25 months until 15 months of age.

Table 13 gives details of the assignment of infants to dominance experience conditions.

The aim, initially, was to have equal sex representation in all 4 conditions. This however was precluded by the uneven birth ratio. In addition, the poor birth rate in 1975 meant that the size of the experimental groups were smaller than expected.

MANIPULATION OF DOMINANCE EXPERIENCE

Only the sample of 13 infants, plus 1 stimulus infant, were involved in the manipulation of dominance experience.

The manipulation of dominance experience was achieved mainly by assigning individuals to different dominance conditions by age.

Thus, the 4 first born infants (regardless of personality or any other factors) were assigned to the dominant condition; the 3 last born to the subordinate condition; while the 6 mid born were assigned to either the intermediate or mixed condition.

Table 13. Assignment of individuals to dominance experience conditions in the DIMS study.

Name and birth order of individuals	Birth date (all 1975)	Sex	Dominance Experience
25	3rd April	F	
26	7th April	M	
27	20th April	F	Dominant
28	22nd April	M	
30	7th May	F	
31	18th May	M	Intermediate
36	3rd July	M	
29	27th April	F	
34	28th June	M	Mixed
35	2nd July	M	
33	18th June	F	
36	3rd July	M	Subordinate
38	8th August	M	
N.B. 37	7th July	M	Used as stimulus infant

It was hoped in this way to take advantage of some of the physical factors determining dominance rank (Koyama 1958) in order to ensure experimentally-appropriate dominance experience.

The first social experience of infants assigned to the dominant condition (i.e., D-gp) was with a stimulus infant of under 1 month of age. In theory, this ensured that the first social experiences of D-gp animals were as alpha animals.

By the time the other animals reached 3.25 months of age, D-gp animals had had fairly extensive experience as alpha individuals. This ensured that the other animals did not have the opportunity to be alpha when a D-gp animal was present in a given dyad or triad: they could however, be intermediate (I-gp) or omega (S-gp; M-gp). M-gp individuals had the opportunity to be alpha when no D-gp animals were included in a given dyad or triad.

Infants assigned to the same experimental condition were never allowed to interact together during the peer experience phase. In theory, however, they did have the opportunity to interact with all other infants in all possible dyadic and triadic combinations. In practice, the dyadic and triadic groups had to be confined to those where the participants allowed a given individual to experience its appropriate rank history.

A sample schedule for dyadic and triadic groupings is given in appendix VII. It will be noted that in order for I-gp infants to interact only as a midranking animal, all of their interactions had to take place in triads.

Throughout the peer experience phase, the behaviour of individuals in their various dyads/triads was sampled according to an experimental schedule. This enabled the developmental progression of the infants to be recorded.

Details of the sampling are given in table 14. However, due to limitations of time and space, the results of the developmental observations will not be reported until a later date. Here, the focus will be on the findings of tests given at the end of the peer experience phase, i.e., at 15 months of age.

Details of the tests given at 15 months are given in table 15.

3. Group-living phase

At 15 months of age, the subjects (now referred to as juveniles, see figure 10) were moved into the main primate colony.

They were assigned to 1 of 4 heterosexual groups - 2 triads; 2 tetrads - each of which was housed in a

Table 14. Sampling schedule for peer experience phase in the DIMS study.

Test	Age of testing (in months)	Situation
social test 1	3.5	a dyadic social test with either infant 26 or infant 37
next 14 days	3.25 - 4	14 dyadic or triadic tests with member(s) of appropriate group(s)
weeks 1, 2 and 3	4.25 4.5 4.75	dyad or triad with any member(s) of appropriate group(s)
test 4	5 - 5.25	dyad and triad with any member(s) of appropriate group(s); also competitive toy tests; competitive milk tests and competitive diaper tests in dyads
week 4	5.75	dyad or triad with any member(s) of appropriate group(s)
test 5	6.5 - 7.5	individuals assigned to dominant, subordinate and mixed groups were observed in all possible dyadic combinations; individuals assigned to the intermediate group were observed in a sample of 6 triads
test 6	7.5 - 9	6 triads for each individual were observed

Table 15. Tests given at 15 months of age in the DIMS study.

Test	Situation
slides and calls tests	<p>individuals were tested in 3 conditions a) slides alone; b) calls alone; c) slides and calls. Conditions given on consecutive days. Detailed description is given in chapter 5.</p>
stimulus animal tests	<p>individuals put in a cage with an unfamiliar stimulus animal. Each individual was tested with 5 different stimulus animals. These included</p> <ul style="list-style-type: none"> a) 3 year old peer-reared female (number 5 from group 2; see chapter 3). b) 2.5 year old social-reared female (number 22 from group 5). c) 2.5 year old social-reared male (number 20 from a group in the breeding colony). d) an adult feral female (kid from the feral group; chapter 3). e) an adult feral male (Angus from the feral group; chapter 3).



Figure 10. A juvenile stump-tail macaque (number 30).
(Photo by G. Cameron).



Figure 10. A juvenile stump-tail macaque (number 30).
(Photo by G. Cameron).

separate section of colony caging.

The composition of these groups was arranged so as to maintain, as far as possible, the previous rank history of individuals. Thus each group consisted of 1 animal from the D-gp, 1 from the I-gp, and 1 from the M-gp and/or S-gp. Individuals from the M-gp became midranking animals in this phase.

Two types of test situation were employed in this phase. The first consisted of grouping together in triads, individuals of similar rank experience, who had never previously interacted together. This situation was used to examine the dominance strategy behaviour of juvenile stumptail macaques and is reported in Walker Leonard (1979).

The second test situation consisted of firstly, grouping together all the females in one group then introducing the males individually to the group and secondly, grouping together all the males in one group then introducing the females individually to the group. This was used to compare the behaviour of different individuals in a similar social situation. The findings will be reported in a later paper and not in this thesis.

MAIN AIMS

It can be seen that although the experimental design

resulted in a fairly comprehensive coverage of the infant's behavioural development, it provided too much data to be reported in a single thesis.

Thus, in the present thesis, the focus is solely on identifying and examining some of the sources of behavioural differences among individuals. The details of developmental progression, and investigation of how the sources of development produce the observed differences in behaviour, will be examined at a later date. However, some hypotheses about the mechanisms involved will be discussed in chapter 10.

In this thesis, then, the main aims were:

- 1) to examine the communicative abilities of socially isolated stumptail macaques, i.e., to examine the importance of innate factors in the development of social communication.
- 2) to examine the personality characteristics of infant and juvenile stumptail macaques, and investigate whether early personality dispositions were predictive of later personality characteristics.
- 3) to examine whether specific dominance experiences had specific effects on the development of social communication or on the development of personality characteristics.

CHAPTER SEVEN

The communicative abilities of socially deprived stumptail macaques.

Communicative behaviour was selected as the dependent variable in the DIMS studies. Emphasis was placed specifically on this aspect of social behaviour for several reasons:

Firstly, it was selected because adequate social interaction depends on processes of communication (Menzel 1973), and secondly, because it implies focusing on fairly molecular units of behaviour, i.e., specific communicative signals, rather than more compound units like aggression, play, and so on.

Compound scores like aggression etc., have several disadvantages: they depend too heavily on value judgements by the investigator; they are motivationally heterogeneous (e.g., aggressive behaviour may be shown in a variety of contexts where the predominant underlying motivation may not be aggression); finally, they are virtually impossible to use for comparative purposes (Hinde 1971).

The more molecular units involved in a communication analysis of social behaviour, on the other hand, have

several advantages. For example, they may be classified objectively according to the specific motor patterns involved (see Van Hoof 1962). Furthermore, measures of such units may be combined in various ways to provide higher-order analyses of behaviour; and it is much better practice to split and then lump measures, than to lump from the beginning and then discover that the unrecorded finer discriminations were probably the more crucial ones.

A third reason for choosing communication as the dependent variable was that a communication analysis of social behaviour has underlying conceptions about the nature of primate social behaviour which tie in with the general emphasis of this investigation. Thus investigators interested in social communication emphasize the dynamic interactional nature of the phenomena involved (see for example, Simpson 1972).

Fourthly, primate non-verbal communication and animal communication in general has received a great deal of attention in the recent literature. However, while the literature has provided much information on the characteristics, functions and determinants of primate non-verbal communication, it has also highlighted many areas which still need to be examined (see Hinde 1972; Marler 1965; Redican 1974; Simpson 1972). It was hoped that by focusing on communication that this study would make some contribution to this field of knowledge.

In the next section, a brief review of the primate communication literature is presented in order to illustrate some of the problems encountered in the study of social communication in primates, and also to show how the present study fits into this general body of knowledge. More extensive reviews may be found in Altmann 1967; Chevalier-Skolnikoff 1973; Marler 1965; Redican 1974.

THE STUDY OF NON VERBAL COMMUNICATION IN THE
NONHUMAN PRIMATE LITERATURE

1. Definitions

In the literature, the problem of defining communication is an aspect which has received much debate. Among the definitions which have been offered are the following:

Sheflen (1964): communication includes all behaviours by which a group forms, sustains, mediates, corrects and intergrates its relationships. In the flow of an interaction, communicative behaviours serve to give continual notification of the states of each participant and of the relationships between them.

Altmann (1967): communication is the process by which the behaviour of an individual affects the

behaviour of others, i.e., changes the probability distribution of the behaviour of others. In looking at communication, we are dealing with contingencies among sequences of events between individuals.

Ploog and Melchenuk (1969): communication is concerned with the elicitation of discriminant responses to non verbal stimuli.

Von Cranach and Vine (1973): a prerequisite of true communication is the existence and operation of a common conventional code, thus communication may be defined as the conventional interchange of messages between individuals in an interaction.

Klopper (1967): communication necessitates the existence of a code shared between two or more individuals whose use is mutually beneficial to its possessors.

As Hinde (1972) points out, the diversity of definitions in the literature may be seen as reflecting the different orientations of the various investigators. Hinde (1972) distinguishes three different orientations in the literature. Firstly, there is the sociobiologist, who is interested in the bases of social organization; secondly, there is the information theorist, who is interested in communication from the point of view of exchange of bits of information; thirdly, there is the

evolutionist, who is interested in behaviour which appears to have become adapted in evolution for a signal function.

Each different orientation results in an interest in slightly different aspects of communication, hence the different emphases placed in definitions of communication.

Primate communication has been studied from a variety of orientations, resulting in the collection of information on many of the characteristics of this behaviour, but here we will focus only on those aspects of primate communication of specific relevance to the present investigation.

In this investigation, communication was defined as the conventional interchange of messages among individuals in an interaction (von Cranach and Vine 1973). In this view, communication depends on the existence and operation of a common conventional code, although this code need not necessarily have been adapted in evolution for a signal function.

Communication codes for various primate species have been described in the literature (for stumptail macaques see Bertrand 1969; Chevalier-Skolnikoff 1974).

2. Methodological problems

Identifying, describing and determining the meaning of the signals involved in communication codes have all presented specific methodological problems for the investigator.

Some of the problems are general ones, encountered in the study of any behaviour in any species. These include the problem of categorizing units in the naturally occurring stream of behaviour; and secondly, the problem of classifying these units according to a useful theoretical scheme.

Other problems are specific to the study of communication. These include the problem of determining whether a specific behaviour pattern is in fact a communication signal, and if it is, what its meaning is for the individuals concerned.

Both sets of problems have been extensively discussed in the literature: the solutions to the problems varying with the interests of the investigator.

Typically, investigators interested in describing the communicative repertoire of a specific primate species have tended to use subjective judgements about what constitutes signalling behaviour (Marler 1965). They have

tended to split up the stream of behaviour into what intuitively seems to be natural communicative units.

As Jolly (1972) comments, at first sight, the units of communication do in fact seem to be "naturally" given. Thus most vocalizations have a beginning and an end; most facial expressions appear as transitory changes, with a "relaxed face" before and after.

In the literature, classification of the signals in communication catalogues has tended to be on the basis of the form of the signal, rather than according to presumed underlying motivation or function. The latter two aspects are probably preferably deduced from empirical analyses of the total context in which a signal appears.

This morphological classification has resulted in much greater advances for the study of nonhuman primate communication compared with the early research on human nonverbal communication which was plagued with classifications according to motivation and/or function (Blurton-Jones 1972; Charlesworth and Kreutzer 1973).

Morphological classification is not, however, without its problems: the very nature of primate communicative behaviour presents several difficulties which must be dealt with.

One striking aspect of primate displays is that few are clearcut: most grade into each other (Jolly 1972), Rowell (1962), for example, pointed out that the agonistic vocalizations of rhesus monkeys form a continuum, and although one can pick out certain modal grunts and barks, there tend to be intermediates between each of the main types.

Chevalier-Skolnikoff (1973) further points out that, not only does there tend to be gradation within a particular class of signal, but also that continua of expressions appear to occur between different affect or emotional states. Thus one can observe expressions which may be classified as representing gradations on a scale from fear to anger, with various degrees or "blends" of fear-anger in between.

Facial expressions also tend to convey degree of emotional intensity. For example, a dominant male stumptail macaque may show in sequence: a "stare" threat; a stare threat with ears flicking forward and raising and lowering of the eyebrows; an "open-mouth" threat; a "round mouth" threat; as he becomes increasingly angry (Chevalier-Skolnikoff 1973 p 26).

A further problem in classifying primate communication signals is that many communicative displays rely on multi-channel expression. Thus, in stumptails, a "round mouth"

threat may be accompanied by a "huh" vocalization and a lunge forward from the threatening monkey. In theory, each channel may vary independently thus altering the message sent.

As Jolly (1972) comments, the very intergradations and variability of primate signals, shows that in primate social life it is important to communicate the nuances of feeling with a certain subtlety.

The early ethologists were partly saved from this type of complexity by the apparent rigidity and stereotypy of most fish and bird displays. It is not until the evolution of the higher mammals that complex systems of facial musculature developed which permit minute variations in expressions to be made.

In the primate literature, this complexity has tended to be dealt with by the use of frame by frame analysis of video or film records, or by spectrographic analysis of audio records.

For analysis of video film, check sheets tend to be used, which record information about body posture; state of the eyes (i.e., open, closed, staring, averted etc); position of the eyebrows, ears, mouth; concurrent vocalizations; and details of the situation or context in which the behaviour occurred (Chevalier-Skolnikoff 1974).

Such detailed description has resulted in the observation that there are certain modal compound expressions which are species-typical. These modal expressions tell us what it is important to communicate clearly in the species observed; and are extremely useful for the beginning analysis of the communicative behaviour of any particular species.

Once a catalogue of such modal expressions is achieved for any particular species, the next step is to discover whether particular expressions do indeed serve a communicative function.

The clue to the occurrence of communication is a change in the behaviour of the receiver on perceiving the signal of the sender (Altmann 1967; Marler 1965).

This can be determined either experimentally (see for example, Miller, Caul and Mirsky 1967), or statistically, i.e., from analysis of the sequential dependencies between behaviours of individuals (see for example, Maurus, Kuhlmann, Hartman-Wiesner and Pruscha 1975).

Again, however, things are not quite as simple as one might hope. For example, there are problems connected with the possibility of imperceptible responses, delayed responses, response interruption etc., (see Simpson 1972).

In theory, some of these problems should be surmounted by detailed classification procedures, the use of permanent records for detailed analyses, and also by the use of various time spans for analysis such that delayed responses, for example, may be included in the analysis.

In addition to determining whether particular expressions serve a communicative function, surface correlations between signals and responses also provide information on the communicative meaning of a given signal for the particular individuals involved. And from correlations between signals and responses of particular individuals, we can abstract the modal communicative meaning for a particular group or species.

3. Causal determinants

Once a communicative catalogue has been established for a particular species, we may then ask questions about the causal determinants of signals.

In primate species, communicative expressions are likely to be determined by any or all of an array of interacting factors (Chevalier-Skolnikoff 1973). These may be classified as follows:

1. *immediate determinants*, i.e., environmental stimuli,

the nervous system and its activity, the hormonal system

2. *ontogenetic determinants*, i.e., the previous experience and genetic potential of the individual
3. *evolutionary determinants*, i.e., selection pressures influencing the genetic makeup of the species.

Here we will focus on the literature investigating the ontogenetic determinants of communicative behaviours.

THE ONTOGENETIC DETERMINANTS OF PRIMATE COMMUNICATIVE BEHAVIOURS

Possible ontogenetic determinants include all those factors which may be conveniently classified as either genetic predispositions or experiential factors.

As with the study of social behaviour in general (see chapter 1), it may be argued that the causal determinants of communicative behaviour may be profitably investigated by means of the deprivation technique. This approach, although it may be criticised on several grounds, should provide information on where gross level factors may be involved in the communication system.

Unfortunately, despite the extensive studies on

experientially deprived rhesus monkeys, very few have focused specifically on the details of communicative behaviour; most appear to have been interested in social behaviour at a more global level.

The few studies which have reported findings on communicative behaviour have suggested that while socially-isolated rhesus monkeys appear to be capable of displaying certain of the species-typical modal signals, e.g., grimace (Evans 1967; Miller, Caul and Mirsky 1967; Sackett 1965); threat (Mitchell and Clark 1968, Sackett 1965); clear calls (Newman and Symmes 1974); crouching (Green 1965); lipsmacking (Cross and Harlow 1965), these tend to be displayed in inappropriate situations or directed towards the self (Miller, Caul and Mirsky 1967; Sackett *et al* 1976).

Newman and Symmes (1974) have further suggested that the actual form of a specific communicative signal may vary with social experience. Thus they report that isolation reared rhesus show various abnormalities in their clear calls compared with more normally reared rhesus. They conclude that adequate manifestation of this call may be dependent on adequate social experience.

It may be, however, that this particular class of vocalization (i.e., contact calls in general) can be varied voluntarily, or that the observed differences are due to other factors, like individuality (Lillihei and

Snowden 1977).

Further findings suggest that social experience does not appear to be essential for a rhesus monkey to recognize some of the species - typical communicative expressions (e.g., threat: Sackett 1966), but it may be essential for the recognition of others (e.g., fear expressions: Miller, Caul and Mirsky 1967; Sackett 1966).

Mason (1965) has concluded that these general findings *suggest* that while for many communicative behaviours, the relation between affective state and the form of a particular signal is independent of social experience, the connection of signals with specific eliciting stimuli, their contextual relevance, and their effectiveness in controlling and co-ordinating social behaviour, are heavily dependent on social experience.

The relevant literature is, however, too piecemeal and too scanty, and the deprivation technique, as used in the early Wisconsin experiments, is too fraught with methodological problems, for any conclusive statements to be made.

What is needed are studies which examine in detail the communicative abilities of socially-deprived primates, and systematically compares these with the abilities of more normally reared individuals at similar ages.

This was done in the present series of studies and the findings are reported in the remainder of this chapter.

GENERAL METHOD

Three major samples were observed.

1. the sample of thirteen infant stumptail macaques used in the DIMS study (details given in chapter 6)
2. five groups of differentially reared juvenile stumptails used in studies of dominance and personality (details given in chapters 3 and 5)
3. one group of feral adult stumptails used for breeding purposes in the main primate colony at Stirling.

STUDY 1

The communicative abilities of socially deprived infant stumptail macaques (<3 months of age).

GENERAL METHOD

Subjects: 13 infant stumptails were observed; 7 males and 6 females with an age range of 4 months.

Details of the name of the infant, its mother, date of birth and sex are given in table 16.

Early experience (8 days to 3 months): Individuals were separated from their mothers at 8 days of age and placed in an incubator for 1 day.

At 9 days of age, they were moved from the incubator to individual wire cages in the nursery. These cages permitted visual and auditory access to the laboratory environment, but no visual or tactual access to any other monkey. Details of caging are given in figure 9 and table 12, chapter 6.

Milk was available *ad lib* throughout the day and overnight. Diapers were always available for contact comfort and infants were handled daily for weighing.

Social experience was not given until the infants reached 3 months of age.

A) NON-SOCIAL TESTS

METHOD

Test situations: A variety of nonsocial test situations were employed throughout the 3 month early social isolation phase in order to assess both the communicative

Table 16. Date of birth, sex and mother of infants observed in DIMS study.

Name and birth order of infant	sex	date of birth (all 1978)	mother
25	F	3:4	Mae West
26	M	7:4	Sexy
27	F	20:4	Ghost
28	M	22:4	Black Scruff
29	F	27:4	Red Glutton
30	F	7:5	Brown Glutton
31	M	18:5	Barelegs
32	F	27:5	Bangla
33	F	18:6	Black Dwarf
34	M	28:6	Buttons
35	M	2:7	Monk
36	M	3:7	Red legs
38	M	8:8	Double Cross

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30	F	7:5	Brown Glutton
31	M	18:5	Barelegs
32	F	27:5	Bangla
33	F	18:6	Black Dwarf
34	M	28:6	Buttons
35	M	2:7	Monk
36	M	3:7	Red legs
38	M	8:8	Double Cross

abilities of the infants and their early personality characteristics. Only data on communicative abilities is presented here; data on early personality characteristics is given in chapter 8.

Details of the test situations are given in table 17. The testing schedule is given in appendix VI.

Data collection: All observations took place between 11.00 hours and 12 noon on Monday through Saturday, from 11th April to 3rd November, 1975. The observer sat in full view of the infants.

Data were collected by means of a handwritten symbol notation method (appendix I) which gave details of the true frequency and sequential patterning of communicative signals of individuals as they responded to the test stimuli. A sample data sheet is given in appendix VIII.

The advantages of the symbol notation method include: flexibility, i.e., new behaviours may be added as they occur; and quietness, i.e., infants were not disturbed by noisy apparatus.

Data was collected for 5 minutes from first presentation of the stimulus object in food tests, diaper tests, etc. In slides and calls tests, data was collected for 1 minute from first presentation of each slide/call stimulus.

Table 17. Non social test situations used in 3 month early social isolation phase of DIMS study.

General parameters	Test name	Age of testing	Description of test
Novel/familiar environments	1. Separation (S)	8 days	Infant taken from mother, wrapped in towelling and placed in an incubator
	2. Prior move 1 (PML)	9 days	Infant observed while in incubator
	3. Environment 1 (E1)	9 days	Infant taken from incubator and placed with diapers in a nursery wire cage
Deprivation of nurturant objects	1. Given diapers 1 (GD1)	29 days (1 month)	Infant given diaper after having been deprived of diapers for $\frac{1}{2}$ hour prior to testing
	2. Given milk 1 (GML)	35 days (5 wks)	Infant given milk after having been deprived of milk for 2 hours prior to testing
	3. Frustration food 1 (FF1)	36 days (5 wks)	Infant given empty milk bottle after having been deprived of milk for 2 hours prior to testing

Table 17 contd.

General parameters	Test name	Age of testing	Description of test
Deprivation of nurturant objects (contd)	4. Given milk 2 (GM2)	55 days (2 months)	Infant given milk after having been deprived of milk for 2 hours prior to testing
	5. Frustration food 2 (FF2)	57 days (2 months)	Infant given empty milk bottle after having been deprived of milk for 2 hours prior to testing
	6. Given diapers 2 (GD2)	64 days (9 wks)	Infant given diapers after having been deprived of diapers $\frac{1}{2}$ hour to testing
Presentation of novel objects	1. Toy 1 (T1)	40 days (6 wks)	An empty milk bottle was placed on the floor of the infant's cage
	2. Toy 2 (T2)	47 days (7 wks)	The milk bottle was removed from the infant's cage on the day prior to testing. On testing a rubber pet toy was placed on the floor of

Table 17 contd.

General parameters	Test name	Age of testing	Description of test
Presentation of novel objects (contd)	2. Toy 2 (T2) (contd)		the infant's cage
	3. Toy test 2 (TT)	54 - 61 days (2 months)	A series of toy tests was given where the toy presented to the infant was one of a series that differed in varying degrees of novelty from Toy 2. Further details are given in table 18.
Presentation of slides and calls of modal communicative expressions of stump-tail macaques	1. Slides Alone (SA)	85 days (3 months)	Details given in table 10 and figure 5, chapter 5.
	2. Calls Alone (CA)	86 days	
	3. Slides and calls (S+C)	87 days	

Table 18. Objects used in toy tests.

Test name	Object(s)
Toy 1 (Ty 1)	Empty plastic milk bottle
Toy 2 (Ty 2)	<p>A rubber pet toy, randomly selected from a set of 7. These included</p> <ol style="list-style-type: none"> 1) blue bone 2) small blue ring 3) large blue ring 4) red ball 5) large red ring 6) orange ball 7) small orange ring <p>These toys were of the type normally supplied by UK pet shops for dogs (see figure 11).</p>
Toy Test 1 (TT1)	<p>All of the pet toys, presented in random order on subsequent test days. These tests were labelled TTA to TTF, depending on degree of familiarity of the presented toy to that given as toy 2 above.</p> <p>Thus TTA = same toy TTB = same shape and size TTC = same colour TTD = same shape TTE = completely different TTF = same colour and shape</p>



Figure 11. A juvenile stump-tail macaque (number 27) with one of the pet toys (large rubber ring) used in TT series. Milk bottle toy shown in foreground.



Figure 11. A juvenile stump-tailed macaque (number 27) with one of the pet toys (large rubber ring) used in TT series. Milk bottle toy shown in foreground.

B) SOCIAL TESTS

METHOD

Test situations: At 3 months of age, each individual was given its first social experience in a dyad.

This experience was either with infant 26 (dominant male) or infant 37 (subordinate male) depending on the experimental condition to which the infant had been assigned. Details are given in table 19.

From the table, it can be seen that this resulted in the testing of 3 month old socially naive infants with partners of various ages, 2 weeks; 1 month; 4 months; 4.5 months; 5 months; 6 months and 7 months.

Infants were tested in the black test cage (fig.9,c hp. 6) and had access to diapers throughout the test situation but no access to milk or toys.

Data collection: All observations took place between 1300 and 1400 hours, Monday through Saturday, from 8th July to 4th November, 1975. The observer sat in full view of the infants.

Data were collected by means of a keyboard event recording system referred to as the DTU. This system

Table 19. First social test of DIMS infants at 3 months of age.

Subject	Experimental Condition	Partner	Partner's age at testing
25	Dominant (D)	37	2 weeks
26		37	2 weeks
27		37	1 month
28		27	1 month
30	Intermediate (I)	26	4 months
31		26	4.5 months
36		26	6 months
29	Mixed (M)	26	4 months
34		26	6 months
35		26	6 months
32	Subordinate (S)	26	5 months
33		26	6 months
38		26	7.5 months

encodes behaviour patterns of interest and the time at which they occurred as numeric entries on paper tape. This general technique can provide information on the duration, frequency and sequential patterning of behaviour which may subsequently be computer analyzed.

In the dyadic social test, a complete record of the ongoing behaviour and direction of this behaviour for both the subject and its partner in a 40 minute test session was obtained.

Appendix III gives the classification of behaviours for recording by DTU. Appendix IX gives a sample print out of the raw data record.

RESULTS

1. Age of first occurrence of modal compound communicative behaviours in socially deprived infant stump-tail macaques.

Details of the age of first occurrence of the compound communicative behaviours recorded in this study are presented in Appendix X.

Table 20 gives details of the median age and range of these first occurrences.

Table 20. Median age of first occurrence of compound communicative signals in socially-deprived infant stump-tail macaques.

Behaviour	Total number of infants exhibiting behaviour	Earliest first occurrence	Latest first occurrence	Median age of first occurrence
<u>submission</u>				
still	11	2 months	3 months	3 months
present	9	3 months	3 months	3 months
teeth chatter	13	9 days	3 months	6 weeks
grimace	12	6 weeks	3 months	3 months
withdraw	13	5 weeks	3 months	6 weeks
freeze	8	3 months	3 months	3 months
jerk	13	8 days	5 weeks	8 days
<u>play</u>				
bounce	10	2 months	3 months	3 months
play initiate*	11	3 months	3 months	3 months
sprawl	5	3 months	3 months	3 months
open mouth	13	2 months	3 months	3 months
chasing*	9	3 months	3 months	3 months
wrestling*	8	3 months	3 months	3 months
open mouth bite*	8	3 months	3 months	3 months
general	12	9 days	3 months	2 months
<u>dominance</u>				
bounce	7	2 months	3 months	3 months
mount	3	3 months	3 months	3 months
yawn	7	5 weeks	3 months	2 months
teeth chomp	7	3 months	3 months	3 months
brow threat	5	9 days	3 months	3 months
open mouth threat	6	5 weeks	3 months	2-3 months
teeth chatter threat	6	2 months	3 months	3 months
scream threat	1	3 months	3 months	3 months
chase*	1	3 months	3 months	3 months
grab/hit	7	5 weeks	3 months	3 months

Table 20 contd.

Behaviour	Total number of infants exhibiting behaviour	Earliest first occurrence	Latest first occurrence	Median age of first occurrence
<u>dominance (contd)</u>				
bite	9	5 weeks	3 months	3 months
<u>affiliation</u>				
groom*	6	3 months	3 months	3 months
present for groom*	1	3 months	3 months	3 months
lipsmack/pout	13	8 days	5 weeks	9 days
square mouth	12	8 days	3 months	3 months
huddle*	12	3 months	3 months	3 months
mouth nibble*	2	3 months	3 months	3 months
<u>sex</u>				
anogenital	8	3 months	3 months	3 months
inspection*	2	3 months	3 months	3 months
mount				
masturbate	12	5 weeks	3 months	2 months
<u>vocalizations</u>				
scream	13	8 days	9 days	8 days
gurgle	13	9 days	3 months	6 weeks
trill/whinney	11	8 days	3 months	8 days
cack/cackle	12	8 days	3 months	9 days-1 mth
whistle	13	8 days	3 months	5 weeks
cheep/squeek	13	8 days	3 months	9 days
bitey	8	8 days	3 months	2 months
<u>other expressions</u>				
tongue protrude	13	8 days	2 months	9 days
open mouth	12	8 days	5 weeks	8-9 days
self huddle	13	1 month	3 months	2 months
follow*	5	3 months	3 months	3 months
approach	13	1 month	5 weeks	5 weeks
self aggression	7	5 weeks	3 months	7 weeks

* behaviours which require a social partner for expression.

Column 2 of this table (earliest first occurrence) may be thought of as demonstrating the communicative competence of socially deprived infant stump-tails at different developmental ages.

Thus at 8 - 9 days of age, it can be seen that socially deprived stump-tail infants are theoretically capable of exhibiting the following communicative behaviours:

1. *submission* - teeth chatter, jerk
2. *play* - general play
3. *dominance* - brow threat
4. *affiliation* - lipsmack/pout
5. *vocalizations* - all vocalizations recorded in this study.
6. *others* - open mouth

By 1 month, they are capable of withdraw, yawn, open mouth threat, grab, hit, bite, self aggression and masturbation.

By 6 weeks, they are also capable of grimace.

By 2 months, they also show still, play bounce, dominance bounce and teeth chatter threat behaviours.

At 3 months, they are capable of showing all of the compound communicative expressions recorded in this study.

Discussion of this section

Chevalier-Skolnikoff (1973) also looked at the age of first appearance of communicative behaviours in infant stump-tails. Her study focused on normative development in three group-raised infants.

The DIMS study was concerned with drawing out the communicative competence of infants, rather than documenting naturalistic development.

If the results of the two studies are compared, it is found that a greater variety of compound communicative expressions are exhibited, at earlier ages, in the DIMS study.

For example, by day 9, infants in this study had exhibited teeth-chatter, general play, brow threat, gurgle, trill/whinney, whistle, and bite behaviours - none of which had made an appearance in Chevalier-Skolnikoff's animals at this age.

The earlier occurrences in this study compared to Chevalier-Skolnikoff's (1973) study are probably due to

differences in sample size (3 vs. 13) as well as differences in method (naturalistic vs. experimental intervention).

The finding that by 3 months of age, these socially deprived infants were capable of showing all of the compound communication expressions recorded in this study, suggests that the ability to exhibit these particular expressions does not depend on social learning mechanisms.

Rather, it seems reasonable to think of the infants as having certain communicative competences which may be demonstrated if the stimulus conditions are appropriate for the specific individual concerned.

2. Efficiency of test situations in eliciting the first occurrence of communicative behaviours.

Appendix XI gives details of the test situations in which the various communicative behaviours first occurred for each of the infants observed.

Table 21 gives details of the test situations which were most frequently effective in eliciting the first occurrence of particular behaviours.

From this table, it can be seen that separation

Table 21. Range of test situations in which compound communicative expressions first occurred in DIMS study.

Behaviour	Range of test situations in which first occurred	Modal situation	Comments on first occurrences
<u>submission</u>			
still	TT, SA, ST1	ST1	first social test
present	SA, ST1, ST2	ST1	common also in slides alone tests
teeth chatter	EL, GDL, T1, T2, TT, SA	TT	common especially in Toy tests where toy very novel
grimace	T1, T2, SA, CA, S+C, ST1, ST2	S+C	most common in slide/calls battery of tests
withdraw	GM1, GM2, FF1, T1, CA, ST1	TL/FF1	first toy test; frustration food test
freeze	SA, CA, S+C, ST1	S+C	most common in slide/calls battery of tests
jerk	S, PML, EL, GDL, GM1	S	separation from mother
<u>play</u>			
bounce	TT, ST1, ST2	ST1	first social test
play initiate*	ST1, ST2	ST1	first social test
sprawl	ST1, ST2	ST1	first social test
open mouth	TT, ST1, ST2	TT/ST1	common in toy tests where toy fairly familiar
chasing*	ST1, ST2	ST1	first social test
wrestling*	ST1, ST2	ST1	first social test
open mouth bite*	ST1, ST2	ST1	first social test
general	PML, GM1, GM2, T2, TT, SA, CA	GM/TT	most common when infant given milk after milk deprivation and when given a familiar toy

Table 21 contd.

Behaviour	Range of test situations in which first occurred	Modal situation	Comments on first occurrence
<u>dominance</u>			
bounce	GM2, SA, ST1, ST2	ST1	first social test
mount	ST2	ST2	second social test
yawn	FF1, T1, T2, TT, CA, ST2	TT	most common in toy tests with very novel toy
teeth chomp	CA, S+C, ST1, ST2	ST2	second social test
brow threat	E1, T2, ST1	ST1	first social test
open mouth threat	FF1, GM2, T2, ST1, ST1	ST1	first social test
teeth chatter threat	FF2, SA, ST2	SA	slides alone test
scream threat	ST1	ST1	first social test
chase*	ST2	ST2	second social test
grab/hit	FF1, ST1, ST2	ST1	first social test
bite	FF1, T2, ST1, ST2	ST1/FF1	common in first social test and also first frustration food test
<u>affiliation</u>			
groom*	ST1, ST2	ST1/ST2	first and second social tests
present for groom*	ST2	ST2	second social test

Table 21 contd.

Behaviour	Range of test situations in which first occurred	Modal situation	Comments on first occurrence
<u>affiliation</u> (contd)			
lipsmack/pout	S, PML, E1, GD1, GM1	S	separation from mother
square mouth	S, E1, SA, CA, S+C	SA	most common in slides/calls battery of tests
huddle*	ST1, ST2	ST1/ST2	first and second social tests
mouth nibble*	ST2	ST2	second social test
<u>sex</u>			
anogenital inspection*	ST1, ST2	ST2	second social test
mount	ST1, ST2	ST2	second social test
masturbate	GM1, T1, T2, FF2, TT, SA, CA, ST2	SA/T	common in slides alone test and toy tests where toy is very novel
<u>vocalizations</u>			
scream	S, E1	S	separation from mother
gurgle	E1, GD1, GM1, FF1, T1, T2, TT, SA	T/GM1	common in toy tests where toy very novel and in tests where infant given milk after milk deprivation
trill/whinney	S, PML, GM1, FF1, SA	S	separation from mother
cack/cackle	S, E1, GD1, GM2, FF1, S+C	S	separation from mother

Table 21 contd.

Behaviour	Range of test situations in which first occurred	Modal situation	Comments on first occurrence
<u>vocalizations (contd)</u>			
whistle	S, PML, E1, GM1, FF1, T1, GM2, SA	GM	most common in tests where infant given milk after milk deprivation
cheep/squeek	S, PML, GDL, GM1, TT, SA	S/PML	separation from mother/tested prior to moving from incubator to wire cage
bitey	S, GM1, FF1, GM2, TT, SA, S+C	GM	most common in tests where infant given milk after milk deprivation
<u>other expressions</u>			
tongue protrude	S, PML, E1, GM1, T2, GM2	GM	most common in tests where infant given milk after milk deprivation
open mouth	S, PML, E1, GDL, GM1	S	separation from mother; also common in tests where infant given diaper after diaper deprivation
self huddle	GDL, FF1, T2, GM2, FF2, TT, SA	SA	most common in slides alone tests
follow*	ST1, ST2	ST2	second social test
approach	GDL, GM1	GM1	first test where infant given milk after milk deprivation
self aggression	FF1, T1, T2, FF2, ST2	T/FF	common in toy tests where toy very novel and also frustration food tests.

*Behaviours which require a social partner for expression

Table 21 contd.

KEY	
S	= Separation
PM1	= Prior move 1
E1	= Environment 1
GDL/2	= Given diapers 1/2
GML/2	= Given milk 1/2
FFL/2	= Frustration food 1/2
T1	= Toy 1
T2	= Toy 2
TT	= Toy test 2 (A to F)
STL/2	= Social test 1/2

from the mother at 8 days of age tended to elicit the following behaviours:

1. *submission* - jerk
2. *affiliation* - lipsmack
3. *vocalizations* - scream; trill/whinney; cheep/squeak; cack/cackle
4. *others* - open mouth.

Tests where the infant was observed in the incubator at 9 days tended to elicit cheep/squeak vocalizations.

Tests where the infant was given a diaper, after being diaper deprived, tended to elicit open mouth behaviour.

Tests where the infant was given milk, after having been deprived of milk for 2 hours prior to testing, elicited the following:

1. *play* - general play
2. *vocalizations* - gurgle; whistle; bitey
3. *others* - tongue protrude; approach.

Frustration food tests, where the infant was given an empty milk bottle after having been deprived of milk for 2 hours, elicited the first occurrences of withdraw, bite and self aggression.

Tests where the infant was presented with a very novel object (i.e., T1, T2, TTC, TTD, TTE) were commonly effective in eliciting teeth chatter, withdraw, yawn, self aggression, masturbate and gurgle behaviour.

Toy tests where the object presented to the infant was fairly familiar (i.e., TTA, TTB) were effective in eliciting open mouth play face and general play behaviour.

The slides/calls battery of tests were most effective in eliciting the following behaviours.

1. slides alone (SA) - present; teeth chatter threat; square mouth; masturbate; self huddle
2. slides and calls (S+C) - grimace; freeze.

Behaviours which by definition require a social partner for expression were first elicited in the social tests. These behaviours included play initiate, play chase, play wrestle, play open mouth bite, dominance chase, groom, present for groom, huddle, mouth nibble, anogenital inspect and follow.

Other behaviours which these tests also first elicited included still, present, play bounce, play sprawl, open mouth play face, dominance bounce, brow threat, open mouth threat, scream threat, grab, hit, bite (all elicited in first social test); dominance mount, teeth chomp, sexual mount (all elicited in second social test).

DISCUSSION OF EFFECTIVENESS OF TEST SITUATIONS

These results point to the importance of the immediate environmental stimulus conditions in eliciting particular behaviours.

Thus, for example, tests where the infant is presented with a very novel object tend to elicit first occurrences of teeth-chatter, withdraw, yawn, self aggression, masturbate and gurgle behaviour. Tests where the infant is presented with a relatively familiar object, on the other hand, tend to elicit first occurrences of open mouth play face and general play behaviour.

These findings suggest that in order to investigate the age at which infants are first capable of exhibiting a particular behaviour, e.g., open mouth play face, it is necessary to test them in a situation which readily elicits this behaviour, e.g., a familiar object test, at various developmental ages.

These findings also give us some idea of the meaning of a particular communication behaviour of these infants: if we examine the environmental context for the first occurrence of each behaviour, we find that the infants' communicative responses tend to be connected with seemingly appropriate contexts.

Thus frustration food tests tend to elicit withdraw, bite and self aggression. Given milk tests elicit approach, tongue protrude, gurgle, general play. Familiar object tests elicit open mouth play face, etc.

In other words, it would appear that the test situations employed are effective in inducing particular affective states in these infants. It would also appear that the relationship between the infant's affective state and the demonstration of particular communication behaviours is fairly independent of social experience.

3. Sex differences in age of first occurrence of communicative behaviours.

Table 22 gives details of sex differences in the age of first occurrence, modal test situation, and total number of infants showing specific communicative behaviours.

Column 7 indicates those behaviours which appear to

Table 22. Sex differences in first occurrences of communicative responses of socially-deprived stump-tail macaques.

Behaviour	MALES (N = 7)			FEMALES (N = 6)			
	Total number showing behaviour	Median age of first occurrence	Modal test situation	Total number showing behaviour	Median age of first occurrence	Modal test situation	Possible significant differences (= 0.05)
<u>submission</u>							
still	6	3 months	ST1	5	3 months	ST1	
present	6	3 months	ST1	3	3 months	no mode	
teeth chatter	7	6 weeks	TT	6	7-8 weeks	T	
grimace	6	3 months	S+C	6	3 months	CA	
withdraw	7	6 weeks	T1	6	5-6 weeks	GM/FF	*T
freeze	4	3 months	S+C	4	3 months	S/C battery	
jerk	7	8 days	S	6	8 days	S	
<u>play</u>							
bounce	6	3 months	ST1	4	3 months	ST1	
play initiate	6	3 months	ST2	5	3 months	ST1	
sprawl	2	3 months	ST1	3	3 months	ST1	
open mouth	7	3 months	ST1/TT	6	2-3 weeks	TT	
chasing	5	3 months	ST1	4	3 months	ST1	
wrestling	5	3 months	ST1	3	3 months	ST1	

Table 22 contd.

Behaviour	MALES (N = 7)			FEMALES (N = 6)			
	Total number showing behaviour	Median age of first occurrence	Modal test situation	Total number showing behaviour	Median age of first occurrence	Modal test situation	Possible significant differences (= 0.05)
<u>play</u> (contd)							
open mouth bite	6	3 months	ST1	3	3 months	ST1	
general	7	2 months	GM2/TT/SA	5	7-8 weeks	GM/CA	
<u>dominance</u>							
bounce	5	3 months	ST1	1	3 months	ST1	*N
mount	3	3 months	ST1	0	-	-	*N
yawn	6	7-8 weeks	T	1	2 months	TT	*N
teeth champ	4	3 months	ST2	3	3 months	ST2	
brow threat	3	3 months	ST1	3	3 months	ST1	
open mouth threat	6	2-3 months	ST1	0	-	-	*N signif. (binomial test)
teeth chatter threat	4	3 months	SA	1	3 months	ST2	*N
scream threat	1	3 months	ST1	0	-	-	
chase	1	3 months	ST2	0	-	-	
grab/hit	5	3 months	ST1	2	5 weeks	FF1	*NAT A and T: signif. (Fisher test)

Table 22 contd.

Behaviour	MALES (N = 7)		FEMALES (N = 6)		Actual significant differences ($\alpha = 0.05$)		
	Total number showing behaviour	Median age of first occurrence	Modal test situation	Total number showing behaviour		Median age of first occurrence	Modal test situation
<u>dominance</u> (contd)							
bite	7	3 months	ST1	2	5 weeks	FF1	*NAT
<u>affiliation</u>							
groom	5	3 months	ST1	1	3 months	ST2	*N
present for groom	0	-	-	1	3 months	ST2	
lipsmack	7	9 days	S/PML/GM1	6	8-9 days	S	
square mouth	7	3 months	SA	5	3 months	S/C battery	
huddle	7	3 months	ST1	5	3 months	ST2	
mouth nibble	0	-	-	2	3 months	ST2	
<u>sex</u>							
anogenital inspection	7	3 months	ST2	1	3 months	ST2	*N
mount	2	3 months	ST2	0	-	-	
masturbate	7	7-8 weeks	T	5	3 months	SA	*AT

Table 22 contd.

Behaviour	MALES (N = 7)			FEMALES (N = 6)				
	Total number showing behaviour	Median age of first occurrence	Modal test situation	Total number showing behaviour	Median age of first occurrence	Modal test situation	Possible significant differences	Actual significant differences ($\alpha = 0.05$)
<u>vocalizations</u>								
scream	7	8 days	S	6	8 days	S		
gurgle	7	5-6 weeks	T	6	5-7 weeks	TT		
trill/whimney	7	8 days	S	4	8-9 days	S		
cack/cackle	6	1 month	S	6	8-9 days	S		
whistle	7	9 days-6 wks	PM1/GM2	6	5 weeks	GM		
cheep/squeek	7	9 days	PM1	6	9 days-1 mth	S		
bitey	4	5-8 weeks	GM	4	2-3 months	no mode		
<u>other expressions</u>								
tongue protrude	7	5 weeks	GM1	6	8-9 days	S		*AT
open mouth	6	8 days	S	6	9 days	S/GDL		
self huddle	7	2 months	SA	6	2-3 months	SA		
follow	4	3 months	ST2/ST1	1	3 months	ST1		
approach	7	5 weeks	GM1	6	5 weeks	GM1		
self aggression	5	7 weeks	T2	2	6 wks-3mths	no mode		*NAT

Table 22 contd.

*T = probable difference in modal test situation
 *N = probable difference in total number
 *AT = probable difference in age of first occurrence and total number
 *NAT = probable difference in all 3

KEY

S = Separation
 PML = Prior novel
 E1 = Environment 1
 GD1/2 = Given diapers 1/2
 GM1/2 = Given milk 1/2
 FF1/2 = Frustration food 1/2
 T1 = Toy 1
 T2 = Toy 2
 TT = Toy test 2 (A to F)
 STL/2 = Social test 1/2

have a different pattern for male and females - mainly dominance and sex behaviours.

The last column of this table indicates those differences which are statistically significant.

Thus for open mouth threat, more males (6) than females (0) exhibited this behaviour (binomial test, 0.05 level of significance).

For grab/hit behaviour, males tend to show this behaviour at 3 months of age in their first social test, while females first show it at 5 weeks of age in frustration food tests (Fisher 1-tailed test, 0.05 level of significance). There was no significant difference in the number of males versus females exhibiting this behaviour.

For anogenital inspect, more males (7) than females (1) showed this behaviour (binomial test, 0.05 level of significance). But both sexes showed the behaviour at the same age (3 months) in the same test situation (social test 2).

DISCUSSION OF SEX DIFFERENCES

The findings indicate that genetic sex may be an important determinant of when infants first show

particular behaviours, and in which test situations. However, only a few behaviours were found to be affected: open mouth threat behaviour, grab/hit, and anogenital inspection.

Two of these behaviours, i.e., open mouth threat and anogenital inspection, showed indications of sexual dimorphism. Thus it was found that while most of the males in this study had exhibited these behaviours within the 3 month observation period; only one female had shown anogenital inspection, and none of the females had shown open mouth threat behaviour.

4. Connections between communicative responses of socially deprived infant stumptails and eliciting communicative stimuli.

A) Slides/calls tests

Appendix XII gives details of the frequency of particular communicative responses recorded for each different slide/call stimulus.

Table 23 gives details of the significance of connections between infant responses and eliciting stimuli (Friedman 2 way analysis of variance). Behaviours and stimuli not included in this table showed no evidence of association.

Table 23. Slides and calls tests: connections between eliciting stimuli and the communication responses of 3 month-old socially-deprived stump-tail macaques.

Infant's response	Test situation	Eliciting stimulus	Significance level
teeth-chatter	SA	slide 1 (human); slide 7 (male open mouth threat); slide 2 (infant explore); slide 3 (infant grimace)	0.05
lipsmack	SA	slide 2 (infant explore); slide 1 (human)	0.001
approach	SA	slide 1 (human); slide 2 (infant explore)	0.01
	S+C (slide only)	slide 1 (mother-infant); slide 6 (juvenile teeth-chatter threat); slide 2 (infant explore)	0.10
	S+C (complex)	slide and call 1 (mother-infant and soft grunts); slide and call 6 (juvenile teeth-chatter threat face and vocalization); slide and call 2 (infant explore and cheep calls)	0.50
withdraw	SA	slide 1 (human);	0.05

Table 23 contd.

Infant's response	Test situation	Eliciting stimulus	Significance level
withdraw (contd)	SA	slide 2 (infant grimace); slide 3 (infant explore)	0.05
	S+C (complex)	slide and call 1 (mother-infant and soft grunts); slide and call 6 (juvenile teeth-chatter threat face and vocalization)	0.50
	CA	call 1 (soft grunts)	0.20
mouth nibble	SA	slide 2 (infant explore); slide 6 (female grimace)	0.20
gurgle	SA	slide 4 (female explore); slide 5 (mother-infant)	0.10
	S+C (complex)	slide and call 1 (mother-infant and soft grunts)	0.30
whistle	SA	slide 7 (male open-mouth threat); slide 8 (male yawn)	0.10
	S+C (call only)	call 9 (male sex rattle)	0.20
scream	S+C (slide only)	slide 6 (juvenile teeth-chatter threat face)	0.10
	CA	call 6 (juvenile teeth-chatter threat call)	0.10

Table 23 contd.

KEY

SA = slides alone test

CA = calls alone test

S+C = slides and calls test

S+C (complex) = response connected to slide and call unit;
rather than to just the slide or the call.

From this table, it can be seen that the submissive responses of teeth chatter and withdraw are significantly connected (0.05 level of significance) with open mouth threat (slide 7) and teeth chatter threat (slide and call 6). They are also significantly connected (0.05 level) with slides 1, 2 and 3, and call 1, which may indicate an order effect.

The affiliative responses lipsmack and mouth nibble tend to be connected with infant explore (slide 2) and female grimace (slide 6).

Approach tends to be connected with teeth chatter threat (slide/call 6). It is also connected with the first two slides which again may indicate an order effect.

Gurgle is connected with female explore (slide 4) and mother cradling infant (slide 1).

Whistle is connected with the male dominance displays, i.e., open mouth threat and yawn, and also with the male sex rattle call.

Scream is connected with teeth chatter threat (slide/call 6).

B) Social test one

Appendix XIII gives details of the distribution of the infants' communicative responses to the behaviour of the stimulus animal in the first social test. Visual explore by the infant was not included as a communicative response in this table.

These transition frequency matrices were subsequently collapsed for analysis. Collapsing rows and columns occurred until none of the expected frequencies was less than zero and no more than 20% of the expected frequencies were less than 5 (Siegel 1956). Behaviours shown infrequently by the infant and/or stimulus animal were excluded from analysis.

Table 24 gives details of the significant associations between the infant's responses and the partner's immediately preceding behaviour.

Behaviours listed in this table show the result of collapsing the matrices presented in appendix XIII.

From this table it can be seen that there was significant association between the infant's communicative response and the partner's prior behaviour in 10 of the 11 infants tested (Contingency coefficient (C); significance level = 0.01).

Table 24. Significant associations between the communicative responses of 3 month old socially-isolated stump-tail macaques and the preceding behaviour of their partner in social test one.

Infant	Partner	Partner's age	Infant's behaviours	Partner's behaviours	Significant associations
25	data missing				
26	37	2 weeks	<ol style="list-style-type: none"> 1. dominance display 2. grab 3. bite 	<ol style="list-style-type: none"> 1. submission (mainly still, jerk and scream) 	$C = 0.31$; $\chi^2 = 10.81$; $df = 2$ C significant at 0.01 level <ol style="list-style-type: none"> 1. dominance display follows visual explore by partner (observed frequency (O) = 6; expected frequency (E) = 3) 2. grab follows visual explore (O = 21; E = 17.9) 3. bite follows submission (O = 27; E = 20.9)
27	37	1 month	<ol style="list-style-type: none"> 1. submission (mainly freeze) 2. affiliation (mainly lipsmack) 3. play (mainly open mouth play face) 	<ol style="list-style-type: none"> 1. visual explore 2. approach 	$C = 0.49$; $\chi^2 = 8.96$; $df = 1$ C significant at 0.01 level <ol style="list-style-type: none"> 1. submission follows approach (O = 9; E = 5.2) 2. affiliation and play follow visual explore (O = 13; E = 9.2)
28	faulty data				
29	26	4 months	<ol style="list-style-type: none"> 1. still/present 2. high intensity submission 	<ol style="list-style-type: none"> 1. dominance 2. affiliation/play 3. visual explore 4. approach 5. contact 	no significant associations

Table 24 contd.

Infant	Partner	Partner's age	Infant's behaviours	Partner's behaviours	Significant associations
30	26	4 months	<ol style="list-style-type: none"> 1. still/present 2. high intensity submission 	<ol style="list-style-type: none"> 1. threat/chase 2. grab 3. bite 4. affiliation (mainly huddle) 5. visual explore 6. approach 	<p>C = 0.39; $\chi^2 = 24.69$; df = 5 C significant at 0.001 level</p> <ol style="list-style-type: none"> 1. still/present follow approach, visual explore and affiliation (0 = 23, 32, 7; E = 16.6, 30.4, 55) 2. high intensity submission follow bite and grab (0 = 15, 9; E = 6.8; 7.1)
31	26	4.5 months	<ol style="list-style-type: none"> 1. still/present 2. high intensity submission 3. open mouth play face 4. play 	<ol style="list-style-type: none"> 1. threat 2. attack 3. affiliation (mainly square mouth and lipsmack) 4. play 5. sex (mainly anogenital inspection) 6. visual explore 7. approach 	<p>C = 0.37; $\chi^2 = 61.48$ df = 18 C significant at 0.001 level</p> <ol style="list-style-type: none"> 1. still/present follow attack, threat and sex (0 = 17, 6, 5; E = 9.5, 6, 3.4) 2. high intensity submission follows threat, visual explore, approach and attack (0 = 17, 24, 16, 22; E = 9, 16.9, 12.3, 20.1) 3. open mouth play face follows visual explore and play (0 = 17, 14; E = 12.4, 12.4) 4. play follows play, affiliation and sex (0 = 52, 14, 20; E = 35.7, 9.8, 15.2)
32	26	5 months	<ol style="list-style-type: none"> 1. still/present 2. high intensity submission 3. open mouth play face 	<ol style="list-style-type: none"> 1. dominance 2. play 3. sex (mainly anogenital inspection) 	<p>C = 0.50; $\chi^2 = 96.16$; df = 12 C significant at 0.001 level</p> <ol style="list-style-type: none"> 1. still/present follow dominance, approach and sex (0 = 20, 22, 6; E = 9.8, 17.1, 3.7)

Table 24 contd.

Infant	Partner	Partner's age	Infant's behaviours	Partner's behaviours	Significant associations
32 (contd)	26	5 months			<p>2. high intensity submission follows dominance, visual explore and sex (0 = 21, 18, 5; E = 10.9, 12.4, 4.1)</p> <p>3. open mouth play face follows play (0 = 20; E = 9)</p> <p>4. play follows play, visual explore and approach (0 = 52, 30, 42; E = 36.1, 26.7, 40.8)</p>
33	26	6 months	<p>1. still/present</p> <p>2. teeth chatter/grinace</p> <p>3. withdraw</p> <p>4. freeze</p> <p>5. jerk/scream</p> <p>6. affiliation (lipsmack)</p>	<p>1. dominance (mainly attack)</p> <p>2. visual explore</p> <p>3. approach</p> <p>4. contact</p>	<p>C = 0.45; $X^2 = 79.2$; df = 15</p> <p>C significant at 0.001 level</p> <p>1. still/present follow dominance and contact (0 = 18, 4; E = 9.4, 3.9)</p> <p>2. teeth chatter/grinace follow approach and visual explore (0 = 56, 26; E = 33.5, 24.4)</p> <p>3. withdraw follows dominance and visual explore (0 = 15, 10; E = 10.8, 9.1)</p> <p>4. freeze follows contact and dominance (0 = 13, 20; E = 7.3, 17.6)</p> <p>5. jerk/scream follow dominance and contact (0 = 21, 7; E = 12, 5)</p> <p>6. lipsmack follows visual explore (0 = 18; E = 8.6)</p>
34	26	6 months	<p>1. dominance (mainly threat)</p> <p>2. open mouth play face</p>	<p>1. dominance</p> <p>2. open mouth play face</p> <p>3. play</p>	<p>C = 0.64; $X^2 = 242.12$; df = 12</p> <p>C significant at 0.001 level</p> <p>1. dominance follows dominance and approach (0 = 20, 4; E = 2.2, 2.5)</p>

Tabel 24 contd.

Infant	Partner	Partner's age	Infant's behaviours	Partner's behaviours	Significant associations
34	26	6 months	3. play initiate 4. play	4. visual explore 5. approach	2. open mouth play face follows visual explore and approach (0 = 37, 17; E = 28.8, 10.7) 3. play initiate follows visual explore (0 = 25; E = 9.5) 4. play follows play and open mouth play face (0 = 75, 64; E = 49.1, 43.4)
35	26	6 months	1. still/present 2. teeth chatter/grinace/withdraw 3. freeze/jerk/scream 4. open mouth play face 5. play	1. threat 2. attack 3. play 4. visual explore 5. approach	C = 0.50; $X^2 = 92.05$; df = 16 C significant at 0.001 level 1. still/present (low intensity submission) follow attack, threat and approach (0 = 15, 9, 12; E = 9.2, 4.7, 11.2) 2. medium intensity submission follows approach, attack and threat (0 = 18, 11, 5; E = 9.7, 8, 4.1) 3. high intensity submission follows attack and threat (0 = 19, 6; E = 9.4, 4.8) 4. open mouth play face follows play and visual explore (0 = 9, 11; E = 5.1, 8.5) 5. play follows play and visual explore (0 = 38, 42; E = 19.7, 33.1)
36	26	6 months	1. still/present 2. high intensity submission 3. open mouth play face 4. play	1. dominance 2. open mouth play face 3. play 4. visual explore 5. approach	C = 0.54; $X^2 = 93.63$; df = 12 C significant at 0.001 level 1. still/present follows dominance and approach (0 = 26, 26; E = 11.8, 13.1) 2. high intensity submission follows dominance, approach and visual explore (0 = 8, 7, 5; E = 5.2, 5.8, 4.2)

Table 24 contd.

Infant	Partner	Partner's age	Infant's behaviours	Partner's behaviours	Significant associations
36 (contd)	26	6 months			<p>3. open mouth play face follows play and visual explore (0 = 24, 10; E = 14.8, 7.2)</p> <p>4. play follows open mouth play face, play and visual explore (0 = 17, 40, 19; E = 8.4, 31.2, 15.2)</p>
38	26	7.5 months	<ol style="list-style-type: none"> 1. still/present 2. high intensity submission 3. open mouth play face 4. play 	<ol style="list-style-type: none"> 1. play 2. sex 3. visual explore 4. approach 5. contact 	<p>C = 0.46; $\chi^2 = 56.47$; df = 12 C significant at 0.001 level</p> <ol style="list-style-type: none"> 1. still/present follow sex, contact and play (0 = 12, 6, 10; E = 3.4, 3.4, 8.4) 2. high intensity submission follows approach and visual explore (0 = 25, 35; E = 16, 28.4) 3. open mouth play face follows contact, play and visual explore (0 = 8, 16, 21; E = 5.6, 14, 19) 4. play follows play and approach (0 = 14, 7; E = 8.9, 6.8)

In general, the significant connections follow an expected pattern, thus submission tends to follow dominance, play follows play, dominance follows submission.

DISCUSSION OF S-R CONNECTIONS

The finding of significant association between the infants' responses and eliciting stimuli, suggests that at least some of the S-R connections in stumptail macaque communication are not dependent on social experience.

Furthermore, the finding that most of these connections seem to be contextually-appropriate, e.g., specific submissive gestures are given in response to specific threat expressions, suggests that the contextual relevance of particular communicative behaviours is not dependent on social experience.

It could be argued then, like Sackett (1966), that certain stimuli appear to function as innate releasing stimuli for certain communication behaviours in these animals. However, whereas Sackett (1966) identified only two such stimuli, i.e., pictures of threatening, and pictures of infant monkeys, this study has pointed to the importance of a range of eliciting stimuli.

In this study, only first-order S-R connections are

reported for the social test situation, however, inspection of the raw data record suggests that higher-order connections may also be important (see Altmann 1965). These higher-order associations will be reported at a later date.

STUDY 2

The communication abilities of socially-deprived juvenile stumptail macaques (groups 1-5, plus feral adult group).

GENERAL METHOD

Subjects: 5 groups of differentially reared juvenile stumptail macaques and 1 group of feral adult stumptail macaques were observed.

Details of age, sex, and rearing experience of the 5 juvenile group is given in table 1, chapter 3.

The feral adult group consisted of 4 animals: Black Bart, an adult male, Isaacs, B. Scruff and Margaret, 3 adult females.

Test situation: The battery of slides/calls tests, previously described in table 10 and figure 5, chapter 5, was given.

Data collection: Data were collected by means of a hand written symbol notation method (appendix I).

RESULTS

Appendix XIV gives details of the distribution of communicative responses to each different slide/call/slide and call stimulus in the S/C battery of tests.

Table 25 lists those S-R connections which were significantly associated (Friedman 2 way analysis of variance, 0.05 level of significance).

From this table, it can be seen that all groups show a significant association between at least one communicative response and one eliciting stimulus in one of the slides/calls tests.

Responses showing significant association include

1. approach
2. withdraw

Table 25. Significant associations between communicative responses and eliciting stimuli in slides/calls tests for 5 groups of differentially-reared juveniles, and 1 group of feral adult stump-tail macaques (Friedman 2 way analysis of variance, 0.05 level of significance).

Group name/ rearing experience	Communicative response	Eliciting stimulus	Test situation
Dark	pout and lipsmack	slide 4 (female explore); slide 7 (male open mouth threat)	SA
Peer	approach	slide and call 1 (mother- infant and soft grunts); slide and call 2 (infant explore and cheeps)	S+C
	withdraw	slide and call 1 (mother- infant and soft grunts; slide and call 5 (female brow threat and threat grunts); slide and call 10 (male ejaculatory face and growl)	S+C
	teeth chatter and grimace	slide 1 (human); slide 7 (male open mouth threat)	SA
Isolate	withdraw	call 1 (soft grunts); call 2 (cheeps); call 6 (teeth- chatter threat vocalization)	CA
Adult-peer	teeth chatter and grimace	slide 1 (human); slide 6 (juvenile teeth chatter threat)	SA

Table 25 contd.

Group name/ rearing experience	Communicative response	Eliciting stimulus	Test situation
Social	teeth chatter and grimace	slide 1 (human); slide 7 (male open mouth threat)	SA
Feral	pout and lipsmack	slide 1 (human); slide 7 (male open mouth-threat)	SA

SA = slides alone; CA = calls alone; S+C = slides and calls

3. teeth chatter and grimace
4. pout and lipsmack.

Stimuli showing significant association include

1. threat stimuli, i.e., male open mouth threat, female brow threat, juvenile teeth chatter threat
2. monkey exploration stimuli, i.e., female explore, infant explore, mother-infant
3. sex stimuli, i.e., male ejaculatory face and call
4. human stimulus.

DISCUSSION OF THIS SECTION

If we ignore response to stimuli presented at the beginning of any test situation, since it cannot be determined whether this was due to the specific properties of the stimulus or due to order effects, then it can be seen that the most important stimulus for all 6 groups was some kind of monkey threat.

Furthermore, the most common response tended to be some kind of submission, i.e., teeth chatter/grimace, withdraw.

From these limited data, however we cannot say anything about similarities or differences

between the different groups. Nor can we say anything about the specific cues inherent in the stimuli which are most important for eliciting specific responses.

We can see, however, that these test situations do not appear to be the best for answering these kinds of questions: most of the stimuli are responded to in like fashion.

In order to investigate the communicative behaviour of such differentially-reared groups it may be more useful to look at their behaviour in a social situation. This is not reported here.

GENERAL DISCUSSION

The main findings of this series of studies are that stumptail macaques, with no previous social experience, are capable of:

1. exhibiting all of the compound communicative expressions examined in this study
2. showing these expressions in apparently appropriate affective contexts
3. responding appropriately to a range of what may be termed *innate releasing stimuli*.

Such findings do not support Mason's (1965) hypothesis that the connection of communication signals with specific eliciting stimuli is dependent on social experience.

These findings extend the range of communicative responses which socially isolated monkeys are capable of exhibiting; and also the range of communicative stimuli which may elicit appropriate communicative responses. Thus table 24 shows that socially isolated stumptail macaques appear to differentiate the following communicative stimuli:

1. various types of threat expressions and calls, including open mouth threat, teeth chatter threat, yawn
2. female explore
3. grimace
4. male sex rattle call.

It is not, however, known from these studies what cues the infants were in fact responding to. This must await future investigation.

It is also not known from these studies whether in

the communicative responses of the infants differed in some of their details, e.g., position of ears, tail, etc., from similar expressions in socially sophisticated infants. This would require a study of the details of signals, perhaps by using video records (see Chevalier-Skolnikoff's 1974).

Finally, these findings may just reflect a species difference in communicative competence. For example, Chevalier-Skolnikoff has suggested that *M. arctoides* develops more rapidly than *M. mulatta*. Future research might examine this question.

A further limitation of these studies, is that no examination of higher-order associations between infant response and partner's behaviour were carried out. Also no investigation of how the infants use their communicative abilities in interaction, e.g., in order to initiate or terminate particular sequences of behaviour. These questions are, however, answerable from the data and will be reported at a future date.

In conclusion, we have seen, from use of the deprivation technique, where social experience is *not* involved in the communication system. Now we must start to investigate where social experience *is* involved, and also determine *how* it is involved.

HYPOTHESES ABOUT THE INVOLVEMENT OF SOCIAL
EXPERIENCE IN THE DEVELOPMENT OF MACAQUE COMMUNICATION

Social experience will obviously be important in any aspect of communication depending on familiarity of individuals.

It is also likely to be involved where individuals exhibit a behaviour pattern outside of the normal species-typical range of behaviours.

In the longitudinal studies of the DIMS infants, several seemingly idiosyncratic behaviour patterns were observed, e.g., dental inspection, open-mouth kissing with hugging. These were exhibited firstly by only one infant (26 showed dental inspection; 28, open-mouth kissing), and then spread to the infants they came into contact with.

In the DIMS infants, not only did learning appear to be involved in the acquisition of novel behaviours, it also appeared to be involved, in certain cases, in the acquisition of species-typical behaviours.

For example, in the manipulation of dominance experience for the dominant-only group, a naive 10 day old infant was used to ensure that D-gp members would receive

the appropriate early experience. At this early age, the naive infant's predominant expressive behaviours were scream and jerk. Screaming elicited attack by the dominant, until constant pairing appeared to inhibit this behaviour.

After such attacks, the dominant would consistently pull up the infant's rear to inspect it. This appeared to result in the shaping of presenting behaviour by the infant to the dominant. No other infant showed presenting behaviour until 3 months of age in the first social test. Then it was exhibited, in sophisticated fashion, along with the various other characteristic submissive expressions.

Given these possibilities for innovation and for shaping, the next step might consist of looking at the development of communication in a rearing situation which maximizes the opportunities for their occurrence, e.g., cross-species rearing situation.

Social experience may also have its effects on the communication system in a more indirect way. Thus different early experiences may affect the relative probability of different types of expression.

For example, in studies of the 5 groups of differentially-reared infants described in chapter 3, it

was found that the 5 groups differed significantly in the mean probability of dominance, submission, play, sex and affiliation, shown in milk test situations ($C = 0.44$; $\chi^2 = 117.82$; significant at 0.001 level).

The data are given in table 26.

From this table, it can be seen that:

- a) the dark group is characterized by a higher probability of play, and a lower probability of affiliation and submission, than expected
- b) the peer group is characterized by a higher probability of dominance and submission, and a lower probability of play, than expected
- c) the isolate group is characterized by a higher probability of dominance and submission, and a lower probability of affiliation, than expected
- d) the adult-peer group is characterized by a higher probability of affiliation and play, and a lower probability of dominance and submission, than expected
- e) the social group is characterized by a higher probability of affiliation and submission, and a lower probability of play and dominance than expected.

Table 26. Observed (O) and expected (E) mean probability of dominance, submission, play, sex and affiliation in 5 groups of differentially-reared stump-tail macaques: milk test situations.

Group	Behaviour					
		Dominance	Submission	Play	Sex	Affiliation
DARK	O	29.4	10.4	40.95	0.35	18.93
	E	30.2	17.6	17.7	1.4	33.2
PEER	O	37.13	24.93	6.65	2.08	29.2
	E	30.2	17.6	17.6	1.4	33.2
ISOLATE	O	37.43	26.55	15.8	0.0	20.25
	E	30.2	17.6	17.7	1.4	33.2
ADULT-PEER	O	22.48	5.8	24.58	3.78	43.35
	E	30.2	17.6	17.6	1.4	33.2
SOCIAL	O	24.45	20.3	0.28	0.8	54.25
	E	30.2	17.6	17.7	1.7	33.2

$C = 0.44$

$\chi^2 = 117.825$

$df = 16$

significant at 0.001 level

In order to investigate any of the above hypotheses about the involvement of social experience in the development of the communication system, a shift must be made from looking at behavioural outcomes, to looking at the sequential and temporal details of inter-individual interaction chains.

CHAPTER EIGHT

Personality in infant stumptail macaques.

This chapter focuses on methods for describing the personality characteristics of infant monkeys.

The main aims were firstly, to develop diagnostic tools enabling objective, valid and reliable measurement of Eysenck's dimensions of personality (neuroticism, extraversion and psychoticism) in infant monkeys, and secondly, to examine the persistence of such personality characteristics in the first 15 months of life.

METHOD

The sample consisted of thirteen stumptail infants, previously described in chapter 7.

These infants had been separated from their mothers at 8 days of age, reared in social isolation until 3 months, and given experimentally controlled social experience with peers from 3 months until 15 months of age. Details of rearing are given in chapter six.

DESIGN

There were three conditions in this study:

- 1) measurement of personality dispositions prior to specific social experience
- 2) measurement of personality dispositions after 1 month social experience with peers
- 3) measurement of personality dispositions after 12 months social experience with peers.

Two types of test situation were used:

- 1) non social tests - used in all 3 conditions
2. social tests - used in condition 3 above.

Non social test situations

- A) prior to social experience (3 months test situations)

The test situations described in chapter 7 for assessment of the communicative abilities of socially deprived infants were used to assess the infant's personality characteristics in this condition.

Details of these tests are given in table 17, chapter 7. Details of the testing schedule is given in appendix VI.

- B) after 1 month of peer experience (4 months test situations)

Personality characteristics were assessed in toy test situations which were essentially a repetition of those described in table 18, chapter 7, with the addition of one very novel object, i.e., TTN (see figure 12).

C) after 12 months peer experience (15 months test situations)

Personality characteristics were assessed in a battery of slides/calls tests. Details of the test stimuli are given in table 10 and figure 5, chapter 5.

Social test situations

These consisted of pairing the infant with an unknown stimulus animal. Stimulus animals examined here included,

- a) peer 5 : a subadult female who had previously been reared as a member of the peer group of animals described in chapter 3,
- b) kid : a feral adult female,
- c) Angus : a feral adult male.



Figure 12. A juvenile stump-tail macaque (number 29) explores TTN.



Figure 12. A juvenile stump-tail macaque (number 29) explores TTN.

DATA COLLECTION

As described in chapter 7: handwritten symbol notation for nonsocial tests; DTU for social tests.

ASSESSING PERSONALITY DIMENSIONS

In the pilot study, reported in chapter 5, the method of measuring neuroticism, i.e., frequency of high intensity expressive behaviours, appeared to be a fairly satisfactory method for assessing this dimension in stump-tails. Therefore, this method was retained here.

The methods of measuring psychoticism and extraversion, however, appeared to be less satisfactory. As a result, these measures were modified as follows:

1. Extraversion

In addition to the measure of switches in the object of the individual's attention, two new measures were included:

- a) total frequency and duration of visual orienting to the test object
- b) total frequency and duration of visual orienting to any object in the test situation.

Frequency measures were obtained in all test situations; duration measures only in the social test situations.

Visual orienting was scored only when the animal looked towards an object, showing no concurrent expressive behaviours. Hence it is a "purer" measure than the switches measure, which was based on both expressive and visual orienting behaviour.

It was reasoned that if visual orienting may be taken as a behavioural indicator of cortical arousal, and if relative introversion may be associated with a relatively high degree of cortical arousal, then those individuals showing the greatest frequency and/or duration of visual orienting behaviour may be labelled introvert. Conversely, individuals showing the least visual orienting behaviour may be labelled extravert.

2. Psychoticism

The original method was expanded to incorporate scores of inappropriate behaviour (i.e., masturbation self huddle), as well as solitary and aggressive behaviour.

The scoring method remained essentially the same as reported in chapter 5. Thus individuals were ranked in

order of psychoticism according to their compound score on aggression, solitary and inappropriate behaviour. Individuals showing the greatest frequency/duration of all three were ranked highest on psychoticism; individuals showing none of these behaviours were ranked lowest in psychoticism.

RESULTS

Appendix XV presents the raw data for assessing neuroticism, extraversion and psychoticism in this study.

Only tests where data for all thirteen animals was available are presented.

1. Reliability of personality measures

Table 27 gives details of the reliability of each personality measure across test situations for given ages.

From this table it can be seen that neuroticism was reliably measured in both 4 month and 15 month test situations, but not in 3 month test situations. Extraversion was reliably measured by at least one method in all test situations (N.B. the three different methods of assessing extraversion were significantly intercorrelated at the 0.01 level). Psychoticism was reliably measured only in 4 month test situations.

Table 27. Reliability of personality measures in DIMS study.

Test situations	Personality dimensions		PSYCHOTICISM
	NEUROTICISM	EXTRAVERSION	
<u>under 3 months</u>			
Separation)))
Toy 1)))
Toy 2)))
Given milk 1)))
frustration food 2)))
Given milk 2)))
slides alone)))
calls alone)))
slides and calls)))
	W = 0.36	W = 0.13	W = 0.56
	$\chi^2 = 21.75$	$\chi^2 = 31.07$	$\chi^2 = 20.12$
	signif. at	signif. at	almost signif. at
	0.05	0.01	0.05
	not signif.	not measured	not signif.
	not signif.	not signif.	not signif.
	not signif.	not signif.	not signif.
	not signif.	not signif.	not signif.

Table 27 contd.

Test situations	Personality dimensions				PSYCHOTICISM
	NEUROTICISM	Visual explore of test object	EXTRAVERSION Visual explore all objects	Switches in object of attention	
<u>4 months</u>					
Toy 3))))) W = 0.53
Toy test B) W = 0.54)) W = 0.42)) $\chi^2 = 25.57$
Toy test D) $\chi^2 = 25.74$) not signif.) $\chi^2 = 20.35$) not measured) signif. at
Toy test N) signif. at 0.05)) almost signif. at 0.05)) 0.05
<u>15 months</u>					
slides alone) W = 0.57)))) not signif.
calls alone) $\chi^2 = 20.51$) not signif.) not signif.) W = 0.61) $\chi^2 = 21.85$
slides and calls) almost signif.))) signif. at 0.05) 0.05
) at 0.05))))
peer 5)) frequency scores:)) not) not signif.
kid) frequency scores:) scores:) W = 0.72) measured)
Angus) W = 0.65) W = 0.71)))

Table 27 contd.

Test situations	Personality dimensions		
	NEUROTICISM	Visual explore of test object	EXTRAVERSION Visual explore all objects
	$\chi^2 = 23.77$ signif. at 0.05	$\chi^2 = 25.47$ signif. at 0.05	Switches in object of attention $\chi^2 = 25.95$ signif. at 0.01
	Duration scores: $W = 0.56$ $\chi^2 = 20.23$ almost signif. at 0.05	$W = 0.8$ $\chi^2 = 28.84$ signif. at 0.01	not signif. $W = 0.84$ $\chi^2 = 30.42$ signif. at 0.01
			PSYCHOTICISM

In the stimulus animal tests, where frequency and duration scores were examined, the rank orderings produced by these two scoring methods were found to be significantly correlated (at the 0.01 level for neuroticism; at the 0.05 level for extraversion).

DISCUSSION OF RELIABILITY OF MEASURES

1. NEUROTICISM

Lack of reliable measurement was found only in tests given at less than 3 months of age, i.e., prior to social experience.

Lack of reliability in this case does not appear to result solely from the choice of test situations, because the same tests (e.g., toy tests; slides/calls tests), given at later ages (i.e., 4 months; 15 months), produce reliable rank orderings for emotionality.

However, it could have resulted from a number of other factors:

For instance, it could be argued that the basic emotional reactivity of these particular infants may have been disturbed by at least two of the early experimental procedures, i.e., separation from the mother (see Hinde 1971), and the period of social isolation. As a result,

emotionality may not be a useful dimension of individuality at this age in these particular infants.

On the other hand, lack of reliable measurement of this dimension may be due, in part, to the differential development of the behaviours scored. Thus, some infants, while they may be basically emotionally reactive, may not actually develop the capacity to exhibit some of the high intensity expressions until later than others. As table 20, chapter 7 shows, there tends to be a range of over 4 weeks in the age of first occurrence of specific high intensity expressions, despite the fact that infants were reared under identical circumstances and exposed to the same test situations at the same age.

Given this variability in the development of the behaviours used to assess emotionality, then it is unlikely that this dimension can be assessed, using this measure, in infants under 3 months of age. Instead, some other method must be sought.

If the interest is mainly in behavioural measures, then if it is found that neuroticism, as assessed in later tests, is correlated with a specific behaviour shown by all infants from a very early age (e.g., diaper contact), then this behaviour may be fruitfully used to assess this dimension in young infants.

The search for behaviours correlated with neuroticism will be discussed in a later section of this chapter.

2. EXTRAVERSION

This dimension was reliably measured in all test situations by at least one of the measures examined; and all measures were highly intercorrelated.

It is likely, then, that the measures can be interchanged, depending on the investigator's interests, without much loss of information. However, switches in the object of the individual's attention does appear to be the most reliable measure.

3. PSYCHOTICISM

This dimension was reliably measured in toy test situations at 4 months of age only.

Lack of reliability in other test situations at other ages may have been due to any of a variety of factors.

For instance, aggression and self huddle behaviours were not shown by these infants until at least 2 months of age (median age of first occurrence for most of the aggressive behaviours = 3 months, for self huddle = 2

months: see table 20, chapter 7, for details). As a result, the method used to assess psychoticism is likely to be unsuitable for infant stumptail macaques less than 3 months old.

For the 15 month test situations, both the slides/calls tests and the stimulus animal tests were ineffective elicitors of aggression in these animals. As a result, the method used to assess psychoticism is likely to be unsuitable in these test situations.

For this dimension, then, we must further investigate both methods for reliable measurement and test situations which effectively elicit the behaviours of interest.

2. Independence of personality dimensions

All three personality dimensions were measured reliably only in toy test situations at 4 months.

It was found that the rank orders for neuroticism, extraversion and psychoticism at this age were not significantly intercorrelated ($W = 0.35$; $X^2 = 12.69$).

Neuroticism and extraversion were both measured reliably in the 15 month test situations.

It was found that the rank orders for these two dimensions were not significantly correlated ($r_s = -0.38$

for slides/calls tests; $r_s = -0.15$ for stimulus animal tests).

Discussion of this section

It would appear that the dimensions of individuality, provisionally labelled neuroticism, extraversion and psychoticism, are fairly independent of each other.

The reason for there being some degree of correlation may be due to the incorporation of aggression and masturbation scores in the measures of both neuroticism and psychoticism.

3. Sex differences in personality

Sex differences in personality were assessed only where dimensions were reliably measured.

A) Under 3 months

No significant sex differences were found in extraversion (Mann Whitney U - 12, $p = 0.117$ for toy tests, food tests etc., U = 17, $p = 0.267$ for slides/calls tests).

B) 4 months

A graphical representation of individuals rankings on

neuroticism, extraversion and psychoticism is given in figure 13.

Significant sex differences were found in neuroticism and psychoticism. Thus it was found that males were significantly more emotional ($U = 7$, $p = 0.026$, signif. at 0.05 level), and significantly more psychotic ($U = 7$, $p = 0.026$, signif. at 0.05 level), than females.

No significant sex differences were found in extraversion ($U = 20$, $p = 0.473$, n.s.).

C) 15 months

No significant sex differences were found in either extraversion or introversion at this age.

Discussion of sex differences

The pattern of sex differences found in the 4 months toy test situations are compatible with other findings in the literature. Thus Sackett (1973) has pointed out that male monkeys are more affected by social isolation than females; Gray (1978) and Chamove *et al* (1972) have suggested that psychoticism is linked to male sexuality.

The lack of a sex difference in neuroticism at 15 months of age may be the result of modification of

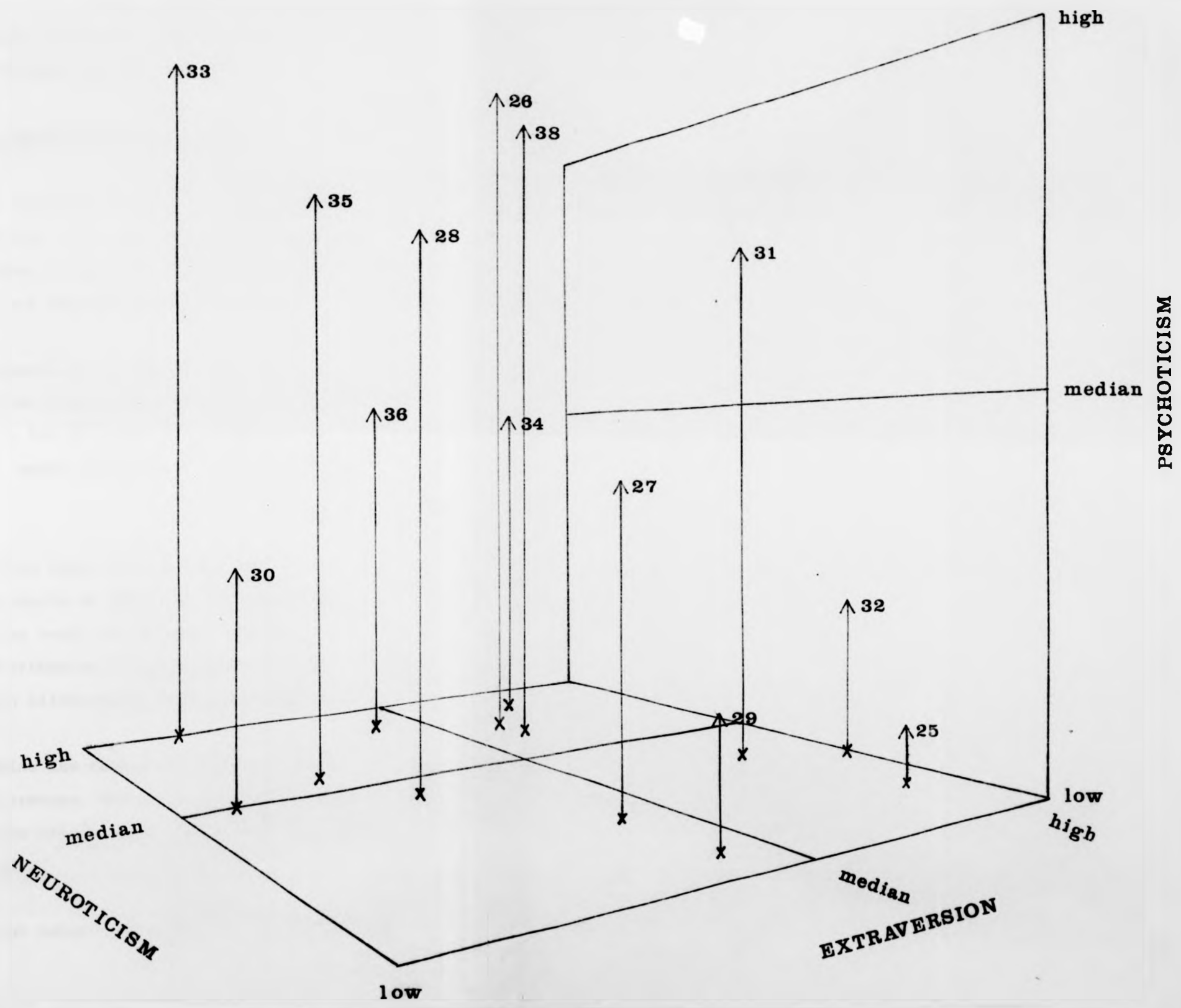


Figure 13. Rankings on neuroticism, extraversion and psychoticism for 13 infant stump-tail macaques : 4 month toy tests.

emotionality by specific dominance experience: a hypothesis which is discussed in the next chapter.

4. Persistence of personality characteristics

Neuroticism and extraversion were the only dimensions of personality which were reliably measured in both early and late test situations, therefore, only these two dimensions are examined for persistence.

Graphical representation of the rankings of individuals on these two dimensions for 4 month toy tests is given in figure 14; for 15 month social tests in figure 15; and for 15 month slides/calls tests in figure 16.

It can be seen from these figures that the distribution of individuals on these two dimensions are similar for 4 month toy tests and 15 month stimulus animal tests; the distribution of individuals on these dimensions in 15 month slides/calls tests is different.

In order to examine the nature and extent of these similarities and differences, the cartesian co-ordinates (with the median as the origin) were transformed to polar co-ordinates (table 28).

Table 29 shows the nature and extent of the differences.

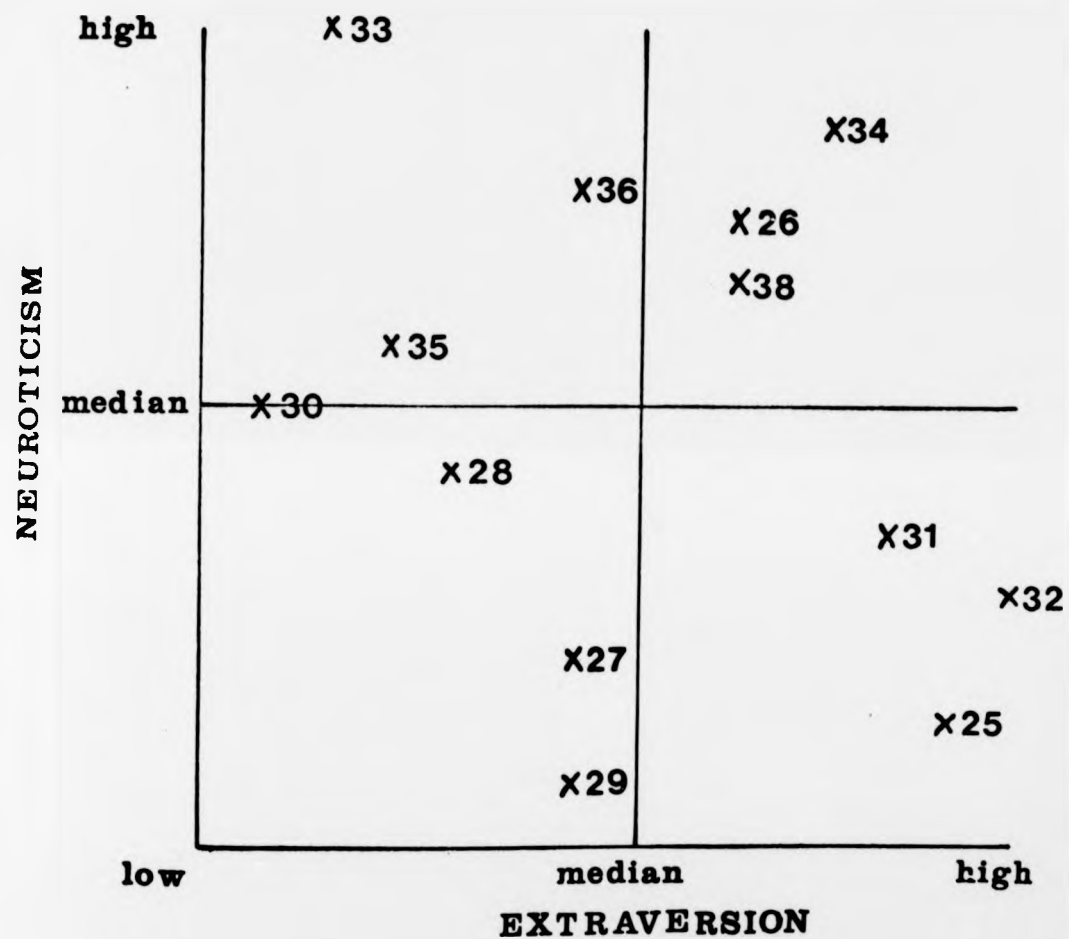


Figure 14. Rankings of 13 stump-tail macaques on neuroticism and extraversion, assessed in toy test situations, at 4 months of age.

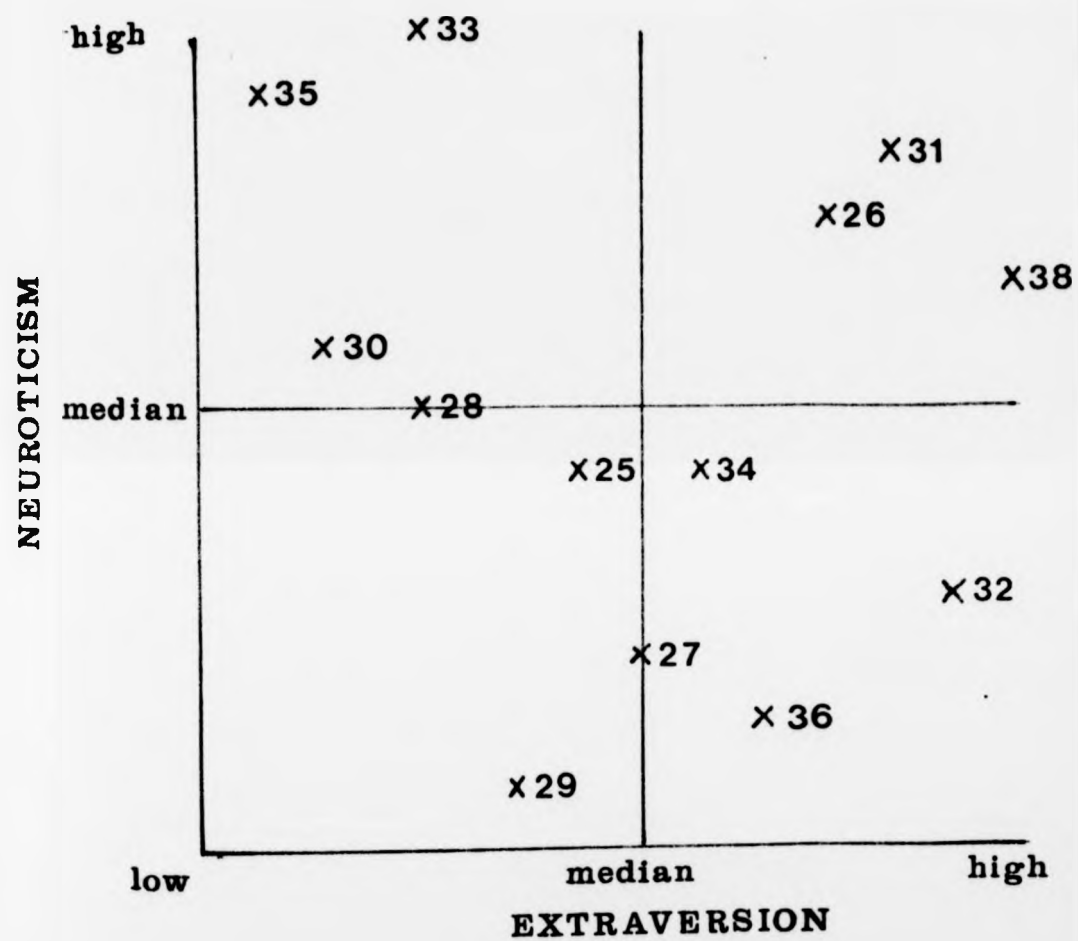


Figure 15. Rankings of 13 stump-tail macaques on neuroticism and extraversion, assessed in stimulus animal tests, at 15 months of age.

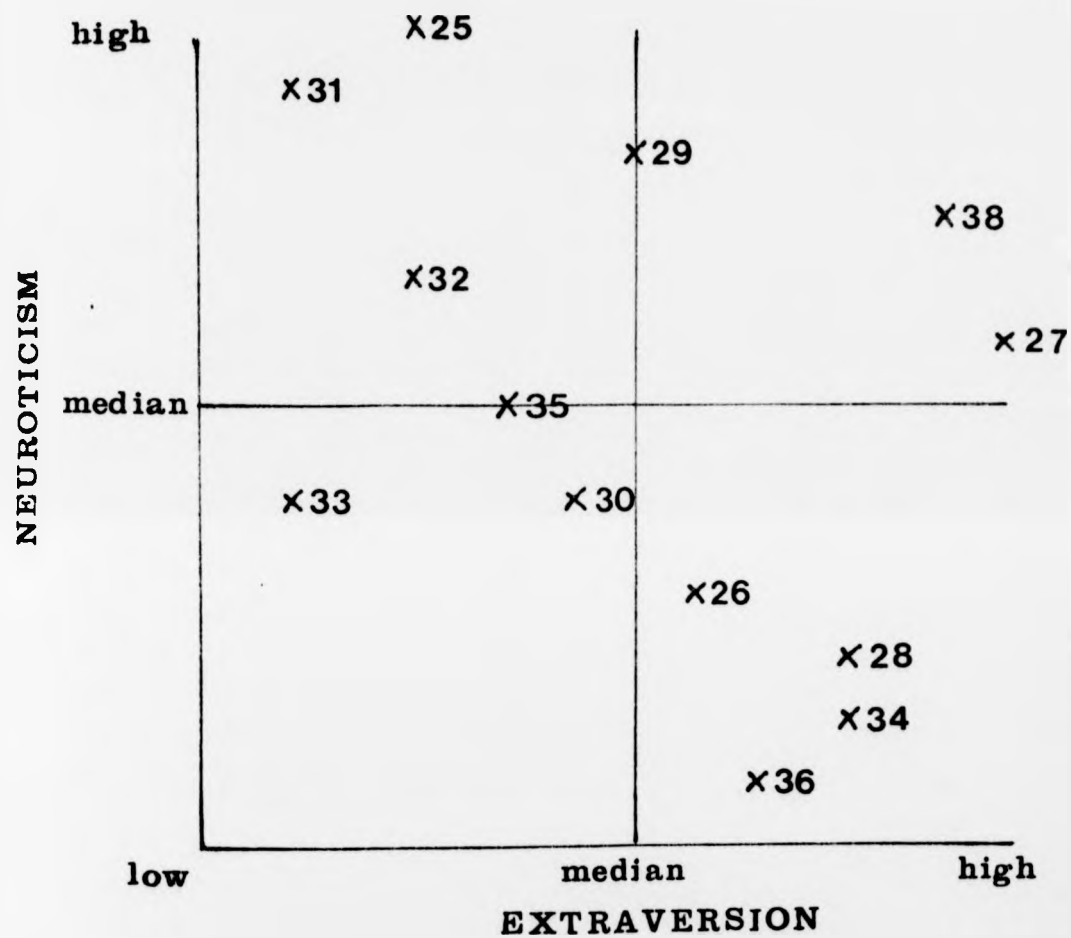


Figure 16. Rankings of 13 stumptail macaques on neuroticism and extraversion, assessed in slides/calls tests, at 15 months of age.

Table 28. Polar co-ordinates for rankings on extraversion and neuroticism in DIMS infants.

Individual	4 months toy tests		15 months stimulus animal tests		15 months SC tests	
	θ	r	θ	r	θ	r
25	315	7.1	243.4	2.2	120.3	7
26	63.4	3.4	45	4.2	288.4	3.2
27	256	4.1	270	4	9.5	6.1
28	198.4	3.2	180	3.5	311.2	5.3
29	260.5	6.1	251.6	6.3	90	4
30	180	6	168.7	5.1	236.3	1.8
31	333.4	4.5	45	5.7	137.7	7.4
32	333.4	6.7	329	5.8	150.3	4.
33	129.8	7.8	120.3	7	195.3	5.7
34	56.3	5.4	315	1.4	305	6.1
35	166	4.1	140.2	7.8	180	2
36	102.5	4.6	291.8	5.4	288.4	6.3
38	53.1	2.5	18.4	6.3	31	5.8

Table 29. Extent of differences in θ and r in different test situations.

Individual	A		B		C	
	θ	r	θ	r	θ	r
25	71.6	4.8	194.7	0.1	123.2	4.7
26	18.4	0.9	225.	0.2	243.4	1.1
27	14	0.1	246.5	2	260.5	2.1
28	18.4	0.3	112.8	2.2	131.2	1.8
29	9	0.2	170.5	2.1	161.6	2.3
30	11.3	0.9	56.3	4.2	67.6	3.2
31	288.4	1.2	195.7	3	92.7	1.8
32	4.4	0.9	183.2	2.7	178.8	1.8
33	9.6	0.9	63.4	2.1	75	1.3
34	258.7	4	248.7	0.7	11	4.7
35	25.8	3.7	14	2.1	39.8	5.8
36	189.3	0.8	185.9	1.7	3.4	0.9
38	34.7	3.8	22.2	3.3	12.5	0.5

A = 4 months toy tests compared with 15 months stimulus animal tests.

B = 4 months toy tests compared with 15 months SC tests.

C = 15 months stimulus animal tests compared with 15 months SC tests.

From this table, the following points are obvious:

1. Comparison of personality in 4 months toy tests with 15 months stimulus animal tests.

a) 10 of the 13 animals had a differences of less than 90° in θ ; and 9 of the 13 had a difference of less than 3 units in τ .

b) Animals with a difference greater than 90° in θ were numbers 31, 34, 36 - all male; 2 reared as intermediates and 1 as a mixed.

Animals with a difference greater than 3 units in τ were numbers 25, 34, 35, 38 - 1 female and 3 males; 1 from each of the 4 rearing conditions.

2. Comparison of personality dimensions in 4 months toy tests with 15 months slides/calls tests.

a) 9 of the 13 animals greater than 90° in θ ; 11 of the 13 animals had a difference of less than 3 units in τ .

b) Animals with a difference of less than 90° in θ were numbers 30, 33, 35, 38 - 2 females and 2 males; 2 subordinate, 1 mixed-, 1 intermediate-reared; 3 of the 4 were emotional introverts on both tests, 1 was an emotional extravert.

3. Comparison of personality dimensions in 15 month stimulus animal tests with 15 month slides/calls tests.
- a) Approximately half of the animals had a difference of more than 90° in θ ; 9 of the 13 animals had a difference of less than 3 units in τ .
- b) Animals with a difference of more than 90° in θ were numbers 25, 26, 27, 28, 29, 32-4 females and 3 males; 4 dominant-, 1 mixed- and 1 subordinate-reared.

Animals with a difference greater than 3 units in τ included numbers 25, 30, 34, 35 - 2 females and 2 males; 2 from the mixed condition and 1 each from the dominant - and intermediate-reared conditions.

DISCUSSION OF PERSISTENCE OF PERSONALITY CHARACTERISTICS

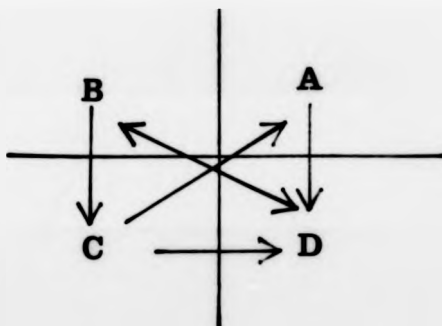
From these results, it can be seen that the personality characteristics of these animals were similar at 4 months of age in toy test situations and at 15 months of age in stimulus animal tests.

It could therefore be argued that personality at 4 months predicts personality at 15 months.

If, however, we compare personality at 4 months with that at 15 months in slides/calls situations, then we find a lack of similarity. This might lead us to query the hypothesis that early personality characteristics may be useful for predicting later personality characteristics.

However, if we examine figures 14 and 15, it can be seen that a pattern is evident in the nature of the differences between the 4 months and 15 months test situations.

Thus we get the following shifts in quadrants:

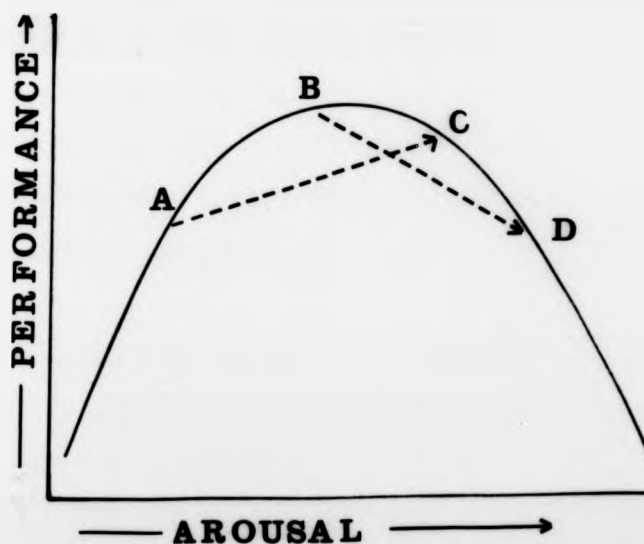


In order to explain this pattern of change, we must examine the nature of the test situations, since it is likely some aspect of the slides/calls test situation is inducing it.

If we look at the raw data, we find that for most animals (i.e., animals 1-23; ferals; infants 25-38), this situation is highly disturbing.

Given the emotional-arousing effect of the slides/calls situations, it was hypothesized that the nature of the personality changes may be explained by recourse to the Yerkes-Dodson law (Broadhurst 1959).

Thus, if we assume a curvilinear relationship between arousal and performance in a particular test situation, then in situations of low arousal we may find normally unaroused (i.e., calm extraverted animals at around point A on the curve below, and normally aroused (i.e., emotional introverted) animals around point B.



If we then assess the animals in a situation of high arousal; then, according to the Yerkes-Dodson law, animals normally at point A might shift to point C, while those normally at point B might shift to point D.

In other words, in situations of high arousal, normally unaroused animals (e.g., calm extraverts) should appear more emotional and/or more introverted; normally aroused animals (e.g., emotional introverts) should appear more calm and/or extraverted.

If we examine figures 14 and 15, we find that, for those animals which changed, these predictions are confirmed.

Thus animals which might be labelled calm extraverts, i.e., 25, 31, 32, in 3 month toy tests became emotional introverts in 15 month slides/calls tests; calm introverts, i.e., 27, 28, 29, became more extravert and/or emotional; emotional extraverts, i.e., 26, 34, 38, became more calm or stayed the same; emotional introverts, i.e., 30, 33, 35, 36, became more calm.

Therefore, it may be concluded that personality assessed at 4 months may be a useful predictor of personality at 15 months.

Of course, the relationship of personality characteristics assessed in the above situations, to personality characteristics observed in natural social settings, remains to be investigated.

5. Personality and Behaviour

Those behaviours not used in assessment of personality were assessed for their relationship to the three dimensions of personality.

These behaviours included:

- 1) frequency of play
- 2) frequency of affiliation
- 3) frequency of contacting the diaper
- 4) frequency of locomotion

In addition, two other measures were examined:

- 1) the total number of different behaviours shown by an individual in a given test situation
- 2) time taken to first contact of a novel object in toy test situations.

Only those behaviours which were significantly intercorrelated over different test situations for a given age are reported here.

Under 3 months

A) Food and toy tests etc.

Frequency of contacting the diaper was the only behaviour meeting the above criterion.

It was found that there were no significant sex differences in this behaviour ($U = 14$; $p = 0.183$; n.s.), and it was not correlated with extraversion ($r_s = -0.03$; n.s.), the only dimension reliably measured in these animals at this age.

B) Slides/calls tests

Frequency of contacting the diaper and locomotory behaviour met the criterion. These behaviours were not intercorrelated.

Neither of those behaviours showed a significant sex difference (contact diaper: $U = 16$; $p = 0.267$; n.s.; locomotion: $U = 13$; $p = 0.147$; n.s.); and only locomotory behaviour was significantly correlated with extraversion ($r_s = -0.82$; signif. at 0.01 level). For contact diaper, $r_s = -0.12$, n.s.

4 months

Toy tests.

5 behaviours met criterion here:

1. time taken to first contact of the novel object
2. frequency of locomtion
3. frequency of play
4. frequency of affiliation
5. frequency of contacting diaper.

These 5 behaviours were found to be significantly intercorrelated ($W = 0.37$; $\chi^2 = 22.11$; signif. at 0.05 level).

Further analyses revealed that animals who were quick to contact the novel object also showed:

- a) the most play ($r_s = -0.55$; signif. at 0.05 level)
- b) the least affiliation ($r_s = 0.57$; signif. at 0.05 level)
- c) the least contacting of the diaper ($r_s = -0.55$; significant at 0.05 level).

Locomotion was not correlated with time to contact novel object ($r_s = 0.38$ n.s.).

No significant sex differences were found for any of the above behaviours, however, frequency of play almost showed a significant sex difference, i.e., $U = 9$; $p = 0.51$, with females showing the least and males showing the most play in this situation.

For locomotion, the only behaviour not correlated with the others, there was found to be a significant correlation with psychoticism at this age ($r_s = 0.63$; signif. at 0.05). There was no significant correlation between this behaviour and the other two dimensions.

The other four behaviours were also found to be significantly correlated with psychoticism ($W = 0.49$; $\chi^2 = 29.6$), and with neuroticism ($W = 0.42$; $\chi^2 = 25.15$). They were not found to be correlated with extraversion ($W = 0.26$; $\chi^2 = 15.86$ n.s.).

15 months

a) Stimulus animal tests.

Locomotory behaviour was the only behaviour which reached criterion.

It was found that there were no significant sex differences in this behaviour ($U = 13$; $p = 0.147$; n.s.), and that it was not correlated with either neuroticism

($r_s = 0.05$; n.s.) or extraversion ($r_s = -0.03$ n.s.) in this test situation.

b) Slides/calls tests

Three behaviours met criterion: frequency of contacting the diaper, frequency of affiliation, and frequency of locomotion.

No intercorrelation among these behaviours was found.

There was a significant sex difference only in frequency of contacting the diaper ($U = 8$; $p = 0.037$; signif. at 0.05 level) with males showing the most, females the least.

Locomotion was the only behaviour found to be significantly correlated with personality. Thus it was found to be correlated with extraversion ($r_s = -0.74$; signif. at 0.05 level); but not with neuroticism ($r_s = 0.07$; n.s.).

Contacting the diaper was not correlated with extraversion ($r_s = -0.35$; n.s.) or neuroticism ($r_s = -0.03$ n.s.). Frequency of affiliation was not correlated with extraversion ($r_s = -0.18$ n.s.) or neuroticism ($r_s = 0.06$ n.s.).

DISCUSSION OF RELATIONSHIPS BETWEEN PERSONALITY AND
BEHAVIOUR

Only behaviours significantly intercorrelated over test situations at any given age were assessed for their relationship to personality. These behaviours, therefore, are characteristic of individuals at the particular age examined.

1. Contacting the diaper

This behaviour was found to be characteristic of individuals, not only at a particular age, but also throughout development. Thus the rank orders for this behaviour correlated across all test situations at all ages ($W = 0.66$; $\chi^2 = 31.89$; significant at 0.01 level).

Under 3 months of age, the only personality dimension reliably measured was extraversion. Frequency of contacting the diaper was not correlated with this dimension either at this age, or at the other two ages examined. It was also not correlated with neuroticism at 15 months of age.

However, at 4 months of age it was found to be correlated with personality. Thus, as a member of an intercorrelated cluster of behaviours (i.e., contacting diaper, time to contact novel object, play and

affiliation), it was found to be significantly correlated with both psychoticism and neuroticism.

The nature of the relationships between the intercorrelated cluster of behaviours and these dimensions was such that two contrasting types of individuals could be discerned.

- A) Those who were quick to contact the novel object; showed a high frequency of play; little affiliation; and little contact of the diaper.

These individuals were calm and non psychotic.

- B) Those who were slow to contact the novel object; showed a low frequency of play; a high frequency of affiliation; and a high frequency of contacting the diaper.

These individuals were emotional and psychotic.

The nature of the test situation itself, i.e., toy test situations, probably magnified these correlations. Thus if infants have contacted the novel object, they are likely to become less fearful of it, and to spend all their time playing with it, thereby excluding the demonstration of other behaviours. Conversely, if infants are fearful and do not contact the object, they are

likely to remain fearful, and thus show a high frequency of contacting and huddling against the diaper, and little or no play.

2. Locomotion

This behaviour was found to be characteristic of individuals at both 4 months and 15 months of age ($W = 0.51$; $\chi^2 = 30.57$; significant at 0.01 level).

At 4 months it was found to be correlated with psychoticism; whereas at 15 months, in slides/calls tests, it was found to be correlated with extraversion.

It has already been argued that the slides/calls test situation is highly arousing and results in normally extraverted individuals appearing as introverted, and normally introverted as extraverted.

Thus it could be argued that the observed correlation between locomotion and extraversion, where the apparently introverted (i.e. more highly aroused) individual shows the most locomotion, can be explained in terms of the arousing nature of the situation.

That is, the more aroused individuals, who therefore have higher cortical facilitation, should show greater output of the effectors (Corcoran 1964). Hence, just as

these individuals show more visual orienting behaviour, they should also show more locomotory behaviour.

The correlation between locomotion and psychoticism at 4 months may also be due to situation effects. Thus, since the most psychotic individuals also appear to be the most fearful of the novel object, they may spend much of their time moving around the cage in order to avoid contacting the object.

On the other hand, locomotion was scored as a rather gross-level category, covering all sorts of movement. It may be that the correlation of this behaviour with psychoticism, at this age in this test situation, is due to a significant contribution of stereotyped pacing behaviours to the category of locomotion.

3. Play and time to first contact of novel object.

These behaviours were only characteristic of individuals in toy test situations at 4 months, and they form part of the cluster of behaviours discussed above.

4. Affiliation

This behaviour was characteristic of individuals at 4 months, and again at 15 months. However the rank orderings of individuals were not significantly correlated between these two ages ($r_s = 0.18$).

At 15 months, frequency of affiliation was not found to be correlated with either extraversion or introversion.

At 4 months, it was part of the cluster of behaviours discussed above.

GENERAL DISCUSSION AND CONCLUSIONS

It would appear that Eysenck's three-dimensional theory of personality may be useful, not only for the characterization of primate personality, but also for the explanation of certain aspects of primate social behaviour.

Thus it was found that:

- a) individuals may be reliably ordered from high to low on each of the three dimensions of personality (neuroticism, extraversion, psychoticism)
- b) a fairly complete description of the individual's personality may be given by the combination of his/her scores on all three dimensions
- c) early personality characteristics may predict later personality in certain situations
- d) personality is correlated with certain aspects of

social behaviour.

However, although reliable methods of measuring these personality dimensions were obtained, the validity of these dimensions was not systematically examined in this study.

Some indication of validity however, was obtained. Thus it was argued that since the measures were deduced directly from Eysenck's theory of the biological bases of personality, then they have considerable face validity. In chapter 5, emotionality measures were found to have criterion validity. In addition, it was found in the DIMS study, that the resulting sex differences in personality, and the correlation of personality with specific social behaviours, appear to go in the directions predicted by the primate literature.

What is needed now, is a systematic examination of the validity of these dimensions of personality, e.g., by looking at physiological correlates, or subjective assessments of primate personality.

CHAPTER NINE

Dominance experience, personality and social behaviour in DIMS-reared stump-tail macaques.

It has been suggested in the primate literature (see chapter 2) that dominance may affect social behaviour either directly, by influencing the occurrence and patterning of particular social behaviours, or indirectly, by affecting the emotionality of the individuals concerned.

Before we can examine these hypotheses, however, we must investigate whether dominance is in fact a pertinent characteristic of social life in the particular species of interest.

In chapter 3, it was shown that, for laboratory stump-tail macaques, dominance appears to be an important characteristic of group life.

In this chapter, the effect of manipulating the infant's dominance experience on the development of its personality characteristics and social behaviour is examined.

METHOD

The sample consisted of 13 stump-tail infants, previously described in chapter 7.

The infants had been separated from their mothers at 8 days of age, reared in social isolation until 3 months of age, then given experimentally-controlled social experience with peers until 15 months of age.

Experience was controlled in such a way that each individual received only one type of dominance experience from 3 months of age until 15 months of age.

Dominance experience conditions consisted of the following:

- a) *Dominant only* - where the individual interacts only with those over whom it is dominant.
- b) *Subordinate only* - where the individual interacts only as the lowest ranking animal in any particular group.
- c) *Intermediate* - where the individual interacts only as a mid-ranking animal.
- d) *Mixed* - where the individual interacts alternately as a dominant and as a subordinate animal.

Details of the manipulation of dominance experience are given in chapter 6.

Regular checks were made on the dominance status of individuals throughout development by measuring priority

of access in milk and novel object tests.

The test situations to be reported here, include the following:

- a) 3 months test situations, i.e., separation, toy tests, food tests etc. Details of the test situations are given in table 18, chapter 7. Details of the testing schedule are given in appendix VI.
- b) 4 months test situations, i.e., toy tests. These were essentially a repetition of those described in table 19, chapter 7, with the addition of a very novel object, i.e., TTN (see figure 12).
- c) 15 months test situations, i.e., slides/calls tests as described in table 10 and figure 5, chapter 5; newly-formed triads as described in Walker Leonard (1979); and stimulus animal tests. Stimulus animal tests consisted of pairing the infant with an unknown stimulus animal. These included:
 1. peer 5 - a member of the peer group, described in chapter 3
 2. kid - a feral adult female
 3. Angus - a feral adult male.

Data collection methods are described in detail in chapter 7. A handwritten symbol notation method, was used for all non-social tests (Appendix I, VIII); the DTU method was used for all social tests (Appendix IX, X).

RESULTS

1. Manipulating dominance status.

Infants assigned to the same experimental condition were never allowed to interact together during the period of peer experience where dominance experience was being experimentally controlled.

In theory, however, they did have the opportunity to interact with all other infants in all possible dyadic and triadic combinations. In practice, the dyadic and triadic groupings had to be confirmed to those where the participants allowed a given individual to experience its appropriate rank history.

Table 30 gives details of the restrictions on the groupings of infants which developed during the attempt to manipulate their dominance experience.

In terms of the least restrictions placed on groupings, it can be seen from this table that:

- a) for the dominant group, 26 was the most successful, as

Table 30. Restrictions on groupings of infants in the manipulation of dominance experience.

A) DOMINANT GROUP

Individual	Restrictions
25	<p>could not be paired with 34 or 35 (mixed-reared males)</p> <p>could not be grouped in a triad with either of the above 2 animals, or with 31 (intermediate-reared male)</p>
26	<p>could be grouped in all possible combinations</p>
27	<p>could not be paired with 33 (subordinate-reared female), 34 or 35 (mixed-reared males)</p> <p>could not be grouped in a triad with any of the above 3 animals, nor with 31 or 36 (intermediate-reared males)</p>
28	<p>could be paired in all possible dyads, but could not be grouped in a triad containing 31 (intermediate-reared male)</p>

Table 30 contd.

B) INTERMEDIATE GROUP

Individual	Restrictions
30	could not be grouped in triads containing either 29 (mixed-reared female) or 35 (mixed-reared male)
31	could not be grouped in triads with either 25 or 27 (dominant-reared females) or 28 (dominant-reared male)
36	could not be grouped in triads containing 33 (subordinate-reared female)

C) MIXED GROUP

Individual	Restrictions
29	could be paired in all possible combinations
	could not be grouped in a triad containing 30 (intermediate-reared female)

Table 30 contd.

C) MIXED GROUP (contd)

Individual	Restrictions
34	could not be paired, or put in triads, with 25 or 27 (dominant-reared females)
35	could not be paired with 25 or 27 (dominant- reared females)
	could not be put in triads containing the above 2 animals or 30 (intermediate- reared female)

D) SUBORDINATE GROUP

Individual	Restrictions
32	could be grouped with all possible partners
33	could not be paired with 27 (dominant-reared female)
	could not be put in a triad containing the above animal or 36 (intermediate-reared male)
38	could be grouped with all possible partners

- a dominant animal, followed by 28, then 25, and finally 27
- b) for the intermediate group, 36 was the most successful intermediate, followed by 30, and finally 31
- c) for the mixed group, 29 was the most successful at being both dominant and subordinate, depending on social context. 34 was the next most successful, and 35 the least successful
- d) for the subordinate group, both 32 and 38 were highly successful subordinates. 33 was the least successful as a subordinate animal.

DISCUSSION OF MANIPULATION OF DOMINANCE STATUS

Intuitively, variation in the success at manipulating dominance status appeared to result from the infants having their own ideas about what their status should be.

Thus, in the dominant group, 25, and particularly, 27, did not appear to *want* to be dominant.

In the subordinate group, 33 seemed determined NOT to be a subordinate animal. In triads, she showed a high frequency of intermediate strategy use.

In the intermediate group, 31 appeared to *want* to be a dominant animal. 36 was rather anti-social; and 30 appeared rather ineffective, although she appeared to try, i.e., she would try to elicit help and showed redirection of aggression, but was often attacked by others.

In the mixed group, 34 and 35 appeared to *want* to be dominant animals. 29 seemed content with any status.

These hypotheses can, of course, be examined by analysis of the longitudinal data.

If we look at the personality characteristics of those animals who appeared to want to be dominant in the majority of their interactions, i.e., 26, 28, 31, 33, 34, 35, we find that in 4 months toy tests, these animals were all ranked as psychotic, and 4 of the 6 were emotional psychotics. 28 and 31 were not as emotional as the other 4, but they were near the median for neuroticism.

Furthermore, if we look at the personality characteristics of those who appeared more interested in being subordinate, i.e., 25, 27, 32 and 38, we find that 3 of the 4 were ranked as calm and non-psychotic. 38 was ranked as an emotional psychotic and hence may have been expected to have striven after dominant status. However, he was very much younger than the other animals, and this may account for the ease of making him a subordinate animal.

This correlation between personality characteristics and ease of manipulating dominance status supports the finding in the literature that there appears to be an interaction between some aspect of individual differences and dominance status (Candland *et al* 1970; Chamove and Bowman 1976; Marsden 1968).

However, the specific relationship discovered in this study appears contrary to the relationship suggested in the literature. Thus, rather than finding that the animals who apparently want to become dominant are relatively non emotional (Candland *et al* 1970), it is found in this study that they tend to be relatively emotional and also psychotic.

This particular correlation may have resulted from two aspects of the experimental paradigm: a) the social situations used to manipulate dominance status; b) the use of the peer-rearing paradigm.

- a) The social situations used to manipulate dominance status were highly unstable, i.e., they involved different groupings of individuals every day, for a period of only 1 or 2 hours interaction (see appendix VII). This resulted in infants having to reassert their status every day. The very nature of the social situations may therefore have produced, or at least enhanced, the observed correlation between emotional psychoticism and dominance.

b) The peer-ranking paradigm has been shown to result in a "Lord of the flies" atmosphere (Goldfoot 1976). compared to the atmosphere found in more normally reared infants. The fact that infants interacted only with agemates in the present study may therefore have also enhanced the observed correlation between emotional psychoticism and dominance.

It is likely then, that in more normally reared infants, if a correlation between personality and dominance behaviour is found, it may be quite different. Thus in chapter 5, for socially-reared infants, it was found that the most dominant individuals were also the most calm individuals. A finding in agreement with the general literature.

Unfortunately, in this study, personality characteristics were not reliably measured (except for extraversion) *before* specific social experience. As a result, we cannot be certain that the relationship between personality and dominance, may be used to predict dominance behaviour.

However, since personality was reliably measured in the 4 months toy tests carried out during the first week of social experience, and since restrictions on groupings only became evident *after* this period, it is likely that this assessment of personality may be used to predict future dominance behaviour.

In this case, it is likely that if the animals had been permitted to remain continuously in peer groups (rather than being switched around every day), then those who appeared emotionally psychotic in 4 months toy tests, would have ended up as high-ranking individuals, whilst those who were relatively calm and non psychotic would have ended up as low-ranking individuals.

Instead, by experimentally manipulating dominance, we now have the opportunity to make the following comparisons:

- A) emotional psychotics who are allowed to become dominant, i.e., D-gp and M-gp animals, vs. emotional psychotics who are not permitted to become dominant, i.e., I-gp and S-gp animals.

- B) calm non-psychotics who are permitted to remain subordinate, i.e., S-gp and M-gp animals, vs. calm non-psychotics who are not allowed to be subordinate, i.e., D-gp and I-gp animals.

These comparisons are examined in the next section.

2. Personality changes after 12 months of specific dominance experience.

Table 31 gives a classification of the individuals according to the above comparison features.

Table 31. Classification of individuals according to personality characteristics (neuroticism and psychoticism only) and experimentally-manipulated dominance experience.

Personality	Allowed to become dominant	Not allowed to become dominant
	Emotional psychotic	Dgp - 26, 28* Mgp - 34, 35
	Allowed to stay subordinate	Not allowed to stay subordinate
Calm nonpsychotic	Sgp - 32 Mgp - 29	Dgp - 25, 27 Igp - 30*

*individuals near the median in neuroticism, but classified according to psychoticism.

The data reported in tables 28 and 29, and figures 14, 15 and 16, chapter 8, are again examined.

Only changes in extraversion and neuroticism are examined, because psychoticism was reliably measured in only one test situation.

From tables 28 and 29, if we examine the nature of the personality changes we find that:

a) in comparing personality in 4 months toy tests with that in 15 months stimulus animal tests:

25 becomes more emotional and less extravert

31 becomes more emotional and less extravert

34 becomes less emotional and less extravert

35 becomes more emotional and less extravert

36 becomes less emotional and more extravert

38 becomes more emotional and more extravert

All other animals, i.e., 26, 27, 28, 29, 30, 32, 33, remain unchanged in these personality attributes.

From these results, it can be seen that emotional psychotics who were allowed to become dominant (i.e., 26/28), did not change their personality characteristics (i.e., their ranking on neuroticism and extraversion) when assessed in a novel stimulus animal situation at 15 months of age.

Emotional psychotics who were allowed to be sometimes dominant, sometimes subordinate (i.e., 34, 35), did change their personality characteristics. Thus 34 became less emotional and 35 became more emotional than before.

Emotional psychotics who were allowed to be dominant over one animal, while being at the same time subordinate to another (i.e., 31 and 36), also changed their personality characteristics. Thus 31 became more emotional, and 36 became less emotional and more extravert.

Emotional psychotics who were never allowed to be dominant (i.e., 33 and 38), were divided. Thus 38 changed his characteristics, becoming more emotional; while 33 did not change hers.

Calm non-psychotics who were allowed to remain subordinate (i.e., 32) did not change.

Calm non-psychotics who were allowed to be sometimes subordinate, sometimes dominant (i.e., 29) did not change.

Calm non-psychotics who were allowed to be subordinate to one animal whilst being dominant to another (i.e., 30) did not change.

Calm non-psychotics who were not allowed to remain

Emotional psychotics who were allowed to be sometimes dominant, sometimes subordinate (i.e., 34, 35), did change their personality characteristics. Thus 34 became less emotional and 35 became more emotional than before.

Emotional psychotics who were allowed to be dominant over one animal, while being at the same time subordinate to another (i.e., 31 and 36), also changed their personality characteristics. Thus 31 became more emotional, and 36 became less emotional and more extravert.

Emotional psychotics who were never allowed to be dominant (i.e., 33 and 38), were divided. Thus 38 changed his characteristics, becoming more emotional; while 33 did not change hers.

Calm non-psychotics who were allowed to remain subordinate (i.e., 32) did not change.

Calm non-psychotics who were allowed to be sometimes subordinate, sometimes dominant (i.e., 29) did not change.

Calm non-psychotics who were allowed to be subordinate to one animal whilst being dominant to another (i.e., 30) did not change.

Calm non-psychotics who were not allowed to remain

subordinate (i.e., 25 and 27) were divided. Thus 25 became more emotional and less extravert; whilst 27 remained the same.

- b) in comparing personality in 4 months toy tests with that in slides/calls tests.

It is found that most animals showed extensive changes in personality. These have already been accounted for in terms of the arousing effect of the slides/calls tests (see chapter 8).

DISCUSSION OF PERSONALITY CHANGES

If we assume that emotional psychoticism is predictive of ease of manipulating dominance in a peer-rearing paradigm; and that calm non-psychotic individuals are likely to become subordinate-ranking, whilst emotional psychotic individuals are likely to become dominant-ranking, then we may deduce the following:

- 1) Emotional psychotics who are permitted to be dominant should not need to change their characteristics in situations which apparently call for similar attributes, i.e., unstable novel social interactions (e.g., stimulus animal tests).

- 2) Emotional psychotics who are not permitted to be dominant for the majority of their social interactions, may change their characteristics as a result of frustrating their "predicted" dominance status.
- 3) Calm non-psychotics who are permitted to be subordinate should not need to change their personality characteristics.
- 4) Calm non-psychotics who are not allowed to be subordinate for the majority of their social interactions may change their characteristics as a result of interfering with their "predicted" dominance status.

These hypotheses are supported, in the main, by the data.

The only exceptions being the cases of individual 27 and individual 33.

The latter was an emotional psychotic female who was not permitted to be dominant, and hence may have been expected to show some change in her personality attributes. However, she was in fact the highest ranking animal on both emotionality and psychoticism, thus, unlike other emotional psychotics, she could not have shown an increase in emotionality (cf. 31, 35). And indeed, this particular

animal never gave up striving to be dominant (i.e., in terms of frequency of dominance strategy use).

Number 27, on the other hand, was a calm non-psychotic female who was an extremely "reluctant" dominant. Thus, although in theory, her experience was as a dominant animal, in practice she was very often subordinate. Hence the lack of change in her characteristics in the stimulus animal tests.

Since the hypotheses concerning personality and dominance experience were supported by these data, this gives tentative support to our original premises.

It may be hypothesized, then, that early environmental experience which in some way thwarts the attainment of "predicted" dominance status, may lead to specific changes in the personality characteristics of individuals. The nature of these changes may depend on the original personality dispositions of the individual.

It may be further hypothesized that early environmental experience which in some way supports the attainment of "predicted" dominance status, may lead to individuals demonstrating similar personality characteristics when tested at later ages in situations calling for similar attributes, e.g., stimulus animal tests.

If, however, these individuals are tested in situations which call for different attributes, e.g., slies/calls tests, then it may be found that their personality characteristics have changed, but in a lawful way (see chapter 8, Yerkes-Dodson law).

Thus it is quite likely that examination of the longitudinal data will show that in stable groups of familiar animals (i.e., tests at around 6 months of age), where it has been shown that dominant status correlates with calmness, that those animals who were not thwarted in attaining their "predicted" dominance status, may never-the-less have changed in personality characteristics, in such a way that individuals allowed to become dominant, may have become relatively non-neurotic, and individuals allowed to remain subordinate, may have become relatively neurotic.

3. Dominance experience, personality and dominance strategy behaviour.

The data reported in Walker Leonard (1979) are again examined.

Table 32 presents the frequency of dominance strategies exhibited by individuals in newly-formed triads of liked-reared animals.

Table 32. Frequency of dominance strategies exhibited by DIMS-reared stump-tail macaques in newly formed triads.

Triad	Resulting rank	Individual	Dominance strategies*	Day of testing			Total frequency
				1	2	3	
Dominants together	1	25	M	4	0	0	4
			I	15	0	0	15
			A	7	1	0	8
			P	3	0	0	3
	2	27	M	0	0	0	0
			I	3	1	0	4
			A	4	0	0	4
			P	4	0	0	4
	3	28	M	0	0	0	0
			I	0	0	0	0
			A	0	0	0	0
			P	0	0	0	0
							42
Intermediates together	1	31	M	3	4	2	9
			I	0	1	0	1
			A	2	6	0	0
			P	0	0	0	0
	2	36	M	0	0	1	1
			I	0	9	1	10
			A	0	4	2	6
			P	0	0	0	0

Table 32 contd.

Triad	Resulting rank	Individual	Dominance strategies*	Day of testing			Total frequency
				1	2	3	
Intermediates together (contd)	3	30	M	0	0	0	0
			I	0	0	0	0
			A	0	0	0	0
			P	0	0	0	0
							27
Mixeds together	1	29	M	13	0	0	13
			I	10	0	0	10
			A	18	1	0	19
			P	0	0	0	0
	2	35	M	2	0	0	2
			I	17	0	0	17
			A	20	0	0	20
			P	6	0	0	6
	3	34	M	0	0	0	0
			I	0	0	0	0
			A	0	0	0	0
			P	0	0	0	0
							87
Subordinates together	1	37	M	8	0	0	8
			I	1	0	0	1
			A	6	2	0	8
			P	1	1	0	2
	2	33	M	5	0	0	5
			I	9	2	2	13
			A	12	4	0	16
			P	0	2	0	2

Table 32 contd.

Triad	Resulting rank	Individual	Dominance strategies*	Day of testing			Total frequency
				1	2	3	
Subordinates together (contd)	3	38	M	0	0	0	0
			I	0	0	0	0
			A	0	0	0	0
			P	0	0	0	0
							57

In these tests, 3 of the dominants were placed together in 1 triad, i.e., 25, 27, 28; the 3 mixeds were placed in another; the 3 intermediates in another; and 3 of the subordinates, i.e., 33, 37, 38, in another.

For dominants-together, the females were included rather than 26 because an earlier investigation of dominance strategy behaviour in groups 1 to 5 had already looked at 3 dominant males together, and also 2 dominant males with 1 dominant female.

For subordinates-together, the males 37 and 38 were included rather than 32, to capitalize on the relatively rare occurrence of males as subordinate animals.

From table 32, it can be seen that the triad showing the highest frequency of dominance strategy behaviour was that of the mixeds-together (total frequency = 87). Subordinates were next highest (57), followed by dominants-together (42). Intermediates-together showed the lowest frequency of dominance strategy behaviour (27).

DISCUSSION OF DOMINANCE STRATEGY BEHAVIOUR

From these results, it would appear that rearing individuals as sometimes dominant, sometimes subordinate, is most conducive to the occurrence of dominance strategy behaviour, regardless of whether the animal is predisposed

to being a calm non-psychotic, i.e., 29, or an emotional psychotic, i.e., 35.

Rearing individuals as mid-ranking animals, on the other hand, appears to result in the least demonstration of dominance strategy behaviour.

This may be because of some attribute of the particular individuals chosen to be intermediate animals. Thus 31 and 36 may have been more interested in asserting status via dyadic rather than triadic interactions. Unfortunately, in this study, no record of the dyadic agonistic interactions was made.

4. Dominance experience, personality and the probability of different motivational types of behaviour.

Classification of behaviour according to presumed underlying motivation is given in appendix III.

Table 33 gives details of the relative percentage of dominance, submission, play, sex and affiliation by infants in slides/calls tests at 3 months of age.

Table 34 gives details of the relative percentage of these same behaviours by the same individuals in the same test situations at 15 months of age (i.e., after specific dominance experience).

Table 33. Relative percentage of dominance, submission, play, sex and affiliation shown by socially isolated stump-tails in slides/calls tests at 3 months of age.

Group	Individual	DOMINANCE			SUBMISSION			PLAY			SEX			AFFILIATION		
		SA	CA	SC	SA	CA	SC	SA	CA	SC	SA	CA	SC	SA	CA	SC
D-gp	25	0	0	0	51	27	91	0	0	0	8	16	1	38	58	7
	26	0	0	0	33	7	74	0	0	0	43	0	0	24	93	26
	27	0	0	0	48	69	91	0	0	0	10	3	0	41	27	9
	28	26	0	0	13	40	60	17	0	0	0	0	0	43	60	40
I-gp	30	0	0	0	51	57	69	0	0	0	0	7	0	49	36	31
	31	10	0	0	20	55	29	58	0	18	0	0	0	12	45	53
	36	4	3	0	42	52	86	15	0	0	0	39	5	40	6	8
M-gp	29	0	8	0	34	76	58	33	0	3	0	0	0	34	16	39
	34	0	4	0	10	40	35	30	4	0	3	0	0	57	52	65
	35	21	0	2	14	63	68	4	3	0	7	0	0	53	34	29
S-gp	32	5	0	0	22	56	37	41	0	28	0	0	0	32	44	35
	33	0	0	0	39	54	83	1	11	0	42	0	6	18	34	12
	38	0	0	13	3	27	38	9	0	31	26	9	13	63	64	6

SA = slides alone; CA = calls alone; SC = slides and calls.

Table 33. Relative percentage of dominance, submission, play, sex and affiliation shown by socially isolated stump-tails in slides/calls tests at 3 months of age.

Group	Individual	DOMINANCE			SUBMISSION			PLAY			SEX			AFFILIATION		
		SA	CA	SC	SA	CA	SC	SA	CA	SC	SA	CA	SC	SA	CA	SC
D-gp	25	0	0	0	51	27	91	0	0	0	8	16	1	38	58	7
	26	0	0	0	33	7	74	0	0	0	43	0	0	24	93	26
	27	0	0	0	48	69	91	0	0	0	10	3	0	41	27	9
	28	26	0	0	13	40	60	17	0	0	0	0	0	43	60	40
I-gp	30	0	0	0	51	57	69	0	0	0	0	7	0	49	36	31
	31	10	0	0	20	55	29	58	0	18	0	0	0	12	45	53
	36	4	3	0	42	52	86	15	0	0	0	39	5	40	6	8
M-gp	29	0	8	0	34	76	58	33	0	3	0	0	0	34	16	39
	34	0	4	0	10	40	35	30	4	0	3	0	0	57	52	65
	35	21	0	2	14	63	68	4	3	0	7	0	0	53	34	29
S-gp	32	5	0	0	22	56	37	41	0	28	0	0	0	32	44	35
	33	0	0	0	39	54	83	1	11	0	42	0	6	18	34	12
	38	0	0	13	3	27	38	9	0	31	26	9	13	63	64	6

SA = slides alone; CA = calls alone; SC = slides and calls.

Table 34. Relative percentage of dominance, submission, play, sex and affiliation shown by DIMS-reared juveniles in slides/calls tests.

Group	Individual	DOMINANCE			SUBMISSION			PLAY			SEX			AFFILIATION		
		SA	CA	SC	SA	CA	SC	SA	CA	SC	SA	CA	SC	SA	CA	SC
D-gp	25	0	3	2	82	46	66	0	3	0	4	46	15	14	3	16
	26	5	0	0	41	38	8	10	0	0	2	8	0	43	54	12
	27	0	0	0	67	81	63	0	0	0	2	0	0	31	19	38
	28	6	0	3	40	50	72	9	0	0	2	0	3	43	50	21
I-gp	30	4	7	17	32	73	38	8	0	0	11	0	3	45	20	41
	31	18	0	5	35	32	46	7	0	5	12	7	8	29	61	36
	36	3	0	0	18	90	89	64	0	7	3	0	0	12	10	4
M-gp	29	1	0	0	45	90	95	18	0	0	0	0	0	36	10	5
	34	8	0	57	22	65	27	47	4	2	0	0	0	19	30	14
	35	1	0	0	51	60	43	7	0	0	0	0	0	40	40	57
S-gp	32	1	0	0	58	13	21	20	69	56	5	4	2	16	13	22
	33	0	0	0	63	26	26	6	48	19	1	0	0	30	26	55
	38	2	0	0	22	43	10	14	0	0	35	29	48	27	29	42

SA = slides alone; CA = calls alone; SC = slides and calls.

Table 35. Relative percentage of dominance, submission, play, sex and affiliation shown by DIMS-reared juveniles in stimulus animal tests.

Group	Individual	DOMINANCE		SUBMISSION		PLAY		SEX		AFFILIATION	
		5	K A	5	K A	5	K A	5	K A	5	K A
D-gp	25	0	1 0	64	33 90	2	0 0	1	14 0	33	52 10
	26	5	1 1	15	61 84	1	0 0	21	9 0	59	29 15
	27	5	2 0	42	35 96	2	0 0	27	45 0	24	18 4
	28	1	2 1	38	59 86	0	1 0	22	15 3	40	24 10
I-gp	30	0	0 0	5	34 85	0	0 0	4	17 0	91	49 15
	31	10	4 0	43	16 82	3	0 2	13	28 7	31	51 10
	36	0	4 0	45	11 68	0	0 0	11	48 11	43	37 21
M-gp	29	0	1 3	23	17 62	20	15 5	23	15 0	35	39 30
	34	0	0 1	55	53 76	11	0 0	4	25 4	30	22 19
	35	0	0 0	86	40 77	0	0 0	1	31 8	13	29 10
S-gp	32	1	2 1	49	32 78	2	0 0	18	18 0	29	48 21
	33	4	0 0	61	30 73	0	1 0	7	32 16	28	38 10
	38	0	0 0	32	17 47	1	1 0	50	45 38	18	37 16

5 = peer 5; K = kid; A = Angus.

Table 35 gives details of the relative percentage of these behaviours in stimulus animal tests at 15 months of age.

It was found that these probabilities were not correlated across the different conditions within the same test situation (Kendall's coefficient of concordance, 0.05 level of significance). Thus, for example, the relative probability of dominance behaviour was not similar for individuals tested in SA, CA or SC conditions within the slides/calls battery of tests.

This finding may reflect the importance of the test situation in influencing the probability of occurrence of these behaviours.

From table 33 it can be seen that in slides/calls tests at 3 months, the two major categories of response are submission and affiliation in these animals. All other categories are shown relatively infrequently.

If we look at the probability of occurrence of the different types of behaviour in terms of subsequent dominance experience, we find that there is no difference between animals assigned to different dominance experience conditions, with respect to probability of dominance, submission or affiliation.

Play and sex behaviour, however, appear to be differentially exhibited.

Thus for play, animals assigned to the D-gp seemed to show the least probability of its occurrence. Only 28 showed this behaviour in this group, and only in the slides alone condition.

Animals assigned to the other 3 groups appeared to show play with similar probability.

For sex, animals assigned to the M-gp showed the least probability of its occurrence. Thus only 34 and 35 showed sexual behaviour, with a very low probability of occurrence (3%; 7%), and only in the slides alone condition.

Animals assigned to the other 3 groups appeared to show sex behaviour with similar probability of occurrence.

From table 34, it can be seen that in slides/calls tests at 15 months, dominance behaviour has a low probability of occurrence in these test situations, whilst submission and affiliation have a high probability of occurrence.

Play appears to be differentially exhibited depending on dominance experience. Thus dominant-reared individuals show the lowest probability of its occurrence; whilst

mixed - and subordinate-reared individuals show a fairly high probability of its occurrence.

Sex behaviour also appears to be differentially exhibited depending on dominance experience. Thus it was never exhibited in any slides/calls test situation by mixed-reared individuals. It was, however, shown by all members of all other groups in at least of the slides/calls conditions.

From table 35, it can be seen that in stimulus animal tests at 15 months, submission, sex and affiliation had a high probability of occurrence for most individuals in most of the stimulus animal conditions. Dominance behaviour had a low probability of occurrence, as did play, except in the case of individual 29, who showed a high probability of play with all 3 stimulus animals.

DISCUSSION OF PROBABILITY OF OCCURRENCE OF BEHAVIOUR

Only two behaviours appear to be differentially affected by different dominance experiences, and then only in slides/calls tests.

These behaviours are probability of play and probability of sex.

Thus in slides/calls tests at 15 months, the D-gp show a low probability of play and the M-gp and I-gp show

a high probability of play. The M-gp show no sex behaviour in this test situation.

However, this same pattern of response was found in slides/calls tests at 3 months of age. Thus rather than reflecting a dominance experience effect, these differences in response must reflect a personal response bias of the individuals who just happened to be grouped together under the same dominance experience condition.

This lack of a dominance experience effect on the probability of different types of behaviour in these novel situations was anticipated by pilot data.

Thus when the probability of dominance, submission, play, sex, and affiliation, was examined in groups 1 to 5 in slides/calls tests, it was found that there was no correlation between the pattern of probable responses and dominance rank.

Conversely, in familiar stable group situations, i.e., milk test situations, it was found that the probability of response type was correlated with dominance rank (see table 5, chapter 3).

Thus it was found, for all 5 groups of differentially-reared juveniles, that both the alphas and the animals ranking second in groups of 4 tend to have a higher

probability of dominance and a lower probability of submission than expected. The omegas and animals ranking third in groups of 4 tend to have a lower probability of dominance and a higher probability of submission than expected.

It is likely then, that if we examine the probability of response type for DIMS-reared infants in stable group situations, we may find an effect of differential dominance experience.

If this is the case, then we might argue that dominance experience effects tend to be confined to the situations in which the experience is gained.

CONCLUSIONS

These findings, then, suggest that throughout development there appears to be an ongoing interaction between personality characteristics and dominance experience in the determination of social behaviour.

It has been possible to tease apart some of the relationships in this study, but of course, the hypotheses presented in this chapter are very preliminary, and must be extensively investigated in both experimental and naturalistic paradigms.

In conclusion, the following relationships were suggested by the data:

1. Personality characteristics prior to specific social experience may predict future dominance status, and affect the ease with which dominance status may be manipulated.

In the peer-rearing paradigm, involving much switching of partners, the relationship between personality and future dominance status appears to be that:

- a) emotional psychotics (who also tend to be males) tend to become dominant
 - b) calm non-psychotics (who also tend to be females) tend to become subordinate.
2. If environmental experience in some way thwarts the attainment of this "predicted" dominance status, this may lead to specific changes in the personality characteristics of individuals. The nature of these changes may depend on the original personality dispositions of the individual.
 3. Rearing individuals as sometimes dominant, sometimes subordinate (i.e., M-gp), appears to be the most conducive to the occurrence of dominance strategy behaviour, regardless of the personality characteristics

of the individual. While rearing individuals as mid-ranking (i.e., I-gp), appears not to be conducive to the occurrence of this behaviour.

4. In novel situations, the probability of dominance, submission, sex, play and affiliation, is not affected by differential dominance experience.

CHAPTER TEN

General discussion and conclusions.

This series of investigations was guided by a specific model for the explanation of the development of social behaviour.

This model, referred to as a transactional model, views the development of social behaviour in the individual as a process involving constant interplay between organismic and experiential sources of variability in behaviour.

In this thesis, the utility of the concept of personality, which may be thought of as an organismic variable, and the concept of dominance, which may be thought of as an experiential variable, was examined.

These sources, and the causal relationships examined in this thesis, are summarized in figure 2, chapter 2.

In brief, it was expected that :

- a) the inherited substratum would have direct effects on the development of social behaviour in the individual, e.g., via IRM's (Sackett 1966).

- b) dominance experience would have direct effects on the development of behaviour, e.g., by influencing the frequency and occurrence of specific communicative behaviours.

- c) personality predispositions (inherited substratum) and specific dominance experiences would interact to affect the development of the individual's personality characteristics, and thereby indirectly affect the development of social behaviour.

In presenting this model, it was emphasized that the principles of dominance and personality were not considered to be the only two possible explanatory principles, or even the two most useful principles, for the study of primate social development.

Similarly, it was emphasized that the causal relationships outlined in the model were not considered to be the only possible relationships among the variables of interest.

Instead, the model was put forward as the simplest version of the potential causal relations among the variables of interest in order to guide the experimental analysis of the development of social behaviour in stumptail macaques.

It was viewed, therefore, as a preliminary theoretical model, to be revised and elaborated in the light of future findings. Consequently, in this chapter, the main findings are reviewed in order to examine the adequacy of the underlying model.

MAIN FINDINGS

1. The communicative abilities of socially deprived stump-tail macaques.

It was found that infant stump-tail macaques, with no previous social experience, are capable of exhibiting *all* of the compound, species-typical, communicative expressions examined in this study (N = 13 ; 7♂, 6♀ ; 48 behaviours).

There appears to be a developmental progression, with certain behaviours appearing before others. However, in this study, it was not extensively investigated whether this reflected an actual maturational progression, or whether it just reflected the use of specific stimulus situations at specific developmental ages.

There appears to be quite a range of individual variation in the first occurrence of specific expressive behaviours, even although infants were reared, up to the age of 3 months, in conditions which were as identical as possible, and were tested in identical test situations.

This individual variation may be related to personality characteristics, but this was not tested in this study, as it was found that personality could not be reliably measured, using the methods developed here, for infants under 3 months of age.

Individual variation did not appear to be dependent on sex differences, except in the case of two behaviours: open mouth threat and anogenital inspection. Both of these behaviours were shown more frequently, and at an earlier age, by the males in the sample.

Not only were these socially deprived infants capable of exhibiting all of the species-typical behaviours examined, but also they were capable of exhibiting them in what appeared to be appropriate affective contexts.

Thus, for example, the first occurrences of withdraw, bite and self-aggression were elicited in response to frustration (frustration food tests, see table 17, chapter 7); whereas the first occurrence of open mouth play face was elicited in response to a familiar object (toy test A or B, see table 18, chapter 7).

And in the very first social test with a peer-reared partner, given when the infants reached 3 months of age, it was found that the infants responded to

dominance behaviour by the partner with submission (if they were younger than, and therefore subordinate to, the partner, i.e., all infants tested with 26); they responded with play to the partner's play; and finally, they responded with dominance to the partner's submission (if they were older than, and therefore dominant to, the partner, e.g., 26 tested with 37).

Furthermore, it would appear that certain communicative stimuli function as innate releasing stimuli for certain of the communicative behaviours of these infants. Thus, when tested in slides/calls situations prior to social experience, the infants were found to differentiate various types of stumptail threat expressions and calls, the grimace expression, and also the male sex rattle call, from other communication signals.

The cues used to differentiate between stimuli were not examined in this study. The infants may have used fairly non-specific cues. For example, in the case of calls, they may have used cues like pitch, length of call, rhythmicity, etc. This must await future investigation.

In addition to the demonstration of fairly molecular units of behaviour, i.e., the individual threat expressions, etc., it was found that socially deprived stumptail macaques are capable of exhibiting these behaviours as units in higher-order behaviour patterns.

The actual data have not been reported here, but it was found that stumptail macaques, who have been isolated from 10 days to 15 months of age, and have subsequently lived together as a group for 3 months, exhibit a high frequency of dominance tactics when placed in a triad with two unfamiliar animals. In addition, stumptail macaques, who have been socially isolated from 8 days of age until 3 months of age, show dominance tactics in their first or second triadic groupings (Walker Leonard unpub. data).

These findings, then, demonstrate that the inherited substratum has important direct effects on the development of social behaviour in stumptail macaques. This gives support to one of the hypotheses of the underlying theoretical model.

These findings also demonstrate that what we have labelled the direct effects of the inherited substratum are more extensive in range than those already reported in the literature for rhesus macaques (see chapters 4 and 7).

This may reflect a species difference, since stumptails appear to develop more quickly than rhesus (Chevalier-Skolnikoff 1973 (b)), or it may point to the significance of differences in rearing conditions among the various studies which have examined the behavioural capabilities of isolated macaques.

Thus, in the present study, while infants were reared in *social* isolation, they had the opportunity to interact with various *non social* objects (presented to them at what was thought to be an adequate pace for promoting development); they had constant contact with an object for contact comfort; they were handled daily for weighing by a technician (wearing a face mask to prevent facial signalling); and they could see and hear whatever was going on in the laboratory environment, although they could not see or interact with other members of their species.

It is likely, then, since this environment was fairly rich in sensory stimulation, although lacking in species-specific social stimulation, that it did not interfere too much with the developing capacities of the infants.

As a consequence, the findings may reflect more accurately the nature and extent of those macaque communicative abilities which do not require species-specific social experience for development.

Support for the hypothesis of direct effects of the inherited substratum does not imply that social experience has no effect on the development of social communication. Social experience is likely to be important in a number of ways, as discussed in chapter 7.

What the findings do emphasize is that infants have certain communicative competences, and these should not be ignored in any experimental study of the effects of social experience, or in any naturalistic study.

These competences consist not only of the ability to recognize and exhibit specific communicative behaviours, but also they are likely to depend on various information-processing capacities of the organism, e.g., attentional strategies, perceptual biases, etc.

2. The importance of personality in the development of social behaviour.

In these studies, it was found that individual stumptail macaques may be reliably ordered from high to low on each of Eysenck's three dimensions of personality, namely, neuroticism, extraversion, and psychoticism. Reliability, however, may be affected by factors like the age of the individual when tested, and the nature of the test situation used.

Sex differences were found in the dimensions of neuroticism (or emotionality) and psychoticism, with the males in the sample tending to be both more emotional and more psychotic than the females.

The validity of the dimensions was not systematically examined. However, it was argued that each of the dimensions had considerable face validity, and demonstrated that emotionality had criterion validity.

Where reliable rank orderings on all three dimensions of personality were obtained, i.e., in 4 months toy tests, it was found that the three dimensions were fairly independent.

It was also found that a fairly complete description of the individual's personality may be given by the combination of its scores on all three dimensions (see figure 13, chapter 8).

Although these findings may be thought of as supporting the idea that Eysenck's (1967) theory of personality may be useful for the characterization of primate personality, it must be emphasized that problems were encountered in developing measures to assess the dimensions. This was particularly the case with psychoticism. Little research has been done on this dimension in humans and although it is suggested here that it may be deduced from the pattern of aggressive, solitary and inappropriate social behaviour in macaques, the human dimension may not be exactly equivalent.

Furthermore, it must be kept in mind that these animals were reared in a very restricted environment, therefore any conclusions must in the first instance be restricted to this experimental situation.

At 3 months and at 15 months, in slides/calls tests, it was found that locomotory behaviour was correlated with the dimension of extraversion, in such a

way that the most introverted individual tended to show the most locomotion.

And at 4 months, in toy tests, a cluster of behaviours was found to be correlated with emotional psychoticism. This correlation was such that animals who were quick to contact a novel object also showed the most play, the least affiliation, the least contact of the diaper, and were ranked as calm non-psychotics.

Although a significant sex difference was found in emotional psychoticism, such that males tended to be emotional and psychotic, and females tended to be calm and nonpsychotic, none of the behaviours correlated with emotional psychoticism showed a significant sex difference.

This points to the importance of looking at both higher-order clusters of behaviour, and the full characterization of the individual's personality attributes, in addition to standard dependent variables.

It also indicates that knowledge about the individual's personality characteristics may enable us to predict certain of his/her behavioural characteristics in certain situations.

This finding supports the hypothesis that personality has certain direct effects on the development

of social behaviour in the individual and permits us to conclude that the individual's personality characteristics should be taken into account in the study of the development of social behaviour.

Not only was it found that personality may be used to predict certain of the individual's behavioural characteristics, but also the personality characteristics of the individual at 4 months of age were found to predict the individual's personality characteristics in certain situations at 15 months of age.

Thus, it was found that the personality characteristics of the 13 infants, in terms of ranking on extraversion and neuroticism, were similar at 4 months of age in toy test situations and at 15 months of age in stimulus animal situations. Personality characteristics in slides/call tests at 15 months of age were different from those at 4 months of age, but they were different in a lawful way, such that personality at 4 months was still a useful predictor of personality at 15 months.

Taken in conjunction with the previous findings, this predictive relationship between early and late personality characteristics indicates that the link between inherited substratum - personality - social behaviour is quite important in these particular animals.

However, it must be remembered that this link was examined only in unstable social situations and in non-social situations. The characterization of the infant's personality in stable social situations has still to be carried out.

It is likely that in such situations, the individual's personality characteristics may be quite different. Thus, it may be found that in stable social situations, the individual's personality characteristics may change as a result of the interaction between the individual's inherited predispositions and his/her specific dominance experiences in these particular situations.

3. The interaction of personality and dominance experience.

In this study it was found that the personality characteristics of the infants, assessed prior to social experience, may be useful for predicting future dominance status. However, because of the small numbers in each experimental group, the findings must be viewed as tentative.

Thus, in the peer-rearing paradigm investigated here, the relationship between early personality characteristics and future dominance status appeared to be such that:

- a) emotional psychotics (who also tend to be male) tend to become dominant

b) calm non-psychotics (who also tend to be female) tend to become subordinate.

This specific correlation between emotional psychoticism and predicted dominance rank may have been enhanced by the particular experimental conditions used. In different situations, calling for different kinds of attributes, it may be found that dominance status is predicted by some other combination of personality characteristics.

It was also found in this study that the infant's early personality characteristics affected the ease with which dominance rank could be manipulated. Thus the dominance experience of the infants could only be manipulated to a degree dependent on the individual's early personality characteristics, and hence the individual's "predicted" dominance status.

If experimentally-manipulated dominance experience thwarted the attainment of this "predicted" status in some way, this was found to lead to specific changes in the personality characteristics of the individual when tested in novel social situations and non social situations.

Conversely, if the experimentally-manipulated dominance experience supported, in some way, the attainment of "predicted" status, then the personality

characteristics of the individual did not change in these situations.

The personality characteristics of the DIMS infants in familiar social situations were not examined in this thesis, however, the personality characteristics of juveniles in groups 1 to 5 in familiar social situations were assessed (see chapter 5).

In groups 1-5, it was found that for group 1 (dark), group 3 (isolate) and group 5 (social), dominance rank was correlated with neuroticism such that the more dominant animals tended to be less emotional than the subordinate animals.

This finding gave support to the findings in the literature (chapter two) that dominance rank affects the emotionality of individuals.

Together with the DIMS data, these findings suggest that the original hypothesis of the underlying theoretical model, which stated that personality dispositions and specific dominance experiences interact to affect the development of the individual's personality characteristics and the development of social behaviour, should be expanded to incorporate the following hypotheses:

- 1) the personality dispositions of the infant (particularly the degree of neuroticism and

psychoticism) may predict the future dominance status of the individual, and may affect the ease with which its dominance experience may be manipulated.

- 2) specific dominance experience may affect the early personality characteristics of the individual such that:
 - a) in familiar stable social situations, animals who become dominant-ranking tend to become relatively calm; animals who become subordinate tend to become relatively emotional.
 - b) in novel social situations, or in non social situations, animals whose "predicted" dominance status has been thwarted in some way may tend to show different personality characteristics: animals whose "predicted" dominance status has been supported may tend to show the same personality characteristics as in similar early test situations.

This may lead to the observation that infants appear to "revert" back to early personality characteristics when tested in novel situations (see Thomas *et al* 1970).

These hypotheses must await future investigation.

4. The influence of dominance experience on social behaviour.

It was found that dominance experience may affect the frequency with which dominance strategy behaviour is exhibited in newly formed triads of like-reared animals.

Thus it was found that rearing individuals as sometimes dominant, sometimes subordinate, i.e., the mixed group, appears to be the most conducive to the occurrence of dominance strategy behaviour. While rearing individuals as midranking, i.e., the intermediate group, appears to result in a low occurrence of such behaviour.

Dominance experience did not appear to affect the probability of dominance, submission, sex, play or affiliation shown by individuals in novel social situations, or in non-social situations. Again, because of small sample size, these results must be viewed as preliminary.

It was not tested whether dominance experience affected the probability of these different types of behaviours in familiar social situations. But pilot data (chapter 3) indicated that it might have some effect.

Thus, in milk test situations, it was found, for the dark, peer, isolate and social groups, that both the alphas and betas tended to have a higher probability of

dominance and a lower probability of submission than expected. Omegas and animals ranking third in these groups of four, on the other hand, tended to have a lower probability of dominance and a higher probability of submission than expected.

CONCLUSIONS

In conclusion, it can be seen that the basic model of causal effects appears to be supported by the main findings of the DIMS study. However, it must again be emphasized that the findings are limited by small sample size, restricted rearing environment, and difficulties in measuring personality. It can also be seen that the hypotheses of this underlying theoretical model are rather too simplistic to account for the actual course of development in these infants. Instead it is suggested that they be replaced by the hypotheses outlined in this chapter.

In this study, the behaviour of individuals, who were reared in an environment where only one major experimental factor was varied, was examined. It is likely that when the factors of personality and dominance experience are examined in a more complex, semi-naturalistic situation, that even the superordinate hypotheses will need to be revised.

The findings do, however, tentatively suggest that personality may be a valid phenomenon in nonhuman primates, worthy of examination in

its own right, and as an intermediate variable or covariate in studies of the effects of environmental influences on the development of social behaviour.

If future work supports the idea that Eysenck's dimensions of personality are useful for the study of monkeys as well as man, then it is likely that future experimental research into the personality of monkeys will make a significant contribution to the study of personality and social behaviour in man. One potential contribution is likely to be in the specification of the neuroendocrine bases of personality differences (see Gray 1973).

SUMMARY

The primate experimental literature on the causal determinants of social behaviour was reviewed, and guidelines for the study of causation of social behaviour were obtained.

A transactional model for the explanation of the development of primate social behaviour was outlined. This model views the development of social behaviour in the individual as a process involving constant interplay between organismic and experiential sources of variability in behaviour.

The utility of two possible explanatory principles was examined: personality, which may be thought of as an organismic variable, and dominance, which may be thought of as an experiential variable. It was found that both of these concepts appear to have potential utility for the explanation of the development of social behaviour in stumptail macaques.

The communicative abilities of socially-deprived stumptail macaques were investigated and it was found that their abilities appeared to be greater than those previously indicated in the literature for macaques.

Diagnostic tools for objective and reliable

measurement of Eysenck's dimensions of personality, i.e., neuroticism, extraversion, and psychoticism, were developed; and the persistence of personality characteristics in the first fifteen months of life examined.

The effect of manipulating the infant's dominance experience on the development of its personality characteristics and its social behaviour was investigated.

It was concluded that the data supported a transactional model of causation, and it was suggested that future experimental research on personality in monkeys is likely to make a significant contribution to the study of personality and social behaviour in man.

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APPENDIX I Symbol notation system.

Behaviour	Symbol	Behaviour	Symbol
<u>submission</u>		<u>exploration</u>	
teeth chatter		visual explore	∂x
grimace	V	locomotion	\xrightarrow{m}
withdraw		contact	\emptyset
freeze			
jerk		<u>dominance</u>	
		bounce	\xrightarrow{D}
<u>play</u>		yawn	Y
bounce	\xrightarrow{P} 	brow threat	\wedge
initiate	PI	open mouth threat	O
sprawl	Pspl	teeth chatter threat	V_T
open mouth face	Po	scream threat	V_T
chasing	\xrightarrow{P} 	chase	\longrightarrow
wrestling	Pwr	grab/hit	gb/ht
open mouth biting	POMB	bite	bt
<u>affiliation</u>		<u>vocalizations</u>	
groom	g	scream	scr
present for groom	pg	gurgle	ggl
lipsmack/pout	ls/pt	trill/whinney	trill/whny
square mouth	\square_m	cack/cackle	ck/ckl
follow	\xrightarrow{f}	whistle	whs
huddle	hd	cheep/squeek	chp/sq
mouth nibble	mn	bitey	bty
		teeth chomp	tc

APPENDIX I (contd)

Behaviour	Symbol	Behaviour	Symbol
<u>sex</u>		<u>others</u>	
present	f Δ	approach	→
mount	m Δ	tongue protrude	tp
anogenital inspect	Δ ins	open mouth	O _m
		solitary	solit
<u>stereotypies</u>		in proximity to	prox
masturbation	Δ ms	drinks	dr
self aggression	Λ s		
self huddle	s.hd.		
withdraw swinging	— s		

APPENDIX II Sample data sheet for milk test situation.

(Data from dark group, milk test 2).

Data record

Supplementary notes

1 - + 3

3 gb bt 1

2 solit.3 P_E4 P 21 prox 32 P 43 gb 14 P 2

APPENDIX III Classification of behaviour according to presumed underlying motivation in stumptail macaques.

Motivation	Behaviours
submission	still; present; teeth chatter; grimace; withdraw; freeze; jerk; scream
play	bounce; initiate; sprawl; open mouth play face; chasing; wrestling; open mouth biting
dominance	bounce; mount; yawn; teeth chomp; brow threat; open mouth threat; teeth chatter threat; scream threat; chase; grab/hit; bite
sex	anogenital inspect; mount; masturbation
affiliation	groom; present for groom; lipsmack; square mouth; follow; huddle; mouth nibble

APPENDIX IV Definitions of emotionally expressive behaviours in stump-tail macaques.

Behaviour	Definition
<u>submission</u>	
still	animal holds its current posture, with eyes averted
present	animal orients perineum towards a partner or object
teeth chatter	rapid opening and closing of mouth lips fully retracted vertically, baring the teeth which chatter audibly
grimace	mouth corners drawn back, lips retracted vertically, baring teeth often accompanied by shrieking vocalization or screams
withdraw	moves away from a stimulus
freeze	tense, rigid posture, with limbs and face held protectively close to body
scream	high pitched noisy vocalization

APPENDIX IV (contd)

Behaviour	Definition
<u>play</u>	
bounce	animal grasps an object and bounces up and down in a very relaxed manner. Often accompanied by eyes closed and open mouth play face.
initiate	animal invites another to join in play by one of a variety of techniques e.g., quick contact then run off
sprawl	animal was on its back in a very relaxed manner. Arms and legs flailing in the air. Eyes often closed. Often accompanied by open mouth play face.
open mouth play face	mouth open wide. Eyes may be closed, or open but unfocused. Posture relaxed.
chasing	as implied. Animals relaxed, often showing open mouth play face
wrestling	as implied. Again animals are relaxed, often showing open mouth play face

APPENDIX IV (contd)

Behaviour

Definition

play (contd)

open mouth biting wrestling play, accompanied by gentle
open mouth biting of partner's body

dominance

bounce animal grabs hold of object or partner,
and bounces vigorously up and down,
with rigid body posture and tense
facial expression

mount individual clasps pelvis of a
presenting animal with its hands and
makes thrusting movements towards the
perineum of the presenting animal

yawn head often thrown back; eyes often
partially or completely closed; mouth
opened slowly and lips withdrawn to
expose the teeth fully

teeth chomp animal nashes teeth together with
characteristic "grinding" or
"squelching" sounds

APPENDIX IV (contd)

Behaviour	Definition
<u>dominance</u> (contd)	
brow threat	intense visual fixation, brows alternately raised and lowered
open mouth threat	as for brow threat, but mouth open and accompanied by low pitched "huh" vocalization
teeth chatter threat	intense visual fixation, accompanied by teeth chattering and an "eh-eh" vocalization
scream threat	intense visual fixation with grimace and screeching vocalization
chase)) grab/hit)) bite)	as implied
<u>sex</u>	
anogenital inspect	animal touches, looks at, or sniffs the anogenital area of another animal

APPENDIX IV (contd)

Behaviour	Definition
<u>sex (contd)</u>	
mount	as for dominance mount, but accompanied by erection and, often, intromission
masturbation	animal manipulates its own genitalia
<u>affiliation</u>	
groom	searching and picking with fingers or mouth through the fur of a partner
present for groom	offering a part of the body (but not the perineum) to another animal
lipsmack	eyes open and directed at partner or object. Lips pursed, and mouth opened and closed rapidly, producing characteristic lipsmacking sound
square mouth	muzzle thrust forward and upward lips protruded and slightly parted to form a square

APPENDIX IV (contd)

Behaviour	Definition
-----------	------------

affiliation (contd)

follow	as implied
--------	------------

huddle	animal sits with arms and head tucked in towards its body, and rests against an object (usually with its side)
--------	--

mouth nibble	animal makes nibbling movements at an object with its mouth. Usually directed at another animal's mouth.
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APPENDIX V Sample data sheet for S/C test situations.

(Data from isolate group : animal 13
responding to slide 9 in SA condition).

slide 9

scr → scr scr why why tr

^m → ~~tr~~ s.hd. ^m → chp scr chp-whs

chp chp whs tr ^m → → ~~tr~~

why why-whn scr

Data to be read from left to right, in sentence form.

APPENDIX VI Testing schedule for non social tests in
social isolation phase of DIMS study (all dates 1975).

ANIMAL	TEST				
	SEPN	PM1	El	ESPrelim*	DkBox1*
25	11-4	15-4	15-4	24-4	1-5
26	15-4	21-4	21-4	1-5	6-5
27	28-4	29-4	29-4	2-5	18-5
28	1-5	2-5	2-5	5-5	20-5
29	5-5	6-5	6-5	9-5	25-5
30	15-5	16-5	16-5	19-5	4-6
31	26-5	27-5	27-5	30-5	15-6
32	4-6	5-6	5-6	8-6	24-6
33	26-6	27-6	27-6	—	18-7
34	6-7	7-7	7-7	—	26-7
35	11-7	12-7	12-7	—	30-7
36	11-7	12-7	12-7	—	31-7
38	16-8	17-8	17-7	—	5-9

APPENDIX VI (contd)

ANIMAL	ES2*	GD1	TEST		
			GM1	FF1	Toy 1
25	2-5	—	8-5	9-5	13-5
26	7-5	—	13-5	14-5	18-5
27	19-5	—	25-5	26-5	30-5
28	21-5	—	27-5	28-5	1-6
29	26-5	—	1-6	2-6	6-6
30	5-6	6-6	11-6	12-6	16-6
31	16-6	17-6	22-6	23-6	27-6
32	25-6	26-6	1-7	2-7	6-7
33	—	19-7	25-7	26-7	30-7
34	—	27-7	2-8	3-8	7-8
35	—	31-7	6-8	7-8	11-8
36	—	1-8	7-8	8-8	12-8
38	—	6-9	12-9	13-9	17-9

APPENDIX VI (contd)

ANIMAL	ESRETEST*	TEST		
		TOY 2	GM2	DkBox 2*
25	14-5	20-5	27-5	28-5
26	19-5	26-5	1-6	2-6
27	31-5	7-6	13-6	14-6
28	2-6	9-6	15-6	16-6
29	7-6	14-6	20-6	21-6
30	17-6	24-6	30-6	1-7
31	28-6	5-7	12-7	13-7
32	7-7	14-7	20-7	21-7
33	—	7-8	13-8	14-8
34	—	15-8	21-8	22-8
35	—	19-8	25-8	26-8
36	—	20-8	26-8	27-8
38	—	10-10	1-10	2-10

APPENDIX VI (contd)

ANIMAL	TEST			
	FF2	TT2	ND2	DkBox 3*
25	29-5	30-5	6-6	26-6
26	3-6	4-6	11-6	1-7
27	15-6	16-6	23-6	12-7
28	17-6	18-6	25-6	15-7
29	22-6	23-6	30-6	20-7
30	2-7	3-7	10-7	30-7
31	14-7	15-7	22-7	11-8
32	22-7	23-7	30-7	19-8
33	15-8	16-8	23-8	11-9
34	23-8	24-8	31-8	20-9
35	27-8	28-8	4-9	24-9
36	28-8	29-8	5-9	25-9
38	3-10	4-10	9-10	31-10

APPENDIX VI (contd)

ANIMAL	SA	TEST	
		CA	S+C
25	27-6	28-6	29-6
26	2-7	3-7	4-7
27	13-7	14-7	15-7
28	16-7	17-7	18-7
29	21-7	22-7	23-7
30	31-7	1-8	2-8
31	12-8	13-8	14-8
32	20-8	21-8	22-8
33	12-9	13-9	14-9
34	21-9	22-9	23-9
35	25-9	26-9	27-9
36	26-9	27-9	28-9
38	1-11	2-11	3-11

APPENDIX VI (contd)

* test not reported in this thesis

KEY

SEPN = Separation from mother
PM1 = Prior move 1
E1 = Environment 1
GD1/2 = Given diapers 1/2
GM1/2 = Given milk 1/2
FF1/2 = Frustration Food 1/2
SA = slides alone
CA = calls alone
S+C = slides and calls

APPENDIX VII Sample schedule for dyadic and triadic groupings in peer experience phase in DIMS study.

Date (1976)	Groupings
10th April	29 + 36 + 33
	26 + 31 + 35
	27 + 30 + 38
	25 + 32
	28 + 34
11th April	34 + 36 + 32
	25 + 30 + 37
	35 + 38
	26 + 29
	27 + 33
12th April	26 + 31 + 34
	27 + 30 + 38
	29 + 32
	28 + 35
	25 + 37

APPENDIX VIII Sample data sheet for non social test situations in isolation phase of DIMS study.

Infant	Test	Date
29	TTC	4/7/75

$\partial X T \text{ is } \overset{m}{\rightarrow} \partial X C \quad \partial X T \overset{m}{\rightarrow} \text{ is}$

$\Theta D \text{ is } \partial X C / T / C / T \quad \Theta D \quad \partial X C / T / E$

$\Theta D \overset{m}{\rightarrow} \partial X T / C / D / T \quad \overset{m}{\rightarrow} \partial X T / E$

$\overset{m}{\rightarrow} \partial X C / T / C / M B \quad \Theta h M B \overset{m}{\rightarrow} \partial X T$

$\overset{m}{\rightarrow} \partial X E / T / C / T / C / T / C / T \quad \overset{m}{\rightarrow} \partial X C / T$

$\partial X E \quad \overset{p}{\underbrace{\quad}} \quad \partial X T \overset{m}{\rightarrow} \partial X C \quad \partial X T$

$\partial X E \quad O_{mth} \quad \partial X T / C \overset{m}{\rightarrow} \partial X C / T$

$\partial X C / T / C / T / C \overset{m}{\rightarrow}$

first two min. only

APPENDIX IX Classification of behaviour of stump-tail
macaques for recording by DTU system.

DTU number	Behaviour	DTU number	Behaviour
11	still	34	open mouth play face
12	present	35	play chasing
13	teeth chatter	36	play wrestling
14	grimace	37	play open mouth biting
15	withdraw	38	play gurgles
16	freeze	39	general play
17	jerk	41	dominance bounce
18	scream	42	dominance mount
19	general submission	43	brow threat
21	visual explore	44	open mouth threat
25	locomotion	45	chase
26	contact	46	grab/hit
31	play bounce	47	bite
32	play initiate	48	teeth chomp
33	play sprawl	49	general dominance
51	groom	71	unknown
52	present for groom	72	scream threat
53	lipsmack	73	excitement teeth chatter
54	square mouth	74	yawn
55	follow	75	approach
56	huddle	76	wheelbarrow huddle
57	mouth nibble	77	self aggression
58	affiliation rattle	78	teeth chatter threat

APPENDIX IX (contd)

DTU number	Behaviour
59	general affiliation
61	sex-mount
63	masturbation

APPENDIX X Sample of DTU record for social test 1 : 33
with 26.

NUMBER	TIMES	EVENTS
1	0	0
2	0	0
3	1	154550
4	33	114250
5	63	182150
6	93	152150
7	123	832150
8	141	212150
9	165	212120
10	185	557550
11	217	117550
12	233	187550
13	255	182650
14	287	154550
15	317	112550
16	343	117040
17	395	803030
18	413	154550
19	443	212150
20	459	112650
21	523	154550
22	547	135650
23	613	137550
24	641	154550
25	671	154650
26	721	137550
27	737	214250
28	793	117350
29	817	162650
30	847	112650
31	871	116150
32	907	112650
33	933	212150
34	959	112650
35	979	215350
36	997	114650
37	1019	154650
38	1051	562110
39	1077	212150
40	1095	114650

Codes for directions:

- 1 = first animal responding to environment; second responding to first
- 2 = second animal responding to environment; first responding to second
- 3 = both responding to environment
- 5 = animals responding to each other

Times are in tenths of a second.

Events are read as follows:

The first two digits give the first animal's behaviour; the second two digits give the second animal's behaviour; the final digit gives the direction of the behaviour of both animals.

Thus, in event number 3, i.e., 15 45 5:

Infant 33 is showing behaviour 15 (withdraw).
Infant 26 is showing behaviour 45 (chase).
The animals are responding to each other (direction = 5).

APPENDIX XI Age of first occurrence of compound communicative expressions in socially deprived infant stump-tail macaques.

Behaviour	Infant												
	25	26	27	28	29	30	31	32	33	34	35	36	38
<u>submission</u>													
still	-	3 mths	3 mths	-	3 mths	3 mths	2 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths
present	3 mths	3 mths	-	-	-	-	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths
teeth chatter	6 wks	2 mths	6 wks	2 mths	2 mths	3 mths	2 mths	7 wks	1 mth	6 wks	1 mth	1 mth	9 days
grimace	3 mths	3 mths	6 wks	-	3 mths	3 mths	2 mths	3 mths	3 mths	3 mths	3 mths	3 mths	6 wks
withdraw	2 mths	5 wks	6 wks	5 wks	5 wks	5 wks	6 wks	5 wks	3 mths	6 wks	5 wks	6 wks	3 mths
freeze	3 mths	-	-	-	-	3 mths	3 mths	3 mths	3 mths	-	3 mths	3 mths	3 mths
jerk	8 days	8 days	8 days	8 days	5 wks	8 days	8 days	8 days	9 days	8 days	8 days	1 mth	9 days
<u>play</u>													
bounce	-	-	2 mths	3 mths	3 mths	3 mths	3 mths	3 mths	-	3 mths	3 mths	3 mths	3 mths
play initiate	-	3 mths	3 mths	-	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths
sprawl	-	-	-	-	-	3 mths	3 mths	3 mths	3 mths	-	-	-	3 mths
open mouth	2 mths	2 mths	2 mths	3 mths	2 mths	3 mths	2 mths	3 mths	3 mths	2 mths	3 mths	3 mths	3 mths
chasing	-	-	-	-	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths
wrestling	-	-	-	-	-	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths
open mouth bite	-	-	-	3 mths	-	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths
general	7 wks	9 days	-	2 mths	5 wks	2 mths	2 mths	2 mths	3 mths	2 mths	3 mths	2 mths	3 mths

APPENDIX XI contd.

Behaviour	Infant												
	25	26	27	28	29	30	31	32	33	34	35	36	38
<u>dominance</u>													
bounce	-	3 mths	-	3 mths	3 mths	-	-	3 mths	3 mths	3 mths	2 mths	3 mths	-
mount	-	-	-	-	-	-	3 mths	-	-	3 mths	-	-	3 mths
yawn	-	2 mths	-	6 wks	2 mths	-	3 mths	-	-	3 mths	-	5 wks	7 wks
teeth chomp	3 mths	3 mths	-	-	3 mths	-	-	3 mths	3 mths	-	3 mths	-	3 mths
brow threat	-	-	9 days	-	-	-	7 wks	-	3 mths	3 mths	-	3 mths	-
open mouth threat	-	-	-	3 mths	-	-	7 wks	-	-	3 mths	2 mths	3 mths	5 wks
teeth chatter	3 mths	-	-	-	-	-	3 mths	3 mths	-	3 mths	2 mths	-	3 mths
threat													
scream threat	-	-	-	-	-	-	-	-	-	-	-	-	3 mths
chase	-	-	-	-	-	-	-	-	-	3 mths	-	-	-
grab/hit	-	3 mths	-	3 mths	5 wks	-	-	-	5 wks	3 mths	3 mths	3 mths	-
bite	-	3 mths	3 mths	5 wks	5 wks	5 wks	7 wks	-	-	3 mths	3 mths	3 mths	5 wks
<u>affiliation</u>													
groom	3 mths	3 mths	-	3 mths	-	-	-	-	-	3 mths	-	3 mths	3 mths
present for groom	-	-	3 mths	-	-	-	-	-	-	-	-	-	-
lipsmack/pout	5 wks	9 days	8 days	5 wks	9 days	8 days	9 days	8 days	1 month	5 wks	8 days	8 days	9 days
square mouth	3 mths	3 mths	8 days	3 mths	9 days	3 mths	3 mths	-	3 mths	3 mths	9 days	8 days	3 mths

APPENDIX XI contd.

	25	26	27	28	29	30	31	32	33	34	35	36	38
Behaviour													
<u>affiliation contd</u>													
huddle	3 mths	3 mths	-	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths	3 mths
mouth nibble	-	-	3 mths	-	-	3 mths	-	-	-	-	-	-	-
<u>sex</u>													
anogenital inspect	3 mths	3 mths	-	3 mths	-	-	3 mths	-	-	3 mths	3 mths	3 mths	3 mths
mount	-	-	-	3 mths	-	-	3 mths	-	-	-	-	-	-
masturbate	6 wks	2 mths	3 mths	6 wks	2 mths	3 mths	3 mths	-	3 mths	2 mths	3 mths	5 wks	7 wks
<u>vocalizations</u>													
scream	8 days	8 days	8 days	8 days	8 days	8 days	8 days	8 days	8 days	8 days	8 days	8 days	8 days
gurgle	5 wks	6 wks	9 days	6 wks	2 mths	7 wks	3 mths	1 month	2 mths	5 wks	5 wks	5 wks	7 wks
trill/whinney	9 days	5 wks	8 days	8 days	-	8 days	8 days	-	3 mths	8 days	9 days	8 days	5 wks
cack/cackle	5 wks	3 mths	9 days	8 days	8 days	8 days	3 mths	5 wks	8 days	1 month	9 days	1 month	-
whistle	5 wks	6 wks	8 days	8 days	2 mths	5 wks	2 mths	9 days	2 mths	3 mths	9 days	2 mths	9 days
cheep/squeek	9 days	9 days	8 days	8 days	2 mths	8 days	8 days	1 month	5 wks	3 mths	9 days	3 mths	9 days
bitey	3 mths	5 wks	-	-	-	5 wks	2 mths	3 mths	2 mths	-	8 days	2 mths	-

APPENDIX XI contd.

	Infant												
	25	26	27	28	29	30	31	32	33	34	35	36	38
Behaviour													
<u>other expressions</u>													
tongue protrude	5 wks	9 days	8 days	9 days	9 days	8 days	2 mths	7 wks	9 days	8 days	5 wks	5 wks	5 wks
open mouth	9 days	-	8 days	5 wks	9 days	8 days	8 days	1 month	1 month	8 days	8 days	1 month	8 days
self huddle	3 mths	2 mths	2 mths	7 wks	3 mths	5 wks	3 mths	2 mths	3 mths	3 mths	1 month	3 mths	2 mths
follow	-	-	-	3 mths	-	-	-	3 mths	-	3 mths	3 mths	3 mths	-
approach	5 wks	5 wks	5 wks	5 wks	5 wks	5 wks	5 wks	5 wks	5 wks	5 wks	1 month	5 wks	5 wks
self aggression	3 mths	2 mths	-	6 wks	6 wks	-	7 wks	-	-	-	-	7 wks	5 wks

APPENDIX XII Test situations in which compound communicative expressions first occurred in DIMS study.

Behaviour	Infant												
	25	26	27	28	29	30	31	32	33	34	35	36	38
<u>submission</u>													
still	-	ST1	SA	-	ST1	ST1	TT	ST1	ST1	ST1	ST1	ST1	ST1
present	ST2	ST1	-	-	-	-	ST1	ST1	SA	SA	SA	ST1	ST1
teeth chatter	T1	TTE	T1	TTE	TTD	SA	TTF	T2	GDI	T1	GDI	GDI	E1
grimace	S+C	S+C	T1	-	CA	CA	T2	ST1	SA	ST2	SA	S+C	T1
withdraw	GM2	GM1	T1	FF1	GM1	FF1	T1	FF1	CA	T1	FF1	T1	ST1
freeze	SA	-	-	-	-	CA	S+C	ST1	S+C	-	S+C	CA	ST1
jerk	S	S	S	S	GM1	S	S	S	E1	S	S	GDI	PM1
<u>play</u>													
bounce	-	-	TTA	ST2	ST1	ST2	ST2	ST1	-	ST1	ST1	ST1	ST1
play initiate*	-	ST1	ST1	-	ST1	ST2	ST1	ST1	ST1	ST1	ST1	ST1	ST1
sprawl	-	-	-	-	-	ST2	ST1	ST1	ST1	-	-	-	ST1
open mouth	T1B	T1B	T1A	ST2	TTA	ST2	TTC	ST1	ST1	TTA	ST1	ST1	ST1
chasing*	-	-	-	-	ST1	ST2	ST1	ST1	ST1	ST1	ST1	ST1	ST1
wrestling*	-	-	-	-	-	ST2	ST1	ST1	ST1	ST1	ST1	ST1	ST1
open mouth bite*	-	-	-	ST2	-	ST2	ST1	ST1	ST1	ST1	ST1	ST1	ST1
general	T2	PM1	-	GM2	GM1	GM2	TTA	TTA	CA	TTA	SA	GM2	CA

APPENDIX XII contd.

Behaviour	25	26	27	28	29	30	31	32	33	34	35	36	38
<u>dominance</u>													
bounce	-	ST1	-	SA	ST1	-	-	ST1	-	ST1	GM2	ST2	-
mount	-	-	-	-	-	-	ST2	-	-	ST2	-	-	ST2
yawn	-	TTE	-	T1	TTE	-	ST2	-	-	CA	-	FF1	T2
teeth chomp	-	ST1	-	-	CA	-	-	-	ST2	ST2	-	ST2	S+C
brow threat	-	-	E1	-	-	-	T2	-	ST1	ST1	-	ST1	-
open mouth threat	-	-	-	ST2	-	-	T2	-	-	ST1	GM2	ST1	FF1
teeth chatter threat	ST2	-	-	-	-	-	SA	SA	-	ST2	FF2	SA	-
scream threat	-	-	-	-	-	-	-	-	-	-	-	-	ST1
chase*	-	-	-	-	-	-	-	-	-	ST2	-	-	-
grab/hit	-	ST1	-	ST2	FF1	-	-	-	FF1	ST1	ST1	ST1	-
bite	-	ST1	-	ST2	FF1	FF1	T2	-	-	ST1	ST1	ST1	FF1
<u>affiliation</u>													
groom*	ST2	ST1	-	ST2	-	-	-	-	-	ST1	-	ST1	ST2
present for groom*	-	-	ST2	-	-	-	-	-	-	-	-	-	-
lipsmack/pout	GM1	PM1	S	GM1	E1	S	E1	S	GD1	GM1	S	S	PM1
square mouth	S+C	SA	S	S+C	E1	CA	SA	-	SA	SA	E1	S	SA
huddle*	ST2	ST1	-	ST2	ST1	ST2	ST1	ST2	ST1	ST2	ST1	ST2	ST1
mouth nibble*	-	-	ST2	-	-	ST2	-	-	-	-	ST2	-	-

APPENDIX XII contd.

	25	26	27	28	29	30	31	32	33	34	35	36	38
Behaviour													
<u>sex</u>													
anogenital inspect*	ST2	ST1	-	ST2	-	-	ST1	-	-	ST2	ST2	ST2	ST2
mount	-	ST2	-	ST2	-	-	ST1	-	-	-	-	-	-
masturbate	T1	FF2	SA	T1	T1D	CA	ST2	-	SA	TTC	SA	GM1	T2
<u>vocalizations</u>													
scream	S	S	S	S	S	S	S	E1	S	S	S	S	S
gurgle	GM1	T1	E1	T1	TTC	T2	SA	GD1	TTA	FF1	GM1	GM1	T2
trill/whinney	PM1	GM1	S	S	-	S	S	-	SA	S	PM1	S	FF1
cack/cackle	GM1	S+C	E1	S	S	S	S+C	FF1	S	GD1	E1	GD1	-
whistle	GM1	T1	S	S	GM2	FF1	GM2	E1	GM2	SA	PM1	GM2	PM1
cheep/squeek	PM1	PM1	S	S	TTA	S	S	GD1	GM1	SA	PM1	SA	PM1
bitey	S+C	GM1	-	-	-	FF1	GM2	SA	TTA	-	S	GM2	-
<u>other expressions</u>													
tongue protrude	GM1	PM1	S	E1	E1	S	GM2	T2	E1	S	GM1	GM1	GM1
open mouth	PM1	-	S	GM1	E1	S	S	GD1	GD1	S	S	GD1	S
self huddle	SA	TTF	GM2	T2	SA	FF1	SA	TTC	SA	SA	GD1	SA	FF2

APPENDIX XII contd.

	25	26	27	28	29	30	31	32	33	34	35	36	38
Behaviour													
other expressions contd													
follow*	-	-	-	ST2	-	-	-	ST1	-	ST2	ST2	ST1	-
approach	GM1	GM1	GM1	GM1	GM1	GM1	GM1	GM1	GM1	GM1	GD1	GM1	GM1
self aggression	ST2	FF2	-	T1	T1	-	T2	-	-	-	-	T2	FF1

*Behaviours which require a social partner for expression.

KEY TO TABLE: (refer to table 17 for description of tests)

S	- Separation	TTA-F	- Toy tests
PM1	- Prior move 1	SA	- Slides alone
E1	- Environment 1	CA	- Calls alone
GD1	- Given diapers 1	S+C	- Slides and calls
GM1	- Given milk 1	ST1	- Social test 1
FF1	- Frustration Food 1	ST2	- Social test 2
GM2	- Given milk 1		
FF2	- Frustration Food 2		
GD2	- Given diapers 2		
T1	- Toy 1		
T2	- Toy 2		

APPENDIX XIII contd.

3) teeth chatter (contd)

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
32	6	2	0	0	0	0	0	0	0
33	4	1	0	0	0	2	2	2	1
34	0	0	0	1	0	0	0	0	0
35	0	0	0	0	0	1	0	0	0

4) grimace

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
33	2	0	0	0	0	0	0	1	0
35	0	0	0	1	0	0	0	0	0

5) withdraw

individual	SLIDE STIMULUS								
	1	2	2	4	5	6	7	8	9
25	2	0	0	0	0	0	0	0	0
26	0	1	0	0	0	0	0	0	0
28	0	0	0	0	1	0	0	0	0
29	7	4	1	2	0	0	0	0	0
30	1	1	2	0	0	0	0	1	1
32	4	2	1	0	0	0	0	0	0
33	3	1	3	0	0	0	0	0	0
34	1	0	0	0	0	0	0	0	0
35	1	0	1	1	0	0	1	0	0

APPENDIX XIII contd.

6) freeze

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
25	0	0	0	0	0	0	1	0	0
35	0	0	0	0	0	0	0	0	1

7) jerk

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
26	1	0	0	0	0	0	0	0	1
27	0	0	0	1	0	0	0	0	0
30	0	0	0	0	0	0	0	0	2
31	1	0	0	0	0	0	0	0	0
32	2	1	0	0	0	0	0	0	0
35	0	0	0	0	1	0	0	0	0

Play responses

1) general play

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
28	0	0	1	0	2	1	0	0	0
29	0	0	0	6	1	2	5	5	7
31	0	1	4	5	5	2	4	5	3
32	1	1	5	4	1	3	9	9	6
34	1	3	0	0	0	0	2	0	3
35	0	0	0	0	0	1	0	4	0
36	0	0	0	1	1	0	0	1	3
38	0	0	1	0	0	0	0	0	2

APPENDIX XIII contd.

Dominance Responses

1) dominance bounce

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
28	0	0	3	1	1	1	0	0	0
35	0	0	0	0	1	2	1	4	0

2) teeth chomp

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
32	0	2	0	0	0	0	0	0	0
35	0	0	0	0	0	0	1	0	0

3) open mouth threat

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
35	0	0	0	1	0	0	0	0	0

4) teeth chatter threat

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
31	1	1	2	0	0	1	0	0	0
32	0	0	0	0	0	3	0	0	0
35	0	0	0	3	2	4	1	1	3
36	0	1	1	0	0	0	0	0	0

APPENDIX XIII contd.

Affiliation Responses

1) lipsmack/pout

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
25	2	6	5	3	2	0	0	1	2
26	2	0	0	0	0	0	0	0	0
27	0	8	1	1	1	3	0	0	1
28	4	3	1	1	0	0	1	0	0
29	1	9	4	2	6	1	1	0	1
30	5	3	0	0	0	3	2	0	0
31	1	1	1	0	1	0	0	0	0
32	6	5	8	3	1	2	3	1	0
33	3	8	1	2	0	4	2	1	0
34	1	0	0	0	0	0	1	0	0
35	9	8	3	4	3	2	6	3	1
36	5	1	0	2	1	1	0	0	0
38	3	3	2	2	2	1	0	0	0

2) square mouth

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
26	2	0	1	0	0	0	0	0	0
30	0	0	0	0	0	0	1	0	1
31	0	0	0	0	0	0	2	0	0
33	0	0	1	0	0	0	0	0	1
34	0	0	1	2	1	0	0	1	0
35	1	0	0	0	0	0	0	0	0
38	0	0	0	3	2	1	0	0	0

APPENDIX XIII contd.

2) gurgle

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
26	4	0	1	0	1	0	0	0	0
28	0	1	0	0	0	0	0	0	0
32	0	0	1	2	0	0	0	0	0
33	0	1	2	4	4	0	0	0	1
34	4	2	2	5	4	4	3	1	4
36	1	3	0	1	0	1	1	0	0
38	0	0	0	1	5	2	0	0	5

3) trill/whinney

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
25	0	0	0	0	2	0	0	3	4
26	0	1	0	0	0	0	0	0	0
31	0	0	0	3	1	1	2	3	0
32	0	0	1	2	1	1	1	0	1
34	0	0	0	0	0	0	1	2	0

4) whistle

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
25	0	0	0	0	0	0	0	2	0
26	1	1	0	1	3	2	7	4	5
29	0	0	0	0	0	0	1	1	1
31	0	0	0	0	1	1	1	0	0

APPENDIX XIII contd.

7) grunt

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
30	0	1	0	0	0	0	0	0	0
31	0	0	0	0	0	0	5	0	1
38	0	0	0	0	0	0	0	0	2

Other Communicative Responses

1) approach

individual	SLIDE STIMULUS								
	1	2	3	4	5	6	7	8	9
25	2	0	0	1	0	0	0	0	0
26	1	0	0	0	0	0	0	0	1
28	1	2	2	0	1	2	1	2	0
29	6	5	1	4	5	2	2	3	4
30	3	1	1	0	0	1	0	0	1
31	3	4	1	3	0	1	0	1	2
32	3	2	4	1	2	3	3	2	1
33	4	4	3	1	0	1	1	2	1
34	4	4	2	0	1	3	1	2	1
35	2	2	3	3	3	3	2	3	2
36	2	3	2	2	0	0	2	0	1
38	1	3	3	1	1	0	1	0	0

APPENDIX XIII contd.

KEY TO TABLE:

SLIDE STIMULUS.

- 1 : human neutral expression
- 2 : infant visual explore
- 3 : infant grimace
- 4 : female visual explore
- 5 : mother with infant on nipple
- 6 : female grimace
- 7 : male open mouth threat
- 8 : male yawn
- 9 : female rear view

APPENDIX XIII contd.

3) withdraw

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	1	1	0	0	0	0	0	0	0	0
27	1	0	0	0	0	0	0	0	1	0
29	2	1	0	1	0	2	0	0	1	0
30	1	0	0	1	0	0	0	0	0	0
31	1	1	1	1	1	1	1	0	0	1
32	1	0	1	0	0	0	0	0	0	0
33	0	0	0	0	0	0	1	0	0	0
34	1	1	1	0	2	1	1	0	0	0
35	1	0	0	0	1	1	1	0	0	1
36	1	1	1	0	1	0	1	0	1	2

4) freeze

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
30	0	1	0	0	0	0	0	0	0	0
36	0	0	1	0	0	0	0	0	0	0

5) jerk

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
26	0	0	0	0	0	1	0	0	0	0
27	0	0	0	0	0	0	1	0	0	0
29	0	0	1	1	0	0	0	2	0	0
30	0	0	1	0	0	0	0	0	0	0
31	0	0	0	0	0	2	0	1	1	1

APPENDIX XIII contd.

Affiliation responses

1) lipsmack/pout

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	3	5	4	1	2	1	1	1	1	1
27	0	3	3	0	1	0	3	0	0	3
28	0	1	0	0	0	0	0	1	0	0
29	0	3	1	0	1	1	0	2	2	2
30	4	3	3	0	4	2	0	1	0	2
31	3	1	0	0	2	2	2	1	3	2
32	0	1	0	1	0	1	3	1	1	0
33	0	1	0	0	0	0	0	0	3	3
34	1	0	0	0	3	0	0	0	1	1
35	0	0	0	1	0	0	3	2	1	2
36	0	0	0	2	0	0	0	0	0	0
38	1	0	0	0	1	0	0	1	1	0

2) square mouth

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
27	1	0	0	0	0	0	2	0	0	0
30	2	1	0	0	2	0	0	1	0	0

Vocal Responses

1) scream

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	1	0	1	0	1	1	2	0	0	1

APPENDIX XIII contd.

3) trill/whinney (contd)

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
35	0	0	0	0	5	6	5	4	7	2
36	0	0	0	0	1	0	0	0	0	0

4) whistle

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
29	0	0	0	0	0	0	0	1	0	1
30	1	2	0	0	1	0	0	0	0	0
33	0	0	0	0	0	0	0	0	1	0
35	0	1	0	0	2	14	2	1	3	2

5) cheep/squeek

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
26	0	0	0	0	2	0	0	0	0	0
30	0	1	2	0	0	0	1	0	5	4
31	0	2	0	1	0	1	0	0	0	0
33	1	1	0	0	0	0	0	0	0	0
34	0	0	1	0	0	0	0	0	0	0
35	0	1	0	0	1	0	0	0	0	0

APPENDIX XIII contd.

6) bitey

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
26	0	0	0	0	1	0	0	0	0	0

7) grunt

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
29	0	0	1	0	0	0	0	0	0	0
32	1	0	0	0	0	0	0	0	0	0
36	1	0	0	0	0	0	0	0	0	0

KEY TO TABLE:

CALL STIMULUS

- 1 : soft grunts
- 2 : cheeps
- 3 : woo calls (contact call)
- 4 : affiliation rattle
- 5 : threat grunts
- 6 : teeth chatter threat call
- 7 : scream
- 8 : teeth chomp
- 9 : sex rattle
- 10 : ejaculatory growl

APPENDIX XIII contd.

C) SLIDES AND CALLS

Submissive Responses

1) still

	SLIDE STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10
27	0	1	1	0	0	0	0	0	0	0

	CALL STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10
27	2	1	0	0	0	0	0	0	0	0
29	1	0	0	0	0	0	0	0	0	0

2) teeth chatter

	SLIDE STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10
25	0	2	3	0	1	0	0	0	0	0
27	0	1	0	0	0	0	0	0	0	0
30	0	0	0	1	0	0	0	0	0	0
33	1	0	0	0	0	0	1	0	0	0
35	1	0	0	1	0	0	0	0	1	0
36	0	0	0	0	0	0	0	0	0	1

	CALL STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10
25	0	0	0	2	0	0	0	0	0	0
27	0	0	0	0	1	0	0	0	0	0

APPENDIX XIII contd.

2) teeth chatter (contd)

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
29	0	0	0	0	0	0	1	0	0	0
31	1	0	0	0	0	0	0	0	0	1
33	0	0	0	2	0	0	0	0	0	1
35	0	0	0	0	0	0	0	1	0	0
38	0	0	1	0	0	0	0	0	0	0

3) grimace

individual	SLIDE STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	0	0	1	1	2	3	1	1	0	0
26	0	0	0	0	0	1	0	0	0	0
33	0	0	0	1	0	0	0	0	0	0

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	0	1	1	2	2	3	1	1	0	0
27	0	0	0	0	0	0	0	1	0	0
36	0	0	0	0	0	1	0	0	0	0

4) withdraw

individual	SLIDE STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	0	0	0	2	0	0	0	0	0	0
26	1	0	0	0	1	1	0	0	0	0

APPENDIX XIII contd.

6) jerk

individual	SLIDE STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	0	0	0	2	0	1	1	2	1	1
26	0	0	0	0	0	1	0	0	0	0
29	0	0	0	0	0	0	0	1	0	0
33	0	0	0	0	0	0	0	0	0	1
35	0	0	0	0	0	1	0	0	0	0

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	0	0	0	3	0	2	2	1	3	2
26	0	0	0	0	0	0	0	0	1	1
27	0	0	1	0	0	0	0	0	0	0
35	0	0	0	0	0	1	0	0	0	4

Play responses

1) general play

individual	SLIDE STIMULUS									
	1	2	3	4	5	6	7	8	9	10
29	0	0	0	0	0	0	0	0	0	1
31	0	0	0	1	1	1	0	0	1	1
32	0	1	0	0	0	0	0	1	2	4

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
31	0	0	0	0	1	0	0	1	0	0

APPENDIX XIII contd.

1) general play (contd)

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
32	0	0	0	0	0	0	0	1	1	2
38	2	2	1	0	0	0	0	0	0	0

Dominance Responses

1) teeth chatter threat (none to call stimuli)

individual	SLIDE STIMULUS									
	1	2	3	4	5	6	7	8	9	10
35	0	0	0	0	1	0	0	0	0	0

Affiliation Responses

1) lipsmack/pout

individual	SLIDE STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	0	0	2	1	0	1	0	1	0	0
26	0	1	0	0	0	0	1	0	0	0
28	0	0	0	0	0	1	0	0	2	0
29	0	0	0	0	0	0	1	0	0	0
30	1	0	0	4	1	0	0	0	0	0
31	0	0	0	0	0	0	0	0	1	0
32	1	2	0	1	0	0	0	0	0	0

APPENDIX XIII contd.

2) square mouth (contd)

		CALL STIMULUS									
individual		1	2	3	4	5	6	7	8	9	10
25		1	0	0	0	0	0	0	0	0	0

3) mouth nibble (none to call stimuli)

		SLIDE STIMULUS									
individual		1	2	3	4	5	6	7	8	9	10
28		1	0	0	0	0	0	0	0	0	0
34		0	0	1	0	0	0	0	0	0	0
36		0	0	0	1	0	0	0	0	0	0

Vocal Responses

1) scream

		SLIDE STIMULUS									
individual		1	2	3	4	5	6	7	8	9	10
25		0	0	0	1	2	4	1	3	8	5
26		0	0	0	0	1	3	2	2	2	3
35		0	0	0	0	0	6	2	1	0	0

		CALL STIMULUS									
individual		1	2	3	4	5	6	7	8	9	10
25		1	1	1	10	1	5	9	17	4	6
26		0	0	0	0	0	2	1	0	1	3
27		0	0	0	0	1	0	0	0	0	0

APPENDIX XIII contd.

1) scream (contd)

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
28	0	0	0	0	0	3	0	0	0	0
29	2	0	0	0	1	0	0	0	0	0
30	1	0	0	0	0	0	2	0	0	0
32	1	0	0	0	0	0	0	0	0	0
33	2	2	3	0	0	0	0	0	1	0
34	1	0	1	0	0	0	1	0	0	0
35	0	0	0	0	0	0	0	0	0	6
36	0	0	0	0	0	1	0	0	0	0

2) gurgle

individual	SLIDE STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	1	0	0	0	0	0	0	0	0	0
26	1	1	0	2	0	0	0	0	0	0
28	0	1	0	0	0	0	0	0	0	0
31	2	0	0	0	0	0	0	0	0	0
34	3	0	4	0	0	0	0	1	0	0
35	0	0	0	1	1	0	0	0	0	0
36	3	3	3	0	0	3	1	0	1	0
38	1	0	0	0	0	0	0	0	0	0

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	1	1	0	0	0	0	0	0	0	0
26	0	0	0	1	0	0	0	0	0	0
34	0	4	0	1	2	0	1	0	0	0
36	1	0	2	0	0	0	0	0	0	0

APPENDIX XIII contd.

3) trill/whinney

		SLIDE STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10	
26	2	0	0	1	2	1	0	0	0	2	
27	0	0	0	0	1	0	0	0	0	1	
31	0	0	0	0	1	2	0	0	0	0	
32	0	0	0	0	0	0	1	0	0	0	
35	0	1	1	0	0	2	0	1	0	1	
36	0	1	0	0	0	0	0	0	0	0	

		CALL STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10	
25	0	0	0	0	0	0	0	0	3	0	
26	0	0	0	3	1	0	0	0	1	2	
27	0	0	0	0	0	0	0	0	0	1	
35	0	0	0	0	2	2	5	1	5	2	

4) whistle

		SLIDE STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10	
25	1	0	0	0	0	2	0	1	1	0	
26	0	0	0	0	3	0	0	0	2	4	
31	0	1	0	0	0	1	0	0	0	0	
32	0	0	0	1	0	1	1	1	0	1	
35	0	2	1	0	0	2	1	0	0	0	

		CALL STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10	
25	1	0	0	0	1	1	1	0	1	0	

APPENDIX XIII contd.

4) whistle (contd)

	CALL STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10
26	0	0	0	4	2	1	3	2	3	2
32	0	0	0	0	0	0	0	0	1	1
33	0	0	0	0	1	0	0	0	0	1
35	0	1	2	2	2	3	5	1	5	2

5) cheep/squeek

	SLIDE STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10
26	0	0	0	0	2	0	0	0	0	0
27	1	1	0	0	2	0	0	2	0	2
33	1	1	0	1	0	0	0	0	0	0
35	0	0	0	1	0	2	0	1	0	1

	CALL STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10
26	0	0	0	3	2	1	1	2	0	0
27	0	0	1	2	0	0	0	0	0	0
33	3	0	0	0	1	0	0	3	0	1
35	1	0	2	0	0	0	1	0	1	0

6) bitey

	SLIDE STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10
25	0	0	0	0	0	0	1	0	1	0

APPENDIX XIII contd.

6) bitey (contd)

	SLIDE STIMULUS									
individual	1	2	3	4	5	6	7	8	9	10

26	0	0	1	0	0	2	0	0	0	0
----	---	---	---	---	---	---	---	---	---	---

CALL STIMULUS

individual	1	2	3	4	5	6	7	8	9	10
------------	---	---	---	---	---	---	---	---	---	----

25	0	0	0	0	0	0	1	3	2	2
----	---	---	---	---	---	---	---	---	---	---

7) grunt

SLIDE STIMULUS

individual	1	2	3	4	5	6	7	8	9	10
------------	---	---	---	---	---	---	---	---	---	----

31	2	0	0	0	0	0	0	0	1	0
----	---	---	---	---	---	---	---	---	---	---

36	0	1	0	0	0	0	0	0	0	0
----	---	---	---	---	---	---	---	---	---	---

1	0	0	0	0	0	0	0	0	0	0
---	---	---	---	---	---	---	---	---	---	---

CALL STIMULUS

individual	1	2	3	4	5	6	7	8	9	10
------------	---	---	---	---	---	---	---	---	---	----

31	0	0	0	0	1	0	0	0	0	1
----	---	---	---	---	---	---	---	---	---	---

Other Responses

1) approach

SLIDE STIMULUS

individual	1	2	3	4	5	6	7	8	9	10
------------	---	---	---	---	---	---	---	---	---	----

25	1	2	1	1	0	0	0	0	0	0
----	---	---	---	---	---	---	---	---	---	---

APPENDIX XIII contd.

1) approach (contd)

individual	SLIDE STIMULUS									
	1	2	3	4	5	6	7	8	9	10
27	0	0	0	0	0	0	0	0	0	1
28	1	1	2	2	1	2	1	2	1	1
29	1	0	0	0	0	0	0	1	0	0
31	1	1	0	1	0	1	0	0	1	0
32	2	1	0	0	0	1	0	1	0	0
33	0	1	0	0	0	0	0	0	0	0
34	2	0	2	1	1	0	0	0	0	0
36	1	1	0	0	0	2	1	0	1	0
38	1	0	0	0	0	1	0	0	0	0

individual	CALL STIMULUS									
	1	2	3	4	5	6	7	8	9	10
25	0	0	0	1	0	0	0	0	0	0
28	0	0	1	0	0	0	0	1	1	0
29	0	0	0	0	0	0	1	1	0	0
31	1	1	1	1	1	1	0	0	1	1
32	0	0	1	1	1	1	1	1	0	1
34	1	2	0	0	1	0	0	0	0	0
36	0	0	0	0	0	0	0	1	0	0
38	0	0	0	1	0	1	0	0	0	0

KEY TO TABLE.

SLIDE STIMULUS

- 1 : mother cradling infant
- 2 : infant visual explore
- 3 : female visual explore
- 4 : male cradling infant

CALL STIMULUS

- 1 : soft grunts
- 2 : cheeps
- 3 : woo calls
- 4 : affiliation rattle

APPENDIX XIII contd.

KEY TO TABLE

SLIDE STIMULUS

5 : female brow threat
6 : juvenile teeth chatter threat
7 : infant grimace
8 : male masturbation
9 : male teeth chatter invite
10 : male ejaculatory face

CALL STIMULUS

5 : threat grunts
6 : teeth chatter threat call
7 : scream
8 : teeth chomp
9 : sex rattle
10 : ejaculatory growl

APPENDIX XIV S-R connections in behaviour of infant and partner in social test one.

a) Infant 26 with 37 (partner).

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	PARTNER'S BEHAVIOUR					affiliation		others	
	still/ present	teeth chatter/ grimace	withdraw	jerk/ scream	huddle	visual explore	approach		
<u>submission</u>									
still/present	1	0	0	0	0	0	0		
withdraw	0	0	0	0	0	1	0		
jerk/scream	1	0	0	0	1	6	0		
<u>dominance</u>									
display	3	1	0	0	0	0	0		
grab	16	1	1	20	0	3	0		
bite	22	0	0	5	0	0	2		
<u>affiliation</u>									
lipsmack	0	0	1	0	0	0	2		
huddle	0	0	0	1	0	0	0		
<u>others</u>									
approach	0	0	0	2	0	1	0		

APPENDIX XIV contd.

b) Infant 27 with 37

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR

	<u>affiliation</u>		<u>others</u>	
	lipsmack	visual explore	visual explore	approach
<u>submission</u>				
still/present	0	0	1	1
withdraw	0	0	2	2
freeze	0	6	6	6
<u>affiliation</u>				
lipsmack	1	5	1	1
square mouth	0	1	0	0
<u>play</u>				
open mouth play face	0	4	0	0
play initiate	0	1	0	0
play chase	0	2	0	0
<u>others</u>				
approach	0	1	0	0

APPENDIX XIV contd.

c) Infant 29 with 26 (partner).

INFANT'S BEHAVIOUR	PARTNER'S BEHAVIOUR												
	<u>dominance</u>		<u>affiliation</u>			<u>play</u>		<u>others</u>					
	display	threat	chase	grab	bite	mouth nibble	lipsmack	huddle	open mouth	play face	visual explore	approach	contact
<u>submission</u>													
still/present	2	5	4	9	3	1	1	3	1	1	15	21	14
withdraw	1	2	0	3	2	0	0	0	0	1	12	10	1
freeze	0	0	0	0	0	0	0	0	0	0	0	1	0
jerk/scream	1	1	2	0	0	0	0	0	0	0	0	0	0
<u>affiliation</u>													
lipsmack	0	1	0	0	0	0	0	0	0	1	9	6	0
<u>play</u>													
open mouth	0	0	0	0	0	0	0	0	0	0	2	0	0
play face													

APPENDIX XIV contd.

d) Infant 30 with 26.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	<u>dominance</u>			<u>affiliation</u>			<u>sex</u>		<u>others</u>		
	display	threat	chase	grab	bite	square mouth	huddle	anogenital inspect	visual explore	approach	contact
<u>submission</u>											
still/present	4	6	3	14	7	2	5	0	32	23	8
teeth chatter/ grimace	0	0	1	0	0	0	0	0	4	0	0
withdraw	2	1	0	5	12	0	1	2	12	1	1
freeze	1	0	0	2	1	0	0	0	2	1	2
jerk/scream	0	0	0	2	2	0	0	0	2	0	0
<u>affiliation</u>											
lipsmack	0	0	0	0	0	0	0	0	2	0	0
<u>others</u>											
approach	0	0	0	0	0	0	0	0	8	0	0

APPENDIX XIV contd.

e) Infant 31 with 26.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	<u>dominance</u>				<u>affiliation</u>			<u>play</u>				
	display	threat	chase	grab	bite	lipsmack	square mouth	huddle	open mouth play face	initiate	chase	wrestle
<u>submission</u>												
still/present	4	2	5	10	2	1	1	0	0	1	0	1
teeth chatter/ grimace	3	2	0	0	1	0	0	0	1	0	2	0
withdraw	5	1	1	7	2	0	0	0	1	1	0	0
freeze	2	1	2	4	0	0	1	0	0	0	0	0
jerk/scream	2	1	2	1	1	1	0	0	0	0	0	0
<u>affiliation</u>												
lipsmack	0	0	0	0	0	0	0	0	0	0	0	0
huddle	1	0	0	2	1	0	0	0	0	0	1	1
<u>play</u>												
open mouth play face	2	1	3	6	5	0	2	0	5	0	8	1
play initiate	0	1	0	0	0	0	0	0	0	0	1	0

APPENDIX XIV contd.

INFANT'S BEHAVIOUR	PARTNER'S BEHAVIOUR											
	<u>dominance</u>		<u>affiliation</u>			<u>play</u>			<u>play</u>			
	display	threat	chase	grab	bite	lipsmack	square	huddle	open mouth	initiate	chase	wrestle
<u>play</u> (contd)												
play chase	2	2	2	3	4	4	1	0	6	7	1	8
play wrestle	6	2	4	14	7	4	4	1	8	1	6	14
<u>others</u>												
approach	0	0	0	0	0	0	0	0	1	0	1	0

e) Infant 31 with 26 contd.

INFANT'S BEHAVIOUR	PARTNER'S BEHAVIOUR									
	<u>sex</u>		<u>others</u>			<u>others</u>			<u>others</u>	
	anogenital	inspect	visual	approach	contact	excitement	teeth	chatter		
<u>submission</u>										
still/present	3	0	4	5	0	2	0	0		
teeth chatter/grimace	0	0	9	4	0	0	0	0		
withdraw	1	0	14	6	0	0	0	0		
freeze	0	0	2	3	0	0	0	0		
jerk/scream	0	0	0	3	0	0	0	0		

APPENDIX XIV contd.

e) Infant 31 with 26 contd.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	sex		PARTNER'S BEHAVIOUR			
	anogenital inspect	mount	visual explore	approach	contact	others
<u>affiliation</u>						
lipsmack	0	0	5	1	0	0
huddle	0	1	8	1	0	0
<u>play</u>						
open mouth play face	3	0	17	9	0	2
play initiate	0	0	3	2	2	2
play chase	3	2	24	14	0	2
play wrestle	9	1	1	7	0	3
<u>others</u>						
approach	0	0	23	1	0	0

APPENDIX XIV contd.

f) Infant 32 with 26.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	<u>dominance</u>				<u>affiliation</u>			<u>play</u>			<u>sex</u>		<u>others</u>	
	display	threat	chase	grab bite	lipsmack	huddle	open mouth	play initiate	play chase	play wrestle	anogenital inspect	visual explore	approach	contact
<u>submission</u>														
still/present	4	3	6	5	3	0	3	1	0	2	1	4	22	6
teeth chatter/grinace	0	0	0	1	0	0	0	0	0	0	0	6	4	0
withdraw	5	2	0	3	2	1	0	1	0	0	0	9	11	3
freeze	0	0	0	1	0	0	0	0	0	0	0	1	2	1
jerk/scream	3	0	1	2	1	0	1	0	0	0	0	2	1	0
<u>affiliation</u>														
lipsmack	0	0	0	0	0	0	0	0	0	0	0	1	1	0
huddle	0	0	1	0	2	1	1	0	1	0	2	1	1	0
<u>play</u>														
open mouth play face	1	1	0	1	0	0	0	4	0	3	13	5	5	0
play initiate	0	0	0	0	0	0	0	0	1	1	0	7	3	0
play chase	1	0	0	0	1	0	1	3	1	5	10	23	34	0
play wrestle	0	1	0	1	1	0	1	5	2	5	19	0	5	0
<u>others</u>														
approach	0	0	0	0	0	0	0	0	0	0	0	23	1	0

APPENDIX XIV contd.

g) Infant 33 with 26.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	<u>dominance</u>			<u>affiliation</u>		<u>sex</u>		<u>others</u>		
	display	threat	chase	grab	bite	lipsmack	anogenital inspect	mount	visual explore	approach contact
<u>submission</u>										
still/present	2	2	2	11		2	0	3	5	5
teeth chatter/ grimace	0	0	4	5		8	1	1	26	56
withdraw	0	0	0	13		1	1	1	10	8
freeze	3	1	1	13		0	3	2	12	15
jerk/scream	5	0	6	0		0	1	2	4	9
<u>affiliation</u>										
lipsmack	4	0	0	0		0	1	0	17	10
huddle	0	0	0	0		0	0	0	1	0

APPENDIX XIV contd.

h) Infant 34 with 26.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	<u>dominance</u>			<u>affiliation</u>			<u>play</u>			<u>sex</u>		<u>others</u>	
	display	threat	chase grab bite	lipsmack	open play	play initiate	play chase	play wrestle	anogenital mount	visual explore	approach	contact	
<u>submission</u>													
still/ present	0	0	0	1	0	1	0	1	0	0	0	0	0
withdraw	0	1	0	0	0	0	0	0	0	0	0	2	0
jerk/scream	0	0	1	0	0	1	0	0	0	0	0	2	1
<u>dominance</u>													
display	1	2	0	0	0	0	0	0	0	0	1	1	0
threat	0	11	0	1	1	0	0	1	0	0	1	3	0
bite	0	1	0	2	0	0	0	0	0	0	0	0	0
<u>affiliation</u>													
lipsmack	1	0	0	0	0	0	0	0	0	0	0	0	0
groom	0	0	0	1	0	0	0	0	0	0	0	0	0
<u>play</u>													
open mouth	0	1	1	0	22	10	2	22	0	0	37	17	0
play face													

4 3 1

APPENDIX XIV contd.

h) Infant 34 with 26 contd.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	<u>dominance</u>		<u>affiliation</u>		<u>play</u>		<u>sex</u>		<u>others</u>						
	display	threat	chase	grab	bite	lipsmack	open mouth	play initiate	play chase	play wrestle	anogenital inspect	mount	visual explore	approach	contact
<u>play contd</u>															
play initiate	2	0	0	1	0	0	6	0	2	2	0	0	25	1	0
play chase	1	0	0	0	0	1	7	0	6	16	0	0	9	2	0
play wrestle	0	0	0	0	0	0	57	6	3	34	1	1	13	7	2
<u>others</u>															
approach	3	0	0	0	0	1	3	2	10	2	0	0	48	0	0

APPENDIX XIV contd.

i) Infant 35 with 26.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	dominance					affiliation			play			
	display	threat	chase	grab	bite	lipsmack	square mouth	groom	open mouth play face	play initiate	play chase	play wrestle
<u>submission</u>												
still/present	4	5	3	10	2	0	1	0	0	0	1	1
teeth chatter/ grimace	0	0	0	3	1	0	0	0	0	0	0	0
withdraw	4	1	2	3	2	0	1	0	1	0	1	2
freeze	1	1	0	1	0	0	0	0	0	0	2	0
jerk/scream	3	1	3	12	3	0	0	1	0	0	0	2
<u>dominance</u>												
grab	0	0	0	1	1	0	0	0	0	0	0	0
bite	0	1	0	0	0	0	0	0	0	0	0	0
<u>affiliation</u>												
lipsmack	0	1	0	0	0	0	0	0	0	0	0	0
<u>play</u>												
open mouth play face	0	1	0	0	0	1	0	0	1	2	4	2

APPENDIX XIV contd.

i) Infant 35 with 26 contd.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	<u>dominance</u>				<u>affiliation</u>			<u>play</u>				
	display	threat	chase	grab	bite	lipsmack	square mouth	groom	open mouth play face	play initiate	play chase	play wrestle
<u>play (contd)</u>												
play initiate	0	0	0	0	0	0	1	0	0	0	0	0
play chase	1	2	0	2	0	0	0	0	3	4	11	11
play wrestle	0	0	0	0	0	1	0	0	0	0	3	6
<u>others</u>												
approach	0	0	0	0	0	0	0	0	0	0	0	0

i) Infant 35 with 26 contd.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	<u>sex</u>		<u>others</u>		
	anogenital inspect	mount	visual explore	approach contact	excitement teeth chatter
<u>submission</u>					
still/present	2	0	17	12	7
teeth chatter/ grimace	0	0	6	7	0

APPENDIX XIV contd.

i) Infant 35 with 26 contd.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	<u>sex</u>		<u>others</u>			
	anogenital inspect	mount	visual explore	approach	contact	excitement teeth chatter
<u>submission</u> (contd)						
withdraw	2	2	4	11	2	0
freeze	0	0	4	8	2	0
jerk/scream	2	1	12	3	1	1
<u>dominance</u>						
grab	0	0	0	0	0	0
bite	0	0	0	0	0	0
<u>affiliation</u>						
lipsmack	0	0	7	3	0	0
<u>play</u>						
open mouth play face	1	1	11	4	1	0
play initiate	0	0	6	0	0	0
play chase	1	0	36	10	3	0
play wrestle	0	0	0	2	1	0
<u>others</u>						
approach	0	0	19	1	0	1

APPENDIX XIV : (contd)

j) Infant 36 with 26 (contd).

INFANT'S BEHAVIOUR	PARTNER'S BEHAVIOUR											
	<u>dominance</u>			<u>affiliation</u>				<u>play</u>				
	display	threat	chase	grab	bite	lipsmack	square mouth	huddle	open mouth play face	play initiate	play chase	play wrestle
<u>play</u> (contd)												
play initiate	0	0	0	0	0	0	0	0	0	0	2	0
play chase	5	1	0	3	0	0	1	1	9	1	12	16
play wrestle	0	0	0	0	0	0	0	0	8	1	2	6
<u>others</u>												
approach	0	0	0	0	0	0	0	0	0	0	5	0

j) Infant 36 with 26 (contd).

INFANT'S BEHAVIOUR	PARTNER'S BEHAVIOUR			
	<u>sex</u>	<u>others</u>	<u>visual</u>	<u>contact</u>
	anogenital inspect	explore	approach	contact
<u>submission</u>				
still/present	2	2	26	2

APPENDIX XIV : (contd)

j) Infant 36 with 26 (contd) .

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	sex		visual explore	others	
	anogenital inspect	mount		approach	contact
<u>submission</u> (contd)	0	0			
teeth chatter/grinace	0	0	2	3	3
withdraw	0	0	3	4	0
jerk/scream					
<u>dominance</u>					
<u>display</u>	0	0	1	0	0
threat	0	0	0	0	0
grab	0	0	0	0	0
bite	0	0	0	1	0
<u>affiliation</u>					
<u>groom</u>	0	0	0	0	0
<u>play</u>					
open mouth play face	1	0	10	7	2
play initiate	1	0	2	0	0

APPENDIX XIV : (contd)

j) Infant 36 with 26 (contd).

INFANT'S BEHAVIOUR	PARTNER'S BEHAVIOUR			
	sex anogenital inspect	mount	visual explore	others approach contact
<u>play</u> (contd)				
play chase	0	0	17	9 4
play wrestle	0	0	8	4 0
<u>others</u> approach	0	0	8	4 0

APPENDIX XIV : (contd)

k) Infant 38 with 26.

INFANT'S BEHAVIOUR	PARTNER'S BEHAVIOUR													
	<u>dominance</u>		<u>affiliation</u>			<u>play</u>			<u>sex</u>		<u>others</u>			
	threat	grab	lipsmack	square	huddle	open	play	play	play	anogenital	mount	visual	approach	contact
			mouth	mouth		mouth	initiate	chase	wrestle	inspect		explore		
<u>submission</u>														
still/present	2	2	1	0	0	1	0	5	4	11	1	4	1	6
teeth chatter/ grimace	0	0	5	0	1	1	2	2	0	1	0	16	13	2
withdraw	0	1	0	0	0	0	0	1	2	3	0	13	5	2
freeze	0	0	0	0	0	0	0	0	0	2	0	0	0	0
jerk/scream	0	0	0	0	0	1	1	2	0	1	0	6	7	1
<u>dominance</u>														
display	0	0	0	0	0	0	0	0	0	0	0	1	0	0
threat	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<u>affiliation</u>														
lipsmack	0	0	2	0	0	0	0	2	0	0	0	12	0	0
square mouth	0	0	0	0	0	0	0	0	0	0	0	0	0	1

APPENDIX XIV : (contd)

k) Infant 38 with 26.

PARTNER'S BEHAVIOUR

INFANT'S BEHAVIOUR	dominance		affiliation		play			sex		others			
	threat	grab	lipsmack	square mouth	huddle	open mouth play face	play initiate	play chase	play wrestle	anogenital inspect	mount	visual explore	approach contact
<u>play</u>													
open mouth	0	2	1	0	0	2	1	7	6	2	1	21	7
play face													
play chase	0	0	1	0	0	1	0	5	1	1	0	11	7
play wrestle	0	0	0	0	0	5	0	0	2	0	0	1	0
<u>others</u>													
approach	0	0	1	0	0	0	0	0	0	0	0	21	1
													0

APPENDIX XV Distribution of communicative responses to
slide and call stimuli in 5 groups of differentially
reared juvenile stumptail macaques and 1 group of
adult feral stumptail macaques.

A) SLIDES ALONE

<u>Submissive responses</u>		1) present *								
		SLIDE STIMULUS								
Group	Individual	1	2	3	4	5	6	7	8	9
dark	1	0	0	0	1	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0
peer	5	1	0	0	4	0	3	0	0	0
	6	0	0	0	0	0	2	2	0	0
	7	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
isolate	10	0	0	0	0	0	0	3	2	0
	11	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0
adult-peer	14	0	0	0	0	0	0	0	0	0
	15	0	0	0	0	0	0	0	0	0
	16	1	0	0	0	0	0	5	0	0
	17	0	0	0	0	0	0	0	0	0

* no present shown by any members of the social group or the adult feral group.

APPENDIX XV contd.

3) withdraw

Group	Individual	SLIDE STIMULUS								
		1	2	3	4	5	6	7	8	9
dark	1	1	0	0	0	0	1	3	1	0
	2	4	2	0	0	1	0	2	0	0
	3	4	0	0	0	0	0	1	1	0
	4	2	1	1	1	0	0	0	0	0
peer	5	3	2	1	3	0	0	0	1	1
	6	4	2	2	5	2	4	5	0	0
	7	4	4	1	4	2	1	1	0	2
	8	3	2	2	0	1	0	2	0	3
isolate	10	1	1	0	1	0	3	1	0	0
	11	10	2	0	3	1	0	1	0	0
	12	9	4	1	2	1	1	3	2	0
	13	1	1	1	2	2	1	4	1	2
adult-peer	14	1	5	2	2	0	2	4	2	3
	15	2	0	1	4	0	2	3	3	2
	16	3	3	3	4	2	2	2	4	4
	17	1	0	2	1	2	2	1	2	3
social	18	2	0	1	2	1	2	2	0	1
	19	2	2	0	1	1	1	4	1	1
	22	1	4	2	1	0	1	0	2	3
	23	1	4	2	1	0	1	0	2	3
Feral	Bart	1	1	0	0	0	0	0	0	0
	B.Susan	2	1	0	0	0	0	0	0	0
	Isaacs	1	0	0	0	0	1	0	0	1
	Margaret	1	1	2	0	0	1	0	0	1

APPENDIX XV contd.

4) freeze *

SLIDE STIMULUS

group	Individual	1	2	3	4	5	6	7	8	9
peer	5	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0
	7	0	1	1	0	0	1	0	2	7
	8	4	2	0	0	0	0	2	1	0
isolate	10	0	1	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0
	13	0	2	1	0	0	0	0	0	0
adult-peer	14	0	0	0	4	0	0	0	1	0
	15	0	0	0	0	0	0	0	0	0
	16	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0
social	18	2	0	0	0	0	0	0	0	0
	19	0	0	0	0	0	0	0	0	0
	22	0	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0	0

* no freeze shown by any members of the dark group or adult feral group.

APPENDIX XV contd.

Dominance Responses

1) dominance bounce *

Group	Individual	SLIDE STIMULUS								
		1	2	3	4	5	6	7	8	9
dark	1	0	0	0	0	1	0	0	0	0
	2	0	0	1	0	0	0	1	1	0
	3	0	0	0	0	0	0	0	0	3
	4	0	0	0	0	0	0	0	1	0
peer	5	0	0	0	0	0	0	1	5	2
	6	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
isolate	10	0	0	0	0	0	0	0	0	0
	11	0	1	2	1	2	0	3	2	3
	12	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0
adult-peer	14	0	0	0	0	0	0	0	0	0
	15	0	0	1	0	0	0	0	0	3
	16	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0
feral	Bart	0	1	1	0	1	0	0	0	0
	B.Susan	0	0	0	0	0	0	0	0	0
	Isaacs	0	0	0	0	0	0	0	0	0
	Margaret	0	0	0	0	0	0	0	0	0

* no dominance bounce shown by any members of social group.

APPENDIX XV contd.

2) yawn/teeth chomp

		SLIDE STIMULUS								
Group	Individual	1	2	3	4	5	6	7	8	9
dark	1	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	3	0	0	0	1	1	6	7	0	0
	4	0	0	0	0	0	0	0	0	0
peer	5	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0
	8	0	0	0	1	0	1	0	0	0
isolate	10	0	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	1	0
	12	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0
adult-peer	14	0	0	0	0	0	0	0	0	0
	15	0	0	0	0	0	0	0	0	0
	16	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	4	8	2	1	0
social	18	0	0	2	2	3	5	3	0	0
	19	0	0	0	0	0	0	0	0	0
	22	0	0	0	0	1	0	3	1	0
	23	0	0	0	0	0	0	0	0	0
feral	Bart	2	0	0	0	0	1	0	1	0
	B. Susan	0	0	0	0	0	0	0	0	0
	Isaacs	0	0	0	0	0	0	0	2	1
	Margaret	0	0	0	0	0	0	0	0	0

KEY TO TABLE

SLIDE STIMULUS

1 : human neutral expression
 2 : infant visual explore
 3 : infant grimace
 4 : female visual explore
 5 : mother with infant on nipple

6 : female grimace
 7 : male open mouth threat
 8 : male yawn
 9 : female rear view

APPENDIX XV contd.

3) all types of threat expression *

		SLIDE STIMULUS								
Group	Individual	1	2	3	4	5	6	7	8	9
dark	1	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	1	0	0
	4	0	0	0	0	0	0	0	0	0
isolate	10	0	0	0	0	0	0	0	0	0
	11	2	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	1	0	0	0
adult-peer	14	0	0	0	0	0	0	0	0	0
	15	0	0	0	0	0	0	0	0	1
	16	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0
social	18	0	0	0	1	1	0	2	0	2
	19	1	1	1	6	5	6	1	1	1
	22	0	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0	0

* no threats shown by any members of peer group or adult feral group.

APPENDIX XV contd.

4) all attacks *

		STIMULUS SLIDE								
Group	Individual	1	2	3	4	5	6	7	8	9
dark	1	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	1	1	0
	4	0	0	0	0	0	0	0	0	0
adult-peer	14	0	0	0	0	0	0	0	0	0
	15	0	0	0	1	0	0	0	0	0
	16	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0
social	18	0	0	0	0	0	0	0	0	0
	19	0	1	0	1	1	1	0	0	0
	22	0	0	1	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0	0
feral	Bart	0	0	0	2	0	1	0	1	0
	B. Susan	0	0	0	0	1	0	3	0	1
	Isaacs	0	0	0	0	0	0	0	0	0
	Margaret	0	0	1	0	1	0	0	0	0

* no attacks shown by any members of peer or isolate groups.

APPENDIX XV contd.

1) lipsmack/pout

SLIDE STIMULUS

Group	Individual	1	2	3	4	5	6	7	8	9
dark	1	0	1	6	7	1	1	2	0	0
	2	0	0	0	2	0	1	2	0	0
	3	1	0	0	4	3	1	3	0	0
	4	1	1	0	3	0	1	0	0	0
peer	5	0	1	1	5	5	4	1	1	0
	6	0	0	0	0	0	0	0	0	0
	7	0	1	0	0	0	0	0	0	0
	8	0	1	5	2	2	0	0	0	0
isolate	10	0	0	0	0	0	0	0	0	0
	11	1	1	2	0	2	1	1	0	2
	12	0	2	1	1	0	1	1	0	0
	13	0	0	1	0	0	0	0	0	0
adult peer	14	2	9	1	1	0	0	4	0	1
	15	1	3	0	3	5	7	0	2	1
	16	0	1	0	3	0	1	0	0	0
	17	0	1	3	0	0	2	3	0	0
social	18	0	0	0	0	0	2	0	0	2
	19	0	0	0	0	0	1	0	0	0
	22	0	0	2	0	0	0	0	1	2
	23	0	0	0	1	0	0	0	0	0
feral	Bart	3	1	0	2	1	1	2	0	2
	B.Susan	4	4	0	0	0	2	5	0	1
	Isaacs	3	6	4	0	0	0	4	1	0
	Margaret	14	1	0	0	0	0	6	0	0

APPENDIX XV contd.

Other Responses

1) approach

SLIDE STIMULUS

Group	Individual	1	2	3	4	5	6	7	8	9
dark	1	2	1	4	2	3	2	2	2	2
	2	3	2	0	0	1	1	4	2	1
	3	3	0	0	0	0	0	1	2	1
	4	2	1	2	3	0	1	1	0	1
peer	5	6	6	1	3	2	2	4	3	2
	6	3	2	2	5	3	4	5	1	3
	7	1	2	0	1	4	1	1	0	0
	8	0	2	4	0	1	0	0	0	2
isolate	10	1	0	0	0	0	0	0	0	1
	11	7	6	2	2	2	2	3	1	1
	12	7	2	3	0	1	2	4	1	3
	13	0	0	0	3	3	0	3	0	0
adult peer	14	2	4	2	1	0	0	4	0	3
	15	0	2	2	3	1	2	4	1	1
	16	0	1	3	2	3	3	0	0	1
	17	0	0	1	0	0	0	0	0	0
social	18	3	3	2	3	2	2	2	1	2
	19	3	2	1	0	2	2	3	2	1
	22	0	5	1	1	2	1	0	2	2
	23	2	2	1	2	1	2	2	2	0
feral	Bart.	2	0	1	2	0	0	0	0	0
	B. Susan	0	2	1	1	1	1	0	1	1
	Isaacs	0	0	2	1	1	2	1	0	1
	Margaret	0	2	3	1	1	1	1	1	1

APPENDIX XV contd.

		2) contact								
		SLIDE STIMULUS								
Group	Individual	1	2	3	4	5	6	7	8	9
dark	1	0	0	2	0	4	3	1	3	2
	2	0	5	4	4	7	3	3	2	1
	3	0	0	0	3	4	3	1	3	2
	4	4	5	4	4	0	1	1	0	1
peer	5	6	6	1	2	0	2	4	8	6
	6	1	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
isolate	10	0	0	0	0	0	0	0	1	0
	11	0	10	7	7	3	4	4	3	6
	12	3	3	5	2	3	4	4	3	5
	13	0	0	0	0	2	0	0	0	0
adult-peer	14	0	5	0	0	0	0	0	0	0
	15	0	4	5	1	3	0	0	3	2
	16	0	1	3	1	3	1	1	0	0
	17	0	0	0	0	0	0	0	0	0
social	18	1	3	1	2	1	0	2	0	1
	19	2	4	1	0	2	1	6	3	3
	22	0	1	3	0	0	0	0	1	1
	23	0	4	0	1	0	1	4	1	1
feral	Bart.	1	4	0	3	0	0	7	1	2
	B.Susan	0	4	1	2	1	0	2	1	1
	Isaacs	0	0	1	4	1	2	1	0	1
	Margaret	0	5	6	2	1	0	0	2	2

APPENDIX XV

B) CALLS ALONE

Submissive Responses

1) teeth chatter/grimace *

Group	Individual	CALL STIMULUS									
		1	2	3	4	5	6	7	8	9	10
dark	1	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0
	4	2	0	0	0	1	0	0	0	0	0
peer	5	0	0	0	0	0	0	0	0	0	0
	6	1	0	1	0	0	0	1	0	0	0
	7	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0	0
isolate	10	0	0	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0	2
	13	0	0	0	0	0	0	0	0	0	0
adult-peer	14	0	0	0	0	0	0	0	0	0	0
	15	0	0	0	0	0	0	0	0	0	0
	16	0	0	0	0	0	0	0	0	0	0
	17	0	0	1	0	0	0	0	0	1	1
social	18	2	0	0	0	0	0	0	0	0	0
	19	0	0	0	0	0	0	0	0	0	0
	22	0	0	0	0	0	0	0	0	0	0
	23	0	2	0	0	0	1	0	0	0	0

* no teeth chatter or grimace shown by any members of adult feral group.

APPENDIX XV contd.

2) withdraw *

		CALL STIMULUS									
Group	Individual	1	2	3	4	5	6	7	8	9	10
dark	1	0	0	1	0	2	1	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	1	0	0	0
	4	0	0	0	0	0	0	0	0	0	0
peer	5	3	1	1	0	1	3	3	1	1	2
	6	7	3	2	0	0	2	3	0	0	0
	7	3	1	1	1	1	3	3	0	0	0
	8	3	3	0	0	0	1	2	1	0	0
isolate	10	4	3	1	0	0	2	1	0	1	0
	11	3	0	1	0	1	1	1	0	0	1
	12	2	1	1	0	1	1	1	0	0	2
	13	1	2	1	1	0	1	1	1	0	0
adult-peer	14	1	0	1	0	0	1	0	1	0	0
	15	0	1	1	1	0	1	1	0	1	0
	16	0	1	0	0	0	1	1	1	1	0
	17	3	0	0	0	0	1	3	0	1	0
social	18	1	1	1	0	1	1	0	0	0	1
	19	0	0	0	0	0	0	0	0	0	1
	22	2	0	0	0	0	0	0	0	0	1
	23	0	0	0	0	0	1	0	0	0	0

* withdraw not shown by any members of adult feral group.

APPENDIX XV contd.

1) approach * (contd.)

		CALL STIMULUS									
Group	Individual	1	2	3	4	5	6	7	8	9	10
adult-peer	14	0	0	0	0	0	0	0	0	0	0
	15	1	0	1	0	2	0	1	1	0	0
	16	1	1	0	0	1	0	1	0	1	0
	17	0	1	0	1	0	2	0	1	1	0
social	18	0	0	2	1	1	2	1	1	1	0
	19	0	1	0	0	0	0	1	0	0	0
	22	0	1	0	0	0	0	0	0	1	1
	23	0	0	0	0	0	0	0	0	0	0
feral Bart.		0	0	0	0	0	0	2	0	0	0
	B.Susan	0	0	0	0	0	0	0	0	0	0
	Isaacs	0	0	0	0	0	0	0	0	0	0
	Margaret	0	0	1	0	0	0	0	1	0	0

* approach not shown by any member of isolate group.

KEY TO TABLE

CALL STIMULUS

1 : soft grunts

2 : cheeps

3 : woo calls (Contact call)

4 : affiliation rattle

5 : threat grunts

6 : teeth chatter threat call

7 : scream

8 : teeth chomp

9 : sex rattle

10 : ejaculatory growl

APPENDIX XV contd.

C) SLIDES AND CALLS

Submissive Responses

1) present *

SLIDE AND CALL STIMULUS

Group	Individual	1	2	3	4	5	6	7	8	9	10
dark	1	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0
	3	4	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0
peer	5	0	0	0	0	2	0	0	0	0	2
	6	0	0	0	0	1	0	0	0	0	1
	7	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0	0
isolate	10	3	0	0	0	1	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0	0

* present not shown by any members of adult peer, social or adult feral groups.

2) teeth chatter/grimace

SLIDE AND CALL STIMULUS

Group	Individual	1	2	3	4	5	6	7	8	9	10
dark	1	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	13
	4	2	0	0	0	0	1	0	0	2	0
peer	5	3	1	0	0	3	0	0	0	0	3
	6	3	0	1	4	0	1	0	0	0	3
	7	3	2	5	3	4	3	0	5	2	12
	8	6	5	5	5	4	1	2	2	1	7

APPENDIX XV contd.

2) teeth chatter/grimace

SLIDE AND CALL STIMULUS

Group	Individual	1	2	3	4	5	6	7	8	9	10
isolate	10	3	0	2	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	2
	12	0	0	0	0	0	0	0	0	0	0
	13	1	0	0	1	0	0	0	0	0	0
adult-peer	14	0	0	0	0	0	0	0	0	0	0
	15	0	0	0	1	5	0	0	0	0	3
	16	0	0	0	0	3	0	0	0	0	1
	17	4	1	1	2	1	0	0	0	0	1
social	18	2	0	0	4	15	2	0	1	1	1
	19	0	0	0	0	0	0	0	0	0	0
	22	3	0	10	3	17	0	0	0	2	5
	23	0	0	0	0	0	0	0	3	0	1
feral Bart.		0	0	1	0	4	0	0	0	0	0
	B.Susan	0	0	0	0	0	0	0	0	0	0
	Isaacs	0	0	0	0	0	0	0	0	0	0
	Margaret	0	0	0	0	0	0	0	0	0	0

3) withdraw

SLIDE AND CALL STIMULUS

Group	Individual	1	2	3	4	5	6	7	8	9	10
dark	1	1	2	2	1	2	5	5	2	2	2
	2	2	2	3	4	2	2	2	3	4	3
	3	1	1	0	2	0	1	2	1	0	6
	4	3	1	0	1	1	0	1	0	0	0
peer	5	2	2	1	1	3	0	1	1	0	3
	6	2	3	1	0	2	1	0	0	0	1
	7	4	4	3	2	3	2	2	2	2	4
	8	5	2	3	6	4	2	0	5	1	4

APPENDIX XV contd.

3) withdraw (contd.)

SLIDE AND CALL STIMULUS

Group	Individual	1	2	3	4	5	6	7	8	9	10
isolate	10	4	1	0	3	1	0	0	1	1	1
	11	1	1	1	0	1	3	1	1	0	0
	12	1	0	0	0	0	1	1	1	1	0
	13	3	2	3	0	1	2	3	1	1	1
adult-peer	14	3	1	1	1	1	1	1	1	0	0
	15	0	1	0	1	4	1	1	0	0	1
	16	2	2	0	1	1	0	1	2	2	2
	17	3	0	1	0	0	0	0	0	0	0
social	18	3	1	1	2	4	2	3	1	2	0
	19	0	0	0	0	0	0	0	0	0	1
	22	4	1	3	1	1	1	2	2	0	1
	23	1	1	2	0	1	0	0	0	1	1
feral Bart.		0	1	0	1	1	1	0	2	1	0
B.Susan		0	0	0	0	0	0	0	0	0	0
Isaacs		1	0	0	0	0	0	0	0	0	0
Margaret		2	0	1	0	0	0	0	0	0	0

4) freeze *

SLIDE AND CALL STIMULUS

Group	Individual	1	2	3	4	5	6	7	8	9	10
peer	5	1	1	0	0	0	1	0	0	0	0
	6	1	0	2	0	0	0	0	0	0	0
	7	0	0	1	1	2	4	2	3	2	2
feral Bart.		0	0	0	0	0	0	0	0	0	0
B.Susan		0	0	0	0	0	0	0	0	0	0
Isaacs		0	1	0	0	0	0	0	0	0	0
Margaret		0	0	0	0	0	0	0	0	0	0

* freeze not shown by any members of dark, isolate, adult-peer or social groups.

APPENDIX XV contd.

Dominance responses

1) dominance bounce

		SLIDE AND CALL STIMULUS									
Group	Individual	1	2	3	4	5	6	7	8	9	10
dark	1	0	0	0	0	0	0	0	0	0	0
	2	0	1	0	0	0	2	0	1	2	0
	3	0	0	0	0	0	0	1	0	0	0
	4	0	0	0	0	0	0	0	0	0	0
peer	5	0	0	0	0	0	0	1	1	1	0
	6	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0	0
isolate	10	0	0	0	0	0	0	0	0	0	0
	11	1	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	1	0	0	0
	13	0	0	0	0	0	0	0	0	0	0
adult-peer	14	0	0	0	0	0	1	0	0	1	0
	15	0	1	0	1	0	0	1	1	0	0
	16	0	0	0	0	0	0	0	0	0	1
	17	0	0	0	0	0	0	0	0	0	0
social	18	0	0	0	0	0	0	0	0	0	0
	19	0	0	1	0	0	0	0	1	1	0
	22	0	0	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0	0	0
feral Bart.	1	1	1	0	0	0	0	0	0	0	0
	B.Susan	0	0	0	0	0	0	0	0	0	0
	Isaacs	0	0	0	0	0	0	0	0	0	0
	Margaret	0	0	0	0	0	0	0	0	0	0

2) yawn/teeth chomp

		SLIDE AND CALL STIMULUS									
Group	Individual	1	2	3	4	5	6	7	8	9	10
dark	1	1	1	0	1	0	0	0	1	2	0
	2	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	1	0	0	0	0	0
	4	0	0	0	2	3	0	0	1	0	0

APPENDIX XV contd.

3) threat expressions * (contd.)

SLIDE AND CALL STIMULUS

group	individual	1	2	3	4	5	6	7	8	9	10
peer	5	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0
	7	1	0	0	0	0	0	0	0	0	0
	8	1	0	0	0	0	0	0	0	0	0
social	18	0	0	0	0	0	0	0	0	0	0
	19	2	0	0	0	1	0	0	2	0	1
	22	1	0	0	0	0	0	2	0	0	0
	23	0	0	2	0	0	0	0	1	1	0
feral Bart.		0	0	0	0	0	0	0	0	0	0
	B.Susan	0	0	0	0	0	0	0	0	0	0
	Isaacs	0	0	0	0	1	0	0	0	0	1
	Margaret	0	0	0	0	0	0	0	0	0	0

* threat not exhibited by any members of isolate or adult-peer groups.

4) attack behaviours *

SLIDE AND CALL STIMULUS

group	individual	1	2	3	4	5	6	7	8	9	10
peer	5	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	2	0	0	0	0	0	0
	X										
social	18	0	0	0	0	0	0	0	0	0	0
	19	0	0	0	0	1	0	0	0	1	0
	22	0	0	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0	0	0
feral Bart.		1	1	0	0	0	0	0	0	0	0
	B.Susan	2	0	0	0	0	0	0	0	0	0
	Isaacs	0	0	0	0	0	0	0	0	0	0
	Margaret	0	0	0	1	0	0	0	0	0	0

* attack not shown by any members of dark, isolate or adult-peer groups.

APPENDIX XV contd.

Affiliation responses

1) lipsmack/pout

		SLIDE AND CALL STIMULUS									
Group	Individual	1	2	3	4	5	6	7	8	9	10
dark	1	0	1	3	1	1	0	1	0	1	3
	2	1	0	0	2	0	0	0	1	0	1
	3	0	0	2	2	1	3	4	0	0	3
	4	0	0	0	0	0	0	0	0	0	1
peer	5	0	0	0	2	1	0	0	0	0	3
	6	0	0	0	0	3	0	2	0	0	0
	7	1	1	0	0	0	2	0	1	1	0
	8	0	2	0	0	0	0	0	0	0	1
isolate	10	2	1	2	2	1	0	0	0	0	1
	11	1	1	0	0	1	0	0	0	0	0
	12	1	0	1	0	0	0	0	0	0	0
	13	3	1	2	2	2	3	1	0	0	1
adult-peer	14	1	0	0	0	1	0	0	1	0	3
	15	1	0	3	2	3	1	0	2	3	4
	16	1	0	0	1	0	0	0	0	0	0
	17	4	0	0	0	0	0	2	1	2	3
social	18	1	1	1	6	0	0	1	3	2	0
	19	0	0	0	0	0	0	0	0	1	1
	22	4	0	1	5	0	0	1	3	1	2
	23	0	0	1	0	2	0	0	2	0	6
feral	Bart.	3	0	3	3	0	0	0	0	0	0
	B.Susan	2	1	2	2	4	2	0	0	0	0
	Isaacs	0	0	1	2	0	1	0	2	0	1
	Margaret	2	0	0	2	0	1	0	0	0	0

Other responses

1) approach

		SLIDE AND CALL STIMULUS									
Group	Individual	1	2	3	4	5	6	7	8	9	10
dark	1	4	0	2	1	2	3	3	2	2	3
	2	2	3	6	5	4	3	5	6	4	3
	3	3	2	1	3	1	1	3	1	3	5
	4	1	0	1	1	0	1	2	0	1	0

APPENDIX XV contd.

2) contact (contd.)

SLIDE AND CALL STIMULUS

Group	Individual	1	2	3	4	5	6	7	8	9	10
peer	5	0	0	0	2	1	0	0	0	0	3
	6	0	0	0	0	3	0	2	0	0	0
	7	1	1	0	0	0	2	0	1	1	0
	8	0	2	0	0	0	0	0	0	0	1
isolate	10	2	1	2	2	1	0	0	0	0	1
	11	1	1	0	0	1	0	0	0	0	0
	12	1	0	1	0	0	0	0	0	0	0
	13	3	1	2	2	2	3	1	0	0	1
adult-peer	14	1	0	0	0	1	0	0	1	0	3
	15	1	0	3	2	3	1	0	2	3	4
	16	1	0	0	1	0	0	0	0	0	0
	17	4	0	0	0	0	0	2	1	2	3
social	18	1	1	1	6	0	0	1	3	2	0
	19	0	0	0	0	0	0	0	0	1	1
	22	4	0	1	5	0	0	1	3	1	2
	23	0	0	1	0	2	0	0	2	0	6
feral	Bart.	1	0	0	2	0	0	0	0	1	0
	B.Susan	1	1	1	0	0	0	0	0	0	0
	Isaacs	2	1	1	0	2	0	0	0	0	0
	Margaret	2	0	1	1	3	0	0	2	0	0

KEY TO TABLE

SLIDE AND CALL STIMULUS

- | | |
|---|--|
| 1 : mother cradling infant; soft grunts | 6 : juvenile teeth-chatter
threat; teeth-chatter
threat call |
| 2 : infant visual explore; cheeper | 7 : infant grimace |
| 3 : female visual explore; woo calls | 8 : male masturbation; teeth chomp |
| 4 : male cradling infant | 9 : male teeth chatter invite; sex
rattle |
| 5 : female brow threat; threat grunts | 10 : male ejaculatory face;
ejaculatory growl. |

APPENDIX XV contd.

2) contact (contd.)

SLIDE AND CALL STIMULUS

Group	Individual	1	2	3	4	5	6	7	8	9	10
peer	5	0	0	0	2	1	0	0	0	0	3
	6	0	0	0	0	3	0	2	0	0	0
	7	1	1	0	0	0	2	0	1	1	0
	8	0	2	0	0	0	0	0	0	0	1
isolate	10	2	1	2	2	1	0	0	0	0	1
	11	1	1	0	0	1	0	0	0	0	0
	12	1	0	1	0	0	0	0	0	0	0
	13	3	1	2	2	2	3	1	0	0	1
adult-peer	14	1	0	0	0	1	0	0	1	0	3
	15	1	0	3	2	3	1	0	2	3	4
	16	1	0	0	1	0	0	0	0	0	0
	17	4	0	0	0	0	0	2	1	2	3
social	18	1	1	1	6	0	0	1	3	2	0
	19	0	0	0	0	0	0	0	0	1	1
	22	4	0	1	5	0	0	1	3	1	2
	23	0	0	1	0	2	0	0	2	0	6
feral	Bart.	1	0	0	2	0	0	0	0	1	0
	B.Susan	1	1	1	0	0	0	0	0	0	0
	Isaacs	2	1	1	0	2	0	0	0	0	0
	Margaret	2	0	1	1	3	0	0	2	0	0

KEY TO TABLE

SLIDE AND CALL STIMULUS

- | | |
|---|--|
| 1 : mother cradling infant; soft grunts | 6 : juvenile teeth-chatter threat; teeth-chatter threat call |
| 2 : infant visual explore; cheeper | 7 : infant grimace |
| 3 : female visual explore; woo calls | 8 : male masturbation; teeth chomp |
| 4 : male cradling infant | 9 : male teeth chatter invite; sex rattle |
| 5 : female brow threat; threat grunts | 10 : male ejaculatory face; ejaculatory growl. |

APPENDIX XVI Raw data for assessing neuroticism, extraversion and psychotism in DIMS study (frequency data for all non-social tests; frequency and duration for stimulus animal tests).

NEUROTICISM

Infant	Test				
	S	GM1	Ty1	Ty2	GM2
25	39	0	8	2	1
26	31	4	1	6	0
27	14	0	5	0	0
28	46	1	4	0	0
29	19	1	5	5	0
30	62	1	5	2	0
31	41	2	0	2	10
32	1	0	1	2	0
33	39	2	4	1	0
34	34	0	5	8	0
35	59	0	0	1	4
36	40	1	5	0	4
38	46	0	2	7	3

APPENDIX XVI contd.

NEUROTICISM (contd.)

Test

Infant	FF2	Ty3	TTB	TTD	TIN
25	9	0	0	0	7
26	63	3	2	8	7
27	0	3	0	0	2
28	2	1	1	3	3
29	4	0	0	0	3
30	1	2	3	3	1
31	1	1	1	3	2
32	1	1	0	0	8
33	0	13	11	16	33
34	0	10	3	2	11
35	4	1	2	3	31
36	0	0	10	5	17
38	4	7	9	2	5

APPENDIX XVI contd.

NEUROTICISM (contd.)

Test

Infant	SA(3)	CA(3)	S+C(3)	SA(15)	CA(15)	S+C(15)
25	31	16	38	115	28	90
26	5	1	29	36	5	0
27	13	31	5	58	2	8
28	8	0	3	19	0	14
29	11	26	5	42	16	87
30	12	39	4	23	2	13
31	9	27	3	45	24	44
32	15	18	2	78	5	6
33	27	10	24	55	1	5
34	1	3	3	11	2	6
35	41	16	33	26	17	1
36	3	17	7	4	3	1
38	9	4	3	33	25	27

APPENDIX XVI contd.

NEUROTICISM (Contd.)

Infant	Test					
	5		Kid		Angus	
	freq.	durn.	freq.	durn.	freq.	durn.
25	46	173.7	14	40	77	141.7
26	27	63	49	104.5	101	185.7
27	26	56.8	9	13.9	48	90.6
28	25	45.2	30	57.2	86	17.3
29	15	49.9	5	22.0	1	1.5
30	75	173.7	14	28.5	70	123
31	74	201.3	19	52.7	128	436.3
32	29	62.3	16	32.2	65	115.4
33	87	154.8	46	85.5	112	214.9
34	66	117.8	35	56.8	30	61.9
35	140	203.1	38	61.9	108	186
36	15	24.3	10	26.9	52	211
38	155	666.8	23	93.4	45	107.8

APPENDIX XVI

EXTRAVERSION

Infant	Test						
	S	GMI		Ty1		Ty2	
	TVX	TVX	VXO	TVX	VXO	TVX	VXO
25	3	8	1	19	9	31	16
26	0	24	6	44	29	30	25
27	0	18	2	51	29	78	35
28	0	23	3	47	24	8	0
29	0	15	6	56	28	67	37
30	0	20	3	66	36	53	25
31	1	53	12	30	9	41	24
32	0	27	13	42	17	70	27
33	0	58	8	73	29	62	29
34	0	36	11	74	37	81	35
35	18	59	22	82	35	100	47
36	23	44	11	69	29	46	21
38	0	42	8	89	38	66	23

APPENDIX XVI contd.

EXTRAVERSION (Contd.)

Infant	Test							
	GM2		FF2		Ty3		TTB	
	TVX	VXO	TVX	VXO	TVX	VXO	TVX	VXO
25	29	6	20	5	32	18	24	10
26	15	5	20	14	42	26	23	9
27	18	7	36	26	51	31	19	7
28	34	16	34	17	17	11	37	13
29	36	9	38	16	68	28	13	7
30	21	8	46	19	99	49	25	4
31	55	21	32	14	63	30	19	7
32	38	10	41	14	10	5	4	3
33	65	23	29	13	55	25	52	22
34	47	21	62	25	17	9	24	5
35	41	24	42	13	77	41	23	11
36	57	11	50	17	78	29	19	8
38	38	11	45	18	63	31	15	5

APPENDIX XVI contd.

EXTRAVERSION (Contd.)

Infant	Test						
	TTD		TTN		SA(3)		
	TVX	VXO	TVX	VXO	TVX	VXO	SW
25	4	1	20	15	83	45	101
26	4	2	51	33	52	22	83
27	14	3	83	40	113	59	121
28	14	5	58	38	85	40	131
29	36	20	29	14	73	50	75
30	61	28	100	42	182	94	194
31	9	5	26	18	77	32	125
32	13	4	52	37	91	54	147
33	62	31	73	43	116	52	161
34	11	4	27	21	74	31	112
35	14	3	87	47	93	48	134
36	31	14	18	11	84	34	144
38	21	2	11	8	127	52	139

APPENDIX XVI contd.

EXTRAVERSION (contd.)

Infant	Test					
	CA(3)			S+C(3)		
	TVX	VXO	SW	TVX	VXO	SW
25	47	8	130	61	33	92
26	43	16	88	73	42	113
27	37	0	53	76	34	87
28	20	1	66	100	64	123
29	35	2	65	46	17	88
30	32	0	56	216	110	244
31	43	8	104	75	27	130
32	30	7	51	95	45	158
33	61	13	139	90	38	140
34	45	11	135	92	42	177
35	98	30	146	113	54	139
36	75	24	154	119	56	191
38	32	2	77	81	37	113

APPENDIX XVI contd.

EXTRAVERSION (contd.)

Infant	Test								
	SA(15)			CA(15)			S+C(15)		
	TVX	VXO	SW	TVX	VXO	SW	TVX	VXO	SW
25	205	114	210	64	8	58	177	90	204
26	162	88	190	35	2	50	130	62	158
27	67	46	48	20	1	16	84	52	97
28	129	75	150	64	19	57	119	63	153
29	135	78	166	77	23	62	49	34	160
30	146	82	185	23	5	32	232	121	230
31	133	68	172	96	34	108	134	71	207
32	131	81	193	63	14	94	128	72	197
33	161	97	217	79	12	56	226	119	243
34	71	38	103	46	0	47	192	88	200
35	103	62	155	48	19	89	110	69	202
36	67	35	75	50	16	60	157	82	190
38	94	61	136	14	3	37	51	18	100

APPENDIX XVI (Contd.)

EXTRAVERSION (contd.)

Infant	Test							
	5				Kid			
	freq.		durn.		freq.		durn.	
TVX	VXO	TVX	VXO	TVX	VXO	TVX	VXO	
25	534	345	1489	1013	430	310	1062.3	790.6
26	432	269	1193.4	711.5	387	229	1072.1	518.8
27	463	238	1796.5	725.7	518	324	1490.2	797.5
28	492	321	1133.9	659.9	642	446	1244.7	882.8
29	507	350	1300.1	939.2	484	337	955.8	645.7
30	593	369	1405.2	755.4	609	353	1383.1	653.5
31	477	331	994.4	648.6	356	248	806.9	529.1
32	395	262	796.5	479.7	354	235	719.6	482.9
33	511	336	1014.8	624	509	364	857.5	594.5
34	371	226	840.1	451.5	448	308	890.6	559.9
35	745	473	1504.7	814.8	632	400	1000.1	901.8
36	610	366	1288.7	565.2	373	235	746.3	333.9
38	348	265	618.2	475	355	245	799.8	506.6

APPENDIX XVI (Contd.)

EXTRAVERSION (Contd.)

Infant	freq.		Test Angus durn.	
	TVX	VXO	TVX	VXO
25	510	334	1595.7	1080.2
26	459	262	1243.1	585.9
27	350	183	2187.7	529.2
28	565	357	1379.1	776.4
27	534	349	1227.8	761.5
30	568	363	1434.5	772.3
31	439	312	837.7	558.8
32	329	232	606.3	424.6
33	571	376	1033	549.9
34	551	334	1266.1	559.5
35	573	407	1068.1	690
36	269	143	837.6	242
38	321	207	852.3	505.6

APPENDIX XVI (Contd.)

PSYCHOTICISM

Infant	Test								
	Ty1			Ty2			GM2		
	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.
25	0	0	0	0	3	1	0	0	0
26	0	0	0	0	1	0	0	0	0
27	0	0	0	0	0	0	0	1	0
28	4	9	1	0	4	0	0	0	0
29	1	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0
31	0	5	0	0	3	0	0	4	0
32	0	0	0	0	0	0	0	1	0
33	0	6	0	0	0	0	0	6	0
34	0	0	0	0	2	0	0	0	0
35	0	3	0	0	6	0	3	0	0
36	0	2	0	1	3	1	0	1	0
38	0	1	0	3	5	5	0	0	3

APPENDIX XVI (Contd.)

PSYCHOTICISM (contd.)

Infant	Test								
	FF2			Ty3			TTB		
	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.
25	0	0	0	0	0	0	0	0	0
26	1	1	1	2	0	1	2	0	0
27	0	0	0	1	0	3	0	4	0
28	0	1	0	0	0	1	0	4	1
29	0	0	0	0	0	0	0	0	0
30	0	0	0	2	1	0	0	0	2
31	0	3	0	1	0	0	1	12	0
32	0	1	0	0	0	1	2	0	0
33	0	0	0	0	4	13	4	0	7
34	0	0	0	0	0	5	0	0	2
35	2	3	0	0	9	0	2	7	0
36	0	0	0	0	0	1	0	0	8
38	1	1	1	0	13	3	2	0	8

APPENDIX XVI (Contd.)

PSYCHOTICISM (Contd.)

Infant	Test								
	TTD			TTN			SA(3)		
	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.
25	0	2	0	0	0	0	0	10	5
26	11	0	4	5	0	0	0	2	1
27	0	0	0	0	0	0	0	0	3
28	3	2	0	0	0	0	6	0	0
29	0	0	0	0	0	2	0	2	0
30	0	0	2	0	2	0	0	0	0
31	2	0	1	0	0	0	5	6	0
32	0	0	0	0	0	0	5	3	0
33	8	0	9	19	0	14	0	5	11
34	3	0	1	0	0	2	0	1	0
35	4	10	0	3	1	0	24	0	5
36	0	0	4	18	0	1	2	22	0
38	1	0	1	2	0	0	0	1	9

APPENDIX XVI (Contd.)

PSYCHOTICISM (Contd.)

Infant	Test								
	CA(3)			S+C(3)			SA(15)		
	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.
25	0	1	7	0	7	2	0	0	5
26	0	0	0	0	7	0	5	1	2
27	0	10	2	0	14	0	0	13	1
28	0	6	0	0	0	0	3	0	1
29	6	25	1	0	8	0	1	0	0
30	0	4	5	0	20	0	3	0	7
31	0	0	0	0	4	0	18	0	9
32	0	0	0	0	8	0	1	1	6
33	0	8	0	0	22	3	0	0	0
34	1	0	0	0	0	0	8	2	0
35	0	1	0	1	0	0	1	4	0
36	1	4	12	0	23	2	1	3	1
38	0	0	1	2	4	2	2	1	13

APPENDIX XVI (Contd.)

PSYCHOTICISM (Contd.)

Infant	Test					
	CA(15)			S+C(15)		
	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.
25	1	2	17	3	0	16
26	0	0	2	0	0	0
27	0	13	0	0	15	0
28	0	0	0	1	0	1
29	0	1	0	0	19	0
30	1	7	0	5	0	1
31	0	0	5	5	2	7
32	0	0	2	0	1	1
33	0	0	0	0	0	0
34	0	0	0	28	0	0
35	0	8	0	0	22	0
36	0	14	0	0	21	0
38	0	0	10	0	0	23

APPENDIX XVI (Contd.)

PSYCHOTICISM (contd.)

Infant	Test					
	freq.			durn.		
	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.
25	0	1	11	0	5.6	38
26	9	1	8	21.1	2.9	17.7
27	6	0	0	18.7	0	0
28	2	1	2	3	3.7	4.5
29	4	0	0	24.6	0	0
30	1	0	48	1.1	0	125.5
31	36	18	5	113.1	65.1	18.3
32	1	0	0	1.9	0	0
33	2	0	0	5.7	0	0
34	42	6	0	73	41.1	0
35	2	2	0	5.8	2.7	0
36	1	19	1	1.1	177.1	4.1
38	0	0	103	0	0	564.6

APPENDIX XVI (Contd.)

PSYCHOTICISM (Contd.)

Infant	Test					
	Kid			Kid		
	freq.			durn.		
	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.
25	1	2	9	1.2	6	31.2
26	7	29	0	22.6	288.9	0
27	3	0	0	4.7	0	0
28	2	0	10	2.5	0	22
29	4	3	0	18	10.7	0
30	7	3	0	15	9.3	0
31	8	0	12	16.1	0	38.5
32	6	1	0	14	5.7	0
33	17	0	5	38.2	0	9.2
34	15	0	0	25.1	0	0
35	0	0	4	0	0	11.7
36	6	0	2	14.8	0	8.7
38	2	0	12	3	0	68.2

APPENDIX XVI (Contd.)

PSYCHOTICISM (contd.)

Infant	Test					
	Angus			durn.		
	freq.			durn.		
	Aggn.	Withd.	Inapp.	Aggn.	Withd.	Inapp.
25	15	1	5	32.1	2.3	7.6
26	8	9	2	17.4	56.2	2.5
27	0	0	0	0	0	0
28	7	0	0	13.6	0	0
29	1	0	0	2.4	0	0
30	1	0	2	2.5	0	2.7
31	100	0	17	302.3	0	87.4
32	4	0	0	10.1	0	0
33	1	0	0	2.5	0	0
34	5	2	0	10.0	3.4	0
35	0	1	11	0	1.9	49.4
36	1	4	0	1.2	10	0
38	0	6	15	0	32.5	61.5

KEY TO TABLETESTS

S :	separation from mother
GML/2 :	given milk 1/2
Tyl/2/3 :	toy 1/2/3
FF2 :	frustration food test 2
TTB/D/N :	toy tests B/D/N at 4 months
SA(3)/(15) :	slides alone at 3 months/15 months
CA(3)/(15) :	calls alone at 3 months/15 months
S+C(3)/(15) :	slides and calls at 3 months/15 months
5 :	stimulus animal test with peer 5.
Kid :	stimulus animal test with kid
Angus :	stimulus animal test with Angus

MEASURES

freq.:	frequency
durn.:	duration (measured in seconds)
TVX :	total visual exploration score
VXO :	visual explore of the test object score
Aggn.:	aggression score
Withd.:	withdrawing in stereotyped fashion
Inapp.:	masturbation score

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