BEHAVIORAL TRAITS IN VERVET MONKEYS: A LONGITUDINAL STUDY OF FOUR SUCCESSIVE BIRTH COHORTS

By

Caroline Desbiolles

Department of Biology

McGill University, Montreal

June, 2007

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Doctor of Philosophy

Your file Votre référence
ISBN: 978-0-494-50808-4
Our file Notre référence
ISBN: 978-0-494-50808-4

ACKNOWLEDGEMENTS

I would like to express my deepest gratitude to all those who have helped me along my journey. I would like to thank my professors and mentors Dr. Roberta Palmour and Dr. Frank Ervin, for making this ambitious project possible. I would like to acknowledge their scientific allegiance, guidance, wisdom, patience, support and encouragement during easier and sometimes more difficult times, and most especially for believing in my ability to achieve this Ph.D. A special thanks also goes to my colleagues and friends, Joshua Fainman, Martine Elbejjani and Dr. Sasha John for their assistance at times, as well as their camaraderie.

I would like to say thank you to Dr. Simon Young for his invaluable assistance and advice. I equally appreciate and thank the statistical guidance of Chantal Mérette for the data analyses.

My heartfelt thanks goes to the Behavioral Science Foundation, St.Kitts and its staff, especially, Dr. Amy Beierschmitt, Gilbert Gordon, Anderson Tross, Dora Louard and Shakima Conrod, for their assistance and support in creating an ideal environment throughout the course of my field work. I would also like to acknowledge the Canadian Institute of Health Research (Medical Research Council of Canada).

I am eternally thankful to my family for their patience and loving support during this entire journey: To my mother (an admirable woman of great strength and determination), my father, Christine, Andrew and Ryan. Mille merci! I salute my grandfather Dr. Tibor Féjérvàry, for whom no words could even begin to express the gratitude I feel for the exemplary role he has played in my life; and to my grandmother, the love of his life, and the pillar of our family. I cherish their memory. Kosenom sepen. Thank you to all of my friends for your sensitivity, your listening ear, your sense of humor, and your encouragement, the sum of which helped me achieve my goals.

A special acknowledgment to one of my earliest mentors, André Giguère, who has not only provided me with wisdom and guidance throughout the years, but whose special haven he created back in 1969, 'La Ferme d'André,' is where my love and intellectual fascination for the behavior of animals and children began.

TABLE OF CONTENTS

CHAPTER VI: Discussion

ABSTRACT

Extensive evidence supports a dimensional approach to the derivation of personality and other behavioral traits in human and animal studies, and suggests that personality traits are hierarchically organized with more specific lower-order traits combining to form higher order-traits. We used this approach in an exploration of the structure of normal behavior in juvenile and adolescent vervet monkeys in a prospective longitudinal study. The goals of this thesis were to determine whether we could successfully identify behavioral traits in >200 African green (or vervet) monkeys (*Chlorocebus aethiops)* based on standard well documented primatological behavioral measures in (1) social groups and (2) novelty challenge tests.

The behavioral data was collected using a systematic methodological approach called focal animal testing (Altmann, 1973) and consisted of direct observations rather than the assigning descriptive adjectives. The data was subsequently analyzed using factor analysis to derive interpretable behavioral dimensions.

In the first study presented in this thesis, we extracted five interpretable behavioral dimensions from the Social Juvenile condition. These five behavioral dimensions in order of decreasing proportional variance were "agonism," "energetic sociability," agreeableness," "playfulness," and "behavioral inhibition." The first two factors showed a negative relationship with age, while the remaining three factors were positively correlated with age. Males scored higher on "playfulness," while females had higher scores for "energetic sociability" and "agreeableness." Monkeys which scored highly for "agonism" had significantly higher social rank, while those which scored highly for "behavioral inhibition" had significantly lower rank. Cerebrospinal fluid levels of the serotonin metabolite 5-HIAA were negatively correlated with Factor 3, "agreeableness," and levels of the norepinephrine metabolite MHPG were negatively correlated with Factor 5, "behavioral inhibition."

In the second study presented in this thesis, we identified four interpretable behavioral dimensions from the first of two novelty testing paradigms. Monkeys in late infancy were exposed to a novel environment physically very different from their home cage, and baited with rewards and opportunities for exploration. The four behavioral

dimensions, which emerged, in order of decreasing proportional variance, were termed "energetic exploration," "defensive aggression," "behavioral inhibition," and "calm exploration." Factors 1 and 2 were negatively correlated with age; on average, females had higher scores for Factor 2. "Energetic exploration" was positively correlated with motility, rewards eaten and rewards dropped, while "defensive aggression" was negatively correlated with the first two of these measures. "Behavioral inhibition" was negatively related to motility and to space covered. Multiple regression analysis showed that levels of 5-HIAA, as well as levels of HVA, were positively correlated with Factor 1 ("energetic exploration"), while levels of MHPG were positively correlated with Factor 4 ("calm exploration").

In the third study presented in this thesis, we extracted four interpretable behavioral dimensions from a jungle-gym novelty testing exposure in adolescent monkeys. In order of decreasing proportional variance, the behavioral dimensions were interpreted as "confident," "cautious", "exploratory" and "defensive aggression." A second-order factor analysis of the individual scores derived from this novel environment paradigm, together with factor scores from the earlier nursery novelty test, yielded four higher-order reactivity traits ("exploratory," "confident-to-inhibited," "defensive," and "cautious"). Thus the response to novelty was both conceptually and statistically replicated at two time points, providing initial evidence for continuity and stability of behavioral traits from late infancy to adolescence.

In summary, the work presented in this thesis validates the hypothesis that interpretable behavioral traits can be identified in young vervet monkeys, using primary behavioral scores; provides initial evidence that the traits observed as a result of challenge tests are stable across developmental time (juvenile to adolescent); and lays the foundation for future studies of the relationship between these behavioral traits and psychopathology, as well as studies of the genes related to each of the behavioral traits.

ABRÉGÉ

Des évidences extensives soutiennent une approche dimensionelle à la dérivation des traits de personnalité et d'autres traits comportementaux chex les humains et les animaux et suggère que les traits de personnalité suivent une hiérarchie organisée de traits plus spécifiques de bas-ordre combinant pour former des traits d'ordre plus élevé. Nous avons employé cette approche dans une exploration de la structure du comportemt normal chez des singes verts (*Chlorocebsu aethiops)* juvéniles et adolescents lors d'une étude longitudinale prospective. Les objectifs de cette thèse étaient de déterminer si nous pourrions réussir a identifier des traits de comportements chez plus de 200 singes verts africains (*Chlorocebus aethiops*) en se basant sur des mesures conformes de comportement primatologique bien documentées dans (1) des groupes sociaux et (2) des essais de défi de nouveauté.

Les données comportementales ont été rassemblées a l'aide d'une approche méthodologique systématique appelée l'examination animale focale, "focal animal testing" (Altmann, 1973), et se constituent d'observations d'ordres directes plutôt que des adjectifs descriptifs attribués. De suite, les données ont été analysées en utilisant l'analyse factorielle pour dériver des dimensions comportementales interprétables.

Dans la première étude présentée dans cette thèse, nous avons extrait cinq dimensions comportementales interprétables à partir du contextejuvénile social, "Social Juvenile condition." Ces cinq dimensions comportementales, citées par ordre de variance proportionelle décroissant, étaient "agonism," "energetic sociability," "agreeableness" "playfulness," and "behavioral inhibition." Les deux premiers facteurs sont négativement reliés à l'age, alors que les trois facteurs restants étaient positivement corrélés avec l'age. Les males ont des scores plus élevé pour "playfulness," tandis que les femelles avaient de plus hauts points pour "energetic sociability," et "agreeableness." Les singes qui ont marqué des points élevés pour "agonism" étaient de rang social remarquablement élevé, alors que ceux qui ont marqué amplement pour "behavioral inhibition" avaient un rang considérablement inférieur. Les niveaux du fluide cérébro-spinaux du métabolite de sérotonine 5-HIAA étaient négativement correlés avec le facteur 3, "agreeableness," et

les niveaux du métabolite de norépinéphrine MHPG étaient négativement correlés avec le facteur 5, "behavioral inhibition."

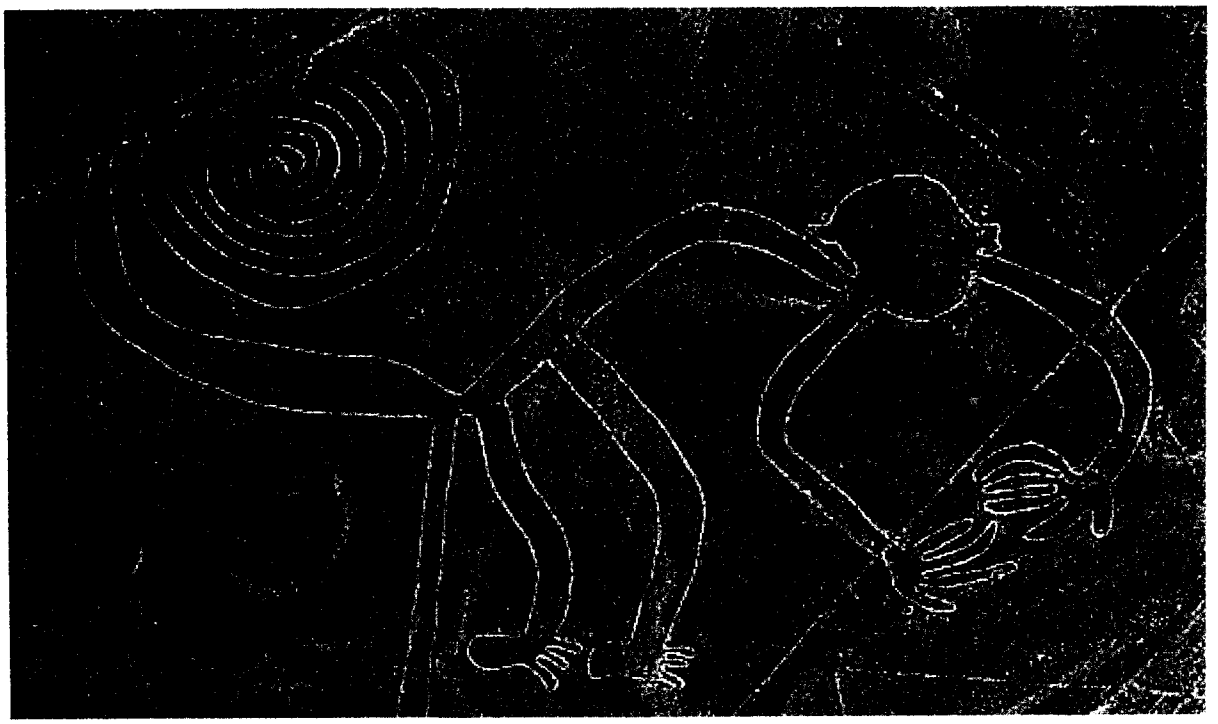
Dans la deuxième étude présentée dans cette thèse, nous avons identifié quatre dimensions comportementales interprétables du premier de deux paradigmes d'épreuve de nouveauté, le "Nursery Novelty test." Des singes en fin d'enfance ont été exposés à un nouvel environement physiquement très different de leur cage habituelle, et séduits par des récompenses et des occasions d'exploration. Les quatre dimensions comportementales extraites, par ordre décroissant de variance proportionnelle, ont été désignées par "energetic exploration," "defensive aggression," "behavioral inhibition," et "calm exploration." Les facteurs 1 et 2 étaient négativement corrélés avec l'âge ; en moyenne, les femelles ont eu de plus hauts points pour le facteur 2 "defensive agression." "Energetic exploration," était positivement corrélée avec la motilité, les récompense mangés et les récompenses échappées, alors que "defensive aggression," était négativement corrélée avec les deux premières de ces mesures. "Behavioral inhibition" était négativement liée à la motilité et l'éspace couverte. L'analyse de régression multiple a prouvé que les niveaux de 5-HIAA et ceux de HVA, étaient positivement corrélés avec le facteur 1 ("energetic exploration"), tandis que les niveaux de MHPG étaient positivement corrélés avec le facteur 4 ("calm exploration").

Dans la troisième étude présentée dans cette thèse, nous avons extrait quatre dimensions comportementales interprétables d'après la pérformance de singe adolescents dans une deuxieme épreuve de nouveauté, la cage jungle gymnastique, "Jungle Gym test." Citées par ordre déclinant de variance proportionnelle, les dimensions comportementales ont été interprétées comme "confident," "cautious", "exploratory" and "defensive aggression." Une analyse factorielle de second ordre employant les scores individuels de cette épreuve de nouveauté, ensemble avec les scores individuels du "Nursery Novelty test" a produit quatre traits d'ordre élevé ("exploratory," "confident-to-inhibited," "defensive," and "cautious"). Le fait que la réponse à l'épreuve de nouveauté a été conceptuellement et statistiquement répliquée à deux temps différents, démontre des preuves initiales pour établire la continuité et la stabilité des traits comportementaux de l'enfance à l'adolescence.

En résumé, le travail présenté dans cette thèse valide l'hypothèse que des traits comportementaux interprétables peuvent être identifiés chez des jeunes singes vervet, en utilisant les points comportementaux primaires; fournit l'évidence initiale que les traits observés suite a des essais de défi sont stables dans le temps développemental (juvénile à l'adolescent); et forme la base pour de futures études du lien entre ces traits comportementaux et la psychopathologie, ainsi que des études des gènes liés à chacun de ces traits comportementaux.

CHAPTER I

HISTORICAL REVIEW



St. Christopher 1774

"She showed me several plantations belonging to Scotch people, who do not reside on them. Amongst these is one belonging to the Millikens. It is situated rather high, and goes by the name of Monkey Hill, from which I suppose it more particularly infested by those gentry, from which indeed no part of the Island is entirely free. As I am no enemy to the Pythagorean system, I do suppose these lively and troublesome companions, [are the successors of] the former Inhabitants of this Island, who you know were French, and truly the difference is so little between one Monkey and another, that the transmigration must have been very easy, and as to the soul, it had undergone no change, but is French in all respects. They grin, they laugh, they chatter and make grimaces. Their frolicks are mischievous, their thefts dextrous. They are subtle enemies and false friends. When pursued, they fly to the mountain and laugh at their pursuers, as they are as little ashamed of a defeat

as a French admiral or general. In short they are the torment of the planters; they destroy whole cane-pieces in a few hours, and come in troops from the mountain, whose trees afford them shelter. No method to get the better of them has yet been found out. I should think strong English dogs the best; as the English is your only animal to humble your French monkey and settle his frolicks."

By Janet Schaw

Journal of a Lady of Quality

Being the Narrative of a Journey
from Scotland to the West Indies,
North Carolina, and Portugal
in the years 1774 to 1776.
Edited by Evangeline Walker Andrews,
in Collaboration with Charles McLean Andrews,
New Haven, Yale University Press 1922.
Pp 131-132.

Vignette

"Early mornings at the Behavioral Science Foundation I make my way towards the enclosures of juvenile vervet monkeys I have been observing for the last few weeks. Every time I approach enclosure number 10, I receive the same consistent but opposite greetings from two specific juveniles in this group. Monkey 'A' always boldly runs up to the front of the cage to greet me, and then proceeds to tilt his head sideways, a sign of a play invite. Meanwhile, monkey 'B' has scurried fearfully towards the back end of the cage, folding himself into a ball, and avoiding any further eye contact with me."

This vignette clearly illustrates that you don't have to be a trained behaviorist in order to notice the presence of behavioral differences between monkeys. Are these behavioral patterns expressed by a given animal indicative of an internally consistent state (which some might refer to as personality) or are they just a series of random behaviors? It is only in the last 30 years that we have begun to address the topic of individual differences in nonhuman primates from a scientific perspective. Prior to that time, the field of primatology merely considered generalized species characteristics. Monkeys were studied according to their behavioral economy, and often all that was measured was the percentage of time allocated to foraging, resting and social activities. The contributions of age, sex and gender were documented, but any sign of individual difference was considered noise and eliminated through statistical group means. Because of the exponentially growing *Zeitgeist* in the behavioral sciences, more specifically individual variability, numerous fields of research addressing both human and nonhuman primates have begun to develop systematic methodological approaches which could ultimately help us to understand the potential scientific and clinical significance of these individual differences. One risk of focusing on behavior *qua* behavior is that it may lead to the reliance on anecdotal rather than systematic data. This may be good for conceptual purposes, but is a poor substitute for rigorous testing. By contrast, systematically observing a monkey's behavior at different developmental time points and in different settings may teach us volumes about his internal consistent state. Therefore, it is only by systematic research using quantitative methods that we will be able to objectively explore

individual behavioral differences in nonhuman primates and to attempt to derive robust, reliable and well-validated behavioral traits. For the clinician, the utility of the behavioral traits will be to discriminate problem and no-problem monkeys, and to flag vulnerable individuals with a high risk for future psychopathology early in the course of development, so as to study the etiological pathway. For the developmentalist, the utility of the behavioral traits depends on the extent to which one can actually observe evidence (not just assumptions) of continuity and stability or instability of these measures for individuals across time and situations.

Animals and Humans on a Continuum

Before the biologist Charles Darwin's (1809-1882) scientific contributions, anthropocentricity reigned. Man was regarded as the center of the universe, and scientists were reluctant to ascribe personality traits, emotions and cognitions to animals. It was Darwin's work (1872: *The expression of the emotions in man and animals*), which stressed a message of continuity in that the difference between man and beast was more a matter of degree than one of quality. Darwin argued that emotions exist in both human and nonhuman animals, and in this fashion, Darwin's work emerged as a springboard for the future study of behavior. It is now a commonly accepted view that animal behavior is closely related to human behavior allowing researchers to espouse the cross-species generality (Harlow et al.,, 1972; Gosling & John, 1999).

Prior to the *Zeitgeist* of individual variability, well-documented examples of cross-species generality could be found in the animal models of psychopathology (Harlow et al.,, 1972). These models served as an experimental effort to reproduce, in nonhuman subjects, the essential features of various human disorders or conditions (Suomi, 1982). A series of longitudinal studies exploring attachment behavior in rhesus monkeys, for example, was created (Harlow et al.,, 1972) largely based upon John Bowlby's (1958) view on mother/infant attachment. Harlow and Suomi manipulated the environment of infant monkeys by removing them from their mothers early on in life. These infants subsequently developed symptoms of depression, which in some cases persisted into adulthood (McKinney and Bunny, 1969; Harlow, Suomi & Novak, 1974; Suomi, 1991). Not only did these studies revolutionize scientific thinking concerning the

socialization process in human children but the existence of compelling nonhuman primate analogues to certain human psychopathologies allowed us to use these models as a means of better understanding the etiology of certain disorders. However, as informative as these models are, they fail to address important questions regarding individual variability: (1) Does every monkey who is separated from his mother at an early age have an equal susceptibility to develop a behavioral disorder? (2) Is the severe manipulation of the rearing environment, at a critical developmental time point, necessary to create a 'depressed' monkey (i.e. state dependent), or could infant monkeys who have not experienced early separation from their mothers also develop symptoms akin to depression (i.e. trait dependent)? And, lastly (3) although these animal models have successfully served to identify the expression of specific pathological conditions (e.g. depression) in monkeys, they do not specify where these depressed monkeys fall on a given distribution. Thus, the critical pursuit of learning about individual variability in animals, much like many other scientific endeavors, raises more questions than it answers. The challenge now is to devise a methodological tool that will help us better understand individual variability in nonhuman primates, while simultaneously enabling us to begin answering many of the raised questions.

The cross-species studies reviewed by Samuel Gosling et al. (1999) demonstrate how far we have come in the field of animal personality. This comparison of 19 factor analytic studies of personality dimensions (in 12 different species) using the human Five-Factor Model (Costa and McCrae, 1992) plus dominance and activity as a preliminary framework showed evidence for a potential underlying biological framework as well as shedding light on some of the current methodological limitations in this field. Gosling concluded that the following three major personality dimensions; extraversion, neuroticism, and agreeableness showed the strongest cross species generality. As stated in his article, the personality dimensions manifested themselves in species-specific manners. Gosling gave the following example "the human scoring low on extraversion stays home on a Saturday night, or tries to blend into a corner at a large party, the octopus scoring low on boldness stays in its protective den during feedings and attempts to hide itself by changing color or releasing ink into the water" (p.71). As a result of these remarkable cross-species commonalities, Gosling suggested that general biological

mechanisms were likely responsible. The fact that such similar factors were discovered, despite the diversity in research groups, methodological approaches, and species involved, indicated to him that this was a productive line of inquiry. However, the use of different semantic terms (i.e. extraversion vs. boldness) to summarize similar behavioral aggregates (i.e. dimensions), leads us to wonder whether we really are comparing apples with apples and not apples with oranges. This kind of comparative work demonstrates the importance and necessity of having both structurally and semantically well-defined behavioral dimensions, not only to gain clarity concerning the measures derived, but also for cross-species and cross-research group comparisons. The field of animal studies has, for the most part, remained rather separate from the study of human development. Only a few pioneers such as Hinde (1987) and Suomi (1997) have encouraged the cross-species generality between human and nonhuman primates.

When it comes to perceiving animals and humans on the same continuum, theorists can take their research into two different directions. Jeffrey Gray (1971) prefers to define basic dimensions of individual differences in behavior at the animal level, where more direct and elegant experimentations is possible, and then to extrapolate their findings to dimensions defined by tests and behavioral observations at the human level. In contrast, Hans Eysenck and Marvin Zuckerman go in the opposite direction, studying humans and attempting to extrapolate down the phylogenetic scale. According to Zuckerman, "As long as the links between human and animal behavior rest only on the judged similarities of behavior, we may run the risk of anthropomorphism (generalizing inappropriately from humans to animals) or zoomorphism (generalizing inappropriately from animals to humans). If we can show that the same biological systems are related to similar behaviors in humans and other animals, the results of experimentation on those systems in animals assumes greater significance for our understanding of humans" (Zuckerman, 1984, pp.413).

Nonhuman primates are useful for modeling human behavior because they have (1) similar brain structures, (2) complex forms of behaviors including social interactions and (3) close evolutionary relationships. Therefore, mapping out robust personality dimensions in nonhuman primates could help provide insights into basic developmental trends in humans.

Temperament versus Personality

The behavioral field has been defined by the two global concepts of temperament and personality. Although there is much overlap in the scientific literature between temperamental dimensions and personality traits (Goldsmith et al., 1987), there are also some distinctions. The most general definition of temperament is that it consists of biologically rooted individual differences in behavioral tendencies. These tendencies, thought to be present early in life, are relatively stable across various kinds of situations and over the course of time (Bates, 1987; Goldsmith et al., 1987; Kohnstamm, 1986). Temperament is the term most often used when describing children's behavioral tendencies, such as the origin of personality differences. As a result of its biological underpinnings, the expression of temperament is purest during early infancy after which it becomes increasingly subject to context and experience. The link between temperament and behavior becomes more complex as the child matures. Thomas and Chess (1977) have suggested that the pure temperamental expression seen during later development is likely to be noticed only at times when novel environmental challenges render coping skills ineffective. It has been argued that the core construct of temperament remains continuous throughout life and that its expression is subject to modification by the environment.

To put things into a conceptual framework, it is worth noting that temperamental dimensions may be regarded as the foundation for later personality. Theorists agree that temperament is a component of personality, but are uncertain as to the clarity of the boundaries between the two concepts. According to Chess and Thomas in the Roundtable discussion (Goldsmith et al., 1987), personality is a structured composite of enduring attributes that constitute the individuality of the person. These included composites are: motivations, abilities, standards, values, defense mechanisms and temperament. In the same article, Rothbart (1981) agrees that personality is a far more inclusive term than temperament, and adds cognitive structures, such as self-concept and specific expectations and attitudes, to its overall definition. By and large, temperament and personality are seen as broadly overlapping domains of study, with temperament providing the biological basis for the developing personality.

What is the exact composition of temperament? There is a general consensus that temperament is not a behavior or a trait itself, but rather a group of related traits. Hinde has remarked (in Goldsmith et al., 1987) that like most psychological terms, temperament is a set of hypothetical constructs. Goldsmith and Riesel-Danner (1986) have referred to temperament as a 'rubric.' A cognition rubric might serve to illustrate as an analogous example, encompassing the following measures: attention, memory, compensation and problem solving. Similarly, a temperament rubric might encompass measures such as: irritability, activity level and fearfulness. Therefore, one could state that temperamental qualities are (1) abstractions and not directly observable behaviors, and (2) inferred by behavioral patterns. The fundamental assumption of these temperamental qualities, which are generally derived by factor analysis, is that it is their underlying latent variables that are causing the observed behaviors. There is still no consensus on the nature of the construct, i.e. how many and which measures define the coherent package of temperament. Until now there is no ready solution to the problem of how to get closest to the abstraction or latent concept.

The interdisciplinary nature of temperament research has received input from diverse disciplines, ranging from developmental psychology, personality theory, psychophysiology, psychosomatic medicine, clinical psychiatry, behavioral genetics, and educational research. Most researchers studying temperament think of it as something underlying the behavior, some sort of endogenous forces shaping the child's individual and social characteristics. A predominant consensus among researchers studying the field of temperament is that, at some level, these biologically based behavioral patterns focus on individual differences rather than species-general characteristics.

The selection and definition of temperamental traits differs depending on the research group. Thomas and Chess (1977) emphasize the notion that temperamental dimensions reflect behavioral tendencies rather than a single behavioral act. They emphasize the 'stylistic' component of the behaviors, (i.e. the "how" rather than the "what" or the "why"). Rothbart (1981) claims the individual differences defined by Thomas and Chess go beyond a simple behavioral style to specify an individual's predisposition to particular reactions. This definition encompasses the relatively stable, and primarily biologically-based individual differences in both reactivity and self-

regulation. Buss and Plomin's (1975) definition of temperament stresses the heritability component, stating that temperaments are inherited personality traits appearing early in infancy, remaining stable across life, thus forming the basic building blocks of personality. Jerome Kagan (1997) defines temperament as an inherited pattern of physiologic and behavioral reactions to particular situations.

Each approach suggests a different boundary for temperament. Different theorists stipulate different criteria of behavioral style, relation to emotional behavior, relative stability, and inheritance. Each research group has used its own definition of the concept of temperament as a means to shed light on different questions using different specific methods. These varying definitions, attempting to describe the same phenomena, understandably confuse outsiders trying to discern what temperament is, and what role it plays in the field of personality. Let us therefore reject once and for all the implication that there ever could be an abstract, pure concept of temperament, which might be as frustrating and "as dangerous as hunting the Snark" (Hinde, 1989, p.28), and focus our energy in a practical sense. In order to move forward in this field we need a good, simple and highly reliable measure of this rubric. There is no right or wrong way to define temperament, but having moderately clear boundaries, which include independent dimensions with some common properties, might increase the utility of the concept. The goal is to turn abstract concepts into objective operational measures, e.g., operationally defining emotionality as the frequency of observed crying by a baby. This approach succeeds in capturing one aspect of only the first level of definition of the emotionality concept. There is an obvious trade-off between the internal validity or objectivity in a measure and its validity as a measure of the inherently abstract and multi-level concept of temperament. This complexity is not cause to despair or abandon the concepts of temperament, but one must keep in mind the conceptual and measurement issues (Bates, 1986). For more information and discussion pertaining to the nuances and subtleties regarding definitions and criteria of temperament see the Roundtable article (Goldsmith et al. 1987).

How does one turn the above concepts into operational measures? This is an important question, ultimately determining the value of the abstract concepts themselves. The first step is to define temperament as a combination of the study of human or animal

social development and psychobiology simultaneously. Secondly, when finally ready to measure temperament, one must consider the conceptual complexity of integrating these disparate foci of interest in the same or complementary measurement tools. In order to achieve this, one might want to perceive temperament as an objective multi-level construct as proposed by Bates (1989). This definition of temperament encompasses three different levels: (1) At the surface is a pattern of observed behaviors, and immediately underneath are two levels of biological underpinnings, including (2) factors of neurological individuality and (3) constitutional factors. For the purpose of this thesis, we will be focusing most of our energy and attention on issues dealing with the first level: patterns of observed behaviors across individuals. These individual differences in behavioral patterns (temperamental qualities) are believed to emerge early in life, and shape the course of personality development, its healthful outcomes and problematic presentations (Rutter, 1987). With this in mind, it seems logical to measure temperament in young children, while the construct is still 'pure' and not yet modified by the external environment. The temperament concept offers advantages especially in discussing the origins of children's personality differences. It is a way of postulating that there are endogenous forces shaping the child's individual and social characteristics.

There are three main ways in which temperament concepts have been operationalized for measuring children's individual differences. The first is parent report, including questionnaires and structured interview of the parent. Second is naturalistic observation in the home (i.e. measurement of spontaneous behavior). Third is observation in a structured laboratory situation. The development of standardized laboratory assessments to supplement parent questionnaires has aided significantly in the definition of temperamental traits. A fourth method for studying temperament is the use of psychophysiological measures as indices of response to particular stimuli. This would be a particularly good approach for exploring level two of Bates (1989) multi-level construct: factors of neurological individuality (i.e. the potential organization of neuroendocrine processes). There are methodological challenges to measuring these theoretical concepts in children. These include, but are not limited to: (1) the potential subjectivity of the parent filling out the temperament questionnaire of their child, given that reports of the child's behavior cannot be easily separated from the parents biases,

values, or expectations; (2) the extreme costs (both temporal and financial) of direct observations in a naturalistic setting or a laboratory context; (3) failing to finding a single pattern of physiological events underlying a particular kind of behavior, but instead finding identical systems underlying a number of different temperament patterns (Buss and Plomin, 1984; Strelau, 1986). The most important point is to be clear about how one is using the construct of temperament, and the operational definition of the measures.

Until there is greater clarity concerning the structure of temperament it will be difficult to investigate continuity (the extent to which the structure of temperament remains similar across age levels). And until the continuity issue is resolved, measurement of stability (the constant ranking over time of individuals on a temperament dimension) will also remain problematic. For the purpose of my thesis, I would like to be clear as to how we will be using the personality/temperament construct. As mentioned above, we will focus our attention on a cross-sectional study of individual patterns of behaviors. We will focus on objective and conceptually simple measures, which are both easy to understand and replicate. To avoid any confusion, I shall be using the term behavioral traits or behavioral dimensions, to define the observed behavioral patterns others have chosen to call personality or temperament.

The Identification of Behavioral Traits

Charles Darwin's work (1872) was a pivotal juncture for all kinds of research on behavior, but he was far from the first scientist to stress the importance of the role of biology in that field. As far back as 2000 years ago, Hippocrates believed behavioral traits were constitutionally based and that they were determined by biological functioning rather than by experience or learning. He thought that there were four basic temperaments: sanguine (cheerful), choleric (irritable), melancholic (gloomy), and phlegmatic (apathetic), which were determined by the predominance of blood, yellow bile, black bile, and phlegm respectively in the person's physical constitution. The ancient theory survives in the form of such expressions as "being in a bad (or good) humor." The theory of four bodily humors did not survive the rise of scientific medicine in the seventeenth century as an explanation for differences in human temperament, but it has not been replaced by any single universally accepted theory of personality either.

In modern times, Gordon Allport was the first to introduce the notion of personality traits which he defined as distinguishing characteristics or qualities, measured on a continuum, that guide behavior. Some of the points he made regarding traits, such as their tangible existence (as opposed to being purely conceptual) and the possibility of empirical demonstration, still stand today. Allport and Odbert (1936) selected 18 000 traits terms in English which were mostly adjectives and reduced them to 4500 descriptors of stable traits. However, many of his other hypotheses did not stand the test of time. The trait approach to personality, and the investigations of the importance of genetic influences, continued to be carried on by contemporary personality 'trait theorists' such as Raymond Cattell and Hans Eysenck. Both these researchers searched for traits that are common to all of us. What was impressive about their approach was that it relied on a rigorous scientific methodology, relying on behavioral observation and the collection of masses of empirical data in each subject to determine common factors. The data collected was subjected to a multivariate statistical procedure, called a factor analysis, whose objective was to assess the relationship between each possible pair of measurements. When two sets of variables showed a high correlation, the conclusion was that they measured similar or related aspects of personality and thus would combine to form a single dimension, factor or in our case behavioral trait.

Raymond Cattell (1943) defined traits as relatively permanent reaction tendencies that according to him, are the basic structural units of personality. While a graduate student, Cattell was hired as a research assistant to Charles Spearman, a mathematician studying the quantification of intelligence. Spearman, a well known name in the field of intellectual assessment, developed a mathematical formula known as factor analysis. This statistical technique allows one to take raw data and determine significant groupings from a correlation matrix. By developing questionnaires and tests consisting of personality characteristics and analyzing data from report cards of students, evaluations from employees, etc., Cattell was the first who applied this new statistical technique factor analysis (1948). Cattell was respected for having organized a huge amount of data in an area often noted for subjective anecdotal histories, intuitions and speculations, and offering new ways of assessing personality. Before then, few theories had been so systematically constructed or firmly grounded in fact. In 1948, he published his findings

in an assessment device known as the 16PF (Cattell, 1948). According to Cattell's research, human personality traits could be summarized by 16 personality factors (PF) or main traits. He described these 16 traits on a continuum, with everybody having some degree of every trait, as assessed by individual positions on the continuum. He derived the following 16 factors (traits), the first three being the most important: (i) reserved/outgoing; (ii) less/more intelligent; (iii) emotional/stable; (iv) humble/assertive; (v) sober/happy-go-lucky; (vi) expedient/conscientious; (vii) shy/venturesome; (viii) tough/determined; (ix) trusting/suspicious; (x) practical/imaginative; (xi) forthright/shrewd; (xii) placid/apprehensive; (xiii) conservative/experimental; (xiv) group-oriented/self-sufficient; (xv) casual/controlled and (xvi) relaxed/tense. Despite all of his endeavors in laying down the groundwork for this scientific approach, his 16 factor solution was criticized for being too subjective and consequently difficult to replicate. As a result, Cattell's theory and research are highly respected yet seldom read. In the late 1980's, he maintained that the factor analytic approach was the only method of value for studying personality, and criticized contemporary psychologists for failing to learn and apply this statistical procedure (Cattell, 1988).

Hans Eysenck agreed with Cattell that personality is composed of some combination of traits, factors or 'behavioral traits' that can be derived by the factor analytic approach (Eysenck, 1987), but he also criticized Raymond Cattell's research for having too many traits and these traits having a high level of subjectivity. In an attempt to objectify his results (thus making them easier to replicate), Eysenck supplemented his method with personality tests and experimental studies and is justly credited with adding science to the field of personality. Eysenck (1947) studied 700 patients in an army unit and, based on his empirical evidence, proposed a personality theory consisting of three dimensions: (1) Extraversion (versus introversion), (2) Neuroticism (versus emotional stability) and (3) Psychoticism (versus impulse control). His extraversion trait was based on measures of sociability, impulsivity, activity, liveliness and excitability. People who scored high on this first behavioral trait would be classified as being more extraverted. Their overall behavior would entail being more talkative, more sexually active, more impulsive, and have higher levels of positive affect. People scoring at the negative end of this vector would be considered introverts. His Neuroticism trait was thought to be a

measure of anxiety. Individuals scoring high on this vector were observed to have more emotional instability, more negative affect, and more social awkwardness. Both extraversion and neuroticism were thought to have normal distributions. Individuals scoring high on psychoticism were thought to be more solitary, troublesome, cruel, insensitive, aggressive, liking odd things, and opposing to social custom. Eysenck emphasized that our behavioral traits are influenced more by our genes than our environment. This view was statistically supported by Rose et al. (1988) who studied 14 000 twin pairs in Finland using Eysenck's behavioral dimensions. Their study concluded a systematically higher correlation (r) for monozygotic twin pairs, as compared to their dizygotic counterparts, for both Extraversion (MZ r= .48; DZ r= .15); and Neuroticism (MZ r= .40; DZ r= .12). Jeffrey Gray (1982) also supported a biologically based, or constitutionally determined, model of behavioral dimensions. However, Gray undertook a major revision of Eysenck's principal dimensions, by rotating his model's axes 45 degrees, making anxiety (behavioral inhibition) and impulsivity (behavioral activation) the basic dimensions of temperament rather than neuroticism and extraversion. Gray's (1982) more simplistic theory viewed behavioral dimensions as representing a balance between an approach (BAS) and an inhibition (BIS) system, with the BIS and BAS being mutually inhibitory so that they compete to control the individual's motor functioning. Despite there not being a consensus on the number or definitional constructs of behavioral dimensions, researchers all seem to agree that at some level and to some degree these traits are biologically based.

Arnold Buss and Robert Plomin (1984) followed Cattell's classification of some personality factors and identified a number of behavioral traits similar to Eysenck (1947). Plomin and his colleagues (Plomin, 1983; Plomin & Dunn, J., 1986) argued that not only should one restrict definitions to a limited number of constitutionally determined, biologically-based characteristics, but that they should also be demonstrably heritable, i.e. having a genetic basis. Their three dimensions, which they believed to be the basic building blocks of personality included: (i) emotionality, (ii) activity, and (iii) sociability. Their definition of emotionality is equivalent to distress, with an almost stoic lack of reaction at one end of the dimension to intense emotional reactions and loss of control at the other end. Activity consisted of two major components, tempo and vigor; at one end

of this dimension, individuals are lethargic, and at the opposite end, a hypomanic push of energetic behavior. Finally, sociability is defined as the preference for being with others rather than alone. Robert Hinde (in Goldsmith et al., 1987), however, did not agree with Buss and Plomin's emphasis on the heritability of traits. He argued that heritability should not form part of the definition of temperament for three reasons: because genetic effects change with age and with context of development; because heritability estimates are notoriously difficult to quantify; and because peri- and postnatal experiences as well as learning potential may confound heritability.

Contemporary theorists agree on a small number of broad traits, which account for the majority of people's personalities, with the two broad traits of Extraversion vs. Introversion and Emotional stability vs. Neuroticism clearly being the most important. There is less agreement concerning the other main dimensions of personality. A large body of research suggests that risk takers tend to be higher in the narrow "Sensation Seeking" trait, a small element of the broader Psychoticism vs. Humaneness trait. Marvin Zuckerman (1991) initially developed the theory of Sensation Seeking in the 1950's following a series of sensory deprivation experiments. He began to suspect that the people who volunteered for these experiments might share a similar set of personality characteristics. These individuals appeared to be especially venturesome and curious, eager to have new and exciting experiences even if they did not contain a degree of social or physical risk. This lead him to the hypothesis that people take risks in order to have exciting, novel and intense new experiences. Zuckerman (1991) used the Factor analytical approach to focus on this single, hypothetically hereditary behavioral Sensation Seeking trait. He described it as "a trait defined by the seeking of varied, novel, complex, and intense sensations and experience, and the willingness to take physical, social, legal, and financial risks for the sake of such experience." Based on this definition, he was able to derive 4 dimensions; (i) Thrill and Adventure Seeking (TAS), (ii) Experience Seeking (ES), (iii) Disinhibition (DIS) and (iv) Boredom Susceptibility (BS). Zuckerman stresses that it would be hard to dampen this trait if you are a high sensation seeker, and hard to encourage its expression if you are a low sensation seeker. Sensation seeking can be expressed in both socially positive and dyssocial ways: Zuckerman explains that if a high sensation seeker comes from a nice middle class family, he expresses himself through

travel, music, and sports, or even through exploration and discovery. But if a high sensation seeker is growing up in a more restrictive ghetto environment, the sensation seeking that is available may be more dangerous, pertaining to criminal behavior, such as drugs, sex and violence. Among other things, this is a clear example of ways in which different environments can shape the expression of relatively immutable behavioral traits. Contemporary personality researchers have expressed dissatisfaction with the above theories, suggesting that Eysenck's was too simple and had too few dimensions, and Cattell's was too complex and had too many behavioral traits. In addition, the early theorists deemphasized hereditary factors and assigned a greater focus to the social stimulus value of individual characteristics as they interact with environmental experience; hence, a more biosocial model was adopted (Thomas, Chess & Birch, 1969; Lerner & Lerner, 1983). Researchers such as Robert McCrae and John Costa conducted independent investigations of personality, finally concluding that personality consists of five broad factors or behavioral traits (McCrae & Costa, 1985; McCrae & Costa, 1987). They derived their factor solution based on a self-report questionnaire, the NEO-PIR. McCrae and Costa identified the so-called Big Five factors of personality, which included the previously mentioned (1) extraversion, and (2) neuroticism, and suggested three further dimensions, (3) openness (to experience), (4) agreeableness and (5) conscientiousness. Each behavioral dimension was analogous to a vector with a positive and a negative end. The overall outcome of the subject's behavior on each specific trait therefore varied depending on what their score for each given vector was. In the case of Costa and McCrae's five factors, the following interpretations can be made: The positive end of the extraversion factor measured items such as sociable, friendly, talkative, and spontaneous, whereas the opposite end of the factor measured more introverted items, such as, retired, aloof, quiet and inhibited. The positive end of the neurotic dimension measured items such as worrying, high strung, nervous and insecure. The negative end of the same dimension measured items such as calm, at ease, relaxed and secure. The positive end of the openness to experience dimension measured items such as original, imaginative, complex and curious and items at the negative end of this dimension were more conventional, down to earth, uncreative and simple. The positive end of the agreeable dimension measured items such as good natured, curious, sympathetic,

agreeable, and the negative end of the dimension had more antagonistic items such as irritable, rude, callous, and disagreeable. Finally, the positive end of the conscientiousness dimension measured items such as, reliable, well organized, and persevering, and at the undirected negative items were more, negligent, undependable, disorganized and quitting. The consistent finding of the same factors from diverse assessment procedures, suggested that these factors may be the major distinguishing aspects of personality. The trait approach led to some theorising as to the role of genetics and environment in determining our personality. Numerous studies have been undertaken looking at the personality scores of monozygotic twins reared together and reared apart, along with comparisons of scores between fraternal or dizygotic twins. Underlying this method is the view that, if genetics underlies personality, the closer the genetic relationship between the individuals, the higher the correlation between the test scores will be. Borkenau et al. (2001) undertook research which suggested that 40% of individual differences in the Big Five are due to heredity, 35% to a non-shared environment, and 25% to a shared environment. In Gosling's cross species review (1999) he concluded that extraversion, neuroticism and agreeableness had the strongest cross species generality, but that conscientiousness was only found in chimps. These five factors were found repeatedly, even when using different data sources, different people, and different tests. There seems to be some stability over time, but the evidence is far from perfect. Despite face plausibility, many findings still lack methodological robustness and fail to make distinctions, for example, between age differences or cohort effects (generational differences). Despite these shortcomings, most investigators in the field believe: (a) that individual differences are stable; (b) that they are more stable over short than long time periods; (c) that they are more stable in adulthood than in childhood; and (d) that the limits of environmental influence are still undetermined.

Robert Cloninger (1986) criticized the factor analytic approach and developed a psychobiological model of personality building upon a synthesis of information from an existing literature concerning personality and temperament (i.e. concept based theories). He based his original three behavioral dimensions: (i) novelty seeking, (ii) harm avoidance and (iii) reward dependence, not on empirical data but on concept alone, and hypothesized they have close correspondence with the underlying genetic structure.

Cloninger's Tridimensional Personality Questionnaire (TPQ) is a self-report inventory designed to assess the above three mentioned primary dimensions of his Biosocial Learning Model of normal and abnormal personality. Conceptual similarities in the literature compared Cloninger's 'harm avoidance,' to Gray's 'behavioral inhibition' (BIS) and Eysenck's 'neuroticism,' as well as Cloninger's 'novelty seeking' to Gray's 'behavioral approach' (BAS) and Eysenck's 'extraversion.' Despite not using empirically derived measures, Cloninger has contributed greatly to the intellectual advancement of the field of personality, more specifically how we think about the interaction between physiology and psychology, but other researchers who have tried to replicate his work through empirical measures failed. The challenge therefore remains to design specific methodological paradigms, which can be easily replicated, while continuing to shed light onto a complex multileveled, multifaceted field.

W. John Livesley et al. (1998) have directed their research at the classification and etiology of personality disorder. Using the dimensional approach, there is an agreement across studies regarding the structure of personality. Personality traits are thought to be hierarchically organized, with more specific lower-order traits combining to form higher-order traits. Eighteen lower-order traits were assessed using the Dimensional Assessment of Personality Disorder-Basic Questionnaire in disordered patients, general population subjects and a voluntary sample of twin pairs. Principal components analysis yielded 4 components, labeled (1) Emotional Dysregulation, (2) Dissocial Behavior, (3) Inhibitedness and (4) Compulsivity. The structures were similar across the three samples. The similarity between the factor structures between normal and clinical populations demonstrated that normal personality and personality disorders are on the same continuum. With this in mind it is expected that knowledge of the biological mechanisms acting in normal personality can contribute to better understanding personality disorders.

Measurement of Behavioral Traits in Children

John B. Watson, founder of the school of behaviorism, which dominated much of North America educational psychology between 1920 and 1960, rejected the notion that inheritance played any part in explaining social behavior. He stressed that learning was the only focus for psychology. This was harmonious with the democratic *Zeitgeist* of the

time stating that all men could be equal in potential if their environments were equally benevolent. However, faced with the growing body of behavioral genetics data, it has been difficult to sustain the simple-minded environmentalist view that children are pliant pieces of putty. The expression of certain behavioral traits has been found to remain stable throughout the life span, from childhood to adulthood, despite the different environmental and social influences to which each of us is exposed.

Much of the current research looking at behavioral traits in children was inspired by the pioneering work of Thomas, Chess and Birch (1977) who, in their New York Longitudinal Study (NYLS), pioneered the systematic application of the concepts of temperament to the measurement of children's individuality. They developed their categories of temperament from parental reports of the detailed behavioral diaries for their first 22 infant subjects. The selection of items was based on the following two criteria; (1) the behavior needed to be present in all children, but at different levels (i.e. individual variability) and (2) the behavior was required to have the potential to influence the psychological development. Based on these criteria, Thomas and Chess proposed nine dimensions of temperament that relied more on the 'stylistic' component of behavior (i.e. the "how" of behavior). These were scored on a three-point scale (medium, high and low): (1) Activity level; (2) Rhythmicity, or degree of regularity, of functions such as eating, elimination and the cycle of sleep and wakefulness; (3) Distractibility or ease of soothing; (4) Approach/Withdrawal, the response to a new object or person; (5) Adaptability of behavior to changes in the environment; (6) Attention span and persistence (7) Intensity of mood expression; (8) Sensory threshold (or sensitivity) of responsiveness to stimuli; (9) Quality of mood, or "disposition", whether cheerful or given to crying, pleasant or cranky. Thomas and Chess stated that their list was "open to revision," and that they would welcome any modification or change in their categories. These indices have been used by many research groups doing longitudinal studies. Subsequent analysis of the correlations among the nine individual attributes showed that certain characteristics tended to cluster together, defining three general types of temperament (although some children did not fit into any of the three): (1) Easy temperament (40%)-- "easy children" presenting very few problems in care and training. (2) Difficult temperament (10%)--"difficult children" are a trial to their parents and

require a high degree of tolerance in the course of their upbringing. (3) Slow to warm up (15%)--"slow to warm up" children typically tend to withdraw on their first exposure, but come around with time. These temperamental classifications became highly influential in child development research. Another important contribution made by Thomas and Chess apart from the derivation of these stylistic behavioral traits which they measured for every child in a longitudinal prospective study, was the emphasis on the biosocial interaction between the child and his or her environment. Domineering authoritarian handling by the parents might make one youngster anxious and submissive and another defiant and antagonistic. Such unpredictability seemed to be the direct consequence of omitting an important factor from the evaluation: the child's own temperament, that is, his own individual style of responding to the environment. Thomas and Chess rejected the "nurture" and the "nature" concepts, stating that 'either by itself is too simplistic to account for the intricate play of forces that form the human character.' They stated in their hypothesis that personality is shaped by the constant interplay of temperament and environment. They maintained that the child's temperament by itself was not the most important consideration in his or her growth and development, but the extent to which that temperament agreed with the values, expectations, and style of the child's environment, whether family, childcare setting, school, or culture. With this in mind, the ideal scenario would be to have an environment that maximized the aptitudes and potential of the child, known as the 'goodness of fit.' For example, a quiet and serious child fits in well with a family of scholars or intellectuals, whereas an intense, active, and easily distracted child may not be accepted as readily in the same context. There may be a certain amount of plasticity to temperamental factors and early environmental interventions could potentially mediate the behavioral course of development by repressing or expressing these behavioral traits. Thomas and Chess' construct of temperament made it possible to begin understanding individual differences in children's response to similar environmental situations. Their groundwork has shed light on a complex, dynamic non-linear construct, and continues to be a constant source of reference and comparison for researchers today.

Mary Rothbart (1981) claimed that the individual differences defined by Thomas and Chess should go beyond behavioral style to specify individual predispositions to

react in particular ways. Rothbart emphasized reactivity and self-regulation as core processes in organizing temperament profiles. Reactivity in this case is related to the Pavlovian concept of individual differences in properties of the nervous system. For example, individuals continuing to function under high intensity stimulation before inhibition are thought to have a strong nervous system, and those with low thresholds, a weak nervous system. Rothbart's model thus comes from Gray's view of behavior as representing a balance between systems underlying approach and inhibition. After considering critical measures, such as smiling, laughter, fear, distress, frustration, soothability, activity level and duration of orientation, derived from parental reports and more importantly, direct behavioral observations of infants in structured laboratory situations, Rothbart's group proposed four major dimensions of temperamental variability. The first two dimensions involved reactivity (i.e. arousability of motor activity); Factor 1, 'negative reactivity', reflected in expressed and felt distress, and behavioral and attentional aversion; and Factor 2, 'positive reactivity', reflected in expressed and felt positive affect, and behavioral and attentional approach. The latter two Factors, comprised of self regulation, Factor 3, 'behavioral inhibition,' was specific to novel or intense stimuli, and a potential Factor 4, the capacity through effort to focus and shift attention. Her Infant Behavior Questionnaire (IBQ), which was developed in the early 1980's, remains one of the most widely used methods of assessing temperament in infants between the ages of three months and 12 months. Rothbart emphasizes the cognitive processes in children as the key to understanding temperament rather than emotions by themselves. For Rothbart and her colleagues, the infant's ability to focus his or her attention is the basis of its later ability to regulate his or her reactions to people and events. In Rothbart's view, what she calls the attentional system allows the child to regulate his or her outward behavior as well as internal reactions to stimuli. Different patterns of self-regulation in turn help to explain differences in temperament. In addition to the questionnaires, Rothbart and colleagues (1994) developed an assessment tool to gauge temperamental dimensions based on systematic observations of behaviors elicited under standard laboratory conditions. The development of an observational protocol or test for assessing temperamental characteristics offers an obvious advantage of objectivity over reliance of questionnaires.

Another major approach to the study of temperament was performed by Jerome Kagan and his colleagues (1997), who used direct behavioral observation in laboratory settings to distinguish between two types of children characterized by different patterns of behavior. Children subjected to novel environments showed a range of responses; the extreme cases on both ends of the distribution interested Kagan and his research group. They considered these extreme clusters as qualitatively distinct behavioral dimensions, each with their own set of phenotypic behavioral aggregates and underlying biological underpinnings. They labeled these two dimensions inhibited and uninhibited to the unfamiliar. Kagan and his laboratory (Kagan, et al., 1987; Kagan, et al., 1988) focused on these two categories and have presently attained initial understanding of their developmental course. Children in the inhibited group, estimated to be about 15-20% of the Caucasian population, are consistently shy, timid, cautious, and emotionally reserved when they confront unfamiliar persons or contexts during the second year of life. Children in the uninhibited group, comprising about 25-30% of the Caucasian population, are consistently sociable, affectively spontaneous, and minimally fearful in the same unfamiliar situations. There is an observed stability of these traits across time and situations. A majority of children in each of these distinctive temperamental groups maintained their behavioral style from the second through the eighth year of life, although the display of temperamental tendencies did vary in accordance with the child's developmental level (Robinson et al., 1992).

Kagan found that the behavioral profiles of these children were accompanied by physiologic profiles that suggested different levels of reactivity in the children's nervous system. The two groups differed in peripheral physiological characteristics that imply different thresholds of reactivity in limbic areas, especially the amygdala and hypothalamus and their varied projections to the sympathetic and skeletal motor systems, as well as to the pituitary-adrenal cortex axis. The inhibited children compared with the uninhibited children, have higher and more stable heart rates, higher levels of stress-related hormones like cortisol and norepinephrine, pupillary dilations, and skeletal muscle tension in response to stressors (Kagan, Reznick and Snidman, 1988). It has also been demonstrated that more inhibited children and their first degree relatives have blue eyes, while more uninhibited children and their relatives have brown eyes (Rosenberg &

Kagan, 1989), suggesting a hereditary component that needs to be further investigated. These differences seem to support the contention that temperamental categories have a biological dimension (Kagan et al., 1987; Kagan et al., 1988; Kagan & Snidman, 1991; Kagan & Zentner, 1996).

Kagan emphasizes that it may be oversimplified to use a single peripheral biologic measure (heart rate, pupillary dilation, cerebrospinal fluid levels) to index a psychological construct, whether that construct be inhibited, uninhibited, or something else. He stresses that investigators should assess several physiological systems, rather than just one, and use a profile of features in diagnosing or classifying children. He insists that no variable, when considered alone, can define a psychological syndrome. He also advises us not to confuse a temperamentally inhibited child, from a shy child who was not born with any temperamental bias favoring limbic reactivity to the unfamiliar, but happened to experience an environment that promoted the acquisition of timidity and restraint. At a behavioral level, this shy child may resemble the temperamentally timid youngster, but can be differentiated from him or her by evaluating early history and physiology. Although the evidence supports that some children are born with a tendency that favors either behavioral inhibition or lack of inhibition to the unfamiliar as a result of low or high thresholds of excitability in limbic structures, Kagan believes that the physiological and the psychological qualities are malleable to alteration with proper experience. The development of standardized laboratory assessments to supplement parent questionnaires has aided significantly in the definition of temperamental traits.

Besides learning about the building blocks of personality constructs, an important question pertaining to the functionality of behavioral traits is determining whether any of these robust dissectible phenotypes may help predict psychopathological disorders. Michel Maziade and his research group (1986) acknowledged the importance of the major work done by the New York Longitudinal Study in child development, but like many other research groups, recognized its methodological flaws. Some examples of pertinent criticism was (1) that temperament should be studied on larger more representative samples in order to verify how it can be generalized and (2) that the typologies (i.e. easy, difficult, slow to warm up) be identified by means of factor analysis on the raw data in order to verify the reproducibility of NYLS profiles. An important

objective in Michel Maziade's longitudinal prospective studies was to use behavioral dimensions as a tool for understanding the antecedents of psychopathology. The New York study's "difficult" typology (i.e. a profile composed of low adaptability, withdrawal from new stimuli, high intensity, negative mood, and a low level of rhythmicity) was replicated by Michel Maziade and his research group in a French-speaking population at four to eight months of age (Maziade et al., 1984a) and at 7-years of age (Maziade et al., 1984b). The question being; Are children who score at the extremes of the distribution, (i.e. reflecting difficult temperaments) more susceptible to serious developmental and psychiatric disorders? Maziade et al., (1985) found that extreme temperamental traits at age 7, predicted clinical disorders at age 12. In addition, in families where discipline lacked parental consensus, and where rule setting and enforcement lacked clarity and consistency, temperamentally difficult children presented more clinical disorders at age 12. In a later study, Maziade and his research group confirmed these earlier findings, suggesting that extreme temperament at age 7 predicts psychiatric status in preadolescence and adolescence, but only when family functioning is taken into account (Maziade et al. 1990b). Maziade observed that in the psychiatric population of children there was an over-proportion of difficult temperament, but also confirmed that of the children referred for a disorder, a large proportion did not present with extreme temperament. From these findings, he concluded that extremely adverse temperament did not automatically equate to a clinical disorder across childhood in the general population (Maziade, 1988) and in clinical populations (Maziade et al., 1990a). By itself, extremely difficult temperament had no strong direct association with later clinical outcome, but an association with family dysfunction in terms of behavioral control seemed to increase the risk: there was a lower rate of clinical disorders among children in superior functioning families than among those in dysfunctional families. This suggests that a higher than average quality of parental behavior control may be a protective factor against the risk associated with difficult temperament. From these findings it is clear that future clinical research must address the complex relationship between extreme temperament and clinical disorders, and take into account potential environmental factors. Maziade et al. (1990a) also suggested a specificity in the relationship between particular temperament factors and the type of clinical problem. Temperament factor 1 (withdrawal from new

stimuli, low adaptability, high intensity, and negative mood) was found to be more associated with externalized disorders (opposition, conduct, or attention deficit disorders), whereas temperament factor 2 (low persistence, high sensory threshold and high mobility) was found to be more associated with specific developmental delays. With the growth and complex nature of this field, it becomes evident that "sound comparisons depend upon researchers making every effort to keep constant their sampling methods and their operational definitions of temperament." (Maziade et al., 1986, pp.50).

Caspi et al. (1995) believed that early emerging individual differences shape the course of personality development, its healthful outcome and problematic presentations. Their goal was to identify the temperamental origins of both internalizing and externalizing behavior problems in late childhood and adolescence. They followed 800 boys and girls from a general population sample across 12 years, initially measuring their temperaments at 3 and 5 years old on a 22-item scale in which each item had 3 scale levels. They came up with 3 dimensions at each age: (1) Lack of control, which was found to be the most stable, is reminiscent of the cluster described as the "difficult child" (Thomas, Chess, & Birch, 1970). (2) Approach, which was found to be the least stable, described a child who is willing and eager to explore. And (3) Sluggishness, which was more stable than approach but less than lack of control, described a child who reacts passively to changing situations. Caspi then independently evaluated measures of child behavior problems by parents from the Rutter Child Behavior Scales and the Revised Behavior Problem Checklist at ages 9, 11, 13 and 15 years old (Rutter, 1987). By doing this he examined the early childhood origins of internalizing and externalizing symptomatology. Caspi found that "lack of control" in early childhood led more strongly to externalizing behavior problems, like hyperactivity and attention problems a decade later. Caspi also found that "approach" led to fewer internalizing problems among boys, and "sluggishness' led to more problems of anxiety, distress and attention among girls. Basically, Caspi was able to support more assertively than Thomas, Chess and Birch had previously, that behavior disorders and temperamental characteristics are potentially different degrees of the same phenomenon. He proposed two possibilies; (1) that some of the extreme individual differences in childhood styles are early subclinical manifestations of later behavior disorders; or (2) that behavioral disorders may represent the cumulative

consequences of early behavioral styles that are "elaborated through evocative, reactive, and proactive person-environment effects" (Caspi et al., 1995, pp.66). In a second paper, Caspi et al. (2003) unable to locate information about the reliability of the previous studies single-assessment examiner ratings, evaluated 1000 3 year olds and this time came up with a 5 temperament types: (1) Well adjusted, (2) Undercontrolled (3) Confident (4) Inhibited and (5) Reserved. In this particular study, Caspi and his group explored whether children's early emerging behavior styles could foretell their characteristic behaviors, thoughts and feelings as adults, since longitudinal evidence now points to the long term continuities of personality characteristics from late childhood and adolescence to adulthood (Caspi, 1998; Shiner, 1998). At 18 and 26 years old, Caspi and his group gave these children the Multidimensional Personality Questionnaire (MPQ) from Tellegen et al. (1988) and from those 10 distinct personality traits, 3 superfactors were derived: (1) Negative Emotionality, (2) Constraint (vs. Disinhibition) and (3) Positive Emotionality. Caspi and his group found that there was some predictability between 3 year old and 18 year old information, but even stronger predictability and more coherence between 3 year old and 26 year old information. Capsi and his group explained this by the period between 18 and 30 years old as brimming with niche-pick opportunities, when young adults can create their own environments in ways that are correlated with their dispositional tendencies (Scarr & McCartney, 1983). Becoming an adult better expresses your true personality. Early-emerging behavioral differences seem to shape the course of development and have some prediction on later outcome, as empirically demonstrated by this study across 23 years.

Advantages of doing Behavioral Research using Nonhuman Primates

Nonhuman primates are a social species with a complex behavioral repertoire, which can be directly observed in a more homogeneous and controlled environment, void of verbal language. Their compressed development allows the study of hereditary behavioral traits across multiple generations in a faster time frame than in humans (female monkeys can breed by age 3). They have similar brain structure and close evolutionary relationships to humans (Fleagle & McGraw, 1999). There also appears to be related causes for the display of anxious and depressive behaviors in monkeys and

humans (Rosenblum & Paully, 1987; Suomi, 1997), evidence of similar behavioral reactions to environmental stimuli (Harlow & Novak, 1973; Rosenblum & Paully, 1987) and evidence for similar underlying neural regulation of these behaviors (Coplan et al. 1995; Kalin et al. 1987; Kraemer & McKinney, 1979). Monkeys also respond to pharmacological agents similarly to humans. Medications that have anxiolytic effects in humans have been shown to abate the expression of related behavioral abnormalities in monkeys. It is legally and ethically permissible to manipulate non-human primates in ways that would be considered improper with human subjects. Until now there have been very few longitudinal studies using nonhuman primates.

Historical Antecedents in the Field of Behavior in Monkeys

Darwin's work established a sense of continuity between humans and monkeys. Initially, monkeys were studied by traditional evolutionary biologists and primatolgists. However, when confronted with the problem of individual differences, which could no longer be perceived only as noise, other disciplines such as psychiatry, genetics, ethology and psychology stepped in with newfound interest. According to researchers such as Stevenson-Hinde and Zunz (1978, p.473), 'even within age/sex classes individuals vary markedly in their behavior in social and non-social contexts.' Using an observational approach, research groups such as Buirski (1973), Stenvenson-Hinde and Zunz (1978), McGuire, Raleigh, and Pollack (1994) and Capitanio (1999) began attempting to assess and identify personality dimensions in non-human primates. These studies have sought to establish whether behavioral traits in socially living monkeys could be reliably identified among individuals and to what extent they can be compared to those found in the human literature.

From the following studies it will be important to understand that the final components (i.e. behavioral traits derived) are not independent of the method of assessment or of the population being assessed. Chamove, Eysenck and Harlow (1972) were one of the first research groups to use a multivariate analysis method to successfully derive 3 factors from a list of 10 descriptors in 168 juvenile macaques. In this case, it was the normalcy of the subjects included in their design, which was questionable, since these 9 to 12 months rhesus monkeys had been separated from their mothers at birth, an

approach generally used to create a model of depression. As a result, it is important to note that their outcome could not be compared to outcomes derived by normal populations. The factors derived still seemed to have face validity, and strongly resembled those factors empirically derived in human personality by Eysenck. Chamove et al's (1972) fearful, hostile, and affectionate factors resembled Eysenck's neuroticism-stability, psychoticism and extraversion-introversion factors respectively.

Buirski et al. (1973) used behaviorally-defined adjectives carefully developed with human subjects, and based on a personality theory (i.e. Plutchik's theory of emotion (1962)), as the items of assessment for evaluating a free-ranging troop of 7 baboons (*Papio anubis*). Observers selected the more appropriate adjective from each possible pair of 12 adjectives. Each adjective was then defined as a combination of two out of the eight basic primary emotions: Protection (fear), Destruction (anger), Incorporation (acceptance), Rejection (disgust), Orientation (surprise), Exploration (expectation), Reproduction (joy), Deprivation (sadness). The end result for each individual was eight scores, representing the relative strength of each emotion. Apart from the small sample size, another methodological issue raised from this study was that the interpretation of the behaviors defined rested heavily on a particular 'human' theory (i.e. with the assumption that the adjectives apply to both humans and lower animals), which could potentially lead to a high risk of anthropomorphism. Amongst the twelve descriptive terms used to describe baboons, were "jealous," "obedient," and "sullen." These descriptors seem like rather complex concepts to operationalize and apply on human beings, let alone baboons. How can an observer know what the monkey is thinking? "Jealousy," is described by the authors as 'a situation where one animal interrupts or interferes with the on-going pleasurable activity himself; e.g., a situation where one female will displace a second female who had begun to groom a third female with whom the first female was very friendly.' In basic terms, the directly observed behavior in this case is a displacement, possibly motivated by hierarchical status (but that is a guess), any explanation more sophisticated than that is an interpretation on the part of the observer and therefore not objective science. This type of approach requires that the observers already have a certain amount of familiarity with the animals and the group dynamic before collecting data. Martau et al. (1985) who did a reliability study on the Emotions Profile Index, deduced

that both observer familiarity and age of subjects (infants and subadults presented particular problems) affected the reliability of ratings in the study. The EPI is less reliable when the observers are unfamiliar with the animals.

If personality is to be measured so individual differences can be identified, it is necessary to develop a psychometric procedure whose reliability and validity are known. It was the seminal paper of Stevenson-Hinde and Zunz (1978) (analogous to the Thomas Chess and Birch paper in children), which provided support for the subjective assessment to characterize individual differences in non-human primates. This paper and its proposed methodological approach snowballed the research interest in exploring quantitative analyses of behavioral characteristics in monkeys. Adjectives commonly used to describe human personality are applied (using a rating scale) to rhesus monkeys. Individual normally raised captive rhesus monkeys were rated on each of the 23 adjectives derived with reference to Sheldon (1942), using a 7-point scale. The data was then subjected to a multivariate analysis and 3 personality dimensions were identified, which they characterized as; (1) Confident-to-Fearful; (2) Active-to-Slow, and (3) Sociable-to-Solitary. It is interesting to note for future comparisons, that each of these derived dimensions clearly measures two polar opposite states. This study involved a more time consuming task for the observers than the Chamove et al. (1972) study, which only included 10 straight forward basic scores (e.g. like 'social play,' 'hostile contact' and 'appropriate withdrawal'), and had the advantage of not relying on an explicit theory based on humans for analysis like in the Buirski et al., (1973) study. What remains problematic on a larger scale, is that the three dimensional measures derived by Stevenson-Hinde and Zunz and the ones derived in the Chamove et al. study, could not be related to one another, even at a superficial level. As Stevenson-Hinde and Zunz (1978) pointed out in their assessment article, 'by definition, components are a product of the subject, the instrument, and even the observers.' Therefore, not being able to make comparisons of results, because of differences in instruments etc., poses difficulties in moving forward in the field of behavior.

Capitanio (1999) attempted to demonstrate the predictive power of personality factors. Their goal was to determine whether personality dimensions, identified in 45 adult male rhesus monkeys, predicted behavior in situations different from the one from

which the dimensions were originally derived, at a time point of up to 4.5 years after the assessment. The observers rated each monkey using a battery of 25 adjectives along a seven-point scale, developed by Stevenson-Hinde et al., (1980) for the rhesus macaques. Twelve adjectives were retained for a factor analysis (these adjectives demonstrated agreement significantly above chance among observers). Finally, 4 personality dimensions were identified in vervets, which he characterized as; (1) Sociability, (2) Confidence, (3) Excitability and (4) Equability. The adjectives that loaded heavily on the Sociable factor were, "sociable," "playful," and "curious." The adjectives "confident," and "aggressive" loaded on the Confidence dimension. The adjectives that loaded heavily on the Excitability Factor were "active," "excitable," and "subordinate." Equable animals were rated highly on three adjectives: "equable," "understanding," and "slow." At the outset, there were already several methodological differences from other studies in nonhuman personality. First, their subjects were much more homogeneous in terms of age/sex, class (i.e. adult male rhesus with mean a mean age of 6.1 years) that has usually been the case in such studies. Second, unlike other studies, the raters were not asked to distribute their ratings for every category approximately normally or according to any pre-specified formula. The rationale being that each characteristic was unlikely going to be normally distributed among the animals in their sample because of the greater homogeneity of their sample. Once the behavioral dimensions derived, another of Capitanio's goals, was to determine if personality dimensions were related to measures of behavioral responsiveness, such as to a threatening human (i.e. approaching the monkey at different distances while staring or not staring at him). They concluded that only the dimension of Excitability (i.e. made up of highly active, over reacting, and easily submissive individuals) was related to the responsiveness measure. More will be said about reactivity level in the next section, when I address the field of novelty testing.

Most investigations of personality in Old World monkeys have examined macaques or baboons. Vervet monkeys attain physical maturity more rapidly and exhibit less sexual dimorphism than macaques. Vervets also differ behaviorally in their styles of play, hierarchical structures, and intergroup relationships (Raleigh & McGuire, 1990). McGuire, Raleigh and Pollack (1994) wanted to determine whether vervets manifested personality profiles similar to those reported among other species, as well as verifying

whether these personality assessments could supplement ethological investigations of nonhuman primate behaviors (i.e. sex, age, social status, and group composition). They rated normally raised socially living captive vervet monkeys, ranging in age from 19 months to 14 years, on 17 items (12 constructs and 5 ethologically coded behaviors). Raters coded each subject using a five-point (modified Likert) scale, and were instructed to try to assign the average score (3 in this case) to approximately 40% of the subjects, each of the two intermediate scores (2 and 4) to about 20% of the subjects, and each of the extreme scores (1 and 5) to about 10%. The data was subsequently subjected to a multivariate analysis, which identified 3 personality dimensions characterized as; (1) socially competent, (2) playful/curious, and (3) opportunistic. The interpretation of the factors and their final label, were based on the cluster of behaviors, which loaded heavily on them. In the case of the 'playful/curious' dimension case, it was difficult to make sense of the 'fearful' heavy factor loading, along with the more logical 'active' and 'playful' heavy loadings. Two other methodological issues worth mentioning in this study were; the extreme age range of the monkeys, and forcing to allocate a specified percentage of individuals to a given score.

Other research groups have also used behaviorally defined adjectives to assess personality dimensions in a variety of nonhuman primate species: Caine et al., (1983) in 10 adolescent Pig-tailed macaques; Figuerdo et al., (1995) in 13 stumptail macaques; King and Figuerdo (1997) in 100 chimpanzees; and Gold and Maple (1994) in 298 gorillas. A subjective assessment instrument consisting of behaviorally based adjectives, called the Gorilla Behavior Index (GBI) was completed for 298 captive gorillas over 1 year of age. The results were subjected to a factor analysis resulting in the identification of four main factors: extroverted, dominant, fearful, and understanding. The study on chimpanzees used 43 trait-descriptive adjectives with representative items from the human Big-Five model to assess the factor structure of personality. They justified this use by stating that 'chimpanzees are humans' closest phylogenetic relatives, sharing a common ancestor species that lived as recently as 5 to 7 million years ago and having DNA about 98% compatible with that of humans.' A six-factor model was derived from 100 chimpanzees, five of which resembled the human Big Five: Surgency, dependability,

agreeableness, emotionality, and openness. The sixth factor was dominance related and was consistent with the central role of dominance in chimpanzee personality.

Although these studies have been able to shed some light onto specific dimensions of personality, the frequent small sample sizes, merely adult populations and subjectivity of the measures (i.e. preconceived adjectives) leave many questions unanswered. A main concern is that by characterizing stable behavioral traits in non-human primates based on human temperament theories or a list of preconceived behavioral adjectives, this approach might (1) bias what we expect to see, and (2) not provide us with the robust empirical construct we require to move forward.

Behavioral Reactivity

Certain behavioral traits, like emotional reactivity, are difficult to observe while monkeys are in their social groups. Some researchers have attempted to measure reactivity in a social context, and have only managed to get indirect measures. Higley (1985) used levels of play as an assessment for reactivity, inferring that monkeys who engage in frequent bouts of play are not reactive, versus monkeys who do not engage in play are highly reactive. Along the same lines, Stevenson-Hinde and Zunz (1978) found that least fearful monkeys were the most social, while the most fearful monkeys were the least social. In the literature, reactivity is occasionally equated to fearfulness alone, but is technically a broader concept including both extremes of a response to a novel stimuli, e.g., approach vs. withdraw; bold vs. shy; curious vs. fearful; inhibited vs. uninhibited. Emotional reactivity, is defined by Higley and Suomi (1989) as reflecting an "effective and behavioral predisposition to respond to novel and challenging stimuli (pp.154)" This behavioral trait has received much attention and research in many different species (Blizard, 1981; Gray, 1971; Scott & Fuller, 1965). Initial withdrawal or behavioral inhibition to the unfamiliar, seems to persist for a longer time than other behavioral traits and is part of a coherent network of characteristics that has reasonable analogies in many mammalian species. The tendency to withdraw from or approach an unfamiliar event emerges at about 8 months in humans, 2 months in monkeys and 1 month in cats and dogs. Schneirla's (1959) suggestion that approach and withdrawal are primary dimensions in animals is affirmed by studies of various mammalian groups, including

rats, cats, dogs, and monkeys. Strains of rats and mice have been selectively bred for levels of reactivity, as measured by levels of exploration and defecation during an open-field test (Blizard, 1981; Gray, 1971). Variation in timidity has been found to be one of the two most differentiating characteristics in five breeds of dogs, (Scott and Fuller, 1965). Suomi (1983) and Stevenson-Hinde, Stillwell-Barnes, and Zunz (1980) have reported similar variations in approach-withdrawal behavior among laboratory reared Macaque monkeys. Such emotional reactivity has been labeled by other names such as timidity, fearfulness, anxiety, introversion, 'uptight,' and more recently, due to the analogous work in humans by Kagan and his lab (1997), behavioral inhibition. These individual differences, often only expressed in the presence of stress, such as a novel challenge, are generally masked during non-stressful baseline periods, but nevertheless appear to be quite stable from infancy to at least adolescence (Suomi, 1987; Kagan, 1997).

A number of paradigms and behaviors have been used to measure reactivity. In general they involve measurements of fearfulness during stressful situations, i.e. novel or possible threatening situations. Some examples are: subjective ratings of fearfulness while being handled by an experimenter (Schneider & Suomi, 1992; Suomi, Kraemer, Baysinger & DeLizio, 1981), latency to approach stimuli in a novel setting, initiation of social interactions with unfamiliar individuals (Thompson, Higley, Byrne, Scanlan, & Suomi, 1986), recording of overall distress behaviors during exposure to a novel room (Suomi et al., 1981; Thompson et al., 1986), and physiological reactivity such as levels of cortisol, heart rate, and central amines (norepinephrine, serotonin, etc.) (Higley, 1985; Suomi, et al., 1981, Thompson et al., 1986). Behaviors that are commonly used to assess "level of anxiety" in an animal include a propensity to inspect of explore a novel object or environment (File, 2001), and reactivity (via vocalizations or facial expressions) to a threatening social or non-social stimulus (Kalin and Shelton, 1989; Kalin et al., 1991). The most familiar use of anxiety models (i.e. reactivity) in the scientific literature have been developed for rodents. A few examples of some of these paradigms are; (1) The elevated plus maze test model, which is the most widely used test to measure fear or anxiety in small rodents. This test is useful because of its relative simplicity, short time, and no required training before testing. This test determines the animal's unconditioned

response to a potentially dangerous environment. It is based upon their natural aversion to heights and open spaces. High anxiety states are directly related to the degree to which the rodent avoids the open arms of the maze and lack of fear is indicated by the "daring" of the animals to enter open arms repeatedly. (2) Light/Dark preference test model is based on the natural tendency of rodents to prefer enclosed environments as well as their innate tendency to explore a new environment. Rodents prefer dark spaces but also want to explore new ones. Therefore, high levels of anxiety can be measured by increased length of time for the animal to emerge into the lighter portion of the apparatus, or the avoidance of the area in general while showing no preference for the dark area of the enclosure suggests low levels of anxiety. (3) Open Field activity test model is used to measure activity in rodents as well as anxiety. Anxiety is determined by the pattern of exploration in the open-field. Individuals exploring the middle open area are considered to be less fearful than individuals that just walk along the borded periphery.

Individual Behavioral Variability through Novelty Testing

Individual variation in reactivity has begun to be utilized in the nonhuman primate literature to describe and to predict responses to demands and challenges (Suomi, 1987; Kalin, 1993; Fairbanks & McGuire, 1988; Schneider et al, 1991; Bolig et al., 1992). Analogous to the concept of behavioral inhibition and disinhibition in humans, more specifically the field of child development (Kagan et al., 1986; Kagan et al., 1987), behavioral reactivity level has not only been associated with specific behavioral responses but also with specific physiological responses to environmental challenges. It was through the research carried out in the laboratory of Stephen Suomi and his group that the issues of individual differences began to be addressed in rhesus monkeys (Suomi, Kraemer, Baysinger and DeLizio, 1981). Suomi (1987) began investigating reactivity level in non-human primates by subjecting them to a novelty situation. Much like the animal models previously mentioned, the monkeys' environment was manipulated by exposing them to a moderately novel situation, thought to induce stress, which produced an array of substantial individual differences in the extent and intensity of their expression of anxious-like behaviors. More specifically, Suomi and his group observed that in these standardized situations some rhesus infants and juveniles consistently

displayed behavioral and physiological signs of fearfulness and anxiety ('uptight,' 20%) where other rhesus monkeys of comparable age and social-rearing background, consistently initiated exploratory behavior and/or playful social interactions ('laid back,' 80%). This approach and the reactions displayed by the rhesus monkeys are comparable to the paradigm described by Kagan, Reznick and Snideman (1987) mentioned in an earlier section, of inhibited and uninhibited human children. In Kagan et al.'s (1987) paradigm, children were scored by observers judging behavioral inhibition while they interacted for the first time in a playroom filled with a variety of toys and objects that promoted physical activity. Predictably, some children took full advantage of the play opportunities in this setting, while others, were more inhibited. These marked distinctive behavioral patterns and their biological correlates are not just analogous between certain groups of children and monkeys, but appear very early in life using a variety of measures, and remain remarkably stable from infancy to adulthood.

For the past 20 years, Ned Kalin has studied fear in people and in monkeys. In his experimental paradigms, he has attempted to demonstrate that fear is not just one thing, but several, and that this palette of fearful, or defensive, behaviors are controlled by different brain mechanisms. Through three tests in a laboratory situation Kalin et al. (1987), tried to identify specific brain processes that regulate fear and its associated behaviors in rhesus monkeys (Macaca mulatta). He tried to find cues that elicit fear, and identify behaviors that reflect different types of anxiety. He exposed rhesus monkeys between 6 and 12 months old to 3 related novel situations; (1) alone in the novel test cage just having been separated from mother and left by itself in a cage for 10 minutes, (2) no eye contact condition (experimenter standing motionless outside the cage and avoided looking at the solitary infant) and (3) stare condition (experimenter assuming a neutral expression peering directly at the monkey). He deduced the following 3 constellations of defensive behaviors; (i) In the alone condition, most monkeys became very active and emitted frequent "coo" calls (ii) In the no-eye-contact situation, the monkeys reduced their activity greatly and sometimes "froze," remaining completely still for prolonged periods of time. (iii) In the stare condition, the monkey made a few hostile gestures, among them "barking," staring back, producing threat faces, baring their teeth and shaking the cage. In this condition "coo" calls also increased in frequency. They

discovered that 9 to 12 weeks is the critical age for the appearance of a monkey's ability to adaptively modulate its defensive activity to meet changing demands. Due to the maturation of the 3 interconnected brain regions; prefrontal cortex, amygdala, and hypothalamus, suspected to underlie selective responding. Their goal was to lay the groundwork for deciphering the relative contributions of various brain systems to inordinate fear in primates, rather than documenting individual difference in reactivity to challenge.

A related study (Mary Schneider et al., 1991) tested the hypothesis that individuals with constitutional weaknesses raised in suboptimal environments are likely to have poor developmental outcomes. The most positive outcomes are anticipated for those individuals without constitutional problems who were reared in enriched environments. The study included 23 rhesus monkey infants separated from their mothers at birth. Assessment of the rhesus infants's relative fearfulness in terms of behavioral measures during the first month of life predicted subsequent performances on problem-solving and motor tests. The temperament assessment, with characteristics such as irritability, consolability, fearfulness, response intensity, and persistence was rated on a 3-point score: "0" none or mild; "1" moderate or average; "2" frequently, continuously. Their operative definition for fear specifically included both 'fear grimaces' and 'trembling,' with a 3-point score: "0" none; "1" fear grimaces early in test session; "2" fear noted frequently. Many other definitions of items on the Early Infancy Assessment were also scored. Fearfulness was chosen as the basis for comparison of the infants for several reasons. First, previous data has demonstrated the importance of this temperamental dimension in rhesus monkeys (Suomi, 1983). In addition, Schneider et al. (1991) opted to use the extreme cases, (i.e. 25% of the fearful and 25% of the bold) based on data from studies of children demonstrating that long-term stability of shyness (i.e. fearful) holds for the behavioral extremes but not for the entire group (Kagan, 1989). The main finding of this study, was that individuals that performed well on 8 months problem-solving and motor tests, and had been reared in enriched environments, rated low on fearfulness during the early laboratory assessment. In contrast, those individuals who scored poorly on 8 months problem-solving and motor tests were the most fearful during early assessments and had been reared without enrichment. Using prior

knowledge, this study investigated the combined effects of early temperamental characteristics (e.g., fearfulness) and environmental enrichment in 23 rhesus monkeys, and despite a modest sample size, they successfully demonstrated the potential of predicting future outcomes.

Another group that used reactivity as a basis for studying temperamental traits is that of Judy Cameron (Cameron et al., (2003). In this study, the authors have used four standardized laboratory paradigms commonly used to assess anxious, fearful, and/or inhibited behavior in 85 young rhesus monkeys. Investigators have begun to recognize that efforts to identify genes underlying the development of anxiety disorders benefit from its broadening of research scope to include assessment of temperamental traits that are precursors to anxiety disorders (Blangero et al., 2000; Gershenfeld and Paul, 1998; Merikangas et al., 2002; Moldin, 1997). The first objective of the study was to refine the "anxious" phenotype for future successful genetic analyses. Cameron et al. (2003), suggest that behavioral traits may represent phenotypes that show more homogeneity than complex anxiety disorders, and therefore serve as a better approach to determine or discover which genes influence which components of the phenotype. The key aspect of this strategy was to "identify robust, dissectable, phenotypes for genetic analysis," (Cameron et al. 2003, pp. 213). As a first step in dissecting the genetics of anxious behavior, Cameron et al., (2003) examined how different testing paradigms (involving exposure to novel objects or environments, and to threatening social and nonsocial stimuli) might influence the display of various behaviors (e.g., inspection of novelty, production of vocalizations and fear grimaces) that have been classified as forms of anxious behavior in infant rhesus macaques (*Macca mulatta*). How these measures of anxious behavior are related to each other has received little study, and what exactly entails the identification of anxious animals remains unanswered. Are the different individuals identified as anxious depending on the test utilized or the specific behavior (e.g., vocalization, level of exploration, production of facial expression) assessed? Four testing paradigms were identified as sufficiently heritable to prove a basis for future analysis of genetic "risk" for anxiety among rhesus infants. Three of the four tests (the Free Play, Remote-Controlled Car, and Human Intruder tests) were based on tests designed by Dr. Hill Goldsmith and collaborators as part of the Laboratory Temperament

Assessment Battery (Goldsmith & Rothbart, 1991). This battery was designed to allow a standardization of temperament and behavior testing in young children, and to provide quantitative and repeatable assessment of behavior in various conditions. The fourth test (Novel Fruit test) was designed to examine the propensity of young monkeys to approach a novel, rewarding stimulus when placed in an unfamiliar environment. Eighty-five rhesus monkeys approximately 4 months of age were used for these studies. To examine the inter-correlations of the behaviors and how they cluster into common factors, factor analyses were performed on all measured behaviors (Williamson et al., 2003). Seven factors explained a total of 56.7% of the overall variability within the behaviors. The results of these analyses support the hypothesis that 'vocalizations' and 'exploration of novelty' are prominent behaviors displaced by monkeys in conditions that can promote anxiety. 'Fear grimacing' was surprisingly only displayed by a small proportion of monkeys, and only in the Stare condition of the Human Intruder test and in the Remote-Controlled Car test. Fear grimacing did not appear in any of the factors explaining the majority of the variance in these tests. Certain attributes that we associate with anxious behavior appear to be uncorrelated, or insignificantly expressed in this study, which could alter our perception on which animals are categorized as anxious. The notion that specific types of anxious behavior are separable from each other, have different etiologies, and may lead to different outcomes is supported by findings from several other groups of investigators, however few studies (like this one), have utilized animal models to help us elucidate the genetic underpinnings of anxious behavior. According to Cameron et al. (2003), work is still required to define how the measurement of various behaviors, in different tests, can help us identify an individual as anxious.

Lynn Fairbanks (1993), using vervet monkeys, focused her attention on a different aspect of reactivity, namely the tendency of juveniles to approach novel and potentially dangerous situations. Three different challenge tests were performed under controlled conditions: (1) latency to enter a new environment; (2) latency to approach a new food source; and (3) latency to approach a strange adult male. Results from all three challenge situations, support the hypothesis that 2- to 3- year-old juveniles are more likely to approach a novel potentially dangerous object or situation than are younger or older group members. In a follow-up study, Fairbanks et al. (2004) tested 36 adolescent

male vervets with the Intruder Challenge test (Fairbanks, 2001), before they were introduced into new matrilineal breeding groups. This standardized resident/intruder test measures an individual's readiness to approach and challenge a social stranger. Social Impulsivity scores were calculated by the latency to approach the intruder along with the number of intervals that males were engaged in risky, assertive, and aggressive behaviors directed towards the intruder. Animals that scored high on social impulsivity immediately approached the intruder and frequently challenged or lunged at the caged conspecific, while those that scored in the moderate range were more cautious and tempered in their responses. Animals with the lowest social impulsivity scores avoided the intruder, and if they interacted at all, did so from a safe distance. One of their findings was that males high in impulsivity as adolescents were more likely to achieve stable alpha male status 1 year following introduction into their new breeding groups. A second index, which was independent of approach to a stranger, was a Social Anxiety score, which was derived by summing the number of intervals that the subject engaged in 'scratching,' 'pacing,' and 'yawning.' Social anxiety from the intruder challenge test was not related to dominance attainment in their sample. Fairbanks et al., (2004) seemingly preconceived their dimensional measures of Social Impulsivity and Social Anxiety, as well as the lower ordered behaviors making up their constructs, prior to subjecting the individual monkeys to their experimental paradigm. In addition, Fairbanks et al., (2004) seemed to focus entirely on the positive end (i.e. high scores) of the Social Impulsivity dimension, while ignoring the lower end. With the data being available, one could focus on the low scores of the Social Impulsivity dimension, and question what exactly is it measuring. Instead of perceiving it as the obvious 'not impulsive,' measure, it could actually be indicative of a different type of fearfulness or avoidance. The advantage to their empirically detailed structure, allows anyone to criticize or challenge their operational definitions of impulsivity and anxiety, as well as their results.

Rosemary Bolig et al., (1992) tried to determine whether the subjective assessment of reactivity level in 22 rhesus macaques, between 1 and 14 years old, is related to assessment of personality traits. They concluded that subjective assessment of reactivity is complementary to that of personality traits. Using experienced observers, this group rated personality traits and tried to assess the inter-rater reliability and convergent

validity of a subjective assessment of reactivity among a small troop of captive rhesus monkeys (*Macaca mulatta*). The goal of this study was to assess the relationships between newly derived personality dimensions and reactivity, social rank, age, and gender; and to determine whether a simple reactivity rating system can capture the essence of a larger collection of tempo-related traits. The number of hours during which the raters had contact with the subject animals was a minimum of 300 hours. Observers first ranked animals as high (3), moderate (2), or low (1) on reactivity. High reactivity was defined as the least likely to approach new stimuli, most anxious, most socially inhibited, and least likely to attempt challenging situations; low reactivity as most likely to approach new stimuli, least anxious, least socially inhibited, and most likely to attempt challenging situations; and moderate reactivity in intermediate positions (Suomi, 1987). The observers also independently assessed the 22 monkeys on the 25-item Stevenson-Hinde et al. (1980) inventory described previously. Principal component analysis was conducted on the data to construct new components, and they tested differences of scores on personality dimensions between reactivity, rank, age, and gender groups. Discriminant analysis was used to determine if animals could be assigned to reactivity level on the basis of their rating on personality traits. They found significant correlations between personality traits and reactivity; animals ranked as highly reactive were also rated as least confident, curious, equable, and understanding, and the most excitable, fearful, insecure, irritable, and tense. The simpler, three-level, reactivity measure, appears to capture salient personality characteristics, and appears to be a reliable instrument, comparable to the 25-item personality assessment.

REFERENCES

Allport, G.W., & Odbert, H.S. (1936). "Trait names: A psycho-lexical study." Psychological Monographs 47 (1, Whole No. 211).

Andrews CM (1922) Journal of a lady of quality; being a narrative of a journey from Scotland to the West Indies, North Carolina and Portugal in the years 1774-1776. Yale University Press, New Haven.

Altmann J (1974). Observational study of behavior: sampling methods. Behavior 49: 227-267.

Bates, J.E. (1986). "The measurement of temperament." In R. Plomin & J.Dunn (Eds), The study of temperament: Changes, continuities and challenges (pp. 1-11). Hillsdale, NJ:Erlbaum.

Bates, J.E. (1987). "Temperament in infancy." In J.D. Osofsky (Ed.), Handbook of infant development, 2nd edition. (pp. 1101-1149). New York: Wiley.

Bates, J.E. (1989). "Concepts and measures of temperament." Temperament in Childhood. G.A. Kohstamm, J.E., Bates, & M.K. Rothbart, Editors. New York: John Wiley and Sons Ltd. Pgs: 1-26.

Blizard, D.A. (1981). "The Maudley reactive and non-reactive strains: A North American perspective." Behavioral Genetics 11: 469-489.

Blangero, J., Williams, J.T., Almasy, L. (2000). "Quantitative trait locus mapping using human pedigrees." Human Biology 72: 35-62.

Boal, S.A., Young, S.N., Sutherland, M., Ervin, F.R. and Coppinger, R. (1988). The effect of breakfast on social behavior and brain amine metabolism in vervet monkeys. Pharmacology Biochemistry and Behavior. 29: 115-123.

Borkenau, P., Riemann, R., Angleitner, A., & Spinath, F.M. (2001). "Genetic and environmental influences on observed personality: evidence from the German Observational Study of Adult Twins." Journal of Social Psychology 80(4): 655-668.

Bolig, R., C. S., Price, S., P. L., O'Neill, & S.J. Suomi, (1992). "Subjective assessment of reactivity level and personality traits of rhesus monkeys." International Journal of Primatology 13(3): 287-306.

Bowlby, J. (1958). "The nature of the child's tie to his mother." International Journal of Psychoanalysis. 39(5): 350-373.

Buirski, P., Kellerman, H., Plutchik, R., Weininger, R., & Buirski, N. (1973). "A field study of emotions, dominance, and social behavior in a group of baboons (Papio anubis)." Primates 14(1): 67-78.

Buss, A.H., & Plomin, R. (1975). "A temperament theory of personality development. New York: Wiley.

Buss, A.H., & Plomin, R. (1984). " Temperament: early developing personality traits, Hillsdale, NJ: Erlbaum.

Caspi, A., Henry, B., McGee, R.O., Moffit, T.E., & Silva, P.A. (1995). "Temperamental origins of child and adolescent behavior problems: from age three to age fifteen." Child Development 66(1): 55-68.

Caspi, A. (1998). "Personality development across the life course. In W. Damon (Series Ed.) & N. Eisenberg (Vol. Ed.), Handbook of child psychology, Volume 3: Social, emotional, and personality development (pp. 311-388). New York: Wiley.

Caspi, A., Harrington, H., Milne, B., Amell, J.W., Theodore, R.F., & Moffit, T.E. (2003). "Children's behavioral styles at age 3 are linked to their adult personality traits at age 26." Journal of Personality 71(4): 495-513.

Capitanio, J.P. (1999). "Personality dimensions in adult male rhesus macacques: prediction of behavior across time and situation." American Journal of Primatology 47: 299-320.

Capitanio, J.P., & Widaman, K.F. (2005). "Confirmatory analysis of personality structure in adult male rhesus monkeys (maccaca mullata)." American Journal of Primatology 65:298-294.

Cattell, R.B. (1943). "The description of personality: Basic traits resolved into clusters." Journal of Abnormal and Social Psychology 38: 476-506.

Cattell, R.B. (1948). "The integration of factor analysis with psychology." Journal of Educational Psychology 39: 227-236.

Cattell, R.B. (1988). "The meaning and strategic use of factor analysis. In J.R. Nesselroade & R.B. Cattell. Handbook of multivariate experimental psychology. (2nd ed.). New York: Plenum.

Caine, N.G., Earle, H., Raite, M. (1983). "Personality traits of adolescent pig-tailed monkeys, (macaca nemestrina): An analysis of social rank and early separation experience." American Journal of Primatology 4: 253-260.

Cameron, J.L., Bacanu, S.B., Coleman, K.D., Dahl, R.E., Devlin, B.J., Rogers, J.A., Ryan, N.D., & Williamson, D.E. (2003). "Dissociating components of anxious behavior in young rhesus monkeys. A precursor to genetic studies." In: Fear & Anxiety: Benefits to Translational Research (Gorman JM, ed). American Psychiatric Press, Washington DC, pp. 211-226.

Chamove, A.S., Eyseck, H.J., & Harlow, H.F. (1972). "Personality in monkeys: Analysis of rhesus social behavior." Quarterly Journal of Experimental Psychology 24: 496-504.

Cheney, D.L., and Seyfarth, R.M. (1990). "How Monkeys See the World." The University of Chicago Press, Ltd. London.

Cloninger., C.R. (1986). "A unified biosocial theory of personality and its role in development of anxiety states." Psychiatric Developments 3: 167-226.

Coplan, J.D., Rosenblum, L.A., & Gorman, J.M. (1995). "Primate models of anxiety. Longitudinal perspectives 18(4): 727-743.

Costa, P.T. Jr., & McCrae, R.R. (1992). "Four ways five factors are basic." Personality Individual Differences 13: 653-665; 861-865.

Darwin, C. (1998). "The expression of the emotions in man and animals." Third Edition. Oxford University Press Inc. New York.

Ervin, F.R., Palmour, R.M., Young, S.N., Guzman-Flores, C. and Juarez, J. (1990). Voluntary consumption of beverage alcohol by vervet monkeys: population screening, descriptive behavior and biochemical measures. Pharmacology Biochemistry. 36: 367-373.

Eysenck, H.J. (1947). "Dimensions of personality." London: Routledge & Kegan Paul.

Eysenck, H.J. (1987). "The role of heredity, environment and 'preparedness' in the genesis of neurosis. In H.J. Eysenck & I. Martin (Eds), Theoretical foundations of behavior therapy (pp. 379-402). New York: Plenum Press.

Fairbanks, L.A. and McGuire, M.T. (1988). "Long-term effects of early mothering behavior or responsiveness to the environment in vervet monkeys." Developmental Psychibiology 21, pp. 711-724.

Fairbanks, L.A. (2001). Individual differences in response to a stranger: social impulsivity as a dimension of temperament in vervet monkeys. Journal of Comp Psychol 115: 22-28.

Fairbanks, L.A., Melaga, W.P., Jorgensen, M.J., Kaplan, J.R., & McGuire, M.T. (2001). "Social impulsivity inversely associated with CSF 5-HIAA and fluoxetine exposure in vervet monkeys." Neuropharmacology 24(4): 370-378.

Fairbanks, L.A., Newman, T.K., Bailey, J.N., Jorgensen, M.J., Breidenthal, S.E., Ophoff, R.A., Comuzzie, A.G., Martin, L.J., & Rogers, J. (2004). Genetic contributions to social impulsivity and aggressiveness in vervet monkeys. Biological Psychiatry. 55: 642-647.

Figuerdo, A.J., Cox, R.L., & Rhine, R.J. (1995). "A generalizability analysis of subjective personality assessments in the stumptail macaque and the zebra finch." Multivariate Behavioral Research 30(2): 167-197.

File, S.E. (2001). "Factors controlling measures of anxiety and responses to novelty in the mouse." Behavioral Brain Res 125: 151-157.

Fleagle, J.G., & McGraw, W.S. (1999). "Skeletal and dental morphology supports diphyletic origin of baboons and mandrills." Proceedings of the National Academy of Sciences USA 96(3): 1157-1161.

Gershenfeld, H.K., & Paul, S.M. (1998). "Towards a genetics of anxious temperament: from mice to men." Acta Psychiatric Scand Supple 393: 56-65.

Gold, K.C., & Maple, T.L. (1994). "Personality assessment in the gorilla and its utility as a management tool." Zoo Biology 13: 509-522.

Goldsmith, H.H., Buss, A.H., Plomin, R., Rothbart, M.K., Thomas, A., Chess, S., Hinde, R.A., & McCall, R.B. (1987). "Roundtable: What is temperament? Four approaches." Child Development (58): 505-529.

Goldsmith, H.H. & Rieser-Danner, L. (1986). "Variation among temperament theories and validation studies of temperament assessment." In G.A. Kohnstamm (Ed.), Temperament discussed (pp. 1-10). Lisse (Neth): Swets & Zeitlinger.

Goldsmith, H.H., & Rothbart, M.K. (1991). "Contemporary instruments for assessing early temperament by questionnaires and in the laboratory, in exploration in temperment." International Perspectives of Theory and Measurement. Edited by Strelau J, Angleitner A, New York, Plenum. Pp. 249-272.

Gosling, S.D., John, O.P. (1999). "Personality dimensions in nonhuman animals: A cross-species review. Current Directions in Psychological Science 8(3): 69-75.

Gray, J.A. (1971). "The psychology of fear and stress." Toronto. NY: McGraw-Hill.

Gray, J.A. (1982). "The neurochemistry of anxiety: An enquiry into the functions of the setpo-hippocampul system. Oxford: Oxford University Press.
Harlow, H.F., Suomi, S.J. (1974). "Induced depression in monkeys." Behavioral Biology 12: 273-296.

Harlow, H.F., Gluck, J.P., & Suomi, S.J. (1972). Generalization of behavioral data between nonhuman and human animals. American Psychologist. 27: 709-716.

Harlow, H.F., & Novak, M.A. (1973). Psychopathological perspectives. Perspectives in Biological Medicine. 16(3): 461-478.

Harlow, H.F., Suomi, S.J. & Novak, M.A. (1974). Reversal of social deficits produced by isolation rearing in monkeys. Journal of Human Evolution. 3: 527-534.

Higley, J.D. (1985). "Continuity of social separation behaviors in rhesus monkeys from infancy to adolescence." Unpublished doctoral dissertation, University of Wisconsin, Madison. WI.

Higley, J.D., & Suomi, S.J. (1989). "Temperamental reactivity in non-human primates. In G.A. Kohnstamm, J.E. Bates, & M.K. Rothbart (Eds.), Temperament in Childhood (pp.153-167). New York.

Higley, J.D., & Suomi, S.J. (1992). "A longitudinal assessment of CSF monoamine metabolite and plasma cortisol concentrations in young rhesus monkeys." Biological Psychiatry 32: 127-145.

Hinde, R.A. (1977). "Mother-infant separation and the nature of inter-individual relationships: Experiment with rhesus monkeys." Proceedings of the Royal Society of London (B) 196: 29-50.

Hinde, R.A. (1987). "Can nonhuman primates help us understand human behavior?" Primate Societies. B.B. Smuts, D.L., Cheney, R.M., Seyfarth, R.W., Wrangham, T.T., Stuhsaker, Editors. Chicago: University of Chicago Press. Pgs: 413- 420.

Hinde, R.A. (1989). "Temperament as an intervening variable." Temperament in Childhood. G.A. Kohstamm, J.E., Bates, & M.K. Rothbart, Editors. New York: John Wiley and Sons Ltd. Pgs: 27-33.

Kagan, J., Reznick, J.S., & Snidman, N. (1987). "The physiology and psychology of behavioral inhibition in children." Child Development 58: 1459-1473.

Kagan, J., Reznick, J.S., & Snidman, N. (1988). "Biological basis of childhood shyness." Science 240: 167-171.

Kagan, J., Reznick, J., & Sniderman, N. (1986). "Temperamental inhibition in early childhood." In Plomin, R., and Dunn, J. (eds), The Study of Temperament, Lawrence Erlbaum Associates, Hillsdale, NJ, pp. 53- 63.

Kagan, J. (1989). "Temperamental contribution to social behavior." American Psychologist 44: 668-674.

Kagan, J., Reznick, S., Gibbons, J. (1989). "Inhibited and uninhibited types of Children." Child Development 60: 838- 845.

Kagan, J., & Snidman, N. (1991). "Temperamental factors in human development." American Pychology 46: 856- 862.

Kagan, J., & Zentner, M. (1996). "Early childhood predictors of adult psychopathology." Harvard Rev Psychiatry 3: 341-350.

Kagan, J. (1997). "Temperament and the reactions to unfamiliarity." Child Development 68(1): 139-143.

Kalin, N.H. & Shelton, S.E. (1989). "Defensive behaviors in infant rhesus monkeys: environmental cues and neurochemical regulation." Science 243: 1718-1721.

Kalin, N.H., Shelton, S.E., & Takahashi, L.K. (1991). "Defensive behaviors in infant rhesus monkeys: ontogeny and context-dependent selective expression." Child Development 62: 1175-1183.

Kalin, N.H. (1993). "The neurobiology of fear." Scientific American pp. 94-101.

Kalin, N.K., Shelton, S.E., & Barkdale, C.M. (1987). "Separation distress in infant rhesus monkeys: Effects of diazepam and Ro 15-1788." Brain Research 408(1-2): 192-198.

King, J.E., & Figuerdo, A.J. (1997). "The five factor model plus dominance in chimpanzee." Journal of Research in Personality 31: 257-271.

Kohnstamm, G.A. (1986). "Temperament discussed: Temperament and development in infancy and childhood. Lisse (Neth.): Swets & Zeitlinger.

Kraemer, G.W., & McKinney, W.T. (1979). "Interaction of alteration in biogenic amine metabolism with the despair response to peer separation in rhesus monkeys." Catecholamines: Basic and Clinical Frontiers, Vol. 2. E. Usdin, I.J. Kopin, J. Barchas, Editors. New York: Pergamon Press. Pgs. 1705-1707.

Lee, P.C., (1983). "Play as a means for developing relationships." In: Primate Social Relationships (Ed. By R.A. Hinde). Pp.82-89. Sunderland, Mass.: Sinauer.

Lerner, J.V., & Lerner, R.M. (1983). Temperament and adaptation across life: Theoretical and empirical issues. In P.B. Baltes & O.G. Brim (Eds), Life-span Development and Behavior. Vol.5 (pp. 197-231). New York: Academic Press.

Livesley, W.J., Jang, K.L., & Vernon, P.A. (1998). "Phenotypic and genetic structure of traits delineating personality disorder." Archives of General Psychiatry 55(10): 941-948.

Martau, P.A., Caine, N.G., & Candland, D.K. (1985). "Reliability of the Emotions Profile Index, primate form, with Papio hamadryas, Maccaca fuscata, and two Saimiri species." Primates 26(4): 501-505.

Maziade, M., Boudreault, M., Thivierge, P.C., Caperaa. J., & Cote, R. (1984a). "Infant temperament: SES and gender differences and reliability of measurement in a large Quebec sample." Merrill-Palmer Quarterly 30(2): 213-226.

Maziade, M., Cote, R., Boudreault, M., Thivierge, J., & Caperaa, P. (1984b). "The New York Longitudinal studies model of temperament gender differences and demographic correlates in a French-speaking population." Journal of American Academy Child Adolescence Psychiatry 23: 582-587.

Maziade, M., Capera, P., Laplante, B., Boudreault, M., Thivierge, J., Cote, R., & Boutin, P. (1985). "Value of difficult temperament among 7-year olds in the general population for predicting psychiatric diagnosis at age 12." American Journal of Psychiatry 142: 943-946.

Maziade, M., Boutin, P., Cote, R., & Thivierge, J. (1986). "Empirical characteristics of the NYLS temperament in middle childhood: Congruities and incongruities with other studies. Child Psychiatry and Human Development 17(1): 38-52.

Maziade, M. (1988). " Child temperament as a developmental or an epidemiological concept: a methodological point of view." Psychiatric Development 3: 195-211.

Maziade, M., Caron, C., & Cote, R. (1990a). "Extreme temperament and diagnosis: a study in a psychiatric sample of consecutive children." Archives of General Psychiatry 47: 477-484.

Maziade, M., Caron, C., Cote, R., Merette, C., Bernier, H., Laplante, B., Boutin, P., & Thivierge, J. (1990b). "Psychiatric status of adolescents who had extreme temperament at age 7." Amercian Journal of Psychiatry 147: 1531-1536.

McCrae, R.R., & Costa, P.T. Jr. (1985). "Updating Norman's 'adequate taxonomy:' Intelligence and personality dimensions in natural language and in questionnaires." Journal of Personality and Social Psychology 49: 710-721.

McCrae, R.R., & Costa, P.T. Jr. (1987). "Validation of the Five-Factor Model of Personality Across Instruments and Observers. Journal of Personality and Social Psychology 52(1): 81-90.

McGuire MT (1974) "The St.Kitts vervet." In: Monographs in primatology, Karger, Basel Merrill, G.C.,: The historical geography of St. Kitts and Nevis, the West Indies (Instituto Panamericano de Geografia e Historia, Mexico 1958).

McGuire, M.T., Raleigh, M.J., & Pollack, D.B. (1994). "Personality features in vervet monkeys: The effects of sex, age, social status, and group composition." American Journal of Primatology 33(1): 1-13.

McKinney, W.T. Jr., & Bunney, W.E., Jr. (1969). "Animal model of depression. I. review of evidence: implications for research." Archives of General Psychiatry 21: 240-248.

Merikangas, K.R., Avenevoli, S., Acharyya, S. (2002). "The spectrum of social phobia in the Zurich cohort study of young adults." Biological Psychiatry 51: 81-91.

Moldin, S.O. (1997). "The maddening hunt for madness genes." Nature Genetics 17: 127-129.

Palmour, RM., Mulligan, J., Howbert, JJ, and Ervin, F. (1997). Insights From Model Systems; Of monkeys and men: vervets and the genetics of human-like behaviors. American Journal of Human Genetics 61: 481-488.

Plomin, R. (1983). "Developmental behavioral genetics." Child Development 54(2): 253-259.

Plomin, R., & Dunn, J. (Eds.) (1986). "The study of early temperament: Changes, continuities and challenges. Hillsdale, NJ: Erlbaum.

Plutchik, R. (1962). "The emotions: facts, theories, and a new model. Random House, New York.

Prior, M. (1992). "Childhood temperament." Journal of Child Psychology and Psychiatry 33(1): 249-279.

Raleigh, M.J., & McGuire, M.T. (1990). "Social influences on endocrine function in male vervet monkeys. Pp. 95-111 in Socioendocrinology of Primate Reproduction. F. Berkovitch, ed. New York, Wiley-Liss.

Robinson, J.L., Kagan, J., Reznick, J.S. & Corley, R. (1992). "The heritability of inhibited and uninhibited behavior: A twin study." Developmental Psychology 28(6): 1030-1037.

Rose, R., & Kaprio, J. (1988). "Frequency of social contact and intrapair resemblance of adult monozygotic co-twins-or does shared experience influence personality after all? Behavior Genetics 18: 309-328.

Rosenblum, L.A., & Paully, G.S. (1987). "Primate models of separation-induced depression." The Psychiatric Clinics of North America 10(3): 437-447.

Rosenberg, A.A., & Kagan, J. (1989). "Physical and physiological correlates of behavioral inhibition." Developmental Psychobiology 22(8): 753-770.

Rothbart, M.K. (1981). "Measurement of temperament in infancy." Child Development 52: 596-578.

Rothbart, M.K., Ahadi, S.A., & Hershey, K.L. (1994). "Temperament and social behavior in childhood." Merrill-Palmer Quarterly 40(1):21-39.

Rutter, M. (1987). "Temperament, personality and personality disorder." British Journal of Psychiatry 150: 443-458.

Scarr, S., & McCartney, K. (1983). " How people make their own environments: A theory of genotype-environmental effects." Child Development 54: 424-435.

Schneider, M.L., Colleen, F.M., Suomi, S.P., & Champoux, M. (1991). "Laboratory assessment of temperament in rhesus monkey infants (Macaca mullata)." American Journal of Primatology 25: 137-155.

Schneider, M.L., & Suomi, S.J. (1992). Neurobehavioral assessment in rhesus monkey neonates (macaca mulatta): developmental changes, behavioral stability, and early experience. Infant Behavior and Development. 15: 155-177.

Schneirla, T.C. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In: MR Jones, ed. Nebraska Symposium of Motivation, Vol.7, U Nebraska Press. pp 1-42.

Shiner, R. (1998). "How shall we speak of children's personalities in middle childhood? A preliminary taxonomy." Psychological Bulletin 124: 308-332.

Stevenson-Hinde, J., & Zunz, M. (1978). "Subjective assessment of individual rhesus monkeys." Primates 19: 473-482.

Stevenson-Hinde, J., Stillwell-Barnes, R., & Zunz, M. (1980). "Subjective assessment of rhesus monkeys over four successive years." Primates 21(1): 66-82.

Strelau, J. (1986). "Do biological mechanisms determine the specificity of temperament?" In G.A. Kohnstamm (Ed.), Temperament discussed. Lisse (Neth.): Swets & Zeitlinger.

Scott, J.P., & Fuller, J.L. (1965). "Genetics and the social behavior of the dog." Chicago: University of Chicago Press.

Seyfarth, R.M. (1977). A model of social grooming among social grooming among adult female monkeys. Journal of Theoretical Biology. 65: 671-698.

Seyfarth, R.M., D.L. Cheney, and P. Marler. 1980. Monkey responses to three different alarm calls: Evidence for predator classification and semantic communication. Science 210: 801-3.

Sheldon, W.H. (1942). "The varieties of temperament. Harper. New York.

Suomi, S.J. (1997). "Early determinants of behaviour: Evidence from primate studies." British Medical Bulletin 53(1): 170-184.

Suomi, S.J., Kraemer, G.U., Baysinger, C.M., & Delizio, R.D. (1981). Inherited and experiential factors associated with individual differences in anxious behavior displayed by rhesus monkeys. In D. Klein & J. Rabkin (Eds.), Anxiety: New Research and Changing Concepts. New York: Raven Press.

Suomi, S.J., (1982). "Abnormal behavior and primate models of psychopathology." Primate Behavior. J. Fobes, J.E. King, Editors. New York: Academic Press. Pages 171-215.

Suomi, S.J. (1983). "Social development in rhesus monkeys: Consideration of individual differences." The Behavior of Human Infants. A. Oliviero; M. Zapella, eds. New York, Plenum. Pp. 71-92.

Suomi, S. (1987). "Individual differences in rhesus monkey behavioral and adrenocortical responses to social challenge: Correlations with measures of heart rate variability. In Fox, N. (chair), Heart Rate Variability and Social Behavior: Behavioral and Biological Correlates, Symposium conducted at the meeting for the Society for Research in Child Development, Baltimore, MD.

Suomi, S.J., (1991). Uptight and laid-back monkeys: Individual differences in response to social challenges. In S.E. Brauth, W.S. Hall, & R.J. Dooling (Eds.), Plasticity of development (pp. 27-56). Cambridge, MA: MIT Press.

Tellegen, A., Lykken, D.T., Bouchard, T.J., Wilcox, K.J., Segal, N.L., & Reich, S. (1998). "Personality similar in twins reared apart and together" Journal of Personality and Social Psychology 6: 1031-1039.
Thomas, A., Chess, S., & Birch, H.G. (1969). "Temperament and behavior disorders in children." New York University Press.

Thomas, A., Chess, S., & Birch, H.G. (1970). "The origins of personality." Scientific American 223, 102-109.

Thomas, A., & Chess, S. (1977). "Temperament and development." New York: Bruner/Mazel.

Thompson, W.W., Higley, J.D., Byrne, E.A., Scanlan, J.M. & Suomi, S.J. (1986). Behavioral inhibition in nonhuman primates: Psychobiological correlates and continuitiy over time. Paper presented at the meeting of the International Society for Developmental Psychobiology, Annapolis, MD.

Tsuang, M.T., Stone, W.S., & Faraone, S.V. (2000). "Toward reformulating the diagnosis of schizophrenia." American Journal of Psychiatry 158(7): 1041-1050.

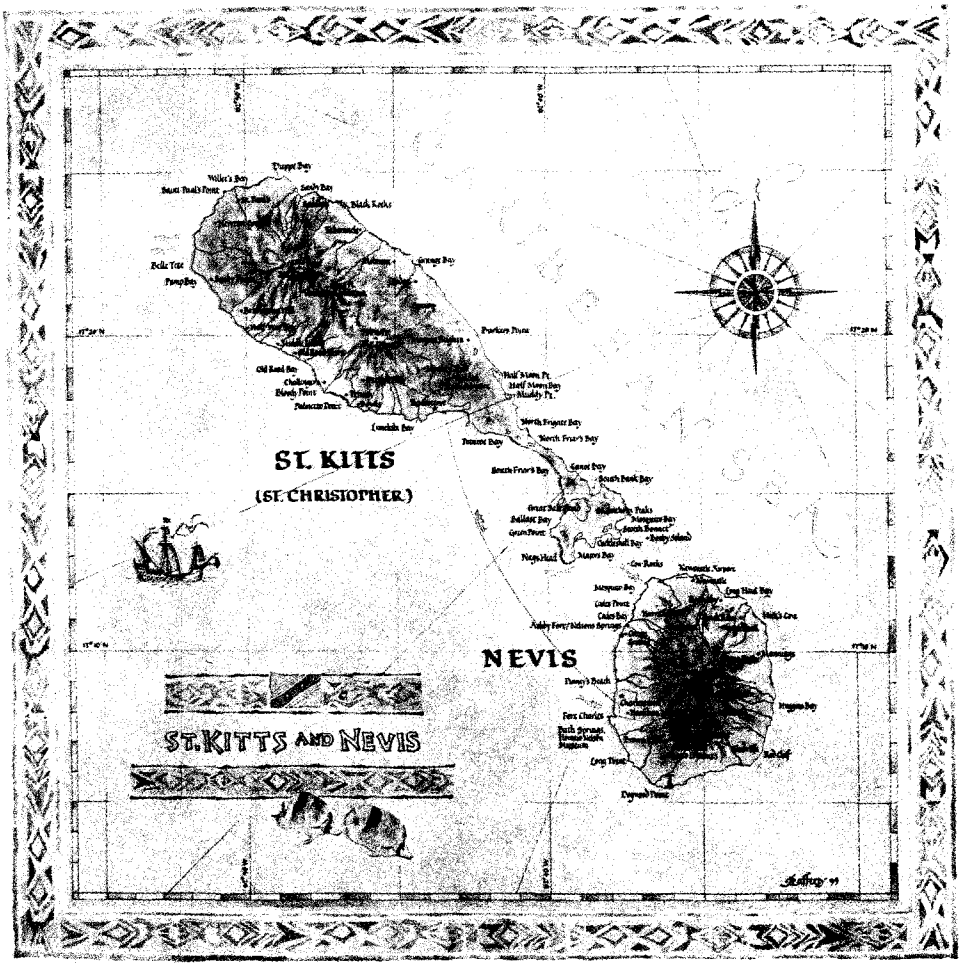
Williamson, D.E., Coleman, K., Devlin, B.J., et al., (2003). "Heritability of fearful/anxious endophenotypes in infant rhesus macaques: a preliminary report." Biological Psychiatry 53: 284-291.

Zuckerman, M. (1984). "Sensation seeking: A comparative approach to a human trait." Behavioral and Brain Sciences (7): 413-471.

Zuckerman, M. (1991). Psychobiology of Personality. Cambridge: Cambridge University Press.

CHAPTER II

CONTEXT OF THE PRESENT STUDY



Vervet monkey

It was not until the early 1960s that the first long-term studies of vervet mokeys were initiated by K.R.L. Hall and Stephen Gartlan (1965) on Lolui Island in Lake Victoria and by Tom Struhsaker (1967a, 1967b) in Amboseli, Kenya. Since then vervets have become one of the most intensively studied primate species; long-term research on vervets has been conducted at a number of sites in East, West, and southern Africa, as well as on several Caribbean islands and in captive colonies in the United States.

The History of the St. Kitts Vervet

St. Christopher, or as it is more commonly known, St. Kitts, was discovered by Colombus on his second voyage to the West Indies in 1493 (Richman, 1920). The island remained unsettled by Europeans until the 17th century until 1624 when 'official' settlement occurred under the direction of the Englishman, Thomas Warner (Merrill, 1958). Upon his arrival he found Indians to be the sole inhabitants of the island, and in his writings, as well as in those of other early settlers, there is no mention of monkeys. The land area of the island was used for agricultural purposes, hence its economy was dependent on slave labor. Because of geographical proximity to the Caribbean, most slaves were brought from West Africa (Boxer, 1969). The vervet's arrival in the Eastern Caribbean most probably occurred around this time since the monkeys were indigenous to Senegambia; also a major source of slaves. The vervets came with a colony of French (white people) when they moved from Senegambia to St.Kitts, after a land-transfer from the English to the French in a war-treaty (Burdon, 1920). The exact date of the vervet's arrival remains unknown, but an edict from the governor of Barbados (Thornton, 1955), states that by the 1650's, there were no more monkeys arriving by ship, hence, a reasonable inference suggests that they started arriving by 1630. The earliest known written report of vervets on the island is provided by Father Labat (1722), a French priest, who visited the island in 1700 (McGuire, 1974). According to Labat, the monkeys were at the time 'wild' and well established. He goes on to report that monkeys escaped from the homes of French settlers during one of the numerous local wars between the English and the French; this suggested to him that they had been pets of the French plantation owners and that the French had been responsible for their presence. Descriptions of the

monkeys today, in fact, differ little from those of two or three centuries ago, the species remains abundant, non-endangered, and a serious agricultural predator (Palmour et al., 1997). Furthermore, ample food and water, and no predators (save man), have allowed the monkeys to reach the present population ranging between 30 000 and 35 000.

The vervet monkey (*Chlorocebus aethiops*), is among the least specialized of the Old World monkeys and perhaps the most abundant monkey in Africa (Struhsaker, 1967a), as well as being the only non-human primate populating the Caribbean islands of St. Kitts, Nevis and Barbados (McGuire, 1974). St. Kitts is an island of 68 square miles of volcanic origin. It is located in the tropical Caribbean Sea, in the northeastern arc of a string of islands extending south from Cuba to South America (17° 15' N - 62° 40' W). The island comprises three distinct biotic zones: (i) a mountainous rain forest, (ii) well forested areas where ghauts cut through sugar cane fields and (iii) a savannah-like peninsula. These diverse zones are familiar to the vervet as they are similar to the kind of environment wild African vervets would have encountered. However, anyone who has attempted to study vervets in the wild has agreed that it is a remarkably challenging task. The generally timid disposition of these monkeys makes them slow to habituate to human observers, and subsequently difficult to locate in their natural habitats, where they find ample opportunities to hide behind thick scrub and up trees. Struhsaker (1967a) reported that there was much individual variability in the degree to which the Amboseli vervet habituated to the observer; some permitting a close approach, while others not. These are only a few of the factors that have limited the number of naturalistic studies in this species.

The first detailed index of behaviors scientifically reported for this species was conducted by Thomas Struhsaker (1967a), based on a one year field study held in the Masai-Amboseli Game Reserve of south central Kenya (East Africa). This study was seminal in that it: derived a catalogue of qualitative and quantitative descriptions of vervet behavior from a natural environment; provided researchers with new information on social group living; facilitated the comparison of species differences and established a template from which behavioral theories could be developed. Struhsaker (1967a) reported that East African vervet monkeys gave different sounding alarm calls to at least three different predators. Vervets responded to playback of leopard alarms by running

into trees; to eagle alarms by looking up in the air or running into bushes and to snake alarms by looking down in the grass around them.

Vervet monkeys are omnivorous and highly adaptable and tolerant of a large range of climates and ecologies (for more details see McGuire, 1974, Cheney & Seyfarth, 1990, Struhsaker, 1967a). The St. Kitts vervet is a well-proportioned and agile animal, as much at home in the trees as on the ground. Average adult males weigh 4 to 5 kg and females 3 to 4 kg; infants under 1 kg. The central part of the face and the ears are black and hairless. The fur-covered chest, abdomen, anterior scrotum, and proximal interiors of the arms and legs are white. The top of the head and the back are gray-yellow as are the arms and legs, which all become gray on the distal parts of the extremities. The tail is approximately two times the length of the back (base of the neck to the base of the tail. Field studies reveal that vervets are social animals mostly living in polygamous, hierarchically structured groups (Struhsaker, 1967a). The sex ratio is 1:1, and the modal troop is composed of several adult males, females, and young juveniles. Juvenile males leave the troop around the time of sexual maturity (5 to 6 years of age) and work their way into neighboring troops. Linear hierarchies exist in this species, with the alpha male and alpha female dominating the social order.

Aspects of Social Behavior

Social Communication: Similar to other non-human behavioral repertoires, this species' behavior can be subdivided categorically into non-communicative and communicative behaviors. Non-commuicative behaviors like locomotion, eating, drinking, sleeping, resting, self-grooming etc., do not evoke immediate social responses, while communicative behavioral patterns, affiliative (i.e. play, groom) and agonistic (i.e. threaten, fight) immediately affect other animals and eventually influence an individual's rank in the hierarchical structure.

***Dominance*:** Many of the early field studies of monkeys suffered from an overemphasis on the behavior of adult males. It seemed to some that the major axis of social organization in primate groups was dominance. Dominance hierarchies clearly have an important adaptive value. They allow individuals in a society to predict the outcome of an interaction when two animals compete for a scarce item in the

environment, be it food, space, an estrous female, or only a safe comfortable seat (Lancaster, 1975). Through experiences, which begin shortly after birth and continue through life, a young monkey learns which animals he can dominate and which he cannot. Dominance is one effective way to organize social interactions, and unorganized social relations can be chaotic. The ability to predict the behavior of others is basic to the evolution of complex social systems.

Grooming: Grooming involves all ages and sexes, and serves as a major integrating and group unifying function. Grooming is probably one of the more well-known and conspicuous behaviors that distinguish primates (Seyfarth, 1977). It is a major behavior pattern, exhibited by captive and free-living primates. The amount of contact through grooming that animals exhibit is one measure of social solidarity and an affectional relationship; mothers groom their infants intensely during the first few months (Fairbank and McGuire, 1985), but the frequency of grooming declines as the infant ages. Vervet females establish long-lasting relationships that are reinforced (if not built around) grooming activities (Simmonds, 1974). High ranking females receive more grooms from subordinate females then the other way around. In most social groups, the majority of grooming among adult females is exchanged between close genetic relatives (Cheney & Seyfarth, 1990).

Play: Play behavior is usually a behavior associated with the more intelligent mammals; the more advanced the mammal, the more important play becomes, since, play presumably serves as a learning experience. Play behavior is one of the most predominant and developmentally important activities in a young primate's life. It is an easily recognizable behavior and, yet, it is difficult to describe and define. Play is ordinarily regarded as behavior patterns not directly linked to daily maintenance needs and survival (Fagan, 1981). Rather, play behavior often involves motor sequences performed without apparent goals; play behavior is often described as repetitive, fragmented, or exaggerated motor behaviors involving diverse movements, and facial expressions (Fedigan, 1982). Anthropologists claim it must be a valuable behavior since primate young invest so much time in it. Juvenile vervet monkeys that play together also tend to groom and sit together (Lee, 1983), therefore demonstrating that play serves to facilitate the development of affiative relationships between individuals (Cheney and Seyfarth, 1990). An example of

useful play is what Lancaster (1975) has termed "play mothering", wherein young juveniles attempt to carry, play and generally take care of infants. The robust and vigorous locomotor movements involved in play contribute to improve coordination and locomotor skills of the playing animals. Play provides a safe setting within which species-specific communicative and social skills can be rehearsed for adulthood, without serious consequences should these behaviors be performed incorrectly.

Mother-infant Interaction: In many ways the most basic theme running through primate social relations is the attachment between a mother and her offspring. This bond between mother and infant is primary in the sense that it is the first bond to be formed in the life of the individual. The basic troop structure of this species is matrifocal (mother-focused) and matrilineal. Breeding in the wild is seasonal, with summer being the peak birth season, after six months gestation. The female is sexually mature by approximately 3 years of old. She will have been completely independent of her mother in terms of feeding and locomotion since the end of her first year, but social adulthood and the responsibilities of raising her own infant do not come for two more years. The first attachment a young infant will form will be to its mother. Initially the infant is able to support its own weight and cling to its mother's fur from birth, in a ventral cling. The emotional content of the bond between mother and infant is very similar in monkeys and humans; it is deep and enduring (Lancaster, 1975). The successful rearing of her own offspring relies on a critical nursing period (~0-6 months) and strict socializing and learning within the group context (Fairbanks and McGuire, 1993).

Studies of mother-infant interactions in vervets demonstrated that juveniles who experience high levels of maternal protectiveness during infancy were more cautious in response to novelty, compared to juveniles who had less protective mothers (Fairbanks, 1993). Adolescent male vervet monkeys that score in the moderate range of impulsivity are more likely to be high ranking in their new groups (Fairbanks, 2001). Measures of monoamine neurotransmitter activity such as low levels of 5-hydroxyindoleacetic acid (5-HIAA), the metabolite of serotonin in cerebrospinal fluid (CSF), are related to earlier age at emigration, higher rates of escalated aggression, higher levels of adolescent mortality, and higher levels of impulsive approach and aggression to an unfamiliar male in captive vervet monkeys (Fairbanks et al., 2001).

Behavioral Science Foundation: The setting for this study

The Caribbean vervet (*Chlorocebus aethiops)* was imported in the 17th century from Western African populations; importation was terminated by about 1650, and stable numbers have been maintained for about 30 generations. Historical evidence suggests that many small groups, rather than a single founder population, were transported from various West African areas. Current estimates of the population ranged from 10,000 to 30,000 individuals three decades ago (Coppinger and McGuire, 1980), and have steadily increased to an estimated 35, 000 individuals today, due to an absence of natural predators. From 1700 to the present, this animal has been considered to be a major agricultural threat, with the local government paying several full-time hunters to control the expanding population.

In 1968, F. R. Ervin established a research base on the island of St. Kitts, and together with a number of colleagues and students, documented the field behavior, distribution and ecology of the resident monkeys. In 1972, land and buildings were leased, enclosures constructed and a basic laboratory was developed. A program was instituted to introduce humane and non-injurious trapping techniques (baited walk-in cages and net trapping, from which monkeys are extracted under ketamine anaesthesia) to replace destructive methods previously used. At the same time, a local staff was developed, many of whom have now worked in the laboratory from more than 15 years. This facility has now been used by a variety of investigators, and students for training, short and long-term projects, thesis studies and research programs. In December 1985, the facility was visited and approved by the Canadian Council for Animal Care. Under current conditions, approximately 400 newly trapped animals are available for study each year.

Husbandry

Babies are born in captivity in the open-air social breeding groups of the Behavioural Sciences Foundation (St. Kitts). In the natal cage, the polygamous breeding groups generally comprise one or two adult males and between six and twelve adult females. Babies typically stay with their mothers until approximately six months, by which age they have already generally been weaned and acquired a certain level of independence. During this time period, in order to provide the most naturalistic

homogenous environment across all animals in this semi-captive colony, animals are rarely disturbed for testing or sampling, except for yearly veterinary inspections.

At approximately 6 months, infants are removed from their birth cages and transferred to an outdoor nursery housing facility. All infants are given a minimum of eight weeks to habituate to their living quarters before being subjected to any behavioral testing. At approximately 1 year of age, infants are placed in social peer groups of 12-15 animals. They typically remain in their peer groups until sexual maturity, after which they are regrouped into polygamous social breeding groups.

Goals and Hypotheses for this project

The goal of this project was to determine the feasibility of deriving interpretable behavioral dimensions, in a semi-captive vervet monkey population, from primary behavioral observations. As reviewed above, previous studies seeking to extract behavioral traits in non-human primate species have used adjective descriptors assigned by experienced behavioral observers after collecting a sample of behavioral observations. This approach is potentially subject to observer bias, and is also difficult to replicate across laboratories. The general question, addressed is: Can interpretable behavioral dimensions be derived, using primary (observational) data (i.e. standard behavioral repertoire already well established in the primatology literature) rather than interpretations (adjective checklists) of those observations? Using a research plan developed for this purpose, I asked the following specific questions: (i) Can interpretable behavioral dimensions be derived using primary (observational) data in a social group context? (ii) Can interpretable behavioral dimensions be derived using primary (observational) data in a novelty test paradigm during late infancy? (iii) Can interpretable behavioral dimensions be derived using primary (observational) data in a novelty test paradigm during adolescence? (iv) If, interpretable behavioral traits can be derived using this specific methodological approach, will they resemble (at least at a conceptual level) behavioral dimensions reported among other research groups? (v) To what extent are those dimensions stable across time? In this particular instance, will the traits identified during adolescent novelty testing be conceptually similar to those identified in the nursery testing paradigm?

Once the interpretable behavioral dimensions are successfully derived, an ultimate goal using this approach is: to consider individuals who score at the extremes of the distribution, as well as those who fall more in the middle range, and speculate about their future potential psychopathology.

Design of the project

This longitudinal project included four successive birth cohorts, comprising 224 captive vervet or African green monkeys (*C. aethiops*). The experimental paradigm was designed with the intention of collecting multiple types of behavioral data over the first three years of life, so as to maximize the amount and kinds of information available for individual animals. Three segments of the study will be presented in this thesis: (i) duplicate responses to a novel testing environment during nursery housing (approximately 13-16 months of age), (ii) repeated social behavioral measures in the juvenile peer cage (18 – 36 months of age) and (iii) duplicate response to a different novel testing environment during the juvenile period (approximately 30 months of age). The novelty tests, which will be described in detail in the following chapters, were designed to match the monkey's size and level of development at the planned time of administration.

In the social context, behavioral data was collected by an observer according to the 5 minute focal animal approach described by Altmann (1974); and prior to the initiation of the study, inter-rater reliability exercises were conducted by an experienced trainer to a criterion of $\kappa > 0.95$. The standard species-appropriate behavioral repertoire was used and the description of the behaviors is consensually operationalized. The presentation of the behavior (i.e. whether it was initiated, received or solitary), the specific behavior and the interacting monkey were recorded at 10 second intervals for the entire bout. In the two novelty testing situations, behavioral data was collected using a modified version of the focal animal approach described by Altmann (1974). In this context (1) the time period was changed, with a total of 15 minutes in the nursery test, 10 minutes in the jungle gym, instead of the 5 minutes mentioned above; and (2) as a result of the individual testing of the monkeys, the social behaviors towards other monkeys were excluded (e.g., receive a groom, or rough and tumble play), and other behaviors

(more specifically related to the testing situation) were added, (e.g., finding a reward, or catatonic fear). At every 10 second intervals, the subjects were scored on their spatial location, the specific behavior, and their physical location in the testing cage. The main analytic plan we chose to use for the analyses of our data sets, was the multivariate statistical procedure called factor analysis. The behavioral data was subjected to a factor analysis, summarizing a matrix of correlations among variables (i.e. behaviors) and thus deriving a limited number of interpretable factors (i.e. behavioral dimensions). In order to enrich our newly derived behavioral dimensions, we also collected subsidiary data at different time points. During the social juvenile paradigm we collected; activity measures (i.e. average motility during each bout), states of arousal at the beginning and at the end of each bout, willingness to approach the observer (i.e. 'eye level'), social rank, individual marginal notes (i.e. descriptive adjectives), and cerebrospinal fluid amine levels. The statistical approach we used to find a possible relationship between orthogonal factor scores for individual monkeys and these above mentioned quantitative measures were evaluated by ANOVA or linear regression analysis, as appropriate. We also looked at the relationship between these orthogonal factor scores and likely covariates such as gender, age and cohort. During the novelty tests we collected; activity measures, rewards obtained, space covered, threshold to enter the main compartment (but only in the jungle gym), individual marginal notes and cerebrospinal fluid amine levels. The possible correlations between the orthogonal factors and likely covariates (gender, age) or the other quantitative measures were evaluated by ANCOVA and stepwise linear regression analysis, respectively.

REFERENCES

Altmann J (1974). Observational study of behavior: sampling methods. Behavior 49: 227-267.

Boxer, C.R.: (1969). "The Portuguese seaborne empire" 1415-1825 (Knopf, New York).

Burdon, C.R. (1920). "A handbook of St.Kitts and Nevis (The West Indian Committee, London).

Cheney, D.L., and Seyfarth, R.M. (1990). "How Monkeys See the World." The University of Chicago Press, Ltd. London.

Coppinger, R.P., & Maguire, J.P. (1980). "Cercopithecus aethiops of St.Kitts: A population estimate based on human predation." Caribbean Journal of Science 15: 1-7.

Fagan, R., (1981). "Animal Play Behavior." New York: Oxford University Press.

Fairbanks, L.A., & M.T. McGuire. (1985). "Relationships of vervet monekey mothers with sons ans daughters from one through three years of age." Animal Behavior 33: 40-50.

Fairbanks, L.A. (1993). "Risk-taking by juvenile vervet monkeys." Behaviour 124(1-2): 57-72.

Fairbanks, L.A. and McGuire, M.T. (1993). "Maternal protectiveness and responses to the unfamiliar in vervet monkeys." American Journal of Primatology 30: 119-129.

Fairbanks, L.A., Melaga, W.P., Jorgensen, M.J., Kaplan, J.R., & McGuire, M.T. (2001). "Social impulsivity inversely associated with CSF 5-HIAA and fluoxetine exposure in vervet monkeys." Neuropharmacology 24(4): 370-378.

Fedigan, L.M., (1982). "Primate Paradigms: Sex Roles and Social Bonds." Eden Press Inc. Montreal, Quebec, Canada.

Hall, K.R.L., & Gartlan, J.S. (1965). "Ecology and behavior of the vervet monkey." Cercopithecus aethiops, Lolui Island, Lake Victoria. Proc. Zool. Soc., London. 145: 37-56.

Labat, J.B. (1722). "Nouveau voyage aux iles de l'Amerique." Paris.

Lancaster, J.B., (1975). "Primate Behavior and the Emergence of Human Culture." New York. Holt, Rinehart &Winston.

Lee, P.C., (1983). "Play as a means for developing relationships." In: Primate Social Relationships (Ed. By R.A. Hinde). Pp.82-89. Sunderland, Mass.: Sinauer.

McGuire MT (1974) "The St.Kitts vervet." In: Monographs in primatology, Karger, Basel Merrill, G.C.,: The historical geography of St. Kitts and Nevis, the West Indies (Instituto Panamericano de Geografia e Historia, Mexico 1958).

Merrill, G.C. (1958). "The historical geography of St.Kitts and Nevis, the West Indies." Instituto Panamericano de Geografia e Historia, Mexico.

Palmour, RM., Mulligan, J., Howbert, JJ, and Ervin, F. (1997). Insights From Model Systems; Of monkeys and men: vervets and the genetics of human-like behaviors. American Journal of Human Genetics 61: 481-488.

Richman, I.B. (1920): "The Spanish conquerors." (Yale University Press, New Haven.)

Seyfarth, R.M. (1977). "A model of social grooming among adult female monkeys." Journal of Theoretical Biology 65: 671-698.

Simmonds, P., (1974). "The Social Primates." New York: Harper and Row.

Struhsaker, T.T.: (1967a). "Behavior of vervet monkeys." (*Cercopithecus aethiops).* University of Calififfornia, Publ. Zool. 82: 1-74.

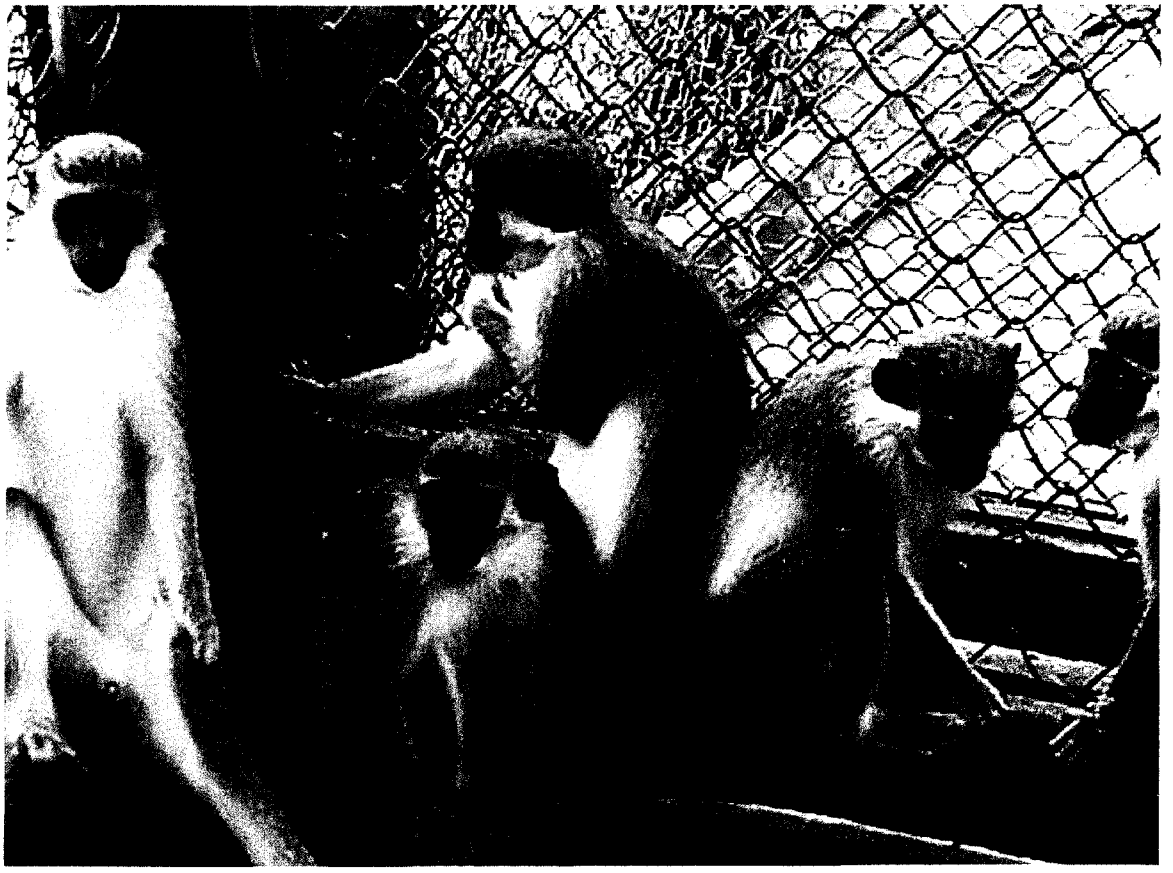
Struhsaker, T.T. (1967b). "Behavior of vervet monkeys and other cercopithecines." Science 156: 1197-1203.

Thornton, A.P. (1955)."The organization of the slave trade in the English west indies 1660-1685." The William and Mary Quarterly. Pp. 399-409.

CHAPTER III

BEHAVIORAL TRAITS IN VERVET MONKEYS:

I. SOCIAL GROUP DURING ADOLESCENCE



BEHAVIORAL TRAITS IN VERVET MONKEYS: I. SOCIAL GROUP BEHAVIOR DURING ADOLESCENCE

Caroline Desbiolles[1], Frank R. Ervin[2,4], Simon N. Young[2], Chantal Mérette[5] and Roberta M. Palmour[1,2,3,4]

[1] Departments of Biology, [2]Psychiatry & [3]Human Genetics, McGill University, Montréal, Québec, Canada; [4]Behavioural Science Foundation, St Kitts, Eastern Caribbean; [5]Centre de recherche université Laval Robert-Giffard, Beauport Québec Canada

Address for correspondence:
Roberta M. Palmour, PhD
Department of Psychiatry
McGill University
1033 Pine Ave West, #326
Montreal Qué H3A 1A1
CANADA
TEL: 514-398-7303 FAX: 514-398-4370
e-mail: roberta.palmour@mcgill.ca

Running title: Behavioral traits in adolescent vervet monkeys

Supported by grants from the Canadian Institutes of Health Research (MT-14526 to RMP, FRE; MOP-15005 to SNY) and generous in-kind support from Behavioural Sciences Foundation, St Kitts

The break down of the contributions for the three papers included in the thesis were made by the following authors:

The studies were designed in collaboration by Caroline Desbiolles, Dr. Roberta Palmour and Dr. Frank Ervin.

The statistical analysis was supervised by Chantale Mérette.

The CSF analysis was done by Dr. Simon Young.

All authors helped in the interpretation of the results.

Caroline Desbiolles and Dr. Roberta Palmour wrote the final manuscripts, which were revised by Dr. Frank Ervin and the other authors.

ABSTRACT

The definition of non-human primate behavioral traits, particularly those which might relate to models of psychopathology, is increasingly topical. This is the first of several communications describing longitudinal behavioral studies in four successive birth cohorts of African green (or vervet) monkeys (*Chlorocebus aethiops*) resident in a captive breeding colony on the island of St Kitts (Eastern Caribbean). All subjects born between January, 1996 and December, 1999 were observed in a social context, using the focal animal method. In contrast to other studies reported in non-human primates, we derived behavioral factors directly from observed behaviors rather than assigning descriptive adjectives on the basis of multiple behavioral observations. Five interpretable factors, with Eigenvalues > 1.3 and accounting for 54.7% of the variance, were extracted. These factors, in order of decreasing proportional variance, were interpreted as "agonism," "energetic sociability," "agreeableness," "playfulness" and "behavioral inhibition." The first two factors show a negative relationship with age, while the remaining factors are positively correlated with age. Males scored higher on "playfulness," while females had higher scores for "energetic sociability" and "agreeableness." Motor activity was positively correlated with "agonism" and negatively correlated with "behavioral inhibition." Monkeys which scored highly for "agonism" had significantly higher social rank, while those which scored highly for "behavioral inhibition" had significantly lower rank. Cerebrospinal fluid levels of the serotonin metabolite 5-HIAA were negatively correlated with Factor 3, "agreeableness," and levels of the norepinephrine metabolite MHPG were negatively correlated with Factor 5, "behavioral inhibition." This factor solution is highly coherent with other solutions identified in human and non-human primates, and supports the hypothesis that meaningful behavioral traits can be derived directly from observed behavior.

INTRODUCTION

The rapid expansion of genomic tools has motivated an increased interest in defining behavioral phenotypes in experimental animals, with particular emphasis on models that can be directly manipulated to test hypotheses concerning human psychopathology. To be useful, these surrogates would ideally have a complex repertoire of behavior, a significant variety of social interactions and a prolonged dependency period for learning, during which time hardwired inborn behavioral responses can be modified. These desiderata apply most cogently to non-human primates in a social group setting.

One of the goals of our group is to identify naturally occurring behavioral phenotypes that can be used subsequently in studies of abnormal behavior and brain/behavior associations. (eg., Ervin et al., 1990; Palmour et al., 1997). While it is relatively straightforward to define behavioral extremes in adult animals, the extent to which phenotypes can be defined at earlier stages of development remains to be examined. This paper reports progress toward defining developmentally relevant dimensional traits in a pedigreed colony of the non-endangered vervet monkey (*Chlorocebus aethiops).*

In the human being, personality and temperament can be conceived as different domains through which behavioral traits are expressed. Hippocrates defined four distinct personality types (sanguine, melancholic, choleric and phlegmatic) with a focus on the bodily fluids or "humors" of the individual. Modern personality theorists have used self-report questionnaires and factor analysis to arrive at conclusions, which are, in some ways, quite consistent with these classical observations. Although there continues to be vigorous argument about the number of traits which best account for human personality, most experts (Costa and McCrae, 1995; Eysenck, 1979, 1984; Livesley et al., 1992, 1998; McCrae and Costa, 1985, 1997) agree that personality is hierarchically organized and that a few domains (extraversion, surgency or positive emotionality; neuroticism, harm avoidance or negative emotionality; sociability, reward dependence or agreeableness) are fundamental.

The notion that one ought to be able to define behavioral dimensions in non-human primates is not new. In one of the earliest studies (Stevenson-Hinde and Zunz, 1978), observers familiar with the behavior of individual animals used a predetermined list of descriptive adjectives with Likert scores (3-7 point scales) assigned for each adjective. Subsequent multivariate analysis yielded a small number of interpretable factors that were postulated to

represent personality dimensions. Others have applied similar paradigms to studies of chimpanzees (King and Figueroda, 1997), rhesus macaques (Capitanio, 1999 and new paper) and vervet monkeys (McGuire et al., 1994). Although each of these studies produced interpretable dimensions of personality, the relatively small sample sizes, the range of individual ages and the potential subjectivity of the measures left many questions unanswered. In addition to evaluating the possibility of defining behavioral traits at an early age, we were interested in determining the feasibility of extracting traits from primary behavioral measures with operationalized definitions and a high degree of inter-observer reliability. If behavioral traits could be extracted directly from primary behavioral measures, it would improve the ability to replicate and extend this type of study across different research groups and species.

Thus the goal of this research was to initiate longitudinal behavioral studies in juvenile and adolescent vervet monkeys, using both normative social behavior and response to challenge situations and evaluate the extent to which behavioral traits could be extracted directly from these observations. The focus was on the behavior of the individual, rather than the social structure of the group. A secondary objective was to evaluate the extent to which trait dimensions, if they could be extracted, were related to cerebrospinal levels of the principal metabolites of serotonin, dopamine and norepinephrine.

METHODS

Animal Subjects

Four successive birth cohorts (March 1996 – February 1999) of vervet or African green monkeys were observed. All infants were born in captivity in the open-air social breeding groups of the Behavioral Sciences Foundation (St. Kitts) colony and lived in natal groups for 8-12 months. The 105 female and 101 male juveniles reported here lived in a nursery for several additional months before moving into juvenile peer groups with a maximum of 8 monkeys per enclosure. Transition from the birth cage to the nursery was done order to protect the infants from illness, while their own immune system has matured. Each group was given a minimum of 10 weeks to habituate to their peers and surroundings before observations began. Purina Primate Chow was supplied once a day (feeding time was 11 am) and fresh water was available *ad libitum*. Local produce supplemented their diet several times weekly. Housing and sanitary conditions met all guidelines of the Canadian Council on Animal Care and the USDA (Fish and

Wildlife). All study protocols were reviewed and approved by the McGill University Animal Care Committee, as well as a local St Kitts Institutional Review Board instructed by the CCAC.

Behavioral Observation

Behavioral data was collected by one of the investigators (CD) according to 5 minute focal procedures described by Altmann (1974). Prior to the initiation of the study, inter-rater reliability exercises were conducted by an experienced trainer to a criterion of $\kappa > 0.95$. The standard species-appropriate behavioral repertoire is used by many groups (eg., Chamberlain et al., 1987; Fairbanks, 2001; Raleigh et al., 1991) and the description of the behaviors is consensually operationalized. The presentation of the behavior (i.e., initiated, received or solitary), the specific behavior and the interacting monkey were recorded at 10 second intervals for the entire bout.

Behavioral testing sessions were collected for each group in two waves, the first occurring between 2.5 and 5 months after group formation, and the second beginning 3-4 months later. Each animal was observed for a minimum of 10 five-minute bouts across each period of data collection. Although the initial goal of this project was to complete social group observations by the end of the third year of life, this was not always possible due to the occurrence of a severe hurricane (1998) approximately 20 months into the study, as well as two less damaging hurricanes in the following year (1999). The observer was situated in a chair placed approximately 3 feet in front of the enclosures. All animals were familiar with the observer from prior exposure during social observation in their natal cages as well as two trials of individual testing during nursery housing (Desbiolles et al., in preparation). Observations occurred during peak activity times (between 7 - 10 am or 3 - 5 pm).

Additional quantitative measures collected for each bout included average motility, willingness to approach the observer ('eye level') and social rank. Motility was scored by estimating imaginary subdivisions of the cage: top vs middle vs bottom, front vs middle vs back and left vs middle vs right. One 'motility point' was counted any time the focal animal crossed from one of the 27 "virtual" compartments into another, throughout the 5 minute bout. For example, if a monkey walks straight across the front or back of the cage once during a bout, the total motility score would be 2. If the monkey explored the entire cage in multiple directions, the score could reach 30. If the animal paced at the bottom of the cage, the score in some instances

could exceed 100 points.Willingness to approach the observer was taken to be the number of times a monkey approached the observer on the ground and at eye level. 'Eye level' was scored as present when monkeys walked up to the front of the cage and climbed the mesh wire to face the observer at eye level. These measures were summed each bout, and averaged for each animal across the period of behavioral observation.

Social rank was estimated on the basis of success in retrieving pieces of banana or other preferred fruit during a 5 minute bout in which 30 pieces of fruit were offered to the cage. During 20 such bouts, two observers (trained to an interrater criterion of 0.98) ranked each animal on a 3 point scale (1 high, 2 intermediate and 3 low) based on the number of threats and displacements initiated and received by individual animals along with their success in obtaining fruit. These rankings were averaged for each animal across the study period.

Qualitative measures

Qualitative information on each monkey was collected in parallel with focal animal scoring by assigning appropriate descriptive adjectives, such as those summarized below. Attention was given to the characteristic activities of an individual animals, the demeanor of the individual (which might vary from day to day) and the manner in which specific activities were conducted: eg., moves confidently, plays aggressively. To minimize recall bias, these descriptors were filed at the end of each test session and were not summarized or evaluated until all focal animal testing for the given individual had been completed.

Cerebrospinal fluid Amine Metabolites

Under ketamine anaesthesia (10 mg/kg, im), 0.5 ml cerebrospinal fluid (CSF) was collected by transcutaneous cisternal puncture at the time each animal was moved from the nursery into the social group cage. Samples were frozen immediately on dry ice, and stored at -70°C until analysis. Amine neurotransmitter precursors (tryptophan) and metabolites (5HIAA: 5-hydroxyindoleacetic acid; HVA: homovanillic acid; MHPG: 3-methyoxy-4-hydroxyphenylethylene glycol) were determined by HPLC with electrochemical detection (Anderson et al., 1979; Anderson et al., 1980), as described previously for this species (Palmour et al., 1998; Young and Ervin, 1989).

Analysis of Data

Behavioral traits were derived by factor analysis of the aggregated focal behavior. In preliminary analyses, behaviors which occurred with an overall frequency below 0.05% (follow, vocalize, pull tail, hit) were excluded, as were received behaviors (eg., being groomed). Behavioral frequencies were then renormalized to provide a constant sum of 600 for each individual animal. Certain relatively uncommon, but highly correlated, behaviors were combined (eg., pick and forage). Orthogonal factors were then extracted by factor analysis with varimax rotation (StatView V, Systat). Possible correlations (i) between the orthogonal factor scores for individual monkeys and likely covariates such as gender, age or cohort, and (ii) between factor scores for individual monkeys and other quantitative measures such as bananas eaten during the determination of social rank and proximity to the observer were evaluated by ANOVA or linear regression analysis, as appropriate.

RESULTS

Factor solution and interpretation

Factor analysis of the scored behaviors (20 bouts for each of 206 monkeys) yielded a 5-factor solution (eigenvalues >1), accounting for 54.7% of the variance ($\chi^2 = 1629$, $p < .0001$). An examination of the scree plots for 4-, 5- and 6-factor solutions also suggested that a 5-factor solution was optimal. Factor scores were constructed using the full continuum of behaviors. The behaviors loading on each factor are detailed in Table 1. Climbing, leaping, watching and threatening the observer load heavily on Factor 1. Because the behaviors which load on this factor are related to occupying a dominant position ('climb') and holding off intruders ('threaten observer'), it is termed "agonism." Behaviors characteristic of activity and interaction ('move horizontally', 'sit near', 'muzzling', 'eat and forage') load positively on Factor 2; pacing and flipping load negatively on this factor. This factor was interpreted to be "energetic sociability." 'Groom,' 'play with object' and 'oral and manual exploration' load heavily on Factor 3, with a weaker loading for 'pace' and 'flip.' 'Look around' loads negatively on this factor. Because of the importance of grooming in vervet social behavior, and because grooming loaded more heavily on this factor than any other, it was called "agreeableness." Factor 4 ("playfulness") comprises play behaviors, including 'chase', 'play fight' and 'self play', as well as secondary loadings for 'oral and manual exploration.' 'Scratch', 'fidget' and 'stare ahead' load heavily on

Factor 5. 'Oral and manual exploration' load weakly on Factor 5, while 'threat' and 'displacement' load negatively. We have interpreted Factor 5 to reflect the construct of "behavioral inhibition."

Relationship of factors to cohort, age and gender

None of the factors was significantly related to birth cohort, but all showed some relationship to age. Factors 1 and 2 were negatively related to age (Factor 1: $r = -0.18$, $p<0.01$; Factor 2: $r = -0.25 = 14.02$, $p<0.001$), while the remaining factors showed a positive relationship with age (Factor 3: $r = 0.48 = 60.44$, $p<0.0001$; Factor 4 : $r = 0.25 = 14.09$, $p<0.001$; Factor 5: $r = 0.39$, $p<0.0001$). The relationship between Factor 3 and age (Figure 1A) was of particular interest, as it illustrates quite clearly the emergence of grooming (a prototypical adult female behavior) around the time of postulated menarche (≈36 months of age in vervet females).

An analysis of variance revealed a significant gender effect for Factors 2, 3 and 4 (Figure 1B). Females displayed significantly higher scores on "energetic sociability" (Factor 2: $F_{1,204} = 18.07$, $p<0.0001$) and "agreeableness" (Factor 3: $F_{1,204} = 4.33$, $p<0.05$) than males. The behavior sit near/muzzle loads on Factor 2 and groom loaded on Factor 3. These differences are entirely consistent with repeatedly demonstrated sex-specific behavioral differences in primates of every species. By contrast, males displayed significantly higher scores for factor 4 ($F_{1,204} = 13.20$, $p<0.001$), consistent with the well-replicated observation that juvenile vervet males are much more playful than juvenile females (Raleigh and Ervin, 1976; Meaney, 1989; Fagen, 1993). Neither Factor 1 nor Factor 5 varied by gender.

Relationship of factors to other quantitative behavioral measures

In order to enrich our interpretation of the factors, we also examined the relationships between each factor and other quantitative measures. These measures, which were collected separately from the focal animal scoring, included average motility, proximity to the observer ('eye level') and social rank, as described above.

Linear regression analysis showed that Factor 1 ("agonism") was positively correlated ($r = 0.15$, $p<0.02$) with willingness to approach the observer ('eye level') and with rank ($r = 0.12$, $p<0.05$). Monkeys with high scores on Factor 1 had higher rankings in the social hierarchy.

After controlling average motility for pacing, this measure was positively related to Factor 1 ($r = 0.30$, $p<0.0001$), in keeping with the extreme types of physical activity ('climb', 'leap') which loaded on this trait. We also found a positive correlation between 'eye level' and Factor 2, "energetic sociability" ($r = 0.22$, $p<0.002$), as well as a more modest positive correlation between this trait and average motility ($r = 0.18$, $p<0.01$).

None of the quantitative measures were related to Factor 3, "agreeableness," but average motility was again weakly correlated ($r = 0.17$, $p = 0.01$) with Factor 4, "playfulness."

Both rank ($r = -0.16$, $p<0.01$) and average motility ($r = -0.26$, $p = 0.0002$) were negatively correlated with Factor 5. Thus behaviorally inhibited monkeys were both lower in the social hierarchy (on average) and relatively immobile, as compared to monkeys with average or low scores on this trait. The face plausibility of these relationships is obvious.

Qualitative exploration of behavioral traits

Qualitative behavioral information, collected as described in Methods, was used to complement understanding of the extracted behavioral traits.

Agonism (Factor 1): Monkeys scoring high on this dimension ($n = 30$) were attentive to everything and exhibited a very high level of energy, as demonstrated by their propensity to climb and leap along the sides of the cage. Despite their willingness to approach the observer, these animals never really habituated to the presence of the observer, and almost always occupied the highest perch in the cage. Factor 1 scores were inversely correlated with total social interaction ($r = 0.27$, $p < 0.0001$), estimated as the sum of groom, sit near, muzzle and play behaviors. Qualitatively the demeanor of animals which scored 1.5 SD above the mean for Factor 1 was fearless, bold and attentive. Monkeys scoring low on this dimension paid little or no attention to the observer and varied from being task oriented to simply "taking it easy."

Energetic sociability (Factor 2): Monkeys scoring high on this dimension ($n = 34$) were often located on the floor of the cage and appeared to be nonchalant in their demeanor, but were typically described as inquisitive, intelligent or curious. They moved purposefully and calmly, and spend much of their time engaged in social interactions (sit nears and muzzles). Individuals with low scores on Factor 2 had high levels of nervous locomotion, with frequent pacing or flipping. Hence they were still very energetic, but in a non-social context. These animals showed marked variations in behavior: one moment they would be pacing vigorously across the cage and

the next moment they would be still. Many had a hyperactive, even stereotypic demeanor and tended to either perseverate or isolate themselves.

Agreeableness (Factor 3): Monkeys scoring high on this dimension (n = 27) quietly explored their environment ('oral/manual explore,' 'play with object') and actively sought social activity, as illustrated by the positive loading of 'groom.' Physically, theywere less purposeful than those with high scores on Factor 2. Their main focus remained inside the group: they did not react much to the observer or to activities taking place outside of the cage. Animals at the positive pole of this dimension form the core of any well-regulated social group for the species. Animals at the negative end of this trait tended to be socially disengaged, physically inactive and considerably more vigilant to the outside (as documented by the high negative loading on 'look around'). Such individuals may also perform a useful social function, as they would be the most likely to perceive a threat to the group.

Playfulness (Factor 4): Monkeys scoring high on this dimension (n = 21) were characteristically unafraid, bold, fearless or even cheeky. Those which score negatively on this dimension not only seemed to play very little, but also displayed low motility. However, they were not necessarily asocial: although the mean level of social activity was low at this end of the distribution, some animals showed high counts for 'sit near' or 'groom.' Instead of spending a lot of energy engaged in play chases and rough and tumble play, they were sociable in a calm manner.

Behaviorally inhibited (Factor 5): Monkeys scoring high on this dimension (n = 33) typically appeared to be uncomfortable in their own skin (i.e. slouched postures, apologetic manner of moving). In extreme cases, these animals were found crouched in a bottom corner of the cage. Monkeys scoring low on this dimension displayed nervous energy channeled into agitation, rather than inhibition. Animals at both ends of this dimension showed low levels of social interaction, as defined above.

Relationship of factors to CSF amine metabolites

Because of extensive and well-documented (Young and Ervin, 1984; Ågren et al., 1986) intercorrelations beween 5-HIAA and HVA and MHPG (the major CSF metabolites of serotonin, dopamine and norepinephrine, respectively), the relation between CSF amine metabolites to dimensional social factors was investigated through multiple regression analysis. The average

age at which CSF was sampled from the 206 monkeys was 28.3 ± 6.3 months. There were no effects of gender at this developmental time period, but 5-HIAA varied according to age ($F_{1,203}$ = 7.73, p = 0.006). The residuals were computed and age-adjusted values were used in all further analyses. In the present study, the partial pairwise correlations were 5-HIAA/HVA = 0.567, 5-HIAA/MHPG = 0.091, HVA/MHPG = 0.070).

Multiple regression analysis showed that the level of 5-HIAA was negatively correlated with Factor 3 ($F_{1,204}$ = 7.93, p = 0.005), while the level of MHPG was negatively correlated with Factor 5 ($F_{1,204}$) = 14.1, p = 0.0002). Thus monkeys with higher factor scores for Factor 3 had lower CSF levels of 5-HIAA (Figure 2A), and those with higher factor scores for Factor 5 had lower CSF levels of MHPG (Figure 2B). However, in no case were these relationships of large magnitude (partial correlations: 5-HIAA and Factor 3: -0.158; MHPG and Factor 5: -0.254). Levels of amine metabolites were not significantly related to any other factor.

DISCUSSION

We conducted repeated observations of 206 vervet monkeys comprising four successive birth cohorts and found that five trait dimensions accounted for 54.7% of the proportional variance. The five extracted dimensions were interpreted as reflecting the traits: "agonism," "energetic sociability," "agreeableness," "playfulness," and "behaviorally inhibited." These traits are isomorphic with those identified by other investigators in this and similar species, as discussed further below. However, to our knowledge, this is the first demonstration that behavioral traits can be extracted from primary observational data, rather than from a list of descriptors generated by observers familiar with the behavior of individual animals.

Because we were interested in the overall structure of personality in this species, we used factor analysis rather than cluster analysis, but this is not to suggest that a cluster analysis might not also be instructive. One attractive feature of factor analysis is the fact that each animal is placed on a continuum for every trait, improving the potential for making longitudinal comparisons. As is always the case, some arbitrary decisions had to be made; for example, the rotational scheme was chosen to optimize orthogonality, and the final number of factors reflects meaningful interpretation as well as statistical criteria. The use of full birth cohorts was intended to minimize selection bias as well as to provide a suitable ratio of subjects-to-variables (12:1 in

the present analysis). Other methodological choices included regular inter-rater reliability studies to ensure stability of scoring (Marteau et al., 1985) and a scoring system derived from classical primatological inquiries (Altmann, 1974; Chamberlain et al., 1987) that leaves little room for subjectivity. The consistency of rearing and housing conditions also might improve the ability to identify inherent (rather than environmentally influenced) individual variability.

In conducting this analysis, we combined the information for 20 observational bouts per animal, with each animal being observed in two relatively intense blocks at least 6 months apart. While this approach may improve the robustness of our solution, it obliterates the opportunity to evaluate developmental behavioral trajectories. Although further detailed analysis is clearly in order, a split sample comparison between the first 10 and the last 10 observations for each individual yielded factor structures with identical trait loadings, but somewhat different trait orders (data not shown).

Behavioral traits in non-human primate species

The specific dimensions identified by representative studies of personality traits in non-human primate species are summarized in Table 2. Not surprisingly, various traits related to sociability are central to primate group behavior. In the present analysis, the distinction between "sociability" (Factor 2) and "agreeableness" (Factor 3) was unanticipated, but is highly robust, emerging in exploratory analysis of the full sample split by early (first 10) vs late (last 10) observations, and also in sensitivity analyses that sequentially remove individual birth cohorts from the dataset prior to factor analysis. A similar distinction (sociable vs. equable) is reported by Capitanio (1999) in macaques, and is suggested by the split between extraversion and understanding in Gold and Maple's (1994) analysis. It is also noteworthy that the negative pole of "energetic sociability" is not necessarily just "solitary," as it appears to be in the solutions of Chamove et al. (1972) and Stevenson-Hinde and Zunz (1978). Instead, animals with low trait scores for "energetic sociability" are hyperactive, excitable and eccentric (the positive end of Stevenson-Hinde and Zunz's active-to-slow dimension), resembling Capitanio's (1999) trait termed "excitable." That being said, animals at the negative ends of all three dimensions which reflect sociability (Factors 2, 3 and 4) exhibit low levels of social interaction and thus by definition are relatively solitary.

Despite the fact that play in non-human primates is a frequent behavior only during the juvenile developmental stage, play contributes to the dimensional structure in many different analyses, but is often subsumed under a more general dimension--affiliative, sociable, extraverted, playful-curious (Capitanio, 1999; Chamove, 1972; Gold and Maple, 1994; King et al., 1997; McGuire et al., 1994; Stevenson-Hinde and Zunz, 1978). In both our study and those of many others, rates of play are higher in males than in females, particularly with respect to rough-and-tumble forms (Fagen, 1993; Meaney, 1989; Raleigh and Ervin, 1976; Symons, 1978). While it is undeniable that Factor 4 ("playfulness") represents positive activity and agonism, it is not apparent how animals high in Factor 4 will differ from those high in Factors 2 and 3 when they are adults.

Historically, the best validated behavioral dimension in non-human primates is that of fearfulness or behavioral inhibition, perhaps most effectively characterized as "up-tight" (Schneider and Suomi, 1992; Suomi, 1986, 1991). However, the conceptualization of the dimensions varies significantly between studies, such that those behaviors which define fearfulness often load negatively on a dimension termed confident-to-fearful or simply confident (Capitanio, 1999; Stevenson-Hinde and Zunz, 1978). In terms both of the structure of the behavior and the conceptualization of the dimension, the dimension "tense/insecure" from the Bolig et al. (1992) study in macaques is most congruent with Factor 5 in the present report. Surprisingly, in the other published study of vervet monkeys (McGuire et al., 1994), the descriptive adjective 'fearful' loaded positively on two dimensions which were interpreted to represent "curious/playful" and "opportunistic."

The factor "agonism" is the most difficult to align with factor solutions reported elsewhere, but is coherent in part with Chamove's (1972) dimension of "hostility," which includes non-contact aggressive behaviors such as threaten and displace. In all other reports, behaviors which load on this dimension are split between two or more factors: dominant and extravert (Gold and Maple, 1994); aggressive and confident (Bolig et al., 1992); confident and active (Stevenson-Hinde and Zunz, 1978); confident and excitable (Capitanio, 1999). As noted above, animals with high trait scores for "agonism" have higher social rank and are more likely to be dominant as adults. Rather than forming an independent trait, behaviors characterizing animals at the positive end of the "agonism" dimension were distributed between three factors in the only other published trait study of vervet monkeys (McGuire et al., 1994).

Primate behavioral traits and human personality

The dimensions revealed in the present study are highly reminiscent of constructs well established in the literature concerning human personality traits. As noted above, convergent evidence is strongest for the primate trait of fearfulness or behavioral inhibition, and according to many experts, the same is true for the human construct of neuroticism, negative affect or harm avoidance (Cloninger, 1993; Costa and McCrae, 1992; Eysenck, 1991; Livesley et al., 1998; Rothbart and Ahadi, 1994). In addition to being highly heritable (Fulker, 1981; Hershberger et al., 1995; Weiss et al., 2000) and temporally stable throughout development (Costa and McCrae, 1994), behavioral inhibition is also readily observed in a wide range of animal species (Gosling, 1999) and at least some expressions of fearfulness have been genetically mapped in humans (Cloninger et al., 1998; Smoller et al., 2003), rodents (Turri et all, 1999) and fruit flies (Leal and Neckemeyer, 2002). It is trivial to relate the vervet trait of "behavioral inhibition" to the avoidant aspects of negative emotionality, but rather more challenging to encompass other aspects of the human factor. Given that human beings who score highly on this dimension have a tendency to perceive or react to the world as threatening, irritating, or punishing, then those aspects of Factor 1 ("agonism") which reflect defensive aggression may also be related to a superfactor of emotional instability (Livesley et al., 1998) or harm avoidance (Cloninger, 1993).

A dimension which includes positive activity, positive affect and agonism is also universally identified, regardless of whether it is termed Extraversion, Surgency or Novelty Seeking (Cloninger, 1993; Costa and McCrae, 1992; Eysenck, 1979; Goldberg, 1992; Tellegren, 1985). The relationship between these constructs and primate traits of positive emotionality are obvious, although rather more complex. In the present study, the traits "energetic sociability" and "playfulness" clearly encompass alternate aspects of both positive activity and social interaction, while "agreeableness" describes an animal with lower physical energy and a more passive style of reacting. Although conceptually overlapping, these traits do not show any statistical intercorrelations. The same distinction between Agreeableness and Surgency is explicit in the Costa and McCrae (1992, 1995) Five-Factor solution.

Psychoticism, as originally postulated by Eysenck (1979), has been extensively questioned and revised, but core aspects are clearly identified in several contemporary factor analyses. Among these, a factor termed "dissocial behavior" and observed in both clinical and

population samples (Livesley et al., 1998) is perhaps the most informative. Dissocial behavior reportedly resembles the negative end of Agreeableness in Costa and McCrae's Five-Factor solution, and includes stimulus seeking, callousness, rejection (hostility) and conduct problems. This formulation is conceptually the inverse of Buss and Plomin's (1984) Sociable/Oppositional dimension. In the adolescent vervet, the closest parallel to dissocial or oppositional behavior is seen in the trait "agonism," which is both statistically and conceptually quite distinct from sociability or agreeableness. In the chimpanzee, a behavioral measure of psychopathy was derived from adjective ratings based on observational measures of agonism, sexual activity, volatility of temper and daring behavior (Lilienfeld et al., 1999). The vervet trait "agonism" clearly comprises a degree of hostility and volatility, but there is also a component of defensiveness ('threaten observer') not present in the human or chimpanzee descriptions. The possibility that this tendency might manifest at a later age as volatility or conduct problems remains to be explored.

Relationship between CSF amine metabolites and juvenile social behavior

In the present study, CSF levels of 5-HIAA were negatively correlated with age-adjusted trait scores for Factor 3 ("agreeableness"), while trait scores for Factor 5 ("behaviorally inhibited") were negatively correlated with levels of the norepinephrine metabolite MHPG. Previous clinical studies also found evidence for an inverse relationship of MHPG and negative emotionality. For example, Ballenger et al. (1983) reported a negative correlation of MHPG with trait measures of anxiety and neuroticism in a clinical population, while Post et al. (1984) found a weak relationship between depression and CSF norepinephrine. It may also be the case that behaviorally inhibited animals expose themselves to fewer stressors, resulting in less activation of norepinephrine neurons (Redmond, 1987) and lower turnover of norepinephrine.

The negative correlation of 5-HIAA with "agreeableness" (Factor 3) is less obvious. Experimental elevation of serotonin levels reduces irritability and dysphoric ideation, and in some cases may promote social cooperation. In some studies, there is evidence that animals with low CSF 5-HIAA have low rates of social interaction (Higley et al., 1996), yet monkeys with high scores for Factor 3 are active social participants. There is also substantial evidence of a relation between levels of serotonin and dominance behavior. In vervet monkeys, dominant adult males virtually always have high levels of whole blood serotonin (Dillon et al., 1992;

Raleigh et al., 1991), and a fall in social position is typically accompanied by a reduction in CSF 5-HIAA levels (Raleigh and McGuire, 1991). In normal people, dominance in social relations increased after repeated oral administration of tryptophan, the precursor of serotonin (Moskowitz et al., 2001). The relative lack of motor activity in agreeable animals may also contribute to the negative correlation between Factor 3 scores and CSF 5-HIAA (Jacobs and Fornal, 1995).

Implications for models of psychopathology

Charles Darwin (1872) argued that emotions exist in both human and nonhuman animals, and the similarity between behavioral traits identified in humans and other mammalian species (eg., Gosling, 1999) implicitly validates the development of models for the study of psychopathology. In previous work, we and others have reported primate analogs of psychopathology in atypical adults from large captive populations (Ervin et al., 1990; Insel and Young, 2001; Palmour et al., 1997) or those individuals whose normal social developmental patterns have been disrupted or impaired in some way (Harlow, 1962; Higley et al., 1996; Higley and Suomi, 1989; Kraemer et al., 1989; Schneider and Suomi, 1992; Suomi, 1977, 1981, 1986), but there has been very little attention to the possibility that dimensional traits might contribute to the expression of individual psychopathology.

In human beings, the extent to which personality domains are stable across the lifespan remains contentious (Carmichael and McGue, 1994; Caspi et al., 1995; Chess and Thomas, 1990; Maziade et al., 1990; McCrae et al., 2000; Moskowitz et al., 1985, 1989; Rutter, 1987; Thomas and Chess, 1968), with early studies emphasizing continuity only at the extremes of trait distributions. Recent studies in large, representative populations suggest a moderate degree of dimensional continuity (Caspi, 2000; McCrae et al., 2000; Roberts and DelVecchio, 2000; Robins et al., 2001), but also emphasize developmentally relevant changes both in intensity and presentation (eg., Helson and Kwan, 2000; Roberts et al., 2001). It is quite clear that expressing a specific personality trait does not determine eventual outcome, but there is a substantial degree of specificity between trait and outcome (Caspi, 2000; Caspi et al., 2003; Hirschfeld-Becker et al., 2003). Thus, undercontrolled (impulsive, restless, affectively labile) children in the Dunedin study were significantly more likely to exhibit antisocial personality disorder or alcohol dependence at age 21, while inhibited children were more likely to develop depression (Caspi, 2000).

Arguing from these admittedly fragmentary generalizations, the type of dimensional analysis presented here should help to delineate animals at the extremes of factor distributions which are most vulnerable to the development of psychopathology in response to appropriate challenge. For example, monkeys with high scores on the agonistic trait seem to be particularly susceptible to "paranoid" suspiciousness and hypervigilance as illustrated by always keeping an eye on the observer, looking over his shoulder, not committing to any other normal monkey behaviors because he is so focused on threatening and staring at the observer. Climbing at high levels, in a spread eagle position and staring in a hyper-aroused state at the observer. when challenged with amphetamine or cholecystokinin analogs (personal observations). Those with high scores on "behavioral inhibition" would obviously be vulnerable to social anxiety and perhaps to depression. We have previously reported on the characteristics of animals which have classic panic attacks in response to cholecystokinin-4 (Bradwejn et al., 1992; Palmour et al., 1992). These animals were carefully selected from the population with phenotypes which would have loaded on factor 5 in the present study. The cohorts reported here have now entered adulthood and reproductive responsibility. We will continue to explore the outcome of these developmental trajectories and their applicability to understanding human psychopathology.

Limitations

This study has a number of limitations. First, the solution must be considered to be preliminary until replication. Second, it would be instructive to compare this solution with other statistical methods (such as cluster and trajectory analysis) not selected for this initial analysis. Third, it will be important in future to evaluate the robustness of the present solution in the context of adult social behavior. To our knowledge, this is the first study of behavioral traits in a large sample of exclusively adolescent individuals, but the similarity of the extracted factors to those reported by other investigators in adult or mixed populations is encouraging. What is completely unknown, however, is the extent to which an individual animal's behavioral profile at 3-4 years of age will predict the behavioral profile in adult life. More explicitly, the extent to which the chaotic nature of adolescent behavior is indicative of the individual's normative behavior is also not known, but is highly relevant both to normal and psychopathological personality development.

External factors may also have influenced the outcome of this project in ways which cannot be fully controlled. Chief among these were two periods of severe hurricane weather, in the fall of 1998 and again in the fall of 1999. The most obvious consequence of these events was a delay in completing social group testing, resulting in a broader age range than had been initially planned. However, none of the extracted factors vary by birth cohort and a split sample analysis (youngest half vs oldest half) again produces traits with the same factor loading but different trait orders (data not shown). As noted above, however, several of the factor traits do vary by age, and in at least one case ("agreeableness"), the age at which grooming becomes a predominant behavior can be appreciated visually (Figure 1A).

Sample attrition posed another limitation. To the greatest extent possible, we tried to hold the interindividual environmental variation to a minimum. Thus all animals in the study were fed on exactly the same diet, at the same time of day, and received the same husbandry care. Nonetheless, some animals died or were lost to follow-up at each of the four data collection periods. Occasionally, this was simple misadventure, but more frequently, there was a clear interaction with the behavioral profile of the affected individual. Most typically, anxious and inhibited monkeys fall to the bottom of the social hierarchy in peer groups, and as a result become poorly nourished and more vulnerable to viruses and other infections. In a few cases, injury or death followed episodes of hyperactivity or impulsivity. A clinical summary of such cases may be instructive.

Conclusion

In summary, we show here that interpretable behavioral traits can be derived by factor analysis of standard focal animal observations, and that the extracted traits have a high degree of face plausibility, when compared to previously published studies of personality in human and non-human primates. This study lays the groundwork for several related lines of research. First, it suggests that the same behavioral traits observed in adult animals can be identified in juveniles, thus facilitating the possibility of longitudinal investigations. Second, it provides the basis for evaluating the extent to which the observed traits are heritable. Third, as outlined above, it offers clear basis for testing the types of psychopathology which might be related to extreme representations for each dimension. In addition to informing the development of models of psychopathology based on individual vulnerabilities, these predictions form the basis for testing

hypotheses regarding developmental trajectories for several common disorders, as well as a resource for testing possible interventional strategies.

REFERENCES

Ågren H, Mefford IN, Rudorfer MV, Linnoila M, Potter WZ (1986) Interacting neurotransmitter systems: A non-experimental approach to the 5-HIAA-HVA correlation in human CSF. *J Psychiatr Res* 20: 175-193.

Altmann J (1974) Observational study of behavior: sampling methods. *Behavior* 49: 227-267.

Anderson GM, Young JG, Dohen DJ (1979) Rapid liquid chromatographic determination of tryptophan, tyrosine, 5-hydroxyindole acetic acid and homovanillic acid in cerebrospinal fluid. *J Chromatogr* 164: 501-505.

Anderson GM, Young JG, Cohen DJ, Shaywitz BA, Batter DK (1981) Amperometric determination of 3-methyoxy-4-hydroxyphenylethyleneglycol in human cerebrospinal fluid. *J Chromatogr* 222: 112-115.

Ballenger JC, Post RM, Jimerson DC, Lake CR, Murphy DL, Zuckerman M, Cronin C (1983) Biochemical correlates of personality traits in normals: an exploratory study. *Personality Individ Diff* 4: 615-625.

Bolig R, Price CS, O'Neill PL, Suomi SJ (1992) Subjective assessment of reactivity level and personality traits of rhesus monkeys. *Intl JPrimatol* 13: 287- 306.

Bradwejn J, Kosycki D, Deutre-Decouteaux A, Bourin M, Palmour RM, Ervin FR (1992) The cholecystokinin hypothesis of panic and anxiety disorders: A review. *J Psychopharm* 6: 345-351

*Buirski P, Plutchik R, Kellerman H (1978) Sex differences, dominance, and personality in chimpanzees. *Anim Behav* 26: 123- 129.

Buss AH, Plomin R (1975) *A Temperament Theory of Personality Development.* New York: Wiley-Interscience.

Capitanio JP (1999) Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation. *Am J Primatol* 47: 299- 320.

Capitanio JP (2002) Sociability and responses to video playbacks in adult male rhesus monkeys (Macaca mulatta). *Primates* 43:169-77.

Capitanio, confirmatory factor analysis to add

Carmichael CM, McGue M (1994) A longitudinal family study of personality change and stability. J *Personality* 62:1-20.

Caspi A (2000) The child is father of the man: Personality continuities from childhood to adulthood. *J Personality Soc Psychol* 78: 158-172.

Caspi A, Harrington H, Milne B, Amell JW, Theodore RF, Moffitt TE (2003) Children's behavioral styles at age 3 are linked to their adult personality traits at age 26. *J Personality* 71:495-513.

Caspi A, Hernry B, McGee R O, Moffit T E, Silva PA (1995) Temperamental origin of child and adolescent behavior problems: from age three to age fifteen. *Child Dev.* 66: 55-68.

Chess S, Thomas A (1990) Continuities and discontinuities in temperament. In: Robins L, Rutter M (eds). *Straight and Devious Pathways from Childhood to Adulthood.* New York: Cambridge University Press, pp 205-220.

Cloninger CR, Svrakic DM, Przybeck TR (1993) A psychobiological model of temperament and character. *Arch Gen Psychiatry* 50: 975-990.

Cloninger CR, Van Eerdewegh P, Goate A, Edenberg HJ, Blangero J, Hesselbrock V, Reich T, Nurnberger J Jr, Schuckit M, Porjesz B, Crowe R, Rice JP, Foroud T, Przybeck TR, Almasy L, Bucholz K, Wu W, Shears S, Carr K, Crose C, Willig C, Zhao J, Tischfield JA, Li TK, Conneally PM, et al. (1998) Anxiety proneness linked to epistatic loci in genome scan of human personality traits. *Am J Med Genet* 81:313-7.

Costa PT, Jr., McCrae RR (1992) Four ways five factors are basic. *Personality Individ Diff* 13: 653- 665.

Costa PT, Jr., McCrae RR (1994) Stability and change in personality from adolescence to through adulthood. In CF Halverson, Jr., GA Kohnstamm and RP Martin (eds.) *The Developing Structure of Temperament and Personality from Infancy to Adulthood* (pp. 139-150). Hillsdale, NJ: Lawrence Erlbaum.

Costa PT, Jr, McCrae RR (1995) Domains and facets: Hierarchical personality assessment using the Revised NEO Personality Inventory. *J Personality Assess* 64: 21-50.

Chamberlain B, Ervin F R, Pihl R O, and Young S N. 1987. The effects of raising or lowering tryptophan levels on aggression in vervet monkeys. *Pharmacol Biochem Behav* 28: 510 – 513.

Chamove A S, Eysenck H J, and Harlow H F.1972. Personality in monkeys: factor analysis of rhesus social behavior. *Quart J Exp Psychol* 24: 496 – 504.

Darwin C (1872) *The expression of emotions in man and animals.* Oxford, England: Oxford University Press. (Reprinted in 1998).

Desbiolles C, Ervin FR, Mérette C, Young SN, Palmour RM Behavioral traits in vervet monkeys: II. Response to a novel environment, submitted in parallel

Dillon JE, Raleigh MJ, McGuire MT, Bergin-Pollack D, Yuwiler A (1992) Plasma catecholamines and social behavior in male vervet monkeys (*Cercopithecus aethiops sabaeus*). *Physiol Behav* 973-977.

Ervin FR, Palmour RM, Young SN (1990) Voluntary consumption of beverage alcohol by vervet monkeys: Population screening, descriptive behavior and biochemical measures. *Pharmacol Biochem Behav* 36: 367 - 373.

Eysenck HJ (1979) Personality factors in a random sample of the population. *Psycholog Rep* 44: 1023-1027.

Eysenck HJ (1984) The comparative approach in personality study. *Behav Brain Sci* 7: 440-441.

Eysenck HJ (1991) Dimensions of personality: 16, 5 or 3?--Criteria for a taxonomic paradigm. *Personality Individ Diff* 12: 773-790.

Fagen R (1981) *Animal Play Behavior.* New York: Oxford University Press.

Fagen R (1993) Sociobiological considerations on exploration and play. In H Keller and K Schneider (eds.) *Curiosity and Exploration.* New York: Springer.

Fairbanks LA (2001) Individual differences in response to a stranger: Social impulsivity as a dimension of temperament in vervet monkeys (*Cercopithecus aethiops sabaeus*). *J Comp Psychol* 115: 22-28.

Fulker DW (1981) The genetic and environmental architecture of psychoticism, extraversion and neuroticism. In: Eysenck HJ, ed. *A Model for Personality.* New York NY: Springer-Verlag, pp 88-122.

Gold KC, Maple T L (1994) Personality assessment in the gorilla and its utility as a management tool. *Zoo Biology* 13: 509 – 522.

Goldberg LR (1992) The development of markers for the big-five factor structure. *Psychol Assess* 4: 26-42.

Gosling SD, Oliver PJ (1999) Personality dimensions in nonhuman animals: A cross-species review. *Curr Directions Psychol Sci*, 8: 69 – 75.

Harlow HF (1962) The effects of early experiences upon the personal-social, heterosexual and maternal behavior f rhesus monkeys. *Trans Am Neurol Soc* 87: 9-10.

Helson R, Kwan VSY (2000) Personality development in adulthood: The broad picture and processes in one longitudinal sample. In: Hampson S(ed.) *Advances in Personality and Social Psychology*, 53: 176-186.

Hershberger SL, Plomin R, Pedersen NL (1995) Traits and metatraits: their reliability, stability, and shared genetic influence. *J Pers Soc Psychol* 69:673-85.

Higley JD, Suomi SJ (1989) Temperamental reactivity in non-human primates. In: Kohnstamm GA, Bates JE, Rothbart MK, eds. *Temperament in Childhood.* New York: John Wiley & Sons, pp. 153-167.

Higley JD, Suomi SJ, Linnoila M (1996) A nonhuman primate model of type II alcoholism? Part 2. Diminished social competence and excessive aggression correlates with low cerebrospinal fluid 5-hydroxyindoleacetic acid concentrations. *Alcoholism: Clin Exp Res* 20: 643-650.

Hirschfeld-Becker DR, Biederman J, Calltharp S, Rosenbaum ED, Faraone SV, Rosenbaum JF (2003) Behavioral inhibition and disinhibition as hypothesized precursors to psychopathology: Implications for pediatric bipolar disorder. *Biol Psychiatr* 55: 985-999.

Jacobs BL, Fornal CA (1995) Activation of 5-HT neuronal activity during motor behavior. *Semin Neurosci* 7:401-408.

King JE, Figuerdo JF (1997) The five-factor model plus dominance in chimpanzees personality. *J Res Personality* 31: 257- 271.

Kraemer GW, Ebert MH, Schmidt DE, McKinney WT (1989) A longitudinal study of the effect of different social rearing conditions on cerebrospinal fluid norepinephrine and biogenic amine metabolites in rhesus monkeys. *Neuropsychopharmacol* 2: 175-189.

Leal SM, Neckameyer WS (2002) Pharmacological evidence for GABAergic regulation of specific behaviors in Drosophila melanogaster. *J Neurobiol* 50:245-61.

Lilienfeld SO, Gershon J, Duke M, Marino L, de Waal FB (1999) A preliminary investigation of the construct of psychopathic personality (psychopathy) in chimpanzees (Pan troglodytes). *J Comp Psychol* 113:365-75.

Livesley WJ, Jackson DN, Schroeder ML (1992) Factorial structure of traits delineating personality disorders in clinical and general population samples *J Abnormal Psychol* 101: 432-440.

Livesley WJ, Jang KL, Vernon PA (1998) Phenotypic and genetic structure of traits delineating personality disorder. *Arch Gen Psychiatry* 55: 941-948.

Marteau P, Caine N, Candland D (1985) Reliability of the Emotions Profile Index Primate form with Papio hamdryas, Macaca fuscata and two Samimiri species. *Primates* 26: 501- 505.

Maziade M, Caron C, Cote R, Merette C, Bernier H, Laplante B, Boutin P, Thivierge J (1990) Psychiatric status of adolescents who had extreme temperament at age 7. *Am J Psychiatry* 147: 1531- 1536.

McCrae RR, Costa PT, Jr. (1985) Comparison of EPI and psychotocism scales with measures of the five-factor model of personality *Personality Individ Diff* 6: 587-597.

McCrae RR, Costa PT, Jr. (1997) Personality trait structure as a human universal *Amer Psychologist* 52: 509-516.

McCrae RR, Costa PT, Jr., Ostendorf F, Angleiner A, Hrebickova M, Avia MD, Sanz J, Sanchez-Bernardos ML, Kusdil ME, Woodfield R, Saunders PR, Smith PB (2000) Nature over nurture: Temperament, personality and life span development *J Personality Socl Psychol* 78: 175-186.

McGuire MT, Raleigh MJ, Pollack DB (1994) Personality features in vervet monkeys. The effects of sex, age, social status, and group composition. *Am J Primatol* 33: 1- 13.

Meaney MJ (1989) The sexual differentiation of social play. *Psychiatr Dev* 7:247-61.

Moskowitz DS, Pinard G, Zuroff DC, Annable L, Young SN (2001) The effect of tryptophan on social interaction in every day life: A placebo-controlled study. *Neuropsychopharmacol* 25: 277-289.

Moskowitz DS, Schwartzman AE (1989) Painting group portraits: Studying life outcomes for aggressive and withdrawn children. *J Personality* 57: 723-746.

Moskowitz DS, Schwartzman AE, Ledingham JE (1985) Stability and change in aggression and withdrawal in middle childhood and early adolescence. *J Abnormal Psychol* 94: 30 – 41.

Palmour RM, Bradwejn J, Ervin FR (1992) The anxiogenic effects of CCK-4 in vervet monkeys are blocked by benzodiazepines, CCK-B antagonists and adenosine A2 agonists. Eur *Neuropsychopharmacol* 2: 193-195.

Palmour RM, Mulligan J, Howbert JJ, Ervin FR (1997) Of monkeys and men: vervets and the genetics of human-like behaviors. *Amer J Hum Genet* 61: 481-488.

Palmour RM, Young SN, Baker GB, Ervin FR (1998) Effects of acute tryptophan depletion and acute tyrosine/ phenylalanine depletion on CSF amine metabolite levels and voluntary alcohol consumption in vervet monkeys. *Psychopharmacol* 136: 1-7

Post RM, Jimerson D, Ballenger JC, Lake CR, Uhde TW, Goodwin FK (1984) Cerebrospinal fluid norepinephrine and its metabolites in manic-depressive illness. In: Post RM, Ballenger JC, eds. *Neurobiology of Mood Disorders.* Baltimore MD: Williams & Wilkins, pp 245-270.

Raleigh MJ, Ervin FR (1976) Human language and primate communication. *Ann NY Acad Sci* 280: 539-541.

Raleigh MJ, McGuire MT (1991) Bidirectional relationships between tryptophan and social behavior in vervet monkeys. *Adv Exp Biol Med* 294: 289-298.

Raleigh MJ, McGuire MT, Brammer GL, Pollack DB, Yuwiler A (1991) Serotonergic mechanisms promote dominance acquisition in adult male vervet monkeys. *Brain Res* 559: 181-190.

Roberts BW, Caspi A, Moffitt TE (2001) The kids are alright: Growth and stability in personality development from adolescence to adulthood. *J Personality Soc Psychol* 81: 670-683.

Roberts BW, DelVecchio WF (2000) The rank-order consistency of personality from childhood to old age: A quantitative review of longitudinal studies. *Psychol Bull* 126: 3-25.

Robins RW, Fraley C, Roberts BW, Trzesniewski K (2001) A longitudinal study of personality change in young adulthood. *J Personality* 69:617-640.

Rothbart MK, Ahadi SA (1994) Temperament and the development of personality. *J Abnorm Psychol* 103: 55-66.

Rutter M (1987) Temperament, personality and personality disorder *Br J Psychiatry* 150: 443-458

Schneider ML, Suomi SJ (1992) Neurobehavioral assessment in rhesus monkey neonates (macaca mulatta): developmental changes, behavioral stability, and early experience. *Infant Behav Devel*, 15, 155-177.

Smoller JW, Rosenbaum JF, Biederman J, Kennedy J, Dai D, Racette SR, Laird NM, Kagan J, Snidman N, Hirshfeld-Becker D, Tsuang MT, Sklar PB, Slaugenhaupt SA (2003) Association of a genetic marker at the corticotropin-releasing hormone locus with behavioral inhibition. *Biol Psychiatry* 54:1376-81.

Stevenson-Hinde J, Still-Barnes R, Zunz M (1980) Subjective assessment of rhesus monkeys over successive years. *Primates* 21: 66- 88.

Stevenson-Hinde J, Zunz M (1978) Subjective assessment of individual rhesus monkeys. *Primates* 19: 473- 483.

Suomi SJ (1981) Genetic, maternal, and environmental influences on social development in rhesus monkeys. in: Chiarelli AB, Corrunccini RS, eds, *Primate Behavior and Sociobiology*. New York, Springer Verlag. Pp.81-87.

Suomi SJ (1986) Anxiety-like disorders in young non-human primates. In: Gittelman R, ed., *Anxiety Disorders of Childhood.* New York, NY: Guilford Press, 1-23.

Suomi SJ (1991) Uptight and laid-back monkeys: Individual differences in the response to social challenges. In: Brauth SE, Hall WS, Dooling RJ, eds. *Plasticity of Development*. Cambridge MA: MIT Press, pp 27-50.

Suomi SJ (1997) Early determinants of behaviour: Evidence from primate studies. *Brit Med Bull* 53: 170-184 .

Symons D (1978) *Play and Aggression: A study of Rhesus Monkeys.* New York: Columbia University Press.

Tellegren A (1985) Structures of mood and personality and their relevance to assessing anxiety, with an emphasis on self-report. In: AH Tuma and JD Maser, eds. *Anxiety and the Anxiety Disorders.* Hillside NJ: Erlbaum, pp 681-706.

Thomas A, Chess S (1968) Temperament and Behavior Disorders in Children New York: New York University Press, pp 64-67.

Turri MG, Talbot CJ, Radcliffe RA, Wehner JM, Flint J (1999) High-resolution mapping of quantitative trait loci for emotionality in selected strains of mice. *Mamm Genome* 10:1098-101.

Weiss A, King JE, Figueredo AJ (2000) The heritability of personality factors in chimpanzees (*Pan troglodytes*). *Behav Genet* 30: 213-21.

Young SN, Ervin FR (1989) Cerebrospinal fluid measurements suggest precursor availability and sex are involved in the control of biogenic metabolism in a primate. *J Neurochem* 42: 1570-1573.

TABLE 1 ***Factor loadings for focal observation of 206 vervet monkeys in a social juvenile environment.***

	Eigenvalue magnitude	Proportional variance
Factor 1	**2.643**	**.155**
Factor 2	**2.444**	**.144**
Factor 3	**1.568**	**.092**
Factor 4	**1.339**	**.079**
Factor 5	**1.312**	**.077**

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Climb/Leap	**0.464**	0.229	-0.247	0.146	-0.258
Watch Observer	**0.635**	*0.326*	-0.145	-0.254	-0.132
Threaten Observer	**0.787**	-0.236	0.146	0.012	0.153
Move Horizontally	0.167	**0.679**	0.076	0.172	-0.095
Sit Near/Muzzle	-0.118	**0.651**	-0.014	-0.252	-0.251
Eat/Forage	-0.361	**0.434**	0.100	0.100	0.182
Look Around	-0.283	**0.394**	***-0.630***	-0.179	0.210
Pace/Flip	-0.105	***-0.776***	*0.259*	0.036	-0.349
Groom	-0.260	*0.266*	**0.469**	-0.229	*0.292*
Play with Object	-0.018	0.007	**0.695**	0.004	-0.037
Oral/Manual Exploration	-0.131	-0.001	**0.636**	*0.290*	*0.289*
Play Behaviors	-0.070	-0.097	0.040	**0.801**	-0.005
Self Play	-0.009	0.116	0.071	**0.736**	0.030
Scratch	-0.031	0.211	-0.035	-0.149	**0.615**
Fidget	-0.023	-0.042	0.112	0.020	**0.600**
Stare Ahead	-0.367	-0.089	-0.154	0.066	**0.664**
Threat/Displace	-0.034	0.083	-0.163	-0.297	***-0.480***

Primary loadings are in BOLD, and secondary loadings are shown in italics

Loadings of specific behaviors on all factors with eigenvalues greater than 1, obtained from factor analysis (orthogonal solution, varimax rotation) of behaviors emitted during social group observation using focal animal sampling, as described further in the text. Each animal was observed a minimum of 10 times in each of 2 waves of observation occurring at approximately 33 ± 4 months of age and at approximately 42 ± 4 months of age. Behavioral measures were cumulated across trials. After initial examination of eigenvalues and scree plots, the solution was constrained to five factors.

TABLE 2 ***Factor-derived behavioral traits identified in Old World primates***

Species	*Context*	*Dimensions*	*Reference*
M mulatta	social	affiliative, fearful, hostile	Chamove et al, 1972
M mulatta	social	confident-to-fearful, active-to-slow, sociable-to-solitary	Stevenson-Hinde et al., 1978
M mulatta	social + challenge	"up-tight," "laid-back"	Suomi, 1986; Suomi, 1991
M mulatta	social + challenge	tense/insecure, confident/popular, playful/active, aggressive/iritable	Bolig et al., 1992
M mulatta	social	sociability, confidence, excitability, equability	Capitanio, 1999; Capitanio, 2005
C aethiops	social	social competence, playful-curious, opportunistic	McGuire et al, 1994
C aethiops	social	agonism, energetic sociability, agreeableness, playfulness, behaviorally inhibited	This report
Pan sp.	social	surgency, emotional stability, agreeableness, dependability, openness	Weiss et al., 2000

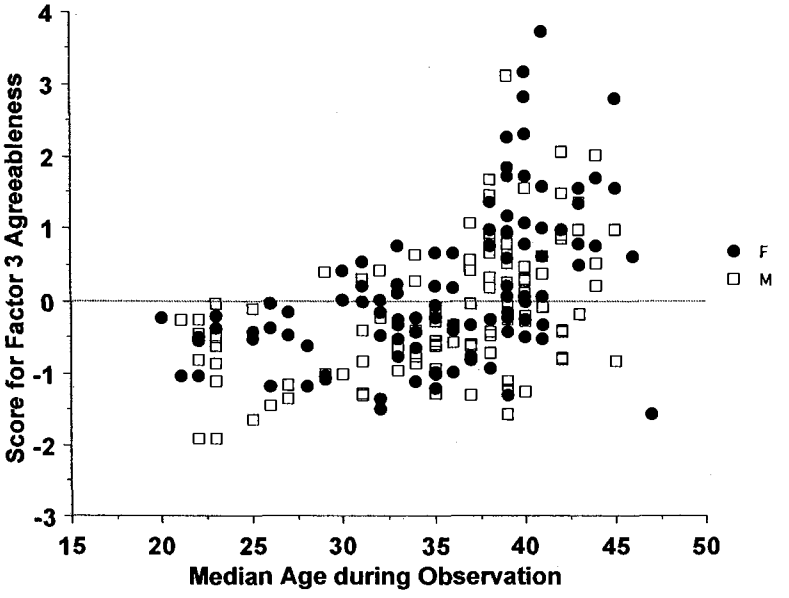


Figure 1A. Standardized scores (Z-scores) on Factor 3 ("Agreeableness") are positively correlatedwith average median age (in months) in social juvenile groups (r= 0.478, $F_{1,204}$= 60.4, p<0.0001). Orthogonal factors were extracted by factor analysis, with varimax rotation, from quantitative scores of standard behaviors in 206 adolescent monkeys across 20 observational bouts. Monkeys age ranged between 20 and 47 months at the median time point.

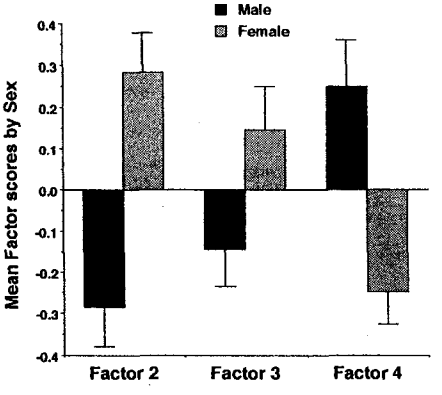


Figure 1B. Females have higher average scores on Factor 2 ("Sociability") and Factor 3 ("Agreeableness"), while males have higher average scores for Factor 4 ("Playful").

FIGURE 2A

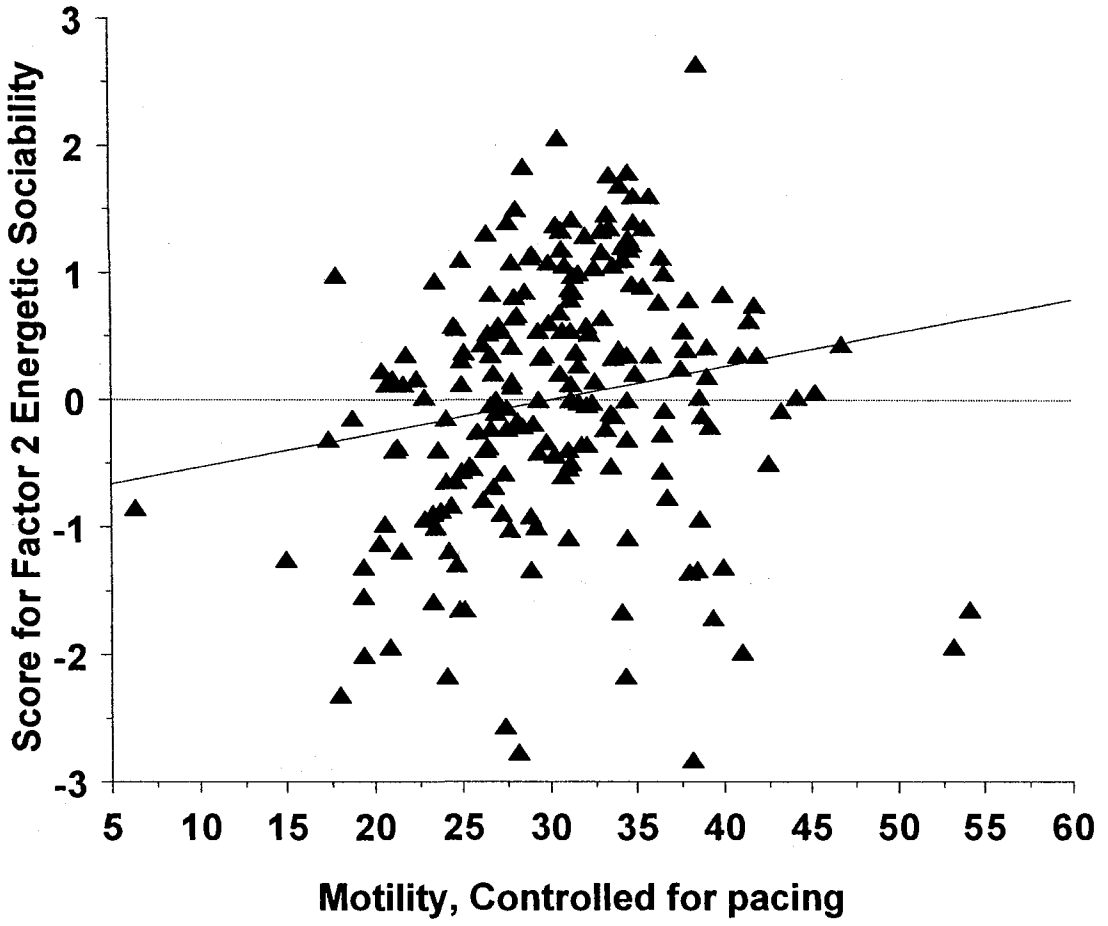


Figure 2. Panel A. Factor 2 ("Energetic sociability") is positively correlated with average motility, controlled for pacing ($r = 0.179$, $F_{1,204} = 6.8$, $p<0.01$). Orthogonal factors were extracted by factor analysis, with varimax rotation, from quantitative scores of standard behaviors in 206 adolescent monkeys across 20 observational bouts. Monkeys age ranged between 20 and 47 months at the median time point.

.FIGURE 2B

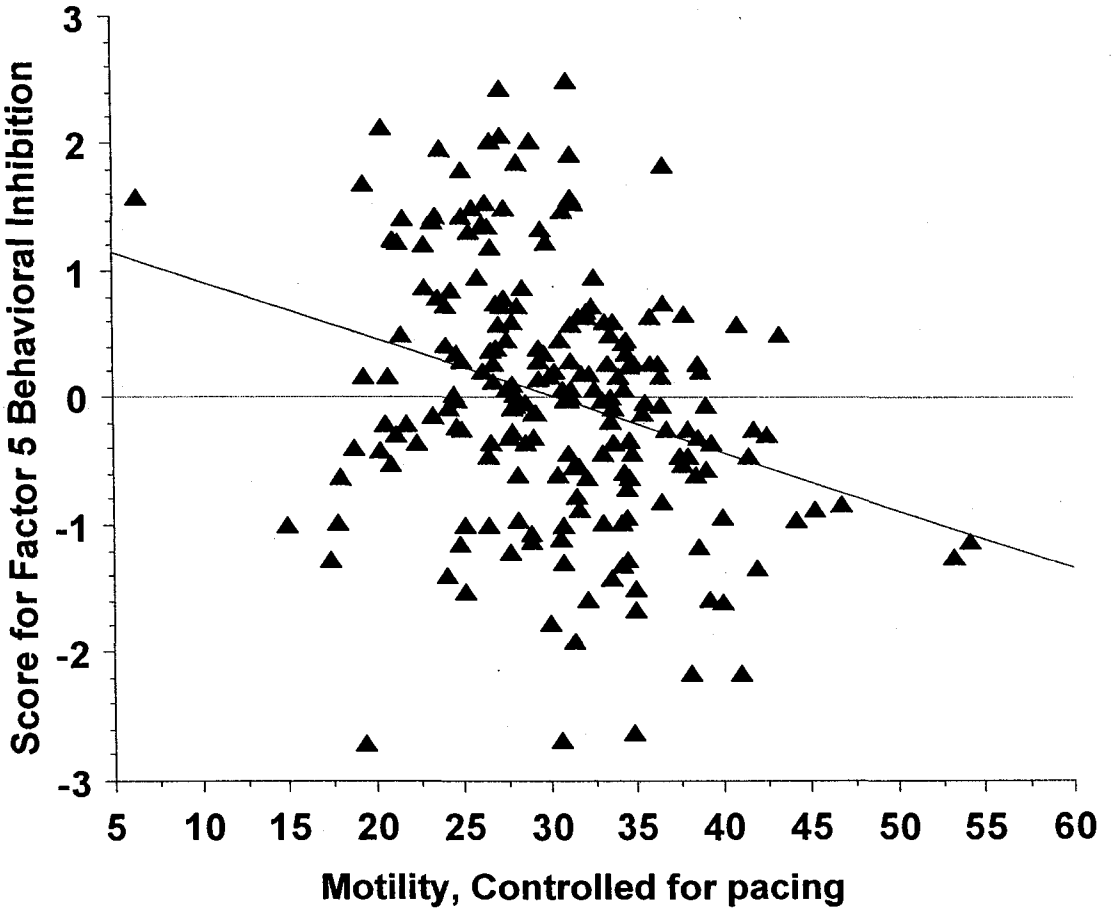


Figure 2. Panel B. Factor 5 ("Inhibited") is negatively correlated with average motility ($r = -0.302$, $F_{1,204} = 14.7$, $p = 0.0002$). Orthogonal factors were extracted by factor analysis, with varimax rotation, from quantitative scores of standard behaviors in 206 adolescent monkeys across 20 observational bouts. Monkeys age ranged between 20 and 47 months at the median time point.

FIGURE 3A

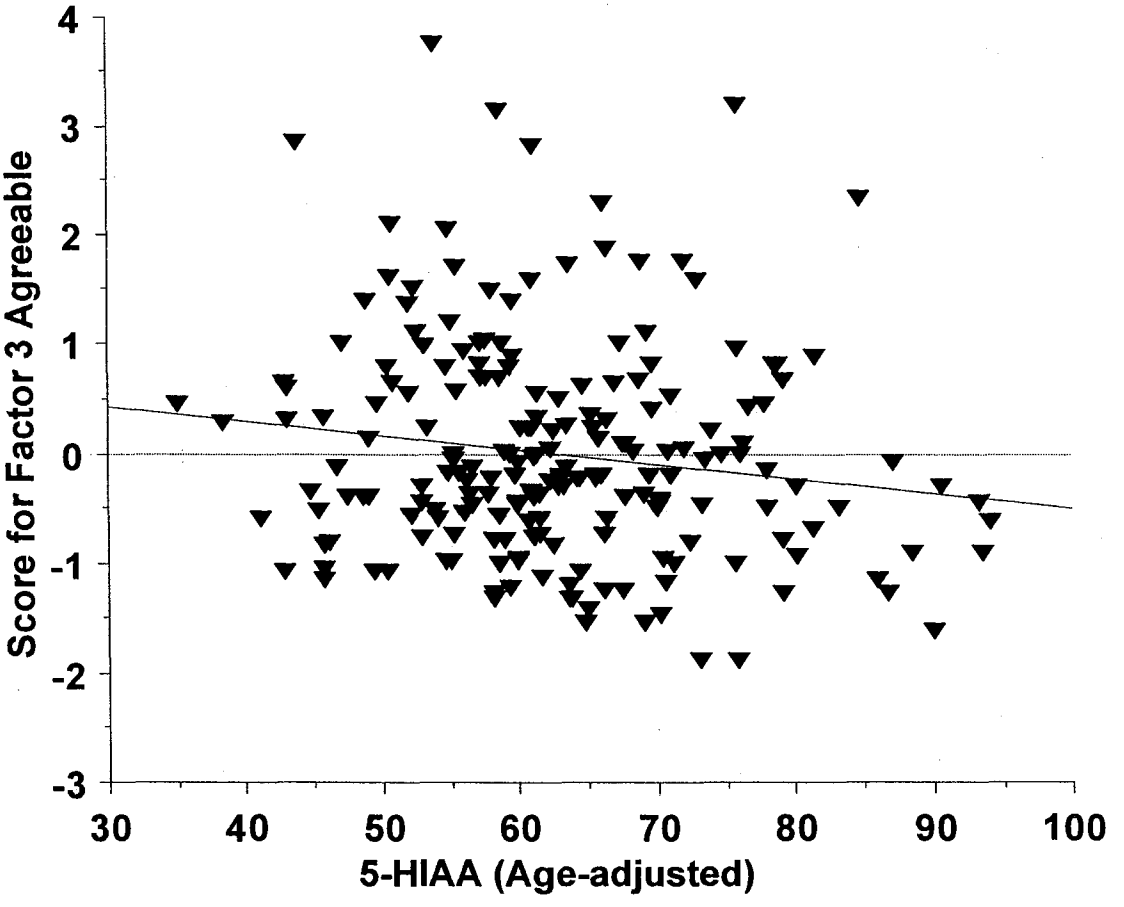


Figure 3. Panel A. Cerebrospinal fluid levels of the serotonin metabolite 5-hydroxyindole acetic acid, adjusted for age, were negatively correlated ($F_{1,204} = 7.93$, $p = 0.005$, $r = -0.158$) with Factor 3 ("Agreeableness") in a stepwise multiple regression analysis to control for partial correlations between CSF amine metabolites.

FIGURE 3B

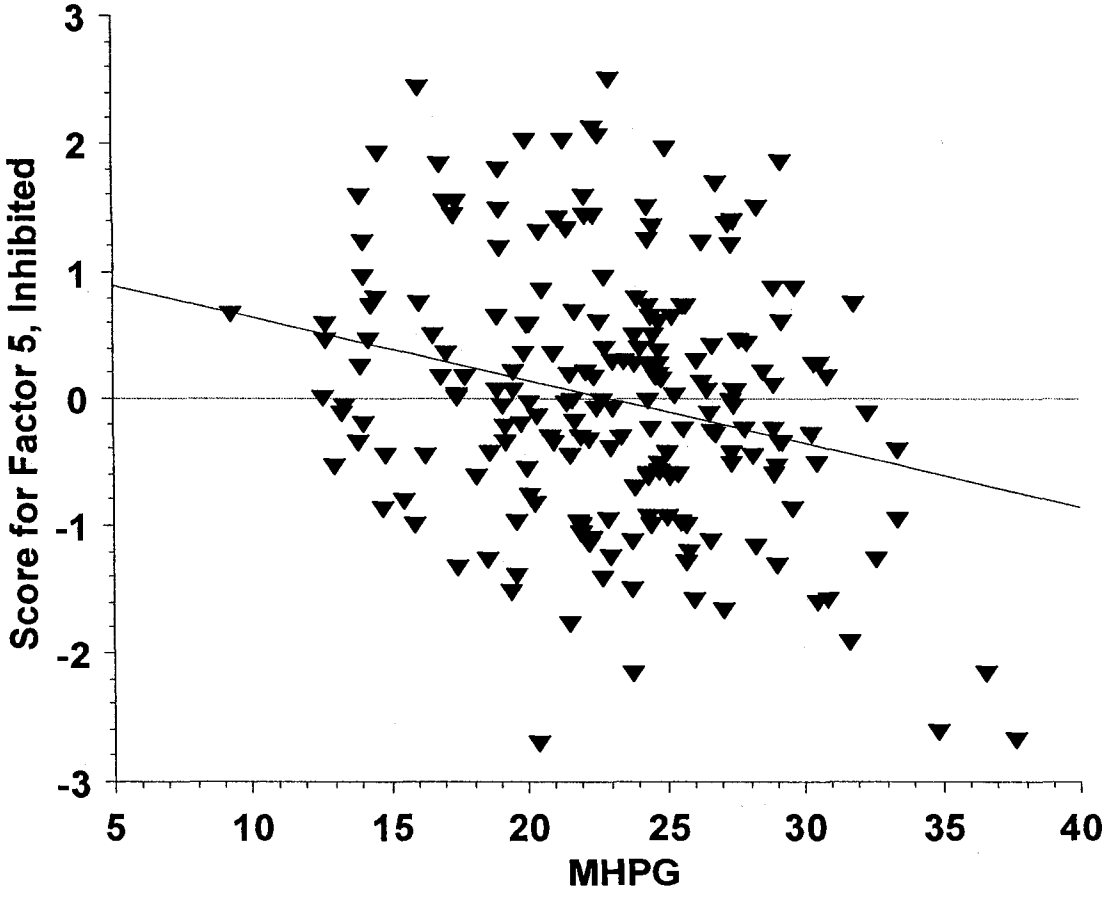


Figure 3. Panel B Cerebrospinal fluid levels of the norepinephrine metabolite MHPG were negatively corelated with Factor 5 ("Inhibited") in a stepwise multiple regression analysis ($F_{1,204}$ = 14.1, p = 0.0002, r = -0.254) which considered the levels of all three amine neurotransmitter metabolites jointly.

BRIDGE I

Our group has managed to derive interpretable behavioral traits or dimensions by collecting observational data from a social juvenile setting. This popular approach has been replicated by many other research groups since the seminal work of Stevenson, Hinde and Zunz (1978), and has obvious significant strengths. One being that socially derived data allows us to gain specific information on the social performance of these animals and consequently derive one or more social dimensions along with a score for each monkey. In order to make the behavioral traits as objective as possible, our group used focal animal testing and collected basic primatological measures, instead of the subjective descriptive adjectives used by other groups. However, by virtue of being in a heterogeneous social context, since monkeys are in groups of 7 and 8, one can argue that the behavioral expressions of these monkeys can be influenced by the varying dynamics in each cage. Example, monkey A, an otherwise sociable monkey might be spending lots of time on his own merely to avoid any confrontation with the four bullies in his group. In another group dynamic, monkey B, an extremely inhibited monkey, might also spend lots of time alone, but in this case as a result of his underlying intrinsic state. In the same group, monkey C might share the same underlying anxious predisposition as monkey B, but engage in a completely different array of behavioral expressions. Monkey C may have learned to cope with her anxiety by adapting to her environment through extreme sociability (ex. grooming and receiving grooms from others), thus masking her anxious state. Therefore in the short term, a monkey's behavior may have been influenced by others in the cage, and in the long term, animals with a certain underlying predisposition may adapt enough to their social environments as to dilute the expression of their extreme states, making these more difficult to identify.

Behavioral traits derived using a social group, may provide a lot of information on the social construct of the species studied (especially when using a large n), as well as insight into specific animals. However, you can only truly get a global picture of these monkeys, by also subjecting them to individual testing. Novelty testing has been performed both in human and non-human primate populations. The premise of this type

of testing paradigm is that a novel environment should raise the level of stress for every given animal. The subject no longer in a familiar environment will be challenged and react in a way true to his internal state, consequently flushing out what potentially may not have been overtly obvious in a social context. Contrary to the social group, the experimental milieu is homogeneous and constant for every animal. Therefore the individual variability in reaction levels for each given monkey should be directly concordant to his internal state. The goal of testing them early on is to measure these underpinnings before they become diluted by either development or the mere interaction they will have with a given environment. The monkeys were subjected twice to the same novelty test as a means of investigating potential habituation, but also to ensure more robustness. By adding a performance component to the experimental design (i.e. finding rewards), we can also further gage the potential level of stress these animals are under. An illustrative example would be, overwhelmed by their anxiety, monkeys who are very nervous will be unable to seek out rewards. By contrast, monkeys who are barely phased by the novel setting will nonchalantly find and eat all of the bated rewards.

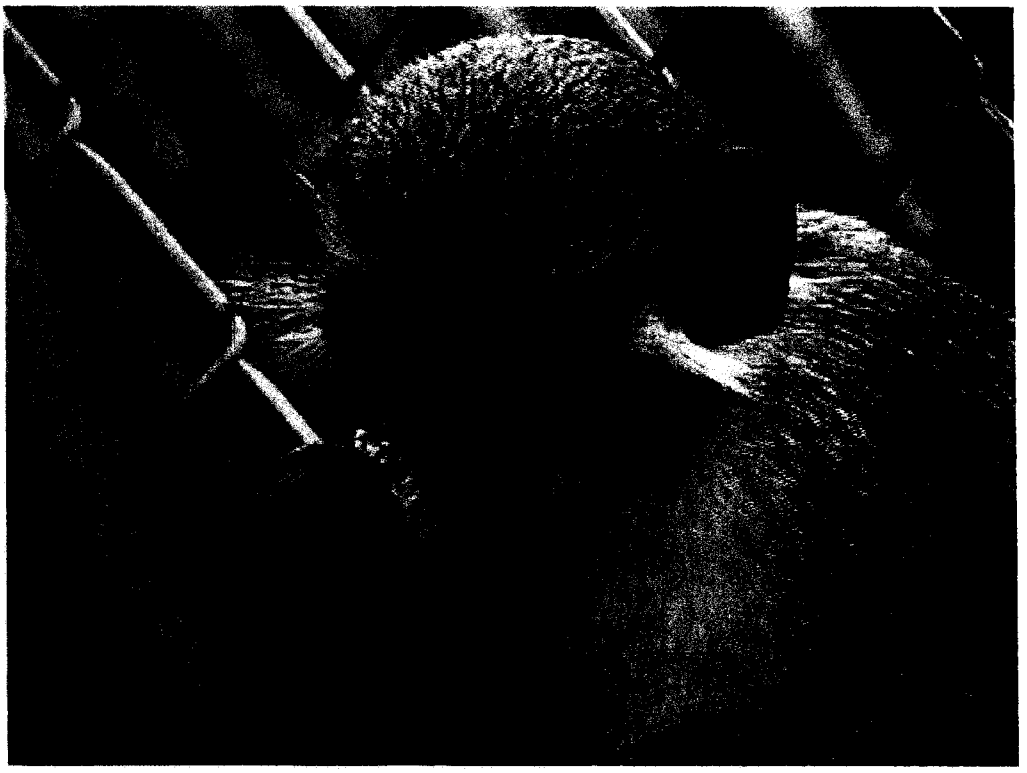
Our research group designed this novelty paradigm, by considering the level of difficulty and stress to suit the age and species of monkeys tested. There is no sense in making a design so stressful that it overwhelms the majority of the animals into a catatonic state. Although it may be interesting to note which select few animals were not phased by this test, and consequently performed well, it will give us very little information on the overall individual variability of this given population. The metric is meant to provide an interesting and diverse range of reactions, which can then derive some behavioral traits. The social data of a given animal sometimes served as an intuitively good predictor of the kind of performance this monkey would have in the novelty challenge, and sometimes not. As a result of an absence of social interaction, the behavioral dimensions derived are more reflective of the approach/avoid, exploration/fearfulness, and uninhibited/inhibited dimensions well documented in the scientific literature.

The goal of having such a metric, which would not only provide an overall description of the given population tested, but specific information for every given animal, would give us the ability to ask and answer many other questions. How do these phenotypic behavioral expressions relate to neurotransmitter levels, and how will they change if the animals are given drugs or alcohol etc. The purpose of this metric is not only to provide more information in order to make some well rounded profiles, but also a means of systematically answering more questions.

CHAPTER IV

BEHAVIORAL TRAITS IN VERVET MONKEYS:

II. RESPONSE TO A NOVEL ENVIRONMENT DURING LATE INFANCY



BEHAVIORAL TRAITS IN VERVET MONKEYS: II. RESPONSE TO A NOVEL ENVIRONMENT DURING LATE INFANCY

Caroline Desbiolles[1], Frank R. Ervin[2,4], Simon N. Young[2,], Chantal Mérette[5] and Roberta M. Palmour[1,2,3,4]

[1]Departments of Biology, [2]Psychiatry & [3]Human Genetics, McGill University, Montréal, Québec, Canada; [4]Behavioural Science Foundation, St Kitts, Eastern Caribbean; [5]Centre de Récherche, Hôpital Robert-Giffard, U Laval, Beauport Québec Canada
Adv Pharmacol. 1998;42:707-11

Address for correspondence:
Roberta M. Palmour, PhD
Department of Psychiatry
McGill University
1033 Pine Ave West, #326
Montreal Qué H3A 1A1
CANADA
TEL: 514-398-7303 FAX: 514-398-4370
roberta.palmour@mcgill.ca

Acknowledgment: This work was supported by grants from the Canadian Institutes of Health Research (MT-14526 to RMP, FRE; MOP-15005 to SNY) and by generous funding from Behavioural Sciences Foundation, St Kitts. We thank the staff of Behavioral Sciences Foundation (especially Amy Beierschmitt, DVM and Mrs. Dora Louard) for their tireless devotion to animal care and handling, and Franceen Lenoff (McGill University) for skilled technical assistance.

The break down of the contributions for the three papers included in the thesis were made by the following authors:

The studies were designed in collaboration by Caroline Desbiolles, Dr. Roberta Palmour and Dr. Frank Ervin.

The statistical analysis was supervised by Chantale Mérette.

The CSF analysis was done by Dr. Simon Young.

All authors helped in the interpretation of the results.

Caroline Desbiolles and Dr. Roberta Palmour wrote the final manuscripts, which were revised by Dr. Frank Ervin and the other authors.

ABSTRACT

Reactivity to a standardized behavioral challenge is thought to reflect inherent patterns of coping in human subjects and in experimental animals. In the first paper of this series (Desbiolles et al., 2007a), we identified five behavioral traits in a birth cohort sample of juvenile vervet monkeys (*Chlorocebus aethiops*) on the basis of focal observations in the peer social group. The present report concerns the response of the same animals (n = 224) to a novel environment during the early juvenile period (13 ± 6 months of age). Each animal experienced two brief (15 min) exposures to a large, novel cage equipped with unfamiliar objects and several food treats hidden in readily accessible openings in the cage wall. Testing occurred at 10 day intervals, and was monitored by a familiar observer collecting standard focal data. As was the case for the social group study, we extracted behavioral factors directly from observational data. Four factors, each with an Eigenvalue > 1.2, explained 54.9% of the variance. These factors, in order of decreasing proportional variance, were interpreted as "energetic exploration," "defensive aggression," "behavioral inhibition" and "cautious exploration." Factors 1 and 2 were negatively correlated with age; on average, females had significantly higher scores for Factor 2. "Energetic exploration" was positively correlated with motility, rewards eaten and rewards dropped, while "defensive aggression" was negatively correlated with the first two of these measures. "Behavioral inhibition" was negatively related to motility and to space covered. Multiple regression analysis showed that levels of 5-HIAA, as well as levels of HVA, were positively correlated with Factor 1 ("energetic exploration"), while levels of MHPG were positively correlated with Factor 4 ("cautious exploration"). The extracted traits coincide well with some of the constructs already well-documented in the human and primate literature, and suggest possible relationships between systematically identified behavioral traits and vulnerability to later psychosocial dysfunction.

INTRODUCTION

In human beings and, more recently, in non-human primates, individual styles of responding or patterns of reactivity are considered to be central to the concept of temperament (Clarke and Boinski, 1995; Goldsmith et al., 1987; Heath-Lange et al., 1999; Kagan et al., 1984; Suomi, 1981, 1986). Much of the current research was inspired by studies of children enrolled in the New York Longitudinal Study. In this work, Chess, Thomas and their colleagues elicited detailed parental reports of nine clinically derived behavioral variables, then used this data to define a major behavioral dimension (difficult-to-easy), which has since been validated with minor differences demographically and across cultures (Thomas and Chess, 1968; Torgersen, 1982; Maziade et al., 1984). Two additional factors, termed undercontrolled and slow-to-warm-up, are less strongly supported and may have age-dependent differences in expression (Caspi et al., 1996; Rothbart and Derryberry, 1981). In their seminal work, and in later reviews, Thomas and Chess (Thomas and Chess, 1968; Chess and Thomas, 1990) emphasize the principle that temperament, though inherent, is always expressed as a response to external stimuli. Despite this understanding, the dimensions of Chess and Thomas may be methodologically limited by strict reliance upon parental report information.

In contrast, researchers such as Rothbart and Kagan derived their dimensions from direct behavioral observations of infants in laboratory situations (Kagan et al., 1988, 1989; Rothbart, 1981). Rothbart's factors of "reactivity" and "self-regulation" are conceptually very similar to the first two Chess/Thomas factors, although more systematically delineated (Rothbart, 1981; Rothbart and Posner, 1985). Kagan focussed on children whose reactions were at opposite extremes of the dimension of behavioral inhibition, as defined by their response to multiple aspects of novelty in structured tests (Kagan et al., 1988, 1989, 1991). In a population sample, willingness to approach strangers or novel objects shows a Gaussian spread, but distinct behavioral styles can be defined at the extremes (approximately 15%) of the distribution. Inhibited children are consistently shy, timid and reluctant to approach novelty, while uninhibited children are spontaneous, outgoing and talkative in the presence of the unfamiliar (Kagan et al., 1986; Resnick et al., 1986). Longitudinal studies suggested that these traits were stable over time ($r = 0.44$) and were gender independent (Resnick et al., 1986), and also that they were well correlated with external variables such as stress hormone release and differential

patterns of brain activation when presented with novel stimuli (Kagan et al., 1987; Schwartz et al., 2003).

In non-human primates, Suomi's studies (Suomi et al., 1981; Suomi, 1986; Thompson et al., 1986; Higley and Suomi, 1989) of behavioral reactivity in rhesus macaque infants closely parallel those of Kagan and document essentially the same phenomenon. Relying primarily on structured exposure of macaque infants to novel places, objects, conspecifics and handlers, two extreme categories of responsivity were defined: inhibited-reactive-avoidant ("uptight") and uninhibited-nonreactive-approaching ("laid-back"). These patterns of reactivity are not confined to primate species, but rather can be readily observed in all vertebrates (eg., Gosling and Oliver, 1999; Piazza et al., 1990) and in many well-studied invertebrates (eg., *Drosophila, Caenorhabditis*). The characteristic response of a given individual to a difficult or stressful situation not only provides an indication of coping strategies, but has also been shown to reflect underlying behavioral vulnerabilities and to predict differential response to psychoactive compounds in both humans and experimental animals (Dellu et al., 1996; DiMascio and Barratt, 1965).

The present report is part of a longitudinal study of four successive birth cohorts of captive vervet (*Chlorocebus aethiops*) monkeys, designed with the intention of collecting multiple types of behavioral data over the first three years of life, so as to maximize the amount and kinds of information available for individual animals. The study comprises three segments: (i) duplicate response to a novel testing environment during nursery housing (approximately 13-16 months of age), (ii) repeated social behavioural measures in the juvenile peer cage (18 – 36 months) and (iv) duplicate response to a different novel testing environment during the juvenile period (approximately 30 months of age). An analysis of the social group behavior of this cohort is reported in the previous paper (Desbiolles et al.,). The present study was carried out in the same animals, tested at a younger age, and reports behavioral response patterns of nursery-housed juvenile vervets observed during two brief exposures to a novel enriched environment (i).

The primary goal of this component was to test all animals in a standardized challenge which would drive the expression of each monkey's behavior in ways which cannot readily be achieved in the social group. By comparison to the social setting, the novelty test: (1) standardizes the environment and makes the context homogeneous for each individual; (2) eliminates the social component and potentially emphasizes the presence of intrinsic traits; (3)

decreases the number of standardized basic behavioral measures scored and reduces the extent of context dependence of the remaining behavioral measures. A secondary goal was to determine whether meaningful traits could be extracted from primary behavioral measures, using well documented and standardized primatological conventions.

METHODS

Animal Subjects

Four successive birth cohorts, comprising 224 vervet or African green monkeys (*C. aethiops)* were tested in the novel environment. All were born in captivity in the open-air social breeding groups of the Behavioral Sciences Foundation (St.Kitts) colony between 1996 and 1999. The 115 female and 109 male infants had lived in their respective birth cages until approximately 6 to 8 months of age before being transferred to an outdoor nursery housing facility for husbandry purposes. In the natal cage, all animals were nursed and began to eat solid food in the species-specific fashion. After being moved to the nursery, Purina Primate Chow was supplied twice a day (feeding times: 8 am and 1 pm for the nursery) and fresh water from a piped central supply was available ad lib. The diet was also supplemented with fresh fruit and produce several times weekly. Housing and sanitary conditions met the guidelines of the Canadian Council on Animal Care, and the protocols were reviewed and approved by an Institutional Review Board established under these auspices.

All infants were given a minimum of eight weeks to habituate to their new living quarters and were on average 13 months of age before being subjected to their first novel challenge. The age range was 6 to 23 months, which also allowed us to study age-related differences in behavior. From the total population of 224 monkeys, six were excluded because they could only be tested once. Each remaining monkey completed two testing trials, each of 15 minutes duration, 10 days apart. As discussed further below, two additional animals paced the majority of the time and therefore were not included in this analysis. The final sample for analysis included 112 females and 104 males.

Novelty Testing Cage

The novel enriched environment illustrated in Figure 1 is in part a complex analogue of the more familiar rodent open-field test of exploration with many similar behavioral measures (for example, level of exploration, motility and number of rewards found). The cage is 6 feet high, 3 feet 7 inches deep and 2 feet 7 inches wide. Three of the cage sides were made of solid wood and the fourth side, facing the observer, was constructed of chicken wire in order to facilitate observation. The inside of the cage, including the top, was entirely meshed with

chicken wire so that the animals could climb around freely. In addition, the cage included three perches, two exits leading to boxes that could be entered by the animal, six holes on the wooden sides which hold the rewards (i.e. bananas) during the testing trials, a square mirror and a 3 foot rope hanging from the middle of the ceiling. The interior of the cage was painted in primary colors to provide additional visual stimulus. The novelty testing cage was placed in a quiet area where external distractions were minimized.

Behavioral Observation

(Observations were made from a point six feet in front of the testing cage. The animals were all familiar with the observer from numerous hours of social observation in the natal cages.) Testing generally occurred between 9 and 11 in the morning and 2 and 4 in the afternoon. Animals tested on a given day were sampled randomly and had not been fed during the 2 hours prior to testing.

Focal animal behavior was collected according to procedures described by Altmann (1974) in which all important observable behaviors are recorded. The spatial location, specific behavior and physical habitus of the animal was scored every 10 seconds from the time the monkey was placed in the novel setting. Hence, in a 15 minute testing bout a total of 90 behaviors were scored. Recorded behaviors are briefly described in Table 1. We also scored a number of features occurring within the 15 minute bout, but not included in standard focal animal scoring. These included the total number of rewards found, the total number of rewards dropped, total motility, and the proportion of space covered throughout the novel testing cage.

Rewards were tucked away in small holes on three sides of the novelty test cage. Total number of rewards found included rewards eaten and rewards dropped. If the monkey reached into the hole to grab a reward and immediately ate it, it counted as 'reward eaten'. If for any reason, the monkey failed to consume the banana, this was scored as 'reward dropped'.

Total motility was scored by dividing the cage into six imaginary segments (top front, top back, middle front and back, bottom front and back). One 'motility point' was counted any time the monkey crossed from one of the six "virtual" compartments into another, throughout the 15 minute bout. For example, if a monkey walked across the bottom of the cage only once during a testing episode, the total motility score would be 1. If the monkey explored the entire novel cage from top to bottom numerous times, the score could easily go up to 30 or more (which is the

average). If the animal paced at the bottom of the cage, the score in some instances could exceed 100 points.

Space covered was scored by keeping track of the spatial location in the cage every 10 seconds. If a monkey spent all of its time in one compartment of the cage (i.e., front bottom), the total space covered would be 1, even if this time was spent walking back and forth across the front bottom of the cage. If the monkey visited all areas of the cage, the maximum score of 6 would be assigned. This measure was intended to give an aggregate view of the proportion of the cage explored by a given individual during the 15 minute exposure.

CSF Amine Metabolites

Under ketamine anaesthesia (10 mg/kg, im), cerebrospinal fluid (0.5 ml) was collected by transcutaneous cisternal puncture at the time each animal was moved from the natal cage into the nursery. Samples were frozen immediately on dry ice, and stored at -70°C until analysis. The neurotransmitter amine metabolites (5HIAA: 5-hydroxyindoleacetic acid; HVA: homovanillic acid; MHPG: 3-methyoxy-4-hydroxyphenylethylene glycol) were determined by HPLC with electrochemical detection (Anderson et al., 1979; Anderson et al., 1980), as described previously for this species (Young and Ervin, 1989; Palmour et al., 1998).

Analysis of Data

Behavioral traits exhibited in this novelty testing paradigm were identified by factor analysis of the focal behavior measures. Prior to conducting this analysis, behaviors which displayed very low frequencies (pace, leap, groom) were excluded. With the exception of the two animals excluded for repetitive pacing, the behavioral frequencies for those few animals with scores on pace, leap or groom were renormalized to provide a constant sum of 90 for each individual. Pilot testing showed that behavior in trial 2 was not significantly different from that in trial 1 indicating that the animals did not habituate to the novel environment by the second test. Therefore, all data for trials 1 and 2 were combined. Orthogonal factors were extracted from the focal behavior measures by principal components analysis with varimax rotation (StatView V: Systat). The possible correlations between the orthogonal factors and likely covariates (gender, age) or other quantitative measures (space covered, motility, rewards obtained, CSF amine metabolite levels) were evaluated by ANCOVA and stepwise linear

regression analysis, respectively. In order to protect against inflation of significance by multiple testing, results were corrected according to the method of Bonferroni, and only corrected p values are reported below.

RESULTS

Factor solution and interpretation

Factor analysis of behavioral data for 216 monkeys tested twice in a novel environmental paradigm yielded a 4-factor solution, with satisfactory statistical properties (all Eigenvalues greater than 1; $\chi^2 = 2267$, $p < 0.0001$) and factors exhibiting high face plausibility. This factor solution accounted for 54.9% of the variance (Table 2). An examination of the scree plots also suggested that a 4-factor solution was optimal. The specific behaviors included in the analysis had commonality estimates of 0.88 - 0.99.

The behaviors loading on each factor are detailed in Table 3. Locomotion, climbing, vocalizing, eating and investigating objects load heavily on Factor 1, suggesting that this factor reflects a construct labelled as "energetic exploration." Factor 2 includes the behaviors 'threaten observer' and adopting a defensive position in the back of the cage (descriptively termed 'spread-eagle'). Vocalizing and watching the observer load less strongly on this factor, which is interpreted as "defensive aggression." Frozen immobility and fixed stare loaded heavily on Factor 3, which we have labeled as "behavioral inhibition." Vigilant watching of the observer loads more weakly on Factor 3. Factor 4 includes oral and manual exploration, as well as staring at the observer. Investigating objects showed a secondary loading on Factor 4. We interpreted Factor 4 as measuring a calmer form of exploration together with caution, have labeled this Factor as "cautious exploration." Looking around (surveying the external environment) did not load positively on any of the factors, but was negatively correlated with both Factors 2 and 3.

Relationship of factors to age and gender

The relationship of the individual factors to age and gender was examined. As shown in Figures 2 and 3, Factor 1 was negatively related to age ($r = -0.27$, $p<0.0001$), as was Factor 2 ($F_{1,214} = -0.21$, $p = 0.003$). Factor 2 was related to gender ($F_{1,214} = 5.14$, $p = 0.024$), with females showing slightly higher mean scores than males (female: 0.145 ± 0.1 ; male: -0.161 ± 0.09). Neither Factor 3 nor Factor 4 were significantly related to either age or gender.

Relationship of factors to other quantitative behavioral measures

Using linear regression, we also examined the relationship between factors and additional variables, such as rewards found, then either eaten or dropped, amount of space covered, and total mobility, defined as described in Methods. Energetic exploration (factor 1) was positively correlated with three external variables ($F_{3,212} = 211.7$, $p < 0.002$). The strongest correlation was with total motility ($r = 0.84$, $p < 0.0001$), followed by rewards eaten ($r = 0.69$, $p < 0.0001$) and rewards dropped ($r = 0.51$, $p < 0.0001$). These relationships are depicted graphically in Figures 4 and 5.

Defensive aggression (factor 2) displayed a significant negative relationship to two external variables: proportion of space occupied, controlled for motility ($r = -0.26$, $p < 0.0001$) and rewards eaten ($r = -0.192$, $p = 0.005$). Factor 3 ("behavioral inhibition") also showed a negative relationship to two external variables: proportion of space occupied, controlled for motor activity (Figure 6: $r = -0.37$, $p < 0.0001$) and rewards eaten ($r = -0.33$, $p < 0.0001$). Cautious exploration (factor 4) showed no relationship with other quantitative behavioral measures.

Qualitative exploration of behavioral traits

The extracted factors were explored further by qualitatively examining the details of behavior in monkeys that scored ≥ 1 SD above the mean for a given factor.

Energetic exploration (Factor 1): Monkeys with high (positive) scores on this dimension ($n = 31$) productively explore most of the area within the novel testing environment, moving both horizontally and vertically, investigating novel objects and finding rewards. Qualitatively their demeanor is energetic and bold, and their focus seems to be on external goals (i.e. motility, exploration and reward seeking). They are curious and clever, and in a social group setting (Desbiolles et al., 2006a) tend to be either dominant or "loners." Monkeys with high scores on Factor 1 also have a high propensity for displacing cagemates, and may thus appear to be frightening. Several aspects of exploratory behavior (investigating new objects, manual exploration) loaded heavily on Factor 1 as well.

Defensive aggression (Factor 2): Monkeys scoring high on this dimension (n = 29) demonstrate more frequent defensive behaviors (eg., threats, challenging postures) towards the observer. Qualitatively their demeanor is more aroused and vigilant, and their focus mainly revolves around the heightened interaction with the observer. These animals may be afraid of the test situation or of the observer, but they counteract this threat to their safety proactively through their vigilance. The defensive monkey will either position itself in the top front or the top back of the cage. Some monkeys which score highly on Factor 2 exhibit a 'spread eagle' position on the back top right or left corner of the cage. However, the more time such animals spend threatening the observer, the less successful they seem to be at finding rewards. In a social group setting (Desbiolles et al., 2006a), these monkeys may also be curious and appear to be fearless, but when taking food from an observer, they are likely to snatch it and retreat. Animals with high scores on this dimension are often characterized as dramatic and intense.

Behavioral inhibition (Factor 3): Monkeys scoring high on this dimension (n = 32) frequently adopt catatonic postures, remaining immobile for the entire duration of the novelty test in seemingly awkward positions. They generally stare ahead at nothing specific with their eyelids closing for long periods of time. Qualitatively their demeanor is inhibited, their movements are labored and their focus seems to be directed inwards. In a social group setting (Desbiolles et al., 2006a), these individuals are more likely to be low ranking and socially isolated.

Cautious exploration (Factor 4): Monkeys scoring high on this dimension (n = 29) display reward-seeking behavior, but are not as successful in finding rewards as monkeys which score highly on the first dimension. Although these animals often stare at or watch the observer, they do not seem aroused or fearful and rarely exhibit threatening facial grimaces. In the social group (Desbiolles et al., 2006a), these animals are more likely to groom than be groomed, and to react, rather than initiate. In the test cage, their demeanor is calm and curious. It is easy to think of this as 'modal' or 'normal' monkey behavior: an average monkey would keep a wandering eye on the observer just to be safe.

Relationship of factors to CSF amine metabolites

The relationship of CSF amine metabolites to the extracted factors was also examined by multiple regression analysis, which takes into account the previously documented (Ågren et al.,

1986, Young and Ervin, 1984) intercorrelations between 5-HIAA, HVA and MHPG (the major CSF metabolites respectively of serotonin, dopamine and norepinephrine). Baseline CSF determinations were available for 210 monkeys sampled within the 3 month period preceding novelty testing. There was no effect of gender, but there were negative correlations with age for each metabolite. Accordingly, residuals were computed and used in the following analyses. As in previous studies, significant partial correlations were observed for all amine metabolites (5-HIAA/HVA = 0.504, 5-HIAA/MHPG = 0.288, HVA/MHPG = 0.142).

Multiple regression analysis showed that levels of 5-HIAA, as well as levels of HVA, were positively correlated with Factor 1 ($F_{2,207} = 6.1$, $p<0.005$; F-to-remove 5-HIAA = 11.45, F-to-remove HVA = 6.73), while levels of MHPG were positively correlated with Factor 4 ($F_{1,208}$) = 5.24, p = 0.03). Thus monkeys with higher factor scores for Factor 1 had higher CSF levels of 5-HIAA and HVA, and those with higher factor scores for Factor 4 had higher CSF levels of MHPG. However, in no case were these relationships of large magnitude (partial correlations: 5-HIAA and Factor 1: 0.226; HVA and Factor 1: 0.171; MHPG and Factor 4: 0.123). Levels of amine metabolites were not significantly related to either Factor 2 or Factor 3.

DISCUSSION

As was the case for social group behaviors (Desbiolles et al., 2006a), this analysis shows that behavioral trait factors can be extracted directly from a standard repertoire of operationally defined measures, taken in this instance in a novel environmental paradigm. In this study of 216 vervet monkeys from four successive birth cohorts, dimensions interpreted as reflecting "energetic exploration," "defensive aggression," "behavioral inhibition" and "cautious exploration" accounted for 54.9% of the proportional variance. In addition to being statistically robust, these dimensions have high face plausibility and are solidly embedded in the literature of primatology and of clinical psychology, as discussed further below. Moreover, the relationships between specific factors and external variables, such as total motility, number of rewards gained and proportion of space occupied, as well as cerebrospinal fluid levels of particular monoamine metabolites, are internally coherent. Finally, as discussed in further detail below, the identified

factors are congruent with behavioral traits which emerge at a later age in the context of a social group (Desbiolles et al., submitted in parallel).

In the aggregate, our findings can be conceptualized as representing alternate expressions of exploration and fearfulness, which can also be understood within the context of approach - avoidance (Schneirla, 1959) or of Gray's (1979) behavioral activating and inhibiting systems. To be precise, the traits which emerged in the factor solution can be grouped into the two domains of approach/exploration (active and passive) and avoidance/fear (defensive aggression and behavioral inhibition). These domains are not only characteristic of vervets (McGuire et al., 1994) and other species of monkey, such as the rhesus (Stevenson-Hinde, 1978; Kalin and Shelton, 1988; Kalin et al., 1989; Bolig et al., 1992; Suomi et al., 1997; Capitanio; 1999), but are also concordant with studies in humans (eg., Kagan et al., 1986, 1987), thereby reinforcing the validity of nonhuman primates as models for human behavior research.

Relationship to behavioral traits identified in the social group

Four of the five factors identified in the social group situation (Desbiolles et al., 2006a) are conceptually similar to the factors reported here. Both studies used the focal animal (Altmann, 1974) approach and a species-specific behavioral repertoire, but the social group observations were intended to profile behavior under daily social conditions, while the novel environment was an opportunity to evaluate behavior in a stressful situation. Another obvious difference was the appearance of interactional behaviors (eg, groom, muzzle, sit near, threaten and displace) in the social juvenile paradigm. The "agonistic" dimension derived in the social juvenile context resembles the "defensive aggression" dimension in the novelty paradigm, both with respect to the behaviors which load on the two factors and with respect to individual animals found at the ends of the distributions. Failure to habituate to the observer, despite repeated exposure, was striking, as was the defensive approach to an uncomfortable situation. Similarly, "energetic sociability" derived in the social juvenile context was strongly related to the "energetic exploration" dimension in the novelty paradigm. Moving across the cage, occupying a large proportion of available space, eating and foraging behaviors loaded heavily on both dimensions. Again, the same animals were found at the ends of the distributions, and as well, the two dimensions were significantly correlated across the whole distribution (data not shown).

The social dimension termed "agreeable" was most coherent with the trait of "cautious exploration" in the novelty test, particularly with respect to the behaviors of oral and manual exploration and explore object. As noted previously (Desbiolles et al., 2006a), overt affiliative behaviors do not load on a single dimension in the juvenile peer group, but rather are distributed between "energetic sociability" (sit near, muzzle) and "agreeable" (groom). The "play" dimension derived in the social juvenile context had no counterpart in the novelty test since by definition play behaviors involved interacting with other monkeys. Finally, the "behavioral inhibition" dimension in the novelty testing paradigm most closely resembled the dimension of "behavioral inhibition" identified in the social group analysis. Both traits were heavily dependent upon fixed staring behavior and were negatively correlatedwith motility in the cage. In summary, these comparisons suggest an internal consistency between the dimensions derived from juvenile peer group observations and the novelty challenge situation. The mathematical comparisons of these two factor solutions will be presented at a later date, in the context of an overall evaluation of the entire data collection scheme.

Behavior in the context of a novel environment

That humans or animals often reveal unanticipated aspects of behavior and biology when faced with a challenge situation is well known. We designed the novel testing paradigm used in these studies with this in mind, and with explicit attention to the goal of constructing a species appropriate (i.e., relatively more complex) analogue of familiar rodent novelty testing paradigms. While the primary behavioral scoring methodology is taken from the primatological domain, most of the so-called external variables were extrapolated from measures used more frequently in rodent experiments. The multi-colored 6' high rectangular boxed cage meshed with chicken wire was supplied with poles and a rope to allow locomotion in 3 dimensions, but is large enough to resemble some aspects of the rodent open field test, while the baited holes recall the holeboard test or other maze-like designs.

However, our analytic approach differs significantly from that used in many novelty tests reported in the literature. Typically, only a few selected dimensions of behavior are measured and then interpreted *a priori.* An example would be the number of head dips in the holeboard test, which is used as an indication of exploration, while the latency to approach a reward is thought to reflect fearfulness. In an attempt to obtain more informative, yet objective and

replicable behavioral measures, we used the standard focal animal method of Altmann (1974), in which any behavior present at the beginning of a 10 second epoch was scored. Thereafter, the actual behavioral frequencies were directly analyzed, rather than deriving adjective checklists to be analyzed subsequently.

Relatively few tests of non-human primate reactivity to novel environments have been reported. In studies of infant rhesus monkeys, Kalin and colleagues (1989, 1991) discriminated alternate behavioral responses, hypothetically mediated by different brain pathways, in response to the presence of unfamiliar humans and direct staring with or without eye contact. In these studies, contact with unfamiliar persons, particularly in the absence of the monkey mother, elicited distress vocalizations ('coo' and 'bark'). Two of their response discriminants, 'barking' and 'freezing,' are identical to behaviors which load on factors 2 and 3 ("defensive aggression," "behavioral inhibition") of the present study, but Kalin and Shelton (1989) noted these responses in the same individuals under different challenge situations (and to some extent, at different ages), rather than in different individuals tested with a single challenge. In contrast, Suomi and colleagues (Suomi, 1986; Higley & Suomi, 1989; Schneider et al., 1991; Schneider and Suomi, 1992) found that some infants, juveniles, and adolescents consistently displayed behavioral and physiological signs of fearfulness and anxiety in novel situations ("uptight"), whereas others of comparable age and social-rearing background consistently initiated exploratory behavior and/or playful social interactions ("laidback"). This is similar to the distinction between approach/exploration and avoidance/fear described above.

In addition to the range of novelty exposure used in Suomi's studies (Schneider et al., 1991), Cameron et al. (2003) describe a battery of behavioral tests which intend to elicit different aspects of reactivity: the "Free Play" test measures physical activity in an unfamiliar playroom containing children's toys and a sedated mother monkey; the "Remote-Controlled Car" elicits fear and distress in response to a brightly-colored unfamiliar moving object; the "Human Intruder" test is a modification of the challenges of Kalin (Kalin and Shelton, 1989) described above, and the "Novel Fruit" test measures the willingness of an individual to overcome neophobia in light of the potentially rewarding experience of eating a preferred food.

Reactivity dimensions in non-human primates

Most of the challenge testing in non-human primates concentrates on one or a few behavioral measures, rather than using a focal animal scoring approach. As a consequence, the majority of reports concern categorical, rather than dimensional, distinctions (eg., Suomi's "uptight" vs "laidback"). In *Macaca radiata,* for example, infants reared under two different levels of environmental demand were tested in a large tile-walled pen which contained colorful climbing cables, a metal feeding box and several novel objects (Andrews & Rosenblum, 1993). Focal animal observations demonstrated a reluctance of environmentally stressed animals to explore the test chamber as compared to the control group, but individual differences were not further explored. In a study using components of the Cameron et al. (2003) test battery described above, there was a significant correlation between blunted growth hormone release (a marker widely reported in children and adults with anxiety disorders) and time spent reacting to the intruder in the Human Intruder test (Cameron et al., 2003). In further studies from this group (Williamson et al., 2003), seven factors were extracted from the aggregate behavior, each interpreted as reflecting different aspects of stress response. Three of these factors showed substantial evidence for heritability, as did five of the individual scored behaviors. Nonetheless, the focus on only a few specific behaviors is more similar to the coding methods typical of rodent studies, as compared to the comprehensive behavioral assessment used in the present investigation.

Using a very different challenge paradigm in older vervet male monkeys of the same geographic origin as those reported here, Fairbanks (2001) located impulsivity and inhibition on a common vector. Impulsivity was not measured explicitly in the present study, but there was no indication that monkeys at the negative pole of Factor 3 (closely related to behavioral inhibition) were impulsive. The extent to which this is a consequence of the methods of data collection or analysis remains to be explored, but the Fairbanks (2001) study is notable in also using primary behavioral data, thus limiting the necessity for interpretation and increasing the potential for replication.

CSF amine metabolites and personality factors

In the present study, cerebrospinal fluid levels of 5-HIAA and HVA, the principal metabolites of serotonin and dopamine, respectively, were significantly correlated with Z-scores

on Factor 1 ("energetic exploration"). There is a robust and varied literature relating dopamine to motor activity and to exploration (Beninger, 1983; Carlsson, 1993;), and also many reports of positive relationships between dopamine and attention (Chudasama and Robbins, 2004; Robbins, 2000). More explicitly, the current notion is that an optimum level of dopamine facilitates positive activity and focused attention (eg., Goldman-Rakic, 1998; Robbins, 2000; Sawaguchi and Goldman-Rakic, 1991; Williams and Goldman-Rakic, 1995), but that concentrations above this level lead to hyperactivity and inattention and suboptimal concentrations are likely associated with passivity and lethargy. A role for serotonin at the positive pole of an "energetic exploration" factor is less well developed, but there is ample evidence of a postive correlation between levels of serotonin and dominance behaviors. In vervet monkeys, Raleigh et al. (1991) established that elevated brain serotonin function promotes the acquisition of a dominant social position and more recently, Moskovitz et al. (2001) have reported that the serotonin precursor tryptophan, given orally to normal humans promotes dominance in daily social interaction. Direct measures of dominance were not collected until the monkeys reported here were moved into juvenile social groups. While not all energetic and exploratory animals will be at the top of the social hierarchy, most of animals which are high in the social hierarchy will be energetic and outgoing.

Contrary to the studies of some other groups of investigators (Kraemer, 1985, 1989; Redmond, 1987), we observed no relationship between baseline CSF MHPG (the principal metabolite of norepinephrine) and those dimensions ("defensive aggression," "behavioral inhibition") which might be thought to be most closely related to fearful or inhibited behavior. Rather, there was a weak (but significant) positive correlation between CSF MHPG and the dimension which we have termed "passive exploration." Rats that exhibit rapid habituation and low locomotor response to an open field challenge are also characterized by a high functional activity of nucleus accumbens norepinephrine (Cools et al., 1990).

Coherence with human personality and temperament

Even though they may change with age, the dimensions revealed in the present study are also related to the better validated human personality traits, described more fully in the previous paper (Desbiolles et al., 2005a). To be explicit, parallels between the dimension of positive activity/affect (Eysenck, 1979; Costa & McCrae, 1992; Tellegren, 1985; Goldberg, 1992;

Cloninger, 1993) and Factor 1 are obvious. Similarly, Factors 2 ("defensive aggression") and 3 ("behavioral inhibition") are related to aspects of the human trait of negative affect or emotional instability (Eysenck, 1979, 1991; Costa & McCrae, 1992; Goldberg, 1992; Cloninger, 1993; Livesley et al., 1998). To be explicit, the trait of "emotional instability" in man include several lower level facets (Livesley et al., 1998), including anxious perceptions and behaviors, suspiciousness, anger, resentment and guilt, as well as some degree of emotional lability. These facets comprise the superfactor of "emotional instability" in population samples, but a given individual may express a specific facet to a greater or lesser extent. In the analysis reported here, there was no statistical evidence that any superfactors could be constructed, yet the specific behaviors which load on Factor 2 (threat, defensive posturing, barking) and Factor 3 (freezing, staring in the face of a new environment) are explicitly related to anger and suspiciousness and to fear and behavioral inhibition, respectively.

It is not immediately clear how the behavioral factors identified in this study relate to the temperamental categories (difficult-to-easy, undercontrolled and slow-to-warm-up) of Thomas and Chess (Thomas and Chess, 1977; Graham et al., 1978; Maziade et al., 1984). Significant differences in statistical methodology (eg., unrotated principal components analysis vs varimax orthogonal extraction) led these workers to interpret both the positive and negative poles of their factors, but we have almost exclusively emphasized the positive loadings as determinants of traits. A factor analysis of similar data in the Dunedin longitudinal study (Caspi et al., 2003) produce a five-trait solution (undercontrolled, confident, inhibited, reserved and well-adjusted) with similar conceptual characteristics, but somewhat better discrimination between constructs. As compared to these two systems, reluctance to approach new stimuli is a key component of "difficult" (Thomas/ Chess) and "inhibited" (Caspi) and also intuitively a significant determinant of Factor 3 ("behavioral inhibition") described above. Motor activity loads strongly on the second Chess/Thomas factor in most studies, and is the chief determinant of Factor 1 ("active exploration") in the present investigation. Some facets of the Chess/Thomas dimensions (eg., adaptability, threshhold) can be construed as being analogous to behaviors which load heavily on Factor 4 ("passive exploration") or Factor 2 ("defensive aggression"). Other constructs (eg., approach/withdrawal) are clearly separated in our analysis, as they are in the Caspi solution, such that tendency to approach is most obvious in Factor 1 (and in "confident"), while tendency to withdraw is strongest in Factor 3 (and in "inhibited"). It may also be noteworthy that the factor

solution described here for the Chess/Thomas categories pertains primarily to samples of children from infancy up to about age 7 (Thomas and Chess, 1977; Matheny et al., 1984; Maziade et al., 1984), but thereafter different trait groupings emerge (Maziade et al., 1989, 1990; Caspi et al., 1995, 2003). The monkeys described here had a mean age of 13 months, which would be approximately equivalent to a human age of 3-5 years (sexual maturity: 32-42 months in female vervets). It will thus be of interest to see whether new behavioral groupings emerge in the analysis of a different novelty paradigm which was conducted on the same monkeys as they entered puberty (Desbiolles et al., 2006c).

Implications for models of psychopathology

The constructs of internalizing and externalizing dimensions (Rutter, 1987; Achenbach) emerged primarily from a clinical perspective, but are conceptually well-related to the findings presented in this report (Graham et al., 1973). Our Factor 1 clearly defines a dimension which, at one pole, would be likely to include cases with externalizing dysfunction. To be explicit, among the animals which had high scores on "energetic exploration," there was a small subset which were not successful at finding rewards despite active exploration of the entire space. Typically these monkeys displayed a hyperactive manner, with poor attention to rewards, or alternately, they found food, but dropped it before they could eat. This notion is confirmed by the positive correlation between Factor 1 and the number of rewards dropped, as well as the number of rewards eaten. One could speculate that these individuals showed characteristics of attention deficit or hyperactivity, and might be particularly vulnerable to extremes of behavior in the social group.

A classical internalizing dimension is well-reflected in those animals which score highly on Factor 3 ("behavioral inhibition"). Behaviorally, the most extreme animals show perceptible dis-ease in their novel environment, to the point of exhibiting a frozen catatonic state. Even those with somewhat less dramatic positive trait scores display behaviors which fit well into Kagan's extreme of "behavioral inhibition," a trait which has been shown to increase the probablility of social phobia and generalized anxiety in later life (Reznick et al., 1986).

It will also be interesting to follow animals with high scores on Factor 2 ("defensive aggression") over time. Many are dominant in a social setting, but in a challenge situation, they are vigilant and aggressive (barking, threatening) in a situation which is clearly not threatening.

Athough they appear to be confronting the situation, is this in fact a overreaction to a fear-provoking stimulus. In the human situation, there is evidence that such individuals have an excess of both internalizing and externalizing traits or symptoms (Thomas and Chess, 1977; Graham et al., 1978; Mazaide et al., 1984). Moskowitz and Schwartzman (1985) have noted that the most aggressive adolescents are those with high childhood evidence of both internalizing and externalizing traits.

Methodological issues

There are a number of methodological choices which must be made in any study, and although some of these are always arbitrary, this is particularly the case in an analysis such as that reported here. As discussed in greater detail in the initial paper of this series (Desbiolles et al., 2005a) we chose to use factor, rather than cluster, analysis because of a focus on the structure of behavior in a longitudinal and developmental context, as compared to the characteristics of extreme individuals, and because we were interested in positioning this study in relation to the human and animal literature. Both cluster and latent class analyses may provide interesting contrasts in future analyses.

We also intentionally examined full birth cohorts in order to minimize selection bias insofar as possible in a captive population and also to achieve a suitable subjects: variables ratio (16:1 in the present analysis). Other methodological choices included regular inter-rater reliability studies to ensure stability of scoring (Marteau et al., 1985), and a scoring system derived from classical primatological inquiries (Altmann, 1974). Among other advantages, this should significantly improve the opportunities for independent replication. Finally, the young age of animals at testing and the consistency of rearing and housing conditions are considerations which, according to some authorities (Kalin and Shelton, 1989; Kalin et al., 1991; Rothbart, 1981; Kagin, 1997) might improve the ability to identify inherent (rather than environmentally influenced) individual variability.

Because preliminary evaluation of the raw behavioral scores in the replicate trials showed no evidence of temporal variation, we combined the data for robustness in this initial study. In future studies, it will be important to conduct additional replicate trials so that test-retest reliability can be examined and so that measurement error can be estimated. An initial analysis of the first trial episode for each animal enrolled in the present study produced a factor solution

(data not shown) which did not differ from the factor solution obtained in the composite data, except that factors 2 and 3 were reversed. However, the correlation between the individual factors produced in the complete solution and the analogous factors which emerged from the solution for trial 1 were all highly significant.

A major goal of this study was to determine the feasibility of extracting meaningful factor scores from primary behavioral scoring. Although our data superficially support this approach, much remains to be done to determine its global utility. For example, without extensive studies using multiple rating systems and several observers it is premature to make definitive statements about the validity of the behavioral traits described here. That the factors which emerged have face plausibility is nonetheless encouraging.

Conclusion

In summary, this study shows that it is possible to extract behavioral traits with high face plausibility and some degree of internal validity (corrrelations with external variables, including cerebrospinal fluid amine metabolites) from primary observational measures. The extracted traits coincide well with some of the constructs already well-documented in the human and primate literature, but because the analysis is restricted to individual response to a novel environment, those dimensions which are heavily influenced by social interactions are either absent or incompletely described.

Of interest to the long-term goal of providing models which will help to advance the understanding of the behavioral neurobiology of health and disease is the identification of behavioral traits which might increase vulnerability to dysfunction. Those monkeys which score highly on the trait of "behavioral inhibition" are perhaps the most obvious, as their strongly inhibited behavior in response to the novel environment clearly indicates a potential risk for anxious behavior and social phobia in the peer group cage. On the basis of more than three decades of observational study with this species, such animals are historically highly vulnerable to isolation and premature death in the social environment. Although only a proportion of predisposed individuals will go on to develop overt disorder, these studies lay a foundation for beginning to evaluate the extent to which early interventions, whether pharmacological or environmental, may modulate the expression of dysfunctional behavioral tendencies.

REFERENCES

Ågren H, Mefford IN, Rudorfer MV, Linnoila M, Potter WZ. 1986. Interacting neurotransmitter systems: A non-experimental approach to the 5-HIAA-HVA correlation in human CSF. J Psychiatr Res 20: 175-193.

Altmann J. 1974. Observational study of behavior: sampling methods. Behavior 49: 227-267.

Anderson GM, Young JG, Dohen DJ. 1979. Rapid liquid chromatographic determination of tryptophan, tyrosine, 5-hydroxyindole acetic acid and homovanillic acid in cerebrospinal fluid. J Chromatogr 164: 501-505.

Anderson GM, Young JG, Cohen DJ, Shaywitz BA, Batter DK. 1981. Amperometric determination of 3-methyoxy-4-hydroxyphenylethyleneglycol in human cerebrospinal fluid. J Chromatogr 222: 112-115.

Andrews MW, Rosenblum LA. 1993. Assessment of attachment in differentially reared infant monkeys (*Macaca radiata*): Response to separation and a novel environment. J Compar Psychol 107: 84-90.

Beninger RJ. 1983. The role of dopamine in locomotor activity and learning. Brain Res 287: 273-196.

Bolig R, Price CS, O'Neill L, Suomi S. 1992. Subjective assessment of reactivity level and personality traits of rhesus monkeys. Intl J Primatol 13: 287-306.

Buirski P, Kellerman H, Plutchik R, Weininger R. 1973. A field study of emotions, dominance, and social behavior in a group of baboons (papio anubis). Primates 14: 67-78.

Cameron JL, Becanu S, Coleman KD, Dahl RE, Devlin BJ, Rogers JA, Ryan ND, Williamson DE. 2003. Dissociating components of anxious behavior in young rhesus monkeys. A precursor to genetic studies. In: Gorman JM, ed., Fear & Anxiety: Benefits of Translational Research. American Psychiatric Press, Washington DC. p 211-226.

Capitanio JP. 1999. Personality dimensions in adult rhesus macaques: prediction of behaviors across time and situation. Amer J Primatol 47:299-320.

Carlsson A. 1993. On the neuronal circuitries and neurotransmittes involved in the control of locomotor activity J Neural Transm (Suppl. 1) 40: 1-12.

Caspi A, Harrington HL, Milne B, Amell JW, Theodore RF, Moffitt TE. 2003. Children's behavioral styles at age 3 are linked to their adult personality traits at age 26. J Personality 71: 495-513.

Caspi A, Hernry B, McGee RO, Moffit TE, Silva PA. 1995 Temperamental origin of child and adolescent behavior problems: from age three to age fifteen. Child Dev 66: 55-68.

Chudasama Y, Robbins TW. 2004. Psychopharmacological approaches to modulating attention in the five-choice serial reaction time task: implications for schizophrenia. Psychopharmacology (Berl). 174:86-98.

Clarke AS, Boinski S. 1995. Temperament in nonhuman primates. Amer J Primatol 37:103-125.

Chamberlain B, Ervin FR, Pihl RO, Young SN. 1987. The effects of raising or lowering tryptophan levels on aggression in vervet monkeys. Pharmacol Biochem Behav 28: 513-510.

Cloninger CR, Svrakic DM, Przybeck TR. 1993. A psychobiological model of temperament and character. Arch Gen Psychiatry 50: 975-990.

Cools AR, Brachten R, Heeren D, Willemen A, Ellenbroek B. 1995. Search after neurobiological profile of individual-specific features of Wistar rats. Brain Res Bull 24: 49-69.

Costa PT, Jr, McCrae RR. 1992. Four ways five factors are basic. Personality Individ Diff 13: 653-665; 861-865.

Dellu F, Piazza PV, Mayo W, Le Moal M, Simon H. 1996. Novelty-seeking in rats--biobehavioral characteristics and possible relationship with the sensation-seeking trait in man. Neuropsychobiology 34:136-45.

Desbiolles C, Ervin FR, Mérette C, Young SN, Palmour RM Behavioral traits in vervet monkeys: I. Social group behavior during adolescence, submitted in parallel.

Desbiolles C, Ervin FR, Mérette C, Young SN, Palmour RM Behavioral traits in vervet monkeys: III. Response of adolescent animals to a novel environment, submitted in parallel.

Dillon JE, Raleigh MJ, McGuire MT, Bergin-Pollack D, Yuwiler A. 1992. Plasma catecholamines and social behavior in male vervet monkeys (*Cercopithecus aethiops sabaeus*). Physiol Behav 973-977.

DiMascio A, Barrett J. 1965. Comparative effects of oxazepam in "high" and "low" anxious student volunteers. Psychosomatics 6:298-302.

Eysenck HJ. 1979. Personality factors in a random sample of the population. Psycholog Rep 44: 1023-1027.

Eysenck HJ. 1991. Dimensions of personality: 16, 5 or 3?--Criteria for a taxonomic paradigm. Personality Individ Diff 12: 773-790

Fairbanks LA. 2001. Individual differences in response to a stranger: Social impulsivity as a dimension of temperament in vervet monkeys (Cercopithecus aethiops sabaeus). J Comp Psychol 115: 22-28.

Goldberg LR. 1992. The development of markers for the big-five factor structure. Psychol Assess 4: 26-42.

Goldsmith HH, Buss AH, Plomin R, Rothbart MK, Thomas A, Chess S, Hine RA, McCall RB. 1987. Roundtable: What is temperament? Four approaches. Child Development 58: 505-529.

Goldman-Rakic PS, Rakic P. 1998. The cortical dopamine system: role in memory and cognition Adv Pharmacol 42:707-11.

Graham F, Rutter M, George S. 1978. Temperamental characteristics as predictors of behavior disorders in children. Am J Orthopsychiatry 43: 328-329.

Gray JA. 1979. Emotionality in male and female rodents. Brit J Psychol 70: 425-440.

Gray JA. 1987. The Psychology of Fear and Stress (2nd ed) Cambridge, England: Cambridge University Press.

Heath-Lange S, Ha JC, Sackett GP. 1999. Behavioral measurement of temperament in male nursery-raised infant macaques and baboons. Amer J Primatol 47: 43-50.

Higley JD, Suomi SJ. 1989. Temperamental reactivity in non-human primates. In: Kohnstamm GA, Bates JE, Rothbart MK, eds. Temperament in Childhood. New York: John Wiley & Sons. p 153-167.

Kagan J. 1989. Temperamental contributions to social behavior. Amer Psychologist 44: 688-674.

Kagan J, Resnick JS, Snidman N. 1987. The physiology and psychology of behavioral inhibition in children. Child Dev 58:1459-73.

Kagan J, Resnick JS, Snidman N. 1988. Biological bases of childhood shyness. Science 240: 167-171.

Kagan J, Reznick JS, Snidman N, Gibbons J, Johnson MO. 1988. Childhood derivatives of inhibition and lack of inhibition to the unfamiliar. Child Dev 59:1580-9.

Kagan J, Reznick JS, Gibbons J. 1989. Inhibited and uninhibited types of children. Child Dev 60:838-45.

Kagan J, Snidman N. 1991. Temperamental factors in human development. Am Psychol. 46:856-62.

Kagan J, Zentner M. 1996. Early childhood predictors of adult psychopathology. Harv Rev Psychiatry 3: 341-350.

Kalin NH, Shelton SE. 1989. Defensive behaviors in infant rhesus monkeys: Environmental cues and neurochemical regulation. Science 243: 1718-1721.

Kalin NH, Shelton SE, Rickman M, Davidson RJ. 1998. Individual differences in freezing and cortisol in infant and mother rhesus monkeys. Behav Neurosci 122: 251-254.

Kalin NH, Shelton SE, Takahashi LK. 1991. Defensive behaviors in infant rhesus monkeys: Ontogeny and context-dependent selective expression. Child Develop 62: 1175-1183.

Kraemer GW. 1985. The primate social environment, brain neurochemical changes and psychopathology. Trends Neuro Sci 8: 339-40.

Kraemer GW, Ebert MH, Schmidt DE, McKinney WT. 1989. A longitudinal study of the effect of different social rearing conditions on cerebrospinal fluid norepinephrine and biogenic amine metabolites in rhesus monkeys. Neuropsychopharmacol 2: 175-189.

Livesley WJ, Jang KL, Vernon PA. 1998. Phenotypic and genetic structure of traits delineating personality disorder. Arch Gen Psychiatry 55: 941-948.

Marteau P, Caine N, Candland D. 1985. Reliability of the Emotions Profile Index Primate form with Papio hamdryas, Macaca fuscata and two Samimiri species. Primates 26: 501- 505.

Matheny AP, Wilson RS, Nuss SM. 1984. Toddler temperament: stability across settings and over ages. Child Dev 55: 1200-1213.

Maziade M, Coté R, Boudreault M, Thivierge J, Capéraà P. 1984. The New York longitudinal studies model of temperament: gender differences and demographic correlates in a French-speaking population. J Am Acad Child Adoles Psychiatry 23: 582-587.

Maziade M, Caron C, Coté R, Mérette C, Bernier H, Laplante B, Boutin P, Thivierge J. 1990. Psychiatric status of adolescents who had extreme temperaments at age 7. Am J Psychiatry 147: 1531-1536.

Maziade M, Coté R, Thivierge J, Boutin P, Bernier H. 1989. Significance of extreme temperament in infancy for clinical status in preschool years. II: patterns of temperament change and implications for the appearance of disorders. Brit J Psychiatr 154: 544-551.

McGuire MT, Raleigh MJ, Pollack DB. 1994. Personality features in vervet monkeys: the effects of sex, age, social status, and group composition. Amer J Primatol 33:1-13.

Moskowitz DS, Pinard G, Zuroff DC, Annable L, Young SN. 2001. The effect of tryptophan on social interaction in every day life: A placebo-controlled study Neuropsychopharmacol 27: 277-289.

Moskowitz DS, Schwartzman AE. 1989. Painting group portraits: Studying life outcomes for aggressive and withdrawn children. J Personality 57: 723-746.

Palmour RM, Young SN, Baker GB, Ervin FR. 1998. Effects of acute tryptophan depletion and acute tyrosine/ phenylalanine depletion on CSF amine metabolite levels and voluntary alcohol consumption in vervet monkeys. Psychopharmacol 136: 1-7.

Piazza PV, Deminiere JM, Maccari S, Mormede P, Le Moal M, Simon H. 1990. Individual reactivity to novelty predicts probability of amphetamine self-administration. Behav Pharmacol 1:339-345.

Raleigh MJ, McGuire MT, Brammer GL, Pollack DB, Yuwiler A. 1991. Serotonergic mechanisms promote dominance acquisition in adult male vervet monkeys. Brain Res 559: 181-190.

Redmond DE. 1987. Studies of the nucleus locus coeruleus in monkeys and hypotheses for neuropsychopharmacology. In Meltzer HY, ed., Psychopharmacology: The Third Generation of Progress. New York, Raven Press. p 967-975.

Resnick JS, Kagan J, Snidman N, Gersten M, Baak K, Rosenberg A. 1986. Inhibited and uninhibited children: a follow-up study. Child Dev 57: 660-689.

Robbins TW. 1997. Arousal systems and attentional processes. Biol Psychol 45: 57-75.

Rothbart MK. 1981. Measurement of temperament in infancy. Child Development 52: 569-578.

Rothbart MK, Derryberry D. 1981. Development of individual differences in temperament. Adv Developmental Psychol 1: 37-86.

Rothbart MK, Posner MI. 1985. Temperament and the development of self-regulation. In: Hartlage LC, Telzrow CF, eds., The Neuropsychology of Individual Differences: A Developmental Perspective. New York: Plenum. p 933-123.

Sawaguchi, T. & Goldman-Rakic, P. 1991. D1 dopamine receptors in prefrontal cortex: involvement in working memory. Science 251: 947-950.

Schneider ML, Moore CF, Suomi SJ, Champoux M. 1991. Laboratory assessment of temperament and environmental enrichment in rhesus monkey infants (*Macaca mulatta*). Am J Primatol 25:137-155.

Schneider ML, Suomi SJ. 1992. Neurobehavioral assessment in rhesus monkey neonates (macaca mulatta): developmental changes, behavioral stability, and early experience. Inf Behav Develop 15, 155-177.

Schneirla TC. 1959. An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In: MR Jones, ed. Nebraska Symposium on Motivation, Vol 7, U Nebraska Press. p 1-42.

Schwartz CE, Wright CL, Shin LM, Kagan J, Rauch SL. 2003. Inhibited and uninhibited infants "grown up": Adult amygdalar response to novelty. Science 300: 1952-1953.

Stevenson-Hinde J, Zunz M. 1978. Subjective assessment of individual monkeys. Primates 19:473-482.

Suomi SJ. 1981. Genetic, maternal, and environmental influences on social development in rhesus monkeys. in: Chiarelli AB, Corrunccini RS, eds, Primate Behavior and Sociobiology. New York, Springer Verlag. p 81-87.
Suomi SJ. 1986. Anxiety-like disorders in young non-human primates. In: Gittelman R, ed., Anxiety Disorders of Childhood. New York, NY: Guilford Press. p 1-23.

Suomi SJ. 1991. Uptight and laid-back monkeys: Individual differences in the response to social challenges. In: Brauth SE, Hall WS, Dooling RJ, eds. Plasticity of Development. Cambridge MA: MIT Press. p 27-50.

Suomi SJ. 1997. Early determinants of behaviour: Evidence from primate studies. Brit Med Bull 53: 170-184.

Tellegren A. 1985. Structures of mood and personality and their relevance to assessing anxiety, with an emphasis on self-report. In: AH Tuma and JD Maser, eds. Anxiety and the Anxiety Disorders. Hillside NJ: Erlbaum. p 681-706.

Thomas A, Chess S. 1968. Temperament and Behavior Disorders in Children. New York: New York University Press. p 64-67.

Thomas A, Chess S. 1977. Temperament and development. New York: Brunner/Mazel.

Torgersen AM. 1982. Influence of genetic factors on temperament development in early childhood. In: Temperamental Differences in Infants and Young Children, Ciba Foundation Symposium 89: 141-154.

Williams GV, Goldman-Rakic PS. 1995. Modulation of memory fields by dopamine D1 receptors in prefrontal cortex. Nature 376:572-5.

Williamson DE, Coleman K, Bacanu S-A, Devlin BJ, Rogers J, Ryan ND, Cameron JL. 2003. Heritability of fearful-anxious endophenotypes in infant rhesus macaques: A preliminary report. Biol Psychiatr 53: 284-291.

Young SN, Ervin FR. 1989. Cerebrospinal fluid measurements suggest precursor availability and sex are involved in the control of biogenic metabolism in a primate. J Neurochem 42: 1570-1573.

TABLE I Behavioral Repertoire in Novel Environment Testing

Behavior	*Description*
Locomotion	Walking or running on the ground
Climb	Climbing along the sides and/or ceiling of the cage
Eat/Pick/Forage	Activities related to eating
Investigate object	Approaching and smelling or watching a foreign object (example: mirror, rope or pole)
Oral Exploration	Exploring objects and cage wall with mouth and/or tongue
Manual Exploration	Exploring objects and cage wall with hands
Freeze	Immobilized and closing eyes as if falling asleep
Fixed Stare	Immobile while watching straight ahead at nothing specific
Vocalize	Repertoire of vocalizations ranging from cooing to cackling
Threaten Observer	Antagonistic interaction with the observer, involving any of the following behaviors: raising eyebrows, lunging head forward, gaping
Spread-eagle	Looking out or at the observer from a position in the top back corner of the cage; arms and legs spread out in a tense erect position.
Watch Observer	Watching the observer (with no underlying signs of threat)
Look Around	Moving head around, looking in different directions with relaxed muscle tone
Autogroom	Licking and picking at his own fur
Leap	Jumping from one part of the cage to another
Pace	Walking or running repetitively back and forth on the cage bottom.

TABLE 2 ***Eigenvalues and proportional variance for significant factors emerging from analysis of initial and repeat exposure to a novel test environment***

	Eigenvalue magnitude	Proportional variance
Factor 1	3.164	0.244
Factor 2	1.489	0.115
Factor 3	1.243	0.096
Factor 4	1.216	0.094

Data obtained from factor analysis (orthogonal solution, varimax rotation) of behaviors emitted during a 15 minute exposure to a novel cage environment, as detailed in the text. Each animal was tested twice, 10 days apart, and behavioral measures were cumulated across trials. The focal animal method of scoring was used, as described further in methods, with a new behavior scored every 10 seconds. After initial examination of eigenvalues and scree plots, the solution was constrained to four factors.

TABLE 3 *Factor loadings for replicate testing of 216 vervet monkeys in a novel environment*

	Factor 1	Factor 2	Factor 3	Factor 4
Locomotion	**0.612**	-0.022	0.007	-0.216
Climb	**0.771**	-0.004	-0.280	0.034
Investigate object	**0.706**	-0.039	0.082	-0.002
Eat/pick/forage	**0.808**	-0.180	-0.230	*0.252*
Oral exploration	**0.494**	0.004	-0.120	**0.494**
Vocalize	**0.343**	*0.257*	0.004	***-0.540***
Threaten observer	-0.053	**0.803**	-0.165	-0.020
Spread-eagle	-0.114	**0.282**	-0.134	-0.007
Freeze	-0.034	-0.193	**0.660**	-0.060
Fixed stare	-0.457	-0.119	**0.728**	-0.014
Watch observer	-0.135	*0.252*	0.239	**0.478**
Manual exploration	0.158	-0.013	-0.126	**0.611**
Look around	-0.439	***-0.669***	***-0.538***	-0.075

Primary loadings are in BOLD, and secondary loadings are shown in italics

Loadings of specific behaviors on all factors with eigenvalues greater than 1, obtained from factor analysis (orthogonal solution, varimax rotation) of behaviors emitted during a 15 minute exposure to a novel cage environment, as detailed in the text. Each animal was tested twice, 10 days apart, and behavioral measures were cumulated across trials. The focal animal method of scoring was used, as described further in methods, with a new behavior scored every 10 seconds. Primary loadings are in BOLD, and secondary loadings are shown in italics

FIGURE 1 Testing cage

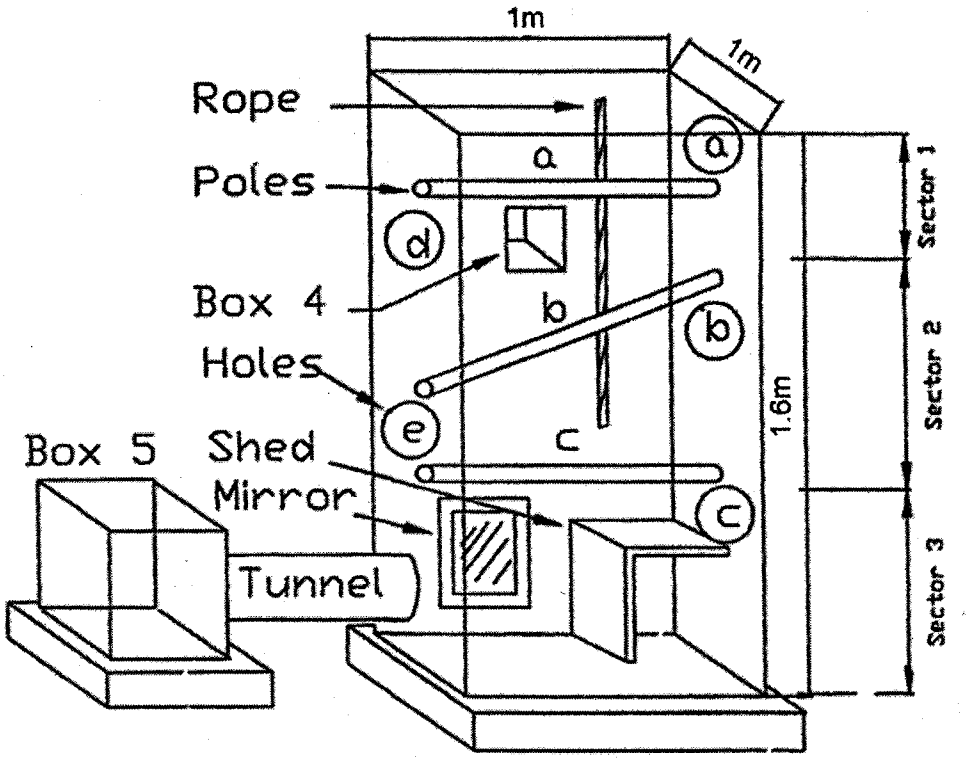


Figure 1. The novelty testing cage. The physical parameters of the novelty test cage are 6' high x 3' 7'' deep x 2'' 7' wide. The subject was introduced in the testing cage by a back door. Three of the sides were made of solid wood and entirely meshed with chicken wire from the inside. The fourth side facing the observer was only constructed of chicken wire in order to monitor the infant during the testing bout. In addition, the cage included three perches, two exits leading to other compartments, six holes on the wooden sides in order to hold rewards (i.e. bananas), a square mirror, a small shed on the floor of the cage, and a 3 foot rope hanging from the middle of the ceiling.

FIGURE 2.

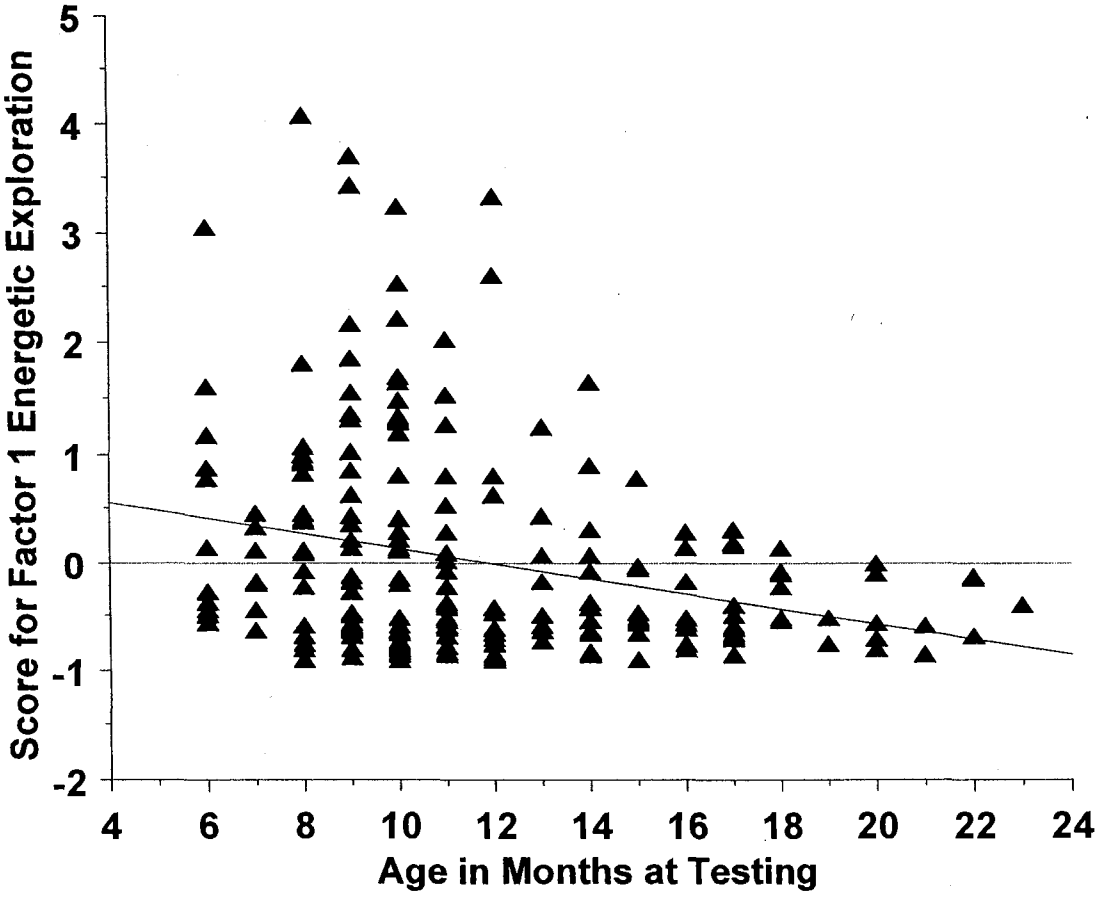


Figure 2. Standardized scores (Z-scores) on Factor 1 ("energetic exploration"), depicted in Panel A, are negatively correlated with average age (in months) at testing in the novelty test cage ($r = -0.234$, $F_{1,214} = 12.4$, $p<0.0005$). Orthogonal factors were extracted by factor analysis, with varimax rotation, from quantitative scores of standard behaviors in 216 young juvenile monkeys tested twice in a novel environment paradigm at approximately 10 day intervals. Monkeys ranged from 6 to 22 months of age at first testing.

FIGURE 3.

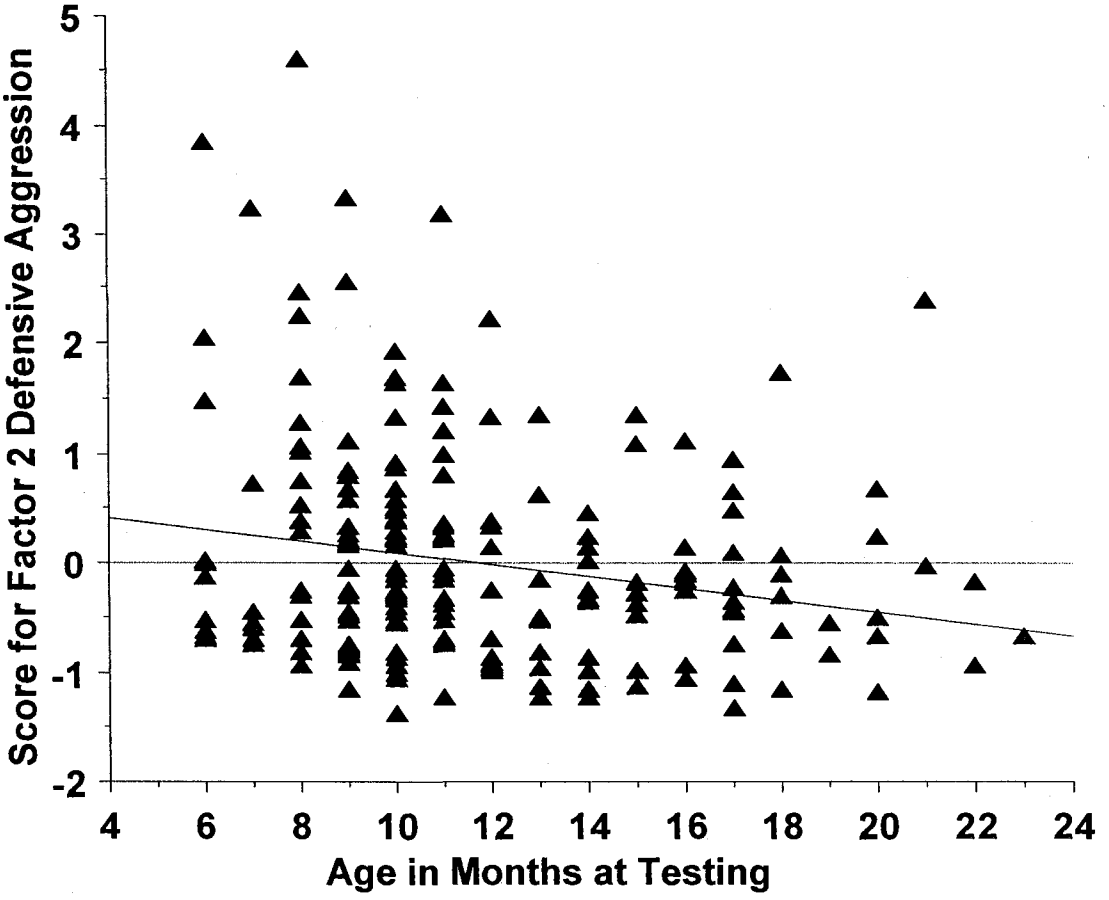


Figure 3. Standardized scores (Z-scores) on Factor 2 ("defensive aggression") are also negatively correlated with average age (in months) at testing ($r = -0.202$, $F_{1,214} = 9.13$, $p<0.003$). Orthogonal factors were extracted by factor analysis, with varimax rotation, from quantitative scores of standard behaviors in 216 young juvenile monkeys tested twice in a novel environment paradigm at approximately 10 day intervals. Monkeys ranged from 6 to 22 months of age at first testing.

FIGURE 4.

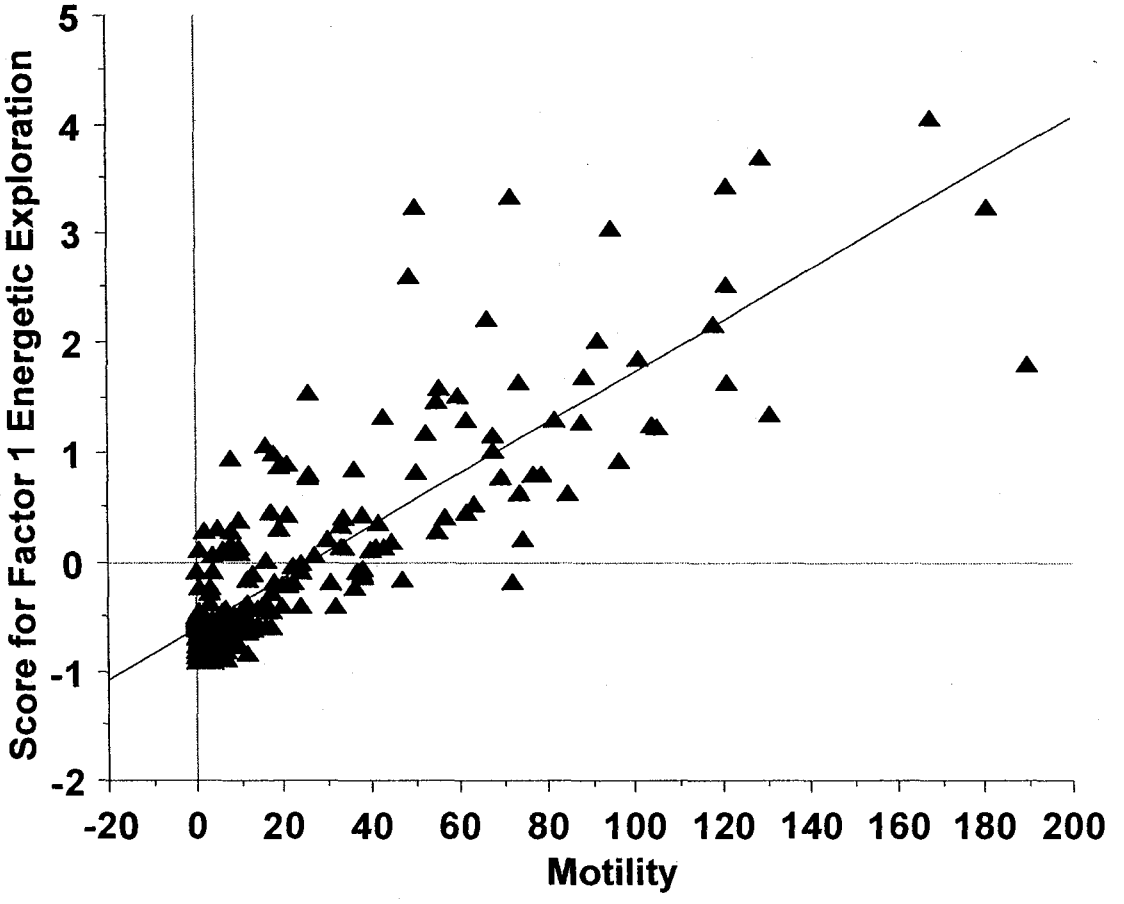


Figure 4. Total motility is positively correlated ($r=0.837$, $F_{1,214} = 499.2$, $p=<0.0001$) with the behavioral trait of "energetic exploration," extracted by factor analysis from quantitative scores of standard behaviors in 216 young juvenile monkeys tested twice in a novel environment paradigm at approximately 10 day intervals. Monkeys ranged from 6 to 22 months of age at first testing. Factor scores are plotted as Z-scores for each individual.

FIGURE 5.

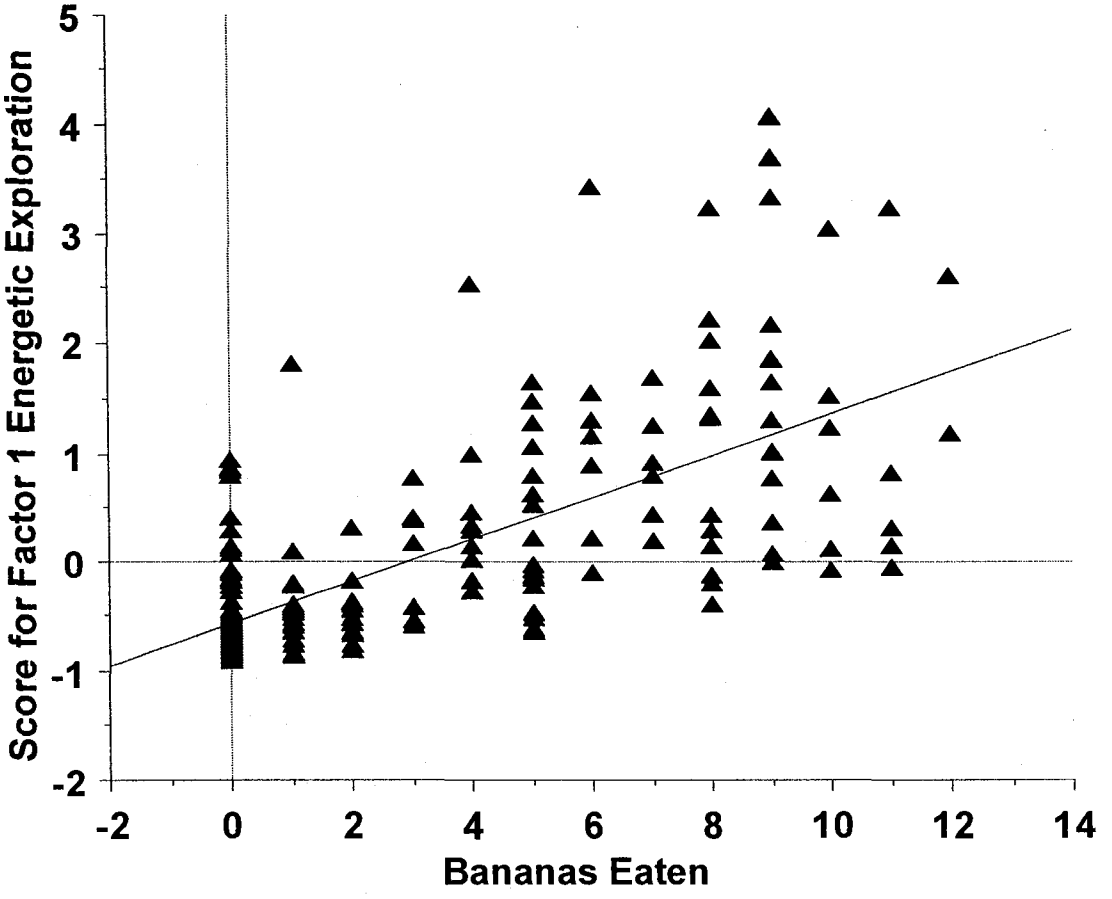


Figure 5. Factor 1 ("energetic exploration") is also positively correlated with the total number of rewards found ($r = 0.739$, $F_{1,214} = 117.7$, $p = <0.0001$) and [data not shown] the number of rewards eaten ($r = 0.687$, $F_{1,214} = 191.7$, $p = <0.0001$). As described before, factor scores (Z-scores) were extracted from from quantitative scores of standard behaviors in 216 young juvenile monkeys tested twice in a novel environment paradigm at approximately 10 day intervals. Monkeys ranged from 6 to 22 months of age at first testing.

FIGURE 6.

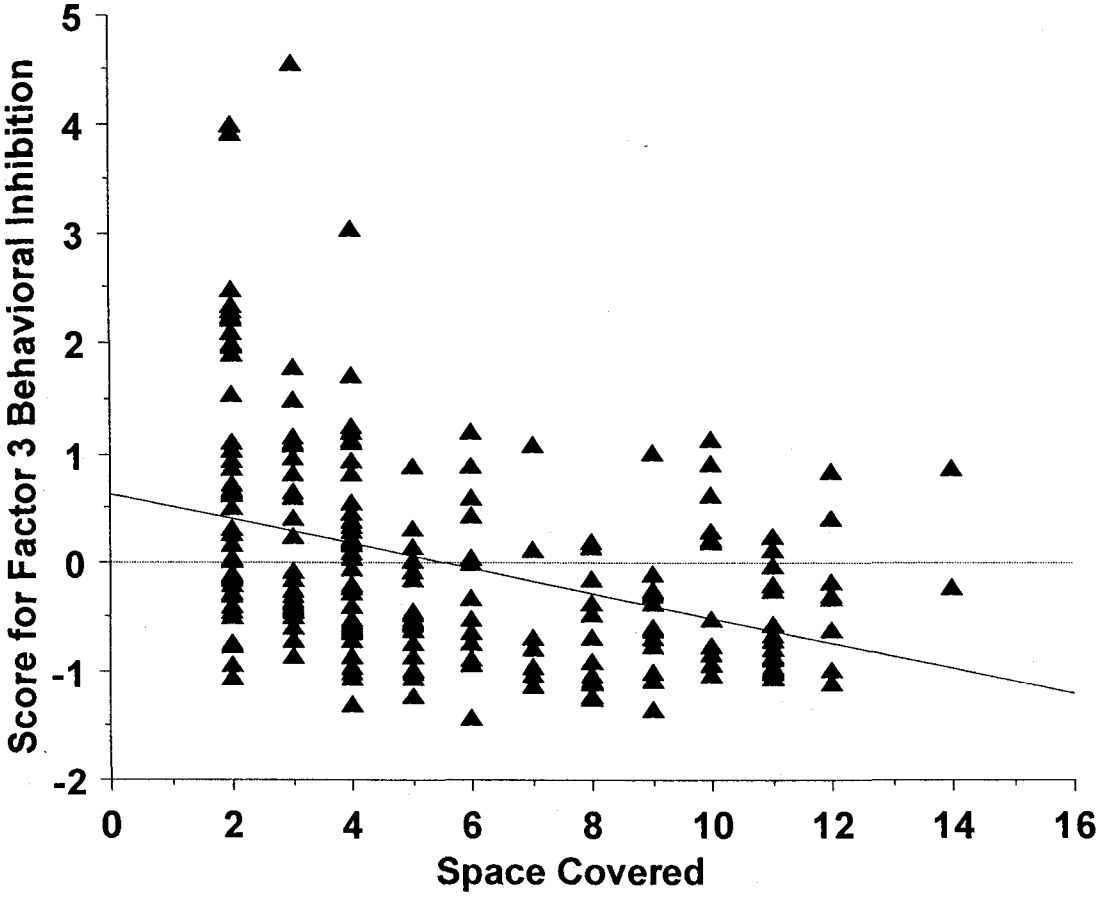
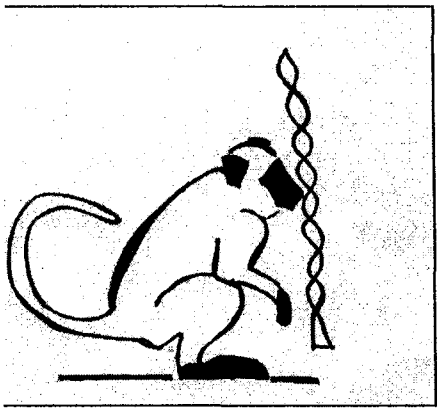
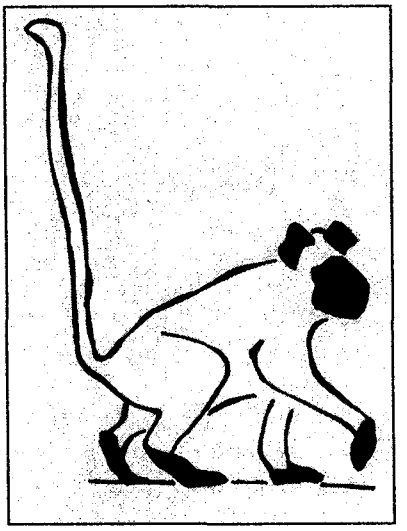


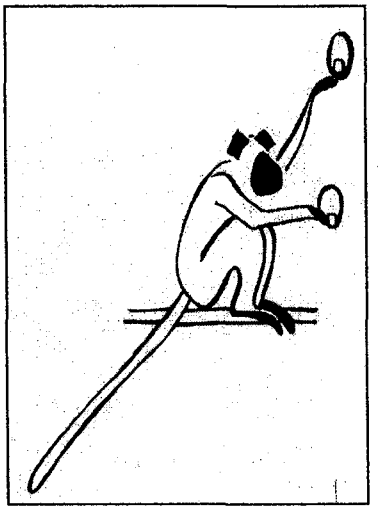
Figure 6. The amount of space covered in the test case is negatively associated (r=0.372, $F_{1,214}$ = 34.4, p=<0.0001) with Factor 3 ("behavioral inhibition"), extracted by factor analysis from quantitative scores of standard behaviors in 216 young juvenile monkeys tested twice in a novel environment paradigm at approximately 10 day intervals. Monkeys ranged from 6 to 22 months of age at first testing. Factor scores are plotted as Z-scores for each individual.

Illustrations: Response to a Novel Environment during Late Infancy

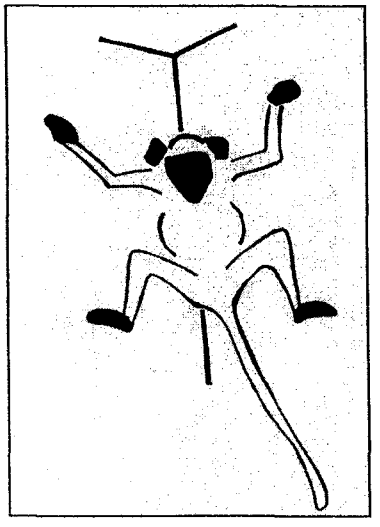
Energetic Exploration (Factor 1)

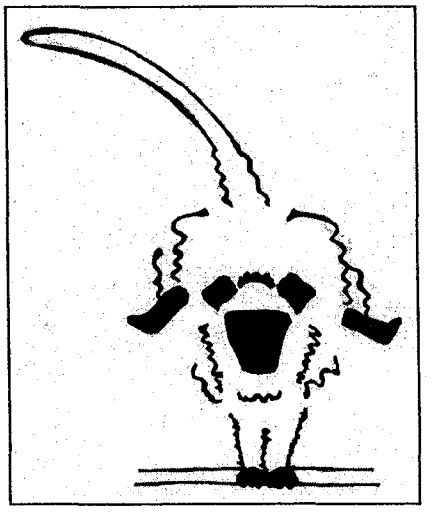




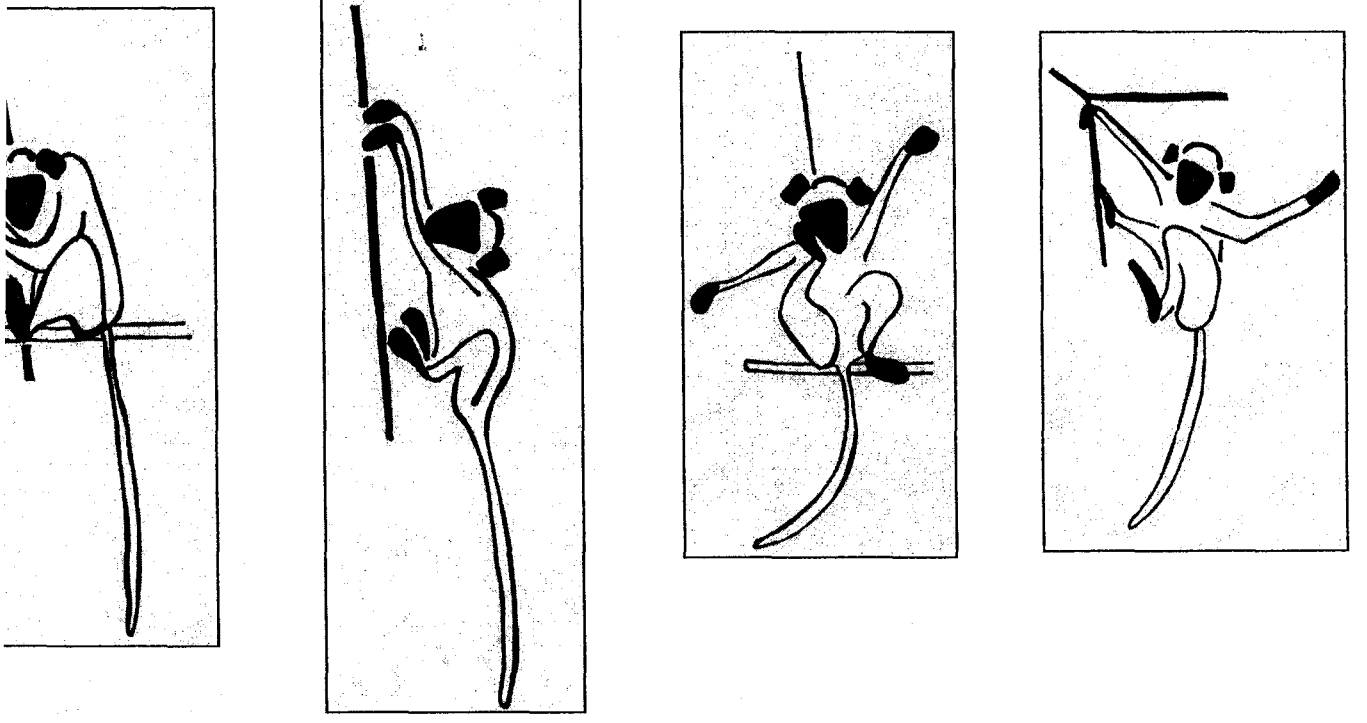


Defensive Aggression (Factor 2)

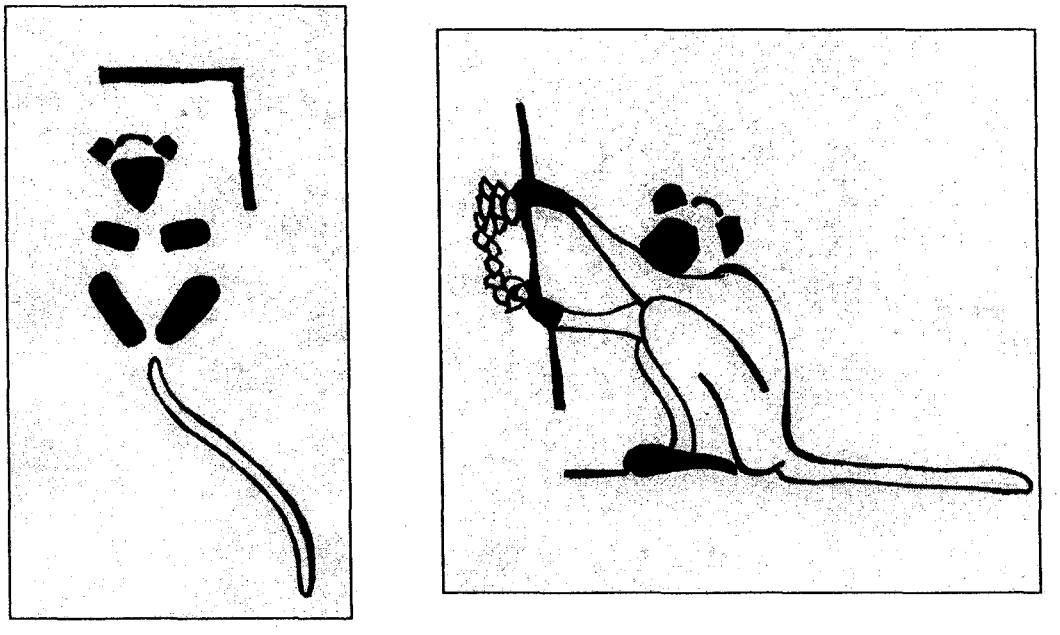




Behavioral Inhibition (Factor 3)



Cautious Exploration (Factor 4)



BRIDGE II

During the course of this longitudinal study, by the time the subjects followed reached adolescence, our research group had already collected social data for each given animal at two specific time points, as well as data systematically measuring their reaction levels and overall performances in a novelty challenge condition. Monkeys were subjected to this first novelty test during late infancy. The goal of testing these monkeys at an early age was to successfully identify the expression of underlying behavioral traits, which could become more difficult to observe with time as animals learn to mask or modify their initial intrinsic states in order to adapt to their environment.

To optimize an interesting and informative range of individual variability, the test paradigm designed by our research group, considered both the species of monkey as well as the subject's developmental age. The behavioral dimensions derived by this metric, depicted different levels of exploration and fearfulness. These two categories have shown evidence of stability across time, especially at the extremes of the distribution, in various primate and non-human primate longitudinal studies. Monkeys who tend to be curious and explorative during infancy, demonstrate these same attributes in adolescence. Similarly, monkeys who are fearful during infancy also remain this way across time. Based on these findings, we asked ourselves what we could implement in our study to verify whether these traits were stable in our subjects. We concluded that in order to answer this question it would be essential for our research group to design another novelty test paradigm, this time more appropriately suited for juveniles testing.

The juvenile testing cage needed to have as many similarities to the nursery testing cage as possible so as to facilitate the comparison of performances of each animal at two different time points. Like in the nursery condition, juveniles would be individually tested on two separate trials, and satisfy a performance component by searching for rewards in an open space. It was essential for the juvenile testing cage to be physically bigger than the nursery cage to match the monkey's growing size. A higher level of difficulty was implemented in the design to challenge the juvenile's precocious

development. The monkeys had already been subjected to a novelty challenge. The testing cage was composed of two sections. The first section was a tunnel like maze leading up a plastic pipe into the second section, an open space bated with rewards. This compartmentalization serves to disguise what would otherwise be an identical cage to the ones these juveniles live in. The plastic pipe linking both sections is a position of great individual variability as it becomes a source of stress for many animals. Some monkeys impulsively or nonchalantly move through it, while others, adamantly resist despite a certain level of coaxing on the part of the experimenter, and therefore must be transferred to the second section by hand. The resulting range of reactions suggests that this experimental design is a source of interesting information, which will further serve to profile the individual animals. The goal of this second novelty test is not only to derive behavioral traits, but also to verify whether there could be a significant correlation, thus evidence of stability between the nursery and jungle gym conditions.

CHAPTER V

BEHAVIORAL TRAITS IN VERVET MONKEYS:

III. RESPONSE OF ADOLESCENT ANIMALS TO A NOVEL ENVIRONMENT

BEHAVIORAL TRAITS IN VERVET MONKEYS: III. RESPONSE OF ADOLESCENT ANIMALS TO A NOVEL ENVIRONMENT

Caroline Desbiolles[1], Frank R. Ervin[2,4], Simon N. Young[2], Chantal Mérette[5] and Roberta M. Palmour[1,2,3,4]

[1]Departments of Biology, [2]Psychiatry & [3]Human Genetics, McGill University, Montréal, Québec, Canada; [4]Behavioural Science Foundation, St Kitts, Eastern Caribbean; [5]Centre de Récherche, Hôpital Robert-Giffard, U Laval, Beauport Québec Canada

Address for correspondence:

Roberta M. Palmour, PhD
Department of Psychiatry, McGill University
1033 Pine Ave West, #326
Montreal Qué H3A 1A1
CANADA
TEL: 514-398-7303 FAX: 514-398-4370
roberta.palmour@mcgill.ca

Acknowledgment: This work was supported by grants from the Canadian Institutes of Health Research (MT-14526 to RMP, FRE; MOP-15005 to SNY) and by generous funding from Behavioural Sciences Foundation, St Kitts. We thank the staff of Behavioral Sciences Foundation (especially Amy Beierschmitt, DVM and Mrs. Dora Louard) for their tireless devotion to animal care and handling, and Franceen Lenoff (McGill University) for skilled technical assistance.

The break down of the contributions for the three papers included in the thesis were made by the following authors:

The studies were designed in collaboration by Caroline Desbiolles, Dr. Roberta Palmour and Dr. Frank Ervin.

The statistical analysis was supervised by Chantale Mérette.

The CSF analysis was done by Dr. Simon Young.

All authors helped in the interpretation of the results.

Caroline Desbiolles and Dr. Roberta Palmour wrote the final manuscripts, which were revised by Dr. Frank Ervin and the other authors.

ABSTRACT

In companion papers, we reported the identification of behavioral traits in four successive birth cohorts of captive vervet monkeys, by factor analysis of focal social group observations (Desbiolles et al., 2006a) or of behavioral response to a novel environment during infancy (Desbiolles et al., 2006b). In the present study, we tested the same animals when adolescents in an investigator-designed analogue of the open field environment, enriched with problem-solving opportunities and hidden food rewards. In these adolescent animals, we extracted four orthogonal factors (varimax rotation) with Eigenvalues > 1.0 that explained 60.1% of the variance in behavior. These behavioral dimensions, termed "confident," "cautious, "exploratory," and "defensive" were related to measures such as motor activity and resembled (at least at a conceptual level) behavioral dimensions previously described in both the human and non-human primate literatures. A second-order factor analysis of the individual scores derived from this novel environment paradigm, together with factor scores from the earlier nursery novelty test (Desbiolles et al., 2006b), yielded four higher-order reactivity traits ("exploratory," "confident-to-inhibited," "defensive" and "cautious") that explained 61.6% of the variance. This analysis provides initial evidence for continuity in behavioral traits from late infancy to adolescence and suggests a substantial stability of trait expression for individuals across time. Taken together, these investigations provide a baseline for a longitudinal evaluation of social and health outcomes in this population, and lay the groundwork for identification of behavioral tendencies which predispose to later psychopathology.

INTRODUCTION

The novel environment paradigm is well accepted and often used in non-human primate and rodent studies (Blizard, 1981; Bolig et al., 1992; Capitanio et al., 1999; Clarke and Boinski, 1995; Schneider et al., 1991; Spencer-Boothe and Hinde, 1969; Suomi, 1991). By highlighting the underlying behaviors which may be masked in social groups, novel environments afford an objective measure of reactivity levels which may be difficult to extract from social data. This paper is the third in a series reporting an integrated longitudinal study of four successive birth cohorts of captive vervet monkeys (*Chlorocebus aethiops*), the goal of which was to identify behavioral traits under social and novelty conditions (Desbiolles et al., 2006a, b). The previous papers in this series were concerned with response to a different novel environment designed for testing younger animals (Desbiolles et al., 2006b) and with social behavioral measures collected during the juvenile period (18 – 36 months - Desbiolles et al., 2006a). The present study was carried out in the same animals, tested at an older age (~30 months of age), and reports behavioral response patterns of socially-housed juvenile vervets observed during two brief exposures to a novel enriched environment.

While novelty testing paradigms may currently be underrepresented in the primatological literature there is little doubt that they are on the rise. Some components of novelty testing in primates, such as Suomi's play-room exposure (Suomi, 1986; Higley and Suomi, 1989), the free play test from the Cameron et al. (2003) battery or the open-field apparatus of Morgan et al. (2000), are derived directly from rodent tests such as the open-field or elevated plus-maze (Carola et al., 2002). Other challenges utilize social interactions with unknown conspecifics (Suomi, 1991; Fairbanks, 2001) or with human primates (eg., Kalin and Shelton, 1989; Kalin et al., 1998; Heath-Lange et al., 1999). Rounding out these batteries are items such as response to capture (eg., Heath-Lange et al., 1999), willingness to take a novel food-stuff (Cameron et al., 2003) and response to social separation (Boccia et al., 1994; Kraemer, 1997). Preceding, and setting the stage for our own study was the work of Bolig et al (1992) who used two separate modal approaches to assess the personality traits in 22 rhesus monkeys with the goal of identifying relationships between reactivity levels and behavioral dimensions. Of particular interest to us in this work was assessing the stability between behavioral traits derived from the

novelty paradigm and those identified in the infant novelty paradigm described previously for these same birth cohorts (Desbiolles et al., 2006b).

The primary goal of this study was thus to challenge all animals previously tested at a younger age to an age-appropriate version of the initial standardized challenge condition, and to attempt to extract interpretable behavioral traits from the observed behavioral scores, as reported in two earlier reports (Desbiolles et al. 2006a, b). In addition to standardizing the environment the jungle gym setting differs from the original nursery novelty test in two ways: (i) with the addition of an increased degree of difficulty, created by incorporating a maze like component meant to further challenge problem-solving skills; (ii) with a much larger surface area in order to facilitate motility in these almost fully-grown monkeys. The secondary goal was to determine whether traits identified during the adolescent novelty testing (Desbiolles et al., 2006b) would be similar to those identified in the nursery testing paradigm and whether individual animals would display stability in their behavioral patterns.

METHODS

Animal Subjects

The juvenile (105 female, 101 male) vervet monkeys (*C.aethiops)* studied in this test paradigm comprised four succesive birth cohorts described in greater detail in the two preceeding papers (Desbiolles et al., 2006a, b). Each animal was born in an outdoor social group enclosure at the Behavioral Science Foundation (St.Kitts) colony between 1996 and 1999. All infants lived with their parents in the harem group until approximately 6 to 8 months of age, at which time they were transferred to a nursery for husbandry purposes. At about one year they were moved into peer groups of no more than 8 animals and lived in these groups until sexual maturity. The present experiment was conducted approximately 8 months after peer group formation. At this time, all animals were either adolescent or in transition from the late juvenile period into adolescence (mean age: 30 ± 4 months).

Throughout this project, care was taken to ensure that all animals had as similar a nutritional environment as possible. In the birth cage, all animals were nursed and began to eat solid food in the species-specific fashion. After being moved to the nursery, Purina Primate Chow was supplied twice a day and fresh water from a piped central supply was available ad lib. In the peer social cages, about 30% of the daily calories were fed between 8 and 9 am, and the main chow feeding occurred was typically between 11 am and 12 noon. The diet was also supplemented with fresh fruit and produce several times weekly. Housing and sanitary conditions met the guideline of the Canadian Council on Animal Care, and the protocols were reviewed and approved by an Institutional Review Board under these auspices.

Experimental Plan

The "jungle gym" environment differed from an earlier novelty test in that the paradigm contained large open and closed spaces (Figure 1), and optimal exploration of space and securing of rewards was intentionally made to be more difficult, taking into account the older age and prior experience of each animal with a novel challenge. Focal animal scoring of behavior was used in the open compartment. Each monkey was tested twice, with the second trial conducted after a rest period of 2 days.

Novelty Testing Cage Physical parameters of the novelty test cage were 8 x 12 x 10 feet (see Figure 1 for more details). The "jungle gym" was subdivided into two distinct physical sections. The first section comprised a closed wooden tunnel stretching along the entire length of the novel cage (12 feet), and half way along the width of the novel cage (5 feet). This tunnel opened into an opaque PVC culvert pipe (diameter, 2 ft) slanted at a 45 degree angle across the mid-line of the open cage segment (12 x 6 x 6 ft) and ended in a 2 x 2 feet wooden box. While in the tunnel or pipe, monkeys could not see out, but they were well adapted to the tunnel from prior experience with the same configuration in the home cage. Five sides of the wooden box were opaque and one was open to the main cage segment. Pieces of banana were scattered on the ground along the entire tunnel section in order to encourage monkeys to move through the tunnel and into the main enclosure. The outer wall of the tunnel was constructed of wire mesh, facilitating observation of animals in the tunnel. The novelty test cage was in a quiet and relatively isolated area of the compound to reduce the extent to which monkeys were distracted by daily husbandry and agricultural activities.

As each monkey exited the wooden box through an opening located on the top, he or she entered the second section of the "jungle gym." This open area had the same dimensions and exterior construction as the standard social group cage in which juvenile monkeys habitually lived. In contrast to the usual cage (which had only perches and climbing apparatus, the "jungle gym" was constructed with additional poles (for climbing or running) positioned across the width of the cage, a small wooden box nestled in the top corner and 10 small plastic containers each holding a reward (i.e. piece of banana). These containers were wired securely to the chain link making up the main cage structure so that they could not be pulled off. The opening of each container was designed to be large enough for the animals to obtain treats, but small enough that a certain amount of precision and dexterity was required.

Procedure for testing. A single social group of monkeys (n = 8) was moved from its home cage to an identical enclosure adjacent to the "jungle gym" the day before the first novelty test occurred. A visual barrier was placed between the housing enclosure and the "jungle gym" enclosure so that animals could not see into the testing environment. Testing occurred between 7 am and 11 am, and food was restricted for at least 2 hours prior to the challenge. In random order, monkeys were individually allowed to enter a single compartment which led to the tunnel section. Each animal was given a maximum of 5 minutes to move from the tunnel segment

through the large pipe and into the wooden box which gave access to the main "jungle gym." A small exit in the ceiling of the wooden box allowed the monkey to exit into an open space making up the second section. The monkey was then free to move around the cage and look for rewards. Focal observations (Altmann, 1974) were collected at 10 sec intervals for the next 5 min period. Recorded behaviors are briefly described in Table 1.

Behavioral Observation

Observations were made from a point ten feet in front of the testing cage. The animals were all familiar with the observer from numerous hours of social observation in the natal and juvenile cages as well as their first novelty test paradigm. In addition to recording the observed behavior (Table 1), the spatial location and specific physical habitus of the animal was scored, as described previously (Desbiolles et al., 2006a, b). In addition, we scored the threshold to enter the main (open) compartment and the total motility of the monkey during time in the open cage, and counted the total number of rewards (bananas) obtained in the large open cage (maximum: 10 per trial). With respect to threshold to enter the open compartment, a score of '0' was assigned if the monkey spontaneously ran through the tunnel and up the pipe in less than 5 minutes. A score of '1' would be assigned if an animal required coaxing to leave the tunnel and move up the plastic pipe into the second section. Animals which stayed in the tunnel section for a full 5 minutes, were resistant to coaxing and had to be moved into the open compartment by hand were assigned a score of '2.' Total motility was scored as described in the first paper of this series (Desbiolles et al., 2006a). Briefly, the cage was divided into 27 "virtual" compartments by estimating imaginary lines going across the length and width of the novelty cage, front vs middle vs back. One "motility point" was counted any time the monkey crossed any of these 27 "virtual" compartments into another, throughout the 10 minute bout.

Cerebrospinal fluid Amine Metabolites

During a physical examination conducted within 3 months of Jungle Gym testing, 0.5 ml cerebrospinal fluid (CSF) was collected under ketamine anaesthesia (10 mg/kg, im), by transcutaneous cisternal puncture. Samples were frozen immediately on dry ice, and stored at -70°C until analysis. Amine neurotransmitter precursors (tryptophan) and metabolites (5HIAA: 5-hydroxyindoleacetic acid; HVA: homovanillic acid; MHPG: 3-methyoxy-4-

hydroxyphenylethylene glycol) were determined by HPLC with fluorometric and electrochemical detection (Anderson et al., 1979; Anderson et al., 1980).

Analysis of Data

As in the preceding experiments (Desbiolles et al., 2006a, b), behavioral traits were identified by factor analysis of the focal behaviors summed over the two trials. Prior to conducting this analysis, similar behaviors with low frequencies were combined (eg., walk with run, explore with pick and forage) and data for trials 1 and trial 2 were compared to ensure that the overall behavioral profiles were not significantly different. Thereafter, data from trials 1 and 2 were summed to enhance robustness of the statistical solution. Orthogonal factors were extracted by factor analysis with varimax rotation (StatView V, Systat). The possible correlations (i) between the orthogonal factors and likely covariates, such as gender or age, and (ii) between factors and other quantitative measures such as motility and rewards obtained were evaluated by ANOVA and stepwise linear regression analysis, respectively.

We also evaluated the coherence of traits identified in the jungle gym novelty paradigm and in an earlier novel test paradigm (Desbiolles et al, 2006a) by performing a secondary factor analysis of the factor scores extracted for each individual tested at boh occasions (Livesley et al., 1998).

RESULTS

Factor solution and interpretation

Prior to making the decision to combine the data from separate trials, we first examined the correlations between individual behaviors scored from trials 1 and 2. There were significant between-trial differences for three behaviors [walk/run' ($p < 0.01$), 'look around' ($p < 0.001$) and 'pace' ($p < 0.001$)] and a trend toward a difference for the behavior 'spread-eagle' ($p = 0.07$). Despite minor differences in the order of loadings, the general factor solution was quite similar between trials 1 and 2 (data not shown), and we chose to sum the data across trials to increase the robustness and generalizability of the final solution.

Factor analysis of behavioral data for 206 monkeys tested twice in a novel environment paradigm yielded a 4-factor solution, with satisfactory statistical properties (all Eigenvalues greater than 1; $\chi^2 = 1830.35$, $p < .0001$) and factors exhibiting high face plausibility. This factor solution accounted for 60.1% of the variance (Table 2). An examination of the scree plots also suggested that a 4-factor solution was optimal. All behaviors included in the analysis had commonality estimates > 0.89.

The behaviors loading on each factor are detailed in Table 3. 'Climb' and 'eat' loaded heavily on Factor 1, with a weaker loading for 'look around.' Factor 1 also had a heavy negative loading for 'watch observer' and stereotypic pacing. We interpreted this factor as representing the construct "confident." Factor 2 comprised the behaviors of 'stare ahead,' 'look around' and 'spread eagle' with heavy negative loadings for 'leap' and stereotypic pacing. We labeled this factor "cautious." 'Walk/run,' 'exploration' and 'foraging' loaded on Factor 3, which was interpreted as "exploratory." Finally, 'spread eagle' and 'threaten observer' loaded positively on Factor 4, while 'pace' loaded negatively on this factor. We labeled this factor "defensive aggression."

Relationship of factors to gender and age

None of the factors was significantly related to the sex of the subjects, but linear regression showed that Factors 1 ($r = 0.18$, $p < 0.01$) and 2 ($r = 0.37$, $p < 0.0001$) were positively related to age (Figures 2 and 3). Neither Factor 3 nor Factor 4 varied as a function of age. Age-adjusted factor scores were used in the following analyses of relationships between behavioral traits and other variables.

Relationship of factors to other quantitative behavioural measures

We examined the relationship between factor scores and other quantitative measures by linear regression. There was a significant positive correlation ($r = 0.84$, $p < 0.0001$) between Factor 1 and total rewards found (Figure 4) and a weaker positive correlation with Factor 3 ($r = 0.184$, $p < 0.01$). This is consistent with the observation that monkeys with high scores on Factor 1 ("confident") spent most of their time climbing in the upper third of the cage, visually examining the territory and successfully finding rewards, while monkeys high on Factor 3 ("exploratory") spent more time foraging on the bottom of the cage, and despite a high level of motor activity, did not actively search out or retrieve as many rewards. There was no relation between Factors 2 or 4 and rewards found. For this analysis, rewards were summed over the two trials, but the same patterns of relationship were found for each trial independently (data not shown).

In the course of observations, it became evident that overall motility was significantly related ($r = 0.87$, $p < 0.0001$) to pacing, which was scored at least occasionally in about half of the animals. After adjustment of motility for pace, there remained a positive relationship with Factor 1 ($r = 0.33$, $p < 0.0001$), and a negative relationship with Factors 2 ($r = -0.26$, $p = 0.0002$) and 4 ($r = -0.19$, $p < 0.01$). Thus monkeys with high scores for "confident" generally moved more and covered more physical space, while high-scoring "cautious" monkeys were less mobile. There was no relationship between the motility adjusted measure and Factor 3, consistent with observational notes suggesting that these animals went about their explorations in a calm and unhurried fashion.

Because threshold to enter the main cage was defined nominally, the relationship between this measure and factor scores was evaluated by analysis of variance. Factors 1 ($F_{2,203} = 5.11$, $p < 0.01$) and 2 ($F_{2,203} = 3.84$, $p < 0.02$) were significantly related to willingness to enter

the main cage. Monkeys with high scores for either Factor 1 ("confident") or Factor 2 ("cautious") were less likely to spontaneously enter the main cage section (Figures 5 and 6). Consistent with this finding, and contrary to expectations, monkeys with a score of '0' on the threshold measure did not seek out and find more rewards ($F_{2,203} = 1.27$, $p = 0.28$). With respect to Factor 2 ("cautious"), once in the main compartment, monkeys with high factor scores spent the majority of time staring ahead and looking around, often occupying a spread-eagle position in one of the top corners of the cage. By contrast, monkeys that readily left the tunnel (threshold score of '0') had lower mean scores on both Factors 1 and 2, and tended to spend their time pacing on the bottom of the cage. These observations are consistent with the negative loading of the behavior 'pace' on both Factors 1 (-0.620) and 2 (-0.499).

Habituation between trials 1 and 2

As noted above, in contrast to the findings from the first novelty test conducted at a mean age of 13 months (Desbiolles et al., 2006a), the frequencies of three behaviors in the jungle gym test were significantly different between trials 1 and 2. One behavior related to vigilance ('look around') decreased, while two behaviors related to motor activity ('walk/run,' 'pace') increased. Except for 'walk/run' ($p < 0.01$), these differences were significant at the 0.0001 level. On the one hand, monkeys exposed to a novel environment often spend most of their time scanning the environment ('look around') until such time as their original apprehension has waned, after which they will begin to explore more freely ('walk/run'). However, the increase in pacing during the second trial may indicate increased excitability, or may be a consequence of becoming more comfortable in a new setting, so that inherent traits surface more prominently.

Another example of habituation was the change in threshold to enter the main test cage compartment. In trial 1, only 33 animals spontaneously ran up the plastic pipe during the alloted 5 min time period, but this number increased to 85 in trial 2. There was also a decrease in the number of monkeys which had to be manually transferred to the main test compartment ($n = 24$ for trial 1, $n = 7$ for trial 2). This categorical measure of habituation was significantly related to factor scores for "cautiousness" ($F_{1,179} = 12.98$, $p < 0.001$), as shown in Figure 7.

Relationship of factors to CSF amine metabolites

As in each of the preceding two reports (Desbiolles et al., 2006a, b), possible relationships between CSF amine metabolites and behavioral traits were investigated by multiple regression analysis, after correcting Factors 1 and 2 for the effects of age. The average age at which CSF was sampled from the 206 monkeys was 32.3 ± 3.1 months. There were no effects of gender at this developmental time period, but 5-HIAA varied according to age ($F_{1,203} = 4.8$, $p = 0.03$). The residuals were computed and age-adjusted values were used in all further analyses. In the present study, the partial pairwise correlations were 5-HIAA/HVA = 0.583, 5-HIAA/MHPG = 0.087, HVA/MHPG = 0.060).

Multiple regression analysis showed that the level of MHPG was negatively correlated with Factor 1 ($F_{1,203} = 5.15$, $p < 0.03$), while the level of HVA was negatively correlated with Factor 2 ($F_{1,203} = 4.11$, $p < 0.05$). Levels of amine metabolites were not significantly related to any other factor.

Comparison of the Jungle Gym and Nursery factors

Higher order factors were extracted when individual factor scores from the two (infant, jungle gym) novelty tests were compared to one another by a secondary factor analysis. Complete data was available for 202 monkeys. A (4-factor solution, with satisfactory statistical properties (all Eigenvalues greater than 1; $\chi^2 = 86.51$, $p < .0001$) accounted for 61.6% of the variance (Table 4). The behaviors loading on each factor are detailed in Table 4. "Energetic exploration" from the nursery test paradigm and "exploratory" from the jungle gym load heavily on Factor 1. Factor 3 comprises strong positive loading of "defensive aggression" from both novelty test paradigms. The positive end of "behavioral inhibition" from the nursery novelty test and the negative end of "confident" from the jungle gym constitute Factor 2 in the higher order solution, while "cautious exploration" from the nursery novelty paradigm and "cautious" from the jungle gym load on Factor 4. The relationships of the facets from each novelty test to these higher order factors is self-evident.

DISCUSSION

Summary

The stress of adapting to a novel or challenging situation reveals aspects of behavior in both humans and animals which may be obscured when subjects are observed in their everyday social context. In designing this "jungle gym" paradigm, we tried to construct an age-appropriate (i.e. relatively more demanding) novel environment to contrast with the novelty testing paradigm used earlier to test these same monkeys (Desbiolles et al., 2006b). The major findings of this study are first, that interpretable factors can be derived directly from observational behavior, and, second, that the specific traits identified in this analysis show substantial consistency with the behavioral traits identified in the same individuals tested at a younger age in the nursery testing cage (Desbiolles et al., 2006b). In the present study of 206 vervet monkeys, four factors ('confident' 'cautious' 'exploratory' and 'defensive aggression') explained 60.1% of the proportional variance. Correlations between individual factors and other measures such as age and sex, number of rewards obtained, motility, willingness to enter the main testing cage and cerebrospinal fluid levels of monoamine metabolites enrich the understanding of individual factors and further validate the factor solution. The factors derived in this solution not only conceptually resembled the factors obtained in the first novelty test, but also produced an interpretable higher-order factor solution when all of the nursery and jungle gym dimensions were subjected to a secondary factor analysis.

As was the case for factors identified in the nursery testing situation, traits emerging in the jungle gym factor solution are readily grouped into the well-studied (Schneirla, 1959; Gray, 1971, 1979; Kagan et al., 1988, 1989; Suomi, 1991) domains of approach ("confident" and "exploratory") and avoidance ("cautious", and "defensive aggression.") As reviewed previously (Desbiolles et al., 2006b), these factors also have high face-plausibility and are straightforwardly related to factor structures of behavior reported in both the human and the non-human primate literature (Kagan, 1986, 1987; Stevenson-Hinde and Zunz, 1978; Kalin and Shelton, 1989; Kalin et al., 1998; Bolig et al., 1992; Capitanio; 1999). In addition, the factors emerging from the jungle-gym testing situation resembled, both in concept and in specific defining behaviors, the four-factor solution derived from the nursery novelty test (Desbiolles et al, 2006b). This apparent similarity was confirmed mathematically when the individual factor scores from the

two novelty test paradigms were submitted to a secondary factor analysis. To be explicit, three of the four higher order factors were almost identical in their overall structure: Factor 1 (termed "exploratory") had similar strong behavioral loadings for moving horizontally, exploring space and objects and foraging for food [nursery Factor 1 ("energetic exploration" and jungle gym Factor 3 ("exploratory.")] Higher order Factor 3 comprises nursery Factor 2 ("defensive aggression") and jungle gym Factor 4 (also labeled "defensive aggression"). Again, the same primary behaviors ('threaten' and 'spread eagle') define the positive ends of both dimensions. Nursery Factor 4 ("cautious exploration") and jungle gym Factor 2 ("cautiousness") load on higher order Factor 4 ("cautious"). Nursery Factor 4 comprises the behaviors 'watch observer" and 'oral /manual exploration", while in jungle gym Factor 2, the defining behaviors are 'look around,' 'spread eagle' and 'fixed stare,' with a secondary loading of 'explore and forage.' In both cases, individuals at the positive end of the dimension spend a disproportionate amount of time scanning the observer and the environment.

Interpretation of the final higher order Factor 2 ("confident-to-inhibited") is a bit more complex. In this instance, Factor 1 from the jungle gym ("confident") loads positively, while Factor 3 ("behavioral inhibition") from the nursery testing loads negatively. At the behavioral item level, 'stare ahead' and 'watch observer,' which load on the positive end in the nursery test factor load on the negative end ("not confident") of the jungle gym test factor, "confident." Conversely, the behaviors ('climb,' 'look around' and 'eat') that load on the negative end of "behavioral inhibition" (i.e. not inhibited) also load on the positive end of "confident." The last behavioral items, 'frozen' in the nursery factor and 'pace' in the jungle gym factor are clearly distinct, but may also reflect alternate expressions of the 'nervous energy' which characterizes monkeys with high scores on both traits.

Novelty testing at different developmental stages

There are also, of course, a number of distinctions between the factor solutions obtained at the two different testing times, and some remaining conundrums in the higher order factor solution. We note above that "exploratory" monkeys in the nursery test environment were highly effective in obtaining rewards, but this was less the case in the jungle gym. The decrease in reward seeking in the jungle gym suggests that, although these monkeys are still exploring, they may be less active than when they were younger. Monkeys with high scores on "cautious"

generally sat quietly on the floor of the nursery test cage, keeping the observer in view, but not exhibiting overt vigilance. In the jungle gym, animals scoring high on this dimension spent a great part of their time in the corner of the testing cage in a spread eagle position watching vigilantly both inside and outside of the testing cage. In the nursery test cage, individuals with high scores for "behavioral inhibition" were often in a frozen, almost catatonic state, while in the jungle gym, the same monkeys seemed to diffuse their stress by pacing. These observations are of course subject to multiple interpretations: maturation, habituation to the test environment or to the observer, the fact that the jungle gym testing was conducted in a cage similar in many ways to the juvenile peer group cage, or simply developmental differences in the way underlying behavioral traits were expressed. Making an informed choice between these alternatives would most likely require additional observations and different experimental paradigms.

What is important, however, is that the similarity between factors revealed in the nursery testing environment (mean age = 12 ± 4 months) and those revealed in the jungle gym test (mean age: 30 ± 4 months) provides evidence for the validity of the behavioral constructs identified, while the emergence of higher order factors with highly consistent item loadings provides evidence for the stability of the traits, at least over the time-frame of the present set of studies. Most interesting is the observation that the correlation between individually variable factor scores at the two different testing times is not restricted to animals at the ends of factor distributions, but rather pertains across the entire dimension.

Although many scientists have investigated reactivity directly, by exposing nonhuman primates to novel situations, or indirectly, by assessing overall traits of curiousity, impulsivity and fearfulness, there are very few experimental designs which have investigated the potential stability of these reactive measures (dimensions) across time (Clarke and Boinski, 1995). In the earliest study of this type, Stevenson-Hinde and colleagues (1980a, 1980b) reported little stability in rhesus removed from their social setting to a novel setting in which they were presented with novel objects, masked persons and operant procedures. However Suomi (1986, 1991) found the trait of high stress reactivity to be relatively stable in individual monkeys across major periods of development even though the trait was often masked under stress free-conditions. In addition, Suomi et al. (1981) noted that monkey infants which are behaviorally highly reactive to mild challenge or stress also tend to be highly reactive physiologically, as compared to to their less (behaviorally) reactive peers. These findings are also consistent with

Higley's (1984) report that infant rhesus displaying fearful anxious reactions to the standardized stimuli tend to show anxious reactions to comparable situations during adolescence.

One possible reason for the dearth of information relating to developmental stability of reactivity measures would be developmental differences in the expression of reactivity (Kalin et al., 1991; Schneider and Suomi, 1992). In our own project, for example, reward-seeking behavior seems to be toned down in the jungle gym, as compared to the infant test cage, yet many of the same behaviors load on trait "exploration" across tests. However, others have suggested that some trait expressions may be increased with age. There are reports, for example, that increased behavioral withdrawal, immobility and flight becomes more prevalent during adolescence in reactive monkeys presented with stressful or fearful stimuli (Higley et al, 1984; Suomi, 1991). This might be interpreted as sensitization, or could suggest that behaviors characteristic of reactivity show age-related changes based on the individual predeliction of he animal. Suomi (1991) also reports that, while the underlying dimension may be continuous across time, the behaviors characterizing the dimension differ between infants and adolescents, in that highly reactive monkeys in the first 2 years of life display withdrawal and inactivity, but the same individuals during adolescence become agitated and hyperactive, with excessive repetitive stereotypic activity. The second-order factor "confident-to-inhibited" described above is entirely consistent with this conceptualization.

Other behavioral issues

Another contrast between the two novelty tests conducted in this cohort was the emergence of a modest degree of habituation during the second exposure to the jungle gym test, as compared to the absence of habituation in the nursery test (Desbiolles et al., 2006b). Several factors are likely to underlie these differences. First, in the nursery test, vervets were (on average) only 13 months old, and according to the precepts of classic investigators in the field (eg., Chess & Thomas, 1990; Rothbart and Ahadi, 1994; Rothbart and Derryberry, 1981), the exhibited behavioral expression should be closer to innate temperament. Effective coping strategies may not have emerged and presumably neither cognition nor socialization has yet modified intrinsic behavior. By the time of the second (jungle gym) challenge test, these animals have lived in social group settings and have arguably learned to modulate their behavior in order to maximize adaptation. As a consequence, rapid adaptation may be less influenced by

individual behavioral predisposition. Second, the perceived novelty of the test situation could be quite different between paradigms. The nursery novelty cage is physically very different from the nursery housing cage and resembles no enclosure previously experienced, while the jungle gym is a physically and structurally modified version of the social group cage in which adolescent monkeys were housed for at least 6 months prior to testing. As described above, the jungle gym was intended to be more cognitively demanding and also more appropriate to the rapid physical growth which had occurred in all individuals between use of the different paradigms. Finally, the interval between trials was also quite different (10 days for the nursery test, 2 days for the jungle gym). Because failure to habituate to novelty is likely to indicate a potential risk for psychopathology (Gilmer and McKinney, 2003), it would be of great interest to explore alternative research designs with the nursery novelty test (eg., a greater number of trials, reduced time between trials).

In designing the jungle gym novelty test paradigm, we had no intention to measure pre-conceived traits, but did intend to challenge problem-solving abilities by requiring monkeys to leave a closed compartment (the tunnel) in order to enter the main testing cage. The willingness to do this was measured as a latency, termed 'threshold to enter the main cage,' which in retrospect may have been an ambiguous or confounded measure. Counter-intuitively, those monkeys that spontaneously ran up the opaque pipe did not immediately explore the main cage or seek out rewards, but rather proceeded to pace stereotypically on the floor of the cage. Similarly, many monkeys that could not be coaxed out of the tunnel, once placed by hand into the second section, readily explored the cage and effectively secured rewards. It is unlikely that the overall design was too fear-provoking, as the majority of animals did leave the tunnel on their own. Perhaps moving down the tunnel was, for some animals, too reminiscent of the procedure through which animals are typically isolated for veterinary examination, innoculation and other husbandry purposes. If this was the case, then refusing to go up the pipe could have simply been an expression of conditioned avoidance of an unpleasant situation. Clearly, other experimental designs would be required to test the validity of this interpretation.

Implications for models of psychopathology

Attempting to predict psychopathology on the basis of personality or reactivity factors, while provocative, is fraught with many difficulties (Chess et al., 1983; Kagan and Zentner,

1996; Maziade et al., 1989, 1990; Moskowitz and Schwartzman, 1989; Prior, 1992; Rutter, 1987; Thomas and Chess, 1968). The modest success in achieving this goal (eg., Caspi et al., 1995, 2003) has been thoroughly reviewed in previous communications of this series (Desbiolles et al., 2006a, b) and will not be further discussed here. Nonetheless, a few conceptual issues inevitably arise when trying to incorporate behavioral measures taken at different developmental times into an assessment of predisposition. First, there are clearly some situations in which displays of fear and/or anxiety represent perfectly normal, developmentally appropriate reactions that most likely have been shaped by natural selection. In these circumstances, when a particular individual fails to display fear and anxiety, something is probably amiss. When studying reactivity levels, it is thus always important to consider the situational context. Indeed, in the type of paradigm presented here, it may not be the initial extreme reaction, but rather failure to habituate after repeated challenge, which indicates a potential risk of future psychopathology. Second, it is important to consider the developmental stage of the subject before focusing on the reaction. For example, in our study we observed high levels of stereotypic pacing in some monkeys, as compared to much lower levels of this behavior in others. Before we can infer that high levels of pacing are indicative of risk, it may be important to consider whether pacing occurs more frequently in adolescent animals. If this behavior peaks during adolescence and declines with maturity (Fairbanks and McGuire, 1993; McGuire et al., 1994; Washburn et al., 1965), we may need to be more conservative when making risk predictions. Hence, it is not just the expression or the frequency of the behavior that is important to consider, but also the developmental time point during which the behavior is scored. The third important point to consider is that even if there are genetic distinctions between high-reacting and low-reacting vervet monkeys, and even if such hypothesized genetically determined individual differences generalize to human infants and children, a predisposition does not always give rise to a disorder. There is no reason to believe that high-reactive infants will inevitably develop childhood anxiety disorders or other forms of psychopathology when they grow up.

There is now a degree of consensus about the existence of compelling nonhuman primate analogues to human anxiety disorders (Kalin et al., 1998; Cameron et al., 2003; Higley and Suomi, 1989; Palmour et al., 1997) and considerable evidence that these traits can be measured across the lifespan, from infancy (Kalin et al., 1991; Cameron et al., 2003) through adolescence (Higley and Suomi, 1989; Suomi, 1991) and into adulthood (Palmour et al., 1997). It may also

be the case that anxious behaviors in early life may predispose individual animals to become socially isolated and to display behaviors which have been interpreted to be analogous to involutional depression (Kraemer, 1985; Capitanio, 1999; Gilmer and McKinney, 2003). Suomi and colleagues (Suomi et al., 1985; Higley et al., 1991; Suomi, 1997) have also reported that highly reactive monkeys, especially those separated from their mothers in early life, are more likely to develop drug abuse behaviors during adolescence and early adulthood. What is lacking is a prospective study in which individuals were tested at an early age and followed into adulthood in a relatively naturalistic context. Providing such baseline information has been an important goal of the present work.

Limitations

This study has all of the limitations noted in the two preceding tests reported for the same vervet monkey birth cohorts (Desbiolles et al., 2006a, b). In addition, the design of the novelty test paradigm is very different from that used either in rodent novelty tests or in any other non-human primate studies known to us. As a consequence, validation of any constructs which might emerge will require further testing. To counter this problem, we have explicitly used highly validated focal animal behavioral methods, and an analytic method which makes no assumptions save those related to the normal distribution of collected measures. As was the case for the previous study (Desbiolles et al., 2006b), the extent to which stable lifetime phenotypes can be identified through the analysis of directly observed behavior will require further study of social group behavior, reproductive success and survival into adulthood.

Conclusion

In summary, we report here the identification of four behavioral traits in a population of vervet monkeys tested during mid-to-late adolescence in an investigator-designed novel environmental challenge. The extracted traits show face plausibility and are interpretably related to external measures, such as motor activity. We were also able to combine the extracted traits with similar traits extracted in a prior novelty test in late infancy (Desbiolles et al., 2006b) to identify second-order traits of reactivity ("exploratory," "confident-to-inhibited," "defensive" and "cautious"). An item analysis further validates the second-order structure. Taken together, these

data demonstrate a significant degree of continuity in behavioral traits from late infancy through adolescence and substantial stability of trait expression for individuals across time.

REFERENCES

Altmann J. 1974. Observational study of behavior: sampling methods. Behavior 49: 227-267.

Anderson GM, Young JG, Dohen DJ. 1979. Rapid liquid chromatographic determination of tryptophan, tyrosine, 5-hydroxyindole acetic acid and homovanillic acid in cerebrospinal fluid. J Chromatogr 164: 501-505.

Anderson GM, Young JG, Cohen DJ, Shaywitz BA, Batter DK. 1981. Amperometric determination of 3-methyoxy-4-hydroxyphenylethyleneglycol in human cerebrospinal fluid. J Chromatogr 222: 112-115.

Blizard DA. 1981. The Maudsley reactive and nonreactive strains: a North American perspective. Behaviour Genetics, 11, 914-916.

Boccia MI, Laudenslager MI, Reite ML. 1994. Intrinsic and extrinsic factors affect infant response to maternal separation. Psychiatry 57: 43-50.

Bolig R, Price CS, O'Neill L, Suomi S. 1992. Subjective assessment of reactivity level and personality traits of rhesus monkeys. International Journal of Primatology 13, 287-306.

Cameron JL, Becanu S, Coleman KD, Dahl RE, Devlin BJ, Rogers JA, Ryan ND, Williamson DE.2003. Dissociating components of anxious behavior in young rhesus monkeys. A precursor to genetic studies. In: Fear & Anxiety: Benefits of Translational Research (Gorman JM, ed). American Psychiatric Press, Washington DC. p 211-226.

Capitanio JP. 1999. Personality dimensions in adult rhesus macaques: prediction of behaviors across time and situation. American Journal of Primatology 47:299-320.

Carola V, D'OlimpioF, Brunamont E. 2002. Evaluation of the elevated plus-maze and open-field tests for the assessment of anxiety-related behaviour in inbred mice. Behav Brain Res 134: 49-57.

Caspi A, Harrington HL, Milne B, Amell JW, Theodore RF, Moffitt TE. 2003. Children's behavioral styles at age 3 are linked to their adult personality traits at age 26. J Personality 71: 495-513.

Caspi A, Hernry B, McGee RO, Moffit TE, Silva PA. 1995. Temperamental origin of child and adolescent behavior problems: from age three to age fifteen. Child Dev 66: 55-68.

Chess S, Thomas A, Habibi. 1983.

Chess S, Thomas A. 1990. Continuities and discontinuities in temperament. In L Robins, M Rutter (eds). Straight and Devious Pathways from Childhood to Adulthood. New York: Cambridge University Press. p 205-220.

Clarke AS, Boinski S. 1995. Temperament in nonhuman primates. Amer J Primatol 37:103-125.

Desbiolles C, Ervin FR, Mérette C, Young SN, Palmour RM Behavioral traits in vervet monkeys: I. Social group behavior during adolescence, submitted.

Desbiolles C, Ervin FR, Mérette C, Young SN, Palmour RM Behavioral traits in vervet monkeys: III. Response to a novel environment during late infancy. Submitted.

Fairbanks LA. 2001. Individual differences in response to a stranger: Social impulsivity as a dimension of temperament in vervet monkeys (Cercopithecus aethiops sabaeus). J Comp Psychol 115: 22-28.

Fairbanks LA, McGuire MT. 1993. Maternal protectiveness and response to the unfamiliar in vervet monkeys. Amer J Primatol 30:119-129.

Gilmer WS, McKinney WT. 2003. Early experience and depressive disorders: human and non-human primate studies. J Affective Disorders 75: 97-113.

Gray JA. 1971. The psychology of fear and stress. Toronto, NY: McGraw-Hill.

Gray JA. 1979. Emotionality in male and female rodents. Brit J Psychol 70: 425-440.

Heath-Lange S, Ha JC, Sackett GP. 1999. Behavioral measurement of temperament in male nursery-raised infant macaques and baboons. Amer J Primatol 47: 43-50.

Higley JD, Hasert MR, Suomi SJ, Linnoila M. 1991. Nonhuman primate model of alcoholism: effects of early experience, personality and stress on alcohol consumption. Proc Natl Acad Sci (USA) 88: 7261-65.

Higley JD, Suomi SJ & Delizio RD. 1984. Continuity of social seperation behaviors from infancy to adolescence. Paper presented at the 7th meeting of the American Society of Primatologists, Arcata, Calif.

Higley JD, Suomi SJ. 1989. Temperamental reactivity in nonhuman primates. In: Kohnstamm G, Bates J, Rothbart M (eds), Temperament in Childhood, John Wiley & Sons, New York. p 153-167.

Kagan J, Reznick JS, Gibbons J. 1989. Inhibited and uninhibited types of children. Child Dev. 60:838-45.

Kagan J, Reznick JS, Snidman N, Gibbons J, Johnson MO. 1988. Childhood derivatives of inhibition and lack of inhibition to the unfamiliar. Child Dev 59:1580-9.

Kagan J, Reznick JS, Snidman N. 1987. The physiology and psychology of behavioral inhibition in children. Child Dev 58:1459-73.

Kagan J, Zentner M. 1996. Early childhood predictors of adult psychopathology. Harv Rev Psychiatry 3: 341-350.

Kalin NH, Shelton SE. 1989. Defensive behaviors in infant rhesus monkeys: Environmental cues and neurochemical regulation. Science 243: 1718-1721.

Kalin NH, Shelton SE, Takahashi LK. 1991. Defensive behaviors in infant rhesus monkeys: Ontogeny and context-dependent selective expression. Child Develop 62: 1175-1183.

Kalin NH, Shelton SE, Rickman M, Davidson RJ. 1998. Individual differences in freezing and cortisol in infant and mother rhesus monkeys. Behav Neurosci 122: 251-254

Kraemer GW. 1985. The primate social environment, brain neurochemical changes and psychopathology. Trends Neurosci 8: 339-40.

Kraemer GW 1997 Psychobiology of early social attachment in rhesus monkeys: Clinical implications. Ann NY Acad Sci 807: 401-418.

Livesley WJ, Jang KL, Vernon PA. 1998. Phenotypic and genetic structure of traits delineating personality disorder. Arch Gen Psychiatry 55: 941-948.

Maziade M, Caron C, Coté R, Mérette C, Bernier H, Laplante B, Boutin P, Thivierge J. 1990. Psychiatric status of adolescents who had extreme temperaments at age 7. Am J Psychiatry 147: 1531-1536.

Maziade M, Coté R, Thivierge J, Boutin P, Bernier H. 1989. Significance of extreme temperament in infancy for clinical status in preschool years. II: patterns of temperament change and implications for the appearance of disorders. Brit J Psychiatr 154: 544-551.

McGuire MT, Raleigh MJ, Pollack DB. 1994. Personality features in vervet monkeys: the effects of sex, age, social status, and group composition. Amer J Primatol 33:1-13.

Moskowitz DS, Schwartzman AE. 1989. Painting group portraits: Studying life outcomes for aggressive and withdrawn children. J Personality 57: 723-746.

Morgan D, Grant KA, Prioleau OA, Nader SH, Kaplan JR, Nader MA. 2000. Predictors of social status in cynomolgus monkeys (Macaca fascicularis) after group formation. Am J Primatol 52:115-31.

Palmour RM, Mulligan J, Howbert JJ, Ervin FR. 1997. Of monkeys and men: vervets and the genetics of human-like behaviors. Amer J Hum Genet 61: 481-488.

Prior M. 1989. Childhood temperament. J Child Psychol Psychiatry 33: 249-79.

Rothbart MK, Ahadi SA. 1994. Temperament and the development of personality. J Abnorm Psychol 103: 55-66.

Rothbart MK, Derryberry D. 1981. Development of individual differences in temperament. Adv Developmental Psychol 1: 37-86.

Rutter M. 1987. Temperament, personality and personality disorder. Br J Psychiatry 150: 443-458

Schneider ML, Suomi SJ. 1992. Neurobehavioral assessment in rhesus monkey neonates (macaca mulatta): developmental changes, behavioral stability, and early experience. Inf Behav Develop 15, 155-177.

Schneider ML, Moore CF, Suomi SJ, Champoux M. 1991. Laboratory assessment of temperament and environmental enrichment in rhesus monkey infants (Macaca mulatta). Am J Primatol 25:137-155.

Schneider ML, Suomi SJ. 1992. Neurobehavioral assessment in rhesus monkey neonates (macaca mulatta): developmental changes, behavioral stability, and early experience. Inf Behav Develop 15, 155-177.

Schneirla TC. 1959. An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In: MR Jones, ed. Nebraska Symposium on Motivation, Vol 7, U Nebraska Press. p 1-42.

Spencer-Booth Y. Hinde RA. 1969. Tests of behavioral characteristics for rhesus monkeys. Behaviour 33: 180-211.

Stevenson-Hinde J, Zunz M. 1978. Subjective assessment of individual monkeys. Primates 19:473-482.

Stevenson-Hinde J, Stillwell-Barnes R, Zunz M. 1980a. Subjective assessment of rhesus monkeys over four successive years. Primates 21, 66-82.

Stevenson-Hinde J, Zunz M, Stillwellbarnes R. 1980b. Behavior of one-year-old rhesus monkeys in a strange situation. Animal Behavior 28, 266-277.

Suomi SJ. 1981. Genetic, maternal and environmental influences on social development in rhesus monkeys. In B. Chiarelli & R Corruccini (Eds), Primate behavior and sociobiology. Berlin: Springer-Verlag.

Suomi SJ. 1986. Anxiety-like disorders in young non-human primates. In: Gittelman R, ed., Anxiety Disorders of Childhood. New York, NY: Guilford Press. p 1-23.

Suomi SJ. 1991. Uptight and laid-back monkeys: Individual differences in the response to social challenges. In: SE Brauth, WS Hall and RJ Dooling, eds. Plasticity of Development. Cambridge MA: MIT Press. p 27-50.

Suomi SJ, Kraemer GW, Baysinger CM, & DeLizio RD. 1981. Inherited and experimental factors associated with individual differences in anxious behavior displayed by rhesus monkeys. In DF Klein & J Rabkin (Eds), Anxiety: New research and changing concepts. New York: Raven Press. p 179-200.

Suomi SJ. 1997. Early determinants of behaviour: Evidence from primate studies. Brit Med Bull 53: 170-184

Thomas A, Chess S. 1968. Temperament and Behavior Disorders in Children. New York: New York University Press. p 64-67.

Washburn SL, Jay PC, Lancaster JB. 1965. Field studies of old world monkeys and apes. Science 150:1541-

TABLE I Behavioral Repertoire in the Jungle Gym Test Environment

Behavior	*Description*
Locomotion	Walking or running on the ground
Climb	Climbing along the sides and/or ceiling of the cage
Eat	Eating pieces of food along the path of the novelty cage and rewards
Forage	Foraging on the ground for food.
Exploration	Exploring objects and cage wall with hands, mouth or tongue
Freeze	Immobilized and closing eyes as if falling asleep
Fixed Stare	Immobile while watching straight ahead at nothing specific
Vocalize	Repertoire of vocalizations ranging from cooing to cackling
Threaten Observer	Antagonistic interaction with the observer, involving any of the following behaviors: raising eyebrows, lunging head forward, gaping
Spread-eagle	Looking out or at the observer from a position in the top back corner of the cage; arms and legs spread out in a tense erect position.
Watch Observer	Watching the observer (with no underlying signs of threat)
Look Around	Moving head around, looking in different directions with relaxed muscle tone
Leap	Jumping from one part of the cage to another
Pace	Walking or running repetitively back and forth on the cage bottom.

TABLE 2 ***Eigenvalues and proportional variance for significant factors emerging from analysis of initial and repeat exposure to a novel test environment***

	Eigenvalue magnitude	Proportional variance
Factor 1	2.737	0.239
Factor 2	1.646	0.150
Factor 3	1.252	0.114
Factor 4	1.074	0.098

Data obtained from factor analysis (orthogonal solution, varimax rotation) of behaviors emitted during a 10 minute exposure to a novel jungle gym environment, as detailed in the text. Each animal was tested twice, 2 days apart, and behavioral measures were cumulated across trials. The focal animal method of scoring was used, as described further in methods, with a new behavior scored every 10 seconds. After initial examination of eigenvalues and scree plots, the solution was constrained to four factors.

TABLE 3 *Factor loadings for replicate testing of 206 vervet monkeys in the jungle gym environment*

	Factor 1	Factor 2	Factor 3	Factor 4
Climb	**0.904**	0.077	0.03	-0.109
Eat	**0.869**	-0.093	0.170	-0.090
Look around	*0.278*	**0.738**	-0.046	-0.086
Stare ahead	-0.257	**0.388**	0.127	0.047
Spread-eagle	-0.212	**0.433**	-0.191	**0.453**
Explore and forage	0.042	*0.244*	**0.726**	-0.087
Locomotion	0.030	-0.034	**0.849**	-0.007
Threaten observer	-0.199	-0.252	-0.007	**0.818**
Pace	***-0.620***	***-0.499***	-0.208	***-0.516***
Watch observer	***-0.541***	0.018	0.065	0.106
Leap	0.023	***-0.595***	-0.160	-0.083

Loadings of specific behaviors on all factors with eigenvalues greater than 1, obtained from factor analysis (orthogonal solution, varimax rotation) of behaviors emitted during a 10 minute exposure to a novel cage environment, as detailed in the text. Each animal was tested twice, with the second testing occurring after a rest interval of 2 days; behavioral measures were cumulated across trials. The focal animal method of scoring was used, as described further in methods, with a new behavior scored every 10 seconds. Primary loadings are in BOLD, and secondary loadings are shown in italics.

TABLE 4: ***Higher order reactivity factors derived from comparison of novelty testing during the nursery period and in the jungle gym***

	Factor 1	Factor 2	Factor 3	Factor 4
Nurs: energetic exploration	**0.843**	-0.007	-0.153	-0.022
JG: exploratory	**0.851**	0.041	0.175	0.034
Nurs: inhibited	0.107	**0.803**	-0.072	0.139
JG: confident	0.084	**-0.645**	-0.206	0.113
Nurs: defensive aggression	0.103	-0.028	**0.789**	-0.121
JG: defensive aggression	-0.071	0.168	**0.628**	0.181
Nurs: calm exploration	0.062	0.263	-0.117	**0.680**
JG: cautious	-0.043	-0.165	0.117	**0.726**

Reactivity factors (orthogonal solution, varimax rotation) were extracted from individual factor scores of 206 monkeys tested in both the nursery novelty paradigm (Nurs) and in the "jungle gym" paradigm (JG). The nursery novelty testing was conducted at 13 ± 3 months of age, while jungle gym testing was conducted at 30 ± 4 months of age. All animals were tested twice in each paradigm. The eigenvalues and proportional variance for the higher order reactivity factors are as follows: Factor 1, eigenvalue 1.504, proportional variance 0.188; Factor 2, 1.322, 0.165; Factor 3, 1.078, 0.135; Factor 4, 1.025, 0.128.

Figure 1: JUNGLE GYM TEST ENVIRONMENT

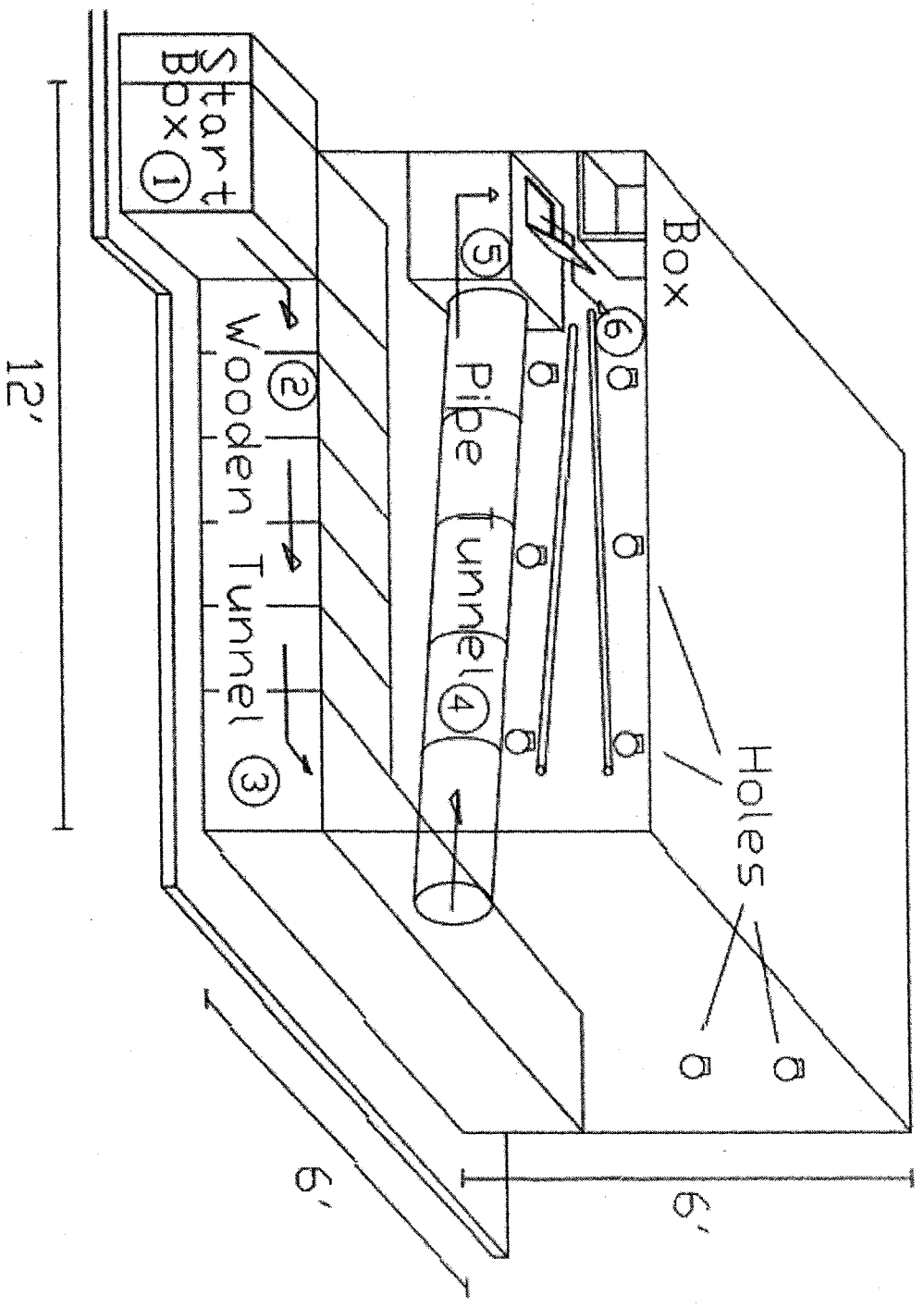


Figure 1: This cartoon of the "jungle gym" novelty testing cage illustrates the relationships between the physical subdivision to which animals were subjected. Each animal began testing by moving from an adjacent housing cage into the L-shaped wooden tunnel (2 x 2 x 2 ft) which streched along the entire length (12 ft) and half of the width (5 ft) of the larger (8 x 12 x 10 ft) open environment. The exterior wall of the tunnel was constructed of wire mesh to facilitate observation, but the remaining walls were opaque. This tunnel opened into an opaque plastic pipe (2 feet), slanted at a 45 degree angle across the mid-line of the test paradigm (12 feet) and ended in a 2 x 2 feet wooden bàox constructed inside the main cage enclosure. The wooden box was closed off on all sides, so the monkey could not see out, but rather exited into the main open space from an opening on the top of box. Once in this space, the monkey was free for 5 min to move around the cage at will and seek out food rewards, which were place out of direct view in 10 small plastic containers wired to the chain link cage sides. The opening of each container was designed to be large enough for the animals to obtain treats, but small enough that a certain amount of precision and dexterity was required. During the 5 min observation period, normative behaviors (1 behavior each 10 sec) as enumerated in Table 1, the number of rewards found, amd overall motility were recorded.

Figure 2:

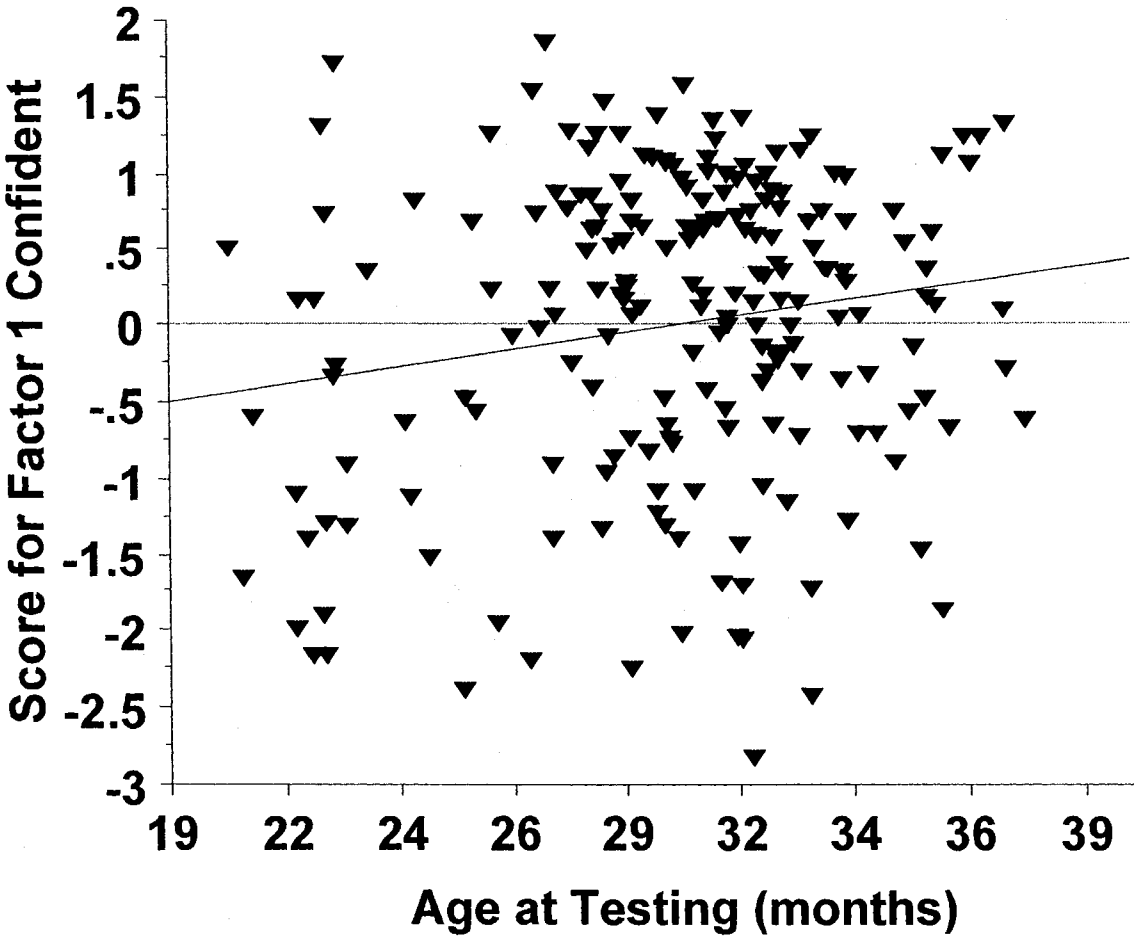


Figure 2. Standardized scores (Z-scores) on Factor 1 ("confident") were positively correlated with average age (in months) at testing ($r = 0.183$, $F_{1,204} = 7.17$, $p < 0.01$). Orthogonal factors were extracted by factor analysis, with varimax rotation, from quantitative scores of standard behaviors in 206 young juvenile monkeys tested twice in a novel environment paradigm at approximately 2 day intervals. Monkeys ranged from 20 to 38 months of age at testing.

Figure 3:

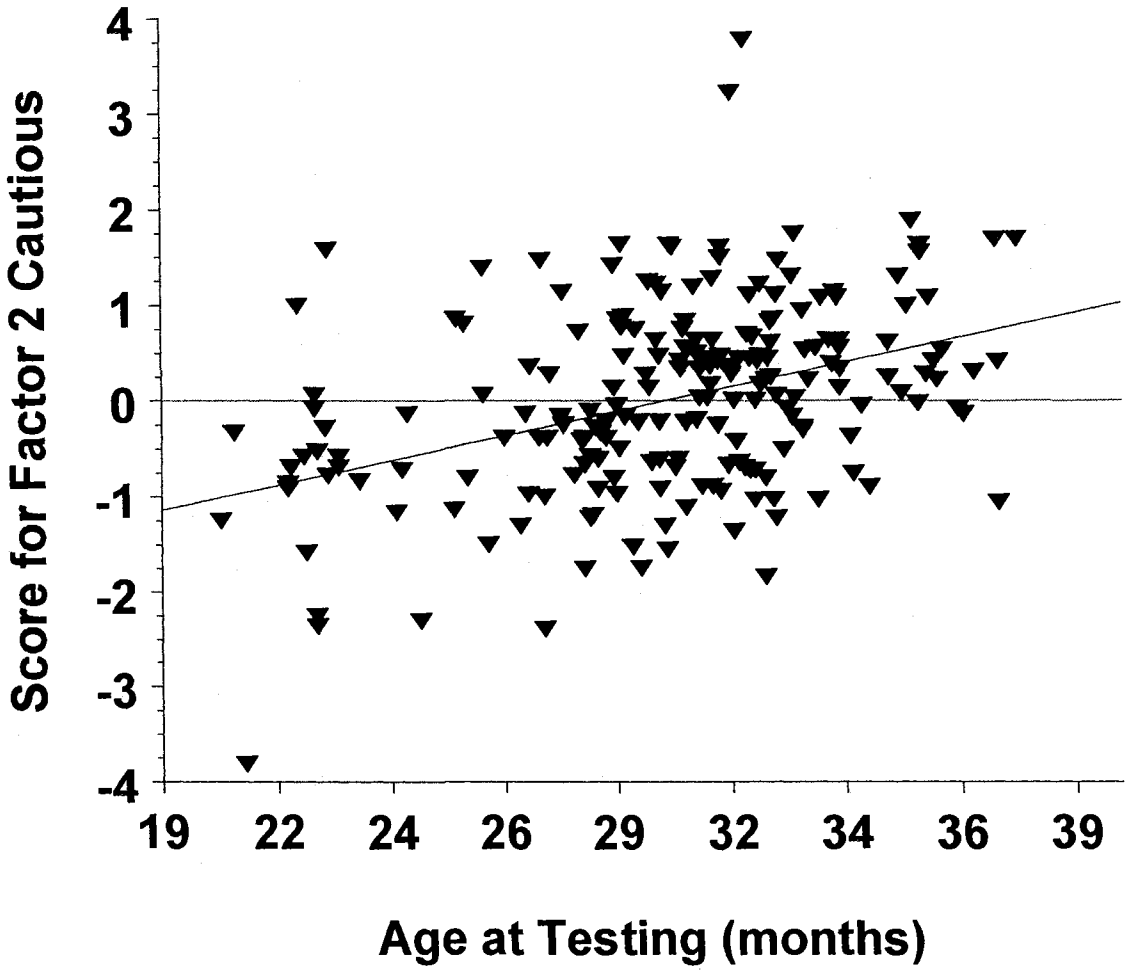


Figure 3. Standardized scores (Z-scores) on Factor 2 ("cautious") were also positively correlated with average age (in months at testing ($r = 0.378$, $F_{1,204} = 33.07$, $p < 0.0001$). Orthogonal factors were extracted by factor analysis, with varimax rotation, from quantitative scores of standard behaviors in 206 young juvenile monkeys tested twice in a novel environment paradigm at approximately 2 day intervals. Monkeys ranged from 20 to 38 months of age at testing.

Figure 4:

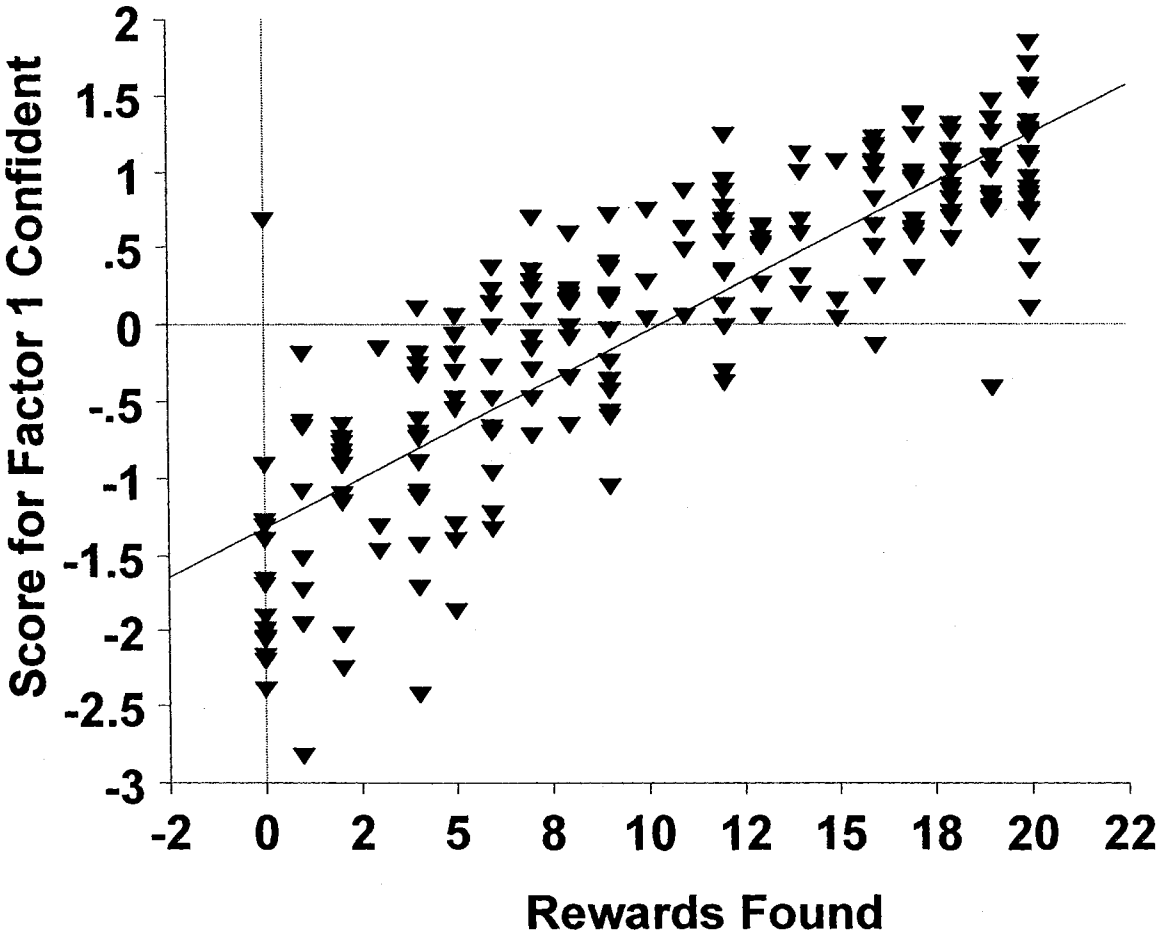


Figure 4. Factor 1 ("confident") was also positively correlated with the total number of rewards found ($r = 0.843$, $F_{1,204} = 447.5$, $p < 0.0001$) As described before, factor scores (Z-scores) were extracted from quantitative scores of standard behaviors in 206 young juvenile monkeys tested twice in a novel environment paradigm at approximately 2 day intervals.

Figure 5

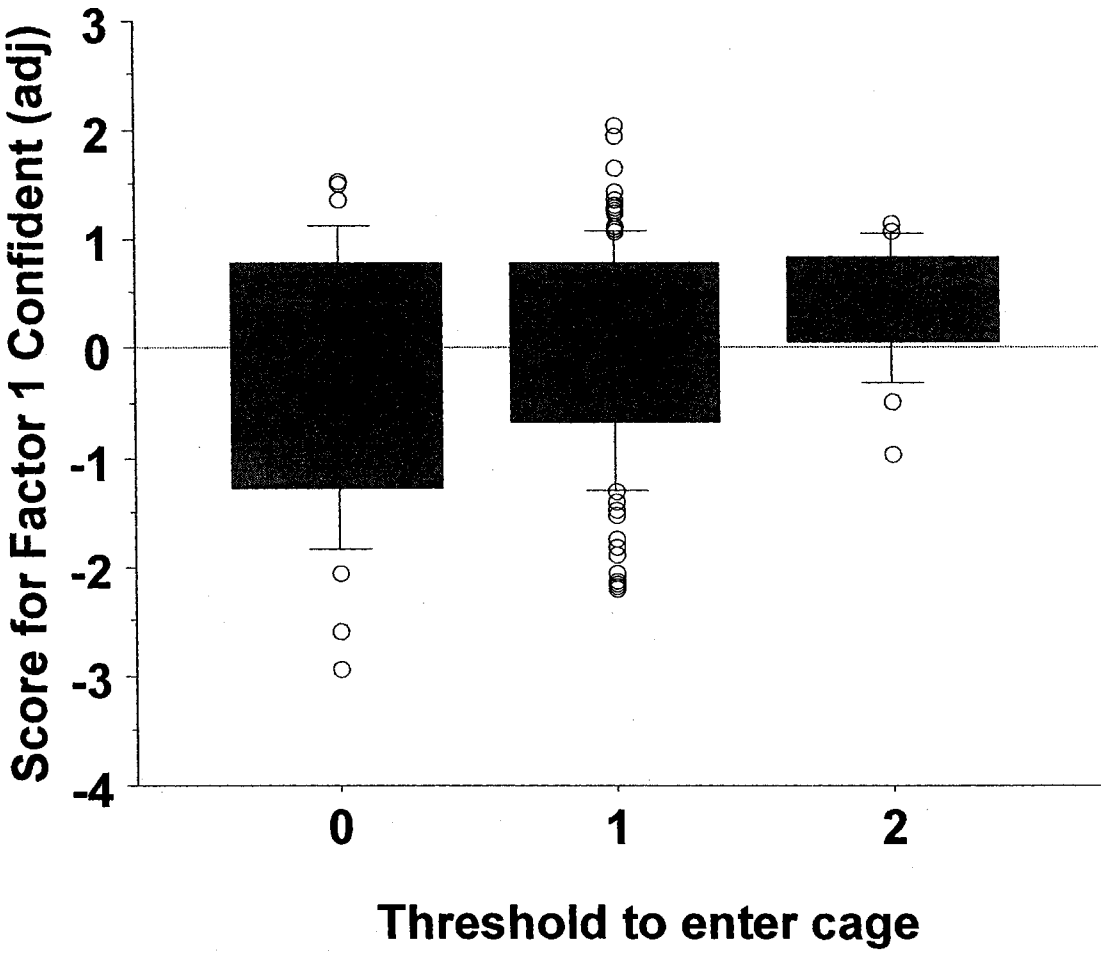


Figure 5: Latency to leave the tunnel and enter the main cage was significantly related to scores for Factor 1: confident, as shown by ANOVA ($F_{2,203} = 5.11$, $p < 0.01$). Threshold to enter the main cage was scored as follows: 0 = animal spontaneously entered the main cage in less than 5 minutes; 1 = animal required coaxin to leave the tunnel and move into the main cage; 2 = animal resisted entering the main cage and had to be moved manually. Data are presented as box plots of Z-transformed factor scores, in which the box defines ± 1 SD, the error bars define ± 2 SD, the horizontal line across the box defines the mean and the points outside the error bars are outliers. As can be seen, monkeys which are resistant to moving into the main cage have higher mean scores for Factor 1.

Figure 6

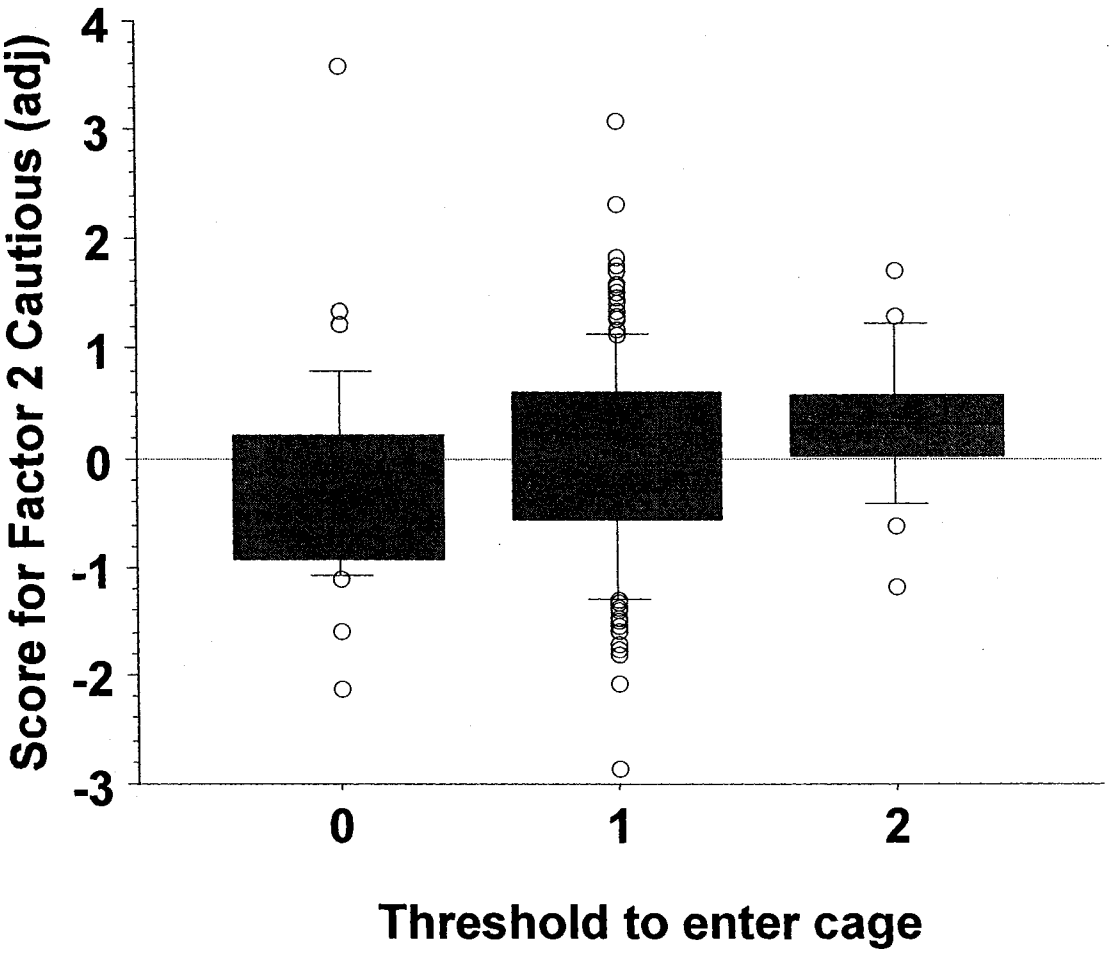


Figure 6: Latency to leave the tunnel and enter the main cage was also significantly related to scores for Factor 2: cautious, as shown by ANOVA ($F_{2,203} = 3.84$, $p < 0.02$). Threshold to enter the main cage was scored as described in the caption for Figure 5. Data are presented as box plots of Z-transformed factor scores, in which the box defines ± 1 SD, the error bars define ± 2 SD, the horizontal line across the box defines the mean and the points outside the error bars are outliers.

Figure 7

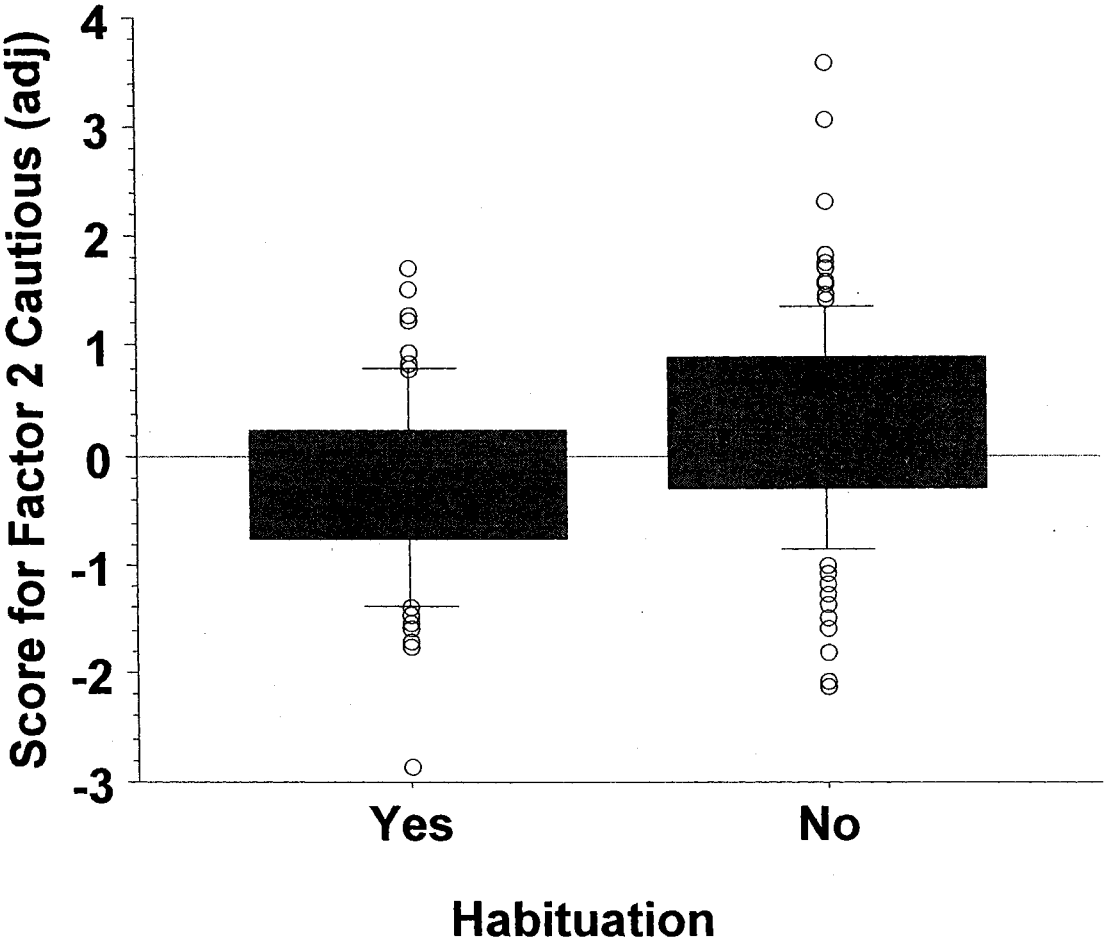
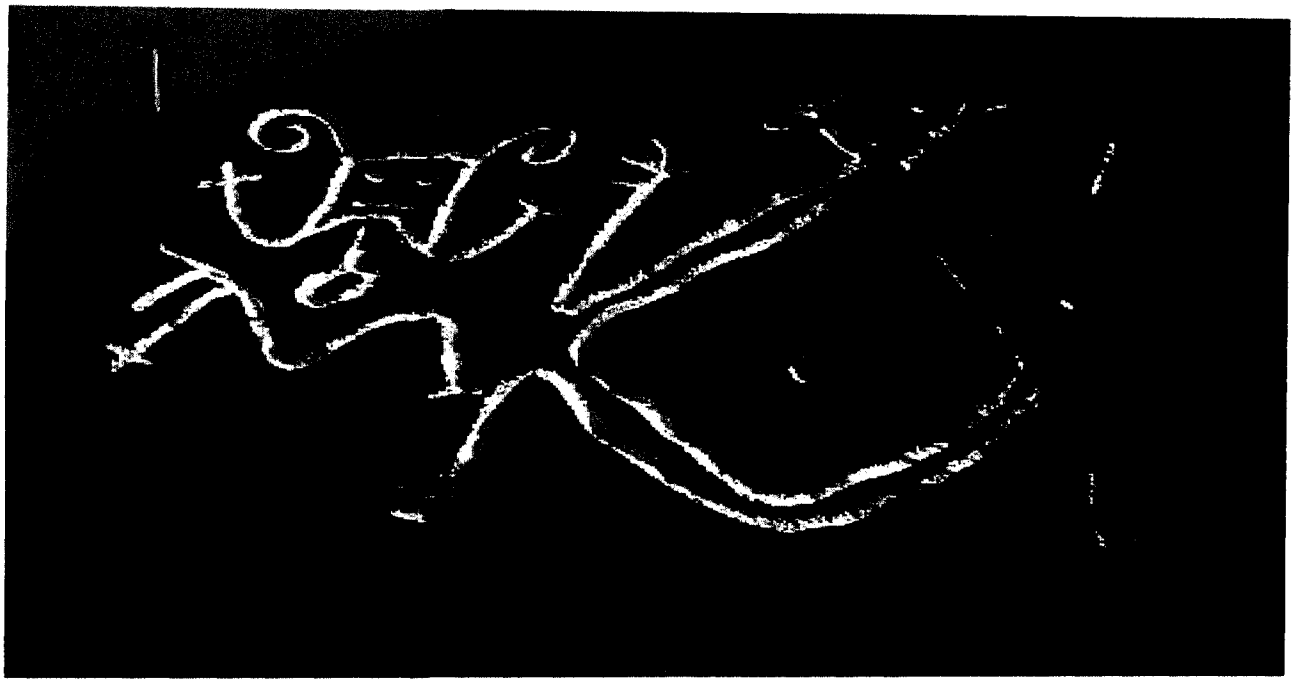


Figure 7: The extent of habituation between trials 1 and 2, as measured by the change in threshold to enter the main cage, was significantly related to Z-scores for Factor 2: cautious ($F_{1,179} = 12.98$, $p < 0.001$). A positive change in threshold was scored if an animal with a threshold score of 2 in trial 1 achieved a score of either 1 or 0 in trial 2, or an animal with a threshold score of 1 in trial 1 achieved a score of 0 in trial 2. Factor scores were computed by factor analysis of summations of standard behavioral measures in 206 young juvenile monkeys tested twice in a novel environment paradigm at approximately 2 day intervals. Monkeys ranged from 20 to 38 months of age at testing.

CHAPTER VI

DISCUSSION



SUMMARY

Our goal was to obtain a parsimonious model for the underlying structure of personality in the vervet monkey. The overall main finding is that it is possible to utilize direct observational data to extract meaningful behavioral dimensions across three different paradigms: Social juvenile, nursery novelty test, and jungle gym novelty test. From the social juvenile context we were able to derive a factorial structure comprising of five behavioral traits: (1) agonism, (2) energetic sociability, (3) agreeableness, (4) playfulness, and (5) behavioral inhibition. These traits not only turned out to be interpretable, but also conceptually resembled other behavioral traits found in the non-human primate literature: Stevenson-Hinde and Zunz (1978) confident-to-fearful, active-to-slow, sociable-to-solitary; McGuire and Raleigh (1994) socially competent, playful-curious, opportunistic; Capitanio (1999) sociability, confidence, excitability, equability; and Bolig et al., (1992) tense-insecure, confident-popular, playful-active, aggressive-irritable. The use of novelty tests were added to our experimental paradigm as a means of bringing out less obvious inherent traits that might otherwise be masked under normal social non-stressful conditions. In late infancy, the four behavioral dimensions derived through the nursery novelty test paradigm were labeled: (1) energetic exploration, (2) defensive aggression, (3) behavioral inhibition, and (4) cautious exploration. During early adolescence, four conceptually similar behavioral dimensions were derived through the jungle gym novelty test paradigm, and interpreted as: (1) confident, (2) cautious, (3) exploratory, and (4) defensive aggression. These factors not only have high face-plausibility but also resemble factor structures of behavior readily grouped into the well-studied domains of approach and avoidance, also known as inhibited and uninhibited; "up-tight" and 'laid-back" reported in both the human and the experimental animal literature (Schneirla, 1959; Gray, 1971, 1979; Kagan, 1988, 1989; Kalin and Shelton, 1989; Suomi, 1991). These two sets of behavioral traits derived using a novelty test paradigm demonstrated internal conceptual similarity, and was mathematically confirmed when the individual factor scores for all eight dimensions (i.e. 4 from the nursery and 4 from the jungle gym) were submitted to a secondary factor analysis. The resulting four interpretable super factors were labeled: (1) exploratory, (2) confident-to-inhibited, (3) defensive, and (4) cautious. Using this systematic quantitative methodological approach has improved the definitional clarity of our behavioral structures, laying down a robust preliminary behavioral index for the vervet monkey,

and provided us with a tool to begin investigating the continuity and stability of these structures across time.

The similarity of the extracted factors across paradigms is more obvious for some dimensions than others. For example, some of the exact same behaviors load on "agonism" in the social juvenile context (threaten the observer, climb, leap and watch the observer), "defensive aggression" in the nursery novelty test, (spread eagle, watch observer, vigilant to the observer), and "defensive aggression" in the jungle gym novelty test (spread eagle and threaten observer). In both novelty tests, the individuals scoring high on "defensive aggression" showed low levels of motility, but in the social context, these animals readily approached the observer at eye level. Perhaps when these monkeys are subjected to a stressful situation and confined to a smaller space, their reactivity (i.e. in this case threatening behavior) increases and their motility decreases. These dimensions all involved an element of vigilance and demonstrated that these individual monkeys spent the majority of their time reacting to the observer, displaying some sort of boldness, but clearly without seeming easy going. A similar argument can be made for the dimensions of "energetic sociability" in the social juvenile context, "energetic exploration" in the nursery novelty test and "exploratory" in the jungle gym test, in that identical behaviors (physical activity, eating and foraging, and exploring the environment) load on all three dimensions.

Another similarity in dimensions across paradigms is "behavioral inhibition" in the social juvenile context, made up of scratch, fidget, and stare ahead, and "behavioral inhibition" in the nursery novelty test, comprising frozen immobility and fixed stare. In both contexts, the trait of "behavioral inhibition" is negatively correlated with motor activity. "Behavioral inhibition" from the nursery novelty test is also inversely related to "confident" from the jungle gym novelty test (as demonstrated in the mathematical results of the super factor solution), which comprises climb and finds rewards. These animals have very low rates of watching the observer and pacing. These dimensions, in both social and individual contexts, display different expressions, whether positive or negative, of fearful behaviors.

Those dimensions, which relate directly to social activity are more difficult to compare across paradigms. Nonetheless, there are some commonalities between "energetic sociability" and the nursery novelty test dimension labeled "energetic exploration," as well as the jungle gym novelty test trait "exploratory." The behaviors walk and run load on all three dimensions, eating

(or finding rewards) and behaviors related to environmental exploration (forage, look around, investigating). All three dimensions are positively correlated with motility, and individuals scoring high on these dimensions were calm, easy going, void of fearful behavior, and successful at achieving food and other rewards. Similarly there are some correlations between "agreeableness" in the social juvenile context, "cautious exploration" in the nursery novelty test and "cautious" in the jungle gym test, particularly with respect to a non-energetic exploration of the environment. However, for both of these groups, the definitive social behaviors of sit near, join, muzzle and groom or be groomed can only be observed in the social context. Similarly, the dimension of "playful" has no analogy in the novelty tests.

METHODOLOGICAL CHALLENGES

As is apparent from the background review, the non-human primate literature is lacking in prospective longitudinal studies. Many of the studies that attempt to shed light on personality features are based on small sample size and typically examine adult animals with a history of multiple experimental studies (Stevenson-Hinde & Zunz, 1978; Caine et al., 1983; Bolig et al., 1992; Figueredo et al., 1995; Capitanio, 1999). The most common methodological approach in the nonhuman primate literature until now has been to use a list of descriptive adjectives to score animals retrospectively in their social milieu. This approach, although successful at deriving interpretable behavioral traits, makes replication of studies, as well as comparison of results between groups, difficult, if not impossible. Although research groups exploring behavior in nonhuman primates have come up with good insights regarding personality traits, there is still much work to be done in order to validate these constructs.

In conducting our studies, we tried to avoid interpretation and remain as close as possible to observed behaviors. The strength of this approach stems from its methodological simplicity and basic objectivity. From a practical standpoint in collecting the data, this removes the necessity to agree about the semantic meaning of descriptors used to summarize the monkeys, or to operationally define selected descriptive adjectives. Unlike retrospective studies in which you need to remember or recall information, a prospective study such as ours requires just scoring what you see at the moment you see it. Naïve observers need only be trained to recognize specific behaviors with reliability, and observers do not require a significant time period prior to

the first scoring bout to become familiar with the monkeys. More importantly, instead of requiring up to 200 h of observation to know an animal well enough to assign behavioral rating scores, as few as 40 5-min focal segments can be used to extract behavioral trait scores. As a consequence, a large number of monkeys can be observed in a time efficient manner. The final behavioral trait index provides us with information on both the group (i.e. species), as well as the individual. In our study, we collected basic primatological behavioral measures from 206 vervet monkeys all of the same age range. The simplicity and transparency of our mathematically derived solutions gave us interpretable behavioral dimensions that can easily be replicated. Our behavioral traits can be conceptually compared to other pre-established behavioral dimensions already published in the scientific literature, or evaluated based on the level of concordance between their interpretation (i.e. semantic labeling) and their empirical structure. It could also provide us with the mathematical means of testing the reliability of behavioral traits across time. These more specific behavioral traits can help us better understand the effects of age, sex and species on behavior. In addition, these behavioral traits allow us to create controlled studies in order to begin answering more specific questions pertaining to the relationship between these behavioral traits with other biological and psychopathological entities, such as gene expression, neurobiology and substance abuse (more specifically alcohol abuse). In using a scientific paradigm that permitted the data to speak for itself, we introduced a level of objectivity that could potentially get us one step closer to the internal validity of these inherent measures.

However, in every methodological approach, there is a trade off between information gained and information lost. Certain questions can be satisfactorily answered using a specific approach, while attempting to answer other questions may not be possible and require complementary information or alternative approaches. Following are some of the methodological challenges or limitations posed by the approach we have used.

The Role of Challenge Tests

There are two main reasons we included novelty tests in our longitudinal research paradigm; (1) The novelty test environment is controlled and therefore more homogeneous than the social environment; (2) the novelty test serves as an ideal tool to flesh out inherent behavioral traits (such as fear), which may not be overtly expressed in everyday social situations. Thomas, Chess and Birch (1977) have suggested that relatively pure temperamental expressions during

later development are likely to be apparent only at times when novel environmental challenges render coping skills ineffective. The stress of the novel environment also taps more directly into the typologies of nervous systems and accounts for individual differences (Pavlov 1927). Monkeys that function effectively under high intensity stress are considered to have a stronger nervous system, (thought to be dominated by the parasympathetic nervous system). These individuals generally have high scores on the uninhibited behavioral dimensions. Their phenotypic behaviors are predominantly exploration and reward seeking. Physiological confirmations for these monkeys might demonstrate low heart rate, smaller pupils, and dilated blood vessels (Suomi, 1987). By contrast, individuals that cannot function under high stress are thought to have a weaker nervous system, (thought to be dominated by the sympathetic nervous system). These individuals generally have high scores on the inhibited behavioral dimensions. Their phenotypic behaviors are fear-based, with low activity (sometimes even catatonic), facial grimaces and threats. There have been physiological confirmations for these 'fight or flight reactions' by other research groups (Strelau, 1983, 1986; Kagan et al., 1988; Suomi, 1987), including high stable heart rates, dilated pupils and constriction of blood vessels. Studies have shown that one third of individuals scored as inhibited based on their patterns of behaviors in a novelty test, do not show a high stable heart rate (Scarr & McCartney, 1983). In future work, it could be interesting to contrast these two groups.

Having both challenge data and normative social data on the same animals, while conceptually interesting, is also challenging. It remains important to find a meaningful way to mathematically combine these data sets. What is the extent of cross-situational consistency? Can we make any predictions on how an individual will perform in a challenge test by knowing something about him in a social context or vice versa? We have observed conceptual intuitive predictions between both socially derived behavioral measures and novelty test derived behavioral measures but we have not yet been able to mathematically compare them (this will be one of our future work endeavors). For example, monkeys scoring high on "behavioral inhibition" on Factor 4 may be the most obvious in a 'performance required challenge test,' but the same individuals may be difficult to pick out in a social milieu, either because they may have learned to mask their inherent anxiety by engaging in 'compensatory' activities such as pacing or grooming others, or as a consequence of mistaking a monkey sitting in the corner of a cage as being inhibited and anxious instead of simply lethargic and lazy.

Estimation of Adaptability

A direct measure of adaptability is unrealistic using this methodological approach for two reasons. We could conceivably have been able to examine the period of adaptation to social group living, but this was not feasible given the large sample size. As a consequence, our monkeys had already been given a period of time to adapt to their newly formed groups before we began our observational bouts. This critical time period of group formation, during which monkeys adjust to one another, is very interesting and informative, but too messy (i.e. heterogeneous) for the purpose of our experimental design. This fruitful undertaking should be addressed using another experimental design.

Second, in our experimental design we combined the data across twenty behavioral bouts in the social context; and two test trials in the novelty tests before deriving our mathematical constructs. This manipulation improved robustness, but blurred information, which might have potentially been important for measuring adaptation or change over time. A trajectory approach or multiple testing trials might be an informative way to measure adaptation. That being said, we can speculate from our factor solutions which monkeys will most likely be adaptable. In the scientific literature it has been demonstrated that there is an empirical clustering between adaptability and approach (Bates, 1989). In addition, infant monkeys that readily approach novel situations are likely to adapt easily, have a more positive attitude and be more sociable later in life. With this in mind, we might predict in our study that monkeys that have a higher score on an exploration measure in the novelty test paradigm will be the same monkeys to have a higher score on a social measure in the social juvenile context and are therefore by definition more adaptable.

Stability of traits across time

Another issue, which poses a methodological challenge to longitudinal behavioral studies, is the extent to which certain behavioral traits are stable across developmental time. If one looks across developmental time, it is generally thought that "the child is father to the man," but that adolescence is a period of fluctuation, sometimes extreme, followed eventually by a return to a normative temperament or personality. If individuals are characterized by their rank or position within a behavioral dimension, then despite some fluctuation with developmental stage and circumstance, a basic pattern of continuity or stability and over time is critical to the validity of the concept. Orthogonally, it is important to establish the stability (or lack thereof) of a behavioral dimension or factor, per se. If successive cohorts of individuals of the same population, at about the same age and under similar environmental circumstances are documented, will the same behavioral dimensions emerge from a factor analysis? If not, instability may be a function of discontinuity of the structure of behavioral dimensions rather than individual variability in responses. In some documents, continuity is used interchangeably with stability, but this term relates only to individuals, not to traits.

In part because of a lack of precision, but also because of methodological problems such as small sample size and paucity of longitudinal data, the issue of stability remains contentious (Prior, 1992). In the human and non-human primate literature the correlational data is modest overall, with stability higher in individuals who score at the extremes of temperament factors or dimensions than it is in those in the middle ranges (Stevenson-Hinde et al. 1980; Kagan, 1989; Suomi, 1987; Maziade et al., 1990a; Sanson et al. 1991). Stability is also strongest when temperament is measured across relatively brief time intervals (Prior, 1992). The exception to the previous statement is the stability demonstrated by Caspi et al., (2003) in a very large sample of children in a 26-year period, where they stated, "show me the child and I'll show you the man."(pp.496). This group observed 1000 3-year-old children with five temperament types: Under-controlled, Inhibited, Confident, Reserved and Well-adjusted and re-examined 96% of the children 23 years later using multiple methods of comprehensive personality assessment. The goal of their work was to test the links between behavioral qualities observed at age 3 and personality functioning measured at age 26. These longitudinal data provide the longest and strongest empirical evidence to date that children's early emerging behavioral styles can foretell their characteristic behaviors as adults.

For the purpose of this thesis, the methodological approach we used allowed us to investigate the stability of behavioral dimensions between the two challenge tests. The mathematical solution derived by the higher order solution demonstrated that there is evidence of stability both for individuals and in the conceptualization of behavioral dimensions. That we were able to derive a second-order solution, which explained 61.6% of the variance, speaks to the fact that at least some individuals scored similarly at the two different time points. The similarity of groupings of individual behaviors into factors at two different points in time (discussed in detail in Manuscript 3 and earlier in the discussion) speaks to a degree of stability in the behavioral traits across developmental time.

What remains very interesting in this social context would be to identify individuals with high stability and individuals with high instability. Is there a large fluctuation in mood, energy level and social interaction within an individual? Are these differences a reflection of normal developmental periods or of individual instability? Certain individuals are hyperactive and impulsively curious one moment and lethargic and unmotivated the next. The way we have analyzed this data does not capture all of this information, and it is therefore impossible to assess using our approach. Our focal animal approach clearly can flag individuals demonstrating stability versus instability, but would provide weak empirical evidence. Our peripheral measure of activity (i.e. motility) could be a good way of capturing some of this information, along a specific vector, without the need to collect a new sample of behavior. The stable monkeys would exhibit consistent scores across all or most observations. Unstable monkeys would oscillate across a range of scores, sometimes within a single day and sometimes across days. It is important to note that simply plotting mean scores across a time frame would not necessarily reveal this type of instability. Rather, it would be necessary to look at the individual data points or at the deviations from the mean value. From an observational point-of-view all event scoring at the same time every day could provide us with some answers and, statistically, trajectory analysis might be a good approach, if raw data or variance measures could be used.

Another interesting topic in this domain is a possible relationship between behavioral instability and rhythmicity, a measure highly valued by research groups like Thomas & Chess (1977) and Prior (1992), but absent from the dimensions extracted by other scientific groups. Thomas, Chess and Birch (1969) measured rhythmicity as one of their nine categories of reactivity. This category was derived from information about sleep/wake cycles and the

regularity of repetitive biological functions, such as eating and appetite, bowel and bladder functions and rest and activity. Infants were scored as 'regular' if the pattern of behavior was displayed at the same time each day, 'variable' if there was some deviation from this pattern on occasion or 'irregular,' which denoted the failure to establish even a partial pattern. In our study, a measure of rhythmicity could have easily been extracted in infancy had we focused on those repetitive biological functions. Once again, our focal animal approach flagged individuals that were unstable versus stable, but returned weak empirical evidence. There is little doubt that scoring some of these variables on a quantitative scale would provide better information from which we could potentially hypothesize both stability and instability at later time points.

Behaviors absent from the final solution

The factor solution defines the structure of behavior overall but may miss nuances of a specific individual's behavior. The more obvious example is that rare behaviors fall out of the factor solution because of their rarity, yet may be very important to defining an individual. The less obvious example has to do with negative space, and with the difficulty of interpreting what the 'absence' rather than the presence of a particular behavior (i.e. play) might mean.

Certain salient behaviors may occur so infrequently that they do not show up in the final factor solution, but if identified, could be the key to help or confirm an individual's profile in a single snap shot. The critical cue then is not so much 'which' behaviors, but rather 'when' are these behaviors expressed during an observational bout. Specific rhythms and patterns of behaviors are beyond the scope of this thesis, but will be considered in future work.

The following is an illustrative example of an important salient behavior: An alpha monkey, with a pre-established high-ranking status in his own social group, may only have to 'raise his head' once, very slightly, thus expressing a mild threat, to maintain the order (e.g. his high ranking position in that group). This subtle but critical behavior during an observational bout could easily be overlooked by the observer, yet has the ability to betray his alpha status in a single snap shot.

In other circumstances it is the absence of the behavior that is meaningful. Certain behavioral traits or disorders may be measured not by the presence of certain overt behaviors, but rather by the absence of these behaviors. It is for that reason that internalizing disorders are more difficult to assess than externalizing disorders (Rutter, 1987) (further discussed in the

psychopathology section). For example some research groups have extrapolated levels of play in monkeys to estimate the presence or absence of anxiety (Higley, 1985) monkeys that play very little or not at all are thought to be more anxious than monkeys that play a lot. This inference may have some validity, since play is thought to be an important component of a healthy social development, and its absence could be an early sub-clinical manifestation of underlying psychopathology (Fagan, 1981). This deductive approach raises other pertinent questions, such as how one can be certain that the lack of play is in fact an indirect measure of anxiety and not simply the result of general lethargy? It seems sensible that along with our objective, systematic and mathematical model of behavioral traits we will require additional complementary pieces of data to answer certain questions.

Measures not generally mentioned in the scientific literature

The following behaviors have continuously been scored by our research group, but have rarely been mentioned in the scientific literature: (1) Pace, (2) Threaten the observer and (3) Watch the observer. One possible reason these behaviors may have been ignored by other research groups is that they seem more like side effects of captivity than spontaneous behaviors occurring in the wild. Nonetheless, we feel these behaviors are worth investigating if only because the frequency of occurrence is highly variable across monkeys. In addition, these behaviors may provide some insight into the monkey's activity level, state of arousal, and level of social participation (even if the interaction happens to be with a human observer now arguably part of the social milieu).

The different possible interpretations of Pace

Pace is defined as a stereotypical, fast, walk in changing directions. Pace is a behavior rarely addressed and elaborated upon by primate researchers. Partly, I suspect, because it is unofficially considered a side effect of captivity and more importantly because we still have not come to a unanimous scientific conclusion as to what it actually measures in a given individual (i.e. an underlying stress response versus hyper-activity). That being said, what remains interesting is its individual variability.

In our study, pace was part of our behavioral repertoire. In the nursery novelty test pace was only observed in two individuals, as noted in Chapter IV. These individuals were removed

from the analysis because their pacing was incessant. In the social group context, a wide range of pacing was observed across animals, consequently deriving a weak positive loading for pace on the "agreeable" factor. In the jungle gym novelty test, a significant portion of monkeys spent their time pacing and as a result, the factor solution demonstrated, pace loading negatively on numerous factors (i.e. three of the four factors). This outcome suggests that pace could mean something different depending on which behavioral trait it falls on. We have observed and speculated on four potential meanings for "pace." The first two interpretations of "pace" result directly from an external cue: (1) pacing as a result of excitement (ex. in anticipation of food); (2) pacing as a result of fear or aggression (ex. in response to a new person walking in the vicinity of the cage, or directly following an event that was perceived threatening to the monkey). The last two interpretations of "pace" are independent of external cues, occurring both spontaneously and randomly, and are more likely to be related to a monkey's internal state; (3) endogenous predisposed hyperactivity, and (4) boredom or cage stereotypy (i.e. under-arousal). In order to discriminate between these different forms of "pace," one would need to pay more attention to the to the monkey's modal reaction across various situations, (including social or environmental contexts), and to potentially correlated underlying physiological markers. This measure has clearly raised more questions than it has answered.

The different possible interpretations of Watch and Threatening the Observer

Other behaviors that may also be considered the outcome of captivity and scientific testing, and are therefore not natural, are watching and threatening the observer. We have observed both of these behaviors in our cohorts during observation and have noted individual variability, as in pacing. In the beginning, we assumed that these behaviors would dissipate once the animals became habituated to the observer. Interestingly, this was not the case for all monkeys. The monkey's reaction to the observer (some unanticipated by our group) ranged from: (1) as predicted, quickly habituating to the observer and resuming their "normal" behavior routine; (2) never even bothering with the observer from the very beginning and minding their own business, and (3) an extreme few individuals who stopped everything they were doing to stare at and threaten the observer for the entirety of the observational bouts, without any sign of habituation. .

Excluded behavior

Another limitation of the chosen method of analysis was that certain types of behavioral information could not be included either because they did not form part of the focal animal observations or their inclusion impaired the robustness of the final solution. Two such examples are described below.

Marginal Notes: The challenge is that there are no clear rules about combining these types of qualitative and quantitative data.

Descriptive notes taken during observational bouts, along the margins of systematically coded behaviors, could provide qualitative information to complement the behavioral trait scores. For every single observational bout, each monkey had both; (a) a string of coded behaviors (collected at ten second intervals during focal animal testing), making up the overall behavioral trait solution, and (b) descriptive marginal notes consisting of various items (eg. an overall state of arousal, quality of movement, presentation of self, posture, and occasional anecdotal descriptions of events including reactions to external cues and social interactions). As mentioned in the manuscripts (Chapters 3-5), the descriptive notes have been used to enrich the interpretations of the mathematically derived behavioral traits, rather than being incorporated in any statistical sense. However, in the future it could be interesting to quantify these repetitive descriptors (eg., as a 5- or 7-point scale) as a means to verify whether there could be a mathematical relationship between the descriptors and the behavioral traits. Using this behavioral information along with the individual scores on behavioral dimensions may yet be another way of obtaining a more global profile on each animal.

Received behaviors

Another methodological issue deals with the 'received behaviors' collected during focal animal scoring. Received behaviors (eg., being groomed) were excluded from the preliminary analyses and the behavioral frequencies were then renormalized to provide a constant sum of 600 for each individual animal. Thomas Chess and Birch (1970) emphasized the importance of the interaction between an individual's inherent traits and his environment. The unique environment every individual creates for himself when his own constitutional behavioral range interacts with his social environment is a topic of much current research (Livesley et al., 1998). This suggests that the behaviors received by the individual may be as important as the behaviors initiated when trying to assess the individual's overall behavioral phenotype. A perfect example of this is that a monkey that receives many "grooms" certainly does not occupy the same social niche as a monkey initiating many "grooms," and may have a very different behavioral trait profile. In our social group factor solution, the first monkey would like have a high score on Factor 2 (sociable), while the second monkey would score highly on Factor 3 (agreeable). In our factor analysis of the social paradigm we chose to use all 'initiated behaviors' and none of the 'received behaviors' collected. The conceptual reason for this was that our focus was on what every individual did, not what was done to him or her. Second, preliminary statistical analyses using both initiated and received behaviors yielded solutions, which were not robust and could not be readily interpreted. If the individual's inherent behavioral traits influence and modify his environment (i.e. the reaction of others towards him), as theoretically described in the scientific literature, then it would be interesting to investigate in future work the information contained in the 'received behaviors' data set. Despite omission of the 'received behaviors', the data derived from the social group context still allowed us to observe how an individual behaves in a social environment; giving us insight as to whether he prefers to be sociable or isolated; interacts in an agonistic or affiliative manner; high or low ranking in the social hierarchy; and functions in an adaptive or maladaptive manner. What we do not have in our mathematical solution is a quantitative means to verify whether others in the group can assess something about the individual that the observer may have missed.

BEHAVIORAL TRAITS AND PSYCHOPATHOLOGY

One of the major motivations for conducting work on behavioral traits is that there is reason to think that inherent behavior styles may contribute to, or even predict, the expression of specific psychopathologies. Despite the continuing debate over the definition and measurement of individual differences in temperament, there is general agreement that these differences matter in terms of their implications for later development and psychiatric risks (Maziade et al., 1990a; Caspi, 1998; Prior, 1992; Rutter, 1987). The traditional way of looking at psychopathology remains the categorical tool used by clinicians referred to as the DSM IV. Individuals with a common cluster of 'problematic' behaviors are labeled under the same semantic label (i.e. diagnosis). Although these grouped individuals may not be completely homogeneous to one another (for example, there are clear differences in the presentation of various symptoms), this remains the most consensually-validated solution at present amongst behavioral experts. With the recognition that behavioral traits are biologically based, are potentially discernable early in life and persist over time and across situations, behavioral experts have begun to reconsider the categorical clinical approach altogether, and to further investigate the dimensional approach as a means of speculating about psychopathology (Tsuang et al 2000; Livesley 1998). A particularly important demonstration in this field (Livesley et al., 1998) was that an identical higher order personality structure could be derived using either a normal or a psychiatric population sample. This important evidence suggests that both normal and psychiatric individuals are on the same behavioral continuum, and that having information about the behavioral and biological mechanisms acting in normal personality could eventually provide us with a better understanding of overt psychopathology, as well as personality disorders. From the inception of this project, and encouraged by Livesley's work, we have been interested in relating the behavioral traits we derived to early indicators of incipient psychopathology in young vervet monkeys. As is obvious, over the developmental time frame of the present data collection, we can only speculate about early sub-clinical manifestations of future psychopathologies. Theoretically, the advantage of the longitudinal approach is that behaviors can be observed before they become a side effect or a symptom of a psychopathology. By contrast, if one observed the behavior or physiology of an already established alcoholic, you would need to determine to what extent the measure was

related to the cause of abusive drinking, and to what extent the behavior or physiology was a consequence of excessive drinking.

How are descriptors validated in clinical medicine? These categories are assumed to represent different underlying biological diseases that have psychological and mental manifestations. One of the main issues when dealing with psychopathology, or abnormal behavior, is the problem with semantics and definitions. In the case of "anxious" behavior for example; (1) how do we know whether the term "anxious" means the same thing for every research group, and (2) how do we ensure that our operational definition of "anxious" is actually measuring what we think it should be measuring?

Clinicians use the DSM-IV as the main tool to label individuals with specific disorders, since it is one of only a very small number of recognized instruments with an established consensus amongst experts regarding the criteria required for psychopathological definitions. Using the DSM-IV as a diagnostic tool permits individuals with common symptoms to be grouped into the same categories (i.e. clusters), and subsequently provided with a treatment plan. There are a number of limitations to this well-defined categorical approach: (1) A lack of homogeneity within the categories; eg., individuals within a category may all be "hyperactive," but a few may also show signs of impulsivity, or fearfulness. In labeling individuals as "hyperactive," we have lost the impulsive and fearful information. (2) The approach gives us no information on the intensity of the behavior; eg., how do we distinguish between an individual who is very hyperactive from one who is only a little hyperactive? (3) There is also no information on the etiology of the behavior; eg., when did this hyperactivity begin? How did it progress? Did it start as excessive fidgeting and develop into pacing? This information lost using a categorical approach could be salvaged and further addressed using a dimensional approach.
The truth of the matter is that there is still no consensus amongst scientists on how to define and measure 'abnormal' behavior. How do we know for example, whether an individual labeled "anxious" meets psychopathological criteria or not? Certain researchers argue that there is no such thing as a pathological temperament since a behavior disorder is very much a function of the reactions and response of significant others in the child's environment to individual behavioral differences. However there is a broad agreement that some kinds of temperament perceived as adverse or difficult may make a child more vulnerable to poor outcome. Conversely, easy temperament may serve to protect a child against maladjustment in a situation

of psychosocial risk. Rutter (1987) stated that despite the continuing debate over the definition and measurement of individual differences in temperament, there is a general agreement that these differences matter in terms of their implications for later development and psychiatric risk. The first definition of 'abnormal' is a statistical one. Individuals at the extremes of the distribution, sometimes even as much as two standard deviations from the mean are thought to be outside of the norm. There is clinical data demonstrating that children who score at the extremes of the distributions have a higher probability of psychopathology then children who are in the middle range. However, certain research groups such as Maziade's (1990) have not been able to see this one to one ratio, as they observed that not all children coming in for psychiatric consults scored at the extremes of behavioral trait distributions. Although individuals scoring at the extremes of the distributions are more susceptible to psychopathology, they may just be 'eccentric,' but still capable of successfully functioning in their social milieu. Rutter (1987) and Maziade have stated that extremes of temperament cannot be equated with psychiatric symptoms alone. Temperament by itself is minimally predictive of psychopathology from infancy to later ages. There is lack of perfect association between the two. It seems to be the temperament interaction with other factors or the 'social meaning' of the behaviors, which lead to disorder rather than temperament alone.

This leads us to our second definition of 'abnormal'. Perhaps it is not 'where' they are situated on the distribution that determines whether they are 'abnormal', but 'how' they are perceived by the others in their environment, and how the others react to them. For example, a child might not consider himself to be aggressive, but might be considered aggressive by the others in his environment. It is the negative perception and reaction of others that might exacerbate his behavior. The following is an example illustrating risks for psychopathology: Children were asked to write down who they would prefer to sit next to in their classroom. A diagram was drawn up with the children's wishful seating arrangements, with in the middle were the most popular children that everybody wanted to sit next to, and the outskirts of the diagram, were the least popular children that nobody wanted to sit next to. It turns out that the highest risk of future psychopathology was being one of the least popular children on the outskirts of the diagram. The chicken or the egg question: Are the other children picking up on early sub-clinical manifestations of future psychopathology in these unpopular children and staying away? Or, are the problematic inherent behavioral traits already present early in development in these

susceptible children, causing them to withdraw away from their peers, so that the lack of social support and social reference now makes them even more susceptible to their predisposed psychopathologies?

A third definition of 'abnormal' behavior is physiological. Is the body in homeostasis? Is the brain producing an adequate level of neurotransmitters? Does the central nervous system have a 'normal' reactivity threshold? Although there are numerous studies that have looked at correlates of physiological measures with behavior, the one to one ratio between biological markers and behavior is still a long way from understanding cause and effect of their relationship. Strelau (1986) offers empirical support for the fact that there are systematic patterns of neuroendocrine functioning beneath psychological traits and behaviors relevant to behavior (i.e.reactivity). However there is not a simple pattern of physiological events underlying a particular kind of behavior and that the same systems might underlie a number of different temperamental patterns. According to Rutter, it is not clear whether neuroendocrine correlates will increase understanding of the mechanisms underling psychological functions. However by showing that the same biological systems are related to similar behaviors in humans and other animals, the results of experimentation on those systems in animals assumes greater significance for our understanding of humans (Zuckerman, 1991). The above 3 mentioned definitions of 'abnormal' behavior could be studied and verified by using our objective dimensional approach.

There is great debate on what is considered 'abnormal' behavior, but clinicians in the field of psychopathology agree on a commonly researched 'cluster' described as the 'difficult temperament' (Bates, 1986; Thomas & Chess, 1977, 1982; Plomin, 1983; Thomas, Chess and Korn, 1982). Although there have been problems with concept of difficult temperament its value to clinicians has been great. Difficult children are more likely to be targeted for parental criticism and irritable reactions. Easy children are less likely to be criticized and more able to cope with adversity (Rutter, 1987). This concept may lack universal agreement on its specific temperamental components, but it has been shown to correlate with concurrent and future behavioral adjustments in children of varying ages, and social and ethnic groups (e.g. Carey and McDevitt, 1989; Earls, 1981; Earls and Jung, 1987; Prior et al., 1989b; Kyrios, Prior, Oberklaid & Demetriou, 1989; Maziade, Cote Thivierge, Boutin & Bernier, 1989a, b). Although they all agree that there are associations between difficult temperament and later adjustment problems, researchers all have different ways of defining difficult temperament. Buss and Plomin label

temperamental difficulty as negative emotionality and consider it consists of low sociability, high emotionality/distress (negative), and high activity. Thomas and Chess (1968) definition of difficult temperament was based on a typology approach identifying 5 of their 9 dimensions: Negative mood, withdrawal, poor adaptation to new stimuli, high intensity, low regular biological rhythmicity. They were able to hand pick the subjects that scored high on 5 of the 9 dimensions, and determine they might have long term behavioral problems, but they could not derive them empirically (i.e. cluster them together mathematically). Based on how they scored on these dimensions Thomas Chess and Birch created 4 categories of children; easy temperament, difficult temperament, slow-to-warm up and intermediate. Prior used a continuous scaling approach, easy to most difficult. Rothbart considered difficult temperament as being relative, and therefore did not perceive a difficult construct. They argued that what is perceived as difficult in one context is an advantage in another context. Difficult temperament is thought to be integrally tied up with notions of caretaker evaluations and appropriateness or behavioral expressions in particular contexts. Ex. Children considered to have difficult temperaments are not praised by teachers in the school system, but these same children during a famine situation in the Sahara desert have been observed to have a higher survival rate. Other research groups have not confirmed this "difficult" cluster as robust psychometrically or as a predictive marker. This cluster still remains very informative for clinicians but the challenge now is making this 'difficult temperament' meet the scientific concept. Our dimensional approach could serve as a tool to compare some of the prior definitions of difficult temperament with our newly derived behavioral traits.

There is insufficient research to date demonstrating a specific association between types of temperament and types of behavior disorder, but several reports have shown that difficult temperament is more frequently associated with externalizing disorders versus internalizing disorders. Part of the reason is most likely because childhood internalizing problems are difficult to discern, whereas oppositional, acting out, externalizing problems are more obvious, especially in a social mileu. Thomas and Chess (1982) found associations between temperament and later adjustment problems. The Australian temperament Project (ATP) led by Prior (1992) demonstrates consistent and moderately strong relationships between temperamental difficulty and externalizing, internalizing, and total behavior problems at every age from toddler to 8 years old. Maziade et al. (1990b) found associations between temperament in early childhood and

behavioral disorders, such as oppositional disorders at 12 years old. Kagan's group (1989) showed that the longer term outcome for children who are inhibited may develop anxiety later on in life. Caspi et al. (1995) demonstrated a significant link between specific behavioral traits and later forms of psychopathology. He found relations between early temperament and behavioral problems across 12 years in an unselected sample of 800 children. Factor analysis revealed 3 dimensions at ages 3, 5, 7 and 9. These were: Lack of control; approach; sluggishness. Temperament at ages 3 and 5 were correlated in theoretical coherent ways with behavior problems. Lack of control, which resembles "difficult temperament" (Thomas, Chess & Birch, 1968) with its emotional lability, restlessness, short attention span, negativism, was the most stable of the 3 traits and predicted future externalizing problems such as hyperactivity and attention problems. In another study Caspi (et al. 2003) used 1000 3 year olds. Factor and cluster analysis derived 5 behavioral traits; Well adjusted, under-controlled, confident, inhibited, and reserved. Twenty-three years later they re-examined 96% of these children as adults, and found important connections in two of the 5 behavioral traits. (1) When observed at age 3, children classified as Undercontrolled (10% of the sample) were rated as irritable, impulsive emotionally labile, and impersistent on tasks. At age 26, there were intolerant and scored high on behaviors indexing Negative Emotionality; they were easily upset, likely to overreact to minor events, and reported feeling mistreated, deceived, and betrayed by others. (2) When observed at age 3, children classified as Inhibited (8% of the sample) were shy, fearful, and socially ill at ease. At age 26, they were characterized by an overcontrolled and nonassertive personality style; they expressed little desire to exert influence over others and expressed little pleasure in life. The remaining three temperament groups did not display such dramatic personality profiles as adults, but continuity was discernible in each group.

Having successfully derived interpretable behavioral traits for vervet monkeys in our longitudinal study, we wanted to speculate about the ways in which the extremes of our distributions, or individual monkeys that seemed to display abnormal behavior, might lead to future psychopathological tendencies. Looking at the individual case studies is very informative but a poor scientific benchmark. Hence, going back and forth from the specific case studies to the derived behavioral dimensions can be much more informative. Similarly, going back and forth from the social juvenile data to the novelty test paradigm is also another excellent way to learn more about the different individuals and behavioral traits. Understanding in depth an

individual's role and behavior in a given social context versus the role of the same individual under stress and verifying the potential presence or absence of a relationship between the two.

One approach to do this is by looking at individuals displaying vulnerabilities in their social context, (i.e. individuals that don't seem to smoothly fit into their social environment), and verify where they are located on the behavioral dimensions. Another way, is by looking at which individuals score at the extreme ends of the behavioral distributions, and verify their individual anecdotal qualitative. Three profiles will suffice to illustrate this concept:

PROFILE 1

Monkey A: Impulsive, very energetic, bully. **Nursery Novelty test:**

Capture: Challenging to catch. Put up a fight (instead of flight).

Scored HIGH on "energetic exploration:" Runs around and climbs excessively. Initially seems to be exploring, but ultimately too "restless". Acts as if "driven by a motor."

Scored LOW on "behavioral inhibition:" Never stops moving, and therefore challenging to score for the experimenter.

Dropped most of the rewards found. While attempting to grab the reward, the monkey either extends his arm too forcefully or with bad aim, consequently knocking off the banana onto the ground (> 4 times).

Scored HIGH on motility.

When this monkey is not engaged in locomotion, he fidgets.

Jungle Gym Novelty test:

Tunnel: He went up in the tunnel spontaneously (without any coaxing from the part of the experimenter).

Scored HIGH on "exploratory:" Exploring and walking on the bottom of the testing cage. (Would have anticipated to see him scoring HIGH on "confident," but this was not the case. He spent more time on the bottom of the cage, and very little time climbing and seeking rewards).

Scored LOW on "defensive aggression" and "cautious:" He was always moving around the cage, and consequently spent no time looking around, looking ahead, threatening the observer or in a spread eagle position. Engaged in frequent bouts of pacing.

Found no rewards. As a result of not climbing along the sides of the cage, he failed to find any of the rewards.

Scored HIGH on motility.

Anecdote:

When the Jungle Gym novelty test cage was opened to remove monkey A, he impulsively leaped out past the observer and ran away. He was found a couple of days later, injured by a tractor, on a remote country path.

PROFILE 2

Monkey B: (Very anxious monkey who eventually develops symptoms of depression)

The anxiety symptoms cause a significant decrease in exploration and seeking out rewards.

Nursery Novelty test:

Capture: Became catatonic, when nursery cage was opened to catch the monkey. The monkey seemed to physiological "shut down" when being handled by the experimenter (i.e. motionless, eyes closing, heart racing).

Scored HIGH on "behavioral inhibition:" Frozen, with a fixed stare but no eye contact with the experimenter. Was catatonic throughout the entire testing bout and remained in awkward and seemingly uncomfortable positions.

Scored LOW on "energetic exploration" and "cautious exploration:" No attempt at any exploration, visual or physical.

Obtained zero rewards. At close proximity to rewards (i.e. reachable distance) and never even attempted to reach out for them.

Scored LOW on motility. Never moved.

Never habituated, despite repetitive trials.

Jungle Gym Novelty test:

Tunnel: Refused to go up into the tunnel, despite extreme coaxing from the part of the experimenter. Had to be manually transferred into the bigger novelty test space.

Scored HIGH on "cautious:" Looking around, staring ahead.

Scored LOW on "exploratory:" Did not move around the cage.

Very low motility.

Ate no bananas (too busy being hyper-vigilant to the outside)

Anecdote: Lethargic. Sits in a corner like a "bump on a log." In a social milieu finds himself at the bottom of the social hierarchy. Is constantly picked on by other higher ranking individuals, and consequently frequently wounded. Has access to the food (i.e. crumbs) last. Injuries and poor nutrition results in a higher susceptibility to sickness and early death. This detrimental outcome occurs despite moving the vulnerable monkey to a new social group.

PROFILE 3

Monkey C: (Very anxious monkey who eventually develops symptoms of OCD)

Compulsive behaviors that monopolize an unreasonable amount of time. These repetitive behaviors seem to interfere with a monkeys "normal" routine.

Compulsions are repetitive behaviors (e.g. checking the same reward holes in a novelty test over and over again). The goal of which seems to prevent or reduce anxiety or distress, and not to provide pleasure or gratification?

Nursery Novelty test:

Capture: Difficult to catch. Pacing frantically up and down the cage, stopping occasionally to swat at the experimenter (i.e. "fight") and begins pacing again.

Scored HIGH on "cautious exploration:" Lots of repetitive manual exploration.

Scored HIGH on "defensive aggression:" Repetitively threatening the observer with gapes and other grimaces.

Very LOW motility. Spent more time obsessively exploring or threatening.

Found a couple of rewards, but spent an excessive amount of time inspecting the same holes over and over again, despite the absence of rewards. Behavior seemed to increase with time.

Jungle Gym Novelty test:

Tunnel: Went up the tunnel with some mild coaxing on the part of the experimenterScored HIGH on "defensive aggression:" Threatening experimenter.

Scored LOW on "confident:" Pacing at the bottom of the cage.

Anecdote: Monkey is quite repetitive in his behaviors. Early on in development this compulsivity is observed more specifically in manual behaviors and with age seems to turn into excessive threatening and pacing.

FUTURE DIRECTIONS

The immediate goal of this study was to see whether we could derive interpretable behavioral traits using basic behaviors in both a social context and laboratory conditions. This dimensional approach has served to take a large amount of empirical data and reduce it to a smaller number of interpretable behavioral traits from which we can detect an underlying structure. We have devoted considerable resources to defining these phenotypes in the belief that this information will provide a more homogeneous basis to help us investigate biological factors, such as the mapping of specific vulnerability genes and other biochemical markers. The measurement of cerebrospinal fluid metabolites of neurotransmitters, and the evaluation of their relationship to behavioral traits, as presented in Chapters 2, 3 and 4, is an initial example of this approach. The ultimate goal of this project will be to use this metric tool as an adjunct to studies of complex behavioral traits, including psychiatric phenotypes (such as affective disorder, ADHD and substance abuse) that occur spontaneously in the population, and for which genetic basis might be plausible. These traits might also be useful in studies of the effects of genetic variants of known candidate loci. Abstracts showing that the behavioral traits identified in this project are heritable and may reflect specific genetic variants are cited in the appendix (claims of originality).

Another important activity for the future is to evaluate the stability of the extracted traits in the same individuals as adults. Will the same overall factor structure be maintained? Can we make predictions about adult behavior from adolescent profiles? Will the trait scores be related to disease susceptibility (i.e. morbidity), reproductive success and survival (mortality)? Will trait scores predict social rank? For example, a highly exploratory individual who is impulsive may have a higher reproduction rate (as well as reproducing at an earlier age), but conversely, the same trait may cause him to have an avoidable accident resulting in an early death. A highly anxious individual who takes few risks may fall to the bottom of the social hierarchy, thus preventing him from having easy access to food, leading to malnourishment, an increased vulnerability to diseases and an early death. Other areas that would be interesting to study but that require different methodological approaches have been mentioned previously. Of these, issues of adaptability and resilience, as well as behavioral stability from day-to-day, are particularly interesting.

Although our reported findings already demonstrate face plausibility and can be conceptually compared to behavioral traits derived by other research groups, there is still room for improvement. In order to move towards an even more robust solution, we could replicate these factor structures in another few cohorts, as a means to further improve both the validity and reliability of our measures. It is important to realize that personality phenotypes remain extremely variable. Minor variations in measures and samples influences the number and contents of factors identified. By increasing our already large sample size and sticking to basic behavioral measures, we ensure both robustness and objectivity.

It could also be informative to take the same data used to execute the dimensional factor analysis, and perform a cluster analysis. Would such an analysis identify individuals at the ends of the extracted dimensions, or would it identify a larger number of traits? A cluster analysis using our data could potentially isolate a subgroup of individuals that demonstrate for example, "difficult" temperament. Having both sets of data could allow us to decipher which behavioral traits make up this cluster. As discussed in the psychopathological section, Thomas Chess and Birch's definitional criteria for difficult temperament was based on 5 of their 9 behavioral traits which could not be empirically derived. The dimensional approach provides a mathematical break down of the various behavioral traits, where as the cluster analysis groups together individuals who have similar scores on various behavioral traits. Both approaches seem to provide important and unique information to better understanding behavior.

CONCLUSION

The overall solution provided us with information (i.e. behavioral scores) on all subjects, including the ones in the middle of the distribution, demonstrating individual differences between animals. The bi-directionality of the dimensional vectors permits us to perceive traits from a different perspective. The possibility of single individuals having a specific score on numerous vectors simultaneously can provide us with much more information than a simple categorical approach. The countless permutations and combinations of scores possible between individuals, begins to demonstrate the range of individual variability.

This longitudinal approach also shines a light onto the potential topological changes of behavioral traits across development, with certain outcomes being more intuitive and other outcomes being more counter-intuitive. An example of an intuitive outcome is that young, more adaptable monkeys who spontaneously approach new things may turn out to be much more sociable as they get older than less curious monkeys. An example of a counter-intuitive outcome is that young, more inhibited monkeys who are not very active may turn out to be much more hyperactive as they get older than more uninhibited active monkeys. With the expression of the phenotypic behaviors at hand, such continuity forces us to reflect on what might actually be the underlying commonality between these two behaviors. This illustrates the theoretical assumption that inherent traits do not simply vanish, but instead can be modified and differently expressed across development. In addition, it has been demonstrated that a cluster of correlating behaviors making up a single dimension, is more stable across time than individual behaviors. Hence further supporting the view that we are successfully measuring something underlying the array of overt behaviors.

As a result of the lack of homogeneity in a social context versus a controlled laboratory test situation and the possibility that some inherent traits become masked in non-stressful environments led us to introduce two novelty tests in our longitudinal research paradigm at different time points. Our original contribution to this established body of work was not in the design of our testing apparatus, which included a conglomerate of elements from various other testing conditions, but in the way we chose to analyze our data. Generally these novelty paradigms have pre-conceived measures which quantify and mark the presence or absence of

specific behavioral traits. The latency to approach a novel object, for example, is suggested to be a direct measure of exploration or fearfulness. By contrast, the novelty challenge situation is a more objective approach as it documents responses as they occur in both humans and experimental animals. This paradigm attempts to identify underlying behavioral traits potentially masked while animals are in a social environment. However, the fact that these animals are individually tested both limits the number of behavioral traits derived (i.e. no social dimensions) and adds robustness to the overall solution.

The main strength of the present methodological approach has been to provide us with a behavioral index for the vervet species, as well as yielding information about the relative hierarchical positioning of each individual on a number of traits. The robustness of this solution is the result of systematically collecting quantitative behavioral data on a large number of monkeys.

REFERENCES

Bates, J.E. (1986). "The measurement of temperament." In R. Plomin & J.Dunn (Eds), The study of temperament: Changes, continuities and challenges (pp. 1-11). Hillsdale, NJ:Erlbaum.

Bates, J.E. (1989). "Concepts and measures of temperament." Temperament in Childhood. G.A. Kohstamm, J.E., Bates, & M.K. Rothbart, Editors. New York: John Wiley and Sons Ltd. Pgs: 1-26.

Bolig, R., C. S., Price, S., P. L., O'Neill, & S.J. Suomi, (1992). "Subjective assessment of reactivity level and personality traits of rhesus monkeys." International Journal of Primatology 13(3): 287-306.

Carey, W.B. & McDevitt, S.C. (1989). Clinical and educational application of temperament research. Amsterdam: Swets & Zeitlinger.

Caspi, A., Henry, B., McGee, R.O., Moffit, T.E., & Silva, P.A. (1995). "Temperamental origins of child and adolescent behavior problems: from age three to age fifteen." Child Development 66(1): 55-68.

Caspi, A. (1998). "Personality development across the life course. In W. Damon (Series Ed.) & N. Eisenberg (Vol. Ed.), Handbook of child psychology, Volume 3: Social, emotional, and personality development (pp. 311-388). New York: Wiley.

Caspi, A., Harrington, H., Milne, B., Amell, J.W., Theodore, R.F., & Moffit, T.E. (2003). "Children's behavioral styles at age 3 are linked to their adult personality traits at age 26." Journal of Personality 71(4): 495-513.

Capitanio, J.P. (1999). "Personality dimensions in adult male rhesus macacques: prediction of behavior across time and situation." American Journal of Primatology 47: 299-320.

Caine, N.G., Earle, H., Raite, M. (1983). "Personality traits of adolescent pig-tailed monkeys, (macaca nemestrina): An analysis of social rank and early separation experience." American Journal of Primatology 4: 253-260.

Earls, F. (1981). Temperament characteristics and behaviour problems in three-year-old children. Journal of Nervous and Mental Disease 169: 367-373.

Earls, F. & Jung, K.G. (1987). Temperament and home environment characteristics as causal factors in the early development of child psychopathology. Journal of the American Academy of Child and Adolescent Psychiatry 26: 491-491.

Fagan, R., (1981). "Animal Play Behavior." New York: Oxford University Press.

Figuerdo, A.J., Cox, R.L., & Rhine, R.J. (1995). "A generalizability analysis of subjective personality assessments in the stumptail macaque and the zebra finch." Multivariate Behavioral Research 30(2): 167-197.

Gray, J.A. (1971). "The psychology of fear and stress." Toronto. NY: McGraw-Hill.

Higley, J.D. (1985). "Continuity of social separation behaviors in rhesus monkeys from infancy to adolescence." Unpublished doctoral dissertation, University of Wisconsin, Madison. WI.

Kagan, J., Reznick, J.S., & Snidman, N. (1988). "Biological basis of childhood shyness." Science 240: 167-171.

Kagan, J. (1989). "Temperamental contribution to social behavior." American Psychologist 44: 668-674.

Kagan, J., Reznick, S., Gibbons, J. (1989). "Inhibited and uninhibited types of Children." Child Development 60: 838- 845.

Kalin, N.H. & Shelton, S.E. (1989). "Defensive behaviors in infant rhesus monkeys: environmental cues and neurochemical regulation." Science 243: 1718-1721.

Kyrios, M., Prior, M., Oberklaid, F. & Demetriou, A. (1989). Cross-cultural studies of temperament: Temperament in Greek Infants. Journal of Cross-Cultural Psychology.

Livesley, W.J., Jang, K.L., & Vernon, P.A. (1998). "Phenotypic and genetic structure of traits delineating personality disorder." Archives of General Psychiatry 55(10): 941-948.

Maziade, M., Caron, C., & Cote, R. (1990a). "Extreme temperament and diagnosis: a study in a psychiatric sample of consecutive children." Archives of General Psychiatry 47: 477-484.

Maziade, M., Caron, C., Cote, R., Merette, C., Bernier, H., Laplante, B., Boutin, P., & Thivierge, J. (1990b). "Psychiatric status of adolescents who had extreme temperament at age 7." Amercian Journal of Psychiatry 147: 1531-1536.

Maziade, M., Coté, R., Thivierge, J., Boutin, P. & Bernier, H. (1989a). Significance of extreme temperament in infancy for clinical status in preschool years. I: Value of extreme temperament at 4-8 months for predicting diagnosis at 4.7 years. British Journal of Psychiatry 154: 535-543.

Maziade, M., Coté, R., Thivierge, J., Boutin, P. & Bernier, H. (1989b). Significance of extreme temperament in infancy for clinical status in preschool years. II: Patterns of temperament change and implications for the appearance of disorders. British Journal of Psychiatry 154: 544-551.

McGuire, M.T., Raleigh, M.J., & Pollack, D.B. (1994). "Personality features in vervet monkeys: The effects of sex, age, social status, and group composition." American Journal of Primatology 33(1): 1-13.

Pavlov, I.P. (1927). Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex (translated by G.V. Anrep). London: Oxford University Press.
Prior, M., Sanson, A., Carroll, R. & Oberklaid, F. (1989b). Social class differences in temperament ratings of pre-school children. Merril-Palmer Quarterly 35: 239-248.

Prior, M. (1992). "Childhood temperament." Journal of Child Psychology and Psychiatry 33(1): 249-279.

Rutter, M. (1987). "Temperament, personality and personality disorder." British Journal of Psychiatry 150: 443-458.

Sanson, A., Oberklaid, F., Pedlow, R., & Prior, M. (1991). Risk indicators: Assessment of infancy predictors of preschool behavioural maladjustment. Journal of Child Psychology & Psychiatry 32: 609-626.

Scarr, S. & McCartney, K. (1983). How people make their own environments: A theory of genotype environmental effects. Child Development 54: 424-435.

Schneirla, T.C. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In: MR Jones, ed. Nebraska Symposium of Motivation, Vol.7, U Nebraska Press. pp 1-42.

Stevenson-Hinde, J., & Zunz, M. (1978). "Subjective assessment of individual rhesus monkeys." Primates 19: 473-482.

Stevenson-Hinde, J., Stillwell-Barnes, R., & Zunz, M. (1980). "Subjective assessment of rhesus monkeys over four successive years." Primates 21(1): 66-82.

Strelau, J. (1983). Temperament, personality, activity. New York: Academic Press.

Strelau, J. (1986). "Do biological mechanisms determine the specificity of temperament?" In G.A. Kohnstamm (Ed.), Temperament discussed. Lisse (Neth.): Swets & Zeitlinger.

Suomi, S. (1987). "Individual differences in rhesus monkey behavioral and adrenocortical responses to social challenge: Correlations with measures of heart rate variability. In Fox, N. (chair), Heart Rate Variability and Social Behavior: Behavioral and Biological Correlates, Symposium conducted at the meeting for the Society for Research in Child Development, Baltimore, MD.

Suomi, S.J., (1991). Uptight and laid-back monkeys: Individual differences in response to social challenges. In S.E. Brauth, W.S. Hall, & R.J. Dooling (Eds.), Plasticity of development (pp. 27-56). Cambridge, MA: MIT Press.

Thomas, A., Chess, S., Birch, H. (1968). Temperament and behavioral disorders in childhood. New York: New York University Press.

Thomas, A., Chess, S., & Birch, H.G. (1969). "Temperament and behavior disorders in children." New York University Press.

Thomas, A., Chess, S., & Birch, H.G. (1970). "The origins of personality." Scientific American 223, 102-109.

Thomas, A., & Chess, S. (1977). "Temperament and development." New York: Bruner/Mazel.

Thomas, A. & Chess, S. (1982). Temperament and follow-up to adulthood. In Temperamental differences in infants and young children. Ciba Foundation Symposium No. 89. London: Pitman. P. 168-175.

Thomas, A. & Chess, S. & Korn, S.J. (1982). The reality of difficult temperament. Merrill-Palmer Quarterly 28: 1-20.

Tsuang, M.T., Stone, W.S., & Faraone, S.V. (2000). "Toward reformulating the diagnosis of schizophrenia." American Journal of Psychiatry 158(7): 1041-1050.

Zuckerman, M. (1991). Psychobiology of Personality. Cambridge: Cambridge University Press.

proved Period for Animal Use	Beginning:	Ending:

This protocol has been approved with the modifications noted in Section 13.

Research Personnel and Qualifications: List the names of all individuals who will be in contact with animals in this study (including the Principal Investigator) and their employment classification (investigator, technician, research assistant, undergraduate/graduate student, fellow). Indicate any training received (e.g workshops, lectures, etc.). The PI certifies that all personnel listed here have suitable training and/or experience, or will be provided with the specific training which qualifies them to perform the procedures described in the protocol. Each person listed in this section must sign to indicate that s/he has read this protocol. (Space will expand as needed.)

Name	Classification	Training Information	Signature
erta mour PI	Professor	20 years experience	
ık Ervin, MD	Investigaror	over 40 years experience	
r Beierschmitt, M	Veterinarian	Board certified in US and California	
oline Desbiolles	Graduate student	Training in behavioural observation: no role in animal handling	

an undergraduate student is involved , the role of the student and the supervision received must be described. I was unable to exapnd previous section, so have added an attachment

Summary (In language that will be understood by members of the general public)

a) Rationale: Describe, in a short paragraph, the overall aim of the study and its potential benefit to human/animal health or to the advancement of scientific knowledge.

iety disorders are highly prevalent in our society, affecting up to 20% of the adian population at some period of the life cycle. Recent studies have suggested t anxiety disorders are constitutionally mediated and that some individuals begin express a susceptibility to these disorders in early childhood. There is also son to think that, if identified early, more effective interventions which will ow a modification of dysfunction could be designed or, alternatively, more ective coping mechanisms could be learned and employed. Before this goal can be lized, we require a great deal of basic information, much of which cannot be lected in human experimentation. It would be neither ethical nor practical to duct this type of longitudinal study in human beings, and uninformative to collect s type of data in an animal without a prolonged developmental period or a strong ial context.

b) Specific Objectives of the Study: Summarize in point form the primary objectives of this study.

overall objective of the present proposal to understand the extent to which nerability to anxiety-related traits can be identified in infant and juvenile vet monkeys raised in a naturalistic, family-based environment; to follow the elopment of these traits throughout adolescence, and ultimately to determine the ent to which such traits influence adult function. Two specific objectives will addressed: (1) we will examine the possibility that anxiety-related traits can identified in infant and juvenile monkeys living in an undisturbed normal social text; (2) we will test the hypothesis that such traits can be more robustly ineated by behavioral response to novel environments. In the process of ducting these studies, we will also collect information about growth patterns, ocrine measures and neurotransmitter metabolite levels at 3 distinct periods of elopment (6, 18 and 36 months of age).

c) Progress Report: If this is a renewal of an ongoing project, **briefly** summarize what was accomplished during the prior approval period and indicate if and how the current goals differ from those in the original application.

the first three years of this study, we have completed the about 80% of the data collection of a longitudinal behavioural f about 200 monkeys from birth to 2 years, with social behavioural observation in the natal cage, followed by social ıural observation in peer groups. At two points, infants are tested for response to a novel environment. During regular /early) veterinary examinations, blood and CSF are drawn for neurochemical and genetic measures. This has allowed an :al definition of trait fearfulness and allowed an evaluation of those neurochemical and neuroendocrine variables which ted to this domain. These goals are restricted in scope as compared to the original objectives because of the reduced level ing available.

) Summary of Procedures for Animal Use Report to the CCAC : Using **key words,** describe the procedures used :.g. anaesthesia, breeding colony, injection IP, gavage, drug administration, major survival surgery, euthanasia by xsanguination, behavioural studies). Refer to Appendix 1of the Guidelines for a more complete list of suggested key /ords.

behaviour observation, behavioural/environmental testing, anaesthesia, iv blood .ing, CSF sampling

Animals To Be Used

Purpose of Animal Use (Check one):

- ☐ Studies of a fundamental nature/basic research
- ☒ Studies for medical purposes relating to human/animal diseases/disorders
- ☐ Regulatory testing
- ☐ Development of products/appliances for human/veterinary medicine

Will the project involve breeding animals? NO☒ YES ☐

Will the project involve the generation of genetically altered animals? NO ☒ YES ☐

Will field studies be conducted? NO ☒ YES ☐

ɔcription of Animals

	Species 1	Species 2	Species 3	Species 4	Species 5	Species 6
s	C aethiops					
ier/Source	BSF					
	St Kitts					
	both					
Vt	birth to 3.5 kg					
ɔe purchased	no					
duced by in-breeding						
er eld studies)	SK primate facility					
led at one time	30-40					
cage	8 - 9					
AL# /YEAR	**up to 200**					

ty Control Assurance: To prevent introduction of infectious diseases into animal facilities, a health status report or veterinary tion certificate may be required prior to receiving animals from all non-commercial sources or from commercial sources whose animal status is unknown or questionable. Quarantine and further testing may be required for these animals.

ustification of Animal Usage

ease justify the number of animals requested for each species described above, **based on the experimental objectives of roject.** Include information on experimental and control groups, # per group, and failure rates. Also justify in terms of tical requirements, product yield, etc. For breeding, specify how many adults are used, number of offspring produced, and many offspring are used in experimental procedures. Use the table below when applicable (space will expand as needed).

offspring born into the pedigreed colony of Behavioural Sciences Foundation, St Kitts, animals in this study will be lled in this study. The animals are indigenous to the island, which is both rabies and tuberculosis free by WHO lards. To identify trait variables using non-invasive social behavioural observation, a relatively large sample is ired. Our data to present comprises 193 individuals studied from birth to age 2. Factor analysis of this data als evidence of 5 behavioural vectors, with a power of about 52% to identify vectors with a moderate effect. ɔrdingly, this sample will need to be doubled to reach an acceptable standard of power. This data collection will be pleted in the next 2 years. Procedures such as blood draw and CSF collection are done in the context of twice ly veterinary examination, which is routine for all animals in the colony. In this respect, we are simply "piggy-ɔing" on normal procedures. SOPs have been approved by the local IRB (and are available on request) for each of e procedures.

Agents or ɔdures	# of Animals and Species Per Group	Dosage and/or Route of Administration	# of endpoints	Other variables (i.e. sex, weight, genotypes,etc.)	**Total number of animals**
2 Drugs	6 rats	.03, .05 mg/kg - IM, IP (4 variables)	1, 7, 10 days (3 variables)	Male, Female groups (2 variables)	2 x 6 x 4 x 3 x 2 = 288

lease justify the need for live animals versus alternate methods (e.g. tissue culture, computer simulation).

omplex social behaviour can only be studied in a live animal. We have prevlously conducted a number of studies of K and CCK receptors in tissue culture, but cannot conduct behavioral studies in that manner.

escribe the characteristics of the animal species selected that justifies its use in the proposed study (consider characteristics ı as body size, species, strain, data from previous studies or unique anatomic/physiological features)

The vervet monkey is a very generalized primate, on a direct lineage to man. It is thus highly appropriate for s which will ultimately be related to human health. More importantly, calm and anxious vervet monkeys are elineated, whereas this is not the case for rodents. Also, the neuroanatomy and neurochemistry of the primate parallels that seen in man.

imal Husbandry and Care

ecial cages NO ☐ YES ☐ Specify: NA

ecial diet NO ☐ YES ☐ Specify: NA

ecial handling NO ☐ YES ☐ Specify: NA

here any component to the proposed procedures which will result in immunosuppression or decreased immune function tress, radiation, steroids, chemotherapeutics, genetic modification of the immune system)?

☒ YES ☐ Specify:

le institution facility housing: NO ☐ YES ☐

te all facilities where animals will be housed: Building: St Kitts Room No:

te area(s) where animal use procedures will be conducted: Building: St Kitts Room No:

nal housing and animal use are in different locations, briefly describe procedures for transporting animals:

ndard Operating Procedures (SOPs)

lete this section if you plan to use any of the UACC SOPs listed below. **It is UACC policy that these SOPs be used applicable.** Any proposed variation of the SOPs must be described and justified. The Standard Operating Procedures can nd at the UACC website at **Error! Reference source not found.**. The completed and signed SOP form must be ed to the protocol.

all SOPs that will be used:

Collection (UACC#1)	☐	Production of Monoclonal Antibodies (UACC#7)	☐
thesia (rodents) (UACC#2)	☐	Production of Polyclonal Antibodies(UACC#8)	☐
esia (rodents/larger species) (UACC#3)	☐	Collection of Amphibian Oocytes (UACC#9)	☐
ng (transgenics/knockouts) (UACC#4)	☐	Rodent Surgery (UACC#10)	☐
genic Generation (UACC#5)	☐	Neonatal Rodent Anaesthesia and Euthanasia (UACC#11)	☐
out/in Generation (UACC#6)	☐		☐

escription of Procedures

For each experimental group, describe all procedures and techniques in the order in which they will be performed - surgical procedures, immunizations, behavioural tests, immobilization and restraint, food/water deprivation, requirements for post-operative care, sample collection, substance administration, special monitoring, etc. **If a procedure is covered by an SOP, no further detail is required.** Appendix 2 of the Guidelines provides a sample list of points that should be addressed in this section.

the St Kitts primate facility, the majority of adult female monkeys are housed in social groups with one or more adult ales. These outdoor enclosures provide 2-8 m3 per animal. Most of these animals were born in the facility. Each imal is tatooed at the first veterinary examination with a unique identifying number which it carries throughout its life. project 1, standard primate social behavioural data is collected by focal animal observation at approximately weekly tervals for all infants born during the years 1996, 1997, 1998, 1999, over the period comprising the first two years of life. fants remain in their natal cages for up to 1 year after birth, then are moved to a nursery setting for a brief period (for purposes of husbandry), then promptly move to peer groups of 8 individuals. At two points (about 11 months of age,

ıut 22 months of age), each animal is briefly removed from its home cage for exposure to a novel environment. The 11 nth exposure is repeated twice, at weekly intervals, and comprises a 10 minute exposure to a play cage equipped with ing places for fruit rewards, toys, ropes, ladders, etc. The animal's response to this cage is monitored by standard focal mal observation with documentation of how much time is spent in each location, what proportion of rewards are tained, what the extent of exploration is, etc. The 22 month trial also comprises two 10 minute exposures, two days art, to a larger play cage, equipped with runs, hiding places, fruit rewards, and a maze to be negotiated. For both of se exposures, animals remain in contact with their social group during periods between trials. An adjunct to this periment is the collection of venous blood (for endocrine determinations) and cerebrospinal fluid (for amine metabolite d peptide determinations) at the time of regular twice-yearly veterinary inspections. Monkeys will be anaesthetized with mg/kg ketamine and removed from the home cage. Under anaesthesia, weight and blood pressure will be measured der SOP. After shaving and disinfecting the skin covering the cisterna magna, 1 ml CSF will be removed through a nscutaneous puncture with a 25 gauge needle (SOP). 20 ml venous blood will be collected by femoral puncture (SOP). ıese fluids will be centrifuged as needed, and frozen immediately with an enzyme inhibitor cocktail to protect labile ptides. Both CSF and blood fractions will be analyzed in the laboratories of Drs. Palmour and Young in Montreal, and r. Baker in Edmonton. All monkeys will all be returned to their social group cages at the end of sample collection.

eld Studies – Provide all relevant details. Procedures to be conducted (e.g. surgery, blood collection, tagging etc.) should cribed above.

)d of capture/restraint, duration of captivity, potential injury/mortality, monitoring frequency:

portation and /or housing of animals in the field:

al handling required:

ıre of non-target species, potential injury/mortality:

captured animals be released at or near the capture site YES ☐ NO ☐
, specify if they will be relocated to other locations and/or populations.

ribe any potential ecological disruption this study may cause:

the responsibility of the investigator to obtain all necessary permits for work with wildlife. Copies of these permits t be forwarded to the Research Ethics Officer (Animal Studies) when they are obtained.

Pre-Anaesthetic/Anaesthetic/Analgesic Agents: List all drugs that will be used to minimize pain, distress or discomfort e will expand as needed.

cies	Agent	Dosage (mg/kg)	Total volume(ml) per administration	Route	Frequency
ıethiops	ketamine	10 mg/kg	0.1 ml/kg	im	twice yearly for vet exam

Administration of non-anaesthetic substances: List all non-anaesthetic agents under study in the experimental ponent of the protocol, including but not limited to drugs, infectious agents, viruses (table will expand as needed).

cies	Agent	Dosage (mg/kg)	Total volume (ml) per administration	Route	Frequency
	none				

Endpoints : 1) Experimental – for each experimental group indicate survival time .
2) Clinical - describe the conditions, complications, and criteria (e.g. >20% wt.loss, tumour size, alizing, lack of grooming) that would lead to euthanasia of an animal before the expected completion of the experiment ecify per species and project if multiple projects involved).

Animals will not be sacrificed at the end of these studies. There are no procedures which would impair a normal ial life or impact upon health or well being. Daily clinical rounds are made by trained staff and by the facility erinarian. Any animal which shows any sign of sickness will be quarantined and treated, and any animal which is ured (typically by a cage mate) receives prompt and thorough care.

ecify person(s) who will be responsible for animal monitoring and post-operative care

Amy Beierschmitt, DVM **Phone#:869-465-7280**

hod of Euthanasia – According to CCAC guidelines, justification must be provided for use of any physical method of ısia without prior use of anaesthesia (justify here):

Species	
	☐ anaesthetic overdose, list agent/dose/route:
ops	☐ exsanguination with anaesthesia, list agent/dose/route: performed,
	☐ decapitation without anaesthesia ☐ decapitation with anaesthesia, list agent/dose/route:
	☐ cervical dislocation
	☐ CO_2 chamber
	☐ other (specify)
	☐ not applicable (explain)

ategory of Invasiveness: B ☐ C ☒ D ☐ E ☐

ories of Invasiveness (from the CCAC *Categories of Invasiveness in Animal Experiments).* Please refer to this document for a more d description of categories:

ory A: Studies or experiments on most invertebrates or no entire living material.

ory B: Studies or experiments causing little or no discomfort or stress. These might include holding animals captive, injection, aneous blood sampling, accepted euthanasia for tissue harvest, acute non-survival experiments in which the animals are completely hetized.

ory C: Studies or experiments involving minor stress or pain of short duration. These might include cannulation or erizations of blood vessels or body cavities under anaesthesia, minor surgery under anaesthesia, such as biopsy; short periods of nt, overnight food and/or water deprivation which exceed periods of abstinence in nature; behavioural experiments on conscious ls that involve short-term stressful restraint.

ory D: Studies or experiments that involve moderate to severe distress or discomfort. These might include major surgery under hesia with subsequent recovery, prolonged (several hours or more) periods of physical restraint; induction of behavioural stresses, nization with complete Freund's adjuvant, application of noxious stimuli, procedures that produce pain, production of transgenics (in lance with University policy).

ory E: Procedures that involve inflicting severe pain, near, at or above the pain threshold of unanaesthetized, conscious als. Not confined to but may include exposure to noxious stimuli or agents whose effects are unknown; exposure to drugs or chemicals els that (may) markedly impair physiological systems and which cause death, severe pain or extreme distress or physical trauma on esthetized animals. **According to University policy, E level studies are not permitted.**

Potential Hazards to Personnel and Animals It is the responsibility of the investigator to obtain the necessary azard and/or Radiation Safety permits before this protocol is submitted for review. **A copy of these certificates must be hed, if applicable.**

azardous materials will be used in this study: ☒

dicate which of the following will be used in animals:

oxic chemicals ☐ Radioisotopes ☐ Carcinogens ☐ Infectious agents ☐ Transplantable tumours

omplete the following table for each agent to be used (use additional page as required).

nt			
ge			
te of administration			
uency of administration			
ation of administration			
ber of animals involved			
Survival time after administration			

: administration the animals will be housed in: ☐ the animal care facility
☐ laboratory under supervision of laboratory personnel

se note that cages must be appropriately labeled at all times.

:ribe potential health risk (s) to humans or animals:

monkeys do not carry B-virus, as it is fatal to them. No case of tuberculosis has ever been confirmed in a St Kitts monkey. Staff are instructed not to work with animals if they are sick or if there are any contagious illnesses in the

scribe measures that will be used to reduce risk to the environment and all project and animal facility personnel:

eviewer's Modifications (to be completed by ACC only): The Animal Care Committee has made the following ication(s) to this protocol during the review process. Please make these changes to your copy. You must comply with the mended changes as a condition of approval.