

# **The dimensions of personality in humans and other animals: A comparative and evolutionary perspective**

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## **ABSTRACT**

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### **Abstract:**

This paper considers the structure and proximate mechanisms of personality in humans and other animals. Significant similarities were found between personality structures and mechanisms across species in at least two broad traits: Extraversion and Neuroticism. The factor space tapped by these personality dimensions is viewed as a general integrative framework for comparative and evolutionary studies of personality in humans and other animals. Most probably, the cross-species similarities between the most broad personality dimensions like Extraversion and Neuroticism as well as other Big Five factors reflect conservative evolution: constrains on evolution imposed by physiological, genetic and cognitive mechanisms. Lower-order factors, which are more species- and situation-specific, would be adaptive, reflecting correlated selection on and trade-offs between many traits.

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The differences in behavior between animals of the same species have long been in the focus of ethologists and comparative psychologists (e.g. Caro & Bateson, 1986; Clark & Ehlinger, 1987; Dunbar, 1982; Mendl & Deag, 1995; Slater, 1981). There may be many causes of individual differences, however it is not uncommon to distinguish (1) differences between sexes, ages, etc.; (2) differences due to transitory conditions affecting some individuals; (3) stable differences in phenotypic traits (Clark & Ehlinger, 1987). In this way, variation, that is differences among individuals, is often considered separately from change, differences in the same individuals as time goes on (Clark & Ehlinger, 1987; Langlet, 1971) and the differences observed between individuals are distinguished from those within individuals (Clark & Ehlinger, 1987; Magurran, 1993; Ringler, 1983; Schleidt, 1976). But the term "individual differences" is often used to label different phenomena ranging from behavioral flexibility and decision making to stable behavioral phenotypes. Yet, some core consistency of a behavior pattern is needed for differences to be attributed to individuals.

In this paper I examine individual variation in consistent temperament traits, integrating approaches from comparative psychology, ethology and behavioral ecology with those from personality psychology. Unlike other reviews (e.g. Boissy, 1995; Clarke & Boinski, 1995; Eysenck & Eysenck, 1985; Mendl & Deag, 1995; Ramos & Mormède, 1998; Royce, 1977; Stevenson-Hinde, 1983; Wilson et al., 1994), the present discussion concentrates primarily on similarities of the overall personality structure in humans and other animals (but see Budaev, 1997a; Gosling & John, 1999 for a similar approach) and possible neurobiological and adaptive mechanisms which could account for these similarities. Second, the present article outlines a broad unifying framework, which integrates psychometric structure of phenotypic personality traits, their neurobiological and motivational basis as well as adaptive and evolutionary causes. Thus, the goal of this paper is two-fold: (1) to attract animal researchers to consistent individual differences in temperament, and provide them with a general framework from the personality theory, (2) and to draw attention of human personality psychologists to the animal literature and the current approaches to multivariate evolution, which would enable analysis of the adaptive causes of personality structures.

There exists a wide variety of views on human personality and temperament (Maddi, 1989). Some researchers prefer idiographic approach while others pursue with more scientific, nomothetic explanations (see Lamiell, 1987). Many theorists define personality and temperament depending on specific aims and approaches, for example, as relative to context (see Magnusson & Endler, 1977; Mischel, 1973; Stevenson-Hinde, 1986). However, in the present article I consider only those, which are worth extending to non-human species, namely the theories which try to reify personality and temperament, assuming that they have some tangible biological basis and are not completely determined by culture, social learning and the interactive processes.

## Dimensional Interpretation

It is not surprising, that empirical studies of individual behavioral differences in animals have been conducted by ethologists, behavioral ecologists, and comparative psychologists, but never by human personality psychologists. These disciplines have very different methodologies and follow very different traditions from personality psychology. For example, the current emphasis in ethology and behavioral ecology is on costs and benefits of particular behavioral tactics, behavioral flexibility (e.g. Via et al., 1995; Wilson et al., 1994; Wilson, 1998) and context-specific behaviors (e.g. Coleman & Wilson, 1998; Houston, 1997; Irving & Magurran, 1997), which are often erroneously equated with the lack of stable individual differences. The issues of behavioral consistency and stability, person-situation interactions, as well as the hierarchical approach to individual differences, while developed more than 20 years ago in the personality psychology, are almost unknown in the animal field. Thus, here I give a brief overview of these psychological concepts in less psychological terms, for them to be usable for animal behaviorists.

### **Behavioral Characters: Flexibility, Plasticity, Randomness**

When studying differences between groups and individuals, an investigator is concerned with characters. A character may be conceived as any trait which varies between these units (Langlet, 1971; Michener & Sokal, 1957). In studies of morphological variation characters are usually easy to determine. But in behavioral investigations opposite is often the case. Even in well-controlled experimental conditions it is difficult to create completely identical environments for all individuals. This problem arises even in testing highly homogenous inbred strains, bred under standard conditions, in a standardized test (Harrington & Blizard, 1983). Animals may differ in motivational states or adopt different strategies depending on behavior of others (Davies, 1982; Krebs & Davies, 1987). Finally, one cannot exclude random variation, especially because natural selection could maintain mixed strategies (Maynard Smith, 1982), or truly random "coin-flipping" (Cooper & Kaplan, 1982; Kaplan & Cooper, 1984). Therefore, one can expect significant differences between the actions of even the same individual, which can be further promoted by adaptive phenotypic plasticity and behavioral flexibility (Lima & Dill, 1990; Thompson, 1991; Via et al., 1995; West-Eberhard, 1989). Thus, any separate behavioral measure scored in a particular situation is often unlikely to represent character that could reliably distinguish between individuals.

### **Behavioral Characters: Correlations**

Different phenotypic characters are typically correlated, which may have a variety of causes (Arnold, 1992, 1994; Hahn et al., 1990). Genetic correlations are maintained (see Falconer, 1981), for example, by pleiotropy (multiple action of a particular gene to more than one phenotypic trait) or linkage disequilibrium (nonrandom association of alleles at different loci, for example, by physical linkage). Furthermore, the simple existence of a phenotypic correlation could often suggest, not necessarily however, that a genetic correlation could also be present between these traits (Bakker, 1994; Cheverud, 1988; Falconer, 1981; Roff, 1996), including personality traits (Livesley et al., 1998). There may be developmental constraints – limitations on the set of possible developmental states arising from ontogenetic processes, such as ordering in time, and functional constraints – limitations on the values of traits or trait combinations (i.e. trade-offs), which also bring about correlations between phenotypic characters (see Arnold, 1990, 1992, 1994). Furthermore, an assumption is frequently made (e.g. Bakker, 1994; Depue & Collins, 1999; Gray, 1987; Royce & Powell, 1985) that individual differences in a particular behavior result from different levels of activities of a relatively small set of internal controlling factors for the behavior. Therefore, if a broad motivational system controls a whole array of behavior patterns, they would be associated and change in a consistent manner. Repeatability–type consistency is expected to be high in characters that are highly heritable, indeed repeatability sets the upper limit for heritability (Falconer, 1981).

### **Behavioral Characters: Consistency versus Stability**

There is an important distinction between the terms "stability" and "consistency." When one speaks of stability, this usually means that a particular behavior does not change. However, the word "consistency" does not necessarily imply stability. Rather, it means that a particular behavioral variable correlates over time (temporal consistency or continuity) or across situations (situational consistency) even if its overall level changes (Nunnally, 1967; Ozer, 1986). That is, an individual which is, say, more fearful than others in one situation is likely to be so in another situation, even though the behavior, overall, differs in these situations (Fig. 1). Magnusson & Endler (1977) distinguished absolute consistency, when an individual displays certain behavior to the same extent across situations (i.e. stability), relative consistency, when the rank order of a set of subjects with respect to the behavior is stable across situations, and coherence, when the behavior is predictable without being consistent.

In the field of human personality psychology, Ozer (1986) developed a general theoretical framework, based on the generalizability analysis, in which persons,

situations, response classes and times represent the basic conceptual units for the study of personality. By partitioning the total variability of behavior into a number of specific variance components, each associated with a particular conceptual unit, it is possible to define various kinds of behavioral consistency, in addition to consistency over time and consistency across situations. For example, it can be possible to distinguish consistency of response profiles across situations (e.g. a person may be high on anxiety but low on dominance consistently in various situations) and consistency of time effects across situations (e.g. a person may become more anxious with age consistently in various contexts).

Thus, there is no incompatibility between consistency and situation–specificity: a behavior may be simultaneously highly consistent and highly situation–specific. Even truly domain–specific abilities (cf. Fodor, 1983; Tooby & Cosmides, 1992), in this way, could show very consistent individual differences (e.g. in Fig. 1, if the behavior or ability is displayed well in the domain B but very poorly in C). This means that even very consistent behavioral traits may be adaptive and tailored to particular situations, and individual differences must not necessarily be situation–specific to be adaptive.

### **Behavioral Characters: Dimensions**

Stable correlations between two or several consistent behaviors would imply the existence of a broader dimension. Such more or less general behavioral characteristics which are not directly observable, are abstractions which have to be obtained by inference, are usually called "latent" and are conceived as "constructs" (e.g. see Nunnally, 1967). Buss & Craik (1983) have developed the act frequency approach to personality dispositions, in which traits are considered as aggregated patterns and trends of behavioral responding, characteristic of particular individuals in various situations. Thus, dimensions of individual differences represent a system of intervening variables. They can be measured either by aggregating objectively recorded behavioral activities or by means of ratings made by experienced judges.

It has been also suggested even that "most behavioural measures in animal research are similar to single items of personality or aptitude tests" (Henderson, 1979, p.273; see also Royce, 1977) and the dimensions can be viewed as true behavioral phenes (Fuller, 1979). Consequently, individual behavioral differences may be considered at several levels. On the lowest level one can find specific responses, acts etc., observed one time. Often, they do not characterize an individual. But broad and consistent aggregate constructs appear on the higher levels, which are based on observed covariations of different tests, measures or responses (Eysenck, 1970; Fuller, 1979; Livesley et al., 1998; Royce & Powell, 1985; Royce, 1979; Ozer, 1986).

## Hierarchical Organization, Modularity and Competition

It has long been assumed that animal and human behavior is produced through a modular, hierarchically structured organization or a network of control systems of different levels (Baerends, 1976; Byrne & Russon, 1998; Newell & Simon, 1972; Tinbergen, 1951; Fodor, 1983; Toates, 1986; Gray, 1987; Tooby & Cosmides, 1992; Karmiloff-Smith, 1994). Computational models of brain functioning, in addition, revealed that competition among cognitive modules may be another general principle of behavioral organization (Grossberg, 1982; Rolls & Treves, 1998).

This approach would directly apply to the structure of personality. If personality dimensions depend on Darwinian cognitive algorithms (cf. Tooby & Cosmides, 1992) and basic affective systems (Depue & Collins, 1999; Gray, 1987; Tellegen, 1985), their hierarchical organization would directly translate to patterns of individual variability and would be maintained by natural selection. The multidimensional hierarchical structure of personality traits, often revealed in humans and other species, may thus be a direct result of modular, hierarchical, and mutually competitive organization of behavior control systems.

The ethological concept of behavioral control system, based on the "computer software" metaphor of behavior organization, has been, for example, applied to the analysis of temperament traits associated with inhibition and wariness of strangers in children (Stevenson-Hinde & Shouldice, 1993). A substantial simplicity could be achieved by assigning functionally equivalent behavioral responses to several interacting control systems, such as fear, attachment, exploration and sociability (see Stevenson-Hinde & Shouldice, 1993).

It may be expected, consequently, that the same behavior control systems organized hierarchically will determine sequential associations of cognitive and behavioral activities in groups mutually suppressing each other, correlations between specific behavioral variables in individual subjects within and across situations, similar patterns of changes of related behaviors in response to the same experimental treatments, as well as would bring about various other forms of behavioral consistency, such as consistency of response profiles across situations and consistency of time effects across situations (cf. Ozer, 1986).

## The Concepts of Temperament and Personality

Thus, it could be possible, to apply the terms "personality" and "temperament" to the behavior of animals without any impression of anthropomorphism provided it is defined objectively and precisely, for example, as a system of relatively stable and enduring constitutional features of an individual's behavior presumably associated with specific behavior control

systems.

There are certain points of controversy about the definition of personality and temperament, but both terms are often used interchangeably. The point of consensus between various approaches is that consistency over time and predictability across situations are the two major distinguishing features of temperament and personality traits as distinct from moods and states (Strelau, 1983; Goldschmidt et al., 1987; Buss & Plomin, 1975, 1984; Eysenck, 1970; Eysenck & Eysenck, 1985; Zuckerman, 1994a). Often, additional distinctions are made. For example, it is assumed (Fridhandler, 1986) that traits are abstract, dispositional entities, which are manifested discontinuously, in response to relevant circumstances, while states and moods are concrete, ostensible and in a given episode are manifested continuously.

Temperament is often defined to refer to formal aspects of behavior, its stylistic, dynamic and energetic features, as distinct from content or motivation (Nebylitsyn, 1976; Rothbart & Derryberry, 1981; Strelau, 1983; Rothbart, 1986; Goldschmidt et al., 1987). As well, it is very common to view human temperament as being biologically determined (including genetic influence), expressed in early childhood and relatively unmodifiable (e.g. Buss & Plomin, 1975, 1984; Strelau, 1983). Personality, on the other hand, is most often conceived as a somewhat more inclusive concept, incorporating different aspects of psychological and behavioral individuality (Eysenck, 1970; Eysenck & Eysenck, 1985). Moreover, it may encompass not only individuality as such, but also important conceptual issues such as self concept (Strelau, 1983; Maddi, 1989). When conceived in the latter sense, of course, "personality" may be inapplicable to animals.

However, the distinction between temperament and personality is rather vague (see also Zuckerman, 1994a). How can one separate the "style" from the "content" of behavior? Furthermore, most behavioral traits share to some extent genetic and other biological factors (Eaves et al., 1989; Plomin, 1986; Plomin et al., 1994), and not all genetically influenced traits appear early in childhood. On the contrary, the traits which are expressed early, have often rather lower heritability, which typically increases with age (Eaves et al., 1989; Hahn et al., 1990; Plomin, 1986). Also, there exist many personality traits that are not easily modifiable and animals may have early "temperaments" which are later molded into "personalities" by experience (Mather & Anderson, 1993). Natural selection shapes human psychological traits, which are unequivocally considered a part of personality (e.g. Budaev 1999; Buss, 1991; MacDonald, 1995; Segal & MacDonald, 1998), an important argument to argue that biological factors are not less important in personality than in temperament. Finally, there is a growing, although still controversial evidence for self-awareness and consciousness in some non-human species (Griffin, 1993; Dawkins, 1993). Thus, the term "personality" has a wider applicability to both humans and animals, despite of the fact that it may on the first sight carry somewhat more anthropomorphic content.

The extension of the concepts of temperament and personality to animals is not new. Pavlov (1955) used it in the early 30s to describe individual differences in the

conditioning performance of dogs as well as in the "general picture" of their behavior. Hall (1941) defined temperament in rats "as consisting of the emotional nature, the basic-needs structure, and the activity level of an organism" (p.909). Later, these terms have been used by many investigators (e.g. Boissy & Bouissou, 1995; Buirski et al., 1978; Caine et al., 1983; Champoux et al., 1997; Clarke & Boinski, 1995; Davidson et al., 1993; Korhonen & Niemela, 1996; Le Scolan et al., 1997; Lindzey et al., 1963; Mather & Anderson, 1993; McCune, 1992; McGuire et al., 1994; Pollard et al., 1994; Richards, 1972; Stevenson-Hinde, 1983; Sapolsky, 1988, 1990, 1993; Suomi, 1987, 1991) to denote broad, sometimes genetically determined, aspects of behavior. Among human psychologists, Strelau (1983) and Buss & Plomin (1975, 1984) suggested that temperament exists in animals too. Moreover, it was hypothesized (Royce, 1977; Garcia-Sevilla, 1984; Eysenck & Eysenck, 1985), that there exist particular broad dimensions in many species of mammals, which represent even closer analogies to human personality, including similar physiological and genetic background.

Some people employed the terms "temperament" and "personality" to the behavior of such "low" animals as fish. Prazdnikova (1956) as well as Leshchova & Zhuikov (1989), who studied the Pavlovian basic types of central nervous system in several fish species, admitted the idea of temperament in these species, the more so that Pavlov himself assumed equality of "temperament" and "type of the nervous system" (see Nebylitsyn, 1976). Francis (1990) used the word "temperament" to denote consistent over time differences in aggressiveness in a cichlid fish, a view close to that of Buss & Plomin (1975, 1984) who conceived temperament as "early-developing personality traits". Also, "personality" was used to denote broad behavioral dimensions in the guppy (Budaev, 1997b). Finally, Mather & Anderson (1993) applied the term "personality" for the description of consistent individual differences even in such distant from humans species as the octopus, an invertebrate animal.

### **The Structure of Human Personality**

A consensus appeared during recent decades concerning the number and nature of the basic personality factors in humans. The Five Factor model, representing a synthesis of many studies conducted in several cultures, became the prevailing view on human personality structure. It postulates (see Digman, 1990; Goldberg, 1990, 1993; Goldberg & Rosolack, 1994; Goldberg et al., 1996 for reviews) that human personality variation may be summarized by five major dimensions: Extraversion (or Surgency), Neuroticism vs. Emotional Stability, Agreeableness, Conscientiousness, and Intellect (or Openness to Experience). The Five Factor model has a paradigmatic validity and emerges even in questionnaires specifically developed to assess different factors and in studies devoted to testing alternative personality theories. Several investigators (e.g. Brand, 1984; Depue & Collins, 1999; Digman, 1990; Eysenck, 1970; Eysenck & Eysenck,

1985; Goldberg, 1990, 1993; Zuckerman, 1994a, 1995) reviewed the available data on descriptive factor-analytic personality studies. Almost universally, the dimensions identical to Big Five appeared, even though they were in a few cases rotated somewhat differently from the classical axes (Ashton et al., 1998; Caprara & Perugini, 1994; Zuckerman et al., 1993). For example, the three-factor version of the Zuckerman's (see Zuckerman et al., 1988, 1993; Zuckerman, 1994a, 1995) model includes E-Sociability, P-InpSS (psychoticism-impulsive sensation seeking), and N-Anxiety. The five-factor version also includes Aggression-Hostility and Activity.

However, two dimensions, Extraversion and Neuroticism, have stronger and more clear physiological and genetic background than other Big Five factors, are the most ubiquitous, and produced in almost every study of personality structure (Eaves et al., 1989; Eysenck, 1970; Eysenck & Eysenck, 1985). Loehlin (1982) even suggested that it is very difficult to find not heritable personality traits merely because most traits have some correlations with either Extraversion or Neuroticism, which are the most pervasive and heritable. Extraversion encompasses such traits as sociability, impulsiveness, surgency, novelty seeking, positive affectivity and susceptibility to reward. Neuroticism involves anxiety, fearfulness, negative affect, mood changeability, and susceptibility to punishment and frustration.

According to the arousal theory (Eysenck & Eysenck, 1985), Extraversion reflects individual differences in the levels of cortical arousal as a consequence of different activities of the ascending reticular activation system, the extraverts being chronically underaroused. Neuroticism is associated with differences in the threshold for hypothalamic activity as well as with responsivity of the sympathetic nervous system. In addition to Extraversion and Neuroticism, the Eysenck's personality theory also includes the third dimension, called Psychoticism. This involves such traits as impulsiveness, hostility, aggressiveness and psychopathy.

Gray (1972, 1981, 1987) has proposed a revision of the Eysenckian personality theory, which is primarily based on animal models and shows a better agreement with some neurophysiological experiments (e.g. Corr, Pickering & Gray, 1997). His model involves two interacting neural systems. First is the Behavior Inhibition System (BIS): septo-hippocampial system, temporal and frontal neocortex with its ascending monoaminergic (noradrenergic and serotonergic) pathways. The BIS modulates individual differences in the susceptibility to conditioned fear, frustrative nonreward, and responses to novel and uncertain stimuli through interruption of ongoing behavior, increased arousal and heightened attention. The Behavior Approach System (BAS) includes the basal ganglia, together with ascending dopaminergic pathways from the mesencephalon, associated thalamic nuclei, as well as motor, sensorimotor, and prefrontal cortex areas. This system mediates individual differences in susceptibility to reward and undelivery of anticipated punishment, and at the behavioral level brings about approach to such stimuli. This model also includes an arousal component, stimulated by both BIS and BAS, and a comparator component, which compares the received

reward or punishment signals with the expected consequences, thereby enabling to modify the reward and punishment mechanisms by experience.

On the basis of this neuropsychological model, Gray introduced two major orthogonal personality dimensions, initially rotated 45° from the Neuroticism and Extraversion. The BIS is associated with Anxiety while the BAS is associated with Impulsivity dimensions. However, recent analyses indicated that they should be better placed at a smaller angle, about 30° (see Pickering et al., 1998), or even that the BAS dimension should be aligned with Extraversion and BIS aligned with Neuroticism (Carvers & White, 1994).

Cloninger (1987) and Cloninger et al. (1993) introduced a model of temperament based on certain neurotransmitters mediating individual differences in behavior. According to this model, dopamine and serotonin are associated with, respectively, Novelty Seeking and Harm Avoidance personality traits. The third axis, Reward Dependence, is related to norepinephrine. Here too, Novelty Seeking shares much in common with Extraversion and Harm Avoidance with Neuroticism dimensions (even though these dimensions are also somewhat rotated from the classical factors: Harm Avoidance also correlates with Extraversion and Novelty Seeking correlates with Psychoticism, see Zuckerman, 1995).

The theory of Cattell (1957, 1973) differs from most other in that it assumes as many as 16 basic dimensions of personality in humans. However, these primary factors are not independent, and when subjected to a second-order factor analysis, yield a few second-order factors (Cattell, 1956, 1973), two of which, Exiva and Anxiety, largely correspond to Extraversion and Neuroticism (see Barrett & Kline, 1980 and McKenzie, 1988). In addition, Saville & Blinkhorn (1981) administered both Cattell's 16PF and Eysenck's EPI personality inventories, and when the variance due to Extraversion and Neuroticism was removed from the 16PF, very little amount of information left. Furthermore, several independent studies (see Digman, 1990 for a review) failed to establish any degree of replicability of the Cattell's 16PF – no one was able to identify more than seven factors in the original correlations amongst the scales that were the basis of the whole system, and even these were very similar with the Extraversion and Neuroticism (Barrett & Kline, 1980; McKenzie, 1988) as well as other factors of the Big Five model of personality. Digman (1989) suggested that this was "an unfortunate consequence of the primitive computational facilities available to Cattell" (p., 197) in mid-40s, when he developed his personality model.

Among other temperament theorists, Buss & Plomin (1984) proposed a theory of temperament conceived as a set of early developing personality traits. It involves three basic dimensions, Emotionality, Sociability and Activity, which agrees with other models in that Emotionality has correspondence with Neuroticism while the remaining traits make up Extraversion. Their earlier model (Buss & Plomin, 1975) incorporated also Impulsivity dimension, being most probably a component of Psychoticism.

Kagan et al. (1988; see also Kagan & Snidman,

1991) conducted an analysis of shyness–boldness in children, which was defined as behavioral inhibition versus boldness. But they were not primarily concerned with psychometric evaluation of underlying dimensions of temperament and it is not easy, therefore, to identify this trait with Extraversion–Introversion or Neuroticism. Most probably, as Zuckerman (1994a, see p.267) pointed out, it represents an amalgam of two basic dimensions, running from neurotic introversion (inhibited) to stable extraversion (bold), rather than a single trait. Indeed, when measured separately, sociability and shyness provide distinctive contributions in predicting behavior (Cheek & Buss, 1981). And an evidence is accumulating (see Cheek & Briggs, 1990) that shyness moderately correlates with Neuroticism as well as (inversely) with Extraversion. Within a similar theoretical framework, concerned with the study of shyness in children, Asendorpf (1993) and Rubin & Asendorpf (1993) were led to distinguish two separate dimensions of temperament in children: Approach–Withdrawal (sociability) similar to Extraversion, and Shyness (fearful and inhibited behavior, especially in novel settings) similar to Neuroticism.

Furthermore, the recent evidence revealed a clear convergence of personality structure with the affect structure. Meyer & Shack (1989) found that Extraversion and Neuroticism personality dimensions are associated with, respectively, Positive Affect and Negative Affect, the two basic dimensions of mood, which consistently emerged in many studies and are stable across cultures (see Tellegen, 1985 and Watson & Tellegen, 1985 for reviews). This lends support to the above hypothesis that these two personality dimensions ultimately reflect independent, hierarchically organized and competing behavior control systems.

### **Psychobiology and Animal Models of Human Personality**

Although applying the concept of personality to animals beyond the simple superficial and operational level may seem preposterous, several theories of human personality really found physiologically–based counterparts to human personality traits in some mammalian species: in primates, rats, mice, and dogs. For example, Eysenck & Eysenck (1985) devoted a separate chapter to review animal personality studies within the context of the Eysenck's three-factor model. The conclusion was that "evidence from the animal field is sketchy as far as similarity of personality patterns to humans is concerned, but as far as it goes it tends to be confirmatory rather than critical" (p.102). Zuckerman (1994a) also devoted a separate section in his book to animal models. He believes, however, that although they can be developed to study human personality traits, there are many limitations. To be a safe and reliable model, the animal trait must show the same functional significance as well as similar biological correlates.

### **Eysenck's Dimensions: Extraversion and Neuroticism**

In earlier studies (Broadhurst, 1960; Savage & Eysenck, 1964) emotionality (measured through open field defecation) in rats and mice was regarded as a reliable analogy of Neuroticism. This view was subsequently generalized to both Extraversion and Neuroticism by a series of studies conducted on rats. They involved drug administering, intracranial self-stimulation, avoidance conditioning, factor analysis of multiple test variables etc. (García-Sevilla, 1984; Gomá & Tobeña, 1985) and were directed to test the Eysenck's arousal theory (see above). Overall, the results provided an evidence that the behavioral trait measured by ambulation and rearing in a stress-attenuated open field have similarities with human Extraversion while open field emotionality has much in common with Neuroticism.

For example, it was shown that ambulation in a stress-attenuated open field negatively correlated with resistance to extinction of a Skinner box response, in accord with the prediction of the Eysenck's theory that extraversion is facilitated by reactive inhibition (the higher extraversion, the stronger generation of reactive inhibition, which should reduce resistance to extinction). Also, low ambulation (introverted) rats were able to easily discriminate the situation of extinction during three consecutive training and extinction sessions. As predicted by the Eysenck's drug postulate, stimulant drug (*d*-amphetamine) produced more introverted whereas depressant drug (reserpine) produced more extraverted behavior in the Skinner box extinction paradigm. Furthermore, as expected for human Neuroticism, low-defecation rats were characterized by higher aversive response threshold. Finally, in accord with the Eysenck's hypothesis that spontaneous antisocial behavior should more easily arise in neurotic extraverts (Eysenck & Eysenck, 1985; Passingham, 1972), it was shown that high ambulation and high defecation rats are easier to train to attack a conspecific (see García-Sevilla, 1984 for a review, see also Martí et al., 1987).

### **Extraversion, Sensation Seeking and Novelty Seeking**

The personality theory of Zuckerman (1994b) also utilizes animal models. It primarily focuses on Sensation Seeking, which is conceived between the Extraversion and Eysenck's Psychoticism, and is associated with antisocial tendencies. This psychological trait is presumed to be associated with individual differences in the activity of catecholamine (dopamine and norepinephrine) and serotonin systems, which are known to mediate various behavioral and emotional arousal processes. As in the other theories, open field exploration is regarded as an adequate prototype for human Sensation Seeking. Additionally, high sensation seekers are presumed to show strong orienting responses and weak defense responses. Another model is social behavior, in which sensation-seekers are characterized by elevated sociability,

impulsiveness, aggressiveness and dominance (Zuckerman, 1994b). A more general personality model, the Big Three (see Zuckerman et al., 1993; 1994a, 1995), includes E-Sociability, Impulsive Sensation Seeking (P-ImpSS) and N-Anxiety, which depend on lower-order processes like approach, inhibition and arousal, in turn mediated by interaction between dopamine, serotonin and norepinephrine.

Recent studies by Dellu et al. (1993, 1996) using several tests (free choice of novel environment with various complexity and aversiveness and responses to food and drug reinforcement) strongly suggest that rats show consistent individual differences in a behavioral trait very similar to the human Sensation Seeking. As in humans, high sensation seeker rats tend to actively pursue novelty and emotional stimulation and are more sensitive to reinforcing properties of food and drugs (e.g. unlike low sensation seekers, they developed amphetamine self-administration). In addition, high sensation seeker rats tend to have an enhanced level of dopaminergic activity in the nucleus accumbens, both under standard basal conditions and following a mild stress.

The second class of models of sensation seeking is based on the often found relationship between this psychological trait and visual evoked potential augmenting and reducing. Persons high on sensation seeking consistently demonstrate augmenting whereas low scorers show reducing (see Zuckerman, 1994a,b for a review). To explain this phenomenon, the Pavlovian concept of strength of the nervous system, general arousal, and susceptibility to transmarginal inhibition (capacity of the central nervous system to sustain high level of stimulation), were implicated together with probable involvement of serotonin in the reducing process (Zuckerman, 1994b; Siegel, 1997; Siegel & Driscoll, 1996).

A study on cats indicated that visual evoked potential augmenting and reducing is an extremely stable individual trait – the average values for three sessions showed correlations exceeding 0.9 over as long as one year (Saxton et al., 1987a). Other investigations evidenced that the augments cats, as humans, are more exploratory and active (Lukas & Siegel, 1977), easier to habituate to a novel testing environment, learn quicker an operant response, respond more frequently in the FI schedule, and are significantly less successful in controlling bar pressing behavior in the inhibitory differential reinforcement of low rate of responding task, as well as when mild stressor is introduced (see Saxton et al., 1987b). Furthermore, more recently, it was found that augmenting-reducing and sensation-seeking-like behavioral traits distinguish the Roman strains of rats. The RHA/Verh strain is characterized by higher sensation seeking (activity and exploration in a novel environment, higher aggression and alcohol consumption, lower acoustic startle response) than the RLA/Verh strain. In accordance with human and cat data, the former strain was found to be augmenting, whereas the latter is the reducer (Siegel et al., 1993; Siegel & Driscoll, 1996).

### **Neo-Pavlovian theories: the four temperaments**

It was Pavlov (1955) who first used animals (dogs) to model human temperament types and later work continued this tradition. According to the need-informational theory of Simonov (1987, 1991), the four Pavlovian types of the nervous system are associated with individual differences in the interaction of four specific brain systems: frontal cortex, hippocampus, hypothalamus and amygdala. The "strong" types are characterized by predominance of the system hypothalamus-frontal cortex, which determines such attributes of behavior as confidence, decisiveness and purposefulness. Choleric and phlegmatic subjects learn on the basis of high, whereas sanguine subjects learn on the basis of low probable events. The "weak"-type melancholic temperament is controlled by the amygdala-hippocampus system, with the behavior being unconfident and individuals oriented toward low probable events. Also, it was suggested (Simonov, 1987, 1991) that the relationships between frontal cortex-hippocampus and amygdala-hypothalamus systems constitute the biological basis of Extraversion/Introversion while the relationships between frontal cortex-hypothalamus and amygdala-hippocampus control Neuroticism.

The situation of conflict between the probability and quality of food reinforcement in dogs (Rudenko & Dyakova, 1993, 1994) was used to model the four temperaments. In this test, choleric and phlegmatic subjects prefer high-probable reinforcement and sanguine and melancholic animals preferred better quality of food. In addition, to model the strength of the nervous system in rats, Simonov (1991) used an avoidance learning task in which aversive unconditioned stimuli are provided by a disturbed conspecific. Rats characterized by more rapid learning in this situation showed higher activity in the open field test and higher level of serotonin in hippocampus and hypothalamus.

### **Other Animal Models**

#### **Fear, Anxiety, Emotionality, and Neuroticism.**

In addition to the specifically developed animal models of human personality, there is a significant body of other research on neurobiological mechanisms controlling individual behavioral differences. For example, it is known that the amygdala is involved in anxiety and conditioned fear (see Davis, 1992 for an overview), and fear-potentiated startle, in which it is implicated (Davis, 1992), correlates with freezing (Leaton & Borszcz, 1985) and fear-related heart rate changes (Young & Leaton, 1994). Furthermore, the amygdala is implicated not only in the anxiety state, but also in the consistent individual differences in fearfulness conceived as a temperament trait (Adamec, 1991). Similarly, effects

of lesioning of the septo-hippocampial system on performance in various fear-related tasks coincide with the patterns of consistent between-strain differences in general fearfulness (Gray & McNaughton, 1983; Gray, 1987), which gives raise to the Behavioral Inhibition System and Anxiety dimension of personality in the Gray's model (see above).

At the neurochemical level, there is a substantial interest to the benzodiazepine / GABA receptor system, which is involved in anxiety, implicated in human anxiety disorders (e.g. File, 1991), and affects Neuroticism personality trait (Zuckerman, 1994a). Benzodiazepines have been used for anti-anxiety treatment for more than 20 years, and many animal models have been proposed for developing and testing anxiolytics (see reviews by Blanchard et al., 1990; Fernandez-Teruel et al., 1991; File, 1991, 1996; Gray, 1987; Green, 1991; Gyertyán, 1992; Sanger, 1991; Treit, 1985).

Hormonal influences on personality often involve reactions of the pituitary-adrenal system. In this respect, individuals with shy, fearful and inhibited personality have higher baseline level of cortisol, which is a consistent trait (e.g. Gunnar et al., 1997; Kagan et al., 1988, 1993; Lewis & Ramsay, 1995; Pruessner et al., 1997; Schmidt et al., 1997; Zuckerman, 1994a,b). This pattern was found in many animal species. For example, fearful and inhibited rhesus monkeys exhibit higher levels of cortisol (Kalin et al., 1998; Suomi, 1987, 1991). Dominant baboons, who are bold and uninhibited, exhibit consistently lower levels of corticosteroid hormones (Sapolsky, 1988, 1990, 1993). Similar patterns were documented in rodents (Benus et al., 1991; Dellu et al., 1996; Sgoifo et al., 1996; Zhukov & Vinogradova, 1994), dairy goats (Lyons et al., 1988), wolves (Fox, 1973; McLeod et al., 1996), and fishes (Pottinger & Pickering, 1992; Pottinger et al., 1992; van Raaij et al., 1996).

Also, the serotonin receptor (5-HT) gene polymorphism was found to be associated with anxiety-related personality traits in humans (Lesch et al., 1996), and many animal studies showed that 5-HT is implicated in anxiety, depression as well as in panic (see Graeff et al., 1996, 1997). In a recent quantitative trait loci analysis, Flint et al (1995; see Gershenfeld & Paul, 1997; Gershenfeld et al., 1997; Wehner et al., 1997 for similar studies, see also Eley & Plomin, 1997 for an overview) were able to map several loci on certain chromosomes, involved in various manifestations of emotionality in mice. It was concluded that they may represent the genetic basis of mouse emotionality. It is tempting to suppose, therefore, that similar neural and genetic mechanisms could determine mouse emotionality as well as human anxiety and neuroticism, which might be affected by homologous genes and could have been conserved between species (Eley & Plomin, 1997; Flint et al., 1995; see also Panksepp, 1982).

#### **Sensation Seeking, Novelty Seeking and Extraversion**

Catecholamines, dopamine and norepinephrine, are



involved in individual differences in exploration, novelty and sensation seeking, and sociability. Dopamine mediates and modulates various natural (food, water, sex etc.) and unnatural (intracranial self-stimulation and drugs) rewards (Mason, 1984; Gray, 1987; Wise & Rompre, 1989; Zuckerman, 1994a), as well as positive affectivity (Depue & Iacono, 1989; Depue et al., 1994; Gray, 1987). In terms of personality traits, this means that individual differences in the activity of the dopaminergic system translate to differences in sensation seeking (Zuckerman, 1994a; Dellu et al., 1996), susceptibility to reward (Gray, 1987), novelty seeking (Cloninger et al., 1993) and extraversion in general (Depue et al., 1994; see Depue & Collins, 1999 for an extensive review).

Furthermore, there exists an evidence that the D4 dopamine receptor gene (which is expressed in the limbic areas of brain) polymorphism predicts extraversion and novelty seeking in humans, which was observed in several cultures (Benjamin et al., 1996; Ebstein et al., 1996, 1997a; Ono et al., 1997; but see Pogue-Geile et al., 1998; Jonsson et al., 1997; Sullivan et al., 1998 for negative reports). A similar reduction of behavioral response to novelty was found in knockout mice, lacking the D4 receptor (Dulawa et al., 1999). The D4 receptor polymorphism has also a significant association with neonatal temperament in humans (Ebstein et al., 1998). But these genetic influences on personality are not simple and may involve interactions with serotonin receptors (e.g. Ebstein et al., 1997b, 1998). Serotonin receptor gene (5-HT<sub>2C</sub>) polymorphism, on the other hand, is associated with individual differences in the Reward Dependence personality trait (Ebstein et al., 1997b).

### **Personality and Emotions: Similarity Between Humans and Other Animals**

Various lines of evidence indicate that the fundamental neural circuits mediating basic emotions are fairly similar in all mammalian species and represent "inherited components of the limbic brain, which are to a substantial degree a shared mammalian heritage" (Panksepp, 1982, p. 407; see also Mason, 1984; Gray, 1987). Moreover, there is evidence that "the similarities of the behavioral effects of forebrain ablation on fish and limbic lesions on mammals are quite striking" (Flood et al., 1976, p. 794), and the mediating role of dopamine in novelty seeking, dominance and aggression was also found in fish (e.g. Nechaev, 1991; Nechaev et al., 1991). If personality structure reflects individual differences in functioning of basic motivational and emotional mechanisms, such as negative affect and positive affect (Depue & Collins, 1999; Meyer & Shack, 1989; Tellegen, 1985), these similarities would directly translate to personality structures.

### **The Personality Factor Space**

The above discussion reveals that there exist striking similarities between humans and other animals in the proximate causes of personality variation. However, contrary to the earlier excitement, personality differences, both in animal and humans, are produced through an extremely complex network of behavioral mechanisms at various levels, and there is no simple one-to-one correspondence between particular physiological systems and psychometrically-based personality dimensions (see Zuckerman, 1994a, 1995 for a discussion). It is, of course, possible to rotate behavioral dimensions to coincide with particular neurobiological circuits (see Gray, 1981, 1987; Cloninger, 1987; Cloninger et al., 1993 for some examples). But to adequately analyze the biological bases of personality, it is necessary to understand what factors and how constrain the structure of personality. Even so, the neurobiological evidence reviewed above strongly suggest that two broadly-defined clusters of personality traits have similar biological background across a variety of mammalian species: (1) Extraversion, Exploration, Novelty seeking, Sensation Seeking, Positive Affectivity and Impulsiveness, and (2) Neuroticism, Anxiety, Fearfulness and Negative Affectivity.

These clusters of traits, however, may be correlated and more or less rotated, depending on the psychometric tool, neurobiological mechanism and species. Thus, it is broad clusters of traits in the personality factor space rather than exact position of axes, which have similar physiological and genetic background across species. Nevertheless, this creates a possibility to find similar behavioral dimensions in animals, which define this factor space psychometrically.

### **The Dimensions of Personality in Animals: Psychometric Evaluation**

#### **Personality in Mammals**

Royce (1977) reviewed 12 factor-analytic studies bearing on the issue of broad behavioral dimensions in mice, rats and dogs. It was concluded that for certain dimensions "the similarities in pattern and magnitudes of factor loadings are striking, particularly since there were significant differences in such parameters as sample size and genetic composition" (p. 1099). Generally, three major replicable factors appeared in these investigations. First, Motor Discharge factor encompassed such behaviors as activity in the open field, penetration to its center and latency to move. It is worth noting, that these behaviors are frequently considered to share exploration (Walsh & Cummins, 1976; Russell, 1983) and are considered (see above) as a direct counterpart of human Extraversion-Introversion. The second broad dimension, Autonomic Balance, was based primarily on open field defecation,

which is typically viewed as a measure of emotionality, anxiety (Walsh & Cummins, 1976) and Neuroticism (see above). The third dimension, Territorial Marking, appeared in several but not all studies. It was determined primarily by open field urination, and, in less degree, by defecation. As well, it showed positive correlation with behavioral manifestation of aggression and social dominance. More recently, this fascinating similarity of personality structures between species was corroborated by Budaev (1997a) and Gosling & John (1999).

Royce et al. (1973) conducted the largest factor-analytic study of personality in mice. A sample of 775 animals was tested in 12 tests (open field, activity wheels, straightway, avoidance conditioning, etc.) and 42 measures were taken in total. Factor analysis yielded fifteen broad and specific factors with eigenvalues greater than unity. The dimension interpreted as Motor Discharge was made up of the latency to leave the start section in the open field and straightway, open field activity, penetration into central squares and straightway activity. Autonomic Balance was loaded by defecation scores in stressful situations like open field, and Territorial Marking involved urination in a range of various tests. The relative numerosity of factors and complexity of the structure may be caused by the fact that arbitrary tests and behavioral variables rather than ethologically-defined measures were analyzed, the variables showed low intercorrelations, and unreliable method (eigenvalues > 1, see Zwick & Velicer, 1986 for an evidence that it severely overestimates the number of factors in almost all cases) was chosen to determine the number of factors. Recently I reanalyzed this data set (Budaev, 1998). It was found that, when uncorrelated ( $R^2 < 0.3$ ) and inadequate (Kaiser-Meyer-Olkin measure of sampling adequacy < 0.5) behavioral variables were removed, two factors similar to Activity-Exploration and Fear-Avoidance appeared much more clearly. It seemed that these two factors were largest in terms of explained variance and the most stable.

Maier et al. (1988), tested rats in seven test situations (including emotionality rating, running-wheel, open fields, water maze). Again, several factor solutions revealed sharp separation of factors associated with activity, exploration and fearfulness-anxiety. It is worth noting that emotionality rating and open field defecation loaded on the same factor. Tachibana (1982) tested male rats in the open field test during five consecutive days. Ambulation, rearing and penetration to the center of the field in this study had the major loadings on the first factor Gross Bodily Activity, while various defecation, and urination scores correlated to form the factor Elimination. The results of a more recent investigation of open field behavior of rats (Ossenkopp et al., 1994), in which a three-mode factor analysis model was applied to longitudinal observations (4 consecutive trials), are in close agreement with previous findings. Again, the same separate unitary dimensions were extracted: Exploratory Behavior (activity, particularly in the central area, which gained prominence with repeated test sessions) as well as Emotional Reactivity (defecation, urination and center avoidance, which showed the greatest prominence in the first test session).

The study of Meijsser et al. (1989) showed that open field behavior of rabbits can also be characterized by

the same behavioral dimensions. Factor analysis of 472 subjects revealed Boldness factor, encompassing locomotion, exploration and rearing, and Fear factor, involving immobility. In addition, our study of the behavior of rabbits in an operant test situation (Zworykina, Budaev & Zworykin, 1997) revealed a stable factor encompassing general activity, rearing, as well as tendency to high level of operant responding and a propensity to make many errors, similar to general activity.

The elevated plus maze test has become popular in psychopharmacological studies of anxiety and screening anxiolytic drugs. Several recent factor analytic studies in mice and rats (e.g. Cruz et al., 1994; Fernandes & File, 1996; Rodgers & Johnson, 1995) provided strong evidence for separate replicable factors related to anxiety (measures of the time spent in open arms of the maze) and locomotor activity (rearing, number of closed arms entries). In addition to these two factors, other were also extracted, such as risk assessment and decision making. Importantly, Trullas & Skolnick (1993) found evidence for cross-situational consistency of activity measures in open field and elevated plus maze tests. Their results also replicated the two factors associated with general activity and exploration, and anxiety. Furthermore, the results obtained by Ramos et al. (1997), who also administered several tests to the same rats, confirm this result: the factors of anxiety (approach versus avoidance of aversive stimuli) and general activity in novel environments comprised measures from the open field test, elevated plus maze, and black and white box. The same cross-situationally consistent factors were also extracted in the accompanying study (see Berton et al., 1997).

In the field of applied ethology, similar personality factors were revealed through factor analysis of the behavior of piglets in several tests, including novelty and isolation (see Forkman et al., 1995): Sociability, encompassing variables associated with social dependence (e.g. nose contact, vocalizations when alone), Aggression and Exploration (contact with novel object). Furthermore, Le Neindre (1989) found two factors, corresponding to fearfulness and activity-exploration in the cattle. More recently de Passillé et al. (1995) found three factors in Holstein calves: two separate but correlated factors involving exploration and locomotor activity, and a factor related to fearfulness. Finally, Pollard et al. (1994)'s analysis indicated that two similar factors – Exploratory Behavior and Fearfulness – encompass an important component of temperament in farmed hybrid deer calves.

In dogs, Goddard & Beilharz (1984a) and Plutchik (1971) found evidence that various measures of fearfulness tended to be positively correlated. Moreover, this general fearfulness is largely independent on general activity in innocuous situations (Goddard & Beilharz, 1984b). Also, Goddard & Beilharz (1985) found two factors, Confidence (lack of fearfulness) and Aggression-Dominance, which were consistent across various behavioral domains. Similar dimensions were identified in dogs by means of factor analysis by Cattell & Korth (1973) and Royce (1955). In particular, as Cattell & Korth noted, the factor involving activity, vocalizations, but not involving heart reactivity, which they considered "a kind of animal extraversion" (p. 23), could be perfectly

matched with a similar factor in the Royce's study. In a more recent study, in which the dog temperaments were assessed via a questionnaire given to their owners, Ledger & Baxter (1997) also found similar factors: Excitability, involving general activity and excitation, and Timidity. The Excitability factor also positively correlated with a factor involving social dependence, indicating that it may also be related to sociability.

Furthermore, Gosling (1998), by analyzing personality ratings of spotted hyenas (*Crocuta crocuta*), revealed five broad dimensions resembling those employed in the Five Factor model of human personality: Assertiveness (social dominance, boldness, confidence), Excitability (vigilance, excitability, nervousness, activity), Sociability, Curiosity and Human-related Agreeableness. Interestingly, three factors – Human-related Agreeableness, Sociability and Curiosity – showed modest positive intercorrelations, implying that a more general second-order factor similar to Extraversion could be present in hyenas.

There were also several studies, examining the structure of personality variation, in non-human primates. In rhesus monkeys (*Macaca mulatta*), Chamove, Eysenck & Harlow (1972), conducted factor analysis of multiple measures from several tests involving interactions with one or several conspecific subjects. Three factors which emerged in this analysis were very similar to the Eysenck's Extraversion, Neuroticism and Psychoticism: Affiliative, Fear and Hostile, respectively. This result was later confirmed by the study of Stevenson-Hinde, Zuz and Stillwell-Barnes (1980). Although they used a different approach to data recording, rating scales, based on a list of behaviorally-defined adjectives very similar factors were independently extracted: Sociable, Excitable and Confident. This personality structure was almost replicated by a recent analysis by Capitanio (1999), who found four dimensions in the rhesus monkeys: Sociability (affiliative), Confidence, Excitability, and Equability. This study also revealed a substantial consistency of these personality factors over time and situations.

A generalizability analysis of the descriptive terms derived from this work and applied to 13 stump-tail macaques (*Macaca arctoides*) indicated that these personality factors are highly valid across items, consistent over time and stable across observers (Figueredo et al., 1995). Similar factor structure, with at least an analogue of Extraversion trait – Playful and Curious, were found in vervet monkeys (see McGuire et al., 1994).

More recently, King & Figueredo (1997) factor analyzed a pool of adjectives, which were ascribed to 100 chimpanzees (*Pan troglodytes*) by independent observers. The trait terms were, in fact, those which are commonly used to describe the Big Five personality factors in humans. The analysis revealed five factors in the chimpanzee very similar to the human Big Five dimensions, plus an additional Dominance factor. Thus, the factors Extraversion and Neuroticism can be reliably found in this species. Finally, Gold & Maple (1994) were also able to extract the factors Extraversion and Fearfulness in gorillas.

A similar personality structure was recently revealed (Watson & Ward, 1996) in the small-eared

bushbaby (*Otolemur garnettii*), a prosimian. In this species, 18 behavioral variables were scored in open field, hand preference and problem-solving tasks. Four orthogonal factors describing the lemurs' temperament were extracted: Boldness, Activity, Curiosity and Escape. If, however, the Wherry (1984) oblique hierarchical rotation procedure is used (Budaev, unpublished reanalysis), these four factors appear intercorrelated and give rise to two higher-order traits: Boldness, Activity, Curiosity together form an analogue of Extraversion while Escape, not correlating with the other three factors, may be considered as Neuroticism.

Thus, the preceding review indicates (see Table 1) that at least two broad personality dimensions appear to exist in mammals: (1) stimulus seeking propensity, exploration, activity impulsiveness, sociability and irresistibility to social separation, which sometimes appear as separate but intercorrelated factors, and (2) susceptibility to fear, anxiety, stress, nervousness and emotionality. Even though the relevant evidence is not uncontroversial, there is an indication that these factors generalize across situations.

### Personality in Other Animals

Surprisingly, several investigations evidenced that these two broad personality factors are not limited to mammals and may be observed in other vertebrates: birds, fish, and even in some invertebrates, such as octopuses. For example, Jones & Mills (1983) and Jones et al. (1991) showed, various indicators of fearfulness are not independent in the quail too, and all share the same underlying factor – general fearfulness. It is especially worth noting for the present discussion of the two personality dimensions that sociability (tendency to social reinstatement) can be divorced from this general fearfulness at the genetic level, and the two constructs can be selected for independently (see Mills & Faure, 1991). Figueredo et al. (1995) applied the items measuring the Confident, Excitable, and Sociable factors in the monkey study by Stevenson-Hinde et al. (1980) to five zebra finches (*Poephila guttata*), and found that such factors reliably assess personality in this bird species.

Csányi & Tóth (1985) conducted a study of paradise fish (*Macropodus opercularis*) in two different environments. A separate factor emerged, which was underlied by exploratory swimming and "staccato" behavior, indicative of excitement. Another factor, termed "Emotionality", was determined by the behaviors emitted typically in presence of frightening stimuli. In another study (Gervai & Csányi, 1985), 23 variables from four different tests involving restricted space, novel object and novel environment, were subjected to principal component analysis. Again, all exploratory measures correlated to form a single "Exploration" factor. In addition, fearful, inhibited movements and freezing made up "Timidity" factor. The third (smaller and relatively poor-defined) dimension, called "Defense" was characterized by inhibition of locomotion and intense

fleeing. In the third study (Gerlai & Csányi, 1990) 324 paradise fish were observed in a home tank, two novel environments as well as in a frightening novel environment. Again several broad factors were extracted, which encompassed specific behavior units in more than one situation. One factor involved activity in different novel environments. Furthermore, two fear-indicating factors appeared, which were called "Active Defense" and "Fear". Additionally, broad "Activity" factor was extracted, expressing fast swimming irrespective of situation. Again, as in the Royce et al. (1973) study, the factor pattern could be dramatically simplified if behaviors with low intercorrelations and low factor adequacy (assessed by means of Kaiser–Meyer–Olkin measure) were dropped: two factors interpretable as Activity–Exploration and Fear–Avoidance clearly emerged (see Budaev, 1998).

Recently, I conducted a study (Budaev, 1997b) on guppies (*Poecilia reticulata*) observed in various contexts – in novel environments, near a predator and in presence of conspecifics. Individual differences in these behavioral domains were consistent over several months. Also, as in the above investigations, exploratory measures correlated between situations, giving rise to the Activity–Exploration dimension, and freezing and fleeing determined Fear–Avoidance factor. Moreover, individual propensity to join a conspecific school (Sociability) correlated with the Activity–Exploration factor, which obviously implied the existence of a more general Approach personality dimension.

Interestingly, the second study (Budaev & Zhuikov, 1998), in which guppies with known personalities were tested in an avoidance learning task, revealed a pattern expected on the basis of the Eysenck's (1970) theory and very similar to that observed in rat experiments testing its predictions (see Garcia–Sevilla, 1984). Specifically, human introverts are more sensitive to stimulation than extraverts because they have chronically higher level of cortical arousal. They are expected to have lower aversive threshold, reacting, in fact, as though they respond to higher relative levels of stimulation. In our guppy experiments, non-exploratory and fearful fish ("neurotic introverts") performed the first avoidance response significantly earlier than other subjects. Furthermore, higher fearfulness (tendency to freeze in potentially dangerous situations) was associated with earlier first avoidance response only in non-exploratory individuals, indicating that they were the most sensitive to the aversive action of mild electric shock (Budaev & Zhuikov, 1998).

Finally, three behavioral dimensions were identified in octopuses (*Octopus ruibescens*, see Mather & Anderson, 1993): Activity (active–inactive: staying inside shelter, grasping an object, versus rest posture); Reactivity (anxious–calm: avoiding approaching object); and Avoidance (avoiding–bold: staying in shelter, changing color and injecting ink, but alerting during feeding). Table 1 summarizes the factor–analytic studies involving different species, within the framework of this two–dimensional model.

### **Other Personality Factors**

Are there only two general personality factors in animals? Obviously, the most clear candidate would be a broad dimension associated with aggressiveness and dominance. For example, separate Hostility versus Agreeableness factor is incorporated into the "Big Five", as well as many other humans personality models (e.g. Psychoticism in the Eysenck's three–factor model). Furthermore, aggressiveness factor has been extracted in many animal studies involving a wide variety of species (e.g. Royce, 1977; King & Figueredo, 1997; Gold & Maple, 1994; Chamove et al., 1972; Forkman et al., 1995; Cattell & Korth, 1973; Ledger & Baxter, 1997; Goddard & Beilharz, 1985). There is also some evidence for factors similar to human Openness to Experience and Conscientiousness in the chimpanzee, the closest living relative of *Homo sapiens* (King & Figueredo, 1997). Gosling & John (1999) found evidence for all the Big Five personality factors in various animal species.

Clearly, there exist also no reason why species–specific personality dimensions, reflecting motivational, cognitive and neural mechanisms as well as ecological conditions typical for particular species could not exist. Future research should concentrate not only on similarities of personality structures across species, but also on species–specific personality factors and their proximate and ultimate causation.

### **Inconsistency and the Hierarchical Model**

Thus, the above ethological and psychometric evidence clearly indicates that there are at least two or three broad factors, which tap the personality space in a variety of species, and are similar to human Extraversion and Neuroticism. These factors emerged in data sets collected during more than 50 years and comprising both objective behavioral measurements and subjective ratings. Therefore they are unlikely to represent an artifact unique to a particular investigation, laboratory, or an implicit personality theory used by the investigator. The study by Figueredo et al. (1995), in which the existence of identical personality factors was confirmed in stump-tail monkeys and zebra finches, is important in this respect, because the same model (Cronbach generalizability analysis, see Ozer, 1986) was simultaneously applied to two phylogenetically very different species. In addition, quantitative factor comparisons by Gosling (1998) revealed high correlations between primate–based factors emerged in some previous studies and the hyena personality factors. Personality factor structures found in two different fish species, guppy and the paradise fish, were also almost identical (Budaev, 1998).

Yet, an important problem is that in many investigations more than one factor defined one of these two broad dimensions. As a consequence, the number of dimensions varied widely between studies. For example, there were often separate factors of locomotor activity,

exploration and sociability as well as several fear-related factors (e.g. Cattell & Korth, 1973; Gerlai & Csányi, 1990; Gervai & Csányi, 1985; Goddard & Beilharz, 1984a,b; Ledger & Baxter, 1997; Watson & Ward, 1996). On the other hand, some studies employing several test situations revealed that the behavioral factors emerging were rather specific to particular tests and did not extend to other tests (e.g. Belzung & La Pape, 1994; Griebel et al., 1996; Reed & Pizzimenti, 1995; Spooler et al., 1996; see Archer, 1973 and Ramos & Mormède, 1998 for reviews) or even to repeated exposures to the same test (e.g. File et al., 1993). Thus, the existing evidence for the universality of the general personality factors in animals is not uncontroversial.

However, in some cases when *oblique* factor rotations were used or it was possible to reanalyze the published factor matrices applying the hierarchical rotation approach, separate narrow factors were often intercorrelated and could be naturally collapsed into second-order factors. Thus, at least some of these discrepancies may be caused by the fact that different tests and measures utilized in particular studies tapped different levels in the personality hierarchy. That is, relatively narrow, low level, traits could have been compared to broader, higher level dimensions. If in a particular analysis there are many variables associated with fear and anxiety obtained in different situations but only few activity measures, it may be expected that several anxiety-related factors will be extracted, corresponding to its various facets, as well as a single activity factor. In a different analysis, however, an investigator may be concerned with a different domain of variables, more fully representing activity in various contexts which, similarly, would yield several activity-related factors but only one anxiety. Then, at a first glance, the two factor solutions would appear completely incompatible. However, if second-order factors corresponding to anxiety and activity could really be extracted, a hidden relationship between the factor structures could emerge. Yet, because orthogonal rotations force the factors to be independent, the existence of multiple narrow factors cannot be considered as an evidence against a more general underlying construct.

This raises an important methodological issue, that the factors are merely artificial theoretical constructs, which have no "real" physical existence and explanatory power (e.g. Revelle, 1983; Eysenck & Eysenck, 1985). They could only be used to summarize the pattern of relationship. Therefore, there exist no single "optimal" level of hierarchy at which one should extract factors. However, the existing empirical evidence suggests that broader factors, less affected by random and insignificant influences, are typically more repeatable across studies than narrow factors (e.g. see Barrett & Kline, 1980; Budaev, 1998; Eysenck & Eysenck, 1985; Guilford, 1977; Saville & Blinkhorn, 1981).

At least in some cases the lack of significant correlations across situations could be ascribed to insufficient statistical power (see Tversky & Kahneman, 1971; Schmidt et al., 1976). Although standard in human personality research, large-sample studies of animal behavior are relatively rare because of costs and difficulty of maintaining large animal colonies in captivity, as well

as the need to test these animals in many situations.

Therefore, the power to detect moderate and low correlations is often low. Furthermore, the reliability of behavioral measurement is typically imperfect. Measurement error, however, significantly affects statistical power in correlational research. For example, sample size of 47 is required to detect a correlation equal to 0.4 with power 0.8 at  $\alpha=0.05$ . But if the behavioral measures have reliability of 0.8, judged by most as quite a high level, the necessary sample size increases to 74. To improve data reliability, aggregation of measures over time, situation, judges and so on is often applied, which typically increases correlation coefficients (for more discussion see Epstein, 1983; Ossenkopp & Mazmanian, 1985; Pruessner et al., 1997; Rushton et al., 1983; Funder, 1995).

Unfortunately, applications of hierarchical factor analysis approach and data aggregation, although routinely used in human psychological research, are rare in animal literature. Nonetheless, the relatively scant evidence that exists, is rather confirming the existence of general personality dimensions. For example, Poley & Royce (1976) applied a series of higher order factor analyses, which resulted in a reduction of 12 primary factors to three third-order factors, from which Motor Reactivity and Active Avoidance agree with the two personality dimensions considered in this paper. Also, albeit correlations between various facets of anxiety, as measured in open field and plus maze, typically load on different factors, initial activity in the open field is significantly correlated with the plus-maze indices, pointing to a general behavioral construct (Lamberty & Gower, 1993).

The evidence for cross-situational consistency of at least fearfulness and anxiety in various animals is widespread (e.g. Boissy & Bouissou, 1995; Jones & Mills, 1983; Jones et al., 1991; Le Scolan et al., 1997; Pollard & Littlejohn, 1995; Wolff et al., 1997; see also Clarke & Boinski, 1995). Furthermore, genetic analysis indicated that, even though various domains of anxiety often do not show high phenotypic intercorrelations, they are affected by common quantitative trait loci (e.g. Eley & Plomin, 1998; Flint et al., 1995; see also Gershenfeld et al., 1997; Gershenfeld & Paul, 1997).

Yet, the underlying multidimensionality at lower levels of personality hierarchy is not unimportant and separate lower-order and situation-specific factors may be associated with activity of different behavior control systems. For example, Livesley et al. (1998) found significant residual heritability of lower-order personality traits in humans, not accounted for by higher order factors, indicating that multiple specific genetic components are not unimportant in determining phenotypic personality structures. Concerning the growing evidence for multiple facets of anxiety, each of these facets could have somewhat different neural and physiological substrate (e.g. Courvoisier et al., 1996; Fernandes & File, 1996; File, 1991; Ramos & Mormède, 1998; Rodgers & Johnson, 1995). For example, it was suggested (Griebel et al., 1996) that two separate anxiety factors revealed by factor analysis could reflect subsystems involving either benzodiazepine or serotonin 5-HT receptors. The situation may be further complicated

by the existence of trait as well as state of anxiety in animals (Belzung et al., 1994). Moreover, the multidimensionality of a behavioral construct, such as anxiety, may involve at least three horizons: external input, central emotional or motivational state, and output subsystem. Thus, multiple sub-factors could reflect individual variability at each of these horizons, rather than solely in the central state (Ramos & Mormède, 1998). Finally, on the adaptive grounds, Wilson et al. (1994) suggested that individual differences would be relatively domain-specific but general to the extent they are governed by common physiological mechanisms. In this way, it may be suggested that narrow personality factors, formed by functionally-related behavior patterns would represent clusters of adaptive strategies, maintained by natural selection.

### **Personality Factors: In the Researcher's Mind?**

On the pessimistic side, however, the similarity of personality structures across diverse species may be a purely human mind phenomenon. If a significant portion of human personality variation is really encompassed by the Big Five factors, it would be highly adaptive for humans in the social interactions contexts to have specialized cognitive mechanisms for rapid assessment of personality of others. The same, of course, should apply to many other social species. Indeed, there exists a body of evidence that people can estimate the personality traits of others, even strangers, quite accurately (Albright et al., 1988; Funder & Colvin, 1988; Watson, 1989; Paunonen, 1991). Even though the simulation study by Paunonen (1991) has shown that the correlations between self-ratings and ratings by strangers may be inflated, minimal acquaintance would be enough for rapid assessment of such publicly observable traits as extraversion. Observability is known to increase the accuracy of ratings, and ratings of traits in the Big Five domain are usually more accurate (Gosling et al., 1998).

The cognitive mechanisms enabling rapid assessment of personality traits could then be projected onto other objects, such as animals. For example, people can apply psychological attribution even to inanimate objects, e.g. geometric shapes, even though they do not believe them (Heider & Simmel, 1944). The consensus between raters (inter-observer agreement), sometimes postulated as the basic criterion in research on human personality (e.g. Funder, 1995), could not detect such projections if the observer's cognitive modules use the same cues for the assessment of animal subjects. The raters are expected to agree, since the dimensions they infer would in fact be matched against the same cognitive template. That psychological characterization of various animal species by observers does not depend on physical similarity with humans, familiarity or phylogenetic closeness to humans, but mainly reflects behavior in the context (see Mitchell & Hamm, 1997), and that humans can accurately predict animal behavior on the basis of commonsense characterization (e.g. Hebb, 1946) does

indicate that such characterization is not arbitrary (e.g. is not completely caused by an implicit evolutionary theory). However, it does not provide any evidence against possible template-matching of higher-order personality dimensions.

This problem of "personality as perception" (cf. Fiske, 1974) would be more serious in studies based on human observers' ratings than in studies involving objective ethological measurements of overt behavior or performance measures in standardized tests. The review by Gosling & John (1999), revealing all the Big Five factors in various species is mostly based on studies dealing with the observers' ratings. As appears in the previous sections of this review, personality structures uncovered by objective measurements are usually more complex and are less in concordance with the Big Five. None the less, the agreement between these studies is substantial, at least with respect to Extraversion, Neuroticism and perhaps Aggressiveness. The factors Openness to Experience and Conscientiousness are certainly expected in our closest relatives (King & Figueredo, 1997) or perhaps in species with very similar social structures. However, the problem of unbiased interpretation would make it more difficult to prove their existence in other, more distant and different, species. Also, whereas the similarity of Extraversion, Neuroticism and Aggressiveness factors between humans and other animals is corroborated by substantial physiological and genetic evidence, no comparable evidence exists for Openness and Conscientiousness. It seems that more research is needed to substantiate other Big Five factors in species other than our own.

### **The General Framework**

Thus, the above evidence strongly indicates that (1) individual differences in many behavioral domains may be consistent over time and across situations, (2) they can be organized into a small number of dimensions, which (3) represent a form of a hierarchical organization, (4) these dimensions could be meaningfully interpreted in motivational, affective and cognitive terms, and (5) they are remarkably similar across species, both in psychometric structure, function and underlying physiological mechanisms.

Thus, the hierarchical dimensional structure of personality may be considered as a general integrating framework for the study of individual differences in various species, their function, as well as proximate and ultimate causation. This could integrate individual differences at various levels, from narrow lower-order traits to higher-order dimensions like Extraversion and Neuroticism. A similar hierarchical trait approach has shown its potential utility for classification of psychiatric disorders (see Livesley, 1998; Livesley et al., 1998). The factor space tapped by these general personality dimensions represents an important component of this framework. These broad traits are especially important because of their relatively straightforward interpretability in terms of affective, motivational, and cognitive systems,

similarity across species as well as tangible physiological background. As such, this general framework may be applied to unify a variety of approaches to individual differences in behavior, which could be easily reinterpreted in its terms. The following discussion will show, for example, how alternative coping styles and shyness–boldness continuum could be translated into personality dimensions.

### **Alternative Coping Styles**

There has long been a substantial interest to the problem of coping with stress and challenge in humans. Individual differences in coping were conceptualized as a coherent set of behavioral and neuroendocrine characteristics in terms of approach versus avoidance and problem–focus versus emotion–focus (e.g. Lazarus & Forkman, 1984; Suls & Fletcher, 1985). For example, problem–focused coping involves direct action removing the individual from the source of stress or manipulation of the environment with the same goal. Emotion–focused coping strategy, in contrast, involves primarily the psychological processes to reduce the emotional impact of stress.

Benus et al. (1991) provided an ample evidence that alternative coping strategies could also be observed in rodents. In mice and rats, for example, some individuals tend to behave actively in threatening situations (e.g. social conflict or shuttlebox avoidance learning) whereas other tended to be passive. In addition, active copers were characterized by significantly lower attention to subtle alterations in the environment and a pronounced predisposition to develop routinized behavioral activities (Benus et al., 1990, 1991). Various physiological mechanisms were suggested to underlie these striking differences in behavioral strategy, such as sympathetic reactivity, testosterone and pituitary–adrenal axis (see Benus et al., 1990, 1991; Roosendaal et al., 1997; Sgoifo et al., 1996). Furthermore, very similar alternative coping styles were recently found in other animal species: great tits (Verbeek et al., 1994, 1996), pigs (Hessing et al., 1993, but see Forkman et al., 1995) and even in fish (Budaev, 1997b,c; Pottinger et al., 1992; van Raaij et al., 1996).

However, an important problem with the concept of alternative coping strategies is that they are conceived as a typological dichotomy rather than a continuum. Consequently, they intrinsically depend on the assumption of bimodal variation. Even though bimodal distributions have been confirmed in some studies (e.g. Verbeek et al., 1994; Budaev, 1997b) this was not the case in other (e.g. Dellu et al., 1993, 1996; Forkman et al., 1995). Furthermore, the SAL and LAL mice (Benus et al., 1991) cannot represent "true" dichotomy between the discontinuous coping styles, because the strains were artificially selected for dichotomous patterns.

Nonetheless, alternative coping styles could be incorporated into the hierarchical personality trait framework. Assume that behavior is determined by

competing control systems associated with anxiety and negative affect (Gray's Behavioral Inhibition System) as well as exploration and positive affect (Behavioral Approach System). In stressful situations these systems would be over–aroused, causing the classical phenomenon of conflict between approach and avoidance. According to the Gray BIS–BAS model, active avoidance is governed by the BAS reward–based system whereas passive avoidance is associated with the activity of the BIS system, sensitive to signals of punishment (see Gray, 1987). In conflict situations, when both systems receive the relevant stimuli, the outcome will depend on how the decision module assesses the relative strength of the associations between these stimuli and reward or punishment. Furthermore, even slight differences between the competing BIS and BAS systems would be augmented by the arousal mechanism. Thus, if individual differences in reactivity of these behavior systems underlie personality dimensions, one can expect that a dichotomous pattern of individual differences would appear almost automatically. When the stimulus reaches a very high value, the associated behavioral character would have an increasingly skewed distribution, culminating in a kind of a ceiling at the point of transmarginal inhibition, when all individuals show the same response. A superposition of two such processes would produce a bimodal pattern (Fig. 2), especially if an arbitrary cut–off criterion is used.

In terms of the dimensional personality model outlined above, the dichotomy would be represented by intersections of the basic personality dimensions: active copers would be impulsive, stable and aggressive extraverts whereas passive copers would be neurotic introverts. However, the dichotomous pattern would not occur in less stressful situations, as well as when stimuli, evoking only one behavioral system (BIS or BAS) are provided. Also, active versus passive style of responding would be relatively unstable in neurotic extraverts and stable introverts, and could be changed by relatively minor stimulus alternations. This would explain why dichotomous distribution patterns are not always observed.

This model seems consistent with the empirical data. As active copers, extraverts were shown to have low levels of attention to subtle environmental changes, higher stimulation thresholds and predisposition to routinized activity (Eysenck & Eysenck, 1985). The differences in neuroendocrine profiles between active and passive copers seem to coincide with differences in Neuroticism and Anxiety as well as Extraversion and Sensation Seeking personality dimensions. Shyness is known to correlate with both Extraversion and Neuroticism (Cheek & Briggs, 1990), and two dimensions are required to describe the shy coping patterns in children (Asendorpf, 1993). The study of personality in the guppy (Budaev, 1997b), which tested the relationships between two behavioral dimensions and coping dichotomies, also revealed that the dichotomous clusters of individuals were associated with two dimensions.

### The Shyness–Boldness Continuum

In a recent review, Wilson et al. (1994) presented an interesting evolutionary framework for the study of individual differences in behavior, focusing on the concept of shyness–boldness, which they operationally defined as the "propensity to take risks". Thus, an individual which performs a more risky behavior in a particular situation is considered as bold whereas one which avoids risk is called shy.

It is important, however, to make a distinction between shyness–boldness continuum, conceived in this way, and the concept of personality. The former is blindly operational, applied to the overt behavior and defined ad hoc in terms of likely ecological consequences for an individual, whereas the latter is viewed in terms of putative behavioral systems, emotions and motivation. This fundamental distinction makes both completely independent. For example, it is possible to conceive an individual which is bold with respect to the shyness–boldness continuum but shy (anxious) with respect to underlying personality.

To illustrate this distinction, it may be helpful to employ a part of the original frequency–dependent selection model developed by Wilson et al. to explain the coexistence of shy and bold individuals within a single population (see Box 1 in Wilson et al., 1994). The current evidence indicates that individuals characterized by lower fearfulness, conceived as a temperament trait, would be more likely to win contests, become dominants and, as such, would have higher competitive abilities (Brain et al., 1990; Huntingford et al., 1990; Sapolsky, 1990; Verbeek et al., 1996). Now imagine (cf. Wilson et al., 1994, Box 1) that individuals are sequentially introduced into an environment consisting of a safe and a dangerous habitats. When the safe habitat becomes overcrowded, the benefits of switching to the dangerous habitat may outweigh the costs in the risky habitat and some individuals choose to enter it. It is the more fearful subordinates having poorer competitive abilities that are most likely to be forced to leave the safe habitat. Entering the risky habitat is called, following the blindly operationalistic definition of shyness–boldness, the bold behavior. When no distinction between personality trait of fearfulness and the shyness–boldness continuum is made, this simple scenario leads to a paradox: just being "shy" predisposes individuals to become "bold".

If shyness–boldness continuum is initially measured, for instance, in an anxiety test like elevated plus maze and is then correlated with the shyness–boldness continuum in the above two–habitat situation, the resulting negative correlation can be thought to suggest two separate but correlated shyness–boldness continua. If, however, the second measurement of shyness–boldness involves a test assessing extraversion, two separate continua will seem uncorrelated, leading to a conclusion that shyness–boldness is domain–specific. Thus, it is likely that the two separate and uncorrelated shy–bold continua that were found for response in threatening and unthreatening situations (Coleman & Wilson, 1998) just reflect two distinct personality

dimensions: Neuroticism and Extraversion. Similarly, the lack of correlation between behavioral inhibition in social and non–social situations observed in children (e.g. Asendorpf, 1993; Rubin et al., 1997) might indicate an involvement of two independent motivational and emotional systems, Extraversion and Neuroticism. If so, it can be expected that neurotic introvert children would show the most consistent inhibition across various contexts (see Rubin et al., 1997).

Although the shyness–boldness continuum, viewed as the propensity to take risks, may be applied in a variety of ecological models, it must not be confounded with individual differences in personality. However, by analyzing relationships between personality factors and risk–related behavioral strategies, it could be possible to link individual differences in motivational, emotional and cognitive systems with the behavior of individuals in natural contexts, studying thus ecological and adaptive consequences of psychological variability (see Wilson et al., 1993; Coleman & Wilson, 1998).

### **Adaptive Personality Factors**

The general approach to the study of animal and human personality outlined above could be further extended to analyze adaptive and evolutionary causes and consequences of consistent individual differences in behavior. Frequency–dependent selection, when the costs and benefits of a particular behavior depend on what others in the population are doing, is an important adaptive mechanism promoting individual differences and alternative tactics within a single population, especially in social behavior. This mechanism would be particularly important for personality traits, because most of them are expressed in social behavior. Multiple–niche polymorphisms, when different individuals specialize to exploit distinct ecological niches (e.g. habitats, prey types etc.) can maintain pronounced differences between individuals. Finally, trade–offs between behaviors associated with conflicting costs and benefits (e.g. foraging versus vigilance against predators, see Lima & Dill, 1990, or extensive parenting versus promotion of the offspring individual experience, see Zworykin, Budaev & Mochek, 2000) can also lead to a range of solutions being equally adaptive (see Clark & Ehlinger, 1987; Maynard Smith, 1982; Wilson, 1998; Wilson et al., 1994 for reviews). Thus, specific patterns of individual and sex differences as well as personality structures can be thought to have evolved as a consequence of these evolutionary processes (see Buss, 1991; MacDonald, 1995; Segal & MacDonald, 1998).

The analysis of adaptive individual differences in personality may be considered at two levels. First, one can try to understand what are the adaptive consequences of particular combinations of personality factors for individuals. For example, do extraverts have higher, lower or equal fitness than introverts in a particular situation? Do fitness consequences of these personality profiles in one situation coincide with those in another situation? What sex differences in the personality factors should be



expected? At this horizon, the phenotypic correlational structure of personality traits is fixed a priori. What is analyzed, is the differences in individual or group (e.g. sex) scores on these fixed personality factors. It may be assumed that a particular trait is produced by an involvement of common motivational, emotional and physiological mechanisms, causing correlations between lower-order behaviors. Or the behavioral axis in question may be defined in operational terms, such as shyness–boldness continuum (Wilson et al., 1994; Wilson, 1998). Thus, even though personality dimensions represent the basic conceptual units, in terms of which individual variation is considered at this level, the analysis is conducted conventionally in terms of personality types or alternative strategies (e.g. MacDonald, 1995).

The second level involves consideration of multivariate evolution and a different set of questions: what are the adaptive mechanisms which produce the structure of phenotypic correlations that gives rise to particular personality dimensions? What are the adaptive causes of correlations between several seemingly unrelated behaviors which form a particular behavioral dimension? How constraints imposed by common psychological, physiological and cognitive mechanisms interact with adaptive requirements in producing the observed pattern of correlations which brings about personality dimensions? At this level, the factor space tapped by personality dimensions, rather than dimensions themselves, represent the basic conceptual unit. The structure of personality dimensions may be thought to reflect the adaptive landscape on the collection of behavioral variables which together encompass the personality factor space.

Adaptive landscape is the relationship between average values of traits and their average fitness (see Arnold, 1992; Lande, 1979; Lande & Arnold, 1983). For example, if two traits are considered, a Gaussian adaptive landscape may be visualized as a hill-like surface. Two important sets of parameters describe adaptive landscape: curvature and orientation. Together, they determine how strong are stabilizing and correlational selection effects (see Lande & Arnold, 1983).

Thus, common physiological, motivational and cognitive mechanisms can exert their evolutionary action simply through constraints they impose on orientation and curvature of adaptive landscape. If anxiety in two domains of situations is governed by common control systems, this could bring about a genetic correlation between them, in turn constraining the adaptive landscape. This would be the primary mechanism causing consistency of behavior across situations, which thus reflects constraints on optimization rather than adaptation (see Houston & MacNamara, 1985). However, parameters of the adaptive landscape can not only passively respond to selective constraints, but can depend on patterns of selection pressures. For example, correlational selection could favor certain combinations of primary behavioral traits, which could change the structure of genetic and phenotypic variances and covariances between them (Arnold, 1992; see also Brodie, 1993). The following example illustrates as this adaptive mechanism could be applied to the Big Five personality factor structure in humans.

### **Aggression, Dominance and the Big Five**

In social conflict situations, natural selection may be expected to favor a combination of hostility with high emotional stability as well as a combination of agreeableness and neuroticism, promoting, respectively, social dominance and subordination. Indeed, social dominance is often associated not with just a high level of basic aggressiveness, but rather with a combination of aggressiveness and emotional stability (see Archer, 1988 for a review). Even though aggressiveness itself is likely to be an important prerequisite for social dominance, emotional stability and stress resistance is required to maintain high status for more or less prolonged time. For example, dominant and subordinate baboons show dissimilar stress responsiveness reflected in different levels and dynamics of cortisol (Sapolsky, 1990, 1993). According to the psychophysiological model developed by Mazur (1994), dominance relationships are formed through manipulation of stress during the contest, so that the individual who "outstresses" the opponent becomes the winner.

Thus, a broad personality dimension, encompassing aggression, hostility, boldness and emotional stability versus agreeableness, conformity and inhibition, rotated at 45 degrees between classical Agreeableness and Emotional Stability, as well as the orthogonal dimension involving hostility and neuroticism, could be expected in humans. Indeed, the study of Zuckerman et al. (1988) revealed a coherent cluster of traits, including aggression and anger–hostility, positioned intermediately between Psychoticism and Neuroticism axes. Similarly, another cluster, comprising succorance, conformity and inhibition of aggression, was found in the high–Neuroticism–low–Psychoticism quadrant. Furthermore, a few studies (e.g. Ashton et al., 1998; Caprara & Perugini, 1994) have produced two factors at axes rotated at 45 degrees from the traditional Agreeableness and Emotional Stability vectors in the Five–Factor model. Ashton et al. (1997) argued that such rotated dimensions may provide a more parsimonious description of sex differences in human personality and some factors found in non–humans.

It may be further expected that, if the rotated personality dimension of Hostility–Emotional Stability is really the basic axis of dominance–related aggressiveness in humans, it should be maintained through a frequency–dependent selection mechanism. Dominance tendencies would have both benefits (priority to valued resources, e.g. mating) as well as costs (risk of physical injury, detrimental consequences of social stress, risk to "lose everything" etc.), and the higher proportion of individuals tend to become dominant, the more cost it incurs on them through more intense competition. Consequently, at some point, the fitness costs of competition may become sufficiently high to outweigh the benefits of dominance. Thus, a high level of individual variation is expected.

This mechanism, however, would substantially differ between the sexes. Males in Homo sapiens are significantly more aggressive, less anxious and more concerned about dominance than females (Feingold, 1994; MacDonald, 1995). This reflects different patterns of

natural and sexual selection – it is males, for example, who compete for potentially limited access to good mates (Daly & Wilson, 1983; Eibl-Eibesfeldt, 1989; Geary, 1998). Females, on the contrary, provide the basis for long-term stability of social group and offspring socialization, which requires a more cooperative and less aggressive social style (Eibl-Eibesfeldt, 1989). As a consequence, it may be expected that, whereas high variability of the Hostility–Emotional Stability personality trait is likely to be found in males, such selection pressure would be relaxed in females, leading to lower variability level in this sex.

In a recent investigation (Budaev, 1999), I tested this hypothesis. It was found that males were not only characterized by higher scores on the Hostility–Emotional Stability factor, but this dimension explained significantly more variance in males than in females, both absolutely and in relation to other personality factors. Specifically, the covariance matrices of males and females differed significantly in eigenvalues, but not in factor structure. In terms of the factor space conceptualization, this can be visualized as if the elliptical clouds formed by males and females had the same major axes corresponding to the Big Five factors, but "stretched" in different directions (see Fig. 3). There is, thus, an evidence that the broad personality trait Agreeableness and Neuroticism versus Hostility and Emotional Stability represents the primary dimension of dominance-oriented aggression, maintained by sex-specific frequency-dependent selection mechanism. Further, this behavioral dimension could underlie certain types of psychopathy and may be associated with testosterone level (see Budaev, 1999).

### Concluding Remarks

The large amount of available data strongly suggests that there are striking similarities between humans and other animals in personality structures, especially broad traits depicted by Extraversion and Neuroticism. This may seem surprising at first, given there are so large differences in ecology and behavioral repertoires between species. But, on the other hand, evolution is a historical process, and it may be expected that fundamental affective and cognitive mechanisms underlying personality variation were conserved during its course.

Furthermore, similar selective pressures involved in sexual selection, aggression and social dominance, could be encountered by many species. The basic adaptive mechanisms bringing about individual differences and alternative behaviors, such as frequency dependent selection, behavioral trade-offs and multiple-niche polymorphisms, are also not unique to any single species. Thus, significant similarities across species in patterns of personality variation should, in fact, be expected.

The above review indicates that the structure of the most broad personality dimensions like Extraversion and Neuroticism as well as other Big Five factors would probably reflect conservative evolution: constrains on evolution imposed by physiological, genetic and cognitive

mechanisms. This follows from relatively unitary physiological background as well as because these supertraits are very general and encompass diverse and functionally unrelated behaviors. Adaptation would have difficulty explaining why very different and functionally unrelated behaviors should be correlated. On the other hand, the structure of lower-order factors, which are more species- and situation-specific, would be adaptive, reflecting complex patterns of correlated selection on and trade-offs between many traits. Thus, there would be a continuum of from adaptation to evolutionary constraints. On the lower level, individual behavioral tactics are shaped mostly by adaptive mechanisms while the highest level dimensions would be constrained by homologous brain structures and functioning. Very interesting interactions between adaptive and conservative processes would be expected at some intermediate levels.

Both conservative and adaptive processes are equally important. However, whereas physiological and genetic bases of personality dimensions (i.e. constraining factors) have been studied quite well in various species, adaptive and evolutionary causation of personality is a relatively novel topic in both human and animal field. Furthermore, almost all previous adaptive studies of personality were limited to the analysis of individual or sex differences in scores on specific personality factors. There has been no empirical investigation of adaptive causes of the personality structure per se, based on models of multivariate evolution. Thus, future studies in this interesting area should integrate the theoretical approaches developed during many years of research by human personality psychologists and the current quantitative approaches to multivariate evolution.

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#### FOOTNOTE

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Table 1  
The two major personality dimensions replicable across species

Species	Study references	Personality dimensions		
		Extraversion	Neuroticism	Other
<b>MAMMALS</b>				
Humans	The Big Five model (see Digman 1990; Goldberg 1993; Goldberg et al., 1996)	Extraversion	Neuroticism	Agreeableness, Conscientiousness, Openness to Experience
	Eysenck & Eysenck (1985)	Extraversion	Neuroticism	Psychoticism
	Gray (1987)	Impulsivity	Anxiety	
	Cloninger et al. (1993)	Novelty Seeking <sup>a</sup>	Harm Avoidance	Reward Dependence
	Zuckerman (1994b)	Sensation Seeking <sup>a</sup>		
Various mammals	Royce (1977), review	Motor Discharge	Autonomic Balance	Territorial Marking
Chimpanzee	King & Figueredo (1997)	Surgency	Emotionality	3 other factors
Gorilla	Gold & Maple (1994)	Extraversion	Fearfulness	2 other factors
Rhesus monkeys	Chamove et al. (1972)	Affiliative	Fear	Hostile
	Stevenson- Hinde et al. (1980)	Sociable	Excitable	Confident
	Capitanio (1999)	Sociability	Excitability	Confidence, Equability
Vervet monkey	McGuire et al. (1994)	Playful- Curious		Opportunistic
Bushbaby	Watson & Ward (1996)	Boldness, Activity, Curiosity	Escape	
Pig	Forkman et al. (1995)	Sociability, Exploration		Aggression
Cattle	Le Neindre (1989)	Activity- Exploration	Fearfulness	

Species	Study references	Personality dimensions		
		Extraversion	Neuroticism	Other
	de Passillé et al. (1995)	Exploration and Locomotor Activity (correlated)	Fearfulness	
Hybrid deer calves	Pollard et al. (1994)	Exploratory Behaviour	Fear	
Dog	Royce (1955)	Withdrawal and Motor Discharge	Physiological Discharge	6 other factors
	Plutchik (1971)		General fearfulness	
	Cattell & Korth (1973)	Extraversion	Several emotion-related factors	other factors (12 in total)
	Goddard & Beilharz (1984a,b)	Activity	Fearfulness	other factors
	Goddard & Beilharz (1985)		Confidence	Aggression-Dominance
	Ledger & Baxter (1997)	Excitability	Timidity	3 other factors
Spotted hyena	Gosling (1998)	Curiosity, Sociability	Excitability	2 other factors
Rabbit	Meijsser et al. (1989)	Boldness	Fear	
	Zworykina et al. (in press)	General Activity		
Mice	McClearn & Meredith (1964) <sup>b</sup>	Exploratory Activity	Defecation and Emotionality	3 other factors
	Royce et al. (1973)	Motor Discharge	Autonomic Balance	12 other factors
	Rodgers & Johnson (1995)	Locomotor Activity	Anxiety	4 other factors
Rat	Garau (1982), two-factor solution <sup>c</sup>	Extraversion	Neuroticism	
	Tachibana (1982)	Gross Bodily Activity	Elimination	

Species	Study references	Personality dimensions		
		Extraversion	Neuroticism	Other
	Maier et al. (1988)	Open Field two: Activity, Exploration	Two correlated: Emotionality, Defecation	other factors
	Ossenkopp et al. (1994)	Exploratory Behaviour	Emotional Reactivity	
	Cruz et al. (1994)	Activity	Anxiety	Decision Making, Self-Grooming
	Fernandes & File (1996)	Activity	Anxiety	other factors
<b>BIRDS</b>				
Japanese quail	Jones et al. (1991)		Fearfulness	
	Mills & Faure (1991), selection experiment	Social Reinstatement	Fearfulness (tonic immobility)	
<b>FISH</b>				
Guppy	Budaev (1997a)	Approach	Fear- Avoidance	Locomotion
Paradise fish	Csányi & Tóth (1985)	Exploration	Emotionality	3 other factors
	Gervai & Csányi (1985)	Exploration	Two correlated: Defence, Timidity	4 other factors
	Gerlai & Csányi (1990)	Two correlated: Exploration, Activity	Two correlated: Frightened State, Fear	other specific and broad factors
Three- spined stickleback	Huntingford (1982)	Boldness		other factors not reported
	Huntingford & Giles (1987)	Boldness		other factors

Species	Study references	Personality dimensions		
		Extraversion	Neuroticism	Other
INVERTEBRATES				
Octopus	Mather & Anderson (1994)	Activity	Reactivity, Avoidance	

<sup>a</sup>also correlates with Psychoticism; <sup>b</sup>cited in Royce (1977); <sup>c</sup>cited in Garcia- Sevilla (1984)

## FIGURE CAPTIONS

Figure 1. An illustration of behavioral consistency. Connected points depict four individuals; left panel: the overall individual level of a particular behavior in three situations (A, B, C); right panel: between-situation correlations (scatterplots). Low average level and high variability of the behavior is adaptive in the situation A, high average level and low variability of this behavior is adaptive in the situation B and low average level and low variability is adaptive in C. However, individual differences may be consistent (upper panel) or inconsistent (lower panel).

Figure 2. An illustration of the relationships between alternative coping styles and personality dimensions.

Figure 3. Scatterplot of factors based on separate principal component analyses of covariance matrices of males and females. The 95% confidence ellipses (solid line in males, striped line in females) are also shown. The factor Agreeableness and low Emotional Stability explains more variance in males than in females. Reprinted from Personality and Individual Differences (Copyright 1999, Elsevier Science).







