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The Emergence of Personality in Animals

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Organizers:

Prof. Dr. Fritz Trillmich, Bielefeld University
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Abstracts:

Behavioural syndromes in sticklebacks

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There are several outstanding evolutionary questions about consistent individual differences in behaviour. For example, it is difficult to explain why individual animals should behave consistently over time and across contexts, and why individual animals differ in behaviour. In this talk, I review the existing literature on the repeatability of behaviour to look for patterns. I argue that while there are a growing number of hypotheses for the evolution of personality, our understanding of within-individual consistency lags behind our understanding of between-individual variation. We are taking several strategies to understand the proximate causes underlying within-individual consistency in behavior in threespined sticklebacks (*Gasterosteus aculeatus*). Whole genome expression data are suggesting the molecular mechanisms underlying within-individual consistency in behaviour across contexts (pleiotropy). In addition, early experience and non-genetic parental effects have long-term consequences for behavioral development.

Comparing the strength of behavioural flexibility and consistency in the hermit crab *Pagurus bernhardus*

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Individual differences in behaviour may be examined from the perspective of variation in both mean responses given by individuals (animal 'personality') and the range of responses given by individuals subjected to a series of environmental conditions ('flexibility', also called the 'behavioural reaction norm') in a sample containing multiple individuals. In order to investigate the possible functional significance of such variation it is necessary to compare samples of individuals that have experienced different developmental conditions, either by manipulating

developmental conditions in the laboratory or by taking samples from different populations. Here we examine animal personality and behavioural flexibility in the hermit crab *Pagurus bernhardus*. These crustaceans show a distinct startle response of withdrawing into their gastropod shell when threatened, and the duration of this response serves as an inverse measure of 'boldness'. We have measured boldness under a range of environmental conditions, which we varied by manipulating the chemical presence of a predator, the level of protection afforded by the gastropod shell and the degree of crypticity against the substrate. These studies show that hermit crabs are capable of gathering and assessing subtle information about the ambient level of risk and they use this to make behavioural decisions. But this behavioural flexibility appears to be between populations and is nested within an overarching pattern of consistent differences in mean response.

Direct and indirect effects of personality on immune and health outcomes in rhesus monkeys

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The idea that temperament is associated with health outcomes dates back at least to Greek and Roman times, and psychoneuroimmunology research has identified mechanisms that might explain such associations. For social species, a fundamental individual difference factor is an interest in affiliation, described as Sociability in a variety of species. We have been examining the immune- and health-related consequences of variation in this trait since the mid-1990s, and our data suggest that Sociability can exert its influences on such outcomes in one of two ways. First, Sociability's influence could be direct. This would be suggested if low- and high-sociable animals were "built" differently, in ways that could affect a health outcome. Second, and perhaps more familiar, Sociability's influence could be indirect – the health consequences of variation in this trait might arise as a consequence of how Sociability affects coping: a bad "fit" between the organism's characteristics and the challenges presented by its environment can lead to stress, with attendant consequences for immunity and health. I will review data obtained from our studies with rhesus monkeys to support the idea of both direct and indirect effects. In the experimental situations in which we have placed our animals, high-sociability seems to be beneficial. The question then arises, are there circumstances in which it is advantageous to be low in Sociability?

Sociality and the evolution of animal personality

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Interest in the evolution and maintenance of personality is burgeoning. Strong trade-offs, mutation-selection balance, spatiotemporal fluctuations in selection, frequency-dependence and good-genes mate choice are invoked to explain heritable personality variation, yet a generally applicable selective force remains elusive. Indeed, ever since Darwin, the maintenance of heritable inter individual variation within populations has remained a puzzle; particularly when populations are subject to strong selection pressures. Here I argue that variation itself can act to stimulate further variation in social groups by selecting for information use. This is because the existence of stable inter-individual variation means that there is something to learn from monitoring others, which in turn can select for individual differentiation amongst those being monitored. I illustrate this thesis using evolutionary game theory in two contexts: cooperation

and aggression. This work adds to growing evidence that evolutionary game theorists can no longer afford to ignore the importance of real world inter-individual variation in their models.

The role of animal personality in ameliorating and evaluating animal welfare.

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In an applied setting animal personality is most often reduced to a single trait, typically fearfulness or aggressiveness. The trait may mainly affect the animal itself, e.g. fearfulness resulting in laying hens in organic production refusing to use to outdoor area, or it might directly affect other conspecifics, e.g. the level fighting shown at mixing of litters in pig production. The production relevant parameters are often indirectly included in the breeding goals.

There have been a number of studies that have attempted to use a broader definition of temperament or personality especially in pigs. The theory most commonly tested is the coping theory (see Koolhaas this volume). In contrast with the work on rats and mice the results from the studies on farm animals have however yielded mixed results.

The basic assumption for most methods of evaluating animal welfare is that animals with a given level of stress/emotion respond in the same way. If flight distance is used as a measure of fear this will lead problems if some animals respond with freezing instead. One of the possible ways around this is by using a more qualitative tool to assess the animal's state, e.g. a Qualitative Behaviour Assessment (Wemelsfelder & Lawrence 2001).

Differences among siblings as contributors to the development of personality in mammals

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Most mammals grow up in the company of same- or different-age sibs or half sibs, and yet little attention has been given to how relations among them might contribute to the development of individual differences in behavior of the kind we generally term personality. In this talk I will review the results of collaborative research of several Mexican and German groups. First, I will present evidence from the domestic cat that differences in behavior among littermates that might be considered precursors of personality are present at or soon after birth and persist reliably across the first postnatal month to the start of weaning. Then I will review data from the cat, laboratory rat, and domestic and wild rabbit demonstrating consistent within-litter differences in morphological, behavioral and physiological parameters that may contribute to the differentiation of personalities during development. Finally, I will report that even in genetically identical mice substantial prenatal within-litter differences exist in body mass and placental efficiency. This suggests that individual differences among siblings potentially associated with personality might have their origin, at least to some degree, in differences in the prenatal environment. In conclusion, differences in personality in mammals may arise from developmental trajectories shaped by the early environment of which siblings usually form an important part.

Individual differences in physiological and behavioral coping styles in response to stressful situations.

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Individual variation in behaviour and physiology is a widespread and ecologically functional phenomenon in nature in many, if not all vertebrate species. Individual behavioural characteristics appear to be consistent over time and across situations. Consistency across situations is likely due to the involvement of one and the same underlying mechanism. Recent evidence suggests that the individual variation is multidimensional. Animal personality has at least two dimensions in which the quality of the response to a challenging condition (coping style) is independent from the quantity of that response (emotional reactivity). This paper will address the causal neuroendocrine and neurobiological mechanisms of these two dimensions using studies in rats and mice.

The quantitative dimension of emotional reactivity is physiologically expressed in the reactivity of the hypothalamus pituitary adrenocortical system (HPA) and the sympathetic nervous system. Evidence will be presented showing that the individual variation in these systems is not the cause, but should rather be considered as the consequence of differences in behavior.

The qualitative, coping style dimension is causally related to a differential pattern of activation in a neuronal network that includes the prefrontal cortex, and its dopaminergic and serotonergic input. The function of the prefrontal cortex in behavioral flexibility might explain consistency of individual characteristics across situations. It will be argued that the multidimensional nature of animal personality and the terminology used for the various dimensions should reflect the differential pattern of activation of the underlying neuronal network and the behavioral control function of its components. From an ecological point of view, the various dimensions and their underlying causal mechanisms can be considered as components of individual fitness.

All mice are not equal: Social stratification and personality in semi-naturalistically housed mice

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The mouse, including countless lines of transgenic and knockout mice, has become the most prominent model organism in biomedical research. Behavioral characterization is often conducted in batteries of short tests on locomotion, anxiety, learning and memory, etc. In such tests any individual differences (be it personality, behavioral types, or temperament) within groups are considered to be disturbing variance. Noteworthy, personality differs from mere variability in being correlated across contexts and time. If part of the variance can indeed be assigned to different personalities within a sample this would be of particular importance for biomedical research.

When inbred strains of laboratory mice or even transgenic mice are allowed to live in spacious semi-naturalistic enclosures they show a wide variety of behavioral patterns largely representing the behavioral repertoire of wild mice. A detailed analysis of these spontaneous behavioral patterns renders a sophisticated means to approximate animal personalities. Two lines of research were carried out using an in-depth behavioral characterization of the spontaneous behavior to evaluate genetic and environmental factors in constituting personalities. I will present data of serotonin-transporter knock-out mice that were observed in semi-naturalistic housing conditions. The results underline the capital importance of the serotonergic system in shaping individual differences in personality. Additionally, I will present preliminary results from genetically identical female mice of an inbred strain that were housed in a group of 40 animals in a large indoor enclosure. These mice could be split into active and less active individuals.

Interestingly, activity scores were stable over time, indicating non-genetic individual differences in personality.

Ecological Influences on Fish Personalities

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Fish, like other organisms, live in a heterogeneous world. In this talk I will consider how ecological communities are structured, and ask how this structure might shape individual personalities. For example personalities may be influenced by community richness, community composition, and by the relative abundance of the species (whether it is common or rare) to which the individuals belongs. Community structure influences levels of competition, predation, resource availability; individuals need to deal with these factors simultaneously rather than in isolation as generally happens in experiments. I will also ask how spatial and temporal variation in community structure might affect fish personalities. This variation includes not just natural baseline change but also anthropogenic change, such as disturbance and introductions of exotic species. I will address these questions primarily in the context of the Trinidadian guppy system.

Effects of personality on territorial and spatial behaviour in great tits

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Differences among individuals in the expression of sexually selected signals and in their response to sexually selected signals often are attributed to differences in individual quality. Yet, such differences in signals and in response to signals may reflect more than merely differences in quality or motivation such as more intrinsic differences among individuals. Individuals often differ consistently across time and contexts in behavioural traits and such systematic differences are commonly described as behavioural syndromes or personality. Personality has been shown to have social and fitness correlates, but it remains unclear how individuals actually determine others' personality and if personality is reflected in sexually selected signaling strategies. Here I show relations between personality and undisturbed signing in great tits, *Parus major*, kept under controlled aviary conditions and how vocal responses to playback and spatial movements, determined by radio tracking, vary with male personality in the field. I will discuss the implications of the results for understanding the evolution of sexually selected signals including individually different strategies in territory defense and spatial behaviour.

Stability and Instability of Childhood Traits: Implications for Personality Development of Animals?

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Recent proposals suggest that the concepts of animal personality and temperament are nearly identical, as both emphasize overt behaviors rather than conscious processes, and assume a primary, if not exclusive, role of biology in shaping individual differences. Animal and human

personality scholars are united in their desire to understand the genetic and environmental origins of individual differences. The focus of my argument is that consideration of development, focusing on four differing aspects of stability and instability (absolute, differential, heterotypic, and structural), is critical to this understanding. Whereas most definitions of personality and temperament emphasize differential continuity – the maintenance of individual differences in behavioral tendencies over time – several behaviors relevant to temperament demonstrate absolute discontinuity – age-related changes in mean levels of an attribute. These shifts appear to represent rapid maturation of underlying neural mechanisms, and attention to species-wide changes in behaviors may generate insight regarding the multiple underlying forces that govern individual differences in these and other behaviors. Understanding of stability is also enhanced through consideration of two additional aspects of continuity. First, continuity may be heterotypic – that is, the consistency of an inferred genotypic attribute may be demonstrated in a variety of ways – and because the environmental elicitors and behavioral manifestations of traits may change over time, it is important to consider a diverse range of indicators of these traits. Structural continuity – persistence of correlational patterns among variables at different ages – represent a tool for identifying coherence in the common underpinnings of these diverse behaviors. My presentation will describe empirical research exemplifying these alternate forms of continuity in humans, and suggest potential implications for investigations of the emergence of animal personality.

The impact of an animal's early environment on its behavioural style

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Features of an animal's early developmental environment, such as the presence of litter siblings and maternal characteristics, are usually thought to have a strong impact on its later life. Next to immediate effects on post-weaning development, there is growing evidence that such conditions of the early environment can also affect the behaviour of an individual and most likely also traits of its personality. In this talk, I will report results from our short- and long-term studies on laboratory rats and European rabbits. We conducted standardized emotionality tests in juvenile animals of both species. We found similar and consistent associations between the animals' early physical development - which was mainly the consequence of the number of litter siblings - and their behavioural responses in the tests. These relationships were apparent across different situations and in both study species, overall suggesting a higher degree of boldness and a higher tendency to explore novel environments in heavier animals from smaller litters. Interestingly, our studies in European rabbits living under semi-natural conditions showed that such correlations persist into adulthood, although the apparent differences in peri-weaning physical development rapidly decreased over time. In conclusion, the results strongly indicate long-term consequences of the animals' early developmental environment, although the mechanisms remain open to discussion.

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The social modulation of behavioural profile: mechanisms and function

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Individual differences in behavioural profile develop during ontogeny. This contribution focuses on the role of the social environment for the modulation of behavioural profile in mammals during early phases of life and adolescence.

For gregarious species, the stability of the social environment in which the pregnant and lactating female lives is of major importance for foetal brain development and the behavioural profile of the offspring in later life. Social instability during these critical periods of development generally brings about a behavioural and neuroendocrine masculinisation in daughters and a less pronounced expression of male-typical traits in sons. Moreover, when mothers live in a socially threatening world during this time, anxiety-like behaviour of their offspring often is elevated in adulthood. These effects of the social environment are likely to be mediated by maternal hormones and/or maternal behaviour. In addition, they can be modulated significantly by offspring genotype. The behavioural effects of social stress during this phase of life are not necessarily “pathological” (nonadaptive) consequences or constraints of adverse social conditions. Rather, mothers could be adjusting the offspring to their environment in an adaptive way.

Adolescence is another period in which behavioural development is particularly susceptible to social influences. There is some evidence that social experiences at this time alter and canalize behaviour and endocrine stress responses in an adaptive fashion, so that earlier influences on behavioural profile development can be complemented and readjusted, if necessary, to meet current environmental conditions. Hence the social modulation of behavioural profiles from the prenatal phase through adolescence appears to represent an effective epigenetic mechanism for repeated and rapid adaptation.

Can robots express personality? Challenging complex explanations

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In order for robots to be accepted (and survive) as a product that is being used in everyday situations they need to exhibit specific behavior that is on the one hand useful and on the other hand socially adequate. In short, robots should be likeable and bias users towards accepting and excusing errors they make. We have designed dynamic (behavioral) as well as static (physical appearance) features for different kinds of robots and analysed their effects on users. Our studies show that already very simple behavioral and appearance features are effective in evoking different personality perceptions of robots by the users. We argue that the importance of personality lies in its interactive emergence.

On the adaptive significance of animal personalities (aka behavioural syndromes)

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Individual animals often exhibit behavioural consistency (i.e., a behavioural type, BT) and groups of animals often show variation among individuals in their BT - some being, for example, more bold, aggressive or exploratory than others. Key inter-related questions about the phenomenon include: why do animals exhibit behavioural consistency - i.e., why do they have a BT? What explains differences among individuals in their BT? When do we expect differences among individuals to be stable over a lifetime? When do we expect early experiences to determine later BTs? When do we expect BTs to persist even when conditions change? And, what might explain variation among populations in the above patterns? I present a progress report on my attempt, with Barney Luttbeg, to develop a general theoretical framework that addresses the above questions using adaptive, state-dependent dynamic models. One basic premise of our models is that behavioural variation and apparently limited behavioural plasticity can be explained, in part, by a connection between behaviour and one or more state variables (e.g., energy reserves, condition, size, information state, skill set or social rank). Put simply,

individuals with different states have different adaptive behaviours (e.g., individuals in better condition are more bold or aggressive). As long as individual differences in state persist, differences in BT should persist. The key then is why should individual differences in state and thus BT persist? Our second basic insight is that a key is the nature of the feedback between behaviour and the state variable. Negative feedback (e.g., via asset protection) tends to result in convergence in state and thus behaviour over time, whereas positive feedback tends to drive divergence and persistence of differences in state and behaviour over time. Positive feedback mechanisms include: state-dependent safety or foraging success, learning, winner/loser effects or other social feedbacks associated with social rank, and BT-dependent situation choice. Reality might often involve a mix of negative and positive feedback mechanisms. Factors that affect the relative importance of the two can then predict/explain variations in the expression of animal personalities.

Stress and immune system: The role of personality factors

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Social stress is a potent modifier of the immune system in mammals. Much of our current knowledge stems from social confrontation studies in murine species conducted during the past two decades. Social stress in this paradigm is caused by aggressive interactions between rivaling conspecifics and rank-dependent related factors. Not surprisingly, dominant and subordinate males differ in hormonal and immunological responses to confrontational stress. Importantly, however, also males with the same social rank can show substantial differences in behavioral and physiological responses. For example, the frequency of submissive behavior displayed by rats is strongly related to the antibody response, the activity of Natural killer (NK) cells, or tumor metastasis in subordinate male rats. At least two different coping strategies can often be observed. With respect to the immune system, we found that a passive (submissive) behavioral style was associated e.g. with a much stronger activation of the unspecific immune response compared to active (subdominant) style. Within-rank differences are not restricted to subordinates. For example, winner males that tend to bite the opponent during social conflict show higher sympathetic baseline activities and differ from non-biting dominant males in their endocrine and immunological responses during confrontation. The reasons for these behavioral and physiological differences may relate to the specific condition, but there is strong evidence that personality factors play an equally important role. We recently showed that prenatal stress affects behavior and the immune system in the adult organism: Baseline levels of several immune parameters (e.g. T cell numbers) and the immunological response to environmental challenge was altered in sons of stressed mothers. Thus, prenatal stress is one important environmental factor shaping adult personality and affecting endocrine and immunological response to stressful condition at least in laboratory rats.

The problem of stability in animal personality research: genetics, ontogeny, plasticity, and flexibility

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Personality has proven a valuable concept that focuses attention on limits in the flexibility of animal behaviour. I suggest that personality research approaches the old subject of the organisation of animal motivation introducing a new functional aspect. Leaving semantics aside (personality, behavioural syndrome or phenotype, temperament and other such names), it has

proven difficult to agree on the temporal and context stability of personality that is to be expected or postulated. Here I attempt to chart different levels of stability that may be expected depending on the causation of personality differences. Considering personality one interesting aspect of the system of animal behaviour, differences caused by single gene effects, epigenetic modulation, learning and day to day changes in state and motivation (flexibility?) could be expected to display decreasing stability. I elaborate on this suggestion by reviewing examples from recent research that demonstrate the limits to stability and plasticity. I briefly discuss possibilities by considering single gene effects like MC1R expression in the melanocortin system, epigenetic changes observed in the determination of caste and function within a eusocial society, high stability in the learning context of imprinting and niche construction, and the potential of seasonal and state influences on personality. The latter examples may offer the chance to arrive at the prediction of the duration of stability from functional principles. This requires the evaluation of longterm influences of environmental and state variables on the expression of the behavioural phenotype.

Genes and receptors: the dopamine receptor D4 and exploratory behaviour in great tits

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Various studies have shown that personality traits, like most quantitative traits, have a heritable basis and influence life history characteristics. A quantitative genetic trait is typically affected by numerous genes with small effect. One of the most promising candidate genes that are identified to affect phenotypic variation in novelty seeking in humans and exploratory behaviour in various other animal species is the Dopamine D4 Receptor Gene (DRD4). The dopamine pathway is known to be highly active in the forebrain during behavioural expression of fear and anxiety related behaviour and affects learning. What is unknown, however, is how variation in receptor activity directly influences variation in the measured behaviour. To study this we manipulated dopamine receptor activity in great tits by injecting a selective D4 antagonist (down regulation) or D4 agonist (up regulation) into animals of lines selected for divergent levels of exploratory behaviour. We subsequently measured the influence of these substances on learning, boldness and explorative behaviour. Here I show the preliminary results of this experiment and discuss this in relation to the plasticity of personality traits.