PHILOSOPHICAL TRANSACTIONS B

Opinion Piece

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Diversity in action: exchange of perspectives and reflections on taxonomies of individual differences

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Throughout the last 2500 years, the classification of individual differences in healthy people and their extreme expressions in mental disorders has remained one of the most difficult challenges in science that affects our ability to explore individuals' functioning, underlying psychobiological processes and pathways of development. To facilitate analyses of the principles required for studying individual differences, this theme issue brought together prominent scholars from diverse backgrounds of which many bring unique combinations of cross-disciplinary experiences and perspectives that help establish connections and promote exchange across disciplines. This final paper presents brief commentaries of some of our authors and further scholars exchanging perspectives and reflecting on the contributions of this theme issue.

This article is part of the theme issue 'Diverse perspectives on diversity: multi-disciplinary approaches to taxonomies of individual differences'.

1. Introduction

To taxonomize individual differences, psychologists have invested considerable efforts over the last century. Allport & Odbert [1] scanned more than half a million entries in the English dictionary to filter out 17 953 person-descriptors that formed the basis of numerous lexical models (e.g. Big-Five Model, Hexaco Model and Big Seven Model). Modern studies compete over the largest numbers of cultures studied or participants involved, with some reaching millions [2,3]. But these studies, focused on amassing data, cannot advance our understanding of the underlying psychobiological systems and the processes of individuals' normative and pathological functioning and development. In fact, such mass investigations of a broad range of differential dimensions are possible only by capitalizing on the efficiency of language-based tools such as standardized questionnaires that capture people's beliefs and therefore enable investigators to collect their data online and thus remote from their participants [4–7].

These approaches, although still popular in psychology, have clearly met their limits. Claims that the psychometrically derived Five Factor Model (FFM) reflects a universal structure of individual differences [3] could not be substantiated; no reliable and specific neurophysiological correlates were found, and multiple neurophysiological systems of individual differences reported in the neurosciences were not incorporated [8]. Scholars from various fields, including some

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psychologists, increasingly criticize psychology's focus on language-based models and methods, and demand to intensify the study of physiology and behaviour [5,6,9]. Classifying individual differences is a fundamental and non-trivial task that cannot be solved by a single discipline or single methodology. In this theme issue, we therefore invited contributions from scholars from diverse backgrounds, involving prominent scholars from different scientific disciplines and with unique combinations of multi-disciplinary experience, who are working in different countries and at different research centres, and who have established different multidimensional taxonomic models of individual differences using different methodological approaches and different methods of investigation. This diversity in perspectives is reflected in our contributions.

To promote exchange and to facilitate integration of insights, this final contribution presents brief mutual commentaries of some authors of the issue as well as of some further scholars. Their reflections about the theme issue are organized around basic themes discussed: principles of taxonomy development, the neurophysiology of temperamental traits, developmental perspectives as well as discussions of functional differentiations and physiological underpinnings of specific traits.

2. Reflections on: principles of taxonomy development

(a) Linearity of temperament dimensions

Those papers of the theme issue focusing on ways of taxonomy formation and basic concepts of measurement [10–14] mostly emphasized nonlinearity instead of linear traits, and patterns of phenomena instead of single dimensions required for measurement and taxonomy of temperament. Some of them seem to represent controversial positions like: formation of concepts as a first step and deriving experiments, which fit the model thereafter [10,12], as opposed to others deriving their taxonomies from a data-driven approach [11]. I would like to point out that these approaches are compatible when analysing the basic meanings represented by the term linearity and temperament traits.

We must be aware that any psychological phenomenon, even if defined by a qualitatively distinct separate functional entity (like attention or perception), never represent items of yes/no alternatives, when observed or measured, but can always be conceived as 'more or less', 'larger or smaller', i.e. a dimension. So dimensionality is inherent in any single observation of a certain function.

Therefore, as soon as we wish to infer rules or laws or any type of generality, we usually combine counts or measures within individuals in order to generate broader sets of observations into a common measure (scales or sets of measures) in order to generalize them to other individuals. This is inevitable if theoretically developed taxonomy systems are translated into experimental proof, and this is the basis of empirical validation of traits, which can usually not do without either *a priori* assumptions or correlations between items or single observations of behaviour.

So a certain type of linearity is inherent in every observation of a psychological or physiological variable. This requires a definition of what we mean by nonlinearity. Nonlinearity can only be defined either on the dimension of (i) time or/and (ii) intensity (size of steps being unequal and perhaps including

further qualities like shape of change, number, frequency and size of fluctuations) or (iii) according to its dependence on one or more simultaneously considered variables. The latter can be the case by (a) unidimensional causal relations or by (b) single stimulus-response influences like in a first step of feedback or (c) by modification of the relationship between two variables A and B by one or multiple variables C to X.

The latter approach is taken by analysing intra-individual patterns, as favoured by Cloninger & Zwir [11], which can be statistically tested by non-parametric methods like configural frequency analysis [15] or log-linear models based on Bayesian concepts. It must be emphasized that the term 'pattern' in this approach does not mean that a group characterized by a certain temperament trait (defined by some psychological tool) differs from another group by a set of physiological measures A, B and C, but rather that intra-individual constellations of high and low expressions of certain variables identify a certain individual and that individuals with the same constellations might form a group. This means that the high or low expression of variable A is the condition of a different relationship between variables B and C in the low and high condition of A. This can be extended to higher-order conditional interactions, which can form the basis of intra-individual pattern analysis and can be applied also to temporal relationships. (Variable A at time 1 may mean a positive relation between variables B and C, and at time 2 no or a negative relationship between B and C [16], an approach relevant to developmental analyses; see [17].)

So it seems that both approaches—the one guided by top-down theory and the one using the bottom-up data-driven approach—emphasize nonlinearity and mutual influences between variables relevant to temperament, but just attack the problem from two different ends.

Perhaps future research can identify new basic temperament dimensions defined by the extent to which behaviour and biochemical or physiological variables are coupled and uncoupled across time and/or within an individual, and the regularity and fluctuation of these coupling processes similar to connectivity measures in functional magnetic resonance analysis.

Petra Netter

(b) Analysing the working principles of biological systems: irrelevance of independent dimensions

We should shape our taxonomies of psychiatric disorders and biologically based traits (temperament) in normal populations on the basis of a separation of regulatory systems as have been found in neurophysiology rather than of public opinions or statistics. In addition to neurophysiology studies, I spent all of my career working psychometrically on many questionnaires, and I do not object to using these methods. However, our psychometric obsession with independence of dimensions is irrelevant when we analyse working principles of biological (highly integrated) systems, and not properties of our instruments. For example, systems of habitual and novel behaviour work in tandem, passing control over behaviour to each other, depending on situational challenges. Therefore, they are not at all independent in action, but yet they have a well-identified neuroanatomical and functional specificity. I hope that future investigations will pay attention to functional, neurophysiologically based and not to statistical models of taxonomies.

Vladimir Rusalov

(c) Limitations of language-derived taxonomies for understanding psychobiological underpinnings of individual differences

The most popular models of human individual differences were developed on the basis of human everyday language; this applies to lexical approaches where the person-descriptive words in the lexica are used as starting points for investigations as well as to models developed on the basis of questionnaire responses in which lay people indicate their subjective judgements of a target individual. The efficiency by which questionnaires enable big datasets to be collected about broad domains of individual differences has boosted the development of statistical methods in psychology and has shifted researchers' focus to psychometric theories and methods, away from the individuals under study. But by selecting only those variables that fit particular statistical assumptions and discarding all those that do not fit—as is standard practice in psychometric instrument development—researchers radically adapt the phenomena under study to the research methods rather than vice versa. Such approaches result in straightforwardly structured models that are rather easy to interpret—also because their origins in people's subjective judgements entail a guaranteed match with our everyday beliefs [4–7].

The contributions of this theme issue have impressively shown that language-based approaches are not only a coarse way of taxonomizing the diversity that people perceive among individuals, but are essentially misleading research in several ways.

(1) Studying individuals' beliefs and ideas as encoded in everyday language may be insightful about human socio-cognitive, cultural and linguistic abilities but cannot reveal anything about psychobiological processes. Our belief systems and everyday languages have evolved to provide orientation and to facilitate navigation in our highly complex social world—and not to adequately reflect the intricacies of the highly complex biological systems of our bodies and brains [18,19]. Language is no valid starting point for taxonomizing the psychobiological underpinnings of perceivable individual differences.

(2) The exploration of psychobiological systems requires fundamentally different approaches and methods enabling the study of (brain) morphology, physiology, behaviour and ongoing psychical processes—rather than of just people's judgements and belief systems as in assessment methods [7,9].

(3) The statistical methods most widely used in differential psychology (e.g. Factor Analysis and Structural Equation Modelling) are linear methods that facilitate the identification of structures underlying sets of redundant lexical variables. But such methods are inadequate for analysing the nonlinear relationships found in most psychological and physiological processes in which redundancy rarely occurs [12,20–22]. Instead, statistical methods are needed that enable the identification of fluid processes that interact with one another in a contingent, nonlinear, multi-level and feedback manner that still presents profound challenges for their mathematical formalization [8,10,13].

(4) Finally, language-based methods mislead participants and researchers alike in the understanding and interpretation of the kinds of phenomena that can actually be captured in empirical studies. Our abilities to denote even complex and abstract ideas with single words often mislead us to assume that these complex phenomena constitute real entities (e.g. 'traits') that could thus be measured rather directly. The present contributions highlighted the necessity to develop far more sophisticated models, approaches and methods for studying individual differences than are currently applied in psychology.

Jana Uher

(d) Conceptual principles for 'spectral analysis' of interacting composites

I share the opinions of Cloninger & Zwir [11], Robbins [23] and Rusalov [13] that the principles of our classifications should go beyond the Lego-language of independent 'building blocks'— 'basic kinds' of emotions and 'basic unitary constructs' of traits—as major units of analysis. Diversity, the subject of taxonomies, relates to distributions of types, and the most commonly analysed distributions in psychology are Gaussian normal distributions, defined by its author as the result of actions of multiple random factors. As Gauss [24] pointed out, the more these factors (errors or deviations) are contributing to the distribution, the more stable and well-identified is the mean, and this is important to remember when talking about the most consistent traits. Traits are always non-unitary phenomena. They are the result of holographic interactions between environmental factors and individual capacities (as pointed out in [11,20–22]). If we want to progress in our taxonomies, we need to discuss conceptual principles for a 'spectral analysis' of these interacting composites with a closer look at the entanglement of components (similar to the analysis of the interaction of inseparable quarks in elementary particle physics). The degree of interaction or intercorrelations should not be, therefore, a grouping principle of our taxonomies as it is not very informative. A consensus on the criteria for 'spectral analysis' of neurophysiology of temperament traits is still to be reached, and our FET model offers one such principle: functional architecture of construction and regulation of behaviour.

Irina Trofimova

(e) Integrative taxonomies of temperamental differences and mental disorders

Distinguishing those aspects of behaviour that have a predominantly biological basis (temperament) from those that are apparent in socio-cultural interactions (personality) is important in psychological and psychiatric practices. As a psychiatrist, I am often faced with the task of evaluating clients within what Trofimova [10] has called the 'grey area' between normal function and mental illness. Some people may be transitioning from a state of illness back to normality or be in the process of becoming ill, and the capacities of some people may be so exceptional that they would not fit into our traditional view of normality. Finding correspondences between taxonomies of mental illness and temperament profiles of normative behaviour may facilitate a more structured approach to such transitional states and/or exceptional traits. Many authors in this volume showed that the following temperament traits have a biological basis, even though they were not highlighted as major dimensions in personality: physical endurance, motor retardation or high speed of actions, rigidity–plasticity of behaviour, impulsivity, risk-sensation seeking tendencies, sustained attention or effortful

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control, psychopathy and empathic capacities, verbal abilities, probabilistic thinking, emotional dispositions and sensory processing sensitivity [10,17,20–23,25–30].

For me, as a clinician, it is intriguing to observe the strong convergence between the lists of traits identified in temperament research and the lists of symptoms of mental disorders as identified in the DSM/ICD (when these traits are expressed in extreme, pathological form; [17,21,23,26,29–33]). This correspondence is promising for the development of taxonomies that would cover the continuum between the ideal of 'normality' and mental illness, and, which would be useful for studies in psychopharmacology, psychiatry, neurochemistry and psychophysiology. Moreover, in my psycho-pharmacological practice, I have observed that clinical symptoms similar to these temperament traits can be adjusted by using medications, in line with the view that these traits in healthy people and the corresponding symptoms in psychiatric patients share a common neurochemical aetiology. By contrast, the majority of personality disorders fail to respond to pharmacological interventions. Therefore, I see a great need to distinguish between the concepts of temperament and personality, because the concept of temperament has a better capacity to discriminate features that are crucially monitored in our treatment and counselling practices than the concept of personality.

William Sulis

3. Reflections on: neurophysiology of temperament traits

Plasticity of behaviour, a temperament trait identified over 100 years ago in the Eastern-European experimental tradition of studying temperament, was proved to possess electrophysiological, neuroanatomical correlates and, as Robbins' [23] and Trofimova's [10] reviews pointed out, neurochemical correlates. Similarly, neurophysiological correlates were found for the temperament traits of intellectual ergonicity/endurance (or effortful control, as per [20]), physical ergonicity/endurance, motor tempo, empathy, verbal capacities and neuroticism—all were proved to be regulated by specific neurophysiological systems. Moreover, our activity-specific models (STQ, [34,35] and FET, [36,37]), unlike other models, used differentiation between traits regulating habitual, well-learned elements of behaviour and novel elements. After all, neurophysiologists have known for decades that the first types of elements are regulated primarily by the striatum and the construction of novel elements requires more involvement of frontal cortex. Yet, these temperament traits, which we separated in our models according to neurophysiological studies of intra-individual stability and inter-individual differences, are not within the radar of genetic, longitudinal and neurochemical studies, which use primarily personality questionnaires.

Vladimir Rusalov

In terms of the neurophysiology of temperament traits, pioneers usually walk in darkness and undertake a first set of trials and errors that we all benefit from later. I would only praise the authors of the early neurotransmitter hypotheses of temperament for their bravery, even though our own (FET) model [36,37] might be different from them. The results, which were reported in this volume, support the FET suggestion that the functional role of MA systems is probably not in the regulation of emotionality (considering the inconsistency of the associations of MA with neuroticism and reward-dependence)

[22,25]. This important negative result is worth exploring. The FET model highlights findings in neurochemistry, suggesting that DA systems prioritize and update behavioural programmes, whereas 5-HT maintains the available alternatives. In fact, Netter's [25] studies of the reaction time (i.e. timing of integration of actions) reported a slow-down universally in both extra- and introverts when a DA antagonist is used.

Moreover, when only DA (and not 5-HT) systems were compromised in experiments of Robbins [23], Netter [25] and Dellu-Hagedorn *et al.* [26], an individual could not prioritize behavioural alternatives into situation-adequate actions, but still was able to maintain previous sets of programmes; this results in rigidity and perseveration around the same acts. When a deficiency in 5-HT was added to disturbances in DA release, a low turn-over of the DA led to high impulsivity [23,26]. This is interpreted by the FET as compromised maintenance of the established behavioural alternatives: without a proper functioning cortical 5-HT system, an individual cannot maintain internally established/selected behavioural programmes, and so is more susceptible to building programmes using external stimuli and distractions. Combined with problems in the DA systems that lead to inadequate (for the situation) timing of behavioural acts, this results in behavioural impulsivity. I believe that the following links should be explored in future studies to clear this picture: effects of 5-HT systems in endurance of behaviour, NE-regulated systems in behavioural sensitivity and orientation (such as sensation seeking, empathy and probabilistic thinking) and associations between opioid receptors and temperamental emotional dispositions.

Irina Trofimova

(a) Understanding the function of brain regions and networks with multidimensional representations

The general issue of structure–function mapping is central to the understanding of the mind–brain relations, and this, in turn, determines how psychological taxonomies of biologically based traits can be partitioned on the basis of our understanding of neurophysiological systems. In the past decade, I have developed an approach to characterizing the relationship between emotion and cognition [38] that largely resonates with the framework described by Trofimova [10]. One of the central questions addressed is the following: Are there specialized circuits in the brain for emotion? In an important sense, the answer is 'no' because the very boundary between emotion and the 'rest of the brain' is ill-defined. Because brain regions are involved in multiple functions, and functions can be instantiated by multiple regions, investigators are faced with a challenging many-to-many problem [39]. In previous work, we proposed to characterize the function of brain regions via functional fingerprints [40,41], namely a multidimensional representation based on a relatively small set of mental 'domains'. The functional 'fingerprint' for a given region represents both the set of domains that systematically engage the region and the relative degree of engagement (figure 1*a*). Beyond the descriptive aspects of the approach, it outlines a framework in which a region's function is viewed as inherently multidimensional: a vector defines the fingerprint of a region in the context of a specific domain structure. How should one define the domain structure? One hope is that cognitive ontologies can be defined that meaningfully carve the 'mental' into stable categories [42,43]. However, no single ontology is likely to be sufficient. Instead, it is better to conceive of several task
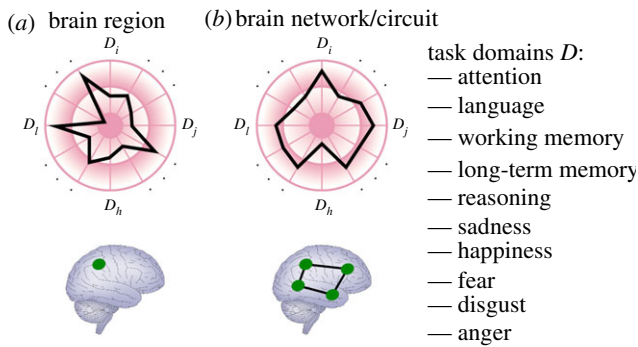
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Figure 1. Multidimensional fingerprints characterize the functional repertoire of brain regions and networks/circuits. (*a*) The polar plot illustrates the fingerprint of a particular brain region, with each vertex corresponding to the degree of involvement in a mental task domain *D* (example domains shown on the right). (*b*) The same idea can be extended to describe the functional repertoire of brain networks/circuits. (Online version in colour.)

domains that are useful and complementary in characterizing brain function and/or behaviour. Thus, a region's functional fingerprint needs to be understood in terms of a family of (possibly related) domains. In the past decade, the field has witnessed a progressive shift to describing mental function in terms of brain networks. Does a description of structure–function relationships in terms of networks allow for a one-to-one mapping? For instance, a network comprised regions R_1, ..., R_n is involved in function F (such as 'executive function'). I suggest that the attempt to map structure to function in a one-to-one manner in terms of networks will be fraught with similar difficulties as the one based on brain regions; the problem is largely passed along to a higher level. Thus, the idea of multidimensional profiles can be profitably extended to networks (figure 1*b*; [40]).

There are multiple reasons for this complexity even at the network level, including the fact that brain networks are not disjoint but overlapping (specific brain regions participate in multiple brain networks [44]) and dynamic (a region's network affiliation evolves in time; [45]). These considerations also imply that, neuroanatomically, there are no specific brain networks for traits of positive or negative emotionality, or neuroticism/extraversion. The ideas above are closely aligned with several principles outlined by Trofimova [10], including functional and physical overlap, and dynamics. A deeper understanding of complex relationship between mind and brain will benefit from frameworks that embrace these types of principles.

Luiz Pessoa

(b) Neurotransmitter systems and brain areas

Many papers of the theme issue converge on opinion that different neurotransmitter systems work differently in different brain areas, responding only to specific tasks, in line with the activity-specific approach offered by Rusalov [13] (i.e. proposing to separate traits related to physical, verbal and mental aspects of behaviour) and also shows that we better tune our taxonomies to the classifications of tasks. For example, in drug challenges reported by Netter [25], people with cognitive impulsivity had more noticeable DA-PRL and NE-cortisol changes than people with high motor impulsivity. The FET suggests that neuropeptides, as a class, play a much stronger role in 'motor-physical' traits, whereas frontal–cortical monoamine systems play a stronger role in 'cognitive traits', and so frontal MA manipulations will affect cognitive functions

more than motor regulation of behaviour. Moreover, the differences in functionality of cortical and basal ganglia regions in the regulation of probabilistic (complex, novel) or more deterministic aspects of behaviour (habits, automatic actions) are rarely discussed, but, as Dellu-Hagedorn *et al*.'s [26], Robbins' [23] and Rusalov's [13] papers suggest, these differences are crucial in understanding the sources of inconsistencies in neurochemical and neurophysiological studies of psychological traits. I agree with Rusalov [13] that Bernstein's [46] classic notion of passing control over the construction of behaviour between several levels of automaticity is often overlooked but should be implemented in taxonomies of psychological traits and mental disorders.

Irina Trofimova

4. Reflections on: developmental perspectives

(a) Development of neural networks

As Hoyniak *et al*. [28] suggested in their interesting paper, the frontal N2 component provides one window on the neural systems of effortful control. The development of effortful control begins at least by seven months, when infants look longer at an error in simple visual problems [47], showing increases in the error-related N2 occur over the same electrode sites shown in adults to involve the anterior cingulate gyrus [48]. However, as Hoyniak *et al*. [28] suggested, even though infants can note errors at seven months, they do not act on them by, for example, slowing their next response until 30–48 months, a time when the executive attention network shows increasing connectivity as shown by resting state MRI. Moreover, we can use specific training methods to enhance N2 by improving responses to conflict [49]. Bringing together questionnaires, observational and behavioural data, such as reaction time with neuroimaging, can greatly enhance our understanding of the role of effortful control in development [50].

Michael I. Posner and Mary K. Rothbart

(b) Using known brain networks to choose candidate genes

Sallis *et al*. [51] say that heritability estimates rest in part on the assumption that gene by environment (GXE) interactions are weak. However, in agreement with a general developmental approach to temperament, there are GXE interactions between effortful control and parenting and with interventions that involve parent training (for a review, see [52]). As the authors pointed out, candidate gene studies have often not been replicable. However, by choosing candidate genes on the basis of knowledge of brain networks related to effortful control, replication may be improved as well as the centrality of the network approach supported by the resulting genetic data [52].

Michael I. Posner and Mary K. Rothbart

(c) Temperament: a complex but useful concept for understanding the development of psychopathology

Temperament, as with many other psychological concepts, is a complex construct as it is not unitary and does not exist as a concrete entity in nature. Yet, it is a useful and important construct that has shown associations with biological and neurochemical regulatory systems. Temperament is defined here as individual differences in reactivity to the environment

and self-regulation that are early appearing, biologically based and relatively stable. Temperamental individual differences, especially in interaction with the environment, are useful for understanding processes of risk and resilience in the development of psychopathology.

A number of the contributions in this theme issue are consistent with the National Institute of Mental Health's Research Domain Criteria (RDoC), which seek to understand the development of underlying phenotypes of psychopathology across multiple developmental stages and at multiple levels of analysis, including genetic and neurodevelopmental pathways [12,21,53]. Farde et al. [22] described the benefits of examining the biological underpinnings of dimensional traits rather than categorical psychological disorders. Hoyniak et al. [28] examined neural correlates of temperamental inhibitory control in toddlers, observing that larger N2 event-related potential amplitudes in a go/no-go task are associated with poorer inhibitory control. Posner & Rothbart [20] reviewed the neural processes supporting attention, and described evidence that executive attention is related to temperamental effortful control. Kagan [17] reviewed the biological underpinnings of behavioural inhibition (high fearfulness and reactivity), including high amygdala activation to novelty and a high but minimally variable resting heart rate. Robbins [23] reviewed the contributions of various monoamine neurotransmitters to different temperament and personality traits, and noted the importance of considering the interactions among multiple neurotransmitter systems, such as the interaction between serotonin and dopamine in impulsivity, examined by Dellu-Hagedorn et al. [26]. Cloninger & Zwir [11] discussed the importance of considering temperament profiles, and not just traits, when examining genetic effects. Collectively, the studies described in this theme issue illustrate the benefit and need of advancing our understanding of how temperament develops across multiple levels of analysis.

Knowing how best to treat or prevent psychopathology hinges on our ability to understand the development of psychopathology at multiple levels and across multiple developmental stages. Temperament is an important window into the early precursors of psychopathology and provides a useful and important avenue to advance our understanding of how psychopathology develops, including why some individuals go on to develop psychopathology in response to stress, whereas others are resilient in the face of stress. As just one example, children who are temperamentally high in negative emotionality have been shown to be more sensitive to their environment, for better and for worse [21,30,54]. Researchers have begun to explore the genetic and biological processes accounting for temperamental differential susceptibility to the environment. Thus, even with its long and rich history, temperament (and its bio-psycho-social levels) remains an important and relevant construct even in the twenty-first century.

Isaac T. Petersen

5. Reflections on specific traits: functional differentiations and physiological underpinnings

(a) Aggression

I think that aggression as a trait is often an overlooked subject, perhaps because it is probably a derivative of several temperament traits—low empathy [25,29] (Netter indeed reported associations with psychoticism), upregulation of integrative traits (impulsivity, plasticity and tempo), dysphoric emotional disposition, low endurance and lowered capacity for probabilistic processing (and so rule learning). I therefore agree with Blair [29] and those who distinguish between several types of aggression (e.g. impulsive–impatience; well-calculated insult; acting-out; bad mood and irritability; and escape from inability to handle situations). This view corresponds to the pattern of associations between impulsivity and aggression with DA and 5-HT systems reported in [22,25].

Irina Trofimova

(b) Attention

Posner & Rothbart's [20] concept of NE-based 'sensitivity and alerting network' is in line with the FET's attribution of NE systems to behavioural sensitivity, especially sensitivity to novelty. However, it might be confusing to see very different uses of the same word 'orientation' in these two models; so let's clarify it. Posner's model [55] call acetylcholine-based component of attention as 'orienting network' in a sense that this network maintains orientational attention to specific stimuli. In contrast to this, the FET model [36,37] uses the word 'orientation' for novelty-related attention, attributed by both models to the NE systems. Despite this difference in wording, both models converge on the idea that ACh systems maintain attention to established elements of situations, whereas NE systems regulate attention to novel aspects of situations as well as many other behavioural sensitivity aspects. In fact, Posner & Rothbart [20] themselves cited [56] study showing that antagonists to ACh block improvement from knowing where the target would occur, but had no effect on RT improvement from warning signals. Hasselmo & Stern [27] also mentioned the well-known role of the ACh in the maintenance of attention. This consensus between Posner's model and the FET model suggests that there are neurochemical basis for differentiation between orientational and attention-maintenance traits of temperament.

Irina Trofimova

(c) Understanding temperamental shyness: reflections on heterogeneity, context and function

There are at least three long-standing issues in the personality and behavioural sciences that are often overlooked in temperament research, but which are critical in order to move towards a unified framework for understanding individual variation in temperament and its predictive utility to typical and atypical socio-emotional development. They are heterogeneity, context and function.

Heterogeneity: Although the extant literature routinely treats temperamental shyness as a homogeneous phenomenon, we have long known that not all temperamentally shy children are alike. Over six decades ago, Litwinski [57] described two types of constitutional shyness, an active form, which he suggested involved chronically avoiding social situations, and a passive form, which emerged from novel situations and the initial avoidance of these situations. Buss [58] later formally described two types of shyness rooted in temperament: an early developing fearful shyness emerging approximately six to nine months, coinciding with the onset of stranger

wariness, and a later developing self-conscious shyness emerging with self-awareness approximately 3–4 years. More recently, others have suggested that there are positive and negative types of shyness, with their antecedents in early infancy [59]: positive shyness is associated with the expression of approach-related behaviours (e.g. averting gaze, but smiling), coyness and sociability, while negative shyness involves more distress, anxiety and avoidance-related behaviours [60]. Considering heterogeneity is important because it enhances conceptual clarity of the phenomena and also prediction.

Context: In personality science, the consideration of context for reliably predicting behaviour has been a central theme for decades. Lewin [61] argued that human behaviour (*B*) was a function of the person's disposition (*P*) and the context or situation (*S*), expressed as $B = f(P,S)$. However, the majority of the work on temperament is based on assessments from limited contexts, involving primarily mothers rating their children at home, teachers rating children in their everyday school environments and/or observational studies of children conducted in controlled laboratory settings. Kagan [17] accurately critiques the limitations of maternal reports. However, laboratory studies also have their own inherent problems, including demand characteristics, experimenter biases, generalizability and external validity. Does temperamental shyness generalize to other contexts? Using a surgical setting as a non-normative ecologically salient context, researchers recently found that temperamentally shy children were consistently less anxious than sociable children in response to impeding elective surgery across two visits: a pre-operative visit and day of surgery [62]. Perhaps all bets are off when it comes to examining consistency of temperament–behaviour relations in shy children in some ecologically salient contexts, such as surgery, arguably one of the most psychologically stressful events one can face. Examining temperamentally shy children only in traditional contexts may limit our interpretations.

Function: What is the evolved function of the behaviour? This is one of the four questions asked by the ethologist and Nobel Laureate, Nikolaas Tinbergen [63] in his seminal model, he used to understand behaviour. However, relatively few ask this question when studying temperament (although see [10,13,36]). What function does temperamental shyness serve? Here, I return to positive and negative shyness. Both types of shyness may be rooted in temperamental fear and

may have different developmental onsets and functions [64]: negative shyness may reflect a sensitivity bias to detect threat of physical harm by conspecifics, be subserved by evolutionary old brain circuits and may have evolved to facilitate withdrawal from danger; negative shyness probably overlaps with Kagan's high reactive infants [17] and Buss' [58] fearful shyness. Positive shyness may reflect more recent human evolution and socio-cognitive processes, which may have evolved to serve simultaneous caution arising from fear and interest, facilitating additional time for learning to take place about conspecifics' motives and intentions; positive shyness has its origins in early infancy but become crystallized in early childhood with cognitive maturation and probably overlaps with Buss' [58] self-conscious shyness and is retained in adulthood, possibly reflecting a neotenous trait [65]. Considering the adaptive value of temperamental phenotypes has implications for how we view normal behaviour and psychopathology. This is particularly relevant in North American culture today where the medicalization of normal variation of some behaviours has become routine [66].

The ideas raised by Kagan [17] and Jones & Sloan [21] in each of their respective review papers shed new light on our understanding of temperament, its definitional issues, origins, correlates and outcomes, and provide fruitful avenues for future research in this domain of inquiry. Kagan's [17] paper illustrates the innate temperamental bias to shyness and attests to the value of conceptualizing temperamental variation as categories versus continua and the need to consider multiple, and observational, measures rather than relying solely on evidence from subjective reports. Jones & Sloan's [21] review illustrates the complex interactions between biology and the prenatal environment in shaping individual differences in temperament, which raise interesting possibilities for developing programming hypotheses of temperamental shyness.

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