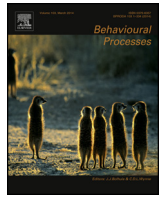




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Plasticity, stereotypy, intra-individual variability and personality: Handle with care

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ABSTRACT

Only recently, variability within individuals has become of importance to evolutionary thinking. The boom in the literature on behavioural variability has led to the emergence of concepts such as behavioural plasticity, stereotypy, imprecision, and intra-individual variability (IIV). The proliferation of new terms has resulted in overlapping concepts, spreading confusion in understanding the origins of variability. Here we provide a critical overview of the concepts related to behavioural variability within the individual. We conclude that although there is no overlapping between behavioural plasticity and IIV, these concepts do overlap with stereotypy; they also face problems with ideas of abnormality and absence of function in stereotyped behaviour. We further provide a critical overview of the sometimes confusing relationship between (1) within individual variability, and (2) consistent variability across individuals (personality). We point out that personality is logically independent of both activational plasticity and IIV, because personality emerges at the population level, whereas plasticity and IIV emerge at the individual level. We conclude that, in personality studies, the failure to acknowledge the existence of either internal variability or consistent between-individual differences in internal variability will result in mixing different phenomena, and inhibit building unified accounts from heterogeneous databases.

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Phenotypic variability is a central concern for evolutionary biology. Geographic correlations with variability reveal incipient speciation processes, and even sympatric variability is connected to speciation. As we progressively understand the evolutionary bases of variability, new concepts emerge in the literature. Part of phenotypic variation, for example, is due to plastic adjustments of the individual, and only recently has this kind of internal variability become important for evolutionary biology.

For behaviour, plasticity is one major source of variability, and this research area has been growing exponentially over the last decades (Fig. 1). As the literature grows, other concepts, such as behavioural imprecision, behavioural reaction norms, behavioural flexibility and intra-individual variability, pop out in order to grasp different aspects of the variability within one individual. The growth of the literature in this area is a clear demonstration of the importance of the theme for behavioural biologists, physicians and psychologists. But the proliferation of new terms has sometimes resulted in overlapping concepts, and also in a diversity of usage of

these terms. We are thus mainly interested in concepts related to the degrees of internal variability in behaviour, that is, concepts that deal with the identification of variability that is either produced autonomously within the individual, without major causal links to (or sometimes even actively buffered against) variations of the external environment, or produced by the individual as a (adaptive or otherwise) reaction to relevant changes in the environment.

In this contribution, we discuss concepts related to internal variability in behaviour, addressing some of the conceptual problems within it, aiming to reduce the polysemy in this large and healthy research field. We provide an overview of such literature, so as to critically discuss the overlap between the concepts that have emerged along with the development of the area. Also, the literature is now proposing associations between these ideas related to internal variability, as well as new concepts related to inter-individual variability in behaviour, concepts such as personality and behavioural syndromes. This shows again the strong expansion of the area, but also adds another layer of possible conceptual confusion between these distinct levels of variability. In this contribution, we will critically analyse the relationship between these distinct levels of variability, with an eye to the problems that emerge when one acknowledges the existence of consistent between-individual differences in internal variability.

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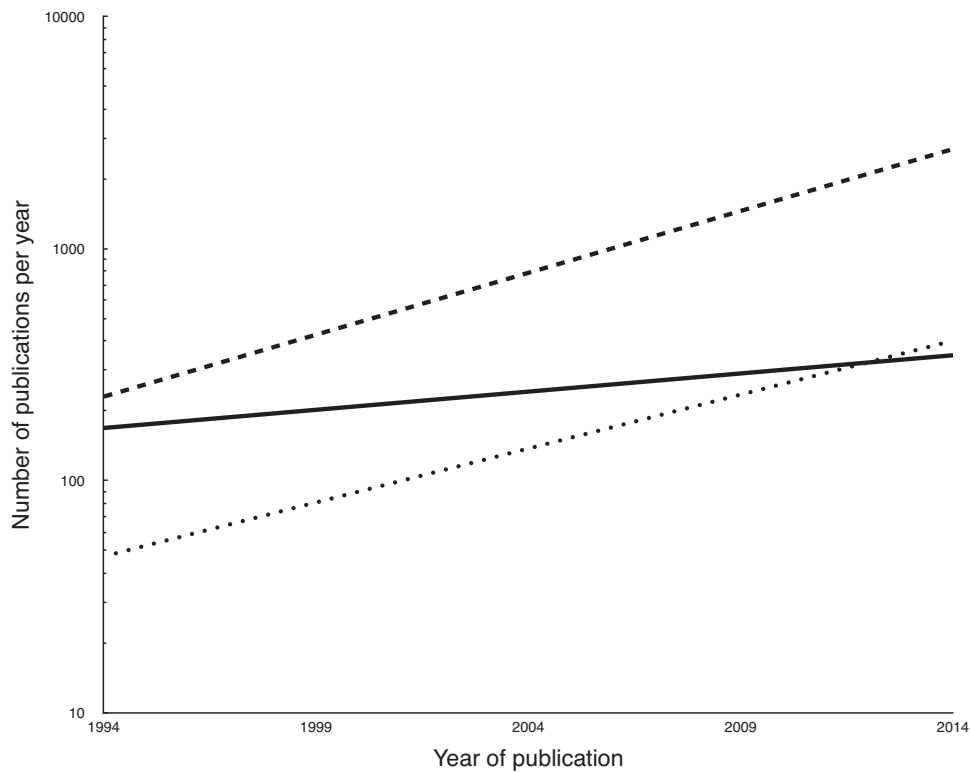


Fig. 1. Yearly publications on behavioural plasticity (dashed line), intra-individual variability in behaviour (dotted line), and behavioural stereotypy (continuous line) in the last 20 years. Plasticity is the most studied area, but all aspects of internal variability in behaviour are growing areas of research. Results from a search with Scopus engine (www.scopus.com), excluding the subject area of physical sciences. Searches were performed including the terms in the title, abstracts or keywords of the documents. The number of publications in 2014, an estimate based on the publications up to August 2014.

1. Overview of internal variability concepts

Behavioural plasticity is a well studied topic (Fig. 1). The top 20 most cited papers converge on the use of the term behavioural plasticity as meaning variability resulting from the exposure of an individual (or genotype) to different stimuli (Appendix 1), which is also in agreement with recent publications in the area (Stamps and Groothuis, 2010; Mathot et al., 2012; Snell-Rood, 2013). One single organism can vary its behaviour as a function of either distinct situations (changes in the external stimulating environment), or distinct contexts¹ (for example, changes in the latency of an aggressive response in the courtship context, as compared to the territorial defense context—Sih et al., 2004), or under changing internal physiological constraints (as most drug induced plasticity studies reviewed in Appendix 1). Plasticity can be measured in the intact organism (variability of any behavioural score in response to distinct stimuli) or with experimental manipulations in the internal functions of the individual, as in most neurophysiological studies. The most straightforward way of measuring plasticity is by fitting a curve through the distinct behavioural scores of the individual, if he/she has been subjected to continuously varying contexts (behavioural reaction norm method), or by evaluating the effect of the environmental factor (analysis of variance or related methods), if the individual has been subjected to discrete environmental changes.

¹ In the remainder of this paper, we will not distinguish between “situation” and “context”, because sometimes it is not straightforward to decide whether one behaviour is related to one or another functional context. To avoid making a priori, and sometimes unjustified distinctions, we will use the term “context” in a broad sense, following Stamps and Groothuis (2010).

Behavioural plasticity has been separated into long versus short-term behavioural changes (for example, Laviola and Terranova, 1998; Brown, 1996), alternatively termed developmental plasticity versus phenotypic flexibility (Piersma and Drent, 2003), or developmental versus activational plasticity (Snell-Rood, 2013).² One should note that long-term changes (developmental plasticity) must not be taken as inflexible, since they indeed refer to alternative developmental pathways guided by switches (West-Eberhard, 2003), in which case the developmental system flexibly adjusts to environmental variable conditions.³ Short-term changes are reversible, and can be connected to flexible processes such as sensitization, habituation, or associative learning (Griffith et al., 1993; Réale et al., 2007), or else can include in-built alternative responses to different contexts (Snell-Rood, 2013). Long-term changes are connected to more complex developmental changes, such as imprinting or the simultaneous change in multiple different behavioural systems (Bolhuis, 1991; Japyassú and Ades, 1998). There is between-individual variation for plasticity (Dingemans et al., 2010), and its presence can have evolutionary outcomes (Moczek et al., 2011).

² When measuring plasticity through reaction norms (RNs), one should differentiate these kinds of plasticity with the appropriate terminology, such as developmental reaction norm versus contextual reaction norm (Stamps and Groothuis, 2010).

³ Although these long-term changes (developmental plasticity) are the very expression of developmental flexibility, they are irreversible once one developmental path is taken. Ideally one could measure the developmental plasticity of one single genotype with the usual reaction norms approach, by artificially cloning the single genotype into multiple individuals, and then developing them in distinct environments. Inbred strains (or lineages, siblings) may be used instead of clones (Fuller et al., 2005).

Although much less studied than behavioural plasticity (Fig. 1), intra-individual variability in behaviour (IIV) has a long research tradition, with a variety of distinct research focuses, and is related to variation in behaviour within the same situation and context. Although it is sometimes referred to as behavioural imprecision (Eberhard, 2007), we prefer the term IIV, because 'imprecision' potentially implies that high levels of variability are maladaptive, whereas there is experimental evidence that high levels of IIV might be adaptive in some situations (Briffa, 2013). One can study the short-term effects of drugs or environment or lesions on IIV, or the long-term developmental patterns in the fluctuations of individual behavioural scores (Stamps et al., 2012). A variety of analytical tools allow, for example, establishing if, and at what exactly critical moment, the behavioural system loses its stability, and increases the IIV (Van Geert and Van Dijk, 2002). The literature is mostly dominated by human oriented research (Appendix 2). Intra-individual variability is usually accessed through successive samplings of the same individual under a single experimental paradigm (e.g. Castellanos et al., 2005; Matthews et al., 2002). It can be measured as departures from the mean individual score, such as variance, coefficient of variation, or standard deviation. In small samples it can be measured as the total variation (maximum–minimum scores) or, with large samples, it can be measured as the skewness of the variability distribution (Van Geert and Van Dijk, 2002).

Stereotypy is still another concept that deals with internal variability, typically small amounts of variability, in the behaviour of one individual. The top 20 most cited papers are mainly dominated by a medical approach (Appendix 3). Stereotypies are most commonly characterized as repetitive, unvarying and functionless (e.g. Mason, 1991) or abnormal behaviour patterns (e.g. Garner, 2005). Nevertheless, some authors adopt a more descriptive approach, defining stereotypy simply as a form of behaviour with little variation (without any reference to the absence of function, or to the abnormality of the behaviour, e.g. Randrup and Munkvad, 1967). Other authors define stereotypies as species typical behaviours that are in one way or another accentuated in relation to normal behaviour (Castellani and Adams, 1981). Many studies are related to the physiological, mechanistic basis of stereotypies, under the experimental paradigm of drug injected subjects (e.g. D-amphetamine, apomorphine, or antagonists of these drugs), and these studies usually measure intra-individual (neurophysiological) features associated to the behaviour of the individual. The animal welfare literature is also strongly represented, with focus on the observable repetitive and unvarying behaviour in intact, whole organisms (Appendix 3).

Up to this point of our outline of the main concepts related to the internal variability in behaviour, we see that there is a general consensus on the meaning of plasticity and IIV, and that there is no overlapping between these two sources of variability. The same is not true about stereotypy, a concept that is always linked to small internal variability, but that is controversial in other aspects, possibly because of its diverging uses in different scientific domains, such as the medical, the animal welfare, or the traditional ethology research programs. In the following section, we will review more closely the concept of stereotypy, showing that in its actual polysemic use, it presents superpositions, sometimes with the concept of activational plasticity, and in other instances with the concept of intra-individual variability.

2. Stereotypy overlaps with activational plasticity and intra-individual variability

As we can see in the outline above, stereotypy has not a consensual definition in literature, and there is no agreement whether

the abnormality or the absence of function of stereotypies should be included in the definition (Mason and Latham, 2004; Edwards et al., 2012; Manning and Dawkins, 2012). For example, from a medical standpoint, there has been a misuse of the idea of abnormality in the literature about movement stereotypies. Potential stereotypies must be evaluated under a more comprehensive diagnosis protocol, one that takes into account not only the phenomenology of the movements, but also other clinical aspects of the potential disorder (Edwards et al., 2012). From an evolutionary standpoint, one must be even more careful about the idea of any potentially abnormal behaviour. Diversity at every phenotypic level of organization (genes, morphology, and behaviour) is one of the major forces driving evolution. In an evolutionary framework, behavioural novelties that at one moment could seem abnormal, can become the rule after unpredictable changes in the selective pressures.

There is also difficulty for accepting the absence of function in the current stereotyped behaviour of an animal due to three reasons at least. Firstly, the function of current behaviour can sometimes become evident only later in the development (Wolf, 1968; Thelen, 1979). Secondly, the seemingly functionless stereotypies could always be considered as a way for an animal to cope with stressful situations (Wiepkema, 1981; Duncan and Wood-Gush, 1972; Dantzer, 1986). Finally, the statement of the absence of function can never be proved right: one would have to review all possible functions before such an assertion, and the function of stereotypies can sometimes be revealed on unsuspected contexts, such as communicative interactions (Garrigues et al., 1982). Indeed, traditional ethological studies introduced the concept of ritualization, whereby behaviour without apparent function evolves to a communicative function by becoming more conspicuous, usually through the frequent rhythmical repetition of movements, reducing both intra and inter-individual variability (e.g. Lorenz, 1966: 276–277; Lorenz, 1981: 248–249). In the literature stemming from this classic ethology tradition, stereotypy has been widely discussed as connected to species typical behaviour, with reference to the classic criteria of homology in comparative studies (Baerends, 1958; Atz, 1970; Hodos, 1976; Lauder, 1986; Wenzel, 1992; Greene, 1994; Penna-Gonçalves et al., 2008; Japyassú and Machado, 2010; Bateson and Gluckman, 2011), and in opposition to the plastic aspects of behaviour (Japyassú and Caires, 2008; Legendre et al., 2008; Sol, 2009; Slagsvold and Wiebe, 2011). Thus, we have different uses for the term stereotypy, stemming from different research traditions: the animal welfare tradition, that conceives stereotypy as functionless or abnormal, repetitive behaviours, and the classic ethology tradition, that conceives stereotypy as behaviour that is repeated always the same way, irrespective of the surrounding context.

This ambiguous usage introduces logical difficulties into the concept of stereotypy. For example, when an animal behaves differently in successive exhibitions in one same context, we talk about intra-individual variability (IIV; Stamps et al., 2012). When this same animal behaves differently, but now in distinct contexts, we talk about activational plasticity. So, we have different terms to express the same phenomenon (change in behavioural expression), depending on whether it occurs as a response to unvarying (one same environment) or varying contexts. This is an important distinction indeed, because in one case it is the organism that changes by itself (IIV), while in the other it is the changed environment that triggers a distinctive response. Different causal systems imply different mechanisms and very different concepts.

Now, what if we apply this same reasoning to the concept of stereotypy? If an animal does not change its behaviour in successive exhibitions, all of them performed in the same context, we refer to this repetitive, and unvarying behaviour, as a stereotypy. But if the animal again do not change its behaviour, and repeat it successively in spite of several changes in the environment, we also

call this repetitive behaviour a stereotyped one. Unlike the previous discussion about IIV/activational plasticity, here we apply the same concept to both cases, no matter if the phenomenon (fixity of behaviour) occurs in the same or in distinct contexts. Thus, the first point we want to make is that there is a logical inconsistency in the way we use the concept of stereotypy. Actually, stereotypy seems to be a purely phenomenological concept, grasping only the repetitive and unvarying nature of successive behaviours, regardless of the diverse causal structures that can lead to the unvarying behaviour.

If a behaviour is repeated without variation, by one same individual, in one same unvarying environment, like when a caged animal repeats one same behaviour on and on, we are talking about stereotypy with the meaning that this concept have in the literature of animal welfare. Nevertheless, for this stereotypy to occur, the animal should also have a low IIV, otherwise it could not repeat precisely the same behaviour. Thus, in the animal welfare literature, the concept of stereotypy overlaps with the concept of IIV.

Now, when behaviour is repeated without variation in different contexts, the system is by definition insensitive to environmental fluctuations, and thus is not plastic (Japyassú and Caires, 2008). This is the usage within the traditional ethology approach, where stereotypy means low activational plasticity. Thus, in this second meaning, the concept of stereotypy overlaps with the concept of activational plasticity.

In order to solve this logical inconsistency one should revise the concept of stereotypy with an eye to the causal structure underlying the exhibition of the behaviour, so as to create different concepts for different causal structures. This logical inconsistency seems to be at the root of the disagreement we have seen in the overview of literature concerning the concept of stereotypy. Our proposal is to use the concept of stereotypy only in its first meaning: as unvarying repetitive routines in one same, unvarying context (for example, a caged animal). Nevertheless, attention should be paid to the development of this concept, as it can be subsumed by IIV; depending on the definition, animal welfare stereotypy will sum up to be simply one special case of (low) IIV. We suggest that the second meaning of the term stereotypy should be simply abandoned, because it is already covered by the concept of activational plasticity.

As our last contribution, we would like to briefly discuss the relationship between the concepts related to internal variability and the concept of personality, which is related to variability between individuals. There has been a rise in the usage of concepts such as temperament, coping style, personality and behavioural syndrome, and these population concepts have been recently discussed in relation to internal variability concepts, such as behavioural plasticity, IIV and stability, a situation that deserves attention, because it raises the possibility of confounding the individual with the population level of analysis.

3. Personality and internal variability

The field of animal personality comprises a much older research tradition, when compared to both behavioural plasticity and intra-individual variability (Appendix 4). Recently (from 2000 on), there has been a resurgence of interest in animal personality, with a more explicit goal of detaching the usage of the term, in the ecological and evolutionary sciences, from its usage in human sciences (Gosling, 2001). In this new resurgence of the field, animal personality is strictly tied to individual differences in behaviour that are consistent across contexts or time (Sih et al., 2012), or that are consistent both across contexts and time (Stamps and Groothuis, 2010).

Most empirical studies of animal personality have relied on coding behavioural scores in standardized tests either in the laboratory (Jenkins, 2011; Carter et al., 2012; Dingemans et al., 2012; Biro and

Adriaenssens, 2013) or in field studies (Betini and Norris, 2012; Dammhahna and Almeling, 2012). The most usual way of assessing behavioural consistency is through repeatability⁴, which is usually evaluated through repeated measures of the individuals (Jenkins 2011; Briffa and Greenaway, 2011; David et al., 2012; Klueen and Broome, 2013; Herde and Eccard 2013; Toscano et al., 2014) under one same context (i.e. differential consistency, *sensu* Stamps and Groothuis, 2010) and/or through repeated measures across distinct contexts (i.e. context generality, *sensu* Stamps and Groothuis, 2010). Statistically, it can be measured through correlations across the contexts and/or across time, through analysis of variance with the individuals taken as a fixed factor, or through linear mixed-effects model-based methods (Nakagawa and Schielzeth, 2010; Dingemans and Dochtermann, 2013).

The relationship between personality and internal variability has been capturing attention recently (Stamps and Groothuis, 2010; Stamps et al., 2012; Brommer, 2013), and we provide a brief overview of this relationship within recent literature (Appendix 5). We will show that the major concerns relate to the fact that, within the literature about animal personality, internal variability is sometimes conceived as a population concept, often it is conceived as similar across individuals and contexts, and even more often it is simply ignored.

A first point of conceptual confusion that appears in this literature refers to the level of analysis, when dealing with behavioural plasticity. As we have seen in the overview above of behavioural plasticity, there is a consensus that plasticity is a property of an individual (Appendix 1). Nevertheless, probably because personality is a property that emerges in a population (or group of individuals), researchers studying personality sometimes mix the levels of analysis, and consider behavioural plasticity as a property of a population (see, for example, Carter et al., 2012). This seems misleading, since plasticity measurements are certainly not supposed to be taken at the level of the population, but instead at the level of the individual.⁵ The expression “population plasticity” is probably only a linguistic shortcut for “mean individual plasticity within a population”. Nevertheless, we think these shortcuts should be avoided, in order to reduce the possibility of misunderstandings.⁶

Sometimes, talking about “population plasticity” is more than a linguistic shortcut. One could argue, for example, that it is possible to have an overall measurement of plasticity without evaluating each individual across the contexts (Crispo and Chapman, 2010).

⁴ It should be noted that repeatability is strictly tied to a design of repeated measures of individuals in one same context, at distinct time points; adjustments have to be performed in order to account for the use of distinct contexts along with repeatability measures (Nakagawa and Schielzeth, 2010).

⁵ Sure, one can always measure plasticity in the individuals of a population, and then calculate the mean individual plasticity in that particular population. If the individuals in the sample show similar plasticity, the mean will be a good central trend estimator, but if there is enough inter-individual variation in plasticity, population means will be less useful. In any case, having a mean value does not imply that the population as an entity is somehow plastic: the individuals are the entities that show plasticity, not the population (but see the next note). In other words, population mean plasticity is caused by individual plasticity, not the other way round, because behavioural plasticity emerges at the level of the individual.

⁶ Misunderstandings may occur because, strictly speaking, one could indeed say that a group, as an entity, could be plastic, for example, when there is a collective behaviour that changes with the environment. The foraging trails of the ant *Pogonomyrmex barbatus* compose a collective behaviour, one that changes in relation to food availability and desiccation risks (Gordon et al., 2013). In this particular case, behavioural plasticity is indeed measured at the level of the foraging group (for example, one could measure the total time to establish a successful trail), because the behavioural character in question (the trail) emerges at the colony, not at the individual level. This is a discussion about levels of individuation; we have shown that authors agree that plasticity must be measured at the level of the individual, but individuality emerges at many distinct levels (Bonabeau et al., 1999). To avoid misunderstandings, plasticity should always refer to the level of organization where the plastic behaviour emerges.

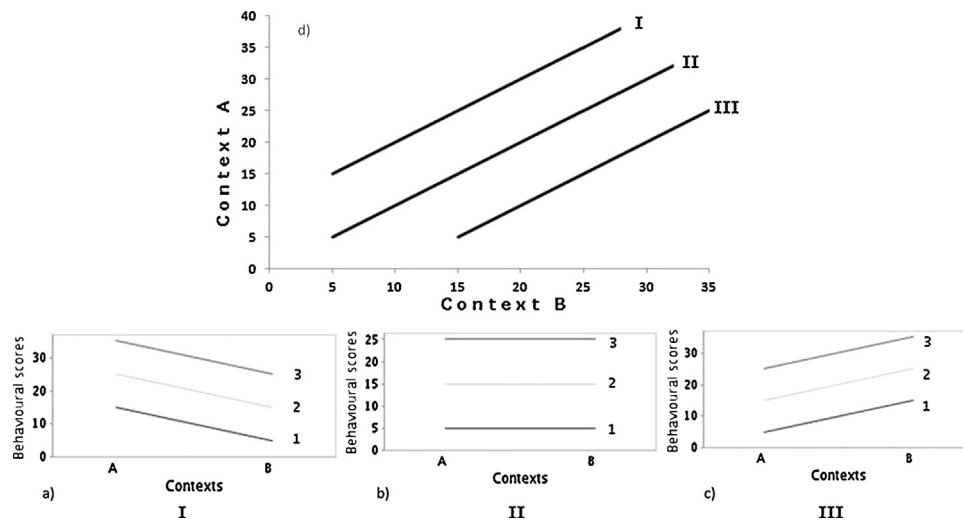


Fig. 2. Internal variability is independent of personality, because the former is defined at the level of the individual, while the latter emerges at the level of the population. Individuals can vary their behaviour (internal variability) with context or time (a–c), with no effect on personality: the correlation between contexts (or between two distinct time points along individual development) is maintained (d) (schematic illustration).

For example, when analysing the effect of the introduction of a predator on the behaviour of a prey, one could measure the mean distance of prey individuals from a retreat, before and after the experimental manipulation (the introduction of a predator), without marking any individual prey; if the mean distance to retreat (population level measurement) does not change with the introduction of the predator, one could be tempted to conclude that there is no activational plasticity (individual level measurement), without measuring activational plasticity for any particular individual. Nevertheless, the absence of change in mean values only allow conclusions about the absence of changes in the individual values, if there is low variability for (individual) activational plasticity within the population, a requisite that calls for experimental evidence, since there is accumulating evidence for large individual variability in activational plasticity (see Brommer, 2013; Dingemans and Wolf, 2013).

The fact that behavioural plasticity is a property of an individual does not mean that plasticity cannot affect the population level. For example, changes in the individual responses of the African striped mouse (*Rhabdomys pumilio*) to conspecifics (individual level, activational plasticity), due to changes in the context (harshness of the environment) may result in changes in the social structure of the species (social flexibility, see Schradin et al., 2012). These changes in the social system scale up to include population level effects, particularly if most individuals have similar reaction norms (Schradin, 2013).

Problems also appear in the relation between personality and the ideas of activational plasticity when it is suggested that the existence of personality constrains activational plasticity (e.g. Neff, 2004; Carter et al., 2012; Toscano et al., 2014; Herde and Eccard, 2014). This reasoning builds upon the intuitive idea that personality itself implies some behavioural stability (thus the opposition to plasticity), an intuition that has been challenged with the documentation of context specific repeatabilities (Brommer, 2013) and developmental changes in animal personality (Stamps and Groothuis, 2010). In order to understand why this intuition is misplaced, we must again stress that personality is not related to the behavioural scores of any particular individual, but instead emerges in the population, since it is related to the existence of significant individual differences in a behavioural score (so that one can rank the individuals) and, more than that, is related to the stability of this ranking, that must be consistent across contexts and/or through time. If personality is related to the ranking of behavioural

scores, and not to the scores themselves, it does not imply stability of any particular behavioural score across contexts (it does not imply low plasticity) or through time (ontogenetic changes can be accommodated with personality). If all individuals are equally plastic, all of them will change their behaviour equally with the context, and the ranking between the individuals will still remain stable despite high levels of plasticity. The same logic applies to consistency through time: if all individuals vary similarly with development, the ranking will still be consistent (Fig. 2).

This confusion has been somehow dissected in recent papers, and it has been clear since then that, under a reaction norms treatment of activational plasticity, personality is connected⁷ to the mean behavioural score of the individual, while plasticity refers to the inclination of the line (if the function is linear) fitting the behavioural scores to the centred environmental gradient (Sih and Bell, 2008; Dingemans et al., 2010; Westneat et al., 2011; ; Dingemans and Dochtermann, 2013). Thus, personality and activational plasticity are not concepts in opposition one to another; instead, they are logically independent concepts, although one should study them in an integrated fashion, and try to see empirically if there is a correlation between them in any specific case (Dingemans et al., 2010; Jenkins, 2011; Westneat et al., 2011; Dammhahn and Almeling, 2012). Indeed, some studies have shown that increasing levels of boldness are sometimes correlated to decreasing levels of activational plasticity (Briffa et al., 2008; Natarajan et al., 2009; Mathot et al., 2012).

The logical independency between activational plasticity and personality (shown above) only occurs when there is no variation for activational plasticity within the population. It is easy to see that whenever there is a large variation in the slope of linear reaction norms, with positive and negative slopes for different individuals⁸, the ranking of behavioural scores will change with the context, reducing or eliminating across context consistency, and thus weakening the strength of the evidence for

⁷ More precisely, we want to stress that personality is not defined by the mean score of any particular individual, but instead by the distribution of the individual scores (individuals must differ from one another) allied to the consistency of this distribution (ranking) across the contexts/time. This is because personality emerges at the population level: it only appears through the comparison of many individuals.

⁸ More precisely, whenever there is no positive correlation between plasticity – inclination of the RN line – and mean behavioural score – elevation of the centered RN line (Brommer, 2013).

personality. Even when the ranking is not altered, individual variation for activational plasticity can result in an enhancement of the variability of behavioural scores in the new context, as when there is a positive correlation between the elevation and the slope of the individual linear reaction norms (Brommer, 2013). Although this positive correlation introduces the problem of heteroscedasticity in the analysis, it is in itself an interesting biological phenomenon. Indeed, an enhancement of variation for activational plasticity is expected when individuals are submitted to unusual contexts (like urban environments), because these new environments may induce non-adaptive plasticity, freeing previously unexpressed genetic variability (Ghalambor et al., 2007; Badyaev, 2005, 2009).

One last problem is that many studies ignore activational plasticity while measuring personality. This is indeed a very common practice, since many studies even omit the context where the measurements were effectively taken (Bell, 2009). If repeated measures are taken in distinct environments, then activational plasticity will inflate the intra-individual variance term in repeatability analyses, reducing artificially the estimate of repeatability (and thus leading to more frequent false negatives in tests of personality). Alternatively, when distinct individuals are measured in distinct environments, activational plasticity inflates artificially the inter-individual variance term of the repeatability statistic, leading to the opposite outcome: more frequent false positives in tests of personality (Nakagawa and Schielzeth, 2010).

The reasoning above could make sense of some general findings, such as the existence of a higher repeatability for field, as compared to laboratory studies (Bell, 2009). Considering variation in a population for each of the dimensions of the ecological niche, and competition for resources in natural habitats, the individuals in a population will usually establish themselves in patches of diverging qualities (differences in food, retreat, predator, or parasite abundance). For each dimension of the niche, there may be a corresponding reaction norm, so that sampling different individuals in nature will most likely mean sampling different points in a multidimensional reaction norm. This will artificially inflate repeatability measurements, thus explaining the higher repeatability for field, as compared to laboratory studies of personality. Activational plasticity must enter into the experimental design of personality studies, otherwise we will take plasticity for personality and, without making these distinctions clear, the literature will turn out to mix different phenomena, and in the never ending struggle to build unified accounts from heterogeneous databases.

4. Conclusion

Behavioural plasticity and intra-individual variability in behaviour are very well established research traditions, with no conceptual overlap or confusion regarding their major themes. On the other hand, another concept related to (low) within individual variability in the behaviour, stereotypy, overlaps with both plasticity and IIV. Based on an analysis of the usage of the term within the literature we conclude that, in one sense (the one employed in the literature derived from the classic ethology approach), stereotypy is opposed to plasticity. In another sense (the one employed in the animal welfare literature), stereotypy overlaps with IIV. We suggest the literature should abandon the first sense of stereotypy: since low stereotypy always means high plasticity, and vice-versa, one could reasonably use only the concept of plasticity to deal with variations in stereotypy. The second sense of the term stereotypy should be further investigated, so as to clarify its underlying causal structure and, consequently, its relation to other levels of within individual variability.

Activational plasticity (and IIV) is a property that emerges at the level of the individual, while personality is a property that emerges

at the level of the population (consistent across contexts/time ranking of the individuals). Thus these concepts are logically independent from one another, and individuals within a population can show personality despite showing high levels of activational plasticity (Fig. 2). This is not to say that activational plasticity will never affect personality, because whenever individuals in a population differ wildly in relation to activational plasticity, there is also a reduction in the contextual generality aspect of personality. Activational plasticity should always be taken into account in personality studies, since it can artificially augment or reduce repeatabilities when excluded from the experimental design, a statistical property that can explain the usually high repeatabilities found in field, as compared to laboratory studies of personality.

Concepts such as stereotypy, IIV, and behavioural plasticity must be continuously examined not only in relation to their empirical content, but also in relation to the logical articulation between the various components of their definitions, as well as to the distinct usages that potentially emerge within their historical development. Continuous critical assessment of the key concepts in a research area, and of the relationships between concepts, such as the relationship between personality and internal variability, will certainly enable the proposition of more self consistent theories.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2014.09.016>.

References

- Asendorpf, J.B., 1990. The measurement of individual consistency. *Methodika* 4, 1–23.
- Atz, J.W., 1970. The application of the idea of homology to behavior. In: Aronson, L.R., Tobach, E., Lehrman, D.S., Rosenblatt, J.S. (Eds.), *Development and Evolution of Behavior*. W.H. Freeman, San Francisco, CA, pp. 53–74.
- Badyaev, A.V., 2005. Stress-induced variation in evolution: from behavioural plasticity to genetic assimilation. *Proc. Biol. Sci./Royal Soc.* 272, 877–878.
- Badyaev, A., 2009. Evolutionary significance of phenotypic accommodation in novel environments: an empirical test of the Baldwin effect. *Philos. Trans. Royal Soc. Lond., Ser. B: Biol. Sci.* 364, 1125–1141.
- Baerends, G.P., 1958. Comparative methods and the concept of homology in the study of behavior. *Arch. Neerlandaises de Zool. Suppl.* 13, 401–417.
- Bateson, P.P.G., Gluckman, P., 2011. *Plasticity, Robustness, Development and Evolution*. Cambridge University Press.
- Bell, A.M., 2009. The repeatability of behavior: a meta-analysis. *Anim. Behav.* 77, 771–783.
- Betini, G.S., Norris, D.R., 2012. The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. *Anim. Beh.* 83 (1), 137–143.
- Biro, P.A., Adriaenssens, B., 2013. Predictability as a personality trait: consistent differences in intraindividual behavioral variation. *The Am. Nat.* 182 (5), 621–629.
- Bolhuis, J.J., 1991. Mechanisms of avian imprinting: a review. *Biol. Rev.* 66 (4), 303–345.
- Bonabeau, E., Dorigo, M., Theraulaz, G., 1999. *Swarm Intelligence: From Natural to Artificial Systems* (No. 1). Oxford University Press.
- Briffa, M., Rundle, S.D., Fryer, A., 2008. Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proc. Royal Soc. Lond. Ser. B (Biol. Sci.)* 275, 1305–1311.
- Briffa, M., Greenaway, J., 2011. High in situ repeatability of behaviour indicates animal personality in the beadlet anemone *Actinia equina* (Cnidaria). *PLoS One* 6 (7), e21963, <http://dx.doi.org/10.1371/journal.pone.0021963>.
- Briffa, M., 2013. Plastic proteans: reduced predictability in the face of predation risk in hermit crabs. *Biol. Lett.* 9 (5), 20130592.
- Brommer, J.E., 2013. Variation in plasticity of personality traits implies that the ranking of personality measures changes between environmental contexts:

- calculating the cross-environmental correlation. *Behav. Ecol. Sociobiol.* 67, 1709–1718.
- Brown, A.C., 1996. Behavioural plasticity as a key factor in the survival and evolution of the macrofauna on exposed sandy beaches. *Rev. Chil. Historia Na* 69, 469–474.
- Carter, A.J., Heinsohn, R., Goldizen, A.W., Biro, P.A., 2012. Boldness, trappability and sampling bias in wild lizards. *Anim. Behav.* 83 (4), 1051–1058.
- Castellani, S., Adams, P.M., 1981. Acute and chronic phencyclidine effects on locomotor activity, stereotypy and ataxia in rats. *Eur. J. Pharmacol.* 73 (2), 143–154.
- Castellanos, F.X., Sonuga-Barke, E.J., Scheres, A., Di Martino, A., Hyde, C., Walters, J.R., 2005. Varieties of attention-deficit/hyperactivity disorder-related intra-individual variability. *Biol. Psychiatry* 57 (11), 1416–1423.
- Crispo, E., Chapman, L.J., 2010. Geographic variation in phenotypic plasticity in response to dissolved oxygen in an African cichlid fish. *J. Evol. Biol.* 23, 2091–2103.
- Dammhahn, M., Almeling, L., 2012. Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. *Anim. Beh.* 84 (5), 1131–1139.
- Dantzer, R., 1986. Behavioural, physiological and functional aspects of stereotyped behaviour. A review and a reinterpretation. *J. Anim. Sci.* 62, 1776–1782.
- David, M., Auclair, Y., Cézilly, F., 2012. Assessing short- and long-term repeatability and stability of personality in captive zebra finches using longitudinal data. *Ethology* 118, 932–942.
- Dingemanse, N.J., Dochtermann, N.A., 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J. Anim. Ecol.* 82 (1), 39–54.
- Dingemanse, N.J., Bouwman, K.M., van de Pol, M., van Overveld, T., Patrick, S.C., Matthysen, E., Quinn, J.L., 2012. Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. *J. Anim. Ecol.* 81 (1), 116–126.
- Dingemanse, N.J., Kazem, A.J.N., Réale, D., Wright, J., 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* 25 (2), 81–89.
- Dingemanse, N.J., Wolf, M., 2013. Between-individual differences in behavioural plasticity within populations: causes and consequences. *Anim. Behav.* 85, 1031–1039.
- Duncan, I.J.H., Wood-Gush, D.G.M., 1972. Thwarting of feeding behaviour in the domestic fowl. *Anim. Behav.* 20, 444–451.
- Edwards, M.J., Lang, A.E., Bhatia, K.P., 2012. Stereotypies: a critical appraisal and suggestion of a clinically useful definition. *Mov. Disord.* 27 (2), 179–185.
- Eberhard, W.G., 1990. Imprecision in the behavior of larval fungus gnats and the origin of new behavior patterns in animals. *J. Insect Behav.* 3, 327–357.
- Eberhard, W.G., 2000. Breaking the mold: behavioral imprecision and evolutionary innovation in *Wendilgarda* spiders (Araneae, Theridiosomatidae). *Ethol. Ecol. Evol.* 12, 223–235.
- Eberhard, W.G., 2007. Miniaturized orb-weaving spiders: behavioural precision is not limited by small size. *Proc. Biol. Sci./R. Soc.* 274, 2203–2209.
- Fuller, T., Sarkar, S., Crews, D., 2005. The use of norms of reaction to analyze genotypic and environmental influences on behavior in mice and rats. *Neurosci. Biobehav. Rev.* 29 (3), 445–456.
- Garrigues, P.J.M., Petersen, A.F., de Roquefeuil, G., Gourdon, N., 1982. On behavioural similarities between animal and human stereotypies. *J. Appl. Anim. Ethol.* 2, 197–198.
- Ghalambor, C.K., McKay, J.K., Carroll, S.P., Reznick, D.N., 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.* 21, 394–407.
- Garner, J.P., 2005. Stereotypies and other abnormal repetitive behaviours: potential impact on validity, reliability, and replicability of scientific outcomes. *ILAR J.* 46 (2), 106–117.
- Gordon, D.M., Dektar, K.N., Pinter-Wollman, N., 2013. Harvester ant colony variation in foraging activity and response to humidity. *PLoS ONE* 8 (5), e63363, <http://dx.doi.org/10.1371/journal.pone.0063363>.
- Gosling, S.D., 2001. From mice to men: what can we learn about personality from animal research. *Psychol. Bull.* 127, 45–86.
- Greene, H.W., 1994. Homology and behavioural repertoires. In: Hall, B.K. (Ed.), *Homology: the Hierarchical Basis of Comparative Biology*. Academic Press, San Diego, CA, pp. 369–391.
- Griffith, L.C., Verselis, L.M., Aitken, K.M., Kyriacou, C.P., Danho, W., Greenspan, R.J., 1993. Inhibition of calcium/calmodulin-dependent protein kinase in *Drosophila* disrupts behavioral plasticity. *Neuron* 10 (3), 501–509.
- Herde, A., Eccard, J.A., 2013. Consistency in boldness, activity and exploration at different stages of life. *BMC Ecol.* 13 (49), 1–10.
- Hodos, W., 1976. The concept of homology and the evolution of behavior. In: Master-ton, R.B., Hodos, W., Jerison, H. (Eds.), *Evolution, Brain, and Behavior: Persistent Problems*. Lawrence Erlbaum Associates, Publishers, Hillsdale, NJ, pp. 153–167.
- Japyassú, H.F., Ades, C., 1998. From complete orb to semi-orb webs: developmental transitions in the web of *Nephilengys cruentata* (Araneae: Tetragnathidae). *Behaviour*, 931–956.
- Japyassú, H.F., Caires, R.A., 2008. Hunting tactics in a cobweb spider (Araneae-Theridiidae) and the evolution of behavioral plasticity. *J. Insect Behav.* 21 (4), 258–284.
- Japyassú, H.F., Machado, F.D.A., 2010. Coding behavioural data for cladistic analysis: using dynamic homology without parsimony. *Cladistics* 26 (6), 625–642.
- Jenkins, S.H., 2011. Sex differences in repeatability of food-hoarding behaviour of kangaroo rats. *Anim. Behav.* 81 (6), 1155–1162.
- Kluen, E., Broomer, J.E., 2013. Context-specific repeatability of personality traits in a wild bird: a reaction-norm perspective. *Behav. Ecol.* 24 (3), 650–658.
- Lauder, G.V., 1986. Homology, analogy, and the evolution of behavior. In: Nitecki, M.H., Kitchell, J.A. (Eds.), *Evolution of Animal Behavior: Paleontological and Field Approaches*. Oxford University Press, New York, pp. 9–40.
- Laviola, G., Terranova, M.L., 1998. The developmental psychobiology of behavioural plasticity in mice: the role of social experiences in the family unit. *Neurosci. Biobehav. Rev.* 23 (2), 197–213.
- Legendre, F., Robillard, T., Desutter-Grandcolas, L.A.U.R.E., Whiting, M.F., Grandcolas, P., 2008. Phylogenetic analysis of non-stereotyped behavioural sequences with a successive event-pairing method. *Biol. J. Linn. Soc.* 94 (4), 853–867.
- Lorenz, K.Z., 1981. *The Foundations of Ethology*. Springer-Verlag, Wien.
- Lorenz, K.Z., 1966. Evolution of ritualization in the biological and cultural spheres. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* 251 (772), 273–284.
- Manning, A., Dawkins, M.S., 2012. *An Introduction to Animal Behaviour* (6th edition). Cambridge University Press, Cambridge.
- Mason, G.J., 1991. Stereotypies: a critical review. *Anim. Behav.* 41, 1015.
- Mason, G.J., Latham, N.R., 2004. Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? *Anim. Welf.* 13, S57–S69.
- Mathot, K.J., Wright, J., Kempenaers, B., Dingemanse, N.J., 2012. Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *OIKOS* 121 (7), 1009–1020.
- Matthews, C.E., Ainsworth, B.E., Thompson, R.W., Bassett Jr., D.R., 2002. Sources of variance in daily physical activity levels as measured by an accelerometer. *Med. Sci. Sports Exerc.* 34 (8), 1376–1381.
- Moczek, A.P., Sultan, S., Foster, S., Ledón-Rettig, C., Dworkin, I., Nijhout, H.F., Pfennig, D.W., 2011. The role of developmental plasticity in evolutionary innovation. *Proc. Royal Soc. B: Biol. Sci.*, rspb20110971.
- Nakagawa, S., Schielzeth, H., 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol. Rev. Camb. Philos. Soc.* 85 (4), 935–956.
- Natarajan, D., et al., 2009. Delineation of violence from functional aggression in mice: an ethological approach. *Behav. Gen.* 39, 73–90.
- Neff, S., et al., 2004. Behavioral syndromes versus Darwinian algorithms. *Trends Ecol. Evol.* 19 (12), 621–622.
- Penna-Gonçalves, V., Garcia, C.R.M., Japyassú, H.F., 2008. Homology in a context dependent predatory behavior in spiders (Araneae). *J. Arachnol.* 36 (2), 352–359.
- Piersma, T., Drent, J., 2003. Phenotypic flexibility and the evolution of organismal design. *Trends Ecol. Evol.* 18, 228–233.
- Randrup, A., Munkvad, I., 1967. Stereotyped activities produced by amphetamine in several animal species and man. *Psychopharmacologia* 11 (4), 300–310.
- Réale, D., Reader, S., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating temperament in ecology and evolutionary biology. *Biol. Rev.* 82, 291–318.
- Réale, D., Dingemanse, N.J., 2010. Personality and individual social specialisation. In: Szekely, T., et al. (Eds.), *Social Behaviour: Genes, Ecology and Evolution*. Cambridge University Press, pp. 417–441.
- Schradin, C., Lindholm, A.K., Johannesen, J.E.S., Schoepf, I., Yuen, C.H., Koenig, B., Pflay, N., 2012. Social flexibility and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*). *Mol. Ecol.* 21 (3), 541–553.
- Schradin, C., 2013. Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Philos. Trans. Royal Soc., Ser. B: Biol. Sci.* 368 (1618), 20120346.
- Sih, A., Bell, A.M., Johnson, C., 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* 19 (7), 372–378.
- Sih, A., Bell, A.M., 2008. Insights for behavioral ecology from behavioral syndromes. *Adv. Study Behav.* 38, 227–281.
- Sih, A., Cote, J., Evans, M., Fogarty, S., Pruitt, J., 2012. Ecological implications of behavioural syndromes. *Ecol. Lett.* 15 (3), 278–289.
- Slagsvold, T., Wiebe, K.L., 2011. Social learning in birds and its role in shaping a foraging niche. *Philos. Trans. Royal Soc., Ser. B: Biol. Sci.* 366 (1567), 969–977.
- Snell-Rood, E.C., 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim. Behav.* 85 (5), 1004–1011.
- Sol, D., 2009. The cognitive-buffer hypothesis for the evolution of large brains. In: Dukas, R., Ratcliffe, J.M. (Eds.), *Cognitive Ecology II*. University of Chicago Press, pp. 111–134.
- Stamps, J., Groothuis, T.G.G., 2010. The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.* 85, 301–325.
- Stamps, J.A., Briffa, M., Biro, P.A., 2012. Unpredictable animals: individual differences in intraindividual variability (IIV). *Anim. Behav.* 83 (6), 1325–1334.
- Toscano, B.J., Gatto, J., Griffen, B.D., 2014. Effect of predation threat on repeatability of individual crab behavior revealed by mark-recapture. *Behav. Ecol. Sociobiol.* 68 (3), 519–527.
- Thelen, E., 1979. Rhythmic stereotypies in normal human infants. *Anim. Behav.* 27, 699–715.
- Van Geert, P., Van Dijk, M., 2002. Focus on variability: new tools to study intra-individual variability in developmental data. *Infant Behav. Dev.* 25 (4), 340–374.
- Westneat, D.F., Hatch, M.I., Wetzel, D.P., Ensminger, A.L., 2011. Individual Variation in Parental Care Reaction Norms: Integration of Personality and Plasticity. *Am. Nat.* 178 (5), 652–667.
- Wenzel, J.W., 1992. Behavioral homology and phylogeny. *Annu. Rev. Ecol. System.* 23, 361–381.
- West-Eberhard, M.J., 2003. *Developmental Plasticity and Evolution*. Oxford University Press.
- Wiepkema, P.R., 1981. On the identity and significance of disturbed behaviour in vertebrates. In: Bessei, W. (Ed.), *Disturbed Behaviour in Farm Animals*. Verlag Eugen Ulmer, Stuttgart, pp. 7–17.
- Wolf, F.P.H., 1968. Stereotypic behaviour and development. *Can. Psychol.* 9, 474–484.

Glossary

Term: Definition

Behavioural plasticity: Expression of different behavioural phenotypes by one same individual/genotype, under distinct environments or behavioural domains (such as territorial defence versus courtship). The diverging behaviours can be a response to context variability in the present time, and in this case we are talking about activational plasticity (behavioural flexibility). The diverging behaviours can also be a response to context variability in the past history of the individual/genotype, and in this case we are talking about developmental plasticity. See the overview of internal variability, in the text, for further discussion.

Consistency: Consistency refers to stability of inter-individual differences in behavioural scores, meaning that the ranking of the behavioural scores of the individuals is maintained across repeated measurements of these same individuals. One can repeat the measurements in one same context (at different time points), or else one can repeat the measurements in different contexts.

Imprecision: A synonym of IIV. To our knowledge, the term was first used by Eberhard (1990, 2000), meaning intra individual variability that is generated by noise in the functioning of the nervous system. We prefer to use IIV because imprecision potentially implies that high levels of variability are maladaptive, whereas there is experimental evidence that high levels of IIV might be adaptive in some situations (Briffa, 2013).

Internal variability: Internal variability refers to the behavioural variability within one individual. It refers both to variability due to changes in the context (behavioural plasticity) and/or variability within the same context, assessed at different time points (intra individual variability).

Intra individual variability (IIV): IIV refers to unpredictable, reversible, and short term changes in the behaviour of one same individual, when she/he is tested repeatedly in one same context (Stamps et al., 2012).

Personality: Consistent inter-individual differences across context and/or time. When the behavioural consistency refers to stability of inter-individual differences across contexts, we are talking about context generality. When the behavioural consistency refers to stability of inter-individual differences through time (in the same context), we are talking about differential consistency (Stamps and Groothuis, 2010).

Repeatability: Repeatability is a standardised measure of the proportion of behavioural variability that is due to differences between the individuals in the sample (inter-individual differences). Different individuals must be assessed repeatedly to estimate the variability among and within individuals (Bell, 2009; Dingemans et al., 2010).

Stability: Stability refers to the measurement of one single individual, without comparison with the scores of other individuals in the study. Thus it is logically unrelated to inter-individual differences (ranking of individuals, see discussion about the relationship between personality and internal variability). A behaviour is considered stable if it is repeated in the same way under different contexts, or at different time points (within the same context). High stability across contexts means low activational plasticity, whereas high stability through time means low intra individual variability. There are several stability indexes, such as the individual stability statistic (Asendorpf, 1990) or the coefficient of relative plasticity (Réale and Dingemans, 2010).

Stereotypy: There is not consensual definition in the literature (see overview of internal variability, in the text), but we suggest that the core of the concept of stereotypy refers to the idea of behaviour that is repeated in the same manner in the same context, as in the case of caged animals repeating routines day to day. This should be distinguished from the repetition of the same behaviour in distinct contexts, because, in this case, stereotypy overlaps with activational plasticity.