



Personality and individual differences in plasticity

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In the last few years, investigators have documented individual differences in many different types of behavioral plasticity. Of particular interest are individual differences in the temporal plasticity of personality traits over extended (ontogenetic) periods of time, because of the relevance of these data to models of behavioral development. We discuss recent empirical studies of the temporal consistency of personality over ontogeny, and models that make contrasting predictions about individual differences in the developmental trajectories of behavioral traits. In addition, we consider recent advances in studies of relationships between personality traits and particular types of behavioral plasticity, including statistical methods which facilitate analyses of relationships between personality traits, contextual plasticity, temporal plasticity and intraindividual variability, and empirical tests of predicted relationships between personality traits and other types of behavioral plasticity (flexibility, learning rates). As the field of animal personality and behavioral plasticity moves from a largely descriptive to a predictive phase, we suggest that there is ample room for empirical tests of recent models that predict individual differences in behavioral developmental trajectories, and for the development of new formal models that make strong predictions about relationships between personality traits and specific types of behavioral plasticity.

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In behavioral ecology, the term ‘personality’ typically refers to individual differences in a given type of behavior that are maintained across contexts and/or across time [1,2]. For instance, ‘aggressiveness’ would be considered to be a personality trait if individuals that attacked a mirror at a high rate in their home cage also quickly

attacked a standard opponent in a neutral arena, and/or if individual differences in the scores in both assays were maintained over time. These days, most students of animal personality attempt to quantify the extent to which individual differences in behavior are maintained across time, but less frequently ask whether individual differences in a presumed personality trait are consistent if the same trait is measured in different contexts [but see 3,4]. Indeed, personality is often scored based on just one assay per trait, a practice which can contribute to the incorrect labeling of personality traits, and to findings which may not extrapolate to the natural settings of interest to behavioral ecologists [5,6].

Behavioral ‘plasticity’ refers to variation in scores for a given behavior as a function of variation in internal or external stimuli. In the case of behavior, the term ‘plasticity’ has been used to describe many different phenomena [7**]. Familiar examples include variation in behavior as a function of the external stimuli that surround the individual when the behavior is expressed (contextual plasticity) and variation in behavior in response to stimuli or experiences that occurred in the near to distant past (developmental plasticity, which includes the many types of learning [2,8]). Plasticity can also describe variation in behavior as a function of variation in internal stimuli, for example, intraindividual variability [9], apparently random within-individual variation in the behavior expressed in a given context that has been attributed to stochastic variation in brain activity [10,11]. In addition, the term plasticity has also been used to simply describe how behavior changes as a function of age or time (temporal plasticity), without attributing such changes to specific causal agents. In recent years, investigators have documented individual differences in all of these types of behavioral plasticity [7**], laying the foundation for current and future studies of the proximate causes and consequences of individual differences in behavioral plasticities.

Individual differences in behavior: change over time

Most recent studies of animal personality include analyses of the extent to which individual differences in behavior are maintained over time (repeatability in the broad sense of the term). Currently, broad-sense repeatability is typically assessed by the statistic R (repeatability in the narrow sense), calculated as the proportion of variance that is accounted for by individual differences in mean values [12,13]. In part, this emphasis on temporal consistency can be traced to the fact that temporal consistency is one of the basic criteria for personality (see

Glossary

Broad-sense repeatability: extent to which individual differences in scores for a given trait are maintained over time.

Context: external stimuli that surround an individual when it expresses behavior.

Contextual plasticity: change in an individual's score for a given trait as a function of a given context.

Developmental plasticity: change in behavior in response to stimuli or experiences that occurred in the recent to distant past; includes learning.

Developmental trajectory: change in an individual's score for a given trait as a function of age; temporal plasticity over extended (ontogenetic) periods of time.

Flexibility: change in behavior in response to a change in a well-learned stimulus situation.

Intraindividual variability: within-individual variability in behavior, after controlling for variability as a function of context and for systematic changes in behavior as a function of time.

R (narrow-sense repeatability): a statistic that is often used to estimate broad-sense repeatability.

Temporal plasticity: change in an individual's score for a given trait as a function of time.

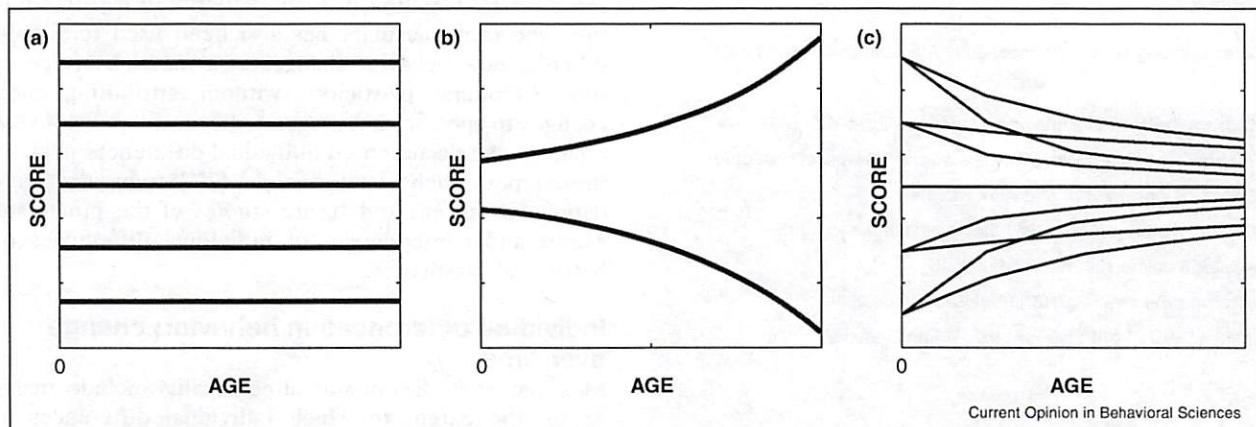
above). However, a more important reason for studying broad-sense repeatability, especially over extended (ontogenetic) periods of time, is the light it can shed on the development of personality and individual differences in plasticity.

The simplest 'null' model of personality assumes that differences in behavior observed in neonates are maintained until death (Figure 1a) [14]. This pattern would imply that individual differences in behavior are established by the effects of genes, parental effects and/or inherited epigenetic factors on the nervous system at

birth or hatching, and are maintained thereafter. In contrast, deviations from this pattern indicate that the individuals within the sample had different developmental trajectories, possibly as a result of differences in post-natal experiences, and/or individual differences in developmental plasticity (responses to the same post-natal experiences).

The developmental implications of age-dependent changes in broad-sense repeatability have encouraged several lines of inquiry. The most basic question is the extent to which individual differences in behavior are maintained across important life-history transitions, or over extended stretches of ontogeny [14,15]. For instance, recent studies of two beetle species indicated that although behavior was temporally consistent in juveniles, adults, or both, individual differences in trait values were not maintained across metamorphosis [16,17]. Recent long-term studies of the temporal consistency of behavior in vertebrates have yielded conflicting results. Zsolt Garamszegi *et al.* [18] measured the behavior of flycatchers, *Ficedula albicollis*, in the field, and reported that the values of R for most traits were low within a given year, and were essentially zero when estimated across years. In contrast, a field study of European roe deer, *Capreolus capreolus*, [19] did not detect any significant differences in the R values of juveniles and adults, or when R was estimated across short versus long time intervals. Similarly, a long-term laboratory study of several different types of behavior in zebra finches, *Taeniopygia guttata*, failed to detect differences in the values of R at different life stages [20].

Figure 1



Predictions about individual differences in developmental trajectories for behavior. A null model (a) assumes that individual differences in mean scores (personality) expressed soon after birth or hatching will be maintained throughout the lifetime. Other models make opposing predictions about individual differences in the temporal plasticity of behavior over ontogenetic periods of time. (b) One set of models, based on positive feedback loops between behavior and state variables [26**], predicts that different individuals begin life with similar scores, but that their scores will gradually diverge from one another as they age (a 'fanning out' pattern). (c) Other models, based on negative feedback loops between behavior and state variables [26**] or assumptions about information-updating across ontogeny [27] predict that individuals begin life with different scores, but that their scores will gradually converge with one another as they age (a 'fanning in' pattern). The latter two sets of models predict that developmental trajectories will be non-linear, that is, that within individuals, behavior will change more rapidly at some ages than others.

More important, a developmental perspective has encouraged renewed interest among theoreticians in the adaptive significance of individual differences in developmental trajectories. For instance, classic studies of behavioral developmental plasticity consider situations in which different experiences early in life (i.e. soon after birth or hatching) encourage divergent developmental trajectories into and through adulthood [21]. Recently Nettle and Bateson [22**] have pointed out there are actually two different reasons why early experience might encourage adaptive differences in behavioral developmental trajectories. The first is the traditional explanation (conditions early in life provide information about conditions later in life); the second is that early conditions have long-lasting effects on an individual's somatic state, and that different behaviors are optimal for individuals with different somatic states. For instance, food restriction early in life might have long-lasting effects on an individual's body size, and hence encourage the development of adult behavior appropriate for smaller individuals. Although there is abundant evidence that early experience can affect the behavior expressed later in life [for recent examples see 23–25], thus far no one has used the framework outlined by Nettle and Bateson to investigate the adaptive significance of these patterns.

The ways that information and somatic state might contribute to individual differences in developmental trajectories have also been the subject of recent formal models of behavioral development. One set of models considers positive or negative feedbacks between an individual's somatic or information state and its behavior, and shows how such feedbacks might contribute to the gradual divergence or convergence of behavioral trajectories across individuals [26**]. For instance, slight (possibly random) differences in state early in life, in conjunction with processes such as winner-loser effects or niche specialization, might result in different experiences for different individuals, and hence encourage divergence, or a 'fanning out', of developmental trajectories over ontogeny (Figure 1b). This perspective is noteworthy because it can explain the emergence of adaptive personalities over time without the need to assume genetic, physiological or life history differences at the outset.

A second set of models considers how changes in an individual's information state over development can affect its developmental trajectory [27]. Some of these models predict a 'fanning in' of developmental trajectories across ontogeny, as individuals who began life with different estimates of the state of the world (i.e. estimates provided by genes, parental effects and/or inherited epigenetic factors) gradually converge on the estimate indicated by the cues from a shared rearing environment [28] (Figure 1c). Such models not only suggest that personality will be expressed early in life, but that it will be more pronounced early than later in life, in contrast to the

positive feedback models discussed above, which predict the opposite.

To date, several investigators have documented 'fanning in' patterns for behavioral developmental trajectories in animals. One field study found that scores for both aggressiveness and activity converged between the juvenile and yearling life-stages in red squirrels (*Tamiasciurus hudsonicus*) [29], while another reported convergence in scores for stress-responsiveness for free-living house sparrows (*Passer domesticus*), that were sampled in their first and second years [30]. Two laboratory studies of the development of boldness in the mangrove killifish (*Kryptolebias marmoratus*) and pigtailed macaques (*Macaca nemestrina*) also provided results consistent with 'fanning in' patterns: in both cases, scores for boldness significantly differed at birth, but gradually converged on similar values over the course of the juvenile period [31,32]. In contrast, laboratory-reared crayfish (*Cherax destructor*) exhibited increases in age-specific values of *R* for boldness from day 1 to day 72, suggesting that their individual trajectories might have been 'fanning out' over this period [33]. We suspect that additional data suitable for investigating this topic may already be available in the files of researchers who have conducted long-term, longitudinal studies of behavioral traits.

Relationships between personality traits and plasticity

Recent methodological advances have facilitated empirical studies of relationships across individuals between differences in their scores for a given personality trait and certain aspects of the plasticity of that trait, including temporal plasticity, contextual plasticity and intraindividual variability (see Box 1). However, students of animal personality have long been interested in correlations between personality traits and other types of behavioral plasticity. For instance, Verbeek *et al.* [34] reported that in great tits (*Parus major*), fast-exploring males responded more slowly to a change in a well-learned location of a food reward (i.e. were less flexible) than slow explorers. Since the 1990s, investigators have advanced hypotheses that predict relationships between personality and a wide range of behavioral plasticities. These range from suggestions that in tit species, fast explorers might be generally less responsive to external stimuli than slow explorers [35*–37], to hypotheses that predict relationships between personality traits and various types of behavioral plasticities for a broader array of taxa [38,39].

Although a growing number of empiricists have begun to test hypotheses about relationships between personality and plasticity, at present support for them is sparse and equivocal. Indeed, one of the most oft-cited relationships (between exploratory speed and flexibility in great tits) has not been confirmed in most studies on this topic; similarly contradictory results have been obtained in tests

Box 1 Using mixed effects models to study personality and individual differences in plasticity

Robust methods for studying individual differences in behavior over time and across contexts have been available to empiricists for some time. Using a single data set, one can use a mixed model (often termed random regression) to test for individual differences in levels of behavior, to determine whether those differences are maintained over time (individual differences in temporal plasticity), whether they are maintained across different contexts (individual differences in contextual plasticity), and whether any correlations exist between these three levels of variation [44–46]. In the last few years, empiricists have used these models to simultaneously quantify individual differences in mean levels of behavior, temporal plasticity, contextual plasticity, and in some cases the among-individual correlations between two or more of these random effect variances [33,47–50]. More recently, doubly hierarchical mixed models which enable flexible modeling of residual variation have been added to the statistical toolbox, making it possible to test for, among other things, individual differences in intraindividual variability, that is, within-individual variability in the behavior in a given context, after controlling for systematic changes in behavior over time [47,48,51*,52].

Although theoreticians and empiricists have become increasingly interested in the temporal consistency of behavior over extended (ontogenetic) periods of time (see text), many empirical studies of this phenomenon do not currently employ the methods described above. Instead, they often rely on pair-wise comparisons of R at different times, ages or life-stages (e.g. R for juveniles vs. R for sub-adults), compute R separately for overlapping time intervals, rely on relatively few subjects, and/or are based on relatively few assays (often only two) at each age or life-stage. Together, these practices have inferential, power and precision limitations that constrain what can be learned from the data [13,53,54]. In addition, using the traditional version of R to make inferences about behavioral stability over a given period of time is problematic when temporal plasticity varies among the subjects over that period (discussed by Biro and Stamps [13]). Instead of separately computing values of R for different time periods, we encourage using mixed models to analyze the temporal consistency of behavior over the long term, using all of the data in a single model.

of predicted relationships between exploratory speed or aggressiveness and flexibility in other animals [7**].

Similarly, predictions about relationships between personality traits and learning rates have met with limited success. For instance, Sih and Del Giudice [39] suggested that as a result of speed-accuracy tradeoffs, individuals with fast exploratory speeds might learn new activity-based tasks more quickly, but learn new avoidance tasks and reversal tasks more slowly, than slow explorers. However, empiricists have had difficulty confirming these predictions [7**]. Recent examples include a study of Florida scrub jays (*Aphelocoma coerulescens*) which detected no relationships between acquisition rates for a new associative learning task or reversal learning and exploratory behavior [40], and a study of mallards (*Anas platyrhynchos*) in which fast explorers learned to a new spatial learning task more slowly than slow explorers [41]. In a recent review, Griffin *et al.* [42*] suggested that such results may not be atypical, and discussed a number of reasons why formulating testable predictions about how

cognition might be related to personality may be more difficult than currently realized.

Finally, we note that animal behaviorists are not alone in having difficulty devising hypotheses that successfully predict relationships between personality and plasticity. For instance, psychologists have suggested that individual differences in neural reactivity to stimuli in the external environment might underlie individual differences in personality traits in humans, but empirical evidence on this point has been contradictory [43]. At this point, current hypotheses about relationships between personality and plasticity are not as well supported as one might assume from a cursory reading of the literature, leaving room for further theoretical and empirical research on this topic.

Conclusions

We know much more about animal personality and individual differences in behavioral plasticities than was the case just a few years ago, but perhaps not as much as we think we do. On the one hand, there is now abundant empirical evidence of personality and of individual differences in many different types of behavioral plasticities in animals, and growing interest among theoreticians and empiricists in the temporal consistency of individual differences in behavior over extended (ontogenetic) periods of time. On the other hand, several predictions about relationships between personality and some types of behavioral plasticity (flexibility, learning rates) have not held up well to empirical scrutiny. We suggest that the field could benefit from new formal models that make strong predictions about relationships between particular personality traits and specific types of behavioral plasticities, especially given the availability of sophisticated methodological and statistical tools that could be used to test those predictions.

Conflict of interest

Nothing declared.

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