Interaction between animal personality and animal cognition

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Abstract The study of animal personality has attracted considerable attention, as it has revealed a number of similarities in personality between humans and several nonhuman species. At the same time the adaptive value and evolutionary maintenance of different personalities are the subject of debate. Since Pavlov’s work on dogs, students of comparative cognition have been aware that animals display vast individual differences on cognitive tasks, and that these differences may not be entirely accounted for differences in cognitive abilities. Here, we argue that personality is an important source of variation that may affect cognitive performance and we hypothesise mutual influences between personality and cognition across an individual’s lifespan. In particular, we suggest that: 1) personality profiles may be markers of different cognitive styles; 2) success or failure in cognitive tasks could affect different personalities differently; 3) ontogenetic changes of personality profiles could be reflected in changes in cognitive performance. The study of such interplay has implications in animal welfare as well as in neuroscience and in translational medicine [Current Zoology 57 (4): 491–498, 2011].

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1 Animal Personalities

Personality refers to stable, long-term behavioural, emotional, and physiological differences in suites of traits among individuals of the same species. A plethora of nonhuman studies, particularly in the last decade, has shown in more than 100 species ranging from insects to mammals that individuals of the same species, independent from sex or age, differ profoundly from each other in their behaviour and underlying physiology, even under standardized laboratory conditions (Carere et al., 2010). Most of this variation is non-random and is consistent across contexts and time. For example, in birds, fish and rodents some individuals are more aggressive than others and the former differ profoundly from each other in their behaviour and underlying physiology, even independent of sex or age. (Carere et al., 2010). These individual differences often become conspicuous and easily measurable when individuals have to cope with challenges in their social and non-social environments (Broom, 2001; Koolhaas et al., 2010; Carere et al., 2010). In the past, such differences were rarely viewed as an expression of biologically meaningful variation; instead, they were often interpreted as either the consequence of inaccurate measurements or non-adaptive variation around an adaptive mean (Wilson, 1998). By contrast, in humans such variation is interpreted as reflecting consistent individual variation in personality or temperament, the science of human personality being already more than one century old. Personality characteristics in humans have a significant heritable and ontogenetic component and they have been shown to predict important life outcomes in health, social and reproductive functioning (Nettle, 2005).

Historically, behaviours that are coherently organized in this way have been referred to in the nonhuman literature as behavioural syndromes, coping styles, predispositions, individualities, or profiles. More recently, these concepts have been shown to be directly comparable to the categories used to describe human personalities (Gosling, 2001; Gosling et al., 2003; Sih et al., 2004; Groothuis and Carere, 2005). Moreover, it appears that the assigning of different personality types to animals is done with approximately the same reliability and validity as is typical in studies of human personality.
Reliability refers to the consistency of measurement across different raters or within the same rater across repeated measurements, as assessed via correlation. In studies of human personality reliabilities tend to be in the range of 0.70 to 0.85. In a review of studies of animal personality, reliabilities averaged 0.73 (Gosling, 2001). The second requirement for the accurate assessment of personality is validity, defined as the extent to which a given measure taps the construct that it is assumed to be marking. Validity is a problem in studies of human personality inasmuch as it is difficult to establish the benchmark measure of a given construct, such as aggression or dominance, against which the validity of other measures can be judged. In the study of personality validity correlations are uniformly lower than reliabilities, but validities in both human and animal studies average about 0.30 to 0.50 (Locurto, 2007).

A major challenge for behavioural biologists has been to understand the origin of variation in personalities and the mechanisms responsible for its maintenance. The study of animal personality is now at the forefront of contemporary behavioural biology especially because of its integrative and holistic approach (Sih et al., 2004) and also because of its strong appeal to public opinion and mass media (e.g. Dall, 2004; Pennisi, 2005). The study of animal personalities is important for several reasons: (i) it is conducted with an interdisciplinary approach that integrates proximate mechanisms with ecology and evolution; (ii) it has implications for evolutionary theory because different but correlated behaviors do not evolve in isolation, but as an integrated pattern that can generate tradeoffs and boundaries to unlimited plasticity (Sih et al., 2004; Wolf et al., 2007; Wolf et al., 2008); (iii) it has to be taken into account in field and laboratory studies because different personality types may react differently to similar environments or experimental treatments; (iv) individuals may show differential vulnerability to stress and artificial housing conditions, leading to differences in welfare; (v) a better knowledge of the mechanisms underlying animal personalities and of the evolutionary causes and consequences of personalities may be extrapolated to humans and help to provide a better understanding of the nature and evolution of human personalities. For instance, studies in birds have shown not only that individual differences in behaviour are heritable, but also that they are systematically related to fitness, with different optima occurring under different environmental conditions (Dingemanse and Rèale, 2005, Rèale et al., 2007). For humans, such a demonstration is necessarily more indirect, both for methodological reasons and because of the profound differences between the contemporary environments in which humans live and that typical of our evolutionary history (Nettle, 2005).

It is finally crucial, though not in the aims of this paper, to highlight the crucial role of early experience in shaping and eventually determining personalities. It is clear, also from recent experimental evidence, that similar or differential fitness might also be achieved by different developmental histories and trajectories affected by environmental conditions early in ontogeny, both social and non social (Caro and Bateson, 1986; Carere and Eens, 2005; Carere et al., 2005; Stamps and Groothuis, 2010). We shall argue here that also cognitive experiences might affect personality.

2 Animal Cognition and Animal Personality: Pavlov’s Foundation

Pavlov (1906; 1941) with his seminal studies on dogs laid a foundation for the study of associative processes and developed the first systematic typology for personality in a nonhuman species. Pavlov identified four personality types as examples from a larger set of personality profiles (Table 1). Pavlov’s typology derived from three properties of the nervous system: Force, Equilibrium, and Mobility (Locurto, 2007). The resulting mixture of these three properties resulted in the four personality types. This system bears similarities to the ancient Greek system of personality types based upon the four humours: Choleric (Excitable), Sanguine (Lively), Phlegmatic (Quiet), and Melancholic (Inhibited).

<table>
<thead>
<tr>
<th>Force (ability to endure external stimulation)</th>
<th>Equilibrium (balance between Excitation (E) and inhibition (I))</th>
<th>Mobility (Flexibility in alternating between excitation and inhibition)</th>
<th>Final Type (Personality designation)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Strong</td>
<td><strong>E &gt; I</strong></td>
<td>Slow</td>
<td>Excitable</td>
</tr>
<tr>
<td>Weak</td>
<td><strong>E = I</strong></td>
<td>Rapid</td>
<td>Lively</td>
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<td><strong>E = I</strong></td>
<td>Moderate</td>
<td>Quiet</td>
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<td></td>
<td><strong>I &gt; E</strong></td>
<td>Slow</td>
<td>Inhibited</td>
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Table 1  Pavlov’s typology (modified from Locurto, 2007): Property of nervous system
Pavlov’s work on personality types in dogs has encouraged a considerable amount of additional work on this topic. In a recent review Jones and Gosling (2005) noted that between 1934 and 2004 51 empirical studies of personality in dogs had been published. Pavlov’s typology was also influential in the later development of Eysenck’s (1967) personality theory, which in its original form captured different personality types within an orthogonal two dimension system consisting of neuroticism/emotional stability on one dimension and extraversion/introversion. Eysenck later added a third dimension, psychoticism, after extensive studies of human psychiatric patients.

Pavlov was convinced that these personality types were markers for different styles of associative learning (Gray, 1964). The Excitable type, for example, showed signs of strong excitatory conditioning, but a limited ability for the acquisition of inhibitory connections. As a consequence, excitatory learning was rapid in these animals but learning that engaged inhibitory processes was often slow. The Lively type was the most balanced of the four types with respect to the transition between excitation and inhibition and these animals displayed rapid associative learning. Pavlov’s Quiet type exhibited consistent but slow learning, the result of low mobility between excitation and inhibition. The weak type, the only one in which inhibition dominated excitation, as might be expected, exhibited slow and difficult excitatory conditioning. These animals possessed little tolerance for intense stimulation and were easily thrown into what Pavlov termed protective inhibition to prevent cortical damage.

As previously outlined, it is by now well established that there are indeed identifiable personality types in animals, often comparable to those found in studies of human personality. Additionally, a number of neuroendocrine correlates of personality types have been identified in animals that appear to correspond to those identified in humans (Koolhaas et al., 1999; Koolhaas et al., 2010; Carere et al., 2010). A question of special importance to researchers of animal cognition is whether an understanding of these types and their neurobiological correlates is relevant for understanding cognition. On the other side, researchers of animal personalities, interested in the proximate basis, the origin, and evolutionary maintenance of personality types, would like to know the degree of covariation between cognitive abilities and the individual profiles (e.g. Sih et al., 2004). Personalities may also shape experience and influence themselves cognition, but to our knowledge there is no animal study directly addressing this question. Interestingly, the relationship between behavioural types (e.g. boldness) and speed of learning varies, depending apparently on the personality and the type of task to be learned. One view is that bold individuals experience more of their environment and thus learn more rapidly. Some studies indeed show that neophobia (avoidance of novel stimuli) is associated with slow learning of foraging tasks in birds (review in Sih et al., 2004). The literature on the proactive-reactive axis, however, emphasizes the opposite: proactive individuals (more aggressive, active, and bold) tend to form set of routines and learn about environmental changes more slowly (Koolhaas et al., 1999; Groothuis and Carere, 2005). Proactive individuals try to manipulate situations, rather than react to them. In colloquial terms, they race through life at high speed and do not appear to notice subtle changes in their environment. In contrast, reactive individuals adapt to situations; they are more sensitive to environmental changes. Putting these views together, it appears that bold individuals might be better at learning novel tasks, while more shy and reactive individuals might be better at sensing environmental changes within a familiar task. Previous work in ravens Corvus corax clearly describes individual differences in acquisition of new tasks in relation to exploration (e.g. Range et al., 2006). A recent work on chickadees Poecile atricapillus showed that slow-exploring birds learn to reverse previously learned category rules more quickly than fast-exploring birds, though it remains unclear whether this is a pure cognitive difference between the type of birds (Guillette et al., 2010). Further empirical and theoretical work should address how the salience, duration, and timing of experience affect personalities. A particularly exciting avenue might be indeed the consequences of ongoing feedback between personalities and cognition (Sih et al., 2004, p. 262).

Pavlov was convinced of such interaction, but admitted after him there has been relatively little work that identifies associations between personalities and differences in cognition (Sih et al., 2004; Locurto, 2007, see also next section). An answer to this question, for which Pavlov’s seminal work makes a clear prediction, needs empirical testing in animals and should constitute a main challenge in animal personality and animal cognition studies.

3 Personality Types versus Cognitive Styles

For those studying comparative cognition an understanding of personality in animals might be crucial in
accounting for unexplained variation in performance much in the manner that Pavlov had assumed that identification and knowledge of personality types helped to predict the effectiveness of his experimental treatments. Reasonably, personality differences are one of the mechanisms that maintain behavioural variability and, accordingly, they constitute one of the prerequisites for natural selection (Dingemanse and Rèale, 2005), whilst it could be expected that personality traits and cognitive abilities have co-evolved. Indeed, artificial selection for personality traits seems to affect performance in tasks that involve cognition in mice and great tits (Groothuis and Carere, 2005). Such an understanding could be crucial from a methodological point of view, as “fearful” or “shy” individuals are often discarded simply because of their reluctance or inhibition to perform, not because of their actual inability.

The argument for the inclusion of personality differences in comparative cognition may face two obstacles. The first is whether Pavlov was indeed correct. Is there evidence that different personality styles predict differences in cognition? Even if the answer to this question is yes, it still remains the question of mechanisms. How exactly would one take personality into consideration in studies of comparative cognition?

Apart from Pavlov, there is little evidence that individual differences in cognitive paradigms relate to differences in personality. Some dimensions of personality may be more reasonably related to cognitive differences than are others. It is not surprising that differences found in exploration are related to differences in learning. In a study involving macaques, subjects were first screened for their exploratory ability by observing their interactions with a novel object and then exposed to an operant contingency that required touching another object in their home cage. Results showed that higher percentage of exploratory subjects acquired the operant response compared to inhibited subjects (75% vs. 22%; Coleman et al., 2005). In corvids it has been shown that neophobia constrains explorative behaviour, learning and innovation, while social context facilitates approach to novel objects and acceptance of novel food (Stöwe et al., 2006). Moreover, different exploratory tendencies (“slow” versus “fast” explorers) interacted with the effect of social context: the presence of a conspecific delayed the approach of fast birds to novel objects. Slow birds, in contrast, approached the novel objects with lower latencies and spent more time close to them when in dyads with fast siblings than when alone (Stöwe and Kotrschal, 2007). There is other evidence that exploratory tendencies co-vary with differences in general learning abilities in laboratory mice, with a positive correlation between propensity to explore and cognitive performance independent of stress and emotional reactivity induced by the exploration challenge (Matzel et al., 2003; Light et al., 2006; Matzel et al., 2008).

The connection between a trait like exploration and simple learning is not surprising, especially in procedures in which novelty responses and speed of conditioning are evaluated using similar responses in the same context, as in the study by Coleman and co-workers (2005). More compelling would be the demonstration that different personalities co-vary with differences in cognition across different paradigms. Such evidence is currently lacking, but it could be speculated that the personality styles identified in the study of primates co-vary with differences in learning and memory. Impulsive monkeys, similarly to Pavlov’s Excitable type, may show deficits in procedures that require an interplay between excitation and inhibition, such as in differential reinforcement of low rate schedules or reverse contingency tasks (e.g. Boysen et al., 1999), or tests of object permanence. Reactive individuals might have difficulties in procedures where high anxiety inhibits performance, or where exploration is required to contact the experimental contingencies. These characteristics may apply to many procedures ranging from aversive conditioning through spatial navigation and problem solving. High arousal, either in the form of anxiety or excitability, has long been known to reduce cue utilization and the span of the attentional field (Easterbrook, 1959). In some cases this feature might be advantageous (e.g., reducing attention to irrelevant cues) but in other cases it may impair performance. This feature of arousal may be relevant to the performance of both impulsive (proactive) and reactive animals in a variety of cognitive paradigms.

Importantly, some neuro-endocrine responses more typical of a given personality profile (e.g. glucocorticoids, Cavigelli and McClintock 2003; Carere et al., 2010) could affect cognitive abilities. For example, in the short term moderate elevations of glucocorticoids can improve learning and memory performance (e.g. Pravosudov et al., 2003), while chronic levels can be detrimental (Sapolsky, 2000). A differential HPA responsiveness is associated with different personality types (Carere et al., 2010; see also Koolhaas et al., 1999 and Koolhaas et al., 2010 for other neuroendocrine correlates). This means that if the cognitive task is perceived at the same time as a novelty, a differential re-
lease of glucocorticoids could differently affect the performance and this may differ between different personality types.

The influences of personality on cognition may depend on which sort of cognition is under consideration. Personality might be less relevant in physical cognition (e.g., spatial navigation, tool use concept formation), while in social cognition (e.g., cooperative problem solving, alliance formation, imitation), it might have greater importance given the reasonable assumption that personalities evolved mainly to mediate the demands of social relationships (Box, 1999). However, this dichotomy could be artificial, since the standard topics of physical cognition may be studied with non-social paradigms, but most of them have commensurate social parallels. For example, transitive inference has clear parallels to an individual animal’s understanding of social rank. Given that evolution is often conservative in the development of mechanisms, it is likely that processes like transitive inference evolved to solve both social and non-social problems. A similar argument suggests that the mechanisms mediating an individual’s ability to distinguish group members bear similarities to the mechanisms found in humans by which the semantic meaning of a word or other symbol is inferred from experiencing that symbol in a variety of contexts. If so, these mechanisms may have contributed to the emergence of the semantic aspects of language (King et al., 1999). Thus, if personality differences influence processes related to sociality, they may similarly affect non-social processes that present similar cognitive demands to the individual. On this point it may be noted that personalities have been described in animals such as octopuses, which spend most of their life solitary and territorial, but greatly rely on cognitive abilities in their life history (Mather, 1991; Mather and Anderson, 1993).

If personality differences affect cognition they are expressed as part of the error term in standard group designs, being part of the noise that constitutes the accepted price of using these designs. The error term is a statement of ignorance; we do not know why all that within group variance is occurring, but we trust that experimental treatments will create more variance between groups thereby resulting in a significant effect. One could label a portion of that error variance and use it as a covariate. Even if one does not wish to study the relationships between personality and cognition directly, as did Pavlov, personality differences can still be used indirectly, that is, statistically.

This can be already pursued at the very beginning of any experiment testing performance in cognitive tasks. For example, corvids are extensively used in trials testing tool use, food caching and problem solving (e.g., Dally et al., 2006; Tebbich et al., 2007; Clayton et al., 2007; Correja et al., 2007; Raby et al., 2007; Seed et al., 2008). It would be very interesting to assess them for behavioural endpoints reflecting personality, such as exploration and neophobia, as some authors did (e.g., Range et al., 2006; Stöwe et al., 2006). To the extent that personality differences affect cognition these differences can be used as a covariate, the variance owing to them extracted, thereby reducing the error term and affording the design greater precision. This is a technique that is already used in some comparative cognition studies when pre-experimental measures of activity and/or exploration are included.

An obstacle in this type of strategy might be the time and effort involved in getting reliable personality ratings and codings from subjects as a part of standard experiments. However, at least in case of birds, longitudinal assessments of activity level, exploration, and styles of coping with several kinds of social and non-social challenges can be made using open fields with artificial trees or novel objects, or responses to social intruders are measured (Carere et al., 2005; Groothuis and Carere, 2005) in parallel with purely cognitive tasks. A related objection might be that in many studies of comparative cognition sample sizes are quite low owing to the rarity of a given species or its low representation in captivity. This problem may apply particularly to corvids or primate species, which need large space and costs for housing and maintenance, but we would also make the case that it would be beneficial if specific assessment of pre- and post- experimental individual differences was made. It may be particularly useful to engage in this type of assessment in small-n designs given that in these designs extreme performance is not counterbalanced by a group average. If a given study uses, say, few jays, and one of these animals happens to be reactive while the second one is more evenly-tempered, there is the chance that variations in their experimental outcomes will be due at least in part to pre-existing personality differences. The observed experimental differences between them may not be entirely cognitive per se, although they may be interpreted in that manner. Such assessments would also have implications on animal welfare, as individuals with different profiles are expected to require different cognitive and physical enrichment. The recently published new animal experi-

4 Methodological Issues

A study on personalities must meet two conditions. First, there must be behavioural variation. Second, for purposes of marking reliability and consistency, individuals need to be measured more than once. The basic procedure, then, is to provide individuals with a set of standardized challenges, and then determine whether individual differences are consistent across challenges. There are some relatively straightforward ways to incorporate these procedures into existing protocols. For example, if the study is investigating problem solving in two different kinds of situations such as in the presence and absence of competition by other individuals or at different densities, the same individuals could be used in the different treatment groups. Therefore, this is an efficient method for measuring both treatment effects and personality. Another way to consider personalities is to collect data on other behaviours that are expressed during the course of the study, even if they are not the main endpoint of interest. For example, individual differences in response to handling and restraint proved to be reliable predictors of behaviour in other situations (Carere and van Oers, 2005) and were related to fitness differences in bighorn sheep (Dingemanse and Réale, 2005). Such situations are easily achievable for species such as laboratory rodents and birds, allowing collecting of a large set of data in a short period of time.

A major practical issue that comes up during studies on personalities may be the large number of correlations that are computed, with the risk of statistical type 1 error. A solution is to perform a factor analysis or another data compression on the entire dataset, and then determine whether behaviours measured in different contexts load on the same factor, which would suggest that they are correlated with each other. This is the basic approach, which has produced five major factors (the ‘Big Five’) of personality variation in humans (McCrae and Costa, 1999). The problem is that if the investigator is comparing different treatment groups or different populations or species, it must be verified that the factor structure is equivalent in the different groups so that factor scores are comparable with each other. Fortunately, analytical tools for comparing factor and matrix structures have been developed in both psychology (Church, 2001) and evolutionary biology (Steppan et al., 2002). These are promising methods for animal personality studies, because one of the most interesting questions is whether behaviours are always related to each other in the same way (Bell, 2007). In general, an unexplored issue is how differences among groups (treatments, populations, species, etc.) in personalities are manifested: whether in average behavioural type (some groups are more bold and aggressive than others), differences in one but not both behaviours (some groups are more aggressive than others, but do not differ in boldness), or covariance (the strength of the relationship between boldness and aggressiveness differs across groups).

There are other statistical tests for analysing data on personalities. For example, one approach is to use path analysis combined with structural equation modelling to test hypotheses about the degree of connectedness of different behaviours. More generally, there is potential for extending statistical methods such as repeatability analysis (Asendorpf, 1990), mixed models and repeated measures ANOVA to apply to personality types in combination with performance in cognitive tasks. We believe that performing such kind of personality assessments in behavioural phenotyping of animals would provide an additional source of data that may be beneficial in interpreting cognitive performance.

5 Concluding Remarks

We have now highlighted the importance of taking into account individual personality profiles in relation to cognitive performance. In sum, to test Pavlov’s predictions about the interactions between personality types and cognitive performance, the following empirical steps are recommended: 1) to quantify inter and intra-individual variation in cognitive performance in parallel with a characterization of the personality profiles of the target populations or cohorts of animals; 2) to test whether personality profiles are predictive markers of different cognitive styles; 3) to test whether ontogenetic changes of personality profiles during early development are reflected in changes in cognitive performance.

The study of such interplay has implications on animal welfare as individuals with different profiles are expected to require different cognitive and physical enrichment. Different behavioural strategies in performing the classical Morris Water Maze spatial learning task have been long recognized in thorough analyses of transgenic mice models for biomedical research (Lipp and Wolfer, 1998). Thus, we suggest taking into account animal personality assessments in those cognitive studies relevant in the field of neuroscience and in transla-
tional medicine, in order to improve the validation of animal models (Branchi et al., 2003; Locurto et al., 2003; Cavigelli, 2005; Crawley, 2008).

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