Opinion

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Cognition and personality: an analysis of an emerging field

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It is now well established that individuals can differ consistently in their average levels of behaviour across different contexts. There have recently been calls to apply the same adaptive framework to interindividual differences in cognition. These calls have culminated in the suggestion that variation in personality and cognition should correlate. We suggest that both these appealing notions are conceptually and logistically problematic. We identify the first crucial step for establishing any cognition–personality relationship. This is to determine the degree to which cognitive abilities yield consistent task performance. We then suggest how to establish whether such consistency exists. Finally, we discuss why formulating predictions about how cognition might be related to personality is much more difficult than is currently realised.

Relating cognition to personality: an introduction to the problem

There has been a recent explosion of interest in quantifying consistent individual differences in behaviour (see Glossary), exploring their adaptive significance, and describing the mechanisms responsible for their maintenance [1–6]. As a result it is now well established that a broad range of species show consistent within-species interindividual variation in a range of behaviours such as aggressiveness, boldness, exploration, activity, and sociability [7–12]. By contrast, there has been much less work to establish whether species show consistent within-species between-individual variation in cognitive abilities such as attention, learning, and memory. Nevertheless, researchers are now attempting to relate consistent individual differences in personality to individual differences in cognition, both theoretically (e.g., [7–9]) and empirically [13–22]. As potential key determinants of interindividual variation in behaviour and its associated evolutionary and ecological consequences, we consider the investigation of the possible relationships between cognition and personality to be an important research endeavour.

Although a relationship of some type between personality and cognition is intuitively appealing, we are concerned, however, that because cognitive ability of one kind

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Glossary

Animal personality: defined as differences between individuals' average level of behaviour that are repeatable across time and/or contexts [6]. Defined statistically as variation between individuals in the intercept of their behavioural reaction norm [42] or the existence of between-individual (co)variance in behaviour [44].
Appetitive conditioning task: a Pavlovian conditioning task in which one cue is associated with a second, desirable cue (e.g., food).
Aversive conditioning task: a Pavlovian conditioning task in which one cue is associated with a second, undesirable cue (e.g., mild foot-shock).
Behaviour: the motor actions performed by an animal. Changes in behaviour are the phenotypic representation of cognition.
Behavioural reaction norm: the function describing the relationship between the behavioural phenotype and environmental gradient within the same individual. We focus here on within-individual reaction norms [42]. Within this context, cognition (e.g., learning) is one source of behavioural change.
Between-individual correlation: phenotypic correlation at the between-individual level where the individual average phenotypic responses of two traits are correlated [44]; also known as a behavioural syndrome [61].
Cognition: the mechanisms that enable the acquisition, processing, storage and use of information, which include perception, learning, memory, and decision making [23].
Cognitive performance: a quantitative measure of continuous variation in a dependent behavioural variable, which can be used to quantify a cognitive trait. For example, the number of trials an animal takes to reach the criterion level of performance on a task where the animal has to remember the distinctive features of an object.
Context: refers to the functional domain in which a test is conducted. Examples include contexts related to food, threat, and reproduction, but can also include stimulus dimensions such as social, novelty, and space.
Instrumental conditioning: a form of associative learning in which an animal learns the association between one of its behaviours (e.g., approaching a conspecific) and its consequence (being attacked).
Pavlovian conditioning: a form of associative learning in which an animal learns the association between two cues.
Personality type: used here to refer to the various degrees of a personality trait (e.g., bold vs shy). Also known as a behavioural type [61] or a temperament phenotype [6].
Plasticity: change in the behaviour of an individual as a function of changing environmental conditions; also defined as the slope of the behavioural reaction norm [44]. Cognition is one mechanism underpinning plasticity.
Repeatability: the proportion of phenotypic variance explained by differences among individuals [42]. If repeatability is >0, a behavioural trait is considered to show some degree of consistency.
Reversal learning: the ability to change behaviour when the environment changes. Its constituents are both the ability to inhibit a previously successful behaviour and the ability to produce a second behaviour to the same stimulus.
Training to criterion: the training on a learning task that an experimental subject receives before that subject reaches a pre-established criterion of performance, at which point it is considered to have learned the task. For example, when on 8 of 10 successive trials the animal selects the correct cue or the correct location in space.
Trait: we define a 'trait' here as the material on which natural selection can act. For a cognitive trait to be favoured it must cause an animal to change its behaviour in such a way that the fitness of the animal is enhanced.
Trial: one experience of a learning event. Examples would be: one pairing of two cues; one pairing of a cue and a consequence; one encounter of food in a given location.
Within-individual variance: amount of phenotypic variance attributable to differences in phenotype among measurements of the same individual [44].

and/or another underpins most, if not all, behaviours, investigating this notion is a more conceptually and practically difficult task than is currently realised. The first and major challenge lies in establishing which cognitive ability underpins the performance of an animal on a task or a change in its behaviour. Only then can we begin to establish whether that performance or change, for example in the ability of an animal to learn the location of food, is repeatable. We suggest how one might approach this issue because, without first addressing it, describing what it means in practice to say that personality is related to cognition will not be possible. Lastly, we identify two factors, one of which is logistical and the other terminological, which we consider restrain progress in this endeavour.

Cognition

Cognition can be defined as the acquisition, processing, storage and use of information [23]. It encompasses a large variety of abilities, including attention, categorisation, rule learning, associative learning, behavioural inhibition, language, self recognition, and social learning, to name only a few [23,24], some of which may themselves be divisible into further subcategories.

Because cognitive abilities are not directly manifested phenotypically, their measurement is achieved through the quantification of a change in behaviour. Thus far, most animal cognition researchers have been interested in identifying and quantifying what cognitive ability(ies) cause observable changes in behaviour (i.e., the mechanistic basis of variation in behaviour). This contrasts with the aim of behavioural ecologists, who are interested in determining the adaptive significance of a trait (i.e., the functional basis for variation in behaviour). For example, the behavioural ecologist would employ a cost/benefit analysis to determine whether the optimal load size that parents deliver to their nest when provisioning their offspring varies as a function of the distance travelled to find food, whereas the animal cognition researcher would want to determine the cognitive abilities parents use to relocate their nest. Evidence for a specific cognitive ability is gathered by using experimental designs that disentangle behavioural responses attributable to, for example, computation of travel distance and direction from their point of departure, an ability known as path integration, from those behavioural responses that are attributable to other underlying cognitive mechanisms (e.g., landmark learning).

Consistent individual differences in cognition

Before we can determine whether there is a relationship between the personality of an individual and its cognitive abilities we need to identify the relevant cognitive abilities and then to confirm that those cognitive abilities cause repeatable behavioural effects. Identification of relevant cognitive abilities and problems therein has been recently discussed elsewhere, however, and we will therefore not elaborate on that issue here [25]. It may seem surprising, then, that consistency in cognitive abilities in nonhuman animals seems to have received very little attention thus far (but see [26,27]). Much of the existing work on individual differences in cognition is to be found within the biomedical sciences, the focus of which has been primarily directed at quantifying variation between genetic strains of rodents, with the view to using them as a human model [28–33].

For most other researchers investigating animal cognition, both within- and among-individual variation are considered sources of undesirable variability that contribute to masking between-group treatment effects. Indeed, considerable effort is made to reduce among-individual variation by incorporating procedures such as routine handling, habituation to test environments, and/or implementing standardised food-deprivation schedules [34].

Nonetheless, the lack of interest in variation in cognitive performance in other nonhuman animals is surprising for two reasons: (i) there is a vast body of work on repeatability in cognition in humans (e.g., [35,36] and references therein), which one might have thought would have lead to the development of nonhuman animal models to investigate the behavioural and neural sources of consistent interindividual differences; and (ii) cognition is a major source of phenotypic plasticity [37–40], and therefore interindividual differences in cognition should play an important part of any discussion of individual variation in plasticity and its adaptive nature [41–43].

Demonstrating consistent individual differences in cognition relies on researchers using the same logic used for demonstrating consistent individual differences in personality, a key feature of which is that individual differences in a given trait are repeatable across time and contexts [5,6]. For example, boldness (e.g., latency to leave shelter) is measured in the same context across two or more timepoints or in two different contexts, such as the latency of an individual to leave shelter when alone and then again when the individual is in a social group.

Similarly, showing that individual differences in cognition are repeatable requires demonstrating consistency in cognitive abilities across time and contexts. Cross-contextual consistency will require demonstrating that an individual performs similarly on two different types of task, such as reaching a given learning criterion faster (than another individual) on both an appetitive conditioning and an aversive conditioning task, on an instrumental conditioning and a spatial learning task, or on a discrimination task across two domains (e.g., auditory and visual [13]; Table 1).

In contrast to personality tests, however, whereby individuals might habituate across repeated tests (e.g., decreased exploration or decreased neophobia), when tested on a learning task individuals might reach criterion increasingly quickly across tests because they either become more experienced at solving the task or they become more motivated to gain reward across successive tests. It is important to note that it is typical when training animals how to perform on a cognitive test that all individuals are trained until they reach the same level of performance (criterion training). Demonstration of between-individual consistency in a cognitive ability requires that the rank order of the performance scores (e.g., the number of trials to criterion) remains the same across successive tests, that is, each time the animals are trained to criterion on a given task.

Table 1. Measurement of cognitive abilities[a]

		Cognitive test methodology and contextual variation		
Cognitive ability	**Cognitive content**	**Threat[b]**	**Appetitive[c]**	**Sexual[d]**
Cognitive abilities with illustration of contextual variation				
Associative learning	Learning of a S–S predictive relationship	Cue predicts a noxious S ('fear conditioning')	Cue predicts an appetitive S ('appetitive conditioning')	Cue predicts access to a mate ('sexual conditioning')
Operant learning	Learning of an action–outcome predictive relationship	An action by the animal is followed by an aversive S	Action followed by an appetitive S	Action followed by access to a mate
Discrimination learning	Learning of S+ and S− predictive relationships	One cue predicts an aversive S, whereas another does not	One cue predicts an appetitive S, whereas another does not	One cue predicts access to a mate whereas another does not
Habituation	Learning that an S is irrelevant	Repeated threat S presentation	Repeated food S presentation	Repeated sexual S presentation
Generalisation	Responses to novel (i.e., not experienced during training) S that share sensory features with the learned S	Fear conditioning followed by tests with similar, novel S	Appetive conditioning followed by tests with similar, novel S	Sexual conditioning followed by tests with similar, novel S
Cognitive abilities without illustration of contextual variation[e]				
	Example tasks	**Cognitive test methodology**		
Contextual learning	Passive avoidance learning	Animals learn to avoid a place in which they have experienced an aversive S		
Behavioural inhibition	Go/no go	In a discrimination learning task, S+ and S− are presented sequentially, such that the S+ requires the animal to perform a response (peck a key), whereas the S− requires it to inhibit a response (withhold from pecking a key)		
	Forced choice	In a discrimination learning task, S+ and S− are presented simultaneously such that the animal must learn to select one cue while ignoring the other		
	Reversal learning	An animal is trained to criterion on a discrimination learning task, at which point the significance of the cues is reversed such that the animal must learn to inhibit previously learned (successful) behaviour		
	Delay discounting	An animal must delay responding to obtain a more valuable reward		
Memory duration	Retention task	The time interval between training and test is extended		
Spatial learning and memory	Morris water maze	A swimming animal must use visual landmarks to locate a platform in a water pool		
	Landmark learning	An animal is trained to find a reward specified by a landmark configuration		
Social learning	Local/S enhancement	A social cue directs the attention of an animal to a particular S or location (local) or category of stimuli/S		
	Social facilitation	An animal increases its frequency of a behaviour after witnessing others perform that behaviour		
	Observational conditioning	An animal learns that a cue predicts a social S		

[a]In the same way that measuring different personality traits (e.g. neophobia; exploration) requires distinct methodologies, methodologies used to measure cognition vary depending on the particular cognitive ability of interest. We provide some examples of commonly measured cognitive abilities. Several of these cognitive abilities are multifaceted, and different tests are used to measure different dimensions. Cues are typically arbitary stimuli with little biological significance, such as a light or a simple tone. Some tests of spatial and social learning can involve association formation where the predictive S is a spatial stimulus or the predicted S is a social stimulus; hence, these types of learning can be viewed as contextual variations of association learning, but we list them here under spatial and social learning to facilitate the development of potential predictions relating these cognitive abilities to personality. Abbreviation: S, stimulus(i).

[b]A predator or a foot-shock are examples of aversive S.

[c]Food or water are examples of appetitive S.

[d]Mates are examples of sexual S.

[e]Some of these tests may also be varied across contexts by changing the nature of the S involved, as illustrated in the traits with contextual variation presented above; for the sake of brevity, these details are not provided here.

In theory, temporal consistency could be established by showing that some individuals learn in consistently fewer trials than do others when trained to criterion multiple times on the same task (e.g., an appetitive conditioning task in which a red light presentation predicts a food reward). In practice, establishing temporal consistency in at least some cognitive measures, especially those related to acquisition of information, will be challenging. As noted above, once an animal has reached criterion on a given task, if the animal remembers any component of that training, then subsequent attempts to measure the rate at which that animal learns that task a second time are likely to be confounded by those memories or the motivation to perform the task, which may increase or decrease. One way that might reduce this effect would be to train the individual on slight modifications of the initial task (e.g., the presentation of a blue light predicts the food reward rather than the red light that predicted the food reward on the initial task). One might still expect that performance on this modified task will be affected by the experience on the first task owing to similarities of the two tasks – for example, that light (of some wavelength) predicts food. For these reasons, cross-contextual, rather than temporal, consistency in cognitive performance might be the more-straightforward approach to

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observing consistent individual differences in cognition, if they exist.

Personality and cognition

Demonstrating a relationship

If consistent individual differences in cognitive performance can be reliably established, either across contexts or across time, then one can begin to examine the relationship between personality and cognition by measuring the extent to which between-individual variation in a cognitive ability (e.g., the number of trials it takes an animal to reach criterion on a task involving memory for the location of food) predicts, or is predicted by, between-individual variation in a behavioural trait, such as boldness. Such a relationship would appear to position both cognition and personality within a 2D space (Figure 1A). In statistical terms, this is equivalent to establishing between-individual correlations between personality and cognition [44]. Although there have been several attempts to show a correlation between personality and cognition [14,20,45–48], they have fallen short of demonstrating consistency in cognitive ability across either context or time because the authors quantified the rate at which their animals reached criterion (i.e., learn) only once and only on a single task (but see [21] and [13] for examples of measuring learning across multiple tasks). In statistical terms, they demonstrated raw phenotypic correlations, which do not allow partitioning of phenotypic (co)-variance of behaviour into between- and within-individual components, a prerequisite for demonstrating that between-individual variation in a behavioural trait, such as boldness, is related to between-individual variation in cognition [44].

A further feature of the existing body of work on the relationship between personality and cognition is the focus on the relationship between a single repeatable behaviour (e.g., boldness) and learning performance on a single learning task (but see [13]). Thus, to our knowledge there are no data that yet address the recent suggestion of Sih and Del Giudice [41] that individuals with a 'fast-inaccurate' cognitive style would differ systematically from individuals with a 'slow-accurate' behavioural style on a collection of

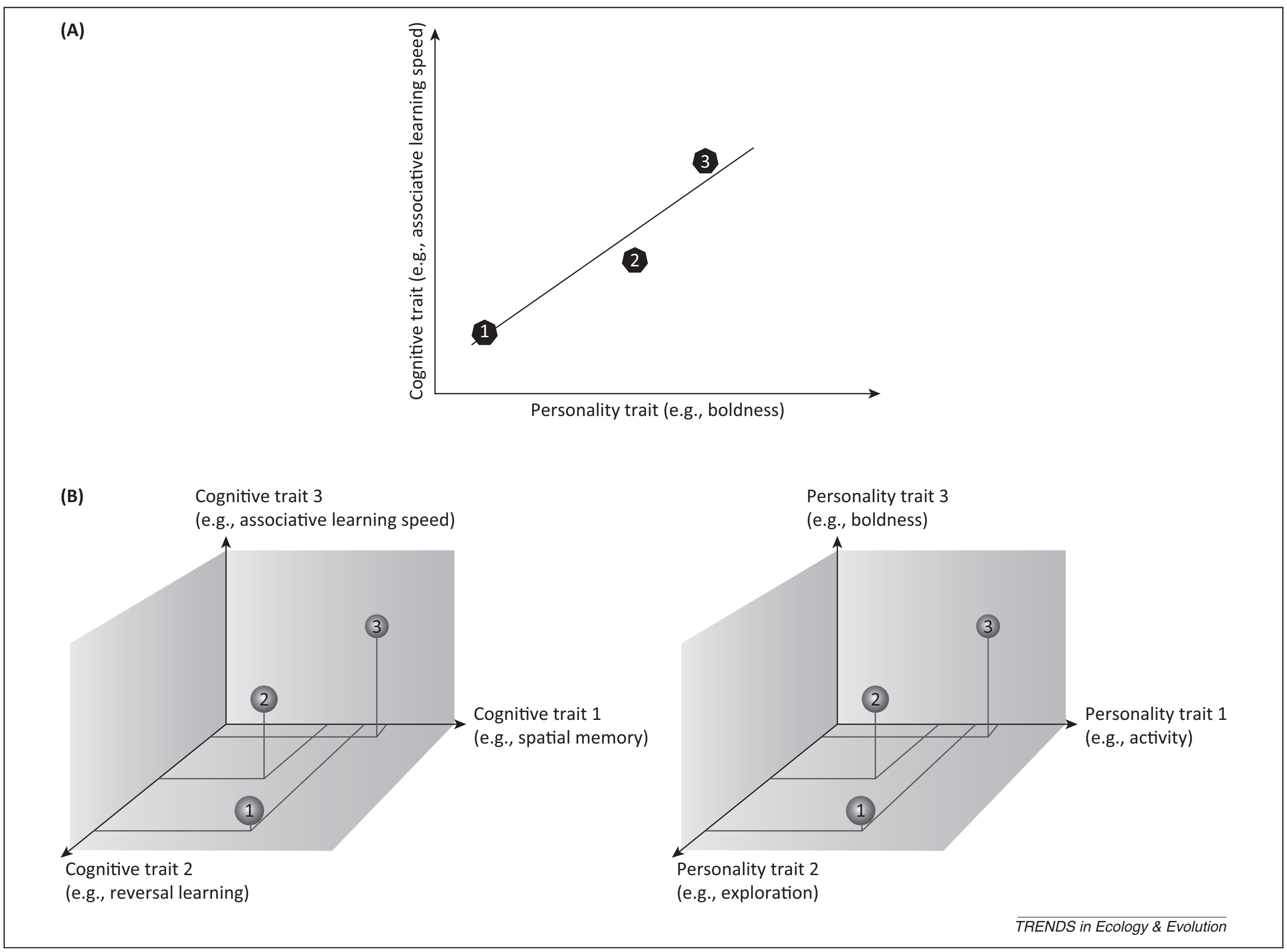

Figure 1. Diagrammatic representations of how personality–cognition relationships can be studied. **(A)** Illustration of a study relating one personality trait and one cognitive ability. Each number represents the cognitive performance measurement (collected once on a single task) of one hypothetical individual relative to its single personality measurement. This is the approach taken by the small body of work to date investigating relationships between personality and cognition [14,20,45–48]. **(B)** Illustration of a study relating multiple personality traits to multiple cognitive abilities. Each number represents the average cognitive performance of one hypothetical individual across multiple measurements relative to its average personality score across multiple measurements. In the latter case, the position of an individual within a multidimensional personality space is predictive of its position within a multidimensional cognition space. The latter scenario would be required to test the prediction that the personality of an animal might be related to its 'cognitive style' [41].

personality and cognitive traits. While it seems plausible that speed of learning and accuracy of the information might be traded off in this way, one can argue equally plausibly, for example, that an individual that learns slowly but accurately that food can be found in a specific location might learn fast and accurately that a specific sound is associated with danger. To attribute a given style (speed and accuracy of performance) to a particular individual one needs to demonstrate that the individual expresses this style across many different learning tasks. It follows that to test whether the personality of an individual is linked to its 'cognitive style' will require a demonstration that individual differences in multiple dimensions of personality (e.g., between-individual variance in boldness, activity, and exploration) predict individual differences in multiple cognitive abilities (e.g., between-individual variance in spatial memory, associative learning, and reversal learning; Figure 1B), often referred to as a general learning ability, or 'G' [26,27].

Basis of a personality–cognition relationship

If personality and cognition are related, it is not clear what shape that relationship might take. One possibility is that particular personality traits, and specific personality types within those traits, facilitate or constrain learning. For example, a bolder individual that approaches and explores novel objects more willingly than does a shyer conspecific is likely to encounter new environmental contingencies more quickly. Therefore, boldness, neophilia, activity, and spatial exploration would be behaviours that might correlate positively with learning because those behaviours determine the rate at which animals encounter the environmental contingencies upon which learning depends. Most experimental measures of learning, however, are less susceptible to such sources of co-variation between learning and personality because performance is quantified as the number of trials to criterion and not as the absolute time it takes the animal to learn a particular contingency (Figure 2). Consequently, if, for example, bolder individuals learn a particular contingency faster than do less-bold individuals, one might then assume that it is because individuals with particular personality types (e.g., more bold) store environmental contingencies faster (i.e., they learn in fewer trials) either because they pay more attention to those contingencies, recognise them sooner, lay them down in memory more readily, or have lower decision thresholds for association formation [49], although which of these it is may not be clear. It may also be the case, however, that animals vary in how they respond to reward (or punishment) [25], perhaps because of their physiological state or prior experience.

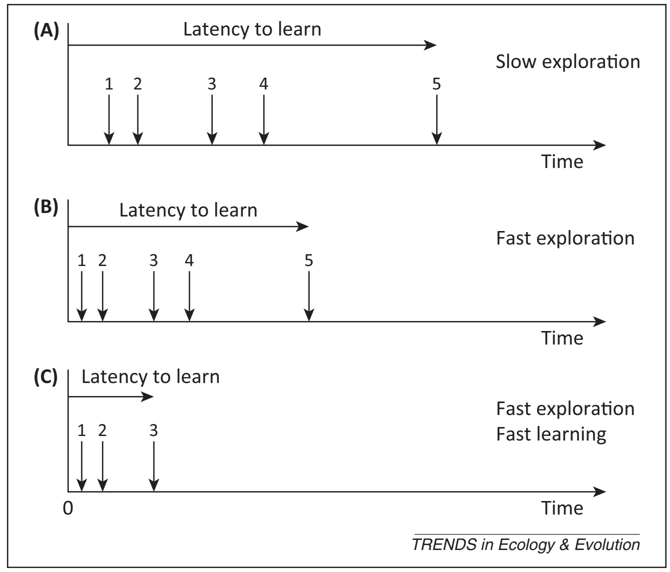

Figure 2. Illustration of how learning tests might reveal meaningful sources of co-variation with personality by quantifying performance as trials to criterion rather than learning latencies. Numbers indicate five successive encounters (i.e., five 'trials') with a given environmental contingency (e.g., a key peck results in food delivery; a light predicts a foot-shock). An animal that explores more quickly will encounter environmental contingencies more quickly than an animal that explores less quickly, and will therefore learn about them in less time (top line vs second line) although the learning performance of the two animals when quantified as trials to criterion will not differ. Consequently, positive correlations between exploration and learning speed, were they to exist, would necessarily indicate that fast explorers learn environmental contingencies faster (i.e., in fewer trials, three in our example) either because they pay more attention to them, recognise them more quickly, and/or because they encode them into memory more quickly than does the individual that explores more slowly (middle line vs bottom line).

Direct facilitatory or inhibitory relationships between personality and cognition are only one possible scenario. Behavioural traits such as boldness, activity, neophilia, and exploration might correlate statistically with cognitive abilities – not because they share a direct relationship but rather because they both are acted on in common by some other process. One plausible candidate for some intervening modifier is stress [50]. For example, individuals prone to high levels of long-term chronic stress, either as a consequence of their genetics or of their developmental history, because of sustained hyper-activation of their hormonal stress pathways might be more likely to be of specific personality types, particularly those associated with avoidance of novelty and shyness. They might also learn more slowly because long-term stress impedes memory consolidation [51,52]. It is important to note that the inhibitory effects of long-term chronic or repetitive stressors are distinct from those of short-lived, transient stressors, which can facilitate memory consolidation [51,52]. For this reason, the patterns of correlations between personality measures, cognition, and responsiveness to transient stressors might be very different to those between personality, cognition, and responses to chronic, repetitive stressors. For those interested in exploring the mechanisms underpinning correlations between personality and cognition it will be important to design testing methodologies that do not conflate the measurement of these distinct types of stress [51,52].

We are reluctant, however, to produce a list of general or specific predictions for two reasons. We see the elaboration of predictions as difficult because, first, any one prediction will depend upon a clear understanding of the mechanistic basis of the trait being measured by a given personality test. For example, a prediction as to how boldness, measured using a novel object test, would be linked to a cognitive ability (e.g., learning) depends on firstly whether boldness is deemed to represent fear, a measure of behavioural inhibition, or a measure of activity [53]. This issue has been raised recently in slightly different terms as the need to develop behavioural assays that unambiguously identify the trait of interest [53]. The second reason why elaboration of predictions is difficult is that the direction of the prediction will depend, separately, on the nature of (i) the stimulus (e.g., light or conspecific), (ii) the response (e.g., a peck or inhibition of a response), and (iii) the outcome (e.g., food or foot-shock, Table 1). Furthermore, any prediction will also depend on the specific individuals (e.g., age, sex, dominance, prior experience), species, and context for which the particular personality trait–cognitive ability hypothesis is developed (see also the discussion [54] of trade-offs between personality traits and contexts). We foresee that, once unambiguous personality assays become available, rapid progress might be made in formulating specific predictions based on the influence of plausible selections/combinations of these parameters.

A way forward

Not only are we concerned as to whether a relationship between cognition and personality should exist, but we also consider that there are two additional challenges that researchers will need to overcome when seeking to establish links between personality and cognition. The first relates to sample sizes and testing protocols, and the second relates to terminology.

Issue 1: methodology. Demonstration that interindividual variation in multiple personality traits is linked in some systematic way to interindividual variation in multiple cognitive abilities (i.e., Sih and Del Guidice's 'cognitive style'; Figure 1B) will require testing large numbers of animals on batteries of personality tests and learning tasks (see [44]). We see this requirement as a significant empirical hurdle to progress in this field. Furthermore, testing large numbers of animals on well-controlled learning tasks is rarely accomplished without resorting to highly automated means of data collection, both of which are likely to be prohibitive for most researchers. One approach might be to develop hypotheses with clear predictions in which a case is made for a correlation between a specific personality trait and a specific cognitive ability [14,20,45–48]. This predictive framework would have to include careful consideration of the factors that are likely to act as confounds in any interpretation of variation in cognition [25]. A second approach might be to quantify individual variation in cognitive ability and personality using artificial selection lines [38]. For example, by using artificial selection for one behavioural trait, such as boldness, one could examine whether a particular cognitive ability correspondingly varies as a result [55–58]. This will be costly and time-consuming for those working on vertebrates, but more feasible if using invertebrates. Finally, researchers that have long-term data on cognitive abilities of their study animals might have sufficient data to allow analysis of variation in cognitive performance in conjunction with data on personality measures of those same animals [59,60]. Without meeting the requirement for individual consistency in cognitive abilities, however, and if measurement of personality is limited to one trait and/or the measure of cognition is limited to one ability, support for a relationship between cognitive and personality styles will remain highly contentious.

Issue 2: terminology. The second hurdle impeding progress in this domain is a terminological one that is caused by the sudden recent surge in the number of terms used to refer to cognitive abilities. Some of these terms are unhelpful because they lack clear operational definitions without which we cannot be sure if it is the same cognitive ability that has been tested. Perhaps the least useful of these new terms are high and low cognition/cognitive abilities and high and low exploration. These terms particularly lack standardised operational definitions.

The enthusiasm to provide the field with new terms is also problematic when a good proportion of them duplicate existing, well-studied, concepts in the cognition literature. Such duplication could lead researchers interested in exploring cognition–personality relationships to overlook existing research on their chosen cognitive ability. We include here terms such as 'choosiness', a concept extensively studied in the cognition literature as 'discrimination' and 'generalisation'; 'sensitivity', a concept that has been studied in the cognition literature as a 'detection threshold'; and 'impulsivity', a concept often studied under the term 'delay gratification'. Such multiplication of terms is unhelpful, and we suggest that researchers new to investigating cognitive abilities put aside the fun of inventing new terminology for the benefits of capitalising on the terminology (and accompanying empirical work) already available in the extensive, extant body that is animal cognition.

Concluding remarks

Between-individual variation in cognitive abilities will be an important part of any discussion on between-individual variation in behaviour and its adaptive significance. As such, an understanding of individual differences in cognition will form a significant complement to the recent upsurge in work on individual differences in personality. Within this context we support, albeit cautiously, burgeoning efforts to understand how between-individual individual variation in cognitive abilities is related to between-individual variation in personality, not least because individual differences in cognitive abilities might drive individual differences in personality, and together they might drive responsiveness to environmental change. Crucial to the success of this work will be the deployment of suitable methodologies that adequately demonstrate that individual variation in cognitive abilities are repeatable, preferably across contexts, before attempts are made to correlate these individual differences with individual differences in personality. Furthermore, more general conclusions about how 'cognitive styles' relate to personality will require studying the relationship between multiple cognitive abilities and multiple personality traits. We argue that this body of research will benefit greatly from a firm scholarship of the vast body of existing research on animal cognition, and all the more so if vague terminological additions can be avoided.

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References

1 Dall, S.R.X. *et al.* (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* 7, 734–739
2 Carere, C. and Maestripieri, D. (2013) Animal personality: who cares and why? In *Animal Personalities: Behaviour, Physiology and Evolution* (Carere, C. and Maestripieri, D., eds), pp. 1–9, The University of Chicago Press
3 Dingemanse, N.J. and Wolf, M. (2010) Recent models for adaptive personality differences: a review. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 365, 3947–3958
4 Réale, D. *et al.* (2010) Evolutionary and ecological approaches to the study of personality. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 365, 3937–3946
5 Stamps, J. and Groothuis, T.G.G. (2010) The development of animal personality: relevance, concepts and perspectives. *Biol. Rev. Camb. Philos. Soc.* 85, 301–325
6 Réale, D. *et al.* (2007) Integrating animal temperament within ecology and evolution. *Biol. Rev. Camb. Philos. Soc.* 82, 291–318
7 Conrad, J.L. *et al.* (2011) Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *J. Fish Biol.* 78, 395–435
8 Réale, D. *et al.* (2009) Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.* 22, 1599–1607
9 Sih, A. *et al.* (2003) Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Anim. Behav.* 65, 29–44
10 Sinn, D.L. and Moltschaniwskyj, N.A. (2005) Personality traits in dumpling squid (*Euprymna tasmanica*): context-specific traits and their correlation with biological characteristics. *J. Comp. Psychol.* 119, 99–110
11 Cote, J. and Clobert, J. (2007) Social personalities influence natal dispersal in a lizard. *Proc. Biol. Sci.* 274, 383–390
12 Groothuis, T.G.G. and Carere, C. (2005) Avian personalities: characterization and epigenesis. *Neurosci. Biobehav. Rev.* 29, 137–150
13 Guillette, L.M. *et al.* (2014) Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. *Anim. Cogn.* 18, 165–178
14 Guillette, L.M. *et al.* (2009) Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. *Behav. Processes* 82, 265–270
15 Guillette, L.M. *et al.* (2011) Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. *Proc. Biol. Sci.* 278, 767–773
16 Amy, M. *et al.* (2012) Worms under cover: relationships between performance in learning tasks and personality in great tits (*Parus major*). *Anim. Cogn.* 15, 763–770
17 Guenther, A. *et al.* (2014) Learning and personality types are related in cavies (*Cavia aperea*). *J. Comp. Psychol.* 128, 74–81
18 Brust, V. *et al.* (2013) Behavioural flexibility and personality in zebra finches. *Ethology* 119, 559–569
19 Griffin, A.S. *et al.* (2013) Tracking changing environments: Innovators are fast, but not flexible learners. *PLoS ONE* 8, e84907
20 Trompf, L. and Brown, C. (2014) Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*. *Anim. Behav.* 88, 99–106
21 Colas-Zelin, D. *et al.* (2012) The imposition of, but not the propensity for, social subordination impairs exploratory behaviors and general cognitive abilities. *Behav. Brain Res.* 232, 294–305
22 Øverli, Ø. *et al.* (2007) Evolutionary background for stress-coping styles: relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. *Neurosci. Biobehav. Rev.* 31, 396–412
23 Shettleworth, S.J. (2010) *Cognition, Evolution, and Behavior*. (2nd edn), Oxford University Press
24 Zentall, T.R. and Wasserman, E.A., eds (2012) *The Oxford Handbook of Comparative Cognition*, Oxford University Press
25 Rowe, C. and Healy, S.D. (2014) Measuring variation in cognition. *Behav. Ecol.* 25, 1287–1292
26 Matzel, L.D. *et al.* (2003) Individual differences in the expression of a 'general' learning ability in mice. *J. Neurosci.* 23, 6423–6433
27 Sauce, B. and Matzel, L.D. (2013) The causes of variation in learning and behavior: why individual differences matter. *Front. Psychol.* 4, 395
28 Caldwell, H.K. *et al.* (2008) Vasopressin: behavioral roles of an 'original' neuropeptide. *Prog. Neurobiol.* 84, 1–24
29 Skuse, D.H. and Gallagher, L. (2009) Dopaminergic–neuropeptide interactions in the social brain. *Trends Cogn. Sci.* 13, 27–35
30 Sweis, B.M. *et al.* (2013) Individual differences in the effects of chronic stress on memory: behavioral and neurochemical correlates of resiliency. *Neuroscience* 246, 142–159
31 Wood, N.I. *et al.* (2010) Responses to environmental enrichment differ with sex and genotype in a transgenic mouse model of Huntington's disease. *PLoS ONE* 5, e9077
32 Posner, M.I. (2005) Genes and experience shape brain networks of conscious control. *Prog. Brain Res.* 150, 173–183
33 Walker, M.D. and Mason, G. (2011) Female C57BL/6 mice show consistent individual differences in spontaneous interaction with environmental enrichment that are predicted by neophobia. *Behav. Brain Res.* 227, 508–513
34 Carere, C. and Locurto, C. (2011) Interaction between animal personality and animal cognition. *Curr. Zool.* 57, 491–498
35 Corr, P.J. (2010) Individual differences in cognition: in search of a general model of behaviour control. In *Handbook of Individual Differences in Cognition* (Gruszka, A. *et al.*, eds), pp. 3–26, Springer
36 Revelle, W. *et al.* (2010) Individual differences in cognition: new methods for examining the personality-cognition link. In *Handbook of Individual Differences in Cognition* (Gruszka, A. *et al.*, eds), pp. 27–50, Springer
37 Domjan, M. (2005) Pavlovian conditioning: a functional perspective. *Annu. Rev. Psychol.* 56, 179–206
38 Dukas, R. (2004) Evolutionary biology of animal cognition. *Annu. Rev. Ecol. Evol. Syst.* 35, 347–374
39 Hollis, K.L. (1997) Contemporary research on Pavlovian conditioning. A 'new' functional analysis. *Am. Psychol.* 52, 956–965
40 Hollis, K.L. (1984) The biological function of Pavlovian conditioning: the best defense is a good offense. *J. Exp. Psychol. Anim. Behav. Process.* 10, 413–425
41 Sih, A. and Del Giudice, M. (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 367, 2762–2772
42 Dingemanse, N.J. *et al.* (2010) Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* 25, 81–89
43 Mathot, K.J. *et al.* (2012) Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos* 121, 1009–1020
44 Dingemanse, N.J. and Dochtermann, N.A. (2013) Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J. Anim. Ecol.* 82, 39–54
45 Dugatkin, L.A. and Alfieri, M.S. (2003) Boldness, behavioral inhibition and learning. *Ethol. Ecol. Evol.* 15, 43–49
46 Boogert, N.J. *et al.* (2006) The relation between social rank, neophobia and individual learning in starlings. *Anim. Behav.* 72, 1229–1239
47 Seok An, Y. *et al.* (2011) Social rank, neophobia and observational learning in black-capped chickadees. *Behaviour* 148, 55–69
48 Carazo, P. *et al.* (2014) Sex and boldness explain individual differences in spatial learning in a lizard. *Proc. R. Soc. B* 281, 20133
49 Gallistel, C.R. *et al.* (2004) The learning curve: implications of a quantitative analysis. *Proc. Natl. Acad. Sci. U.S.A.* 101, 13124–13131
50 Cockrem, J.F. (2007) Stress, corticosterone responses and avian personalities. *J. Ornithol.* 148, 169–178
51 De Kloet, E.R. *et al.* (2005) Stress and the brain: from adaptation to disease. *Nat. Rev. Neurosci.* 6, 463–475
52 Joëls, M. *et al.* (2006) Learning under stress: how does it work? *Trends Cogn. Sci.* 10, 152–158
53 Carter, A.J. *et al.* (2013) Animal personality: what are behavioural ecologists measuring? *Biol. Rev. Camb. Philos. Soc.* 88, 465–475
54 Sih, A. *et al.* (2012) Ecological implications of behavioural syndromes. *Ecol. Lett.* 15, 278–289
55 Coppens, C.M. *et al.* (2010) Coping styles and behavioural flexibility: towards underlying mechanisms. *Philos. Trans. R. Soc. B* 365, 4021–4028

56 Koolhaas, J.M. *et al.* (2010) Neuroendocrinology of coping styles: towards understanding the biology of individual variation. *Front. Neuroendocrinol.* 31, 307–321

57 Van Oers, K. *et al.* (2004) A genetic analysis of avian personality traits: correlated, response to artificial selection. *Behav. Genet.* 34, 611–619

58 Bignami, G. (1965) Selection for high rates and low rates of avoidance conditioning in the rat. *Anim. Behav.* 13, 221–227

59 Thornton, A. and Lukas, D. (2012) Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 367, 2773–2783

60 Vonk, J. and Povinelli, D. (2011) Individual differences in long-term cognitive testing in a group of captive chimpanzees. *Int. J. Comp. Psychol.* 24, 137–167

61 Sih, A. *et al.* (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* 19, 372–378