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Individual consistency in multiple cognitive performance: behavioural versus cognitive syndromes

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Individuals within species differ consistently in their behaviour. Such individual differences may represent adaptations. Recently, researchers have started to implement the same adaptive framework to individual differences in cognition, leading to the suggestion that personality and cognition should covary. To determine the contextual consistency of cognitive traits and their covariation with several personality traits, 24 guinea pigs, *Cavia aperea* f. *porcellus*, were tested using a battery of 12 cognitive tests. Four tests each were conducted to test for problem solving, association learning and social learning. We assessed consistency within each of these three domains and tested for cognitive and behavioural syndromes between domains. Problem solving and social learning were consistent across contexts and positively correlated with each other. In addition, both correlated positively with boldness, and problem solving showed a negative correlation with aggressiveness and sociopositive behaviour. Association learning was neither consistent nor correlated with personality or performance in the other cognition tasks. We showed contextual consistency of two cognitive traits and found multiple links to personality traits that were predicted by recent theory. Surprisingly, associative learning was not consistent, demonstrating the importance of testing the relation between personality and multiple cognitive traits to increase our understanding of individual variation in cognition and personality.

Recently, the intriguing possibility of an association between individual variation in animal behaviour, i.e. personality, and cognitive performance, sparked great research interest (Carere & Locurto, 2011; Griffin, Guillette, & Healy, 2015; Sih & Del Giudice, 2012). To better understand the mechanisms causing such individual variation in cognitive traits we need to learn more about their consistency over time and context and how they covary with each other and with personality traits. Certain personality types are known to be situated along a risk–reward axis. Bold, explorative and aggressive individuals engage in risky behaviours to gather resources quickly whereas shy individuals use more cautious strategies that are less risky but result in lower resource acquisition rates. A risk–reward trade-off is also often found in cognitive performance (Chittka, Skorupski, & Raine, 2009). Some individuals take fast decisions with little knowledge about possible risks, like making a wrong decision or exposing oneself to potential predators. Other individuals need more time to make more accurate decisions, which are often less risky. From these observations emerged the hypothesis that risky personality traits are associated with speed as opposed to accuracy in cognitive performance (Sih & Del Giudice, 2012).

Until now, a handful of studies tested the predicted linkage between personality and cognitive traits (Boogert, Reader, & Laland, 2006; Dugatkin & Alfieri, 2003; Guillette, Reddon, Hurd, & Sturdy, 2009). However, as pointed out by Griffin et al. (2015), studies that aim to reveal the mechanisms behind and the adaptiveness of such a link should investigate the consistency of cognitive performance. Individuals can change their expression of behaviour in response to environmental or motivational changes, called within-individual changes, i.e. plasticity. However, if consistent differences between individuals exist, individuals would maintain their relative behavioural expression across conditions and over time (between-individual differences), i.e. individuals that solve one type of task quickly in relation to other individuals will also solve other types of tasks quickly. Only if cognitive performance measured in a task reflects a consistent cognitive trait can testing for linkages to other traits or suites of traits reveal ecologically and evolutionarily meaningful coherences.

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Consistency in personality research is often reported as repeatability (Hayes & Jenkins, 1997). Repeatability quantifies the amount of phenotypic variance due to differences between individuals (Falconer & Mackay, 1996). Repeatability varies from 0 (no consistency) to 1 (perfect consistency). Low values on this scale indicate small changes between individual performances compared to within-individual changes across contexts and/or over time. High values indicate that within-individual changes are smaller than those between individuals. Behaviour is repeatable when individuals behave consistently through time and differ from one another (Falconer & Mackay, 1996).

The demonstration of consistency in cognitive traits such as learning, attention or memory requires testing individuals in multiple cognitively challenging tasks. Cross-context consistency requires individuals to perform similarly in at least two different tasks, such as reaching criterion in associative and spatial learning. Consistent traits often have a genetic basis and are therefore prone to be influenced by selection because repeatability sets the upper boundary for heritability (Falconer & Mackay, 1996). Thus, these traits hold the potential to change the trajectory of evolution (Boake, 1989).

The existence of between-individual correlations between different traits implies that these traits do not evolve independently. Thus, such correlations might heavily influence a population's or species' response to selection ('correlated selection', Roff, 1992; Stearns, 1992). To date, only a few studies have tested nonhuman animals across multiple cognitive tasks. Matzel et al. (2003) tested mice, *Mus musculus*, for associative fear conditioning, operant avoidance, odour discrimination and spatial learning. They found individual performances correlated between spatial learning and passive avoidance and between odour discrimination and spatial learning. Another study conducted by Herrmann and Call (2012) found clusters of independent cognitive traits for learning, inference and tool use in chimpanzees, *Pan troglodytes*. Guillette et al. (2009) found no correlations between acoustic discrimination, colour association and detour reaching in black-capped chickadees, *Poecile atricapillus*. Given the few studies conducted across very different species, further investigation of cognitive traits is necessary to reveal a broader picture of the consistency of cognitive traits in nonhuman animals.

Trait consistency is also important for investigating correlations between personality and cognitive traits. To estimate the potential influence of correlated traits on evolutionary processes, one needs to estimate between-individual correlations between several traits at a time, which allows one to draw conclusions about their proximate and ultimate causes. Behavioural correlations reflect the joint influences of between- and within-individual correlations (Dingemanse & Dochtermann, 2013; Dingemanse, Dochtermann, & Nakagawa, 2012). Between-individual correlations refer to the correlations between each individual's average performance across several traits, i.e. the correlation between the repeatable parts of traits. Within-individual correlations, in contrast, reflect individual plasticity across traits (Brommer, 2013). To advance our knowledge about consistency of cognitive traits in nonhuman animals, we assessed the consistency of problem-solving performance, associative learning and social learning across each of four contexts (i.e. test situations). We then asked whether cognitive performance in these three domains forms a cognitive syndrome. Finally, we tested whether the cognitive traits correlate with personality traits in guinea pigs, *Cavia aperea* f. *porcellus*.

The repeatability of the personality traits used in this study has already been demonstrated (Brust & Guenther, 2016; Zipser, Kaiser, & Sachser, 2013). In addition, individual differences in learning performance and phenotypic correlations with personality have been established (Brust & Guenther, 2015; Guenther, Brust, Dersen, & Trillmich, 2013). Therefore, guinea pigs are a good model species to study the relationship of personality and cognition. We tested for consistency of problem-solving behaviour across four food extraction tasks based on different mechanisms. We tested problem-solving performance because it has been linked to ecologically relevant traits, such as migration propensity or reproductive success in some species (Cole, Morand-Ferron, Hinks, & Quinn, 2012; Sol, Lefebvre, & Rodríguez-Teijeiro, 2005; Sol, Sayol, Ducatez, & Lefebvre, 2016) and may therefore be expected to differ between individuals. Consistency of associative learning performance was assessed by testing cues across different domains, i.e. colour, size, location and symbol association. In previous studies, we established the temporal consistency of associative learning in guinea pigs when individuals had to associate a food reward with the larger of two similar objects in four different association tasks (Brust & Guenther, 2016). Here, we built on these findings and tested for cross-context consistency of associative learning. Social learning was assessed by confronting animals with novel food, with an unknown terrain and with two novel food extraction apparatuses with which animals were tested alone and after watching a demonstrator. Guinea pigs are highly social and form stable rank hierarchies using a broad range of sociosexual behaviours (Machatschke, Bauer, Schrauf, Dittami, & Wallner, 2008; Sachser & Hendrichs, 1982). Social learning should be important for coping with the social environment in such a species and hence we hypothesized that it would be a consistent trait.

Regarding correlations between cognitive traits and personality traits, the framework proposed by Sih and Del Giudice (2012) included the prediction that bold and/or aggressive and less social individuals should be fast in learning new tasks that require high levels of activity or an interaction with novel set-ups. Hence, bold individuals should outperform shy individuals in our problem-solving tasks that require them to investigate an unknown apparatus and to perform certain motor actions for solving them. From previous studies, we know that boldness is strongly correlated with the number of trials needed to learn to knock over cylinders (Guenther et al., 2013). However, no correlation exists between the time an individual takes to approach a novel test set-up (i.e. boldness) and the trials needed to reach a learning criterion thereafter (Brust & Guenther, 2015). Sih and Del Giudice (2012) also predicted that, beyond individual learning strategies, social tendencies of individuals might contribute to differences in performance. They suggested that social individuals might be more attracted to conspecifics and rely more on social learning while less social individuals that either avoid conspecifics or aggressively drive them away might rely more on individual learning. Our previous findings show that shyer and at the same time more social individuals need more trials to individually learn an association. This finding fits well with the hypothesis stated above. We consequently predicted that shy individuals would outperform bold individuals in tasks requiring social learning.

METHODS

Animals and Housing

Twenty-four (12 male, 12 female) guinea pigs served as test subjects. A power analysis prior to the experiments indicated that a sample size of 24 would be large enough to detect statistical evidence for repeatability of traits when assuming an estimate of $R = 0.37$, the average repeatability across personality traits (Bell, Hankison, & Laskowski, 2009). Likewise, correlations between traits of this magnitude can be detected with this sample size. At the onset of testing, all animals were about 3 months old and sexually mature. They were kept in same-sex groups of four