



The fast and the flexible: cognitive style drives individual variation in cognition in a small mammal

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Patterns of individual differences in cognition have been studied empirically and systematically in the last decade, but causes and consequences of this variation are still largely unclear. A recent hypothesis suggests that one predictor of individual variation in cognition is personality, and specifically that personality types are linked to cognitive styles through a speed–accuracy trade-off. We tested specific predictions of this hypothesis, measuring individual differences in associative learning speed and flexibility, quantified via reversal learning, of 86 bank voles, *Myodes glareolus*, along with their activity and boldness. We found that bolder and more active individuals were fast, inflexible and persistent in the associative learning tasks, whereas shyer and less active individuals were slow and flexible. We also found evidence for a speed–accuracy trade-off: correct choices in the cognitive tasks required more time for all individuals compared to incorrect choices, but bolder, more active voles always made their decisions faster than reactive ones. The difference between the time required for a correct and an incorrect choice was most pronounced in initial learning for shyer and less active individuals, but for bolder, more active individuals it was most pronounced in the reversal learning task. We also found differences related to sex and age: females were faster than males to update information or correct incorrect choices and older animals took longer to initiate the test. Our results confirm the hypothesis that individual differences in behaviour are reflected in different ‘cognitive styles’, differentially trading off speed for flexibility and accuracy in cognitive tasks. Moreover, we provide the first evidence for the mechanisms of such a trade-off in a small mammal.

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Cognitive abilities are part of a species' adaptation to its environment (Dukas, 2004; Shettleworth, 2010). Since cognitive processes are not directly measurable, they are usually inferred by assessing a change in behaviour (e.g. Barron et al., 2015; Bebus, Small, Jones, Elderbrock, & Schoech, 2016; Griffin, Guillette, & Healy, 2015). Hence, the individual's behaviour is used to make inferences about its cognitive abilities (Bebus et al., 2016). Studying individual variation in cognition and individual variation in behaviour, that is, personality, in relation to each other might prove beneficial in multiple contexts. It might help identify responses that underlie specific cognitive abilities (i.e. the mechanistic basis of variation in behaviour), which is the aim of animal cognition researchers, as well as determine the adaptive significance of

behavioural and cognitive traits (i.e. the functional basis for variation in behaviour), which is the focus of behavioural ecologists (according to Griffin et al., 2015). However, up to now we have only limited knowledge about patterns of consistent individual differences in various aspects of cognition (e.g. Brust & Guenther, 2017; Chang, Ng, & Li, 2017; Chittka, Dyer, Bock, & Dornhaus, 2003; Wang, Brennan, Lachlan, & Chittka, 2015), even though this field of research is rapidly expanding (e.g. Cussen, 2017; Griffin et al., 2015; Shaw, 2017; Thornton & Lukas, 2012; van Horik, Langley, Whiteside, & Madden, 2017).

Here we investigated whether individual differences in animal personality are related to individual cognitive traits. Personality is defined as the set of individual differences in behaviour that are consistent across time and contexts (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). This variation extends to physiological traits (e.g. Koolhaas et al., 1999), is ecologically relevant (e.g. Wolf & Weissing, 2012) and may affect cognitive performance (e.g. Carere

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& Locurto, 2011; Locurto, 2007). Specifically, it has been proposed that behavioural types may be markers of different cognitive styles (Carere & Locurto, 2011; Sih & Del Giudice, 2012), defined as the specific strategies by which different individuals perform cognitive tasks (Bebus et al., 2016). Throughout this article, we use the expression 'cognitive style' in this way. It has been suggested that cognitive performance is a combination of cognitive ability and cognitive style (Bebus et al., 2016). Cognitive ability is an individual's capability to acquire, process, store and use information, whereas cognitive style is the specific strategy by which the individual acquires, processes, stores and uses the information (Bebus et al., 2016; Carere & Locurto, 2011; Griffin et al., 2015; Sih & Del Giudice, 2012). For example, two test subjects may have similar capability to discriminate between different cues, associate the characteristics of one with the reward, remember this association and recall it when presented again with the same setting. However, the individual cognitive style (e.g. how the individual focuses its attention) may influence the performance (Bebus et al., 2016). One subject may consistently look for the rewarded cue ignoring the, potentially rewarded, other cues, while the second may keep sampling the other cues as well. In an associative task, the first individual will achieve a better performance. In a reversal task, a measure of behavioural flexibility, the second individual will perform better because of the more complete information acquired through extended sampling (Bebus et al., 2016). Sih and Del Giudice (2012) also suggested that these strategies are related to trade-offs between speed and accuracy/flexibility. Their theoretical framework suggests that 'bolder individuals learn a particular contingency faster (i.e. in fewer trials) than do shyer individuals either because they recognise such contingencies sooner, lay them down in memory more readily, or have lower decision thresholds for association formation' (Griffin et al., 2015, p. 211). However, because such fast changes in the behavioural response (learning) are bound to the formation of routines (e.g. Benus, Den Daas, Koolhaas & Van Oortmerssen, 1990; Koolhaas et al., 1999), they would also be more challenged in reversal learning tasks that require flexible adjustments in response to altered circumstances. Conversely, shyer individuals might take longer to master a cognitive task (e.g. Sih, Bell, Johnson, & Ziemba, 2004) possibly because they depend more on, and are more sensitive to, environmental stimuli and keep sampling the environment, thus acquiring more complete and accurate information (e.g. Bebus et al., 2016; Benus et al., 1990; Groothuis & Carere, 2005). This strategy would enable them to flexibly adjust to altered circumstances and thus perform better in reversal learning tasks. So far, current empirical evidence for the proposed link between personality and cognition is mixed. Studies reporting connections between personality and cognitive performance have often not included direct reference to a speed–accuracy trade-off (e.g. Guillette, Reddon, Hurd, & Sturdy, 2009; Guillette, Reddon, Hoeschele, & Sturdy, 2011), and some of the studies investigating the presence of speed–accuracy/flexibility trade-offs have not included an assessment of the individuals' personality (e.g. Raine & Chittka, 2012; Wang et al., 2015). Finally, studies testing the connection between personality and cognition through a speed–accuracy/flexibility trade-off, in both vertebrates and invertebrates, present contradictory findings within and between species (summarized in Table 1).

Therefore, the main aim of this study was to test whether different personality types adopt different strategies to learn a cognitive task, and to test Sih and Del Giudice's (2012) predictions regarding a speed–accuracy/flexibility trade-off. Our study system was the bank vole, *Myodes glareolus*, a common boreal rodent species that exploits ephemeral food sources (e.g. Imholt, Reil, Plašil, Rödiger, & Jacob, 2016; Reil, Imholt, Eccard, & Jacob, 2015)

and is subject to intense predatory pressure (e.g. Jędrzejewski, Rychlik, & Jędrzejewska, 1993). We tested the voles for their olfactory associative learning speed and flexibility. The reward was the opportunity to return immediately to the vole's own home cage. Believing that associative learning tests should use the predominant sense of a species, we took the set of environmental demands and conditions that shape the species' behaviour and cognition into account when we designed our experiment. We exploited the voles' natural reliance on olfaction to gain information about their environment and the need to find shelter, providing a comparable motivation for all tested individuals. We expected faster learners to be bolder and more active whereas slower learners would show shyer, less active traits. We predicted that bolder, more active faster learners would be less flexible in updating behaviour in response to altered circumstances, and therefore that they would take longer to learn a reversal learning task than shyer, less active slower learners. Since personality might affect learning performance in a sex-dependent way (e.g. Titulaer, van Oers, & Naguib, 2012), we investigated differences between the strategies adopted by males and females to approach the cognitive tasks. Specifically, based on sex differences in space use and territoriality in bank voles (females are territorial and males have large overlapping ranges) and on existing literature on sex differences in cognition, we expected males to be faster learners and females to be more flexible (e.g. Guillamón, Valencia, Calés, & Segovia, 1986; Schuett & Dall, 2009). Lastly, we expected older individuals to be slower learners than younger ones.

METHODS

Animals and Housing

We tested 86 adult bank voles, 45 males and 41 females, born in captivity. Fifty voles originated from laboratory-born mothers; the remaining 36 originated from wild-caught females, trapped in Potsdam (Germany). A maximum of four individuals from the same litter (two males and two females) was included in our sample. At 3–5 weeks of age juveniles were weaned, sexed and assigned a unique identity. From then on, all animals were housed individually in standard polycarbonate cages (Typ III, Ehret GmbH, Mahlberg, Germany; 42 × 27 cm and 16 cm high). Light, temperature and humidity mirrored the natural conditions occurring outside the laboratory. Cages were provided with wood shavings and hay as bedding, and paper rolls for shelter. Water and food pellets (Ssniff V1594 R/M-H Ered II, Soed, Germany) were available ad libitum. Bedding was changed every 2 weeks.

Personality Tests

We assessed differences between individuals in activity, exploration and boldness using two standardized laboratory tests (Réale et al., 2007), developed for common voles (Herde & Eccard, 2013) and adjusted for bank voles. We conducted the first round of tests 2 days after the cognitive trials; the second round of tests took place 2 weeks later.

Open field test

Since bank voles have a polyphasic activity rhythm (e.g. Ylönen, 1988) it is difficult to test all individuals in an active state. However, state differences while testing may account for large variation in behavioural measures in many other studies. We therefore took subjects from their home cage only when they were active, that is, when they were perceived moving in the cage; this allowed us to test all animals during similar activity levels.

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