A general intelligence factor in dogs

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ABSTRACT

Hundreds of studies have shown that, in people, cognitive abilities overlap yielding an underlying 'g' factor, which explains much of the variance. We assessed individual differences in cognitive abilities in 68 border collies to determine the structure of intelligence in dogs. We administered four configurations of a detour test and repeated trials of two choice tasks (point-following and quantity-discrimination). We used confirmatory factor analysis to test alternative models explaining test performance. The best-fitting model was a hierarchical model with three lower-order factors for the detour time, choice time, and choice score and a higher order factor; these accounted jointly for 68% of the variance in task scores. The higher order factor alone accounted for 17% of the variance. Dogs that quickly completed the detour tasks also tended to score highly on the choice tasks; this could be explained by a general intelligence factor. Learning about g in non human species is an essential component of developing a complete theory of g; this is feasible because testing cognitive abilities in other species does not depend on ecologically relevant tests. Discovering the place of g among fitness-bearing traits in other species will constitute a major advance in understanding the evolution of intelligence.

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1. Introduction

In humans cognitive abilities such as navigating through space, understanding written language and number skills correlate positively; a person who is above average at one task is likely to be good at others (Deary, Penke, & Johnson, 2010; Deary, 2013). Hundreds of empirical phenotypic studies show that the structure of human abilities can be represented as a hierarchy with observed manifest measures or tests (such as verbal comprehension or arithmetic) at the bottom level, latent group factors (such as spatial or verbal skills) at the second level and a third factor at the apex (Carroll, 1993). This third factor, called g or Spearman's g after its discoverer Charles Spearman (Spearman, 1927), is a major focus of psychometric studies in the human behavioural sciences (Jensen, 1998; Johnson, Bouchard, Krueger, McGue, & Gottesman, 2004; Spinath, Ronald, Harlaar, Price, & Plomin, 2003).

Quantitative genetic methods developed in the 1970s and applied to data from adoption and twin studies have established the existence of genetic g; that is, abilities are correlated at the genetic as well as the phenotypic level (Bouchard & McGue, 1981; Deary, Spinath, & Bates, 2006; Loehlin, Horn, & Willerman, 1997; Pedersen, Plomin, Nesselroade, & McClearn, 1992). More recently, evidence from molecular genetic studies using DNA from large samples of unrelated people show that g is highly polygenic (Davies et al., 2011). Research on g is motivated partly because it is phenotypically associated with many important life outcomes including health (Batty, Deary, & Gottfredson, 2007; Luciano et al., 2010; Mõttus, Luciano, Starr, & Deary, 2013; Schou, Østergaard, Rasmussen, Rydahl-Hansen, & Phanareth, 2012), physical attractiveness (Langlois et al., 2000; Zebrowitz, Hall, Murphy, & Rhodes, 2002), brain resilience (Santarnecchi, Rossi, & Rossi, 2015), and life-expectancy (Batty et al., 2009; Batty et al., 2007; Whalley & Deary, 2001). The phrase cognitive epidemiology was coined to characterise research into the association between measured intelligence and traits such as health and life-expectancy in people (Deary & Der, 2005). It would be useful to learn whether the pattern of findings linking higher g with better health outcomes (Gottfredson, 2004) is particular to people or common among animals. Links between intelligence and health in non human animals would be especially interesting to probe because other animals neither smoke nor drink alcohol (habits that are lifestyle confounders in human studies). But as the legendary recipe prescribes, 'first catch your hare'; in this case, evidence concerning the structure of cognitive abilities in other species. This 'hare' is an essential first step in probing a link between intelligence and health in other species.

There is some evidence of g in non human animals (reviewed in Chabris, 2007; Galsworthy, Arden, & Chabris, 2013; Matzel, Sauce, & Wass, 2013). Yet evidence of the distribution, structure (phenotypic and genetic correlations among cognitive abilities), and the consequences of those differences in other species is exiguous: relatively

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few studies on general intelligence have been conducted in non human animals since 1920 (one review comprised 21 studies (Chabris, 2007), another comprised 24 studies (Galsworthy et al., 2013)). In order to test whether cognitive abilities are correlated or not, individual-level data on task performance need to be collected, in a sample of reasonable size. This has been done in mice (Galsworthy, Paya-Cano, Monleon, & Plomin, 2002; Locurto, Fortin, & Sullivan, 2002; Matzel et al., 2003; Wass et al., 2012), where a g factor was found, and in chimpanzees (Banerjee et al., 2009; Herrmann & Call, 2012; Hopkins, Russell, & Schaeffer, 2014) where a g factor was found in two out of three studies.

We tested the structure of measured cognitive abilities in dogs. Dogs and dog breeds are good models for within- and between-species spectra of cognitive abilities. The reasons are plural. Dogs are tractable; they enjoy interacting with people and can visit testing facilities, while living in their own homes. Dogs are not subject to confounding arising from lifestyles that may contribute to causal differences such as smoking, alcohol and drug use. Individual differences in dogs' cognitive abilities are not causally confounded with variability in socio-economic status. It is more feasible, cheaper and less intrusive to conduct repeated behavioural testing with dogs. Following phenotypic studies, dogs will be useful in genetic studies; genes associated with complex traits are easier to find in dogs than people because of their longer haplotype structure (Lequarré et al., 2011; Ostrander, Giger, & Lindblad-Toh, 2006). A consequence of their haplotype structure is that sample sizes needed for genomic analyses are much smaller in dogs than people. Some behavioural adaptations are breed-specific (pointing, herding); these involve both innate propensities and learning. Some traits are typical across all breeds, such as a tendency to affiliate with humans (see for review Benksy, Sinn, & Gosling, 2013; Miklosi, 2007; Shipman, 2010).

Our underlying assumption was that cognitive abilities would vary among dogs. This is implied by existing data in the animal behaviour literature but variance is rarely the focus of the work. For example, many animal cognition studies are framed as 'can species X do the Y task?' yet the results usually include animals that did, and did not, pass the test. Behavioural variability is the rule not the exception; since variance supplies evolution with its traction, it is a worthwhile object of study.

The present empirical study owes an intellectual debt to the work of John Paul Scott and John L Fuller (Scott & Fuller, 1965). We examined individual differences on a set of cognitive tasks (four increasingly complex versions of a detour task first designed in 1927 by the German psychologist, Wolfang Kohler (1887–1967)(Frank & Frank, 1982; Scott & Fuller, 1965), a quantity-discrimination task (Bonanni, Natoli, Cafazzo, & Valsecchi, 2011; Macpherson & Roberts, 2013; Prato-Previde, Marshall-Pescini, & Valsecchi, 2008; Ward & Smuts, 2006) and a point-following task (Elgier, Jakovcevic, Mustaca, & Bentosela, 2012; Ittyerah & Gaunet, 2009; Kaminski & Nitzschner, 2013; Lakatos, Gácsi, Topál, & Miklósi, 2012; Miklosi, Soproni, Miklósi, & Soproni, 2006). These tasks were administered to one breed of dog (border collies) selected from similar rearing and living environments. We administered six tasks (of which four were related) to the dogs and, guided by the human psychometrics literature, tested the fit of four basic models against the data.

2. Methods

2.1. Sample

We recruited 68 farm-living border collies from Wales. We chose a single breed to avoid confounds arising from differential selection. Scores from a basset hound tested against a whippet would be uninterpretable (Udell, Ewald, Dorey, & Wynne, 2014) This is because dogs have been selected by people for different behaviours, and they are the most polymorphic species on earth, varying greatly in leg length and other traits relevant to task performance. We selected farm border collies for several reasons. First, we wanted the dogs' backgrounds to be similar (in contrast with pet or companion animals, because variation in

level of enrichment could contribute to cognitive differences). Although border collies have been subject to artificial selection its focus has been on behaviour more than appearance; border collies remain morphologically variable with a reported moderate inbreeding coefficient of around 2.8% (Hoffman, Hamann, & Distl, 2002) but unknown empirically in our sample. Our sample comprised 68 dogs, (males 34, females 34) ranging in age from 1 to 12 years. We chose Wales as our recruitment centre because it is rural and enriched for border collies, having many hill farms where dogs work stock.

The animals in our sample differ from companion animals in background and behaviour that may be relevant to the study. They are kennelled outdoors and, although socialised to respond to their owner in a farmyard setting, they are unaccustomed to games, indoor behaviour and food treats.

2.2. Testing facility

All testing was conducted in a purpose-built barn (see supplementary materials) with a concrete floor that was washed down after each dog's session to eliminate or minimise scents. The same two colleagues administered all the testing. Testers wore plain clothing in all sessions to maintain consistency across dogs, and to reduce distraction in this breed, which is sensitive to visual markers including dress. All equipment was the same for each dog. All start points, and set-up points were marked with tape on the floor. All timings were recorded with a stopwatch.

2.3. Behavioural tests

On entering the barn, each dog was released to wander freely for three minutes among toys and treats scattered on the floor. This allowed the dogs to relax and adjust to the experimental setting. Diagrams of the set up for each test are given in the electronic supplementary materials.

Problem-solving tests were selected and adapted from the literature. All were appetitive—each problem was motivated by a food treat. We administered 4 versions of a detour test that was designed to measure the underlying construct of insight, navigation, and spatial ability. In each detour test a food treat is placed behind a see-through barrier in 4 configurations (short, long, V-shaped and maze-shaped). The test was to gain the food from a start point. We recorded how much time elapsed between the tester releasing the dog from the start point and the dog reaching the food reward.

The next test, point-following, was designed to measure how well each dog would make a behavioural inference from a visual cue (a human pointing towards a beaker). The point-following task was administered by a tester who stood equidistant between two inverted beakers (one was baited) set on the floor. The tester looked straight ahead, and pointed one arm towards an inverted beaker (the pointed beaker was not baited). On release by the second tester, the dog could choose one (or none) of two beakers to probe. Each dog was administered 10 consecutive trials. The pointed side was pseudo-randomised. We measured how many times the dog went to the pointed beaker as well as how quickly the dog went to the beaker. The baited beaker was not strongly olfactory (as far as we could tell), but served the purpose of focusing the challenge on what seems to be an evolved propensity in dogs—to follow human spatial directive points (Riedel, Schumann, Kaminski, Call, & Tomasello, 2008).

Next we tested individual differences in dogs' discrimination between two quantities by counting how many times each dog went to the larger of two presented food treats. Plates were prepared: a circle was drawn on each plate (diameters were: 2.5 cm, 3.5 cm, 4 cm, 6 cm, and 8.5 cm). Wet dog food mixed with tuna was spread inside the drawn circles. In each trial the dog's attention was directed to a tester holding two plates with circles of different diameters of food. The plates were shown to the dog, and then placed on the floor, in front of the tester. When the dog was released (by the second tester), he (or she) could go to a plate and eat. As soon as the dog went to a plate the other plate