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**Individual differences in behaviour and cognitive performance
in domestic dogs**

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“Courage and timidity are extremely variable qualities in the individuals of the same species, as is plainly seen in our dogs. Some dogs and horses are ill-tempered and easily turn sulky; others are good-tempered; and these qualities are certainly inherited.”

Charles Darwin (1871) *The Descent of Man and Selection in Relation to Sex*.
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TABLE OF CONTENTS

Acknowledgements	4
Author contributions	6
Chapter 1 – General Introduction	7
1.1. Individual behaviour differences	7
1.2. The concept of impulsivity	11
1.3. Individuality in problem solving - Unravelling cognitive processes	13
1.4. The science of the domestic dog – cognition, behaviour and relationship with people	15
1.4.1. Individual behaviour differences in dogs	17
1.4.1. Impulsivity in dogs	19
1.4.3. Physical cognition in dogs	21
1.5. Research questions - Chapter outline	24
1.6. References	26
Chapter 2	39
“The predictive value of early behavioural assessments in pet dogs – a longitudinal study from neonates to adults”	
<i>(accepted for publication in PLoS One)</i>	
Chapter 3	81
“Choice of conflict resolution strategy is linked to sociability in dog puppies”	
<i>(published in Applied Animal Behaviour Science)</i>	
Chapter 4	107
“Impulsive for life? The nature of long-term impulsivity in domestic dogs”	
<i>(published in Animal Cognition)</i>	
Chapter 5	118
“Dogs can learn to attend to connectivity in string pulling tasks”	
<i>(published in Journal of Comparative Psychology)</i>	
Chapter 6 – General Discussion	144
6.1. Individual behaviour differences	144
6.3. Impulsivity	149
6.4. Individuality in problem solving - Unravelling cognitive processes	153
6.5. Implications	158
6.6. References	160
Summary	169
Zusammenfassung	171
Curriculum Vitae	173

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AUTHOR CONTRIBUTIONS

Chapter 1.

Stefanie Riemer.

Chapter 2 (Study 1).

I designed this study with input from Corsin Müller, Friederike Range and Zsófia Virányi. I collected and analyzed the data with help by Corsin Müller and wrote the paper. Corsin Müller, Friederike Range and Ludwig Huber were involved in editing and revising the paper.

Chapter 3 (Study 2).

This study came out as part of Study 1. Addressing this research question was my own idea. I analysed the data with statistical input by Corsin Müller and wrote the paper. Corsin Müller, Zsófia Virányi, Ludwig Huber and Friederike Range contributed to editing and revising the paper.

Chapter 4 (Study 3).

This study represents a follow-up of a study by Hannah Wright (2012), employing identical methodology. I collected the data with a student helper, analyzed the data and wrote the paper. Daniel Mills and Hannah Wright contributed to editing and revising the paper.

Chapter 5 (Study 4).

The study design was planned jointly by Corsin Müller, Friederike Range, Ludwig Huber and myself. I collected the data together with Corsin Müller and student volunteers. I analysed the data with statistical support by Corsin Müller and wrote the paper. Corsin Müller, Ludwig Huber and Friederike Range were involved in editing and revising the paper.

Chapter 6.

Stefanie Riemer

CHAPTER 1

1. GENERAL INTRODUCTION

1.1. Individual behaviour differences

Charles Darwin pointed out already in 1871 that individual animals differed in what he called ‘qualities’, such as courage and timidity; nonetheless individual differences in behaviour and cognition in non-human animals have largely been neglected by scientists until the 20th century. Today it is well recognized that consistent inter-individual behavioural differences exist across the animal kingdom, from mammals to fish, birds, reptiles and amphibians to arthropods and molluscs (reviewed Wolf and Weissing, 2012), and a multitude of studies have been published on personality (Gosling, 2001) or the related concepts of temperament (Réale et al., 2007), behavioural syndromes (Sih et al., 2004) or coping styles (Koolhaas et al., 1999) in non-human animals.

Nevertheless, the terminology is still inconsistent in the field. Some authors (Bell, 2007; Dingemanse et al., 2010) consider personality, temperament and behavioural syndromes as analogues, meaning “consistent differences between individuals in their behaviour across time and contexts” (Dingemanse et al., 2010). Others view temperament as a precursor for personality (Freeman and Gosling, 2010). In the human literature, temperament has been defined as “early appearing, constitutionally based, relatively stable individual differences in emotional, motor, and attentional reactivity and self-regulation” (reviewed by Putnam, 2011) and personality as “those characteristics of individuals that describe and account for consistent patterns of feeling, thinking, and behaving” (Pervin and John, 1996). An alternative definition for behavioural syndromes is “suites of correlated behaviours across contexts” (Sih and Del Giudice, 2012), thus disregarding the temporal aspect, while repeatability of behaviour refers to temporal consistency without implying consistency across contexts (Bell et al., 2009). Finally, coping styles are relatively clearly defined as “a coherent set of behavioural and physiological stress responses which is consistent over time” (Koolhaas et al., 1999).

For the purpose of this thesis, I shall adhere to the broad definition of personality as “individual differences in behaviour that are consistent across time and contexts” (Bergmüller

& Taborsky, 2010; Stamps and Groothuis, 2010) and consider temperament as “inherited, early appearing tendencies that continue throughout life and serve as the foundation for personality” (Goldsmith et al., 1987). Furthermore, I use the term “behavioural consistency” to refer to temporal (but not necessarily contextual) stability of behaviour.

At a proximate level, consistent behavioural differences in animals have been shown to be related to distinct brain regions, neurotransmitters and stress physiology, for example via serotonin and dopamine transmitter-receptor systems (Cravchik and Goldman, 2000), gonadal reactivity (Kralj-Fišer et al., 2007), the pituitary-adrenal response (Stamps and Groothuis, 2010) and the functioning of the amygdala (Most et al., 2006). At an ultimate level, several explanations have been proposed for the puzzle of why such consistent inter-individual behavioural differences evolve and why evolution does not select for a single optimal phenotype. These include frequency dependent selection, differential fitness consequences of different strategies depending on the individual’s ‘state’, and fitness tradeoffs for different strategies (reviewed in Bell, 2007). Furthermore, if individuals in a social system consistently adopt alternative behaviour strategies, e.g. producing vs scrounging in resource acquisition, conflicts could be reduced to the benefit of both parties (Bergmüller and Taborsky, 2010), and there is evidence of individual niche selection depending on an individual’s behavioural tendencies (‘role choice’; Bergmüller and Taborsky, 2010).

Research on rodents and birds suggested two main alternative behavioural phenotypes in challenging situations, labelled reactive–proactive (Koolhaas et al., 1999), shy–bold (Frost et al. 2007, Réale et al. 2007), slow–fast (Drent et al., 2003), or passive–active (Martins et al. 2007). These are associated with different physiological responses and have a genetic basis (Koolhaas et al., 1999; Drent et al., 2003; Groothuis and Carere, 2005). Animals with a proactive coping styles generally show an active response to aversive situations and react with fighting or, when defeated with flight, whereas reactive individuals tend to behave passively (Benus et al., 1990; Koolhaas et al., 1999). Moreover, proactive animals show boldness in exploration, form routines quickly and demonstrate lower behavioural flexibility than reactive individuals, which are less explorative, less prone to routine formation and display higher behavioural flexibility (Benus et al., 1990; Koolhaas et al., 1999).

Factor analytical approaches, an empirical method for measuring an unobservable latent construct that accounts for correlations between variables (Budaev 2010), are another common method for classifying inter-individual behaviour differences (Forkman et al. 1995). Some factors commonly found in different animal species are activity/arousal, sociability and reactivity (Forkman et al. 1995). Also, equivalents of the traits extraversion, neuroticism, openness and agreeableness of the widely accepted five-factor model of human personality have been found to be applicable to nonhuman animals (Gosling and John 1999; Gosling et al. 2003). However, while links between conflict resolution strategies and personality factors are well documented in humans (Graziano et al., 1996; Park and Antonioni, 2007; Wood and Bell, 2008), apart from the coping styles model, relations between personality and conflict behaviour have rarely been studied in nonhuman animals (but see Miranda de la Lama et al., 2011).

Although the concept of personality implies consistency across time and situations, surprisingly little is known about the development and stability of individual behavioural differences in non-human animals and which factors, at which time points, influence them (Stamps and Groothuis, 2010). Often experience early in life is considered of prime importance in shaping later behaviour (Stamps and Groothuis, 2010). For example, in a line of great tits *Parus major*, later aggressiveness and speed of exploration could be modified by experimentally limiting food resources available to nestlings (Carere et al., 2005). There is furthermore much evidence that early handling of rodents has positive effects on later stress responsivity (Anisman et al., 1998; Mirescu et al., 2004; Plotsky and Meaney, 1993), but also after weaning, beneficial effects of handling have been demonstrated in farmed blue fox cubs (*Alopex lagopus*, Pedersen et al., 2002). Recent studies have suggested that salient experiences (for example a change of physical or social environment due to natal or breeding dispersal, migration, or joining a new social group) occurring after juveniles have become independent of their parents can also have profound effects on the expression of personality (Stamps and Groothuis, 2010) and that DNA methylation (an important epigenetic mechanism) can be altered by environmental stimuli throughout life (Szyf et al., 2008).

From a physiological perspective, personality changes are most likely to occur during stages of ontogeny when physiological and morphological systems are undergoing major reorganisation such as rapid morphogenesis, metamorphosis, or sexual maturation (Stamps

and Groothuis, 2010). Developmental mechanisms include genetic as well as epigenetic effects, and so behaviour at any point in time is the result of a continuous interaction between genes and experience (Stamps and Groothuis, 2010). Individual behaviour traits are furthermore likely to vary in their stability, depending on the underlying physiological system (Bell et al., 2009; Fratkin et al., 2013), and moreover, behavioural consistency may also be higher for some individuals than for others (Stamps and Groothuis, 2010). For example, in human children behavioural inhibition was more stable in individuals with either very high or very low initial scores compared to those with intermediate scores (reviewed in Stamps and Groothuis, 2010). It has even been suggested that contextual plasticity per se might be considered a personality trait (Stamps and Groothuis, 2010). There is furthermore evidence that behavioural consistency changes with age and varies between the sexes (depending on the trait, Bell et al., 2009). Not surprisingly, behavioural consistency decreases with increasing time between test and retest (reviewed by Bell et al., 2009; Stamps and Groothuis, 2010).

In humans there appears to be moderate stability in personality traits over time, with increasing stability after 2 years of age (Henderson and Wachs, 2007). In particular, rank order of personality features within a cohort (i.e. personality relative to that of other individuals) typically remains stable, while there is a general tendency towards decreases in neuroticism, extraversion, and openness, and small increases in agreeableness and conscientiousness with age (Costa et al. 2000). Although personality consistency according to Lewis (2001) is typically low, other studies found that personality test-retest correlations in adults lie in the range of 0.40–0.60 and above (Costa et al., 2000; Henderson and Wachs, 2007). Generally, it appears that human personalities become increasingly more stable from infancy up to at least 30 years of age (McCrae et al., 2000).

Much less is known about behavioural ontogeny in nonhuman animals. Carere et al. (2005) performed repeated testing of exploratory behaviour in great tits from two lines that were bidirectionally selected for fast or slow exploratory performance. At the level of the line, behavioural differences were stable between juvenile and adult age; however, at the individual level, consistency across time and situations was less evident, with slow birds becoming faster with age and exhibiting less behavioural stability than fast birds (Carere et al., 2005). In the Midas cichlid, *Cichlasoma citrinellum*, two of three tested aggression measures were stable from the juvenile phase through to adulthood (Francis, 1990).

A study on captive rhesus macaques (*Macaca mulatta*) demonstrated that stability was dependent on the trait in question (Stevenson-Hinde et al., 1980a). Confidence was rated to be stable at all ages, while ratings for excitability showed no stability until adulthood and those for sociability became stable after the age of three years. The authors furthermore report some correlations in social behaviour between the ages of 8, 16, and 52 weeks (Stevenson-Hinde et al., 1980a). However, the same authors found no correlation in a series of behavioural tests conducted with rhesus monkeys at one year of age and repeated at 2.5 years (Stevenson-Hinde et al., 1980b).

Also in domestic cats (*Felis catus*, Lowe and Bradshaw, 2001), behavioural consistency between the age of 4 months, 1 and 2 years was variable for different traits, with boldness being one of the most consistent traits (Lowe and Bradshaw, 2001). However, none of the investigated behaviours was significantly correlated between all age classes (Lowe and Bradshaw, 2001). Partial consistency of some traits but not others was reported also for young horses (*Equus caballus*) that were followed up for between 10 and 22 months (Lansade et al., 2008a, 2008b; Visser et al., 2001). In this species, social behaviours, fearfulness and reactivity to humans appear to be among the most stable traits while behaviour in a novel object test and responses to handling were stable only over shorter time intervals (Lansade and Bouissou, 2008; Lansade et al., 2008a, 2008b).

These diverse studies of behavioural development indicate that behaviour is frequently consistent when assessed at shorter time intervals, but often no relationship is found over long time periods. Different traits seem to exhibit different levels of stability, and likewise stability varies between individuals.

1.2. The concept of impulsivity

An individual characteristic with wide implications for behaviour and cognition that has shown high stability over time in humans is impulsivity. A comprehensive definition includes 1) decreased sensitivity to negative consequences, 2) rapid, unplanned reactions to stimuli before complete processing of information, and 3) lack of regard for long-term consequences (Moeller et al., 2001); however there is currently a lack of agreement on the definition of this concept. In part, the disagreement in the literature reflects the fact that many different psychological processes may underlie impulsive behaviour, such as the inability to foresee the

consequences of one's actions or the inability to retain the possible alternatives in memory (Arce and Santisteban, 2006). Several authors make a distinction between motor (or behavioural) impulsivity, i.e. response inhibition, and cognitive (or choice) impulsivity, i.e. the inability to weigh the consequences of immediate and future events (reviewed in Arce and Santisteban, 2006).

Impulsivity has been studied in the laboratory in both humans and nonhuman animals. Motor impulsivity is typically assessed with go/no-go tasks (e.g. Horn et al., 2003), reversal learning tasks (e.g., Pattij et al., 2003), or stop tasks (Avila et al., 2004). Several paradigms have been developed to measure cognitive impulsivity, or ability to wait. In delay of gratification paradigms, the subjects need to wait for a large reward during a delay period while a smaller reward is constantly available. Thus, they can reverse their choice when the delay becomes too long and so this task measures both cognitive and motor impulsivity (inhibitory control) (Reynolds et al., 2002). In tests of delay choice, the subject has to make a choice at the beginning that cannot be reversed (Evans and Beran, 2007). In exchange tasks, the subject is given a food item that it can subsequently exchange for another food item of higher quality or quantity (Leonardi et al., 2012). By varying the time delay until the large reinforcer is given, this task serves to measure cognitive impulsivity in addition to inhibitory control. Similarly, in accumulation tasks the quantity to gain increases regularly with time, so in order to maximise its gain, the subject has to refrain from consuming the available food items (Beran, 2002; Beran et al., 1999). Finally, in reverse reward contingency tasks, subjects need to choose the smaller of two food items in order to receive the larger one (Anderson et al., 2008).

The decrease in the present value of an outcome when its receipt is delayed is often referred to as delay discounting (Odum, 2011). Similar patterns – although at different magnitudes – emerge in a variety of species: Typically the function describing this decreasing preference for a larger but increasingly more delayed reward is hyperbolic (Odum, 2011), i.e., reward value increases as a hyperbolic function of its magnitude and decreases as a hyperbolic function of its delay or likelihood of occurrence (Arce and Santisteban, 2006). In humans, the ability to delay gratification appears to be an extremely stable individual characteristic. For example, preschool children's ability to refrain from eating a marshmallow in order to receive a second one after a time delay has been shown to be related to attentiveness, measures of IQ and academic success later in life (Mischel et al., 1988). Even 40 years after the initial test,

correlations of impulse control abilities with those measured during childhood were still significant (Casey et al., 2011). It has also been suggested that levels of impulsivity are stable from experiment to experiment in rats (*Rattus norvegicus*, Zaichenko and Merzhanova, 2011); however, there is a lack of test-retest data from nonhuman animals.

1.3. Individuality in problem solving - Unravelling cognitive processes

While individual *behavioural* differences have been met with increased interest in the last decades, individual variation in *cognitive* performance – although often quite striking (Thornton and Lukas, 2012) – has received even less attention. Comparative psychologists have long tended to ignore individual differences observed in cognitive testing by treating the variation observed as noise around the population mean (Herrmann and Call, 2012; Thornton and Lukas, 2012). Furthermore the remarkable abilities of a single or a few high-performing individuals – such as Kanzi the bonobo, Alex the African grey parrot and Betty the New Caledonian crow – are often considered as sufficient to demonstrate cognitive abilities at the level of the species (Thornton and Lukas, 2012). However, it has been pointed out that using only success or failure as dependent variable ignores the potentially relevant information of individual differences in problem solving (Thornton and Lukas, 2012), and so Thornton et al. (2012) suggest that focusing on failures as well as successes may shed light on the cognitive mechanisms employed.

An important point to consider is to what extent performance in cognitive tasks really reflects strategy choice versus cognitive constraint (Bensky et al. 2013). I here use the term ‘strategy’ sensu Hunt et al. (2006) and Tecwyn et al. (2012), who do not imply planning or foresight but use the term to denote alternative solutions to a given cognitive problem. Such cognitive strategies may include the use of heuristic rules, simple processes such as chaining, as well as higher level cognitive processes (Tecwyn et al., 2012). Inferring which mental processes animals are employing as they are solving problems in their physical or social environment represents a big challenge in cognitive biology. On the one hand, relatively simple mechanisms may underlie complex behaviours (Thornton et al., 2012). On the other hand, animals may fail in cognitive tasks not because of a lack of causal understanding but because of constraints such as limitations in working memory and attention (Seed et al., 2012; Thornton et al., 2012) or a lack of inhibitory control (Santos et al., 1999).

While some authors suggest that some animals are capable of causal reasoning (Beran et al., 1999; Heinrich, 1995; Huber and Gajdon, 2006; Taylor et al., 2009), others warn against over-interpreting animals' apparent understanding of cause–effect relationships in manipulation tasks (Herrmann et al., 2008; Povinelli et al., 2000; Tomasello and Call, 1997; Visalberghi and Tomasello, 1998). Often it may turn out that animals use simple configurational or perceptual rules to solve physical tasks. Some of the best evidence for causal understanding comes from two bird species, the kea (*Nestor notabilis*, Huber and Gajdon, 2006) and the raven (*Corvus corax*, Heinrich and Bugnyar, 2005). Nonetheless, even New Caledonian crows (*Corvus moneduloides*), corvids renowned as proficient tool users in the wild, seem to rely on operant conditioning and perceptual-motor feedback rather than causal understanding in a means-end task (Taylor et al., 2010). Also, in a series of experiments on chimpanzees' (*Pan troglodytes*) understanding of physical causal mechanisms, Povinelli (2000) concluded that the chimpanzees focused solely on the observable relations and showed no evidence of an understanding of the unobservable causal mechanisms. Conversely, inferential reasoning tasks have shown that apes perform better when causal cues are provided than when they have to form associations between arbitrary stimuli and responses, indicating some understanding of the physical properties of the world (Call, 2006).

In their 2007 review, Penn and Povinelli argue that neither an associationist approach nor a high-level inferential interpretation may adequately depict animals' capabilities in the physical domain. On the one hand, causal cognition in nonhuman animals appears to be more sophisticated than can be accounted for by traditional associationist theories (Penn and Povinelli, 2007). That is, animals appear to have certain domain-specific predispositions that bias their perception and manipulation of objects without the need for instrumental learning (Hauser et al., 2002; reviewed in Penn and Povinelli, 2007). On the other hand, such a heritable discriminative bias does not imply any awareness of the causal mechanisms (Penn and Povinelli, 2007). Taylor et al. (2010) suggest that animals can develop complex behaviour through understanding the consequences of their own actions, without using insight or planning ('embodied cognition', Wilson, 2002). Sometimes, remarkable performances can result from rule abstraction and the formation of representations based on observable features without causal understanding of unobservable forces (Seed et al., 2006); nonetheless under some conditions animals perform better when they can rely on causal rather than arbitrary cues (Call, 2006). Thus, to what extent nonhuman animals understand causal relationships is

still being debated, and carefully controlled experiments are needed to tease out how animals solve physical problems and whether different individuals may follow alternative rules to solve the tasks.

1.4. The science of the domestic dog – cognition, behaviour and relationship with people

Given their evolutionary history intertwined with humans, their easy accessibility and their behavioural versatility, domestic dogs (*Canis familiaris*) are ideally suited for investigating not only questions relating to the evolution and development of social cognition (Cooper et al., 2003; Huber et al., 2009; Miklósi et al., 2004), but also non-social cognition (e.g. Bräuer et al., 2006; Range et al., 2011; reviewed in Miklósi & Topál, 2012) and personality (Gosling, 2001; Gosling et al., 2003). They can be studied in sufficient sample sizes in a standardised way, enabling testing of hypotheses that would be more difficult to investigate in wild species (Bensky et al., 2013). Furthering our understanding of cognition and behaviour in domestic dogs is furthermore of high practical relevance, with domestic being among the most popular pets (e.g. 17% of Austrian households, Kotrschal et al., 2004, 31% of UK households, Murray et al., 2010, 36.5% of U.S. households, American Veterinary Medical Association, 2012, and 39% of Australian households, Richmond, 2013, owned at least one dog). Nonetheless, although dogs have been living alongside humans for some 15,000 years (Freedman et al., 2014), it is only relatively recently that they have become a popular subject in scientific research (Bensky et al., 2013).

Much previous research has addressed dogs' capabilities in the social domain. Over the course of domestication, dogs appear to have evolved unique abilities in reading and interacting with humans (e.g. Hare and Tomasello, 2005). For example, they are better able to interpret human pointing gestures than great apes (Bräuer et al., 2006) and are sensitive to humans' attentional focus (Schwab and Huber, 2006; Virányi et al., 2004). They show a wealth of communicative behaviours directed at humans (e.g. Gácsi et al., 2009), use social referencing from their owners to interpret stimuli in their environment (Merola et al., 2012), look to humans for help when faced with an insoluble problem (Miklósi et al., 2003) and even communicate referentially with humans (Miklósi et al., 2000). Comparative work has investigated parallels in social cognition between humans and dogs (e.g. Hare and Tomasello, 2005; Miklósi et al., 2004; Range et al., 2009, 2007; Topál et al., 2009; Virányi et al., 2006), and parallels between human social groups and dog-human mixed groups have been

suggested for attachment to humans, inequity avoidance, low levels of intragroup aggression, emotional synchronisation, selective imitation, pointing behaviour, initializing eye contact, utilizing human directional gestures, learning by exclusion etc. (reviewed in Topál et al., 2009, Table 1). Conversely, dogs never show other behaviours such as teaching, tool use or tool construction. An evaluation of such similarities and differences can enhance our understanding about the evolutionary origins of behaviour in our own species (Topál et al., 2009). The domestic dog is furthermore utilised as model organism for investigating various diseases (e.g. Russell and Proctor, 2006; Tracy and Randles, 2011), human attention deficit hyperactivity disorder (Lit et al., 2010; Vas et al., 2007), and cognitive ageing (Adams et al., 2000). For instance, a recent study demonstrated parallels in the development of attention and sensorimotor control over the lifespan in humans and dogs (Wallis et al., 2014).

Domestic dogs play various roles in human society. Beneficial effects of dogs on human health and wellbeing are well documented (Barker and Wolen, 2008; Fawcett et al., 2001; McNicholas et al., 2005; Serpell, 2003; Wilks, 1999). It is suggested that humans and pet dogs can form an attachment bond not dissimilar to that between parents and children (Topál et al., 1998), with dogs viewing their human caretakers as secure base (Horn et al., 2013; Palmer and Custance, 2008) and safe haven (Gácsi et al., 2013). Vice versa, there is evidence that dogs may serve as secure bases/ safe havens for people too (Zilcha-Mano et al., 2012). Additionally, highly trained dogs serve a variety of functions, for example as guide dogs for the blind, assistance dogs for people with hearing impairments or in wheelchairs, therapy dogs (Prestrude and O'Shea, 1998), military dogs (Sinn et al., 2010), police dogs (Slabbert and Odendaal, 1999), and search and rescue dogs (Jones et al., 2004).

Crucial to these functions is the recognition of individual behavioural differences between dogs. The number one reason why working dogs are disqualified is fearfulness, which is detrimental to performance in any working context (Overall and Dunham, 2005). However, requirements for different types of working dogs are different. While a very calm, stable predisposition is needed for optimal performance of sniffer dogs, heightened reactivity levels may be considered desirable for dual-purpose dogs that serve as patrol dogs as well (Overall and Dunham, 2005). Sharpness (“a dog’s ability to react in an aggressive way towards a serious or serious-looking attack”, Ruefenacht et al., 2002, p. 120) is suggested to be desirable in military patrol dogs (Haverbeke et al., 2009) whereas guide dogs for the blind should not

display any aggressive behaviour at all (Holdsworth, 1967, as cited by Murphy, 1998). Characteristics such as a calm/ compliant demeanour, high sociability, lack of aggressiveness, and a high energy level are considered as important by people describing the ‘ideal companion dog’ (King et al., 2009). If we can test or predict such individual predispositions, this would be highly valuable for matching puppies or dogs with the right families and selecting suitable dogs for particular jobs. Nonetheless, there is still a lack of consensus about the extent to which personality is temporally consistent in dogs (Fratkin et al., 2013). In fact, this question seems to be an understudied one in non-human animals in general (Stamps and Groothuis, 2010).

1.4.1. Individual behaviour differences in dogs

One of the earliest students of canine personality was Ivan Pavlov (1935 as cited by Rothbart, 2011), who noted distinctive behavioural differences in his dog subjects that affected performance in conditioning experiments. Convinced of strong links between animals’ and humans’ temperament, Pavlov classified these according to the four Hippocratic temperament types as sanguinic, phlegmatic, choleric and melancholic (Rothbart, 2011). His work on conditioning and individual differences was followed up by his student W. Horsley Gantt, who had a special interest in dogs’ susceptibility to experimental neurosis and associated individual differences in dogs’ motor, cardiovascular, and respiratory responses (Feuerbacher and Wynne, 2011). In the 1960s and 1970s, researchers focused on the genetic underpinnings of behaviour. Selective breeding experiments resulted in two strains of pointers, a ‘normal’ line that performed well in the field and a ‘nervous’ line – dogs that showed less exploratory behaviour, tended to freeze in response to a loud noise and tended to avoid or freeze and cower in the presence of humans (reviewed in Feuerbacher and Wynne, 2011). Scott & Fuller (1965) raised and tested some 300 dogs of five breeds under controlled conditions, investigating effects of breed and environmental conditions on confidence, trainability, problem solving ability etc. Despite having set out to investigate genetic influences on behaviour, this study also demonstrated the importance of the early environment and initiated a shift away from the belief in genetic control to a view emphasizing plasticity and flexibility of behaviour (Dewsbury, 2012).

Since Scott and Fuller’s (1965) seminal study, a large body of literature assessing dogs’ behaviour from an applied perspective has accumulated. Nonetheless, there is still very little

standardization in the terms used to describe personality in domestic dogs. In an overview of 51 studies on dog personality, the most frequently assessed traits were reactivity, fearfulness, responsiveness to training, aggression, and sociability (Jones and Gosling, 2005), though investigated traits vary widely. For instance, Gosling et al. (2003) identified four traits as equivalent to four of the five human personality traits in the five-factor model used in human psychology: Energy (c.f. the human personality factor Extraversion), Affection (c.f. human Agreeableness), Emotional Reactivity (c.f. human Neuroticism) and Intelligence (c.f. human Openness/Intellect). Svartberg and Forkman's (2002) factor analytical study based on a personality test for working dogs found five traits – Playfulness, Chase-proneness, Curiosity/Fearlessness, Sociability and Aggressiveness – and one higher-order, broader dimension, interpreted as a shyness–boldness continuum. Using an adjective based questionnaire, Ley et al. (2008) determined five traits labelled extraversion, neuroticism, self-assuredness /motivation, training focus and amicability, while the C-BARQ (Canine Behavioral Assessment and Research Questionnaire) yields 11 traits, stranger-directed aggression, owner-directed aggression, stranger-directed fear, nonsocial fear, dog-directed fear or aggression, separation-related behaviour, attachment or attention-seeking behaviour, trainability, chasing, excitability and pain sensitivity (Hsu and Serpell, 2003). These different findings reflect the different methodologies and research questions, ranging from comparing canine and human personalities to selecting dogs for particular functions to getting an overview over personality traits in dogs and relating them to environmental or genetic factors.

A variety of tests are in use for selecting breeding stock (van der Borg and Graat, 2009), assessment of working dogs (Svartberg, 2002), assessing characteristics of shelter dogs (Bollen and Horowitz, 2008; Christensen et al., 2007; Lucidi et al., 2005; Valsecchi et al., 2011), selecting dogs to be trained as service dogs (Weiss and Greenberg, 1997), and predicting puppies' suitability for work as guide dogs, police dogs or military dogs (Asher et al., 2013; Beaudet et al., 1994; Goddard and Beilharz, 1986; Scott and Beilfelt, 1976; Slabbert and Odendaal, 1999; Svobodova et al., 2008; Wilsson and Sundgren, 1998a). All of these assessments are valuable only if there is a degree of stability in individual dogs' behaviour. However, while a recent review indicated that overall consistency is moderate, there is still a lack of agreement about the temporal consistency of behavioural tendencies in dogs (Fratkin et al., 2013).

One reason why behavioural assessments of dogs are of wide interest is assessing individuals' propensity to react aggressively. Nonetheless, while aggression in dogs has been related to numerous characteristics such as sex, reproductive status, breed or breed groups, environmental variables and characteristics of the owners (e.g. Serpell, 2005; Duffy et al., 2008; Casey et al., 2013), its relationship with other behavioural measures and alternative conflict resolution strategies have been little explored (but see links between impulsivity and aggression, section 1.4.2).

1.4.2. Impulsivity in dogs

One trait that has been associated with aggressive behaviour in both dogs (Fatjó et al., 2005; Reisner et al., 1996; Wright et al., 2012) and other animals (e.g. Winstanley et al., 2006; van den Bergh et al., 2006; Cervantes and Delville, 2009) is impulsivity. Although, conceivably, this trait has wide implications for the dog-human relationship, only a few studies have explored this characteristic in dogs. Some comparative studies suggest that dogs can serve models for investigating the mechanisms underlying human attention deficit hyperactivity disorder (ADHD), such as impulsive behaviours, attention and hyperactivity. For instance, questionnaires originally designed for evaluating ADHD related problems in children have been successfully adapted for dogs (Lit et al., 2010; Vas et al., 2007).

A different approach was taken by Wright et al. (2011), who designed an impulsivity questionnaire especially for dogs based on an expert survey. The Dog Impulsivity Assessment Scale (DIAS, a 19-item questionnaire) yielded an overall questionnaire score and three principal components, labelled 'Behavioural Regulation', 'Aggression and Response to Novelty', and 'Responsiveness'. The questionnaire detected breed and size differences, with smaller and younger dogs scoring higher on impulsivity. Moreover, dogs with behaviour problems had significantly higher impulsivity scores than those whose owners reported no behaviour problems (Wright et al., 2011). This result is in line with previous studies invoking impulse control deficits in relation to behaviour problems, in particular aggressive behaviour, in dogs (Fatjó et al., 2005; Reisner et al., 1996). Additionally, a follow-up study demonstrated that the overall questionnaire score and the 'Behaviour regulation' factor of the DIAS were significantly correlated with levels of dopamine and serotonin metabolites in the urine of the subjects (Wright et al. 2012).

Impulsivity, or aspects of it, have also been studied by means of behavioural tests. Bray et al. (2013) conducted three behavioural tests, which they assumed to measure inhibitory control. In the social task, dogs had to bypass a ‘stingy’ experimenter holding a high value reward who had previously never shared any food with them. Instead, they could obtain a reward – albeit of lower value – by approaching a generous experimenter, who always shared food with them. In the A-not-B task, the dogs had to refrain from searching for food in a previously rewarded location after the food had been displaced – in full view – from this location to a novel hiding place. In the cylinder task, dogs were initially given familiarization trials in which they learned to obtain food out of an opaque cylinder attached horizontally to a wooden board. In the test trials the opaque cylinder was replaced with a transparent one so that the reward was visible but could not be obtained directly. Instead, as in the previous trials, the dogs had to make a detour to obtain the reward and thus needed to control their impulse to approach the now visible reward directly. The dogs demonstrated inhibitory control in all of the tasks. There was a ceiling effect in the A-not-B task, with only 6 of 33 dogs committing the A-not-B error in the first trial. Performances in the social task and the cylinder task were more varied; however, there was no correlation in performance between tasks, possibly because neither test was a pure measure of inhibitory control but required quantity discrimination, reputation-like inferences, learning, or physical problem solving abilities, respectively (Bray et al., 2013).

Two studies to date have experimentally assessed dogs’ ability to delay gratification, with surprisingly good results. Leonardi et al. (2012) tested five domestic dogs in a cooperative exchange task with an experimenter. Not only did all subject consistently exchange lower-value for higher-value rewards, they were also able to perform two and three exchanges in succession. When introducing delays until the higher value reward was given, dogs sustained delays ranging from 10 s up to 10 min for the largest rewards. The data of Leonardi et al. (2012) suggest that the dogs “anticipated delay duration and made decisions according to the relative reward values offered” (p. 107). Moreover, they were willing to sustain longer waits for smaller value rewards than primates (Leonardi et al., 2012).

A different method for assessing individuals’ ability to delay gratification was applied by Wright et al. (2012) in a task they are referring to as “delayed reward choice test”. Following pre-training during which the actions were trained and contingencies were introduced, dogs

were given 15 minutes of free access to two panels. When depressed, one panel delivered a small reward (one piece of food) immediately, the other delivered a larger reward (three pieces of food) but after a delay. This delay increased when the dogs selected the large delayed device. The number of times the dogs pressed the large delayed panel during the waiting period can be considered as a measure of motor impulsivity. Maximum delays reached within 15 minutes of testing ranged from 7 to 27 seconds. The validity of this test was demonstrated by significant correlations between dogs' performance and owner-reported impulsivity according to the DIAS: dogs judged to be more impulsive by their owners reached shorter maximum delays and so demonstrated a greater preference for smaller, more immediate rewards (Wright et al., 2012). The test and the DIAS questionnaire both proved to be robust over shorter time frames (a few weeks, Wright et al., 2012, 2011), but consistency over longer time frames has not been investigated to date.

1.4.3. Physical cognition in dogs

While dogs' outstanding skills related to social interactions with humans are well documented, less is known about physical cognition (comprising skills involving space, quantity, and causality, Herrmann et al., 2010) in dogs. It has been demonstrated that they possess some understanding of object permanence and so can follow visible displacement tasks but fail in invisible displacement tasks (reviewed in Bensky et al., 2013; Fiset and Plourde, 2013; Miklósi, 2009). Furthermore, dogs are easily misled when human-given ostensive cues are conflicting with observations (Kis et al., 2012; Topál et al., 2009). Thus, in a visible displacement task, dogs performed better in noncommunicative or nonsocial hiding contexts than during an ostensive-communicative condition, as communicative cues from the experimenter apparently contributed to the emergence of this perseverative search error (Topál et al., 2009). Also, in a two-way object choice task, in which the experimenter showed either the full or the empty container to the subject before it could make its choice, dogs initially tended to select the container that had been manipulated by the human. However, when both containers were manipulated in the same way, the dogs chose the baited box more frequently than was expected by chance, suggesting that they inferred the location of the reward (Erdőhegyi et al., 2007). The authors conclude that dogs have the ability for simple inference but that social cues can easily override the causal cues (Erdőhegyi et al., 2007; Miklósi, 2009; Topál et al., 2009). Dogs have furthermore demonstrated a gravity bias, i.e. they expect an object to fall down vertically, but they do not understand that this trajectory

can be diverted by diagonal tubes (Osthaus et al., 2003). Both a violation of expectation paradigm (West and Young, 2002) and choice studies (Prato-Previde et al., 2008; Ward and Smuts, 2007) indicated that dogs have some numerical competency and select the larger of two quantities of food significantly above chance level. However, they will be misled if their owners draw their attention to the smaller quantity (Prato-Previde et al., 2008).⁷

Dogs' strong reliance on human cues can be explained by selection in the course of domestication for their ability to communicate and cooperate with humans (Miklósi et al., 2004). In contrast, there is no reason to assume that they were selected for abilities in the physical domain (Bräuer et al., 2006). Rather, it has been suggested that under human custody, selection in this domain may have been relaxed (Miklósi, 2009), or that dogs may even have been selected for special skills which might interfere with physical cognitive abilities (attentiveness towards human actions; Miklósi, 2009; Topál et al., 1997). Several studies demonstrated poor performance of domestic dogs in physical cognition tasks compared to great apes (Bräuer et al., 2006), as well as to their closest relatives, wolves (*Canis lupus*, Frank and Frank, 1985, 1982; Frank, 1980; Hiestand, 2011) whereas others indicated similar capabilities of dogs and wolves in object permanence tasks (Fiset and Plourde, 2013) and means-end tasks (Range et al., 2012).

Bräuer et al. (2006) compared great apes and dogs in a variety of object choice tasks requiring them to infer the location of hidden food by either social (pointing etc.), behavioural (manipulation by the experimenter) or causal cues (e.g. noise when shaken). Consistent with the “Social Dog, Causal Ape-Hypothesis”, apes outperformed dogs in the causal tasks while dogs outperformed apes in the social ones (Bräuer et al., 2006). Also, wolf puppies proved to be more proficient than same aged Malamute puppies in detour tests (Frank, 1980) and in experiments involving puzzle boxes of increasing difficulty (Frank and Frank, 1982). While these results are not entirely conclusive as the differences could also be attributed to different speeds of development in the wolves and the dogs, a recently published study on a vertical string pulling task in adult wolves and German shepherd dogs supports the previous findings (Hiestand, 2011). In contrast, no detrimental effects of domestication on physical cognitive ability were apparent in recent comparative studies on object permanence (Fiset and Plourde, 2013) and on a horizontal string pulling task in dogs and wolves (Range et al., 2012).

The string pulling task is one of the most commonly used tasks to test individuals' understanding of means end connections. It involves an out-of-reach object that is desirable to the subject and can be obtained only by pulling on a string attached to it (Lea et al., 2006). Combinations of several strings laid out at various angles can introduce varying complexity in this task (e.g. Osthaus et al., 2005). Previous studies showed that domestic dogs could solve simple tasks requiring them to pull a single perpendicular or diagonal string or to select the baited one out of a choice of two perpendicular parallel strings. However, they failed in more complex setups such as when strings were crossed or when only one of two rewards was connected with a string (Osthaus et al., 2005; Range et al., 2012). Due to their strong tendency to paw near where they perceived the reward, committing the so-called proximity error, it was suggested that dogs lack an understanding of means-end connections (Osthaus et al., 2005).

Nonetheless, dogs' performance in a different means-end paradigm was suggestive of some means-end understanding: In the support problem, subjects were given a choice between two boards, one with a reward resting on top of it, the other unbaited but with a second reward placed to the side of it (Range et al., 2011). The rewards were inaccessible behind a fence and could thus be obtained only by pulling out the baited board. The dogs spontaneously selected the correct board significantly more often than expected by chance, leading to the conclusion that they possess the ability to consider means-end relationships in this task (Range et al., 2011; but see a new appraisal by Müller et al., 2014). Thus, studies on dogs' understanding of means-end connections remain inconclusive and this topic warrants further investigations.

1.5. Research questions - Chapter outline

This thesis explores individual differences in domestic dogs at the level of both behaviour and cognition. It comprises a combination of pure and applied research by presenting three studies related to individual behavioural differences in dogs and one study on individual problem solving abilities. Chapters 2-5 represent original studies, which have been published or accepted for publication in peer-reviewed scientific journals. The results are discussed and conclusions are drawn in Chapter 6.

Chapter 2 (Study 1, accepted for publication in PLoS One)

It is suggested that temperament characteristics can be distinguished already in newborn dogs (Trumler, 1986; E. Kersting, pers. comm.). However, while ‘temperament tests’ are sometimes performed with neonate dog puppies (E. Kersting, pers. comm.), to my knowledge no peer-reviewed study exists on the validity of such tests. More commonly, tests are conducted with dog puppies during the socialisation period in order to assess their suitability for a particular function such as guide dog work, police or military work. However, this is a period of rapid developmental change (Wilsson and Sundgren, 1998), and results regarding the predictive value of such tests have been mixed, with some studies finding no correspondence between behaviour in puppy tests and behavioural ratings at a later date (Beaudet et al., 1994; Goddard and Beilharz, 1986; Wilsson and Sundgren, 1998) and others suggesting a level of predictability (Asher et al., 2013; Scott, Beilfelt, 1976; Slabbert and Odendaal, 1999; Svobodova et al., 2008). Study 1 reports on longitudinal behavioural data of a cohort of Border Collies. The dogs were assessed in behavioural tests at three points in time, a neonate test at 2-10 days of age, a puppy test at the age of 6-7 weeks and an adult test at the age of 1.5-2 years. The predictive value of early assessments is discussed and an explanation for the diverging results of previous studies is offered.

Chapter 3 (Study 2, published in Applied Animal Behaviour Science)

Few studies have assessed the effect of personality on conflict behaviour in non-human animals. A degree of consistency in dogs’ responses towards a threatening experimenter in repeated tests suggests a relationship between dog personality and conflict behaviour, although certain responses (friendly or threatening behaviour) appear to be more consistent than others (active or passive avoidance; Vas et al., 2008a). Study 2 explores links between puppies’ conflict behaviour and behaviour in other contexts by relating responses to restraint

tests (assumed to represent mild conflict situations) to behaviour in a friendly greeting situation and towards a novel object.

Chapter 4 (Study 3, published in *Animal Cognition*)

Impulsivity is a characteristic that has demonstrated remarkable stability through ontogeny and has numerous implications for everyday life in humans (de Wit et al. 2007; Casey et al., 2011; Mischel et al., 1988). It has furthermore been associated with behaviour problems in domestic dogs (Fatjó et al., 2005; Reisner et al., 1996; Wright et al., 2011); however, long-term data on the consistency of impulsivity in dogs and other non-human animals are lacking. In Study 4, I examined test-retest correlations of convergent measures of impulsivity in pet dogs, including a behavioural test and owner questionnaires, over an interval of over six years, to assess whether impulsivity exhibits stability in dogs.

Chapter 5 (Study 4, published in *Journal of Comparative Psychology*)

Previous studies yielded inconsistent results regarding the question whether dogs can attend to means-end relationships. While studies on string pulling in domestic dogs gave no indication of means-end understanding (Osthaus et al., 2005; Range et al., 2012), dogs spontaneously solved a different means-end paradigm, the support problem (Range et al., 2011, but see Müller et al., 2014). Possibly, contextual differences account for these differences in cognitive performance and decision making between studies. Therefore the aim of Study 4 was to investigate how dogs solve such tasks and to what extent they may possess an understanding of means-end connections. I tested this by presenting pet dogs with several conditions of a string pulling task and report on various choice rules that different dogs appear to follow.

Chapter 6

The main findings and implications of the thesis are discussed.

1.6. References

- Adams, B., Chan, A., Callahan, H., Milgram, N.W., 2000. The canine as a model of human cognitive aging: recent developments. *Prog. Neuro-Psychopharmacology Biol. Psychiatry* 24, 675–692.
- Anderson, J.R., Hattori, Y., Fujita, K., 2008. Quality before quantity: Rapid learning of reverse-reward contingency by capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 122, 445.
- Anisman, H., Zaharia, M.D., Meaney, M.J., Merali, Z., 1998. Do early-life events permanently alter behavioral and hormonal responses to stressors? *Int. J. Dev. Neurosci.* 16, 149–164.
- Arce, E., Santisteban, C., 2006. Impulsivity: a review. *Psicothema* 18, 213–220.
- Asher, L., Blythe, S., Roberts, R., Toothill, L., Craigon, P.J., Evans, K.M., Green, M.J., England, G.C.W., 2013. A standardized behavior test for potential guide dog puppies: Methods and association with subsequent success in guide dog training. *J. Vet. Behav. Clin. Appl. Res.* 8, 431–438.
- Avila, C., Cuenca, I., Félix, V., Parcet, M.-A., Miranda, A., 2004. Measuring impulsivity in school-aged boys and examining its relationship with ADHD and ODD ratings. *J. Abnorm. Child Psychol.* 32, 295–304.
- Barker, S.B., Wolen, A.R., 2008. The benefits of human–companion animal interaction: A review. *J. Vet. Med. Educ.* 35, 487–495.
- Beaudet, R., Chalifoux, A., Dallaire, A., 1994. Predictive value of activity level and behavioral evaluation on future dominance in puppies. *Appl. Anim. Behav. Sci.* 40, 273–284.
- Bell, A.M., 2007. Future directions in behavioural syndromes research. *Proc. R. Soc. B Biol. Sci.* 274, 755–761.
- Bell, A.M., Hankison, S.J., Laskowski, K.L., 2009. The repeatability of behaviour: a meta-analysis. *Anim. Behav.* 77, 771–783.
- Bensky, M.K., Gosling, S.D., Sinn, D.L., 2013. The World from a Dog’s Point of View: A Review and Synthesis of Dog Cognition Research. *Adv. Study Behav.* 45, 209–406.
- Benus, R.F., Den Daas, S., Koolhaas, J.M., Van Oortmerssen, G.A., 1990. Routine formation and flexibility in social and non-social behaviour of aggressive and non-aggressive male mice. *Behaviour* 176–193.
- Beran, M.J., 2002. Maintenance of self-imposed delay of gratification by four chimpanzees (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). *J. Gen. Psychol.* 129, 49–66.

- Beran, M.J., Savage-Rumbaugh, E.S., Pate, J.L., Rumbaugh, D.M., 1999. Delay of gratification in chimpanzees (*Pan troglodytes*). *Dev. Psychobiol.* 34, 119–127.
- Bergmüller, R., Taborsky, M., 2010. Animal personality due to social niche specialisation. *Trends Ecol. Evol.* 25, 504–511.
- Bollen, K.S., Horowitz, J., 2008. Behavioral evaluation and demographic information in the assessment of aggressiveness in shelter dogs. *Appl. Anim. Behav. Sci.* 112, 120–135.
- Bräuer, J., Kaminski, J., Riedel, J., Call, J., Tomasello, M., 2006. Making inferences about the location of hidden food: social dog, causal ape. *J. Comp. Psychol.* 120, 38.
- Bray, E.E., MacLean, E.L., Hare, B.A., 2013. Context specificity of inhibitory control in dogs. *Anim. Cogn.* 1–17.
- Budaev, S.V., 1997. ‘‘Personality’’ in the guppy *Poecilia reticulata*: a correlational study of exploratory behavior and social tendency. *J. Comp. Psychol.* 111, 399–411.
- Call, J., 2006. Descartes’ two errors: Reason and reflection in the great apes, in: S. Hurley, M.N. (Ed.), *Rational Animals?* Oxford University Press, Oxford, pp. 219–234.
- Carere, C., Drent, P.J., Privitera, L., Koolhaas, J.M., Groothuis, T.G.G., 2005. Personalities in great tits, *Parus major*: stability and consistency. *Anim. Behav.* 70, 795–805.
- Casey, B.J., Somerville, L.H., Gotlib, I.H., Ayduk, O., Franklin, N.T., Askren, M.K., Jonides, J., Berman, M.G., Wilson, N.L., Teslovich, T., others, 2011. Behavioral and neural correlates of delay of gratification 40 years later. *Proc. Natl. Acad. Sci.* 108, 14998–15003.
- Christensen, E., Scarlett, J., Campagna, M., Houpt, K.A., 2007. Aggressive behavior in adopted dogs that passed a temperament test. *Appl. Anim. Behav. Sci.* 106, 85–95.
- Cooper, J.J., Ashton, C., Bishop, S., West, R., Mills, D.S., Young, R.J., 2003. Clever hounds: social cognition in the domestic dog (*Canis familiaris*). *Appl. Anim. Behav. Sci.* 81, 229–244.
- Costa, P.T., Herbst, J.H., McCrae, R.R., Siegler, I.C., 2000. Personality at midlife: stability, intrinsic maturation, and response to life events. *Assessment* 7, 365–78.
- Cravchik, A., Goldman, D., 2000. Neurochemical individuality: genetic diversity among human dopamine and serotonin receptors and transporters. *Arch. Gen. Psychiatry* 57, 1105–1114.
- de Wit, H., Flory, J. D., Acheson, A., McCloskey, M., & Manuck, S. B. 2007. IQ and nonplanning impulsivity are independently associated with delay discounting in middle-aged adults. *Pers. Individ. Differ.* 42, 111–121.
- Dewsbury, D.A., 2012. A history of the behavior program at the Jackson Laboratory: An overview. *J. Comp. Psychol.* 126, 31–44.

- Drent, P. J., van Oers, K., & van Noordwijk, A. J. 2003. Realized heritability of personalities in the great tit (*Parus major*). *Proc R Soc Lond [Biol]* 270, 45–51.
- Erdőhegyi, Á., Topál, J., Virányi, Z., Miklósi, Á., 2007. Dog-logic: inferential reasoning in a two-way choice task and its restricted use. *Anim. Behav.* 74, 725–737.
- Evans, T.A., Beran, M.J., 2007. Delay of gratification and delay maintenance by rhesus macaques (*Macaca mulatta*). *J. Gen. Psychol.* 134, 199–216.
- Fatjó, J., Amat, M., Manteca, X., 2005. Aggression and impulsivity in dogs. *Vet. J.* 169, 150.
- Fawcett, N., Gullone, E., others, 2001. Cute and cuddly and a whole lot more? A call for empirical investigation into the therapeutic benefits of human--animal interaction for children. *Behav. Chang.* 18, 124–133.
- Feuerbacher, E.N., Wynne, C.D.L., 2011. A history of dogs as subjects in North American experimental psychological research. *Comp Cogn Behav Rev* 6, 46–71.
- Fiset, S., Plourde, V., 2013. Object permanence in domestic dogs (*Canis lupus familiaris*) and gray wolves (*Canis lupus*). *J. Comp. Psychol.* 127, 115.
- Forkman, B., Furuhaug, L.L., Jensen, P. 1995. Personality, coping patterns, and aggression in piglets. *Appl. Anim. Behav. Sci.* 45, 31–42.
- Francis, R.C., 1990. Temperament in a Fish: A Longitudinal Study of the Development of Individual Differences in Aggression and Social Rank in the Midas Cichlid. *Ethology* 86, 311–325.
- Frank, H., 1980. Evolution of canine information processing under conditions of natural and artificial selection. *Z. Tierpsychol.* 53, 389–399.
- Frank, H., Frank, M.G., 1982. Comparison of problem-solving performance in six-week-old wolves and dogs. *Anim. Behav.* 30, 95–98.
- Frank, H., Frank, M.G., 1985. Comparative manipulation-test performance in ten-week-old wolves (*Canis lupus*) and Alaskan malamutes (*Canis familiaris*): A Piagetian interpretation. *J. Comp. Psychol.* 99, 266.
- Fratkin, J.L., Sinn, D.L., Patall, E.A., Gosling, S.D., 2013. Personality Consistency in Dogs: A Meta-Analysis. *PLoS One* 8, 8:e54907.
- Freedman, A.H., Gronau, I., Schweizer, R.M., Ortega-Del Vecchyo, D., Han, E., Silva, P.M., Galaverni, M., Fan, Z., Marx, P., Lorente-Galdos, B., Al., E., 2014. Genome sequencing highlights the dynamic early history of dogs. *PLoS Genet.* 10, e1004016.
- Freeman, H.D., Gosling, S.D., 2010. Personality in nonhuman primates: a review and evaluation of past research. *Am. J. Primatol.* 72, 653–671.

- Frost, A. J., Winrow-Giffen, A., Ashley, P. J. & Sneddon, L. U. 2007. Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proc R Soc Lond [Biol]* 274, 333–339.
- Gácsi, M., Gyoöri, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B., Miklósi, Á., 2009. Explaining dog wolf differences in utilizing human pointing gestures: selection for synergistic shifts in the development of some social skills. *PLoS One* 4, e6584.
- Gácsi, M., Maros, K., Sernkvist, S., Faragó, T., Miklósi, Á., 2013. Human analogue safe haven effect of the owner: behavioural and heart rate response to stressful social stimuli in dogs. *PLoS One* 8, e58475.
- Goddard, M.E., Beilharz, R.G., 1986. Early prediction of adult behaviour in potential guide dogs. *Appl. Anim. Behav. Sci.* 15, 247–260.
- Goldsmith, H.H., Buss, A.H., Plomin, R., Rothbart, M.K., Thomas, A., Chess, S., Hinde, R.A., McCall, R.B., 1987. Roundtable: What is temperament? Four approaches. *Child Dev.* 505–529.
- Gosling, S.D., 2001. From mice to men: what can we learn about personality from animal research? *Psychol. Bull.* 127, 45.
- Gosling, S. D., & John, O. P. 1999. Personality dimensions in non-human animals: A cross-species review. *Curr. Dir. Psychol. Sci.* 8, 69 –75.
- Gosling, S.D., Kwan, V.S.Y., John, O.P., 2003. A dog's got personality: a cross-species comparative approach to personality judgments in dogs and humans. *J. Pers. Soc. Psychol.* 85, 1161–9.
- Graziano, W.G., Jensen-Campbell, L.A., Hair, E.C., 1996. Perceiving interpersonal conflict and reacting to it: the case for agreeableness. *J. Pers. Soc. Psychol.* 70, 820.
- Groothuis T.G.G., Carere C. 2005. Avian personalities: characterisation and epigenesis. *Neurosci. Biobehav. Rev.* 29, 137-150.
- Hauser, M., Pearson, H., Seelig, D., 2002. Ontogeny of tool use in cottontop tamarins, *Sanguinus oedipus*: innate recognition of functionally relevant features. *Anim. Behav.* 64, 299–311.
- Haverbeke, A., De Smet, A., Depiereux, E., Giffroy, J.-M., Diederich, C., 2009. Assessing undesired aggression in military working dogs. *Appl. Anim. Behav. Sci.* 117, 55–62.
- Heinrich, B., 1995. An experimental investigation of insight in common ravens (*Corvus corax*). *Auk* 994–1003.
- Heinrich, B., Bugnyar, T., 2005. Testing Problem Solving in Ravens: String-Pulling to Reach Food. *Ethology* 111, 962–976.

- Henderson, H.A., Wachs, T.D., 2007. Temperament Theory and the Study of Cognition-Emotion Interactions across Development. *Dev. Rev.* 27, 396–427.
- Herrmann, E., Call, J., 2012. Are there geniuses among the apes? *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2753–2761.
- Herrmann, E., Wobber, V., Call, J., 2008. Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *J. Comp. Psychol.* 122, 220.
- Hiestand, L., 2011. A comparison of problem-solving and spatial orientation in the wolf (*Canis lupus*) and dog (*Canis familiaris*). *Behav. Genet.* 41, 840–857.
- Horn, L., Huber, L., Range, F., 2013. The Importance of the Secure Base Effect for Domestic Dogs--Evidence from a Manipulative Problem-Solving Task. *PLoS One* 8, e65296.
- Horn, N.R., Dolan, M., Elliott, R., Deakin, J.F.W., Woodruff, P.W.R., 2003. Response inhibition and impulsivity: an fMRI study. *Neuropsychologia* 41, 1959–1966.
- Horváth, Z., Igyártó, B.-Z., Magyar, A., Miklósi, Á., 2007. Three different coping styles in police dogs exposed to a short-term challenge. *Horm. Behav.* 52, 621–630.
- Huber, L., Gajdon, G.K., 2006. Technical intelligence in animals: the kea model. *Anim. Cogn.* 9, 295–305.
- Huber, L., Range, F., Voelkl, B., Szucsich, A., Virányi, Z., Miklósi, A., 2009. The evolution of imitation: what do the capacities of non-human animals tell us about the mechanisms of imitation? *Philos. Trans. R. Soc. B Biol. Sci.* 364, 2299–2309.
- Hunt, G.R., Rutledge, R.B., Gray, R.D., 2006. The right tool for the job: what strategies do wild New Caledonian crows use? *Anim. Cogn.* 9, 307–316.
- Jones, K.E., Dashfield, K., Downend, A.B., Otto, C.M., 2004. Search-and-rescue dogs: an overview for veterinarians. *J. Am. Vet. Med. Assoc.* 225, 854–860.
- King, T., Marston, L.C., Bennett, P.C., 2009. Describing the ideal Australian companion dog. *Appl. Anim. Behav. Sci.* 120, 84–93.
- Kis, A., Topál, J., Gácsi, M., Range, F., Huber, L., Miklósi, Á., Virányi, Z., 2012. Does the A-not-B error in adult pet dogs indicate sensitivity to human communication? *Anim. Cogn.* 15, 737–743.
- Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M.A.W., Blokhuis, H.J., 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* 23, 925–935.
- Kralj-Fišer, S., Scheiber, I.B.R., Blejec, A., Moestl, E., Kotrschal, K., 2007. Individualities in a flock of free-roaming greylag geese: behavioral and physiological consistency over time and across situations. *Horm. Behav.* 51, 239–248.

- Lansade, L., Bouissou, M.-F., 2008. Reactivity to humans: A temperament trait of horses which is stable across time and situations. *Appl. Anim. Behav. Sci.* 114, 492–508.
- Lansade, L., Bouissou, M.-F., Erhard, H.W., 2008a. Fearfulness in horses: A temperament trait stable across time and situations. *Appl. Anim. Behav. Sci.* 115, 182–200.
- Lansade, L., Bouissou, M.-F., Erhard, H.W., 2008b. Reactivity to isolation and association with conspecifics: A temperament trait stable across time and situations. *Appl. Anim. Behav. Sci.* 109, 355–373.
- Lea, S.E.G., Goto, K., Osthaus, B., Ryan, C.M.E., 2006. The logic of the stimulus. *Anim. Cogn.* 9, 247–256.
- Leonardi, R.J., Vick, S.-J., Dufour, V., 2012. Waiting for more: the performance of domestic dogs (*Canis familiaris*) on exchange tasks. *Anim. Cogn.* 15, 107–120.
- Lewis, M., 2001. Issues in the Study of Personality Development. *Psychol. Inq.* 12, 67–83.
- Lit, L., Schweitzer, J.B., Iosif, A.-M., Oberbauer, A.M., 2010. Owner reports of attention, activity, and impulsivity in dogs: a replication study. *Behav Brain Funct* 6, 1.
- Lowe, S.E., Bradshaw, J.W.S., 2001. Ontogeny of individuality in the domestic cat in the home environment. *Anim. Behav.* 61, 231–237.
- Lucidi, P., Bernabò, N., Panunzi, M., Villa, P.D., Mattioli, M., 2005. Ethotest: A new model to identify (shelter) dogs' skills as service animals or adoptable pets. *Appl. Anim. Behav. Sci.* 95, 103–122.
- Martins, T. L., Roberts, M. L., Giblin, I., Huxham, R., & Evans, M. R. 2007. Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. *Horm. Behav.* 52, 445-453.
- McCrae, R.R., Costa, P.T., Ostendorf, F., Angleitner, A., Hrebícková, M., Avia, M.D., Sanz, J., Sánchez-Bernardos, M.L., Kusdil, M.E., Woodfield, R., Saunders, P.R., Smith, P.B., 2000. Nature over nurture: temperament, personality, and life span development. *J. Pers. Soc. Psychol.* 78, 173–86.
- McNicholas, J., Gilbey, A., Rennie, A., Ahmedzai, S., Dono, J.-A., Ormerod, E., 2005. Pet ownership and human health: a brief review of evidence and issues. *Bmj* 331, 1252–1254.
- Merola, I., Prato-Previde, E., Marshall-Pescini, S., 2012. Social referencing in dog-owner dyads? *Anim. Cogn.* 15, 175–185.
- Miklósi, Á., 2009. *Dog Behaviour, Evolution, and Cognition* (Oxford Biology). Oxford University Press, Oxford.

- Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., Csányi, V., 2003. A simple reason for a big difference: wolves do not look back at humans, but dogs do. *Curr. Biol.* 13, 763–766.
- Miklósi, A., Polgárdi, R., Topál, J., Csányi, V., 2000. Intentional behaviour in dog-human communication: an experimental analysis of “showing” behaviour in the dog. *Anim. Cogn.* 3, 159–166.
- Miklósi, Á., Topál, J., 2012. The evolution of canine cognition, in: Vonk, J, Shackelford, T. (Ed.), *The Oxford Handbook of Comparative Evolutionary Psychology*. Oxford University Press, Oxford.
- Miklósi, A., Topál, J., Csányi, V., 2004. Comparative social cognition: what can dogs teach us? *Anim. Behav.* 67, 995–1004.
- Miranda de la Lama, G.C., Sepúlveda, W.S., Montaldo, H.H., María, G.A., Galindo, F., 2011. Social strategies associated with identity profiles in dairy goats. *Appl. Anim. Behav. Sci.* 134, 48–55.
- Mirescu, C., Peters, J.D., Gould, E., 2004. Early life experience alters response of adult neurogenesis to stress. *Nat. Neurosci.* 7, 841–846.
- Mischel, W., Shoda, Y., Peake, P.K., 1988. The nature of adolescent competencies predicted by preschool delay of gratification. *J. Pers. Soc. Psychol.* 54, 687.
- Moeller, F.G., Barratt, E.S., Dougherty, D.M., Schmitz, J.M., Swann, A.C., 2001. Psychiatric aspects of impulsivity. *Am. J. Psychiatry* 158, 1783–1793.
- Most, S.B., Chun, M.M., Johnson, M.R., Kiehl, K.A., 2006. Attentional modulation of the amygdala varies with personality. *Neuroimage* 31, 934–944.
- Müller, C.A., Riemer, S., Virányi, Z., Huber, L., Range, F., 2014. Dogs learn to solve the support problem based on perceptual cues. *Anim. Cogn.* 1–10.
- Murphy, J.A., 1998. Describing categories of temperament in potential guide dogs for the blind. *Appl. Anim. Behav. Sci.* 58, 163–178.
- Odum, A.L., 2011. Delay discounting: Trait variable? *Behav. Processes* 87, 1–9.
- Osthaus, B., Lea, S.E.G., Slater, A.M., 2005. Dogs (*Canis lupus familiaris*) fail to show understanding of means-end connections in a string-pulling task. *Anim. Cogn.* 8, 37–47.
- Osthaus, B., Slater, A.M., Lea, S.E.G., 2003. Can dogs defy gravity? A comparison with the human infant and a non-human primate. *Dev. Sci.* 6, 489–497.
- Overall, K.L., Dunham, A.E., 2005. A protocol for predicting performance in military working dogs: roles for anxiety assessment and genetic markers, in: 4 Th International Working Dog Breeding Conference, Queen’s College, Melbourne, Australia, 23-27 January 2005. International Working Dog Breeding Association.

- Palmer, R., Custance, D., 2008. A counterbalanced version of Ainsworth's Strange Situation Procedure reveals secure-base effects in dog--human relationships. *Appl. Anim. Behav. Sci.* 109, 306–319.
- Park, H., Antonioni, D., 2007. Personality, reciprocity, and strength of conflict resolution strategy. *J. Res. Pers.* 41, 110–125.
- Pattij, T., Broersen, L.M., van der Linde, J., Groenink, L., van der Gugten, J., Maes, R.A.A., Olivier, B., 2003. Operant learning and differential-reinforcement-of-low-rate 36-s responding in 5-HT_{1A} and 5-HT_{1B} receptor knockout mice. *Behav. Brain Res.* 141, 137–145.
- Pedersen, V., Moeller, N.H., Jeppesen, L.L., 2002. Behavioural and physiological effects of post-weaning handling and access to shelters in farmed blue foxes (*Alopex lagopus*). *Appl. Anim. Behav. Sci.* 77, 139–154.
- Penn, D.C., Povinelli, D.J., 2007. Causal cognition in human and nonhuman animals: A comparative, critical review. *Annu. Rev. Psychol.* 58, 97–118.
- Pervin, L.A., John, O.P., 1996. *Personality: Theory and Research* (7th Edition). John Wiley & Sons.
- Pilley, J.W., Reid, A.K., 2011. Border collie comprehends object names as verbal referents. *Behav. Processes* 86, 184–195.
- Plotsky, P.M., Meaney, M.J., 1993. Early, postnatal experience alters hypothalamic corticotropin-releasing factor (CRF) mRNA, median eminence CRF content and stress-induced release in adult rats. *Mol. brain Res.* 18, 195–200.
- Povinelli, D.J., Reaux, J.E., Theall, L.A., Giambrone, S., Humphrey, N., 2000. *Folk physics for apes: The chimpanzee's theory of how the world works*. Oxford University Press Oxford.
- Prato-Previde, E., Marshall-Pescini, S., Valsecchi, P., 2008. Is your choice my choice? The owners' effect on pet dogs' (*Canis lupus familiaris*) performance in a food choice task. *Anim. Cogn.* 11, 167–174.
- Prestrude, A., O'Shea, J., 1998. Dogs in service to humans, in: *Comparative Psychology: A Handbook*. Garland Publishing, New York, pp. 386–392.
- Range, F., Hentrup, M., Virányi, Z., 2011. Dogs are able to solve a means-end task. *Anim. Cogn.* 14, 575–583.
- Range, F., Horn, L., Bugnyar, T., Gajdon, G.K., Huber, L., 2009. Social attention in keas, dogs, and human children. *Anim. Cogn.* 12, 181–192.
- Range, F., Möslinger, H., Virányi, Z., 2012. Domestication has not affected the understanding of means-end connections in dogs. *Anim. Cogn.* 15, 597–607.

- Range, F., Viranyi, Z., Huber, L., 2007. Selective imitation in domestic dogs. *Curr. Biol.* 17, 868–872.
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev. Camb. Philos. Soc.* 82, 291–318.
- Reisner, I.R., Mann, J.J., Stanley, M., Huang, Y., Houpt, K.A., 1996. Comparison of cerebrospinal fluid monoamine metabolite levels in dominant-aggressive and non-aggressive dogs. *Brain Res.* 714, 57–64.
- Reynolds, B., De Wit, H., Richards, J.B., 2002. Delay of gratification and delay discounting in rats. *Behav. Processes* 59, 157–168.
- Rothbart, M.K., 2011. *Becoming who we are: Temperament and personality in development.* Guilford Press, New York.
- Ruefenacht, S., Gebhardt-Henrich, S., Miyake, T., Gaillard, C., 2002. A behaviour test on German Shepherd dogs: heritability of seven different traits. *Appl. Anim. Behav. Sci.* 79, 113–132.
- Russell, J.C., Proctor, S.D., 2006. Small animal models of cardiovascular disease: tools for the study of the roles of metabolic syndrome, dyslipidemia, and atherosclerosis. *Cardiovasc. Pathol.* 15, 318–330.
- Santos, L.R., Ericson, B.N., Hauser, M.D., 1999. Constraints on problem solving and inhibition: Object retrieval in cotton-top tamarins (*Saguinus oedipus oedipus*). *J. Comp. Psychol.* 113, 186.
- Santos, L.R., Pearson, H.M., Spaepen, G.M., Tsao, F., Hauser, M.D., 2006. Probing the limits of tool competence: Experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). *Anim. Cogn.* 9, 94–109.
- Schwab, C., Huber, L., 2006. Obey or not obey? Dogs (*Canis familiaris*) behave differently in response to attentional states of their owners. *J. Comp. Psychol.* 120, 169.
- Scott, J.P., Fuller, J.L., 1965. *Genetics and the social behavior of the dog.* University of Chicago Press, Chicago.
- Scott, J.P., Beilfelt, S.W., 1976. Analysis of the puppy testing program., in: Pfaffenberger, C.J., Scott, J.P., Fuller, J.L., Ginsburg, B.E., Bielfelt, S.W. (Ed.), *Guide Dogs for the Blind: Their Selection, Development and Training.* pp. 39–75.
- Seed, A., Seddon, E., Greene, B., Call, J., 2012. Chimpanzee “folk physics”: bringing failures into focus. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2743–2752.
- Seed, A.M., Tebbich, S., Emery, N.J., Clayton, N.S., 2006. Investigating Physical Cognition in Rooks, *Corvus frugilegus*. *Curr. Biol.* 16, 697–701.

- Serpell, J.A., 2003. Anthropomorphism and anthropomorphic selection - Beyond the “cute response”. *Soc. Anim.* 11, 83–100.
- Sih, A., Bell, A., Johnson, J.C., 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* 19, 372–378.
- Sinn, D.L., Gosling, S.D., Hilliard, S., 2010. Personality and performance in military working dogs: Reliability and predictive validity of behavioral tests. *Appl. Anim. Behav. Sci.* 127, 51–65.
- Slabbert, J.M., Odendaal, J.S.J., 1999. Early prediction of adult police dog efficiency - a longitudinal study. *Appl. Anim. Behav. Sci.* 64, 269–288.
- Stamps, J., Groothuis, T., 2010. The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.* 85, 301–325.
- Stevenson-Hinde, J., Stillwell-Barnes, R., Zunz, M., 1980. Subjective assessment of rhesus monkeys over four successive years. *Primates* 21, 66–82.
- Stevenson-Hinde, J., Stillwell-Barnes, R., Zunz, M., 1980. Individual differences in young rhesus monkeys: consistency and change. *Primates* 21, 498–509.
- Svartberg, K., 2002. Shyness--boldness predicts performance in working dogs. *Appl. Anim. Behav. Sci.* 79, 157–174.
- Svobodova, I., Vapenik, P., Pinc, L., Bartos, L., 2008. Testing German shepherd puppies to assess their chances of certification. *Appl. Anim. Behav. Sci.* 113, 139–149.
- Szyf, M., McGowan, P., Meaney, M.J., 2008. The social environment and the epigenome. *Environ. Mol. Mutagen.* 49, 46–60.
- Taylor, A.H., Hunt, G.R., Medina, F.S., Gray, R.D., 2009. Do New Caledonian crows solve physical problems through causal reasoning? *Proc. R. Soc. B Biol. Sci.* 276, 247–254.
- Taylor, A.H., Medina, F.S., Holzhaider, J.C., Hearne, L.J., Hunt, G.R., Gray, R.D., 2010. An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. *PLoS One* 5, e9345.
- Tecwyn, E.C., Thorpe, S.K.S., Chappell, J., 2012. What cognitive strategies do orangutans (*Pongo pygmaeus*) use to solve a trial-unique puzzle-tube task incorporating multiple obstacles? *Anim. Cogn.* 15, 121–133.
- Thornton, A., Clayton, N.S., Grodzinski, U., 2012. Animal minds: from computation to evolution. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2670–2676.
- Thornton, A., Lukas, D., 2012. Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2773–2783.
- Tomasello, M., Call, J., 1997. *Primate cognition*. Oxford University Press.

- Topál, J., Gergely, G., Erdőhegyi, Á., Csibra, G., Miklósi, Á., 2009. Differential sensitivity to human communication in dogs, wolves, and human infants. *Science* 325, 1269–1272.
- Topál, J., Miklósi, A., Csányi, V., 1997. Dog-human relationship affects problem solving behavior in the dog. *Anthrozoos A Multidiscip. J. Interact. People Anim.* 10, 214–224.
- Topál, J., Miklósi, Á., Csányi, V., Dóka, A., 1998. Attachment behavior in dogs (*Canis familiaris*): A new application of Ainsworth's (1969) Strange Situation Test. *J. Comp. Psychol.* 112, 219.
- Topál, J., Miklósi, A., Gácsi, M., Dóka, A., Pongrácz, P., Kubinyi, E., Virányi, Z., Csányi, V., 2009. The dog as a model for understanding human social behavior. *Adv. Study Behav.* 39, 71–116.
- Tracy, J.L., Randles, D., 2011. Four models of basic emotions: a review of Ekman and Cordaro, Izard, Levenson, and Panksepp and Watt. *Emot. Rev.* 3, 397–405.
- Trumler, E., 1986. *Das Jahr des Hundes: ein Jahr im Leben einer Hundefamilie*. Heyne.
- Valsecchi, P., Barnard, S., Stefanini, C., Normando, S., 2011. Temperament test for re-homed dogs validated through direct behavioral observation in shelter and home environment. *J. Vet. Behav. Clin. Appl. Res.* 6, 161–177.
- Van der Borg, J.A.M., Graat, E.A.M., 2009. Effect of behavioral testing on the prevalence of fear and aggression in the dutch rottweiler population. *J. Vet. Behav. Clin. Appl. Res.* 4, 73–74.
- Vas, J., Topál, J., Gácsi, M., Miklósi, A., Csányi, V., 2005. A friend or an enemy? Dogs' reaction to an unfamiliar person showing behavioural cues of threat and friendliness at different times. *Appl. Anim. Behav. Sci.* 94, 99–115.
- Vas, J., Topál, J., Györi, B., Miklósi, A., 2008. Consistency of dogs' reactions to threatening cues of an unfamiliar person. *Appl. Anim. Behav. Sci.* 112, 331–344.
- Vas, J., Topál, J., Péch, E., Miklósi, A., 2007. Measuring attention deficit and activity in dogs: a new application and validation of a human ADHD questionnaire. *Appl. Anim. Behav. Sci.* 103, 105–117.
- Virányi, Z., Topál, J., Gácsi, M., Miklósi, Á., Csányi, V., 2004. Dogs respond appropriately to cues of humans' attentional focus. *Behav. Processes* 66, 161–172.
- Virányi, Z., Topál, J., Miklósi, Á., Csányi, V., 2006. A nonverbal test of knowledge attribution: a comparative study on dogs and children. *Anim. Cogn.* 9, 13–26.
- Visalberghi, E., Tomasello, M., 1998. Primate causal understanding in the physical and psychological domains. *Behav. Processes* 42, 189–203.

- Visser, E., van Reenen, C., Hopster, H., Schilder, M.B., Knaap, J., Barneveld, A., Blokhuis, H., 2001. Quantifying aspects of young horses' temperament: consistency of behavioural variables. *Appl. Anim. Behav. Sci.* 74, 241–258.
- Wallis, L.J., Range, F., Müller, C.A., Serisier, S., Huber, L., Virányi, Z., 2014. Lifespan development of attentiveness in domestic dogs: drawing parallels with humans. *Name Front. Psychol.* 5, 71.
- Ward, C., Smuts, B.B., 2007. Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). *Anim. Cogn.* 10, 71–80.
- Watson, J.S., Gergely, G., Csanyi, V., Topal, J., Gacsi, M., Sarkozi, Z., 2001. Distinguishing logic from association in the solution of an invisible displacement task by children (*Homo sapiens*) and dogs (*Canis familiaris*): Using negation of disjunction. *J. Comp. Psychol.* 115, 219.
- Weiss, E., Greenberg, G., 1997. Service dog selection tests: effectiveness for dogs from animal shelters. *Appl. Anim. Behav. Sci.* 53, 297–308.
- West, R.E., Young, R.J., 2002. Do domestic dogs show any evidence of being able to count? *Anim. Cogn.* 5, 183–186.
- Wilks, K., 1999. When Dogs are Man's Best Friend—the Health Benefits of Companion Animals in the Modern Society, in: UAM 1999 Conference Proceedings. Available Online at [Http://www. Urban-Renaissance. Org/urbanren/publications/dogsandhealth. Pdf](http://www.Urban-Renaissance.Org/urbanren/publications/dogsandhealth.Pdf).
- Wilson, M., 2002. Six views of embodied cognition. *Psychon. Bull. Rev.* 9, 625–636.
- Wilsson, E., Sundgren, P.-E., 1998. Behaviour test for eight-week old puppies—heritabilities of tested behaviour traits and its correspondence to later behaviour. *Appl. Anim. Behav. Sci.* 58, 151–162.
- Wolf, M., Weissing, F.J., 2012. Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.* 27, 452–461.
- Wood, V.F., Bell, P.A., 2008. Predicting interpersonal conflict resolution styles from personality characteristics. *Pers. Individ. Dif.* 45, 126–131.
- Wright, H.F., Mills, D.S., Pollux, P.M.J., 2012. Behavioural and physiological correlates of impulsivity in the domestic dog (*Canis familiaris*). *Physiol. Behav.* 105, 676–682.
- Wright, H.F., Mills, D.S., Pollux, P.M.J., others, 2011. Development and validation of a psychometric tool for assessing impulsivity in the domestic dog (*Canis familiaris*). *Int. J. Comp. Psychol.* 24, 210–225.
- Zaichenko, M.I., Merzhanova, G.K., 2011. Studies of impulsivity in rats in conditions of choice between food reinforcements of different value. *Neurosci. Behav. Physiol.* 41, 445–451.

Zilcha-Mano, S., Mikulincer, M., Shaver, P.R., 2012. Pets as safe havens and secure bases: The moderating role of pet attachment orientations. *J. Res. Pers.* 46, 571–580.

CHAPTER 2

The predictive value of early behavioural assessments in pet dogs – a longitudinal study from neonates to adults

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Abstract

Studies on behavioural development in domestic dogs are of relevance for matching puppies with the right families, identifying predispositions for behavioural problems at an early stage, and predicting suitability for service dog work, police or military service. The literature is, however, inconsistent regarding the predictive value of tests performed during the socialisation period. Additionally, some practitioners use tests with neonates to complement later assessments for selecting puppies as working dogs, but these have not been validated. We here present longitudinal data on a cohort of Border collies, followed up from neonate age until adulthood. A neonate test was conducted with 99 Border collie puppies aged 2-10 days to assess activity, vocalisations when isolated and sucking force. At the age of 40-50 days, 134 puppies (including 93 tested as neonates) were tested in a puppy test at their breeders' homes. All dogs were adopted as pet dogs and 50 of them participated in a behavioural test at the age of 1.5 to 2 years with their owners. Linear mixed models found little correspondence between individuals' behaviour in the neonate, puppy and adult test. Exploratory activity was the only behaviour that was significantly correlated between the puppy and the adult test. We conclude that the predictive validity of early tests for predicting specific behavioural traits in adult pet dogs is limited.

Introduction

It is now widely accepted that nonhuman animals display consistent behavioural differences comparable to human personalities, and moreover that these differences are functional and of evolutionary significance [1]. However, in contrast to the contention that personality means “behavioural differences that are stable across time and situations”, such behaviour differences are often not as fixed as one might expect [2]. Besides influences of situational factors and salient experiences both early and later in life, developmental factors and age can be expected to have major effects on behaviour, and temporal stability over the short term does not preclude behavioural changes over the long term [2]. It is therefore not surprising that behavioural consistency generally decreases as time between test and re-test increases (reviewed in [2,3]).

Behavioural development in humans and nonhuman animals

In humans, personality traits become increasingly more stable with age ([4]; reviewed in [5]). In particular, the rank order of personality features within a cohort (i.e. personality relative to that of other individuals) typically remains stable, while there is a general tendency towards decreases in Neuroticism, Extraversion, and Openness, and small increases in Agreeableness and Conscientiousness with age [6]. Some studies have attempted to make predictions about behavioural predispositions already soon after birth. Although available measurement tools have some shortcomings (moderate internal consistency, low convergent validity, inconsistent findings on concurrent validity; reviewed in [7]), moderate levels of predictive validity of neonate assessments for childhood behaviour have been reported. Among the most predictive traits appear to be levels of irritability or distress, which showed some predictiveness up to the age of 15 months [8,9], reviewed in [10]. Neonate activity was furthermore correlated with activity and openness to new experiences in 4 to 8-year old children [11]. However, often behavioural consistency seems to be limited to relatively short time intervals. For instance, Worobey & Bladja [9] found that infants’ responsivity and activity level were related between 2 weeks and 2 months and between 2 months and 1 year of age, respectively, but not between 2 weeks and 1 year of age. No study seems to have followed up the tested infants’ behaviours beyond the childhood years.

Few studies investigated the development of individual behavioural differences from birth in nonhuman animals. In a study on infant macaques and baboons from birth until 5

months of age, several behaviours were significantly correlated between consecutive age blocks of 50 days, but only three (of a possible 33) correlations turned out to be significant across nonconsecutive age blocks [12]. Sussman & Ha [13] report considerable behavioural changes in infant pigtailed macaques between birth and 10 months of age and no relationship of determined temperament traits to behaviour in a novel context. Also, a study on captive wolves found no correlations between neonate and later behaviour [14].

Similarly, assessments of behavioural development from juvenile to adult age in birds [15], fish [16], primates [12,13,17,18], horses [19,20] and domestic cats [21] yielded mixed results. Some studies support consistency of at least some behavioural traits, while others found no consistency across age or consistency only between adjacent age groups, but not over the longer term, implying a pattern of relative stability or gradual change during development. Furthermore, different traits with a different physiological basis may vary in their ontogeny and consistency [22]. For example, in rhesus macaques (*Macaca mulatta*), confidence was rated as stable at all ages, while ratings for excitability showed no stability until adulthood and those for sociability emerged as significant only after the age of 3 years [17].

Behavioural development in dogs and validity of puppy tests

Behavioural development in domestic dogs has been investigated for practical reasons such as matching puppies, juvenile or adult dogs with the right families, identifying predispositions for behavioural problems at an early stage, and predicting suitability for service dog work, police or military service. A recent meta-analysis suggested that personality is moderately consistent in younger dogs (<1 year, mean $r=0.30$) and older dogs (>1 year, mean $r=0.51$; reviewed in [22], but the predictive value of early tests (prior to 3 months of age), as frequently performed for the selection of guide dogs, police or military dogs, was not specially addressed.

Some dog trainers test dog puppies as early as at 1-10 days of age to complement behavioural assessments during the socialisation period for selecting service or working dogs (E. Kersting, pers. comm.); however, these neonate assessments have not been scientifically validated. Moreover, although several studies investigated the predictive value of puppy tests conducted at 6-12 weeks of age, results are inconclusive. For the purpose of this paper we use

the term puppy test to denote a sequences of behavioural (sub-)tests performed with young dogs during the socialisation period up to the age of 3 months. Such tests are typically aimed at investigating a variety of behavioural predispositions and often include interactions with unfamiliar people, play, exploration of novel environments or objects, and startle stimuli.

Some studies found a level of predictability of puppy test results for the success of guide dogs and police dogs [23–25]; nonetheless, the studies with the largest sample sizes yielded less promising results. Wilsson & Sundgren [26] reported poor correspondence between puppy test results and adult dogs' behaviour and performance as service dogs in a sample of 630 German shepherd dogs. Similarly, Asher et al. [27] followed up 465 dogs assessed in a puppy test and subsequently trained as guide dogs and found low predictability of successful certification. Of the 450 dogs that scored above the proposed cut-off point in the behavioural test, 66% reached certification, compared to 64% in the complete sample. In contrast to success, failure was more accurately predicted by the test, as 14 of the 15 dogs that scored below the cut-off point did not reach certification [27].

Moreover, which combination of subtests is deemed predictive is usually based on an a posteriori selection, and selected tests often differ between studies, although playfulness (fetching a toy or following a rug) emerges as predictive in studies of both guide dogs [23] and police dogs [24,25]. In contrast to the above studies, which used outcomes (i.e. whether or not the dog became certified) as dependent variables, those studies which investigated direct correlations of behaviour traits in puppies of different ages or between puppies and adults generally did not find much evidence of stability [26,28,29]. Beaudet et al. [30] evaluated test-retest performance in 30 puppies at 7 and 16 weeks of age and found no relationship between social behaviour scores within this relatively short time period. Goddard & Beilharz [29] report a low predictive value of tests conducted with 4 to 10-week-old puppies. Fearfulness was the only trait which could be predicted to some degree by the age of 3 months or by a summary score combining subtests from 8 weeks to 3 months [28,29]. Nonetheless, recognizing that predictability increases with age, the authors recommend waiting until the age of 6 months when selecting dogs for breeding based on the fearfulness trait [28].

Published studies differ in the importance attributed to early environment on shaping later behaviour in dogs. Strandberg et al. [31] report little maternal influence, but a larger influence of litter on personality traits in the Swedish Dog Mentality Assessment. In a behavioural assessment of German shepherd dogs at 15 months of age, two of four traits, ‘Confidence’ and ‘Physical Engagement’ (during play with a tennis ball), were affected by factors such as parity, growth rate, litter size or season of birth whereas no early environmental effects were found on the other two components, ‘Social Engagement’ and ‘Aggression’ [32]. Goddard & Beilharz [33] found little effect of variation in the environment prior to 6 weeks of age on success rate in guide dogs for the blind.

In summary, there are some inconsistencies in the puppy test literature, as well as a lack of longitudinal data on behaviour consistency in pet dogs and on the predictive value of neonate assessments in particular. Therefore the aim of the present study was to perform behavioural tests in pet dogs at three ages – during the neonate period (2-10 days of age), during the socialisation period (40-50 days of age) and as adults (1.5-2 years of age) – and to assess the predictability of later behaviour by early behavioural tests.

In the neonate test, activity and vocalisations during a brief isolation period and sucking force were determined. The puppy test and the adult test both included subtests for 1) exploration in a novel environment, 2) interaction with an unfamiliar experimenter, 3) play, 4) a novel object, and 5) a social conflict situation (three restraint tests in the puppy test and a threatening approach by the experimenter in the adult test). As no published study on assessments of neonate dogs are available, predictions were based on findings from neonate assessments in humans, the coping styles model, and personal experiences (E. Kersting, pers. comm.).

In human children, correlations between neonatal movements and high daytime activity at the age of 4-8 years have been reported [34]. Furthermore the coping styles literature indicates that activity, exploration, aggression and boldness are linked, with proactive individuals scoring higher on all of these than reactive individuals [35,36]. Therefore a positive correlation between activity in the neonate test and exploratory activity and boldness in the later assessments was predicted. As the degree of irritability in human infants is typically assessed by frequencies and duration of fussing and crying [37], we

assumed duration and loudness of vocalisations in the neonate dog puppies to be indicative of irritability. In human infants irritability has been linked to distress to limitations or frustration and forms a negative affectivity factor together with fear [10]. Measures of irritability were found to exhibit relatively high stability over time [9]. Thus we predicted neonate vocalisations to be positively correlated with struggling and flight behaviour during restraint tests in the puppy test and with barking or growling during the threatening approach in the adult test; conversely a negative relationship between neonate vocalisations and latency to react to the threatening approach was predicted. Additionally, the following prediction made by practitioners was put to the test: Sucking force in the neonate test is positively related to motivation and thus playfulness in the puppy and the adult test.

We furthermore predicted that corresponding behaviours would be positively correlated between the puppy and the adult test. To test this, we selected those five subtests from the adult test that matched best with subtests from the puppy test (more subtests were conducted in the adult test with the aim of investigating effects of personality on cognitive performance and age differences in behaviour for different studies). Since effects of litter can be expected due to both genetic and early environmental effects, we tested for litter effects on behaviour in the neonate, puppy and adult tests.

Ethics statement

All procedures were performed in compliance with the Austrian Federal Act on the Protection of Animals (Animal Protection Act – TSchG, BGBl. I Nr.118/2004) and with the consent by the breeders or owners. According to the Austrian Animal Experiments Act (§ 2, Federal Law Gazette No. 501/1989), such non-invasive behavioural studies are not considered as animal experiments and no special permission for use of animals in such studies is required. For the small number of adult tests performed at the University of Veterinary Medicine, approval by the ethics committee (Ethik- und Tierschutzkommission) of the Veterinary University Vienna was obtained on 19th April 2012. Since the owners were only required to interact with their dogs in their usual manner during the experiments and their behaviour was not analyzed, approval for human experimentation was not necessary.

Methods

To rule out effects of breed differences in the ontogeny of behaviour [29,38–40], members of a single breed, the Border collie, were included in the study. All tested dogs came from small-scale breeders (with typically 1-2 litters per year) that raised their puppies primarily in the house. We tested 99 puppies from 18 litters in the neonate test (age range: 2-10 days). At the age of 40-50 days, 134 puppies were tested in a puppy test (including 93 puppies tested as neonates). All puppies were subsequently adopted as pet dogs. Fifty of these dogs (29 female, 21 male) were also tested as adults (1.5-2 years of age). Table 1 gives an overview of the subjects. Only three subjects, two males and one female, were neutered during the course of the study (between the age of 6 and 12 months) and thus the data for neutered and intact dogs were pooled.

Table 1. Summary of subjects tested in the neonate test, the puppy test and the adult test

	Age range	Total number of tested dogs	Dogs tested in the neonate test	Dogs tested in the puppy test
Neonate test	2-10 days	99		
Puppy test	40-50 days	134	93	
Adult test	1.5-2 years	50	40	45

Neonate test

Each puppy was tested individually at the breeder's home following a protocol by Erik Kersting (Hundezentrum Canis Familiaris, Roetgen, Germany, pers. comm.; Table 2). Prior to the test, the mother was separated from the litter for a median of 55 min (range 0 – 245 min). According to E. Kersting (pers. comm.), puppies should ideally be separated from the mothers for two hours; however breeder compliance was variable and therefore separation time was variable. We tested whether this affected the puppies' behaviour and controlled for this statistically. The puppy was removed from the litter box and placed at the centre of a blanket, which was visually divided into a grid of 16 squares (22.5 x 22.5 cm). All tests were video-recorded from a set distance (approximately 2 m from the centre of the blanket), and durations of puppies' activity and vocalisations and maximum amplitude of vocalisations were assessed from the videos (Table 2). After two minutes, the experimenter picked up the puppy and tried to elicit the sucking reflex by stimulating the puppy's palate with her finger. Sucking force was determined subjectively but based on an objective scale (Table 2). Experimenters always disinfected their hands prior to handling the puppies.

Table 2. Variables measured in the neonate test.

Variables measured		Definition	Cronbach's alpha
Puppy's behaviour on the blanket			
Duration of activity		Puppy is moving at least one leg, includes tumbling and backwards movements.	0.92
Number of line crossings		Frequency of crossing a line with the head and both forelegs.	0.82
Number of squares visited		Number of different squares entered with the head and both forelegs.	0.95
Duration of vocalisations		Self-explanatory.	
Max. vocal amplitude		Extracted from the audio stream of a video camera, set at a standardised distance of approximately 2 m from the centre of the blanket (range -50 to -3db) and converted to scores of 1-5.	
Amplitude Score	Amplitude		
1	<-20 > -50 or no vocalisation		
2	≤ -15 > -20		
3	≤ -10 > -15		
4	< -5 > -10		
5	≤-3 ≥ -5		

Table 2 continued

Test of sucking force	Sucking Force	
	Score*	Description
Max. sucking force	0	Does not take the finger.
	2	Takes finger, but no sucking.
	4	Sucking, but hardly holds on to finger when removed.
	6	Sucking, holds on to finger when removed but no “plop” noise when finger is removed.
	8	Strong sucking; produces “plop” noise when finger is removed.
	10	Strong sucking; produces “plop” noise when finger is removed; additionally head moves along as finger is removed.
	12	Very strong sucking; able to support its own weight by sucking on the experimenter’s finger.

* Intermediate scores (1, 3 etc.) were given in unclear/ambiguous cases.

Puppy test

As detailed in [41], all tests were carried out in rooms unfamiliar to the puppies at the breeders' homes (only one litter had to be tested in a familiar room because no unfamiliar room was available, so no data was taken in the first part of the test – room exploration). All tests were conducted by the same experimenter (SR), who was unfamiliar to the puppies prior to the test. A cameraman filmed the test for subsequent video analysis. The test, which was originally developed for the selection of service dogs (E. Kersting, pers. comm.), lasted about 20 minutes per puppy and consisted of eleven subtests exposing the puppy to different social and non-social stimuli (see Table 3 for descriptions of the relevant subtests and Table 4 for details on scoring methods; [41]). These form part of a test routinely used for assessing puppies' suitability as service dogs (E. Kersting, pers. comm.).

Table 3. Summary of the subtests of the puppy test that were used for analysis.

Subtest	Description	Duration
Exploration	The puppy was allowed to explore the unfamiliar room for two minutes; experimenter, cameraman and breeder remained passive.	60 s
Greeting test	The experimenter crouched down approximately 2.5 m away from the puppy and encouraged it to make contact by calling its name, chatting in a friendly voice or clicking her tongue. When the puppy approached, she petted the puppy and talked to it in a friendly way for 20 seconds. If the puppy did not want to approach within 45 seconds, the subtest was terminated.	60 s
Play	The experimenter tried to engage the puppy in play by wiggling a soft toy in front of it. When the puppy was following and/or trying to grab the toy for at least 10 seconds, she threw it two metres away and vocally encouraged the puppy to return to her with the toy. This was repeated three times.	2-3 min
Back test	The experimenter was sitting on the floor and gently turned the puppy on its back, holding it in this position with both hands while casually looking at the puppy, but not staring at it in a threatening way.	25 s
Vetcheck test	Simulated veterinary examination. The experimenter, sitting on the floor, stroked the puppy's body, touched its paws, looked into its ears and examined its teeth.	30 s
Staring test	The experimenter lifted the puppy up, holding it upright under its armpits, so that she could look directly into its eyes. When the puppy averted its gaze, the experimenter reoriented the puppy and took up eye contact again.	30 s
Novel object test	A battery-powered toy looking like a paper bag, approx. 20 x 10 x 5 cm, was placed approx. 2 m away from the puppy to assess its reactions to the novel object's erratic movements.	60 s

Table 4. Description of behavioural measurements used in the analysis of the puppy test. As a measure of interobserver reliability, Cohen's kappa is indicated for scores and Cronbach's alpha for durations, counts, and absolute estimates.

Variable	Type	Measure	Description	Cohen's kappa	Cronbach's alpha
<u>Exploration</u>					
Move	Duration	% time	Locomotion (Leg movement followed by body movement. Forwards or backwards movement, coding starts when dog starts to move leg). Does not include moving leg for other purposes e.g. pawing at objects or if dog moves legs but does not change its spatial position.		0.96
Inactive	Duration	% time	Sitting, standing or lying without doing anything else (e.g. exploring). Also includes scratching and shaking.		0.80
Explore	Duration	% time	Puppy's nose is <5cm from ground or from objects, apparently sniffing, mouthing, manipulating, or scratching objects with the paw.		0.98
<u>Greeting test</u>					
Approach	Rating	0	Does not approach the experimenter (10 cm from experimenter's hands) within 45 seconds.	0.71	
		1	Approaches the experimenter within 21-45 seconds after she started calling.		
		2	Approaches the experimenter within 11-20 seconds after she started calling.		
		3	Approaches the experimenter within 10 seconds after she started calling.		
Tail-wagging	Rating	0	Wags tail <30% of interaction time.	0.88	
		1	Wags tail 30-69% of interaction time.		
		2	Wags tail 70% or more of interaction time.		
Jumping up	Absence/	0	Does not jump up or climb into experimenter's lap.	0.70	
	Presence	1	Jumps up or climbs into experimenter's lap.		

Table 4 continued

Variable	Type	Measure	Description	Cohen's kappa	Cronbach's alpha
<u>Play</u>					
Follow toy	Frequenc	0-3		0.83	
	y		Number of times the puppy followed the thrown-away toy (total number of trials: 3).		
Grab toy	Frequenc	0-3		0.72	
	y		Number of times the puppy followed and grabbed the thrown-away toy (total number of trials: 3).		
Return with toy	Frequenc	0-3		0.69	
	y		Number of times (out of 3) the puppy brings the toy back to experimenter so she can grab the toy. Puppies that return to within 20cm of experimenter with the toy and stay there for several seconds but do not bring the toy to experimenter directly, receive half a point.		
<u>Back test</u>					
Struggling	Duration	% time	Quick movements of body, head, and legs. Does not include slow movement of individual limbs or the head. Absolute duration in seconds (precision 0.2 s).		0.95
Vocalising	Duration	% time	Duration of vocalisations. Absolute duration in s (precision 0.2 s).		0.84
<u>Vetcheck test</u>					
Flight	Absence/	0	No escape attempt (trying to move away with the whole body while being held – does not include movement with the head to avoid teeth control or walking away when not held).	0.83	
	Presence	1	Escape attempt.		
Interaction	Absence/	0	Mouthing or licking of experimenter's fingers/ face for <20% of the time.	1.0	
	Presence	1	Mouthing or licking of experimenter's fingers/ face for at least 20% of the time.		
Passive	Absence/	0	Shows interaction or flight behaviour.	1.0	
	Presence	1	Shows neither interaction nor flight behaviour.		

Table 4 continued

Variable	Type	Measure	Description	Cohen's kappa	Cronbach's alpha
<u>Staring test</u>					
Look away	Event	Frequency	Averting gaze (head turn away from the experimenter's face). This is followed by the experimenter reorienting the puppy to look into its eyes again.		0.88
<u>Novel object test</u>					
Novel object - Approach	Rating	1	Does not approach to within 20 cm of the novel object within 30 s.	0.67	
		2	Approaches to within 20 cm of the novel object after 5 s.		
		3	Approaches to within 20 cm of the novel object within 5 s.		
Novel object - Tail	Rating	1	Tail mostly low.	0.92	
		2	Tail partly low, partly medium/high.		
		3	Tail mostly medium to high.		
Novel object - Hunt	Absence/	0	Puppy does not 'hunt' the novel object (jump at the object with the fore paws and/ or bite into it).	0.89	
	Presence	1	Puppy 'hunts' the novel object (i.e., jumps at the object with their fore paws and/ or bites into it).		
Novel object - Distance	Estimate	continuous	Estimated closest distance (cm) of puppy to paper bag.		0.88

Adult test

The adult test was specifically designed for use at the Clever Dog Lab with the primary aim of investigating effects of personality on cognitive performance and age differences in behaviour. Partly, the dogs of the current study were used for these other studies and so the test was not completely tailored to serve as a follow up of the puppy test. To take account of this, only the five subtests that matched best with subtests from the puppy test were selected for the present analysis (Tables 5 and 6).

Tests were conducted in a room (6m x 5m) at the Clever Dog Lab, Nussgasse, Vienna, or in a slightly larger room (6m x 7m) with an identical setup at the new Clever Dog Lab, University of Veterinary Medicine, Veterinärplatz, Vienna. Twenty-five dogs were tested by SR and 25 dogs were tested by another female experimenter of a similar age, Claudia Rosam, as SR had been in contact with many of the tested dogs prior to the adult test. The experimenters were thus unfamiliar to the dogs. An exception were five dogs tested by SR (with four dogs she had had contact at least one year prior to the test, and for one dog the last contact occurred 8 months prior to the test).

Table 5. Summary of the subtests of the adult test that were used for analysis.

Subtest	Description	Duration
Exploration	This was the very first test, conducted in an unfamiliar room. The owner walks in with the dog on the lead, stops in the middle of the room, takes off the lead, gives a “go” command if necessary and thereafter ignores the dog, which is free to explore the room.	120 s
Greeting test	The owner and the dog (on the lead) stand in the centre of the test room. The experimenter enters, steps within reach of the lead, stops and waits whether the dog shows initiative to approach. If it does not, she calls the dog’s name and encourages it to approach. If the dog still does not approach, she steps towards the dog. If the dog has approached or does not withdraw, she pets the dog while continually talking to it. If the dog shows avoidance behaviour, petting is stopped.	30 s
Threatening approach	The owner holds the dog’s leash but takes one step back so that s/he is behind the dog (giving the dog the opportunity to withdraw behind the owner if it wishes to do so). The owner remains passive throughout the test. The experimenter stands at the opposite end of the room, calls the dog’s name once and then starts approaching slowly and haltingly (one step every ~4 s) with a slightly bent upper body. She is looking steadily into the eyes of the dog. The approach is terminated when the experimenter has reached the dog, the dog has approached the experimenter in a friendly way, or the dog shows heightened signs of stress (repeated barking, growling, or withdrawing/ hiding). The experimenter resolves the situation by withdrawing eye contact, crouching down sideways and inviting the dog to come up to her, speaking to the dog in a friendly manner.	30 s
Novel object	A battery-driven toy dog, which rolls on the floor and produces a ‘laughing’ noise is placed on the floor ca. 2 m from the dog while the dog is facing in the other direction with the owner. As soon as the toy starts moving and producing sound, the owner lets go of the dog’s collar/ harness and the dog has one minute to investigate the toy while owner and experimenter remain passive. The toy is motion sensitive and stops acting after about 15 s. If the dog does not approach close enough to turn the toy on again within 30 s, the experimenter walks past the toy once to turn it on a second time.	60 s

Table 5 continued

Subtest	Description	Duration
Ball play	The owner throws a tennis ball for the dog three times. During the first two times, the dog is encouraged to bring back the ball. After throwing for the third time, the owner stops interacting with the dog, stands up straight and ignores the dog.	30 s

Table 6. Description of behavioural measurements used in the analysis of the adult test. As a measure of interobserver reliability, Cohen's kappa is indicated for scores and Cronbach's alpha for durations, counts, and absolute estimates.

Variable	Type	Measure	Description	Cohen's kappa	Cronbach's alpha
<u>Exploration</u>					
Move	Duration	% time	Locomotion, movement of the legs leading to a forward or backward motion.		0.87
Explore	Duration	% time	The dog's nose is in close proximity (max. 10 cm) to the floor or any other surface (e.g., wall, table, objects) or both front paws placed on an elevated surface (e.g., window sill, table). Does not include drinking.		0.80
Inactive	Duration	% time	Sitting, standing or lying without doing anything else (e.g. exploring). Also includes scratching and shaking.		0.96
<u>Greeting test</u>					
Greeting intensity	Score			0.67	
		0	Dog does not approach or may approach initially but then avoid the experimenter so there is no interaction.		
		1	Dog is passive and shows little interest towards the experimenter, with or without tail wagging		
		2	Friendly greeting; tail wagging, may cuddle up, jump or lick		
		3	Very excited/ enthusiastic greeting with intensive searching for contact and tail wagging		
Tail-wagging		0	0 = no or very little wagging	0.71	
		1	1 = wagging intermittently		
		2	2 = wagging most of the time		
Jumping up	Absence/	0	Dog does not jump up in the first greeting phase.	0.82	
	Presence	1	Dog jump ups in the first greeting phase.		

Table 6 continued

Variable	Type	Measure	Description	Cohen's kappa	Cronbach's alpha
<i>Threatening approach</i>					
Latency to react	Latency		Latency to first overt reaction .e. moving away, hiding, barking, growling. This only refers to aversive reactions, but not to approaching the experimenter in a friendly/ appeasing way.		0.77
Bark	Absence/ Presence	0/1	Absence or presence of barking.	0.89	
Growl	Absence/ Presence	0/1	Absence or presence of growling.	0.90	
Retreat	Absence/ Presence	0/1	Absence or presence of retreating.	0.89	
Approach friendly	Absence/ Presence	0/1	Absence or presence of approaching the experimenter in a friendly/ appeasing way during the threatening approach.	0.84	
<i>Novel object test</i>					
Novel object - Approach	Score	0	The dog does not approach the novel object to within 20 cm within 60 s.	0.72	
		1	Upon noticing the novel object, the dog approaches to within 20 cm within 60 s.		
		2	Upon noticing the novel object, the dog approaches to within 20 cm within 30 s.		
		3	Upon noticing the novel object, the dog approaches to within 20 cm within 5 sec.		
Novel object - Proximity	Duration		Time spent within 1 m from the toy.		0.97
Novel object - Orientation	Duration		Time spent looking in the direction of the toy		0.94
Novel object - Grab	Absence/	0	The dog does not grab the novel object with its mouth.	0.84	
	Presence	1	The dog grabs the novel object with its mouth.		

Table 6 continued

Variable	Type	Measure	Description	Cohen's kappa	Cronbach's alpha
<i>Ball play</i>					
Return with toy	Frequency	0-3	Number of times the dog returns to within 1.5 m of the owner within 5 seconds of grabbing the ball after it has been thrown.	0.74	
Encourage			Latency to stop encouraging the owner who is ignoring the dog after the third throwing. Encouraging is defined as looking at the owner or spitting out the ball within 1.5 m from the owner while facing the owner.	0.75	
	Score	1	before 5 s		
		2	before 10 s		
		3	before 15 s		
		4	after 15 s		

Data processing and statistical analysis

For the neonate test, audio streams were extracted from the video recordings, and the maximum amplitude of the vocalisations was determined in CoolEdit 2000 and subsequently converted into scores of 1-5 (Table 2). The dogs' behaviour in the three tests was coded using Solomon coder (© András Péter). The duration of puppies' vocalisations during the neonate test had to be recorded live during the test because on the video recordings, the subject's vocalisations could not be reliably distinguished from those made by its siblings. The neonate test and the puppy test were coded by the first author. To assess reliability, an additional coder coded 20 randomly selected puppies of 20 litters in the neonate test. Reliability coding for the puppy test was split between two more coders, each of whom coded a subset of the test for 20 puppies. The adult personality tests of the sample presented here, and of an additional 124 dogs tested for other studies, were coded by one of three coders (SR, Stephen Jones, Claudia Rosam). Reliability between coders was assessed based on 38 double coded dogs. Details of the coding schemes and reliability measures are presented in Tables 2-6.

Statistical analysis was carried out in R 2.12.0 (R Development Core Team 2010) and SPSS Statistics 21 (IBM Corp. Armonk, NY, 2012). Non-linear principal components analysis (CATPCA in SPSS [42,43]) was performed on selected variables from the neonate, the puppy and the adult tests, respectively, to reduce the number of variables and obtain principle components for further analysis. Tables 7-9 show the variable loadings on the principal components, Eigenvalues and explained variance. In the case of the adult test, the sample used for variable reduction included the 50 dogs from the current study and an additional 124 dogs that were tested for other experiments (some of these dogs were tested by a third experimenter).

Initially, linear mixed models were calculated to assess effects of age, weight and time separated from the mother on the neonate puppies' behaviour, with litter included as a random factor (R package nlme [44], function lme). In case of a significant effect of these covariates, the residuals of the model were used as predictor in subsequent analysis. To assess correlations between earlier and later behaviours, linear mixed models (Type III Sums of Squares) were calculated using either principal components or individual variables, depending on the predictions. To test for litter effects, these models were then compared against models with no random factor included (package nlme [44], function gls). If there was no significant

difference according to likelihood ratio tests, the reduced models are presented (Tables 10-12). For variables that were not included as dependent variables in any models, litter effects were calculated in the same way by using likelihood ratio tests to compare models with and without litter as a random factor. Normality of the residuals was assessed from quantile-quantile-plots and was adequate in all cases. To correct for multiple comparisons, sequential Bonferroni correction [45]) was applied.

Results

Data reduction and covariates

The CATPCA of the neonate test yielded two components, labelled Activity and Vocal/ Sucking force, which accounted for 65.86% of the variance (Table 7). Activity had high positive loadings for all three variables related to activity, i.e. duration of being active, number of line crossings, and number of squares visited. Vocal/ Sucking force had high positive loadings for duration and loudness of vocalisations and a high negative loading for sucking force, reflecting the fact that heavier puppies tended to vocalise more but displayed a lower sucking force (Table S1). The positive effect of puppies' weight on the Vocal/ Sucking force component was significant, while there was a significant negative effect of separation time. To take account of this, the residuals of the model for Vocal/ Sucking force were used as predictors in the subsequent analysis. Activity was unaffected by age, weight or separation time (Table S1).

Table 7. Components and component loadings of the CATPCA over the neonate test

	Activity	Vocal/ Sucking force	Total
Activity	0.77	-0.05	
Line crossings	0.83	-0.36	
Squares visited	0.82	-0.39	
Duration of vocalisations	0.49	0.64	
Max. amplitude of vocalisations (score)	0.44	0.66	
Max. suckingforce	-0.08	-0.67	
<i>Eigenvalue</i>	2.38	1.57	3.95
<i>% variance</i>	39.69	26.17	65.86

Tables 8 and 9 show the results of CATPCA for the puppy and the adult test, respectively. Principal components for activity during room exploration, greeting of the experimenter, play with a human and boldness towards a novel object were extracted for both the puppy and the adult test. Note, however, that the components relating to room exploration and boldness had opposite loadings in the puppy and the adult test so that a negative relationship would be expected between them. Additionally, three components – labelled Flight, Struggle and Passive/ Low Interaction – based on the puppies’ predominant reactions to the restraint tests were extracted from the puppy test (Table 8; see [41]). From the adult test, two components based on dogs’ reactions to the experimenter’s threatening approach were determined. The latter were labelled Threat-Friendly and Threat-Retreat due to high loadings of either friendly approach behaviour or withdrawing from the threatening experimenter, respectively (Table 9). Both components had high negative loadings for barking and growling.

Table 8. Components and component loadings of CATPCA over selected variables from the puppy test

Exploration - Inactivity		Greeting		Play	
Move	-0.75	Approach	0.77	Follow toy	0.88
Explore	-0.86	Tail-wagging	0.82	Grab toy	0.94
Inactive	0.96	Jumping up	0.68	Return with toy	0.66
<i>Eigenvalue</i>	2.22	<i>Eigenvalue</i>	1.74	<i>Eigenvalue</i>	2.09
<i>% variance</i>	73.83	<i>% variance</i>	57.93	<i>% variance</i>	69.77

Novel object – low Boldness		Restraint tests	Passive/ Low Interaction	Play	Struggle	Total
Novel object - Tail	-0.81	Struggling	-0.46	-0.03	0.77	
Novel object - Approach	-0.80	Vocalising	-0.45	-0.42	-0.34	
Novel object - Hunt	-0.72	Flight	-0.25	0.88	0.10	
Novel object - Distance	0.85	Interaction	-0.79	-0.24	-0.37	
		Passive	0.78	-0.53	0.24	
		Look away	-0.59	-0.43	0.41	
<i>Eigenvalue</i>	2.54	<i>Eigenvalue</i>	2.05	1.48	1.08	4.61
<i>% variance</i>	63.48	<i>% variance</i>	34.15	24.59	18.00	76.74

Table 9. Components and component loadings of CATPCA over selected variables from the adult test

Exploration - Activity		Greeting		Play	
Explore - move	0.90	Greeting intensity	0.90	Encourage	0.82
Explore - explore	0.87	Tail wagging	0.73	Return with toy	0.82
Explore - inactive	-0.85	Jumping up	0.85	<i>Eigenvalue</i>	<i>1.34</i>
<i>Eigenvalue</i>	<i>2.30</i>	<i>Eigenvalue</i>	<i>2.06</i>		
<i>% variance</i>	<i>76.50</i>	<i>% variance</i>	<i>68.77</i>	<i>% variance</i>	<i>67.04</i>

Novel Object - Boldness		Threatening approach	Threat - friendly	Threat - retreat	Total
Novel object - grab	0.92	Latency to react	0.84	-0.20	
Novel Object - approach	0.88	Bark	-0.70	-0.52	
Novel Object - proximity	0.47	Growl	-0.71	-0.53	
Novel Object - orientation	0.56	Retreat	-0.59	0.61	
		Approach friendly	0.63	0.11	
<i>Eigenvalue</i>	<i>2.16</i>	<i>Eigenvalue</i>	<i>2.64</i>	<i>1.36</i>	<i>4.01</i>
<i>% variance</i>	<i>54.04</i>	<i>% variance</i>	<i>0.33</i>	<i>0.17</i>	<i>0.50</i>

Associations between behaviour in the neonate test, the puppy test and the adult test

Although struggling in the puppy test was negatively associated with the residuals of the Vocal/ Sucking force component in the neonate test ($F_{1,74}=6.45$, $p=0.013$) this effect disappeared after correcting for multiple testing. None of the other tested variables in either the puppy or the adult test was significantly correlated with the predictors from the neonate test (Tables 10-11), indicating a lack of predictive value of the neonate test used. Regarding associations between behaviour in the puppy test at 6-7 weeks and the adult test, only a single significant correlation emerged: as predicted, Exploration - Inactivity in the puppy test was negatively correlated with Exploration - Activity in the adult test ($F_{1,43}=7.79$, $p=0.008$; significant after correction for multiple testing). None of the other predicted associations turned out to be significant (all $p>0.1$, Table 12).

Table 10. Summary of linear mixed models testing for predicted associations between neonate test components and puppy test components

NEONATE test component	PUPPY test variable/ component	Predicted direction of effect	Random effect of best model	Value	Std. Error	numDF	denDF	F	P
Activity	Exploration – Inactivity	-	Litter (p<0.0001)	0.06	0.08	1	85	0.52	0.47
Activity	Novel object – Low boldness	-	Litter (p=0.002)	0.01	0.10	1	85	0.02	0.89
Vocal/ Sucking force (residuals)	Flight	+	Litter (p=0.005)	0.09	0.12	1	74	0.51	0.48
Vocal/ Sucking force (residuals)	Struggle	+	Litter (p=0.0004)	-0.28	0.11	1	74	6.45	0.013
Vocal/ Sucking force (residuals)	Playfulness	-	Litter (p=0.003)	-0.15	0.12	1	74	1.76	0.19

Table 11. Summary of linear mixed models testing for predicted associations between neonate test components and adult test components

NEONATE test component	ADULT test component	Predicted direction of effect	Random effect of best model	Value	Std. Error	numDF	denDF	F	P
Activity	Exploration – High Activity	+	None	-0.15	0.13	1	40	1.41	0.24
Activity	Novel object – Boldness	+	None	-0.16	0.11	1	40	2.23	0.14
Vocal/ Sucking force (residuals)	Threat-Retreat (no barking or growling)	-	None	0.12	0.23	1	37	0.26	0.61
Vocal/ Sucking force (residuals)	Threat-Friendly (no barking, growling, retreating)	-	None (tendency for litter: p=0.052)	-0.03	0.22	1	24	0.02	0.88
Vocal/ Sucking force (residuals)	Threat reaction latency	-	None	0.10	3.22	1	35	0.001	0.98
Vocal/ Sucking force (residuals)	Playfulness	-	None	0.61	0.32	1	35	3.53	0.07

Table 12. Summary of linear mixed models testing for predicted associations between puppy test components and adult test components

PUPPY test component	ADULT test component	Predicted direction of effect	Random effect of best model	Value	Std. Error	numDF	denDF	F	P
Exploration – Low Activity	Exploration – High Activity	-	None	-0.29	0.10	1	43	7.79	0.008
Novel object – Low Boldness	Novel object – High Boldness	-	None	-0.04	0.06	1	43	0.46	0.50
Greeting	Greeting	+	Litter (p=0.019)	-0.01	0.14	1	29	0.001	0.97
Play	Play	+	None	-0.16	0.18	1	43	0.84	0.37
Passive/ Low Interaction	Threat-Retreat (no barking or growling)	+	None	0.07	0.14	1	41	0.10	0.75
Flight		+	None	-0.17	0.14	1	41	1.52	0.23
Struggle		-	None	-0.24	0.14	1	41	2.74	0.11
Passive/ Low Interaction	Threat-Friendly (no barking, growling, retreating)	-	None	0.06	0.16	1	24	0.11	0.74
Flight		-	None	-0.01	0.16	1	24	0.002	0.96
Struggle		-	None	-0.07	0.16	1	24	0.18	0.68

Litter effects

In the neonate test, Activity was unaffected by litter ($p=0.30$) whereas Vocal/ Sucking force was significantly affected by litter ($p=0.01$; Table S1). All tested variables in the puppy test, Exploration - Inactivity ($p<0.0001$), Low boldness ($p=0.004$), Playfulness ($p=0.0008$; Table 10), as well as Greeting ($p=0.014$), Passive/ Low Interaction ($p<0.0001$), Flight ($p=0.008$) and Struggle ($p=0.0003$), were significantly affected by litter. In the adult test, only Greeting ($p=0.02$), and Threat-Friendly ($p=0.05$) tended to be affected by litter, but this was no longer significant when correcting for multiple testing.

Discussion

We investigated behavioural consistency and the predictive value of early tests in Border collies. The analysis of the neonate test showed that the Vocal/ Sucking force component was affected by puppies' weight, as well as by separation time from the mother, and so these factors would need to be taken into account in assessments of neonate puppies. Nonetheless, although we controlled for these effects, there was a lack of correspondence between the behaviour of neonates and the same dogs during the puppy and adult test, implying a lack of validity of this tool for making predictions regarding future behaviour. The results furthermore indicate low predictive validity of the puppy test conducted at 6-7 weeks of age, as activity during room exploration was the only behaviour that was significantly related between the puppy test and the adult test. Even if some of the results became significant at larger sample sizes, this would be of little use to practitioners when assessing individual dogs.

The lack of the predictability of future behaviour based on our neonate test is in line with a study on the ontogeny of behaviour in a litter of captive wolves: MacDonald [14] tested five wolf cubs' reactions to people and novel objects repeatedly from birth to the age of 6 months. He suggests that some consistency in behaviour, relative to the litter mates, did not emerge before the age of 44 days when the cubs were tested together with their siblings. Moreover, in individual tests, individual behaviour differences did not stabilise until day 86. Some major changes were observed over time, with the initially most fearful individuals becoming most friendly to people or vice versa [14]. While these results are in agreement with the lack of correspondence between neonate and later behaviour found in our study,

unfortunately the animals were not followed up for more than 6 months and so we do not know whether those individual differences which showed some stability between 6 weeks and 6 months remained stable until adulthood. Also, studies on primates found poor correspondence between behaviour as neonates and 5 to 10 months later: Heath-Lange et al. [12] assessed behaviour of infant macaques and baboons in blocks of 50 days and while several traits were correlated between adjacent age blocks, most behaviours were unrelated over longer time spans [12]. Sussman & Ha [13] report no predictive value of neonate pigtailed macaques' behaviour for later behaviour at all.

In the current study, correspondence between dogs' behaviours at 6-7 weeks and 1.5-2 years was low, with only one out of ten investigated traits being significantly correlated between the puppy and the adult test. This implies that either behaviour is not consistent from the age of 6 weeks or a lack of validity of the assessments used. Given that tests such as those used in the present study are routinely used for selecting working dogs, this is a critical question. Clearly one downside of behavioural assessments in general is that generalisations about the dog's overall behavioural tendencies are made from a test spanning a very limited time period and including a limited number of stimuli [46]. Also, all tests were designed to be appropriate for the respective ages and therefore different assessments were used at different ages. However, it should be considered that the use of different measurements will lead to more diverging results than applying the same instrument twice, confounding the consistency estimate with method variance [22]. These factors may have contributed to the low correspondence between earlier and later behaviour traits in our study.

Another factor that could have contributed to the low consistency is the young age of the puppies in the puppy test. At 6-7 weeks, puppies tend to be quite open and will react less fearfully to stimuli [47] before a heightening of fear responses occurs at around 9-10 weeks of age [48]. Thus, by testing the puppy at 6-7 weeks of age, there was a low risk of detrimental effects on the puppies' socialisation due to the presentation of potentially fear eliciting stimuli such as the novel object (table 4, c.f. [27]). At 6 weeks of age, however, the puppies were only one quarter into their sensitive period which lasts from 4 to 12 weeks of age (sensu Friedman et al. [47]; Lord [49] considers this period to end already at 8 weeks), and later events, particularly environmental influences after transition to their new homes are likely to have had a major influence on the puppies' development. Thus, testing at a later age might

have resulted in higher consistency between tests. For instance, when comparing puppies' scores in "fear of object tests" with adult fearfulness, Goddard & Beilharz [29] found no significant correlations between adult fearfulness and behaviour in tests conducted at 6 or 7 weeks of age, but scores in one of three tests conducted at 8 weeks and in two of four tests conducted at 10 weeks were significantly correlated with fearfulness in the adult dogs. Furthermore, trainers' subjective ratings of adult dogs' nervousness, assessed during five different behavioural tests and 3 weeks of training, were significantly positively correlated with "fear on walk" scores at 3, 4, 6 and 12 months of age, respectively, but correlation coefficients increased more than two-fold between 3 and 12 months [28].

While the importance of a sensitive period for socialisation in young puppies is often stressed (e.g. [47,49]), this does not imply that environmental influences occurring at other developmental stages do not have effects as well [50], and so experiences throughout ontogeny can account for the low correspondence between behaviour in the puppy and the adult test. For example, Appleby et al. [51] found that environmental factors (such as being raised in a nondomestic environment and lack of exposure to urban environments) between the ages of 3 and 6 months were significantly associated with aggressive and avoidance behaviour in pet dogs. Moreover a major reorganisation of the central nervous system occurs during puberty [52], and there is growing evidence that adolescence can be considered as an additional sensitive period (beyond the prenatal and early postnatal periods), with profound effects on future behaviour (reviewed in [53]). There is evidence that steroid-dependent adolescent brain and behavioural development can be modified by social experience [54]. Thus, experiences after the first sensitive period of socialisation, and in particular during adolescence, will also play an important role in determining the adult animal's behaviour. For instance, Foyer et al. [55] point out that the experiences and behaviour of the dogs during their first year of life are crucial in determining their later behaviour and temperament, and accordingly, Swedish military dogs are not selected for enrolment within the Swedish Armed Forces until they are 15-18 months old [55].

A reason for the diverging results of previous studies regarding the predictive value of puppy tests may lie in different levels of analysis. Based on the existing puppy test literature, we suggest that the predictive value of a puppy test depends on the level at which a prediction is made: puppy tests may have the potential of predicting outcomes (successful qualification

as guide dogs [23,28] or as police dogs [24,25]) to some extent (but see [26,27]), but not individual behaviour traits [30,56,57]. Based on psychometric principles, a higher reliability can be expected for aggregate measures (i.e., sum or average of multiple observed behaviours) than for single measures due to evening out of the random, nonsystematic errors in the different multiple measures [22]. Although there is some evidence that aggregate measures are more predictive of outcomes [58] and have higher heritability estimates [57] than single measures in dog personality assessments, a meta-analysis on personality consistency in dogs did not find a significant difference between single trait measures and aggregate trait measures [22]. At least in the case of puppy tests, however, the current literature seems to support higher predictability for outcomes (i.e. aggregate measures) than for individual behaviour traits, and accordingly, our results show that correlations between puppies' and adults' behaviour are mostly lacking.

Litter effects differed between assessments at different ages. Vocal/ Sucking force in the neonate test and all puppy test components were significantly affected by litter whereas in the adult test no significant litter effects were found. This indicates that behaviour in the 6-7-week-old puppies was influenced more by either genetic effects, maternal effects or the shared early environment than behaviour in the adult dogs. Accordingly, high maternal effects are often found in puppies' behaviour but for older dogs, these effects are small or negligible (reviewed in [29]). Studies on other species also showed that effects of early experiences became less salient as the animals became older (e.g. sheep [61]; rats [62]). A decline in the effects of early shared environment with age has furthermore been shown in humans: In more than 200 pairs of adoptive siblings, correlations in IQ of 0.26 were found when the children were 8 years old; however, 10 years later these same siblings showed a correlation near 0.0 [63].

Unlike this study, Strandberg et al. [31] did find litter effects (as well as additive genetic effects) on adult dogs' behaviour in behavioural assessments, and also Foyer et al. [32] identified influences of several early environmental variables on the behaviour of dogs tested at approximately 17 months of age. A possible explanation lies in the bigger sample sizes in these studies (N=5959 and N=503, respectively), so that much smaller effect sizes are significant. Heritability of behavioural traits has been estimated at 0.05-0.56 in domestic dogs [59,60], although there appears to be breed-specific variation [26,60]. In general, heritabilities

around 0.20 appear to be the norm. This effect may be too small to turn out as significant with our sample size and may explain the scarcity of litter effects in the adult test. Thus, the absence of litter effects in our study does not necessarily imply that genetics or early environmental influences are unimportant but indicates that litter effects were too small to be detected in our sample. Conversely, the results point to the importance of (later) environmental influences on canine behaviour.

Furthermore, environmental differences can be expected to have a greater effect on behavioural variability in our sample of pet dogs compared to the working dogs of previous studies, which tend to be kept under more uniform conditions and follow standardised training regimes. Given that dogs are highly responsive to their social environment [64], the role of the owner should not be forgotten. For example, parallels in personality dimensions in humans and their dogs have been reported [65], training methods employed by the owners were found to be related to dogs' openness towards an unfamiliar person and how they interacted with their owners in play [66], and owner personality was related to stress coping in human-dog dyads [67].

Conclusions

Our results suggest that early behavioural tests yield poor predictability regarding future behaviour in pet dogs. While there are some indications that puppy tests may have the potential to identify negative extremes (e.g. [27]) and may serve to predict outcomes such as working dog success, we want to caution against over-interpreting results from these early assessments and highlight the importance of experiential factors in the course of ontogeny in influencing the adult dog's behaviour. Despite the blossoming of dog research in the last decades, we are still at the beginning of understanding dogs' behavioural development. Future studies should investigate developmental trajectories by repeatedly assessing dogs between the age of 6 weeks and 1.5 years and by following them up into old age. This will yield further insights into the ontogeny of behaviour in dogs and the question from what age meaningful predictions about later behaviour can be made.

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References

1. Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. *Biol Rev Camb Philos Soc* 82: 291–318.
2. Stamps J, Groothuis T (2010) The development of animal personality: relevance, concepts and perspectives. *Biol Rev* 85: 301–325.
3. Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. *Anim Behav* 77: 771–783.
4. McCrae RR, Costa PT, Ostendorf F, Angleitner A, Hrebícková M, et al. (2000) Nature over nurture: temperament, personality, and life span development. *J Pers Soc Psychol* 78: 173–186.
5. Roberts BW, DelVecchio WF (2000) The rank-order consistency of personality traits from childhood to old age: a quantitative review of longitudinal studies. *Psychol Bull* 126: 3–25.
6. Costa PT, Herbst JH, McCrae RR, Siegler IC (2000) Personality at midlife: stability, intrinsic maturation, and response to life events. *Assessment* 7: 365–378.
7. Hubert NC, Wachs TD, Petersmartin P, Gandour MJ (1982) The study of early temperament: Measurement and conceptual issues. *Child Dev* 53: 571–600.
8. Matheny APJ, Riese ML, Wilson RS (1985) Rudiments of infant temperament: newborn to 9 months. *Dev Psychol* 21: 486–494.
9. Worobey J, Blajda VM (1989) Temperament ratings at 2 weeks, 2 months, and 1 year: Differential stability of activity and emotionality. *Dev Psychol* 25: 257–263.
10. Rothbart MK, Derryberry D, Posner MI (1994) A psychobiological approach to the development of temperament. In: Bates JE, Wachs TD, editor. *Temperament: Individual differences at the interface of biology and behavior*. Washington: American Psychological Association. pp. 83–116.
11. Korner AF (2010) Individual differences at birth: Implications for early experience and later development. *Am J Orthopsychiatry* 41: 608–619.
12. Heath-Lange S, Ha JC, Sackett GP (1999) Behavioral measurement of temperament in male nursery-raised infant macaques and baboons. *Am J Primatol* 47: 43–50.
13. Sussman A, Ha J (2011) Developmental and Cross-Situational Stability in Infant Pigtailed Macaque Temperament. *Dev Psychol* 47: 781–791.
14. MacDonald K (1983) Stability of individual differences in behavior in a litter of wolf cubs (*Canis lupus*). *J Comp Psychol* 97: 99–106.

15. Carere C, Drent PJ, Privitera L, Koolhaas JM, Groothuis TGG (2005) Personalities in great tits, *Parus major*: stability and consistency. *Anim Behav* 70: 795–805.
16. Francis RC (1990) Temperament in a Fish: A Longitudinal Study of the Development of Individual Differences in Aggression and Social Rank in the Midas Cichlid. *Ethology* 86: 311–325.
17. Stevenson-Hinde J, Stillwell-Barnes R, Zunz M (1980) Subjective assessment of rhesus monkeys over four successive years. *Primates* 21: 66–82.
18. Weinstein TAR, Capitanio JP (2008) Individual differences in infant temperament predict social relationships of yearling rhesus monkeys, *Macaca mulatta*. *Anim Behav* 76: 455–465.
19. Visser E., van Reenen C., Hopster H, Schilder MB., Knaap J., et al. (2001) Quantifying aspects of young horses' temperament: consistency of behavioural variables. *Appl Anim Behav Sci* 74: 241–258.
20. Lansade L, Bouissou M-F, Erhard HW (2008) Fearfulness in horses: A temperament trait stable across time and situations. *Appl Anim Behav Sci* 115: 182–200.
21. Lowe SE, Bradshaw JWS (2001) Ontogeny of individuality in the domestic cat in the home environment. *Anim Behav* 61: 231–237.
22. Fratkin JL, Sinn DL, Patall EA, Gosling SD (2013) Personality Consistency in Dogs: A Meta-Analysis. *PLoS One* 8: 8:e54907.
23. Scott, J.P., Beilfelt SW (1976) Analysis of the puppy testing program. In: Pfaffenberger, C.J., Scott, J.P., Fuller, J.L., Ginsburg, B.E., Bielfelt SW, editor. *Guide Dogs for the Blind: Their Selection, Development and Training*. pp. 39–75.
24. Slabbert JM, Odendaal JSJ (1999) Early prediction of adult police dog efficiency - a longitudinal study. *Appl Anim Behav Sci* 64: 269–288.
25. Svobodova I, Vapenik P, Pinc L, Bartos L (2008) Testing German shepherd puppies to assess their chances of certification. *Appl Anim Behav Sci* 113: 139–149.
26. Wilsson E, Sundgren P-E (1998) Behaviour test for eight-week old puppies—heritabilities of tested behaviour traits and its correspondence to later behaviour. *Appl Anim Behav Sci* 58: 151–162.
27. Asher L, Blythe S, Roberts R, Toothill L, Craigon PJ, et al. (2013) A standardized behavior test for potential guide dog puppies: Methods and association with subsequent success in guide dog training. *J Vet Behav Clin Appl Res* 8: 431–438.
28. Goddard ME, Beilharz RG (1984) A factor analysis of fearfulness in potential guide dogs. *Appl Anim Behav Sci* 12: 253–265.

29. Goddard ME, Beilharz RG (1986) Early prediction of adult behaviour in potential guide dogs. *Appl Anim Behav Sci* 15: 247–260.
30. Beaudet R, Chalifoux A, Dallaire A (1994) Predictive value of activity level and behavioral evaluation on future dominance in puppies. *Appl Anim Behav Sci* 40: 273–284.
31. Strandberg E, Jacobsson J, Saetre P (2005) Direct genetic, maternal and litter effects on behaviour in German shepherd dogs in Sweden. *Livest Prod Sci* 93: 33–42.
32. Foyer P, Wilsson E, Wright D, Jensen P (2013) Early experiences modulate stress coping in a population of German shepherd dogs. *Appl Anim Behav Sci* 146: 79–87.
33. Goddard ME, Beilharz RG (1982) Genetic and environmental factors affecting the suitability of dogs as Guide Dogs for the Blind. *Theor Appl Genet* 62: 97–102.
34. Korner AF (1971) Individual differences at birth: Implications for early experience and later development. *Am J Orthopsychiatry* 41: 608.
35. Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, et al. (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neurosci Biobehav Rev* 23: 925–935.
36. Carere C, van Oers K (2004) Shy and bold great tits *Parus major*: body temperature and breath rate in response to handling stress. *Physiol Behav* 82: 905–912.
37. Crockenberg SB, Smith P (1982) Antecedents of mother-infant interaction and infant irritability in the first three months of life. *Infant Behav Dev* 5: 105–119.
38. Scott JP (1965) *Genetics and the Social Behavior of the Dog*. Chicago: University of Chicago Press.
39. Rooney N, Bradshaw J (2004) Breed and sex differences in the behavioural attributes of specialist search dogs—a questionnaire survey of trainers and handlers. *Appl Anim Behav Sci* 86: 123–135.
40. Miklósi Á (2009) *Dog Behaviour, Evolution, and Cognition* (Oxford Biology). Oxford: Oxford University Press.
41. Riemer S, Müller C, Virányi Z, Huber L, Range F (2013) Choice of conflict resolution strategy is linked to sociability in dog puppies. *Appl Anim Behav Sci* 149: 36–44.
42. Linting M, Meulman JJ, Groenen PJF, van der Kooij AJ (2007) Nonlinear principal components analysis: introduction and application. *Psychol Methods* 12: 336.
43. Linting M, van der Kooij A (2012) Nonlinear principal components analysis with CATPCA: a tutorial. *J Pers Assess* 94: 12–25.

44. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. RCT (2013) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3. pp. 1–107.
45. Holm S, 1979. A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70.
46. Taylor KD, Mills DS (2006) The development and assessment of temperament tests for adult companion dogs. *J Vet Behav - Clin Appl Res* 1: 94–108.
47. Freedman DG, King JA, Elliot O (1961) Critical period in the social development of dogs. *Science* 133: 1016–1017.
48. Overall KL, Dyer D (2005) Enrichment strategies for laboratory animals from the viewpoint of clinical veterinary behavioral medicine: emphasis on cats on dogs. *ILAR J* 46: 202–215.
49. Lord K (2013) A Comparison of the Sensory Development of Wolves (*Canis lupus lupus*) and Dogs (*Canis lupus familiaris*). *Ethology* 119: 110–120.
50. Lindsay SR (2000) *Handbook of Applied Dog Behavior and Training, Vol. 1: Adaptation and Learning*. Ames: Iowa State University Press.
51. Appleby DL, Bradshaw JWS, Casey RA (2002) Relationship between aggressive and avoidance behaviour by dogs and their experience in the first six months of life. *Vet Rec* 150: 434–438.
52. Romeo RD (2003) Puberty: a period of both organizational and activational effects of steroid hormones on neurobehavioural development. *J Neuroendocrinol* 15: 1185–1192.
53. Sachser N, Kaiser S, Hennessy MB (2013) Behavioural profiles are shaped by social experience: when, how and why. *Philos Trans R Soc B Biol Sci* 368: 20120344.
54. Schulz KM, Molenda-Figueira HA, Sisk CL (2009) Back to the future: the organizational--activational hypothesis adapted to puberty and adolescence. *Horm Behav* 55: 597–604.
55. Foyer P, Bjällerhag N, Wilsson E, Jensen P (2014) Behaviour and experiences of dogs during the first year of life predict the outcome in a later temperament test. *Appl Anim Behav Sci* in press.
56. Goddard ME, Beilharz RG (1986) Early prediction of adult behaviour in potential guide dogs.
57. Wilsson E, Sundgren P-E (1997) The use of a behaviour test for the selection of dogs for service and breeding, I: Method of testing and evaluating test results in the adult dog, demands on different kinds of service dogs, sex and breed differences. *Appl Anim Behav Sci* 53: 279–295.

58. Sinn DL, Gosling SD, Hilliard S (2010) Personality and performance in military working dogs: Reliability and predictive validity of behavioral tests. *Appl Anim Behav Sci* 127: 51–65.
59. Saetre P, Strandberg E (2006) The genetic contribution to canine personality. *Genes, Brain Behav* 5: 240–248.
60. Van der Waaij EH, Wilsson E, Strandberg E (2008) Genetic analysis of results of a Swedish behavior test on German Shepherd Dogs and Labrador Retrievers. *J Anim Sci* 86: 2853–2861.
61. Mirza SN, Provenza FD (1990) Preference of the mother affects selection and avoidance of foods by lambs differing in age. *Appl Anim Behav Sci* 28: 255–263.
62. Lehmann J, Russig H, Feldon J, Pryce CR (2002) Effect of a single maternal separation at different pup ages on the corticosterone stress response in adult and aged rats. *Pharmacol Biochem Behav* 73: 141–145.
63. Loehlin JC, Horn JM, Willerman L (1989) Modeling IQ change: evidence from the Texas Adoption Project. *Child Dev* 60: 993–1004.
64. Webster SD (1997) Being sensitive to the sensitive period. *Proceedings of the First International Conference on Veterinary Behavioural Medicine. Universities Federation for Animal Welfare, England.* pp. 20–27.
65. Kubinyi E, Turcsán B, Miklósi Á (2009) Dog and owner demographic characteristics and dog personality trait associations. *Behav Processes* 81: 392–401.
66. Rooney NJ, Cowan S (2011) Training methods and owner-dog interactions: Links with dog behaviour and learning ability. *Appl Anim Behav Sci* 132: 169–177.
67. Schöberl I, Wedl M, Bauer B, Day J, Möstl E, Kotrschal K (2012) Effects of Owner-Dog Relationship and Owner Personality on Cortisol Modulation in Human-Dog Dyads. *Anthrozoos* 25: 199–214.

Table S1. Final reduced models of effects of age, separation time and weight on the components Activity and Vigour of the neonate tests (effects of the interaction between predictors and age are not shown because they were removed in the model selection process).

Dependent variable	Predictor	Random effect of best model	Value	Std. Error	numDF	numDF	F	P
Vocal/ Sucking force	Weight	Litter (p=0.003)	6.13	0.02	1	79	0.002	0.0008
	Time separated		6.03	0.02	1	79	-0.005	0.002
Activity	Weight	None	0.00007	0.001	1	34	0.003	0.95
	Time separated		0.003	0.003	1	34	0.84	0.36

CHAPTER 3

Choice of conflict resolution strategy is linked to sociability in dog puppies

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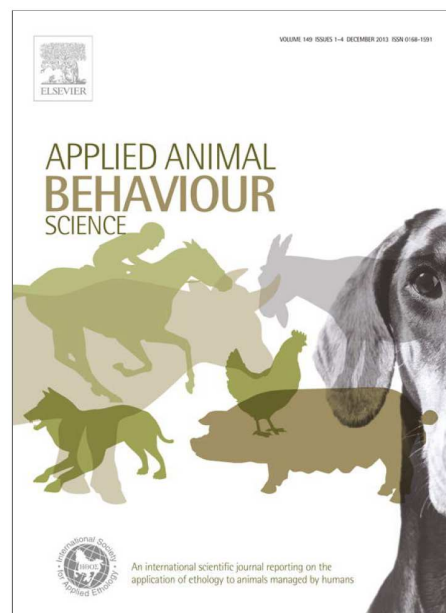
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Abstract

Measures that are likely to increase sociability in dog puppies, such as appropriate socialisation, are considered important in preventing future fear or aggression related problems. However, the interplay between sociability and conflict behaviour has rarely been investigated. Moreover, while many studies have addressed aggression in domestic dogs, alternative, non-aggressive conflict resolution strategies have received less scientific attention. Here we tested 134 Border collie puppies, aged 40-50 days, in a personality test which included friendly interactions with an unfamiliar person, exposure to a novel object, and three brief restraint tests. Considering the latter to be mild ‘conflict’ situations, we analysed whether the puppies’ behaviour in the restraint tests was related to their sociability or to their boldness towards the novel object. Strategies employed by the puppies during restraint tests included trying to interact socially with the experimenter, remaining passive, and attempting to move away. In line with findings from humans and goats, puppies scoring high on sociability were more likely to adopt an interactive conflict resolution strategy, while those with low sociability scores tended to react passively. In contrast, avoidance behaviours were unrelated to sociability, possibly reflecting inconsistency in the flight strategy in dogs. Boldness towards a novel object was not related to sociability or to puppies’ reactions in restraint tests. This is one of the first studies to demonstrate a link between sociability and conflict resolution strategies in non-human animals.

Keywords:

Conflict resolution, personality, sociability, boldness, dog puppies, *Canis familiaris*

1. Introduction

Group-living confers many advantages to animals such as increased foraging or prey-capture efficiency, defence of kills and territory, vigilance and defence against predators, and rearing of young (Krause & Ruxton, 2002). However, there are costs associated with sociality such as increased competition, incompatible goals, or clashes of interest regarding the coordination of activities or travel decisions, which may lead to inter-individual conflicts (Aureli & De Waal, 2000; Preuschoft & van Schaik, 2000; Aureli et al., 2002; Bergmüller & Taborsky, 2010). To maintain the benefits of group living and avoid the costs of aggressive interactions, behavioural conventions such as greeting gestures, reconciliation (affiliative post-conflict behaviours between former adversaries), and the establishment of dominance relationships are common in group living animals (de Waal 2000, Preuschoft & van Schaik 2000, Aureli et al., 2002).

Conflict management strategies such as appeasement, submission, or avoidance serve to increase tolerance within the group, control aggression and reduce conflicts (reviewed in Aureli & de Waal, 2000; Aureli et al., 2002; Miranda-de la Lama et al., 2011). In the behavioural context, a strategy can be defined as a behaviour or collection of behaviour patterns which an individual uses to achieve a goal, whereby different behavioural solutions to the same problem may be equally successful (Mendl & Deag, 1995). It has been suggested that personality represents an important, underlying factor for individuals' choices of strategy (Miranda de la Lama et al., 2011). Work primarily on rodents and some birds has shown that responses to challenge – referred to as 'coping styles' – are often related to a suite of other behavioural tendencies, as well as physiological responses: Proactive individuals are bolder, more explorative, and tend to react to stressful events with a fight-or-flight response, whereas reactive individuals show lower aggressiveness, tend to freeze in aversive situations, and are more flexible to environmental changes (Benus et al., 1991; Koolhaas et al., 1999; Carere et al., 2010).

In humans, personality factors, especially those related to social interactions – extraversion and agreeableness – are suggested to be helpful predictors of individual preferences of conflict resolution strategies (Wood & Bell, 2008). Similarly, it has been suggested that behaviour, such as use of aggression, in non-human animals can be predicted and manipulated based on a knowledge of individual coping strategies (Mendl & Deag, 1995). However, there is a lack of studies on conflict behaviour other than aggression and post-conflict reconciliation

(reviewed in de Waal, 2000, Aureli et al., 2002) in non-human animals, particularly in non-primate species (Judge, 2000; Aureli et al., 2002; but see Miranda-de la Lama et al., 2011). Moreover, apart from the coping styles model, where the presence or absence of a fight/flight response or freezing in a challenging situation is inherent in the definition of two behavioural extremes (proactive and reactive coping styles, Koolhaas et al., 1999), links between personality and behaviour in social conflict situations in non-human animals have received little scientific attention (but see Thierry, 2000; Cote & Clobert, 2007; Miranda-de la Lama et al., 2011).

Domestic dogs (*Canis familiaris*) constitute a suitable model species to investigate the proposed link between personality and conflict resolution for various reasons. Over the course of domestication, they appear to have evolved specialised and flexible social skills for reading human social and communicative behaviour (Hare & Tomasello, 2005), and the human environment and social setting has become their natural ecological niche (Miklósi et al., 2004). Thus, it is possible to test dogs' personality and conflict behaviours outside of the laboratory environment but in a standardised way by using a human test person. Many studies have described different personality traits in domestic dogs including reactivity, fearfulness, trainability, aggressiveness and sociability (reviewed in Jones & Gosling, 2005). Surprisingly, not much scientific information is available on conflict resolution strategies in dogs (but see Cools et al., 2008, for reconciliation following intraspecific conflict). A few papers report dogs' differential responses in inter-group conflicts (Bonnani et al., 2010), or to a threatening human (Vas et al., 2005, 2008; Horváth et al., 2007; De Meester et al., 2008; Györi et al., 2008). Walker et al. (1997) classified dogs' strategies in relation to fear behaviour, adapting the model by Marks (1987a as cited by Walker et al., 1997) - freeze (immobility), flight (withdrawal, escape, avoidance), flirt (deflection of attack and appeasement/ submission), and fight (aggressive defence). Lindsay (2005) similarly suggested the following five behavioural reactions in conflict situations in dogs: fight, flight, flirt, freeze (wait for the situation to change), and forbear (tolerate or accept the situation).

Relating personality and conflict resolution in dogs has been addressed only to the extent that behavioural assessments have aimed at identifying dogs' tendency to react aggressively, typically by threatening or manipulating the dog or by removing resources from the dog (e.g. Netto & Planta, 1997; Bollen & Horowitz, 2008; De Meester et al., 2008; van der Borg et al., 2010; Bennett et al., 2012). There is currently a lack of scientific data on dogs' use of alternative,

non-aggressive, conflict resolution strategies. Our aim was therefore to determine alternative conflict resolution strategies in dogs and to investigate whether dogs' reactions to a perceived conflict situation are related to their personality, particularly their sociability and boldness.

We compared the behaviour of 134 Border collie puppies in a friendly greeting situation with an unfamiliar person to that in three restraint tests (a back test, a simulated veterinary examination and staring into the puppies' eyes), which could be perceived as conflicts by the dogs. We predicted that the puppies' sociability is positively correlated with active but nonaggressive ways of conflict resolution (interaction, c.f. flirt strategy), and negatively with aggressive (fight strategy) or avoidant (flight strategy) strategies (c.f. Walker et al., 1997; Lindsay, 2005). Passivity could either indicate high tolerance (forbearing) or constitute a freeze strategy (c.f. Lindsay, 2005). While highly sociable puppies might potentially be more tolerant of handling, less sociable puppies might be more likely to freeze during handling; therefore no a priori prediction was made. Given a suggested association between boldness and reactions in the back test (e.g. Hessing et al., 1994 – but see Forkman et al., 1995), we furthermore analysed whether boldness towards a novel object was related to behaviour in the restraint tests.

2. Methods

All procedures were performed in compliance with the Austrian animal protection law and the University of Vienna's ethics guidelines, and with the breeders' consent. No special permission for use of animals in such non-invasive socio-cognitive studies is required in Austria.

2.1. Subjects and test setup

We tested 134 Border collie puppies (aged 40-50 days, 72 males and 62 females) from 23 litters of 15 different breeders in a personality test. All breeders were small-scale breeders (with typically 1-2 litters per year) and bred according to FCI (Fédération Cynologique Internationale) standards, and the puppies spent most of their time in the house. Due to the risk of disease contraction for the young puppies, all tests were carried out at the breeders' homes, but in rooms that were unfamiliar to the puppies (only one litter had to be tested in a familiar room because no unfamiliar room was available).

2.2. Behavioural tests

All tests were conducted by the same experimenter (SR), who was unfamiliar to the puppies prior to the test. A cameraman filmed the test for subsequent video analysis. Besides the experimenter and the cameraman, the breeder or a familiar person was present in 62 of the 134 tests – this was accounted for in the analysis (see below).

The test lasted about 20 minutes per puppy and consisted of eleven subtests exposing the puppy to different social and non-social stimuli (see Table 1 for descriptions of the subtests). These form part of a test routinely used for assessing puppies' suitability as service dogs (Erik Kersting, Hundezentrum Canis Familiaris, pers. comm.). Social tests started after an initial exploration phase of two minutes in which the puppy was free to explore the unfamiliar surroundings. None of the people present interacted with the puppy during this time. The first social test was the greeting test (subtest 2) to assess sociability. The three restraint tests (subtests 6-8), back test, vetcheck test and staring test, followed after three subtests that were not used for analysis here (see Table 1). The novel object test constituted the final test in the sequence.

Following the restraint tests, the experimenter resolved the situation by crouching, encouraging the puppies to approach, and interacting with the puppies in a friendly way. Despite constituting potentially stressful situations, the restraint tests did not appear to affect the puppies' ensuing behaviour in a negative way. They did not show strongly submissive or fearful behaviours during the restraint tests; only one puppy that had recently woken up urinated during the back test. After the test, the puppies usually returned to the experimenter when encouraged to exchange affiliative interactions.

Table 1. Summary of the subtests of the puppy personality test. Tests used for the present paper are in bold font.

	Subtest	Description	Aim	Duration
1.	Room exploration	The puppy was allowed to explore the unfamiliar room for two minutes; experimenter, cameraman and breeder remained passive.	Not used for analysis here.	60 s
2.	Greeting test	The experimenter crouched down approximately 2.5 m away from the puppy and encouraged it to make contact by calling its name, chatting in a friendly voice or clicking her tongue. When the puppy approached, she petted the puppy and talked to it in a friendly way for 20 seconds. If the puppy did not want to approach within 45 seconds, the subtest was terminated.	Determining individual sociability.	60 s
3.	Play	The experimenter tried to engage the puppy in play by wiggling a soft toy in front of it. When the puppy was following and/or trying to grab the toy for at least 10 seconds, she threw it two metres away and vocally encouraged the puppy to return to her with the toy. This was repeated three times.	Not used for analysis here.	2-3 min
4.	Following test	The experimenter started walking away from the puppy, encouraging the puppy to follow by calling it, clicking her tongue, and clapping her hands, changing direction of movement several times.	Not used for analysis here.	60 s
5.	Problem solving	The experimenter showed some pieces of sausage to the puppy and then placed them under a transparent cup, which the pup had to knock over to obtain the food. This was repeated three times.	Not used for analysis here.	2-4 min
6.	Back test	The experimenter was sitting on the floor and gently turned the puppy on its back, holding it in this position with both hands while casually looking at the puppy, but not staring at it in a threatening way.	Determining conflict resolution strategies.	25 s
7.	Vetcheck test	Simulated veterinary examination. The experimenter, sitting on the floor, stroked the puppy's body, touched its paws, looked into its ears and examined its teeth.	Determining conflict resolution strategies.	30 s
8.	Staring test	The experimenter lifted the puppy up, holding it upright under its armpits, so that she could look directly into its eyes. When the puppy averted its gaze, the experimenter reoriented the puppy and took up eye contact again.	Determining conflict resolution strategies.	30 s

Table 1 continued

	Subtest	Description	Aim	Durati on
9.	Startle test	A balloon was burst approximately 3 m away from the puppy. Thereafter, the experimenter behaved cheerfully and tried to engage the puppy in play.	Not used for analysis here.	60 s
10.	Table test	The puppy was placed at the centre of a table for one minute. Four different dog toys had been placed in the four corners of the table for the puppy to explore.	Not used for analysis here.	60 s
11.	Novel object test	A battery-powered toy looking like a paper bag, approx. 20 x 10 x 5 cm, was placed approx. 2 m away from the puppy to assess its reactions to the novel object's erratic movements.	Determining boldness.	60 s

2.3. Data processing

The puppies' behaviour was scored by the first author from the videos, using Solomon coder (© András Péter), according to the definitions in Table 2. A range of socio-positive behaviours was scored during the greeting test (subtest 2), using ordinal scores and presence/absence of behaviours. For the back test (subtest 6), durations of struggling and vocalising were coded. In the vetcheck test (subtest 7), attempts to interact with the experimenter by licking or mouthing of the experimenter's fingers/ face and escape behaviour were noted. In the staring test (subtest 8), the number of times the puppy averted its gaze was counted. In the novel object test, approach latency, tail position and whether or not the puppies 'hunted' the novel object (i.e., jumped at the object with their fore paws and/ or bit into it) were scored and minimum distance to the novel object was estimated (Table 2). For tests terminated prematurely due to measurement error (back test: N=12, range 14.6-24.8 s; staring test: N=7, range 14-29.2 s), durations and frequencies were extrapolated to the full duration.

Table 2. Scoring of variables derived from video analysis of behaviour in the various subtests. Subtests are numbered as in Table 1.

	Variable	Type	Score	Description
<u>2</u>	<u>Greeting test</u>			
2a.	Approach latency	Rating	0	Does not approach the experimenter (10 cm from experimenter's hands) within 45 seconds.
			1	Approaches the experimenter within 21-45 seconds after she started calling.
			2	Approaches the experimenter within 11-20 seconds after she started calling.
			3	Approaches the experimenter within 10 seconds after she started calling.
2b.	Tail-wagging	Rating	0	Wags tail <30% of interaction time.
			1	Wags tail 30-69% of interaction time.
			2	Wags tail 70% or more of interaction time.
2c.	Jumping up	Absence/ Presence	0	Does not jump up or climb into experimenter's lap.
			1	Jumps up or climbs into experimenter's lap.
2d.	Pawing/ rolling over	Absence/ Presence	0	Does not give the paw or attempt to roll over.
			1	Gives the paw or rolls over/ performs intention movements to roll over.
<u>6.</u>	<u>Back test</u>			
6a.	Struggling	Duration	% time	Quick movements of body, head, and legs. Does not include slow movement of individual limbs or the head. Absolute duration in seconds (precision 0.2 s).
6b.	Vocalising	Duration	% time	Duration of vocalisations. Absolute duration in s (precision 0.2 s).

Table 2 continued

	Variable	Type	Score	Description
<u>7.</u>	<u>Vetcheck test</u>			
7a.	Flight	Absence/	0	No escape attempt.
		Presence	1	Escape attempt (trying to move away with the whole body while being held – does not include movement with the head to avoid teeth control or walking away when not held).
7b.	Interaction	Absence/	0	Mouthing or licking of experimenter's fingers/ face for <20% of the time.
		Presence	1	Mouthing or licking of experimenter's fingers/ face for at least 20% of the time.
<u>8.</u>	<u>Staring test</u>			
8.	Look away	Event	Frequency	Averting gaze (head turn away from experimenter's face). This is followed by the experimenter reorienting the puppy to look into its eyes again.
<u>10.</u>	<u>Novel object test</u>			
10a.	Approach latency	Rating	1	Does not approach to within 20 cm of the novel object within 30 s.
			2	Approaches to within 20 cm of the novel object after 5 s.
			3	Approaches to within 20 cm of the novel object within 5 s/ does not retreat more than 20cm when approached by the novel object.
10b.	Tail position	Rating	1	Tail mostly low.
			2	Tail partly low, partly medium/high.
			3	Tail mostly medium to high.
		Absence/	0	Puppy did not 'hunt' the novel object (jump at the object with the fore paws and/ or bite into it).
10c.	Hunt	Presence	1	Puppy 'hunted' the novel object (i.e., jumped at the object with their fore paws and/ or bit into it).
10d.	Minimum distance	Estimate	continuous	Estimated closest distance (cm) of puppy to paper bag.

Reliability coding for the above variables was performed by two coders, one not involved in the study for 20 randomly selected puppies, one from each of 20 litters, with one coder coding the greeting test and the restraint tests and the other coding the novel object test. Reliability was assessed using Cohen's weighted kappa for scores and Cronbach's alpha for frequencies, durations and estimated distance. Correspondence of coders was good for all coded variables: Cohen's weighted kappa was 0.71 for approach latency score, 0.88 for jumping up, 0.70 for tail-wagging score, and 0.67 for giving the paw/rolling over in the greeting test, 1.0 for interacting with the experimenter during the vetcheck test, 0.83 for fleeing during the vetcheck test, 1.0 for passive behaviour during the vetcheck test, 0.67 for approach latency score in the novel object test, 0.92 for tail position during the novel object test, and 0.89 for hunting of the novel object. Cronbach's alpha was 0.95 for duration of struggling during the back test, 0.84 for duration of vocalising during the back test, 0.88 for frequency of gaze avoidance during the staring test, and 0.89 for the estimated minimum distance of the puppies to the novel object.

Statistical analysis was carried out using R 2.12.0 (R Development Core Team, 2010) and SPSS Statistics 21. (IBM Corp. Armonk, NY, 2012). Sample size was 134 for all tests. Nonlinear principal components analyses (called CATPCA or categorical principal components analyses in SPSS; Linting et al., 2007, Linting & Kooji, 2012) were performed on relevant subsets of variables to obtain components for sociability, conflict resolution strategies, and boldness.

Linear mixed models (LMM) were calculated to assess effects of sociability and boldness on behaviour in conflict situations. Components derived from the restraint tests were dependent variables, and sociability (assessed in the greeting test), boldness in the novel object test, and presence or absence of the breeder (to account for a possible effect of the breeder's presence on the puppies' behaviour during the test) were included as fixed effects. Interactions between the predictors were included in the initial models, but none of these turned out as significant and so they are not discussed in the results. Also, presence of the breeder did not act as a confounding factor (no effect in any of the models) and is therefore not discussed further. Therefore, we present reduced models where only the main predictors – sociability and boldness – were retained. Litter nested within breeder was included as a random effect in the initial models. Subsequently we computed alternative models without random effects or with breeder only or litter only as a random effect and compared goodness of fit of the different models with likelihood ratio tests.

3. Results

3.1. Greeting Test

Latency to approach the stranger, amount of tail wagging, jumping up and pawing/rolling over all had high positive loadings on the first component of the CATPCA (Table 3), accounting for 44.7% of total variance. This component was labelled ‘Sociability’ and was used in the ensuing analysis.

Table 3. Variable loadings on the CATPCA component ‘Sociability’ and accounted variance.

Original variable	Component 1
	Sociability
Approach latency	0.77
Tail-wagging	0.84
Jumping up	0.62
Pawing/ rolling over	0.34
% of variance	44.72

3.2. Restraint tests

The puppies showed various behavioural reactions when faced with potential conflict situations in the restraint tests. All but two puppies struggled during the back test, and 114 of the 134 puppies also vocalised. The median proportion of time spent struggling and vocalising was 71.7% (Interquartile Range IQR=51.7-85.3%) and 25.3% (IQR=4.7-50.7%) respectively. Only two puppies displayed aggression (snapping at the experimenter’s hand) during the back test. Due to the 1/0 scoring system, only distinct responses were identified in the vetcheck test: 51 puppies (38.1%) were passively tolerating the procedure; 37 puppies (27.6%) tried to interact with the experimenter by mouthing or licking the experimenter’s fingers/ face but did not attempt to escape; 34 puppies (25.4%) tried to move away but did not interact with the tester; and 12 puppies (9.0%) showed both interaction and escape attempts. During these handling procedures, no stiffness or other signs of aggression were shown by the puppies. During the staring test, the number of times the puppies averted their gaze ranged from 0 to 20 (median = 8, IQR=4-11).

The CATPCA of the restraint test variables yielded 3 components accounting for 76.8% of total variance (Table 4). Puppies with high values on the first component ‘Passive/ Low

Interaction’ tended to show passivity or low levels of responses in all three restraint tests. Puppies with low values on the first component tried to diffuse the situation through social interaction or social signalling, such as by licking or mouthing of the experimenter’s hands or face during the vetcheck test, looking away during the staring test, and (to a lesser extent) also struggling and vocalising during the back test. Puppies with high values on the second component ‘Flight’ tried to escape during the vetcheck test and were less likely to show passive behaviour, looking away and vocalising. Puppies with high values on the third component ‘Struggle’ showed a lot of struggling in response to the back test and also tended to look away during the staring test.

Table 4. Variable loadings on the three CATPCA components from the restraint tests and accounted variance.

Restraint Test	Original variable	Component 1	Component2	Component 3
		Passive/ Low Interaction	Flight	Struggle
<u>Back Test</u>	Struggling	-0.46	-0.03	0.77
	Vocalising	-0.45	-0.42	-0.34
<u>Vetcheck Test</u>	Flight	-0.25	0.88	0.10
	Interaction	-0.79	-0.24	-0.37
	Passive	0.78	-0.53	0.24
<u>Staring Test</u>	Look away	-0.59	-0.43	0.41
	% of variance	34.15	24.59	18.00

3.3. Novel Object test

The first component, labelled ‘Boldness’ accounted for 63.48% of variance. A short latency to approach the novel object, tail position and ‘hunting’ of the novel object loaded highly negatively on this component, while minimum distance to the novel object had a high positive loading (Table 5). Thus, high values on this component indicate a lack of boldness.

Table 5. Variable loadings on the CATPCA component ‘Boldness’ and accounted variance.

Original variable	Component 1
	Boldness
Approach latency	-0.80
Tail position	-0.81
Hunt	-0.72
Minimum distance	0.85
% of variance	60.55

3.4. Relationship between ‘Sociability’, ‘Boldness’ and behaviour in restraint tests

Effects on the ‘Passive/ Low Interaction’ component

A LMM assessing the effect of ‘Sociability’ and ‘Boldness’ on a ‘Passive/ Low Interaction’ response yielded a highly significant negative effect of ‘Sociability’ (Table 6, Fig. 1a). That is, more sociable puppies were more likely to interact with the tester and less likely to show a passive response in the potential conflict situations. In contrast, ‘Boldness’ had no significant effect on the dependent variable (Table 6). Likelihood ratio tests showed that goodness of fit of a model with litter nested within breeder as random effect was significantly better than that of a model including only breeder as random effect (L.Ratio=12.59, $p < 0.001$), but did not differ from a model including only litter as random effect (L.Ratio<0.001, $p = 0.99$). The latter model was therefore retained (Table 6). This model was significantly better than a model without random effects (L.Ratio=22.54, $p < 0.001$), demonstrating an effect of litter on the tendency to show a passive or interaction response in restraint tests.

Table 6. Summary of mixed effects models, showing effects of ‘Sociability’ and ‘Boldness’ (fixed effects) on the restraint test components ‘Passive/ Low Interaction’, ‘Flight’, and ‘Struggle’. All presented models include litter as a random effect.

Dependent variable	Model term	Value	Std. Error	numDF	denDF	F	P
Passive/ Low Interaction	Sociability	-0.21	0.08	1	110	7.97	0.006**
	Boldness	-0.04	0.08	1	110	0.26	0.61
Flight	Sociability	0.01	0.09	1	110	0.01	0.91
	Boldness	0.04	0.09	1	110	0.19	0.66
Struggle	Sociability	-0.01	0.08	1	110	0.002	0.97
	Boldness	0.08	0.09	1	110	0.88	0.35

Effects on the ‘Flight’ component

Neither ‘Sociability’ nor ‘Boldness’ had a significant effect on the ‘Flight’ component (Fig. 1b, Table 6). A model with litter nested within breeder as a random effect was significantly better than a model without random effects but did not differ significantly from models with either breeder only (L.Ratio<0.001, p=0.99) or litter only as a random effect (L.Ratio= 1.03, p=0.31; Table 6). Both models were significantly better than a model without random effects (random effect - breeder: L.Ratio=9.85, p=0.0017; random effect - litter: L.Ratio= 8.81, p=0.003), demonstrating that the tendency to flee differed between puppies from different breeders or litters, but was not related to puppies’ ‘Sociability’.

Effects on the ‘Struggle’ component

A model testing for effects of ‘Sociability’ and ‘Boldness’ on the ‘Struggle’ component found no significant effect for either predictor (Table 6, Fig. 1c). A model including litter nested within breeder as a random effect did not differ significantly from a model including only litter (L.Ratio=0.006, p=0.99) but was significantly better than a model including only breeder (L.Ratio=15.53, p=0.001). The model including litter as a random effect was also significantly better than a model without random effects (L.Ratio=19.70, p <0.001) and was therefore selected (Table 6).

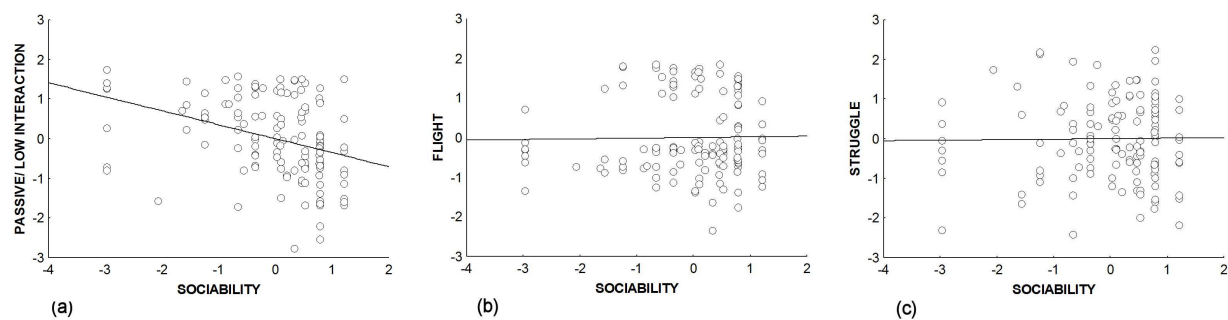


Fig. 1 Individuals' object scores for the 'Sociability' component plotted against object scores for (a) 'Passive/ Low Interaction' (b) 'Flight' and (c) 'Struggle'.

In summary, 'Sociability' was positively associated with interaction during restraint tests and negatively with passivity. In contrast, there was no relationship of 'Sociability' with flight responses and struggling. 'Boldness' was unrelated to reactions in the restraint tests. Responses in restraint tests were, however, affected by litter or breeder.

4. Discussion

The dog puppies showed much variation in their willingness to engage positively with the unfamiliar experimenter during the greeting test, which was assumed to measure sociability. The fourth to eight weeks of life are particularly important in the socialisation of dog puppies (Lord 2013); thus puppies' behavioural responses may have been affected by previous experiences with unfamiliar people and handling procedures. Nonetheless, this does not preclude the notion of personality, as the expression of personality traits is influenced by an interaction of genes and experiential factors (Stamps & Groothuis 2010). Litter or breeder significantly affected responses in all restraint tests, suggesting that the puppies' behaviour was influenced by genetics, maternal factors, and/ or early environment. The relative influences of these cannot be determined from our data.

The CATPCA components of behaviour in the three restraint tests can be considered to reflect three (or four) different conflict resolution strategies. Puppies that showed no or few overt behavioural reactions had high values of the first component ('Passive/ Low Interaction'), which may be comparable to a freeze response (Walker et al., 1997 and Lindsay 2005), forbearing (Lindsay 2005), 'standing still' during a physical examination (Åkerberg et al., 2011), a passive

strategy as found by Vas et al. (2008, 2005), or tolerating (Györi et al., 2010). In contrast, low values on the ‘Passive/ Low Interaction’ component were associated with interaction with the experimenter (licking, mouthing, and gaze aversion). This might correspond to the flirt strategy defined by Walker et al. (1997) and Lindsay (2005), or to dogs’ friendly or contact-seeking responses towards a human who is threatening them (Vas et al., 2008, 2005; Györi et al., 2010) or performing a physical examination (Åkerberg et al., 2011). The second component (‘Flight’) corresponds to a flight strategy (Walker et al., 1997; Lindsay 2005; De Meester et al., 2008) or can be compared to dogs’ active avoidance/ moving off (Vas et al., 2005, 2008; Györi et al., 2010).

Struggling in the back test, the variable that loaded most highly on the third component, could be interpreted as an attempt to escape the situation (thus it could be classified as a flight strategy, c.f. Forkman et al., 1995) or as a fight strategy (Walker et al., 1997). Struggling was not associated with aggressive behaviour (fight strategy), as only two puppies displayed any aggression (snapping during the back test) at all. This lack of aggressive responses could be explained by the young age of the puppies and/ or because they did not perceive the tests as severely threatening. If we interpret struggling as avoidance behaviour, then the puppies with high values on the third component could be said to display both elements of active avoidance (moving away) and passive avoidance (gaze aversion) after Vas et al. (2008). Notably, struggling during the back test seemed to be unrelated to escape responses during the vetcheck test; however, the loading of looking away on the ‘Struggle’ factor would be suggestive of avoidance behaviour, rather than a fight response.

It is possible that flight responses are a more inconsistent strategy in dogs than other forms of conflict resolution: When analysing test-retest responses to a threatening human, Vas et al. (2008) found that dogs exhibiting friendly or threatening behaviour tended to respond consistently in a subsequent test, whereas dogs classified as active avoidant (moved away behind the owner from the approaching stranger whilst keeping eye contact) or passive avoidant (interrupted the eye contact with the stranger and averted its gaze permanently) altered their responses (Vas et al., 2008). If dogs’ avoidance behaviour in social situations is generally inconsistent as suggested by Vas et al. (2008), this could explain the lack of a relationship between the ‘Flight’ and the ‘Struggle’ components and with ‘Sociability’ in our study. Moreover, the main variables on the components ‘Flight’ and ‘Struggle’ differ in that the flight

response was scored as present/ absent, whereas the dominating variable of the ‘Struggle’ component – proportion of time spent struggling – was a continuous variable. The puppies may have perceived the back test as more threatening than the vetcheck test and so nearly all of them exhibited some degree of struggling during the back test, whereas only 25.4% tried to escape during the vetcheck test. Such a situational change in response strategy is in line with Vas et al.’s (2008) interpretation who suggest that the change in behavioural responses of ‘active avoidant’ or ‘passive avoidant’ dogs with repeated testing may can be regarded as different manifestations of the same continuum, for example representing approach/ avoidance motivational conflicts.

No correlation between ‘Boldness’ towards a novel object and the ‘Struggle’ component (or any of the other components of conflict resolution) was found; neither was there an interaction between ‘Boldness’ and ‘Sociability’. This lack of a relationship between social and non-social tests indicates that sociability and conflict behaviour in dog puppies may not reflect a generalised coping style or behavioural syndrome extending to non-social behaviours. Similarly, MacDonald (1987) found fear of objects to be unrelated to attraction towards humans in young wolves, and Forkman et al. (1995) reports the lack of a relationship between numbers of escape attempts during the back test in piglets and their performance in other behavioural tests including a novel object test, extinction of a learned response, aggressiveness and social dependence. We conclude that social behaviour and boldness towards a non-social stimulus and are not related in our sample of well-socialised dog puppies. Clearly higher generalised fearfulness can be expected in puppies that have received little social and non-social stimulation, such as those raised in non-domestic environments (c.f. Appleby et al., 2002), which might explain the reported relationship between the factors ‘Sociability’ and ‘Curiosity/Fearlessness’ in domestic dogs (Svartberg, 2002).

We acknowledge that conclusions about personality should be cautious as no measure of temporal consistency (inherent in the definition of personality) is available in this study. However, our findings are in agreement with results from human children: In developmental psychology, children are often classified into three groups according to their styles of emotional regulation, which seem to be related to both their sociability and their conflict resolution strategies (Blair et al., 2004). Children described as ‘highly inhibited’ tended to show socially withdrawn behaviour and passive coping in conflict situations, which corresponds to those puppies that showed low interest and little affiliative behaviour towards the stranger during the

greeting test and tended to react passively in the restraint tests. Children who are ‘optimally regulated’ were found to exhibit the most positive, adaptive behaviour in conflict situations and were judged as more sociable and socially competent (Blair et al., 2004). These may correspond to puppies with high sociability scores. As aggression was hardly observed in our study, we found no equivalents to children classified as ‘undercontrolled’, who score low in prosocial behaviour and are most likely to employ non-constructive strategies such as reactive aggression when in a social conflict situation (Blair et al., 2004).

There are furthermore parallels between our study and a study on domestic goats (*Capra hircus*) in a related context, third-party intervention in conflicts and use of agonistic or affiliative strategies. Goats with an ‘affiliative profile’ engaged in frequent affiliative interactions during everyday life and primarily used active, non-agonistic strategies when in a conflict situation, aiming to reduce social tension (Miranda-de la Lama et al., 2011). These individuals can be compared to puppies with low ‘Passive/ Low Interaction’ scores, which showed high sociability towards the experimenter and reacted to restraint tests by trying to interact with the experimenter. In contrast, goats with a passive profile seemed indifferent to their social environment, neither engaging in affiliative interactions nor in conflicts – similarly as the puppies scoring high on the ‘Passive/ Low Interaction’ component. The ‘avoider profile’ in goats, characterised by an avoidance of conflicts, could be compared to puppies scoring high on the ‘Flight’ component and presumably also on the ‘Struggle’ component; however, as discussed above, the flight – or avoidance – strategy seemed less consistent in our study and was not related to sociability. Finally, goats with an ‘aggressive’ profile used aggression as the main mechanism of social relationships. At least in the interaction with humans, consistent aggressive strategies may be unlikely to occur in domestic dogs, which have been selected for low levels of aggression and a high level of social tolerance towards humans (e.g. Hare et al., 2012) and developed effective mechanisms to negotiate interactions and avoid the escalation of conflicts in interaction with humans (Györi et al., 2010).

5. Conclusions

We show that conflict resolution strategies are related to sociability in dog puppies. The most sociable puppies were most likely to employ active and communicative ways of conflict resolution, while passive responses were negatively associated with sociability. These results add to previous findings that dogs showing aggression obtained lower sociability scores in a

behavioural assessment (Valsecchi et al., 2011). They are further in agreement with the proposed importance of measures which are likely to increase puppies' sociability (i.e. appropriate socialisation) in preventing future problem behaviour (e.g. Freedman et al., 1961, Serpell, 1995, Duxbury & Anderson, 2003). Even though our sociability measure is rather rough and can only represent a snapshot in time, the observed relationship between dog puppies' sociability and conflict resolution strategies is in line with findings from other species. The relationship of sociability and conflict behaviour in adult dogs, as well as their stability over time, warrants further research.

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References

- Åkerberg, H., Wilsson, E., Sallander, M., Hedhammar, Å., Lagerstedt, A.-S., Larhammar, D. Meyerson, B., 2012. Test for personality characteristics in dogs used in research. *J. Vet. Behav. – Clin. Appl. Res.* 7(6), 327–338
- Appleby, D.L., Bradshaw, J.W., Casey, R.A. 2002. Relationship between aggressive and avoidance behaviour by dogs and their experience in the first six months of life. *Vet. Rec.* 150, 434-438.
- Aureli, F., Cords, M., Van Schaik, C.P., 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Anim. Behav.* 64, 325-343.
- Aureli, F., de Waal, F. B. M., eds., 2000. *Natural Conflict Resolution*. Berkeley, California: University of California Press.
- Bennett, S. L., Litster, A., Weng, H-Y, Walker, Walker, S.L., Luescher, A.U., 2012. Investigating behavior assessment instruments to predict aggression in dogs. *Appl. Anim. Behav. Sci.* 141(3-4), 139-148.
- Benus, R. F., Bohus, B., Koolhaas, J. M. van Oortmerssen, G. A., 1991. Heritable variation for aggression as a reflection of individual coping strategies. *Cell. Mol. Life Sci.* 47, 1008–1019.
- Bergmüller, R. Taborsky, M., 2010. Animal personality due to social niche specialisation. *Trends Ecol. Evol.*, 25(9), 504-511.
- Blair, K., Denham, S., Kochanoff, A., Whipple, B., 2004. Playing it cool: Temperament, emotion regulation, and social behavior in preschoolers. *J. School Psychol.*, 42(6), 419-443.
- Bollen, K.S. Horowitz, J., 2008. Behavioral evaluation and demographic information in the assessment of aggressiveness in shelter dogs. *Appl. Anim. Behav. Sci.* 112, 120–135.
- Bonanni, R., Valsecchi, P., Natoli, E., 2010. Pattern of individual participation and cheating in conflicts between groups of free-ranging dogs. *Anim. Behav.* 79, 957–968.
- Carere, C., Caramaschi, D., Fawcett, T.W. 2010. Covariation between personalities and individual differences in coping with stress: Converging evidence and hypotheses. *Curr. Zool.* 56(6), 728-740.

- Cools, A. K. A., van Hout, A. J. M., Nelissen, M. H. J., 2008. Canine reconciliation and third-party-initiated postconflict affiliation: do peacemaking social mechanism in dogs rival those of higher primates? *Ethology*, 114, 53–63.
- Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proc. Biol. Sci.* 274, 383-390.
- De Meester, R. H., De Bacquer, D., Peremans, K., Vermeire, S., Planta, D., J., Coopman, F. Audenaert, K., 2008. A preliminary study on the use of the Socially Acceptable Behavior test as a test for shyness/confidence in the temperament of dogs. *J. Vet. Behav. – Clin. Appl. Res.* 3(4), 161-170.
- Duxbury, M., Jackson, J. J., Line, S., Anderson, S. 2003. Evaluation of association between retention in the home and attendance at puppy socialization classes. *J. Am. Vet. Med. Assoc.* 223(1), 61-66.
- Forkman, B., Furuhaug, L.L., Jensen, P. 1995. Personality, coping patterns, and aggression in piglets. *Appl. Anim. Behav. Sci.* 45, 31-42.
- Freedman, D.G., King, J.A., Elliot, O., 1961. Critical period in the social development of dogs. *Science* 133(3457), 1016-1017.
- Győri, B., Gácsi, M., Miklósi, Á., 2010. Friend or foe: Context dependent sensitivity to human behaviour in dogs. *Appl. Anim. Behav. Sci.* 128, 69-77.
- Hare, B. Tomasello, M., 2005. Human-like social skills in dogs? *Trends Cogn. Sci.*, 9, 439-444.
- Hare, B., Wobber, V., & Wrangham, R., 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Anim. Behav.* 83, 573-585.
- Hessing, M.J., Hagelsø, A.M., Schouten, W.G., Wiepkema, P.R., Van Beek, J.A., 1994. Individual behavioral and physiological strategies in pigs. *Physiol. Behav.* 55, 39-46.
- Horváth, Z., Igyártó B.Z., Magyar, A., Miklósi, A., 2007. Three different coping styles in police dogs exposed to a short-term challenge. *Horm. Behav.* 52, 621-630.
- Jones, A.C. Gosling, S., 2005. Temperament and personality in dogs *Canis familiaris*: A review and evaluation of past research. *Appl. Anim. Behav. Sci.* 95, 1–53.
- Judge, P.G., 2000. Coping with crowded conditions. In: *Natural Conflict Resolution* (Ed. by F. Aureli F. B. M. de Waal), pp. 129–154. University of California Press, California.

- Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M.A.W. Blokhuis, H.J., 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. R.* 23, 925-935.
- Krause, J., Ruxton, G., 2002. *Living in Groups*. Oxford University Press, United Kingdom.
- Lindsay, S. R., 2005. *Handbook of applied dog behavior and training*. Vol 3, Procedures and Protocols. Blackwell Publishing, Iowa.
- Linting, M., Meulman, J.J., Groenen, P.J. van der Kooij, A.J., 2007. Nonlinear principal components analysis: introduction and application. *Psychol. Methods* 12(3), 336-58.
- Linting, M., van der Kooij, A., 2012. Nonlinear principal components analysis with CATPCA: a tutorial. *J. Pers. Assess.* 94, 12-25.
- Lord, K., 2013. A Comparison of the Sensory Development of Wolves (*Canis lupus lupus*) and Dogs (*Canis lupus familiaris*). *Ethology*, 119, 110-120.
- MacDonald, K. 1987. Development and stability of personality characteristics in pre-pubertal wolves: implications for pack organisation and behaviour. In: Frank, H., ed. *Man and wolf: advances, issues, and problems in captive wolf research*, pp. 293-312. Junk Publishers, Dordrecht.
- Marks, I.M., 1987. *Fears, Phobias, and Rituals*, New York: Oxford University Press,
- Mendl, M., Deag, J.M., 1995. How useful are the concepts of alternative strategy and coping strategy in applied studies of social behaviour. *Appl. Anim. Behav. Sci.* 44, 119–137.
- Miklósi, Á., Topál, J. Csányi, V., 2004. Comparative social cognition: what can dogs teach us? *Anim. Behav.* 67, 995-1004.
- Miranda-de la Lama, G.C., Sepúlveda, W.S., Montaldo, H.H., María, G.A.m Galindo, F., 2011. Social strategies associated with identity profiles in dairy goats. *Appl. Anim. Behav. Sci.* 134, 48-55.
- Netto, W. J., Planta, D. J., 1997. Behavioural testing for aggression in the domestic dog. *Appl. Anim. Behav. Sci.* 52, 243-263.
- Preuschoft, S. van Schaik, C. P., 2000. Dominance and communication: conflict management in various social settings. In: *Natural Conflict Resolution* (Ed. by F. Aureli F. B. M. de Waal), University of California Press, Berkeley, pp. 77–105.

- Serpell, J., ed., 1995. *The Domestic Dog. Its Evolution, Behaviour and Interactions with People*. Cambridge University Press, Cambridge.
- Stamps, J., Groothuis, T. G., 2010. The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.* 85(2), 301-325.
- Svartberg, K., Forkman, B. 2002. Personality traits in the domestic dog (*Canis familiaris*). *Appl. Anim. Behav. Sci.* 79, 133-155.
- Thierry, B., 2000. Covariation of conflict management patterns across macaque species. *Natural Conflict Resolution* (Ed. by F. Aureli F. B. M. de Waal), University of California Press, Berkeley, pp. 106-128.
- Walker, R., Fisher, J. Neville, P., 1997. The treatment of phobias in the dog. *Appl. Anim. Behav. Sci.* 52, 275–289.
- Valsecchi, P., Barnard, S., Stefanini, C., Normando, S. 2011. Temperament test for re-homed dogs validated through direct behavioral observation in shelter and home Environment. *J. Vet. Behav. – Clin. Appl. Res.* 6(3), 161–177.
- van der Borg, J.A.M., Beerda, B., Ooms, M., Silveira de Souza, A., van Hagen, M., Kemp, B. 2010. Evaluation of behaviour testing for human directed aggression in dogs. *Appl. Anim. Behav. Sci.* 128, 78-90.
- Vas, J., Topál, J., Gácsi, M., Miklósi, Á., Csányi, V., 2005. A friend or an enemy? Dogs' reaction to an unfamiliar person showing behavioural cues of threat and friendliness at different times. *Appl. Anim. Behav. Sci.* 94, 99–115.
- Vas, J., Topál, J., Györi, B., Miklósi, Á., 2008. Consistency of dogs' reactions to threatening cues of an unfamiliar person. *Appl. Anim. Behav. Sci.* 112, 331–344.

CHAPTER 4

Impulsive for life? The nature of long-term impulsivity in domestic dogs

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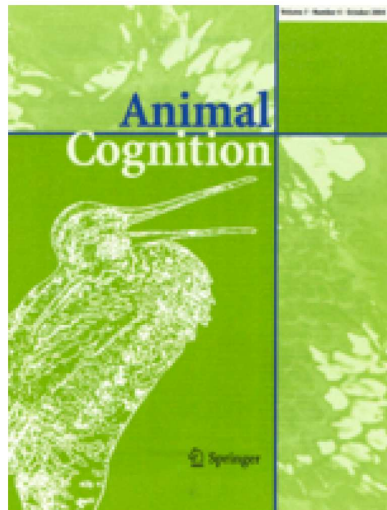
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Abstract

Individual differences in impulsivity occur at a cognitive and/or behavioural level and are associated with differing life outcomes. However there is a lack of empirical evidence to support the long-term stability of these characteristics in non-human animals. This study reports on the stability of convergent measures of impulsivity in domestic dogs assessed more than six years apart. Measures were (1) owner assessment by means of a questionnaire, the validated ‘Dog Impulsivity Assessment Scale’ (DIAS) and (2) dogs’ performance in a delayed reward choice test. Dogs had 15 minutes free access to two food dispensers, one dispensing a piece of food immediately, the other dispensing three pieces after a delay, which increased by one second every other time the dogs sampled it. Maximum delay reached in this task reflects decision making, or cognitive impulsivity, whereas the rate of extra presses on the delayed reward device during the delay can be considered as a measure of motor or behavioural impulsivity. DIAS scores were strongly and significantly correlated across years. The maximum delay reached in the behaviour test was also highly stable, whereas paw pressing rate was uncorrelated between the years. These results demonstrate that cognitive but not motor impulsivity is highly consistent over time in dogs.

Keywords: dogs *Canis familiaris*; impulsivity; delayed reward choice; personality; test-retest reliability; stability

Introduction

Many authors report two major facets of impulsivity, the ability to delay gratification (cognitive impulsivity) and the ability to, inhibit prepotent responses (motor impulsivity), Dougherty et al. 2003, Arce and Santisteban 2006). A common test of these abilities in humans and non-human animals is the delayed reward task in which subjects are given a choice between an immediate lower value reward and a higher value reward after a delay. Humans may be asked questions such as “Would you rather have (X amount) now or (Y amount) in (a given delay period)?”, with hypothetical or real rewards such as money, food, etc. (Odum 2011). Nonhuman animals may be given operant choices via lever presses or key pecks between an immediate lower value reinforcer (e.g. one piece of food) and a delayed higher value reinforcer (e.g. three pieces of food, Wright et al. 2012). Individuals’ delay choice can be considered as a measure of cognitive impulsivity, while the ability to refrain from responding during the delay can be considered as a measure of motor impulsivity.

Across species, individuals tend to discount the value of rewards that are delayed, as reflected by a decreasing preference for an increasingly delayed reward. Nonetheless, this phenomenon, known as delay discounting, exhibits substantial individual differences (Kalenscher et al. 2006; Jimura et al. 2013), which are associated with a variety of life outcomes. High individual levels of impulsivity (fast discounting) are related to attention deficit hyperactivity disorder, substance abuse, pathological gambling, obesity and aggressive behaviour in humans (Cherek et al. 1997, Winstanley et al. 2006, Reynolds 2006, Odum 2011), as well as to aggressiveness in non-human animals (rats: van den Bergh et al. 2006; golden hamsters: Cervantes and Delville 2009) and to owner-reported ‘behaviour problems’ in domestic dogs (Wright et al. 2011).

In their pioneering work, Mischel and colleagues (1988) measured how long preschool children were able to resist taking an immediate reward (e.g. one marshmallow) to obtain a higher value reward later (e.g. two marshmallows). They found that ability to wait in preschoolers was predictive of attentiveness, academic and social competence, and ability to deal with frustration and stress as adolescents (Mischel et al. 1988). Moreover, individuals who were less able to delay gratification in preschool performed more poorly than those more able to delay in a go/no-go task 40 years later (Casey et al. 2011). However these studies remain rare examples, with behavioural tests of temporal stability of impulsivity in humans typically spanning only a few weeks. In behavioural tests, good long-term test-retest reliability has only been reported in relation to monetary rewards (Audrain-McGovern et al. 2009, Kirby 2009, Anokhin et al. 2011).

Models of impulsivity in animals similarly lack a robust demonstration of test-retest reliability over long-term time frames, despite suggestions that impulsivity is a stable characteristic persisting across experiments (Zaichenko and Merzhanova 2011). Although there has been increased interest in ‘animal personality’, defined as “individual differences in behavior that are consistent across time and contexts” (Stamps and Groothuis 2010), in recent years (Réale et al. 2007), the temporal consistency of traits is often neglected, especially over long time intervals. For instance, with one exception (van den Berg et al. 2006 on consistency of aggressive behaviour in dogs), intervals for assessing repeatability of behaviour in dogs have not exceeded 1.5 years (reviewed in Fratkin et al. 2013).

Here, we aimed to assess the stability of two measures of impulsivity in domestic dogs over a six-year period, one using a validated psychometric tool based on owners’ reports (the ‘Dog Impulsivity Assessment Scale’, DIAS), the other assessing performance in a delayed reward choice test. These measures have previously been shown to be related, demonstrating convergent validity (Wright et al. 2011, 2012).

Methods

This study is a follow-up of the work of Wright et al. (2011, 2012), conducted in 2006, with a repetition of two methods for assessing impulsivity on the same dogs. Thirteen dogs of mostly medium-sized breeds (Belgian Shepherd (Tervuren), two Border Collies, Cocker Spaniel, German Shepherd Dog, German Spitz, Labradoodle, Miniature Poodle, Spanish Water Dog, and four cross-breeds) that had participated in the original study were re-tested in 2013. The subjects’ age ranged from 7.5 to 11.5 years (mean 9 years).

Dog owners completed the Dog Impulsivity Assessment Scale (DIAS), a validated 18-item questionnaire (Wright et al. 2011). The questionnaire yields an overall questionnaire score (OQS) and values for three main factors, labelled ‘Behavioural Regulation’ (F1 – reflecting items relating to excitability and behavioural control), ‘Aggression and Response to Novelty’ (F2), and ‘Responsiveness’ (F3 – reflecting items relating to focus and ease to train). The DIAS has previously demonstrated convergent validity with both a delayed reward choice test and physiological markers of serotonergic and dopaminergic functioning (Wright et al. 2012).

Dogs were tested in a delayed reward choice task as in 2006 (described in detail in Wright et al. 2012). After pre-training on a ‘neutral’ device to make sure that the dogs remembered the action of pressing the panel, they were given 10 forced choice trials on each of the two test devices. Pressing of the immediate reward device resulted in immediate delivery of a single piece of dry

food, while pressing of the delayed reward device marked the start point of a three-second delay, after which three pieces of food were delivered. Following the forced choice trials, dogs were given continuous free access to the two devices for a 15 minute period as described in Wright et al. 2012. Starting at three seconds, the delay on the delayed reward device was increased by one second every other time the dogs chose the large reward (consistent with the method used by Wright et al. 2012). When a dog switched to the small immediate device before the delay was over, this cancelled the choice of the large delayed reward and resulted in the dispensing of one piece of food from the small immediate device. When the dogs subsequently selected the delayed reward device again, the time delay continued to increase from the delay that had been reached on the previous press of that panel (i.e. the delay was not reset by the alternative choice of the small immediate device). During testing, the dogs' owners sat in a chair at the back of the test room, filled in the DIAS and did not interact with the dogs.

The maximum delay reached (MaxD) in the 15 minute session and number of extra presses (i.e. presses from first press to delivery of reward) on the delayed reward device during the waiting period were considered to be measures of cognitive and motor impulsivity respectively, since delayed choices reflect the ability to weigh the consequences of immediate and future events and consequently delay gratification (cognitive impulsivity), while rate of paw pressing is a form of response inhibition (motor impulsivity)(Arce & Santisteban 2006). Most dogs show an initial preference for the large delayed device, and although selecting the large delayed device does not lead to gain maximization at longer delays, maximum delay (MaxD) in this test has been found to be inversely correlated with dogs' impulsivity, as assessed in the DIAS (Wright et al. 2012): The overall questionnaire score and 'Behavioural Regulation' factor of the DIAS were significantly negatively correlated with MaxD and significantly positively correlated with the rate of extra presses (Wright et al. 2012).

Intraclass correlation coefficients (two-way random, absolute agreement, single measures. Lessells 1987) were calculated to assess repeatability of dogs' performance in the behaviour test and questionnaire scores. Potential differences were analysed with Wilcoxon Signed Rank tests. To correct for multiple comparisons, False Discovery Rate control (FDR) was applied. Original p-values are indicated in the text. They remained significant after FDR correction unless indicated otherwise. Statistics were computed in PASW Statistics 21.0 software (SPSS Inc. 2012) and figures were produced in Statistica 6.1 (Statsoft Inc. 1984-2004).

Results

13 owners completed the DIAS scale on their dogs, but of these, one had a dog that never selected the delayed reward device in 2006 and two had dogs that did not in 2013. These subjects were therefore excluded from the analysis of the behaviour test since they did not comply with the operational requirement of sampling both devices available in the choice test, leaving 10 subjects in the behaviour test dataset.

DIAS scores remained highly stable over time: Overall Questionnaire Score (ICC=0.76, $n=13$, $p=0.002$), Behavioural Regulation ICC=0.90, $p<0.001$; Figure 1) and Aggression and Response to Novelty (ICC=0.70, $p=0.009$) were highly correlated between 2006 and 2013. Responsiveness was the only factor that differed significantly between the years (Wilcoxon $Z=2.47$, $p=0.01$), showing a decrease over time. Although Responsiveness tended to correlate positively between the years (ICC=0.46, $p=0.033$), this was not significant after FDR correction.

In 2013, the dogs reached maximum delays ranging from 10 - 25 s (median 19 s) in the delayed reward choice test, compared to 7 - 23 s (mean 18 s) in 2006. This slight increase (Wilcoxon, $Z=2.02$, $p=0.04$) was not significant following FDR correction. Individuals' delay choices, reflected by MaxD, were significantly correlated between the years 2006 and 2013 (Intraclass Correlation Coefficient ICC= 0.80, $n=10$, $p<0.001$; Figure 2). In contrast, paw pressing rate was uncorrelated across the years (ICC=0.23, $p=0.228$). There was no statistically significant difference in the median rate of paw pressing in 2006 (median 0.51 presses per second) and 2013 (median 0.89 presses per second, Wilcoxon $Z=1.17$, $p=0.24$).

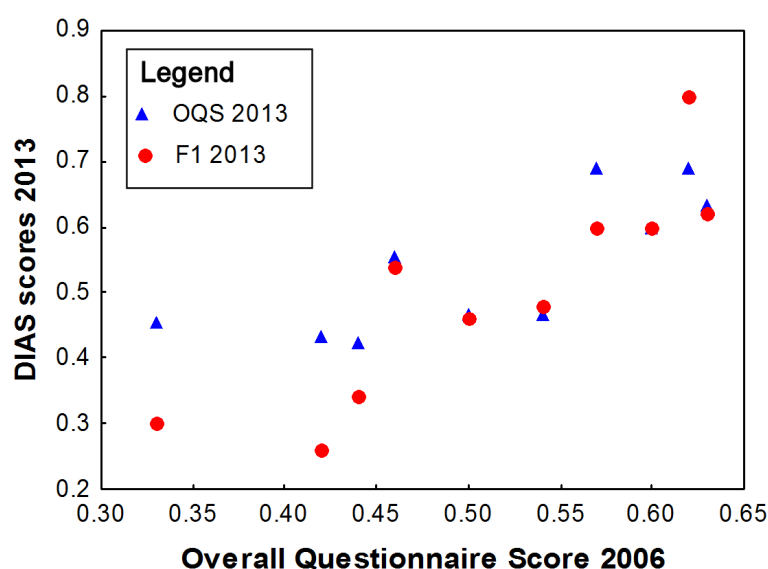


Figure 1 Overall Questionnaire Score (OQS) 2013 and Behavioural Regulation Score (F1) in 2013 plotted against OQS in 2006

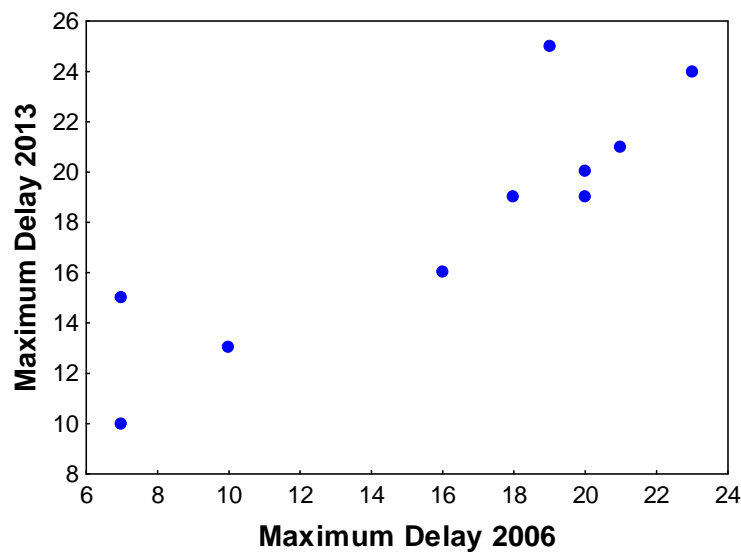


Figure 2 Maximum delay in 2013 plotted against maximum delay in 2006

Discussion

Both the owners' assessments of their dogs' impulsivity according to the DIAS and the dogs' delay choices in the behaviour test indicate that impulsivity remains highly stable in domestic dogs over at least six years (or half a dog's lifetime). To our knowledge, this is longer than has been investigated in any previous study using a delayed reward paradigm in either humans or non-human animals.

The general construct of impulsivity, as assessed by DIAS, and cognitive impulsivity (MaxD), but not motor impulsivity (frequency of paw pressing), were found to be stable across time.

Previous studies support the suggestion that motor and cognitive impulsivity may be independent (Dougherty et al. 2003; van den Bergh et al. 2006), and the results of the current study suggest that motor impulsivity may be more susceptible to changes over time than cognitive impulsivity. Furthermore, in pigeons, the rate of ineffective key pecks made during reinforcer delays in a delayed reward choice task was affected by food deprivation – unlike delay choice (Logue et al. 1985). These results suggest that motor impulsivity may also be more subject to influence from environmental factors (it is worth noting that, in both 2006 and 2013, owners were asked not to feed their dogs prior to the test, by way of control). It is furthermore possible that paw pressing rate simply reflects general motor activity.

However, delay choice and DIAS scores appear to be more accurate measures of trait impulsivity, having high temporal stability. These measures show a significant correlation with each other, demonstrating cross-situational consistency (Wright et al. 2012). Thus, cognitive but not motor

impulsivity appears to be a stable individual characteristic in domestic dogs and can be regarded as a personality trait, being stable across time as well as across contexts (Stamps & Groothuis 2010). This highlights an important distinction between measures which simply allow differentiation between individuals (individual differences) and those relating to behavioural style with a biological basis (true personality traits, *sensu* Mills 2010). Individual differences do not need to be temporally stable, nor necessarily biologically meaningful; they simply need to allow the reliable discrimination between populations at a given time. The correlation coefficients obtained here are considerably higher than temporal correlations reported for other personality traits in adult domestic dogs, ranging from 0.47 to 0.49 (Fratkin et al. 2013), and this may reflect the grounding of the trait in a clear neurobiological basis (Wright et al. 2012).

More research is needed to determine at what age impulsivity can be considered a stable trait in domestic dogs and whether this is dependent on breed and/ or size of the dog. Furthermore, future studies should address the question to what extent individuals' impulsivity can be modified through targeted training. It has been suggested for humans that interventions which increase tolerance to delay of reinforcement in one domain could provide beneficial reductions in impulsive behaviours in other domains that may not be as amenable to direct intervention (Odum 2011), and these results indicate that the domestic dog may be a useful experimental model for testing this question.

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This research was approved by the University of Lincoln's ethics committee and complies with British animal welfare legislation. The authors declare that they have no conflict of interest.

References

- Anokhin AP, Golosheykin S, Grant JD, Heath AC (2011) Heritability of delay discounting in adolescence: A longitudinal twin study. *Behav. Genet.* 41: 175-184. doi: 10.1007/s10519-010-9384-7
- Arce E, Santisteban C (2006) Impulsivity: a review. *Psicothema* 18: 213-220.
- Casey BJ, Somerville LH, Gotlib IH, Ayduk O, Franklin NT, Askren MK, Jonides J, Berman MG, Wilson NL, Teslovich T, Glover G, Zavvas V, Mischel W, Shoda Y (2011) Behavioral and neural correlates of delay of gratification 40 years later. *PNAS* 108: 14998-15003. doi: 10.1073/pnas.1108561108
- Audrain-McGovern J, Rodriguez D, Epstein LH, Cuevas J, Rodgers K, Wileyto EP (2009). Does delay discounting play an etiological role in smoking or is it a consequence of smoking? *Drug Alcohol Depend.* 103(3), 99-106.
- Cervantes MC, Delville Y (2009) Serotonin 5-HT1A and 5-HT3 receptors in an impulsive-aggressive phenotype. *Behav Neurosci.* 123: 589-98. doi: 10.1037/a0015333
- Cherek DR, Moeller FG, Dougherty DM, Rades H (1997) Studies of Violent and Nonviolent Male Parolees: II. Laboratory and Psychometric Measurements of Impulsivity. *Biol. Psychiatry* 41: 523-529.
- Dougherty DM, Bjork JM, Harper RA, Marsh DM, Moeller FG, Mathias CW, Swann AC (2003) Behavioral impulsivity paradigms: a comparison in hospitalized adolescents with disruptive behavior disorders. *J. Child. Psychol. Psychiatry* 44: 1145–1157. doi: 10.1111/1469-7610.00197
- Fratkin L, Sinn DL, Patall EA, Gosling, SD (2013). Personality consistency in dogs: A meta-analysis. *PLoS One* 8: e54907. doi:10.1371/journal.pone.0054907
- Jimura K, Chushak MS, & Braver TS. (2013). Impulsivity and Self-Control during Intertemporal Decision Making Linked to the Neural Dynamics of Reward Value Representation. *J. Neurosci.* 33: 344-357.
- Kalenscher T, Ohmann T, & Güntürkün O. (2006). The neuroscience of impulsive and self-controlled decisions. *Int. J. Psychophysiol.* 62: 203-211.

- Kirby KN (2009). One-year temporal stability of delay-discount rates. *Psychonom. Bull. Rev.* 16, 457–462.
- Lessells CM., Boag PT (1987) Unrepeatable repeatabilities: a common mistake. *Auk* 104: 116-121.
- Logue AW, Peña-Correal TE (1985) The effect of food deprivation on self control. *Behav. Process.* 10: 355–368. doi: 10.1016/0376-63578590036-1
- Mills DS (2010) Personality. In: Mills DS (ed) *Encyclopedia of Applied Animal Behaviour*, Wallingford, CABI, pp. 463-465.
- Mischel W, Shoda Y, Peake EK (1988) The nature of adolescent competencies predicted by preschool delay of gratification. *J. Pers. Soc. Psychol.* 54: 687-696. doi: 10.1037/0012-1649.26.6.978
- Odum AL (2011) Delay discounting: Trait variable? *Behav. Process.* 87: 1-9.
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. *Biol. Rev.* 82: 291-318.
- Reynolds B (2006) A review of delay-discounting research with humans: relations to drug use and gambling. *Behav. Pharmacol.* 17: 651-67. doi:10.1097/FBP.0b013e3280115f99
- Stamps J, Groothuis TG (2010) The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.* 85: 301-325. doi: 10.1111/j.1469-185X.2009.00103.x.
- Van den Berg L, Schilder MBH, de Vries H, Leegwater PAG, van Oost BA (2006) Phenotyping of aggressive behavior in Golden retriever dogs with a questionnaire. *Behav. Genet.* 36: 882–902.
- Van den Bergh F, Spronk M, Ferreira L, Bloemarts E, Groenink L, Olivier B, Oosting R (2006) Relationship of delay aversion and response inhibition to extinction learning, aggression, and sexual behaviour. *Behav. Brain Res.* 175: 75–81. doi:10.1016/j.bbr.2006.08.003
- Winstanley CA, Eagle DM, Robbins TW (2006) Behavioral models of impulsivity in relation to ADHD: translation between clinical and preclinical studies. *Clin. Psychol. Rev.* 26: 379–395. doi: 10.1016/j.cpr.2006.01.001
- Wright HF, Mills DS, Pollux PMJ (2011) Development and validation of a psychometric tool for assessing impulsivity in the domestic dog *Canis familiaris*. *Int. J. Comp. Psychol.* 24: 210-225. doi: 10.1016/j.physbeh.2011.09.019

Wright HF, Mills DS, Pollux PMJ (2012) Behavioural and Physiological correlates of Impulsivity in the Domestic Dog *Canis familiaris*. *Physiol. Behav.* 105: 676–682. doi: 10.1016/j.physbeh.2011.09.019

Zaichenko MI, Merzhanova GK (2011) Studies of Impulsivity in Rats in Conditions of Choice between Food Reinforcements of Different Value. *Neurosci. Behav. Physiol.* 41: 445-451.

CHAPTER 5

Dogs can learn to attend to connectivity in string pulling tasks

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Abstract

String pulling tasks are commonly used to investigate recognition of means-end connections. Previous studies suggested that dogs base their choice on proximity rather than connectivity (Osthaus, Lea, & Slater, 2005), nonetheless, dogs performed successfully in the related support problem (Range, Hentrup, & Virányi, 2011). To re-investigate dogs' means-end understanding, we tested 34 Border collies in string pulling tasks in which the proximity of the reward to the connected string's end was varied. First, subjects were presented with a four-string task (four parallel perpendicular strings, one baited, with the reward in line with the correct string's end). Dogs that performed above chance in this task were tested with a curved string task, involving one straight and one curved string. When the reward was attached to the curved string, it was equidistant from both strings' ends so that choosing by proximity was not possible. While group level performance was significantly above chance, only three of 20 dogs met criterion individually, of which one dog subsequently solved a broken string task upon its first presentation. However, the dogs seemed to be unable to overcome their proximity bias in a parallel diagonal string task where proximity of the unconnected string's end to the reward was misleading. We conclude that although dogs may not demonstrate means-end understanding spontaneously, some can learn to pay attention to connectivity when proximity is not a confounding factor. This study supports the notion that animals may apply several alternative strategies to solve physical problems, which are influenced by the test-setup.

Keywords: string-pulling, means-end connections, proximity, strategy selection, dogs *Canis familiaris*

Introduction

The ability to gain access to an out of reach object by means of pulling a string attached to it has long been regarded as a valid example of non-human animals' apprehension of means-end relationships. However, mere acquisition of the reward by pulling at the string does not necessarily reflect means-end understanding; alternatively, it could be due to associative learning (e.g. Schmidt & Cook 2006) and/ or manipulating the vicinity of the food (Heinrich & Bugnyar 2005; Osthaus, Lea, & Slater, 2005). To distinguish between these possibilities, several strings, which may be laid out at various angle orientations or crossed, are often provided (Heinrich & Bugnyar 2005). Animals as diverse as pigeons (*Columba livia*, Schmidt & Cook, 2006), corvids (Heinrich, 1995), psittacids (Werdenich & Huber, 2006; Schuck-Paim, Borsari, & Ottoni, 2009), several monkey species (Harlow & Settlage, 1934; Cha & King, 1969; Halsey, Bezerra, & Souto, 2006; Gagné, Levesque, Nutile, & Locurto, 2012), and great apes (Herrmann, Wobber, & Call, 2008; Povinelli, 2000) have performed successfully in tasks requiring them to select a baited over an unbaited string or paying attention to a gap between the string and the reward. Based on the performance in these tasks, various cognitive processes have been proposed for different animals, including associative learning (e.g. squirrel monkeys, *Saimiri sciureus*, Cha & King, 1969; pigeons, *Columba livia*, Schmidt & Cook 2006), operant conditioning (New Caledonian crows, *Corvus moneduloides*, Taylor, Medina, Holzhaider, Hearne, Hunt, & Gray, 2010), attending to perceptual contact but not necessarily connectivity (great apes, Herrmann, Wobber, & Call, 2008; Povinelli, 2000) and spontaneous apparently “insightful” solutions (individual ravens, *Corvus corax*, Heinrich 1995; grey parrots, *Psittacus erithacus*, Pepperberg, 2004; and keas, *Nestor notabilis*, Werdenich & Huber, 2006).

In fact, a combination of ontogenetic development and experience may have led to such apparently insightful behavior. For instance, Bruce, a 7-month-old kea fledgling, failed to retrieve food attached to a string initially, but a month later, he showed the same competence as those individuals that were several years old when tested for the first time (Huber & Gajdon, 2006; Werdenich & Huber, 2006). A combination of sensorimotor development (beak-foot coordination) and experience might have facilitated means-end understanding (Werdenich & Huber, 2006). Indeed, experience is of paramount importance in the development of physical cognition: It is through exploration that human children detect and relate affordances between objects, coordinate spatial frames of reference, and incorporate early-appearing action patterns

into instrumental behaviors (Lockman, 2000). Given appropriate experience, young children quickly learn, transfer and extend their current knowledge about physical causality (Brown, 1990). Also in animals, cognitive development comes about through an interaction between the subject and its environment (Doré & Dumas, 1987). Moreover, specific experiences may be necessary for a functional understanding of physical tasks. For instance, in a tool using task, great apes initially failed to select the correct cane tool when it was not in contact with the reward (Herrmann, Wobber, & Call, 2008). However, after only a small amount of experience with the plastic material of the canes (in the context of different experiments), they improved relative to the first experiment (Herrmann, Wobber, & Call, 2008). Besides enhancing physical understanding, certain experiences may furthermore aid animals in overcoming impulsive responses or in examining the task more carefully, leading to improved performance (Seed, Call, Emery, & Clayton, 2009).

Domestic dogs (*Canis familiaris*) have generally shown an inferior performance in physical cognition tasks when compared to primates and some birds (e.g. Osthaus, Lea, & Slater, 2005; Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006). In the string pulling paradigm, they were able to select a baited over an un-baited string when parallel perpendicular strings were presented (Osthaus, Lea, & Slater, 2005). However, they failed in more complex two-choice tasks when the proximity of the unconnected string's end was misleading (Osthaus, Lea, & Slater, 2005; Range, Möslinger, & Virányi, 2012), as well as in a task requiring them to select an entire string connected to a reward over a shorter one that was not connected, but close to a second reward (Range, Möslinger, & Virányi, 2012), with no sign of learning within 20 trials in either task (Osthaus, Lea, & Slater, 2005; Range, Möslinger, & Virányi, 2012). Dogs have a strong tendency to paw near the reward and accordingly perform successfully in tasks where the correct string's end lies closest to the reward, but not when the unconnected string's end is closer to the reward than the connected string's end (Osthaus, Lea, & Slater, 2005; Range, Möslinger, & Virányi, 2012). Based on these results, it is assumed that dogs do not possess means-end understanding but follow a proximity rule instead, pawing near where they perceive the reward (Osthaus, Lea, & Slater, 2005).

In contrast, Range, Hentrup, & Virányi (2011) demonstrated that dogs have the ability to solve a means-end task in the related support problem. In this task, two identical rewards were presented behind a fence, one on top of a board, another one next to a second, parallel board. The

dogs spontaneously chose to pull out the correct board more often than would be expected by chance, even when the food reward on the board was further away than the inaccessible reward. Possible explanations for the better performance in this task are that during their daily experiences dogs have more opportunities to learn something about objects placed on other objects than about objects connected to strings, that the contact is easier to perceive in the support problem than in string pulling tasks, or that only very simple conditions were tested in Range et al.'s (2011) study. In any case, the study does indicate that dogs may possess the capacity to attend to means-end connections.

This led us to predict that, given the right conditions, dogs are capable of tracing means-end connections in the string pulling problem and that they can solve a connectivity task if proximity is not a confounding factor. We also predicted improvement in performance with increasing experience (number of string pulling trials performed), which would reflect learning. To test these predictions, we tested 34 dogs in a series of string pulling tasks, varying the proximity of the reward to the correct and the incorrect strings' accessible ends.

Methods

Subjects

All subjects were Border collies (10 males, 24 females), which participated in a larger research project on physical cognition, of which the string pulling task was the first one tested. In this project, the subjects were restricted to a single breed to rule out breed differences. Border collies were chosen because most individuals of this breed are highly motivated to engage in such tasks and they are quite common. Border collies are neither extremely brachycephalic ("short-nosed") nor dolichocephalic ("long-nosed"), characteristics that may provide advantages or disadvantages in visual discrimination tasks, respectively (McGreevy, Grassi, & Harman, 2004; Gácsi, McGreevy, Kara, & Miklósi, 2009), and we have no reason to assume that Border collies would be selected for performance in means-end tasks. All the dogs were tested at the same age (12-15 months) and had extensive experience with string pulling from a previous experiment conducted when they were 6-8 months old (up to 50 trials with single and two strings, in which they showed no evidence of means-end understanding, unpublished data).

Experimental Setup and Procedure

The tests were performed in a room (6m x 5m) at the Clever Dog Lab, Vienna (Figure 1). One corner of the room was fenced off. Experimenter 1 entered this area through a door from the outside and laid out the strings, which were 1.5 cm in diameter and 60 cm long, with knots at their distal ends (where the rewards could be attached). Rewards were strips of sausage approximately 8 cm long and 0.5 cm wide. A wire-mesh fence prevented the dogs from accessing the baited ends while allowing visual access. The proximal 10 cm of the strings were accessible to the dogs, which could pull out the strings through a 5 cm gap between the floor and the fence. As dogs have dichromatic color vision and can discriminate best between stimuli whose predominant spectral energies lie around 480nm (Miller & Murphy 1995), blue strings were used to ensure that the dogs could distinguish well between the strings and the dark brown floor. The baited location and the configuration of the strings were pseudo-randomised so that no location was baited more often than twice in a sequence and all locations were baited equally often.

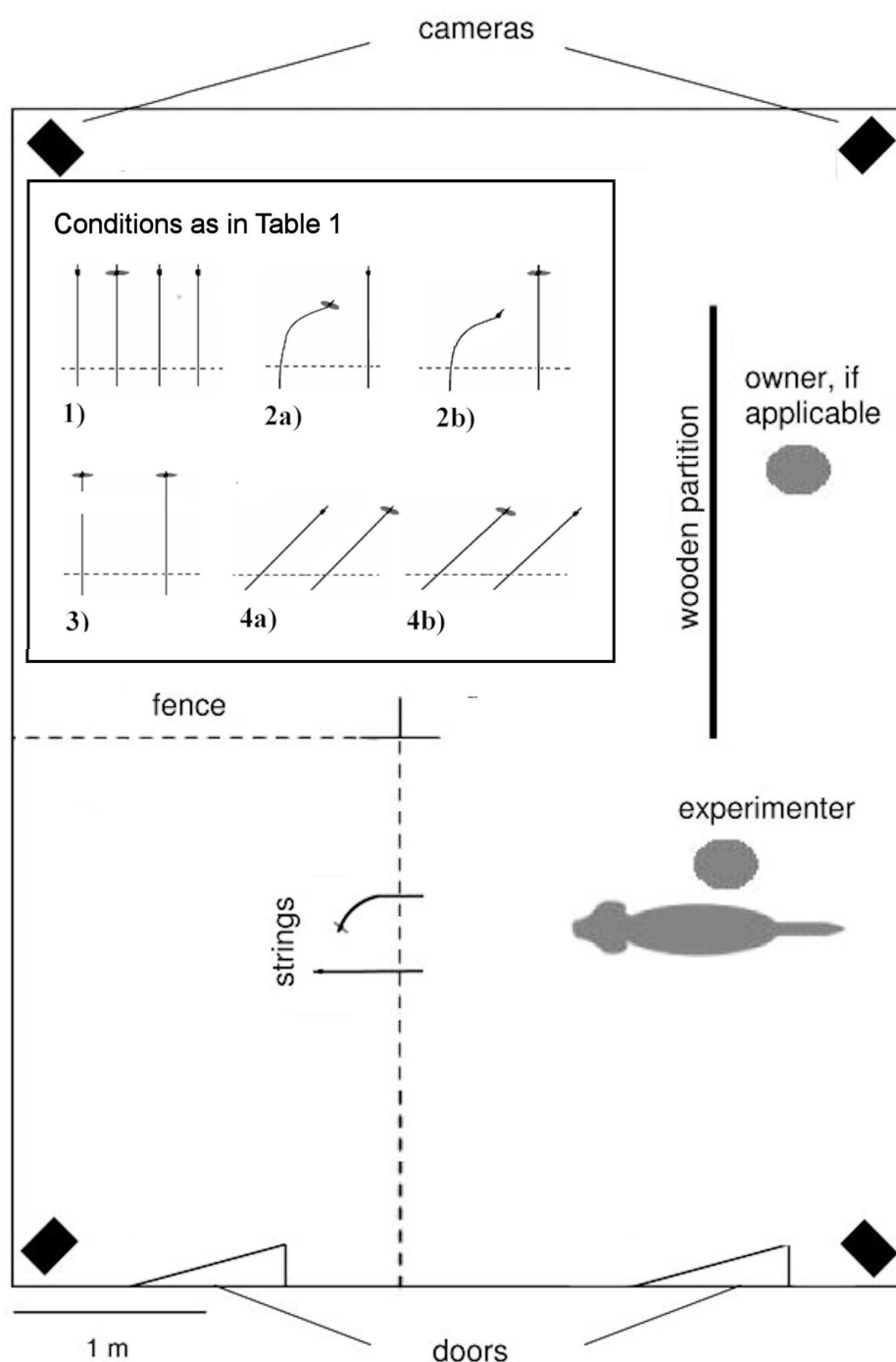


Figure 1. Setup of the test room and depiction of conditions.

During the baiting, the dog waited with experimenter 2 behind a wooden partition preventing it from observing the baiting (Figure 1). After experimenter 1 had laid out the strings and exited the room, experimenter 2 walked the dog to the starting point one meter away from the fence. As soon as the dog had looked at the setup for five seconds (i.e., facing towards the strings and not looking sideways or upwards, regardless of whether it was apparently focusing on

the correct or the incorrect string), she released the dog by letting go of a 30 cm long leash attached to its harness.

When a dog had pulled out an unbaited string, experimenter 2 pushed the baited string behind the fence or led the dog away by its harness to prevent a second choice. Only in the last trial of each session were the dogs allowed to try until they obtained the reward to keep up motivation. During testing, switching to a different string was allowed as long as the first string had not been pulled out more than halfway. However, aiming to draw inferences about means-end understanding and not alterations of responses due to visual feedback, we considered a choice as correct only when the dog touched the correct string first (and subsequently pulled it out completely). Thus, our criterion was more stringent than that used by Osthaus and colleagues (2005), who considered a choice as correct when the first string to be completely pulled out was the one with the food attached.

The dogs were usually given a session of 10 trials followed by a break of at least 5 minutes, with a maximum of 3 sessions per test day. For five dogs, breaks were taken after a smaller number of trials due to decreased focus on the task (not looking at the setup). Their performance was not significantly different from that of the dogs that completed all sessions without additional breaks (Mann Whitney U tests, p-values of 0.24 or higher).

If possible, testing was performed without the owners present in the room; however, during the first condition, three dogs would not work without their owners. Their owners remained in the test room but stayed behind the wooden partition (Figure 1) so that they could not influence their dogs' choices. Mann Whitney U tests yielded no significant differences in performance between dogs working with or without their owners present in the test room (p-values of 0.14 or higher).

Tasks and Conditions

Initially the dogs were given two “warm-up” trials in which they had to pull out single perpendicular strings to obtain an otherwise inaccessible reward behind a fence. These trials were performed to make sure that the dogs still remembered the action of string pulling from the previous experiments several months earlier. All dogs succeeded and were subsequently tested in tasks requiring them to select a baited string out of a choice of two or four strings. The proximity of the reward to the correct and the incorrect strings’ ends was systematically varied: in the four-string task (task 1, Table 1), the reward was directly in line with the correct string’s end so that choosing by proximity would lead to success. Dogs that performed above chance in this task were subsequently tested in the curved string task (task 2, Table 1). Here, the reward was equidistant from both strings’ ends on half of the trials, so that the task could only be solved by tracing the connection between the reward and the string. Finally, dogs that mastered the curved string task were tested in further tasks in which the proximity of the unconnected string’s end to the reward was inconclusive (gap task, task 3, Table 1) or misleading (parallel diagonal string task, task 4, Table 1).

Four-string task (Task 1). The four-string task (task 1, Table 1) involved four parallel perpendicular strings, one of which was baited. It has previously been found that dogs are capable of selecting a baited string out of two options when choosing by proximity is possible (Osthaus, Lea, & Slater, 2005); however, learning may be less likely to occur when success rate is high at 50% (see Tebbich, Seed, Emery, & Clayton, 2007). Therefore, we provided a choice of four, not two strings, one of which was baited, to lower chance probability of success to 25% and thus increase the pressure on the dogs to pay attention and choose correctly. The criterion to proceed to task 2 was at least 11 of 20 correct choices in two consecutive test sessions with 5 or more correct choices in each session (binomial probability: $p < 0.01$). For dogs ($N=13$) that did not meet criterion within 60 trials, testing was terminated.

Curved string task (Task 2). The majority of subjects ($N=21$) succeeded in the four-string task, and 20 subjects were presented with a novel task, the curved string task (task 2, Table 1; one dog did not return for testing). While in previous string pulling studies, dogs’ correct or incorrect choices were facilitated by the linear proximity of the reward to the connected or the unconnected string’s end, respectively, the curved string task is the first string pulling task tested in dogs in which proximity is not a confounding factor (but see e.g. Range, Möslinger, & Virányi,

2012 for a task with two rewards). The curved string task involved one straight and one curved string (Table 1). When the reward was attached to the curved string, it was an equal distance away from both strings' ends so that choosing by proximity was not possible. Dogs that initially committed the proximity error (defined as pawing at the fence near the reward and not at the strings; scored as present/ absent in each trial) had the chance to rectify their decision and pull out the correct string. Proximity errors, likely reflecting an inhibitory problem, were not considered as incorrect choices - only touching one of the strings was considered as a choice.

Each dog received 20 trials of the curved string task. In half of the trials, the straight string was baited and in the other half the curved string was baited. The trials of the two conditions were presented in a random order to exclude associative learning and to disentangle use of the proximity strategy (successful only when the straight string was baited) from attending to connectivity (successful in both conditions). The analysis was performed separately for each condition (10 trials each). This was done to take account of the fact that above chance performance (15/20 correct choices, binomial probability, $p < 0.05$) would theoretically have been possible for dogs that performed at chance level in the curved string baited condition (5/10 correct) if they achieved 10/10 correct choices in the straight string baited condition. Thus, our criterion was at least 8 of 10 correct choices in both the straight string baited and the curved string baited condition (binomial probability, $p < 0.01$).

Gap task (Task 3) and Parallel diagonal string task (Task 4). Most tested dogs (N=17) showed no evidence of means-understanding in the curved string task, and therefore testing was terminated for these individuals. The three dogs that met criterion in the curved string task were tested in further task variations, the gap task and/ or the parallel diagonal string task to distinguish the possible use of a task-specific strategy from the ability to trace means-end connections.

The gap task (task 3, Table 1) involved two rewards attached to two parallel perpendicular strings; one string was entire while the other one was broken, leaving a 10 cm gap between the reward and the inaccessible end. The parallel diagonal string task (task 4, Table 1) involved two strings (one baited), laid in parallel at an acute angle to the fence (see Osthaus, Lea, & Slater, 2005). It was varied randomly whether the tilt of the strings was to the left or to the right and which side was baited. When the exterior string was baited (non-overlapping condition),

the reward did not lie directly in line with any string's end; however, the string closest to the reward was the connected one. Thus this task was solvable by selecting according to proximity. In contrast, when the interior string was baited (overlapping condition), the unconnected string's end was directly in line with the reward and was thus potentially misleading for animals adhering to a proximity strategy (Table 1).

Table 1: Setup of tasks

Task	Criterion	No. of subjects
1. Four-string task: Four parallel, perpendicular strings, 20 cm apart, one baited.	11 of 20 correct choices	34
2. Curved string task: Two strings (one curved) 40 cm apart. The distal end of the curved string at the centre is equidistant from both strings' proximal ends. a) Curved string baited b) Straight string baited	8 of 10 correct choices in both the straight string baited and the curved string baited condition	20
3. Gap task: Two parallel perpendicular strings, 40 cm apart, with two food rewards; one entire string connected to the reward, one short string (45 cm) leaving a 10 cm gap to a 5 cm long string connected to the reward.	8 of 10 correct choices in both sessions	3
4. Parallel diagonal string task: Two parallel diagonal strings, 30 cm from each other, laid out at an angle of approximately 45° with the fence, one baited. a) Overlap b) No overlap	8 of 10 correct choices in both sessions	3

Originally, we intended to counterbalance the order of these additional tests across successful individuals to take order effects into account. However, it turned out that only three individuals mastered the curved string task, leading to an unbalanced distribution: Two dogs were tested in the gap task first, of which one mastered the task and proceeded to the parallel diagonal string task. One dog was tested in the parallel diagonal string task first and was not tested further upon failure.

Coding and Analysis

The trials were video-recorded and experimenter 1 furthermore noted the dogs' choices by pen and paper during testing (based on observations from the video screen outside the testing room). For analysis, the videos were subsequently coded by the first author using Solomon coder (© András Péter). No video was made for five test sessions (of different dogs) due to experimenter error. In these cases, the data noted by experimenter 1 were used for analysis. Correspondence between notes and coded data was excellent (Cohen's weighted kappa, as determined based on 10 randomly selected test sessions, was 0.96). Statistical analysis was carried out using R 2.12.0 (R Core Development Team 2010). One-sample Wilcoxon tests (two-tailed) were performed to test whether group level performance in the first 20 trials and in the last 20 trials was significantly different from chance. To test for differences between the first and the last session of 20 trials, Wilcoxon two-sample tests (two-tailed) were applied. To determine whether the number of proximity errors (defined as pawing at the fence between the strings, near the reward) in the curved string task was related to performance in this task, Spearman rank correlation tests were calculated.

A Wilcoxon signed ranks test was performed (separately for the first and the last 20 trials) to test whether the dogs performed better in the four-string task when the inner two strings (which were in closer proximity to them) were baited compared to when the outer strings were baited. We used binomial tests ($p < 0.05$) to determine whether individual dogs were more likely to pull the inner or the outer strings, whether they chose the right half or the left half of the setup more often than expected by chance, or whether they had specific location preferences.

Results

Four-string task (Task 1). At the group level, the dogs selected the correct string significantly more often than would be expected by chance (25%) within the first 20 trials (one-sample Wilcoxon test, $V = 534$, $p < 0.0001$), with 30 of 34 dogs being above the chance level of 5 correct choices. These results confirm previous findings that dogs are able to select the baited string when parallel perpendicular strings are presented (Osthaus, Lea, & Slater, 2005). Learning was also involved: The dogs' performance improved significantly from the first 20 trials to the last 20 trials (two-sample Wilcoxon test, $W = 321.5$, $p < 0.01$) (Figure 2). At the individual level, four dogs met the criterion of at least 11 of 20 correct choices within the first 20 trials ($p < 0.01$). Another seventeen dogs met this criterion within 30-60 trials. Thirteen dogs did not meet criterion within 60 trials.

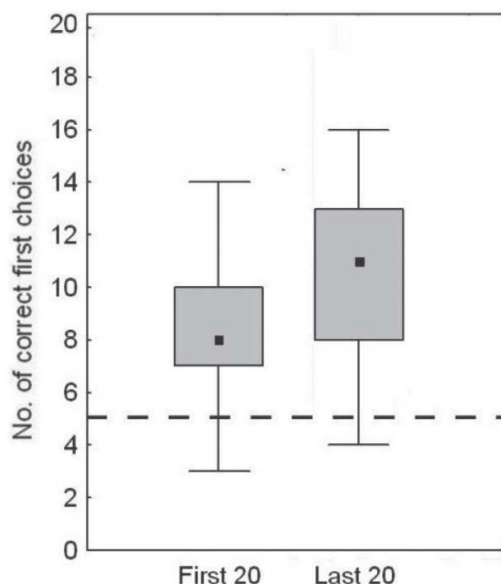


Figure 2. Number of correct choices in the first 20 trials and the last 20 trials in the four-string task (task 1). Median, interquartile range and range are given. The dashed line indicates chance level.

Overall, success rate was significantly higher when the inner string was baited than when the outer string was baited, both in the first 20 trials (Wilcoxon signed ranks test, $Z = 2.34$, $p = 0.019$) and in the last 20 trials ($Z = 2.22$, $p = 0.026$), indicating that the dogs were more prone to pulling those strings in closer proximity to them. Individually, 10 dogs significantly preferred to pull on the inner strings in the first 20 trials, while one dog preferred to pull on the outer strings (location preference for the outer left string, binomial test, $p < 0.05$). In the last 20 trials, nine dogs

significantly preferred to pull on the inner strings, and a different dog from the one in the first 20 trials preferred to pull on the outer strings (binomial test, $p < 0.05$). In the first 20 trials, eight dogs developed a significant bias for the left two strings, and four dogs for the right two strings (binomial tests, $p < 0.05$). In the last 20 trials, one dog significantly preferred the left two strings and five dogs significantly preferred the right two strings. Biases towards particular locations were shown by six dogs in the first 20 trials and also by six dogs in the last 20 trials (three of these showed location biases both in the first and the last 20 trials, of which one dog changed its preferences to a different position). In total, six of the 13 unsuccessful dogs but none of the 21 successful dogs showed a significant location bias in the last 20 trials of the four-string task (binomial tests, $p < 0.05$).

While switching from an incorrect to a correct string was shown by all but two dogs at least once in the course of testing (up to four occasions per session of 10 trials of the four-string task), only seven dogs switched from a correct to an incorrect string on one occasion each. Of these, six dogs made this mistake during the first 20 trials of the four-string task and one dog during the last 20 trials. Note that choices in which dogs switched from a correct to an incorrect string or vice versa were considered as incorrect for analysis.

Curved string task (Task 2). Group level performance ($N = 20$) was significantly above chance both when the straight string was baited (one-sample Wilcoxon test, $V = 171$, $p < 0.001$) and when the curved string was baited ($V = 108$, $p = 0.04$) (Figure 3), indicating that at least some dogs were paying attention to the connection between the reward and the string. However, an analysis of the number of dogs meeting the individual criterion confirms that the proximity rule was favored: 13 of 20 subjects achieved at least 8 of 10 correct choices in the straight string baited condition, whereas only 3 of 20 dogs reached this level also in the curved string baited condition (when choosing by proximity was not possible). One individual had 9 of 10 correct choices in the curved string baited condition but missed criterion with 7 of 10 correct choices in the straight string baited condition. Three dogs did not meet criterion in any condition; of these, one dog consistently corrected its errors very early and switched to the correct string, apparently following a rule of adjusting the behavior according to the visual feedback received (the sausage moving or not). The difference in number of correct choices between the straight string baited condition and the curved string baited condition was highly significant (two-sample Wilcoxon test, $Z = 3.4$, $p < 0.001$).

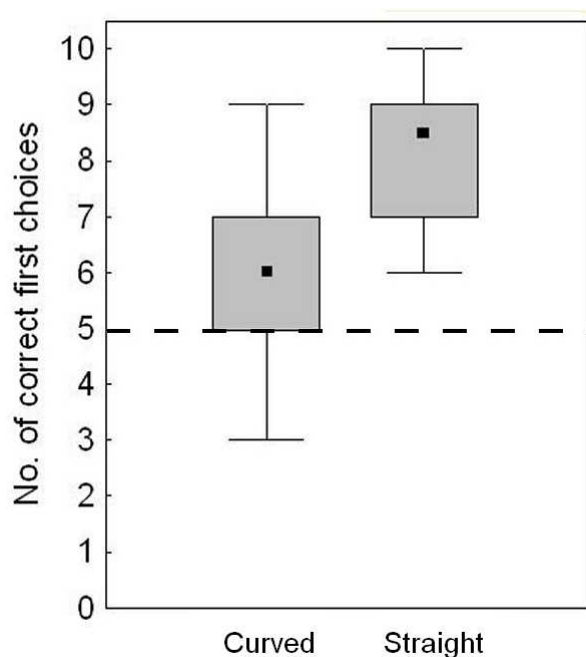


Figure 3. Number of correct choices in the curved string task (task 2) when the curved string was baited and when the straight string was baited, respectively. Median, interquartile range and range are given. The dashed line indicates chance level.

Proximity errors were shown in at least one trial by 10 of 20 dogs in the curved string baited condition (median 0.5; range 0-4). Success in this condition was independent of the number of proximity errors a dog committed in this task (Spearman rank correlation, $Rho = 0.24$, $p = 0.30$). Six of the dogs that failed to meet criterion exhibited a significant side bias (binomial test, $p < 0.05$); four of them preferring the right string and two preferring the left string.

Gap task (Task 3) and Parallel diagonal string task (Task 4). In the gap task, one of the two dogs tested met criterion with 8 of 10 correct choices in two consecutive sessions. The second dog chose at chance level in the first session (5 of 10 correct), but achieved 8 of 10 correct choices in the second session. No dog met criterion in the parallel diagonal string task. One dog (tested only in this and not in the gap task) committed the classical proximity error: He achieved 2 of 10 correct choices in the overlapping condition whereas the success rate was 10 of 10 in the non-overlapping condition. The one dog that proceeded to the parallel diagonal string task after successful performance in the gap task achieved 5 of 10 correct choices in the overlapping condition and 9 of 10 in the non-overlapping condition.

Discussion

We predicted that dogs can solve a connectivity task when proximity is not a confounding factor. Our prediction was confirmed for a subset of our sample of Border collies, those that had already succeeded in the four-string task (note that Osthaus, Lea, & Slater (2005) reported that they found no evidence that breed had an impact on the results). In the curved string task, group level performance was significantly above chance even in the curved string baited condition when choosing by proximity was not possible. Nonetheless, individual performance was relatively poor in this condition, compared to the good performance in the straight string baited condition and in the four-string task. This indicates that the majority of dogs selected the strings according to the proximity rule, confirming previous findings (Osthaus, Lea, & Slater, 2005). (Note, however, that the dogs only had a single chance to master the curved string task and that our criterion was more stringent than in Osthaus, Lea, & Slater (2005) – choices were only considered correct if the dog touched the connected string first and subsequently pulled it out completely).

A few dogs were apparently able to use information on connectivity, at least when there was no useful information on proximity in the curved string task. To further explore their abilities, we tested the successful dogs in the gap task and/ or the parallel diagonal string task. The performance of two individuals in the gap task may suggest that they may have gained at least a vague understanding of connectivity; in contrast, the dogs seemed to be unable to choose correctly when the information on connectivity conflicted with information about reward proximity (parallel diagonal string task, see below). Although a sample of two dogs is not representative, the relatively good performance of our subjects in the gap task is notable in the light of previous evidence that dogs are unable to solve this task (Range, Möslinger, & Virányi, 2012). Our subjects' performance was superior to that of all 10 dogs in Range et al.'s (2012) study, where most subjects developed a preference for the shorter string and none met criterion. This difference could be explained either by the fact that we tested only the most proficient subjects in this difficult task (i.e., only a few animals out of a large sample, which had already proven to be able to solve the curved string task), by the greater amount of experience with string pulling tasks of the successful subjects or by breed and/ or keeping conditions (in the study by Range and colleagues only Huskies kept in kennels were tested).

Despite performing comparatively well in the gap task, the dogs seemed to be unable to choose correctly when the information on connectivity conflicted with information about reward proximity in the parallel diagonal string task. Here, the performance of our two subjects was similar to that by the dogs tested by Osthaus, Lea, & Slater (2005) and Range, Möslinger, & Virányi (2012): They tended to choose correctly when the non-overlapping string was baited (where choosing by proximity led to success), but performance was poor in the overlapping condition (where the incorrect string was closest to the reward). Thus, although some individual dogs apparently attended to connectivity when choosing by proximity was precluded, they were unable to solve a task where proximity and connectivity information conflicted, suggesting that they may favor proximity rules over connectivity rules. Along similar lines, Herrmann, Wobber, & Call (2008, p. 229) suggest that great apes might possess some causal knowledge with respect to tool use, but that certain task features make it hard to express it consistently, suggesting that “motor or attentional biases present in the two-choice situation may have introduced some noise into the data”.

Note that Range, Hentrup, & Virányi (2011) reported that dogs could solve a different means-end task, the on-off problem, even when proximity was misleading. The dogs succeeded in selecting a baited board over an unbaited one, even when the reward placed next to the unbaited board was closer to the dog than the reward placed on the baited board. Two factors may explain why the dogs were able to overcome their proximity bias in the on-off task unlike in the string pulling task. Firstly, the misleading effect of proximity was less pronounced in the on-off task than in the diagonal baited string task, as the inaccessible reward was not directly in line with the incorrect board (even though it was closer to the incorrect board’s end than to the correct board’s end). Secondly, the contact between the board and the reward was most likely easier to perceive for the dogs than the contact between the thin string and the reward.

While our findings suggest that at least in Border collies, some individuals are capable of attending to connectivity, they also indicate that this strategy can easily be overruled by other, simpler strategies. In a different context (logical reasoning), Erdőhegyi, Topál, Virányi, & Miklósi (2007) suggested that dogs base their decisions on a set of rules, preferentially choosing the simplest one and switching to more cognitively demanding ones only under certain circumstances. This may also apply to their decision-making in string-pulling tasks. According to Osthaus, Lea, & Slater (2005), dogs’ two main strategies when encountering food are first

pawing close to the food, even when there is no string attached (thereby committing the proximity error), and – when unsuccessful – switching to pawing at the string where the proximal end is closest to the food. Our data suggest that a third strategy – attending to the connection between the string and the reward – may be activated in some dogs when the proximity strategy failed, as in our curved string task, or when the dogs have experienced that the costs of failing are high. A fourth possible strategy appears to be based on visual feedback (movement of the reward) received by pulling on a string. Still, despite the evidence that paying attention and choosing accordingly is within the cognitive repertoire of the species, there were large individual differences, and many subjects seemed to follow even simpler decision rules, preferentially pulling on the strings that were closest to them (the inner strings in the four-string task), or developing a significant preference for one particular location (c.f. occurrence of side biases in dogs, e.g. Hare & Tomasello, 1999; Gácsi, M., Kara, Belényi, Topál, & Miklósi, 2009).

Despite the occurrence of such alternative problem solving strategies, our results give the first evidence – to our knowledge – that (some) dogs can attend to means-end connections in the string-pulling paradigm. There are a number of possible explanations why some of our subjects were able to solve means-end tasks independent of proximity unlike dogs in previous studies (Osthaus, Lea, & Slater, 2005, Range, Möslinger, & Virányi, 2012).

First, our subjects had considerably more experience with strings and string pulling than dogs in either Osthaus, Lea, & Slater (2005) or Range, Möslinger, & Virányi (2012). Therefore it is likely that the greater amount of experience with string pulling in general (potentially leading to learning about means-end connections) or the specific experience gained from the four-string task contributed to our subjects' better performance. There is much evidence that young humans as well as non-human animals acquire knowledge about objects' affordances, learn perceptual rules, and build up motor representations through exploration (Lockman, 2000; Matsuzawa, Tomonaga, & Tanaka, 2005; Takeshita, Frigaszy, Mizuno, Matsuzawa, Tomonaga, & Tanaka, 2005; Sommerville, Hildebrand, & Crane, 2008). Both tool-using species (e.g. chimpanzees, *Pan troglodytes*, Seed, Call, Emery, & Clayton, 2009) and non-tool-using species, including monkeys and rodents (Spaulding & Hauser, 2005; Santos, Pearson, Spaepen, Tsao, & Hauser, 2006; Okanoya, Tokimoto, Kumazawa, Hihara, & Iriki, 2008), seem to develop some understanding of the functional aspects of objects/ tools through (extensive) experience with them. Also in goldfinches (*Carduelis carduelis*) and siskins (*C. spinus*), an individual's string-pulling

competence seemed to be influenced by prior experience of handling branchlets, but also by trial-and-error learning and social learning (Seibt & Winckler, 2006). Even though the four-string task was solvable by choosing according to proximity, latent learning about the properties of the strings and connectivity may have occurred. Furthermore, the higher cost-benefit tradeoffs in the four-string task may have increased the dogs' awareness that a choice had to be made and that choosing incorrectly meant obtaining no reward, potentially leading to greater attentional focus and better inhibitory control.

Second, a relatively small task modification – precluding choosing by proximity in the curved string task – may have enabled the dogs to utilize an alternative strategy to the proximity rule. Studies on other species have shown how small alterations in the procedure can lead to dramatic improvements in animals' performances in cognitive tasks. Similarly to this study, a recent study on string pulling in marmosets (*Callithrix jacchus*) showed that the animals were initially prone to choosing by proximity, but alterations of the setup enabled the subjects to develop a new strategy, to bypass the spatial proximity rule and to master novel nonlinear tasks (Gagné, Levesque, Natile, & Locurto, 2012). Also, chimpanzees (Mulcahy & Call, 2006, Seed, Call, Emery, & Clayton, 2009, Girndt, Meier, & Call, 2008) and orangutans (*Pongo pygmaeus* and *Pongo abelii*, Mulcahy, Schubiger, & Suddendorf, 2013) performed successfully in some physical cognition tasks only after some task alterations were introduced (modes of tool use were altered or tool use was no longer required).

Third, while a previous study found no effect of breed on dogs' performance in string pulling tasks (Osthaus, Lea, & Slater, 2005), it is nonetheless a possibility that some differences might be accounted for by the different breeds used (Border collies in our study, various breeds in Osthaus, Lea, & Slater, 2005, and Huskies in Range, Möslinger, & Virányi, 2012). There were furthermore environmental differences – dogs in this and Osthaus et al.'s (2005) study were pet dogs while the huskies in Range et al.'s study were kept in kennels.

Fourth, regarding the direct comparison of performance of our dogs and Range et al.'s (2012) dogs in the gap task, the superior performance of our subjects could be explained by the fact that we had only tested the most proficient subjects in this difficult task (i.e., only a few animals out of a large sample, which had already proven to be able to solve the curved string task).

Our study differed from Osthaus, Lea, & Slater (2005) and Range, Möslinger, & Virányi (2012) in that we found a clear learning effect in the four-string task in the course of 30-60 trials, whereas there was no effect of trial number on dogs' performance in Osthaus, Lea, & Slater's (2005) parallel diagonal string task or Range et al.'s (2012) gap task. Task differences and differences in statistical methodology might account for the diverging results of our study and those by Osthaus, Lea, & Slater (2005) and Range, Möslinger, & Virányi (2012). Conceivably, experience with tasks which appear to be too difficult for dogs to solve at all, such as the parallel diagonal strings task, resulted in no learning.

Future research could investigate how much experience is necessary for dogs to develop an (apparent) understanding of connectivity and to be able to trace means-end connections in the curved string task. This could be determined by testing experimentally naïve dogs with the curved string task and assessing learning in the course of e.g. 60 trials. Further control studies, systematically altering the costs of choosing incorrectly, could be performed to disentangle the effect of general experience with string pulling – potentially enabling learning about connectivity – from the benefits of the four-string task, which made random choice more costly.

Like dogs and marmosets, several species have previously failed in tasks involving crossed or parallel diagonal strings, including wolves (*Canis lupus*, Range, Möslinger, & Virányi, 2012), macaws (Schuck-Paim, Borsari, & Ottoni, 2009), hooded crows (*Corvus corone*, Bagotskaya, Smirnova, & Zorina, 2012), and even New Caledonian crows (*Corvus moneduloides*), which are famous for their tool-use competence (Taylor, Medina, Holzhaider, Hearne, Hunt, & Gray, 2010). Re-testing individuals of these species with the curved string task introduced in this study or with some of the non-linear tasks used by Gagné, Levesque, Nutile, & Locurto (2012) would yield further insights into animals' strategy selection when faced with physical problems.

To conclude, our study shows that even though dogs may not demonstrate spontaneous means-end understanding, some can learn to pay attention to connectivity. Our results support the notion that animals may apply several alternative rules or strategies to solve problems in their environment (Erdőhegyi, Topál, Virányi, & Miklósi, 2007). Strategies used by tool-using species such as the great apes and New Caledonian crows, by non-tool using, but dexterous marmosets, and by carnivores, which are less ecologically prepared for object manipulation tasks, may not

be so different after all. Members of different taxonomic groups appear to devise certain rules to deal with physical problems, with species-specific as well as considerable individual differences in associative and perceptual abilities and behavioral flexibility. Some individuals may be better at the formation of concepts or representations, based on observable features of problems (Seed, Tebbich, Emery, & Clayton, 2006), than others, or they may be better at inhibiting prepotent responses (e.g. going for the string nearest the reward; Lea et al., 2006), leading to the large inter-individual variability observed in performance in physical problems. In light of our findings, as well as those of Gagné, Levesque, Nutile, & Locurto (2012), follow-up studies on other species with modified string pulling problems might yield novel insights into animals' selections of strategies to deal with physical problems.

References

- Bagotskaya, M. S., Smirnova, A. A., & Zorina, Z. A. (2012). Corvidae can understand logical structure in baited string-pulling tasks. *Neuroscience and Behavioral Physiology*, 42, 36-42.
- Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology*, 120, 38-47.
- Brown, A. (1990). Domain-specific principles affect learning and transfer in children. *Cognitive Sciences*, 14, 107–133.
- Cha, J. H., & King, J. E. (1969). Learning of patterned strings problems by squirrel monkeys. *Animal Behaviour*, 17, 64-67.
- Doré, F.Y., & Dumas, C. (1987) Psychology of animal cognition: piagetian studies. *Psychological Bulletin*, 102, 219–233.
- Erdőhegyi, Á., Topál, J., Virányi, Zs., & Miklósi Á. (2007). Dog-logic: inferential reasoning in a two-way choice task and its restricted use. *Animal Behaviour*, 74, 725-737.
- Gácsi, M., McGreevy, P., Kara, E., & Miklósi, Á. (2009a). Effects of selection for cooperation and attention in dogs. *Behavioral and Brain Functions*, 5, 31.
- Gácsi, M., Kara, E., Belényi, B., Topál, J., & Miklósi, Á. (2009b). The effect of development and individual differences in pointing comprehension of dogs. *Animal Cognition*, 12, 471-479.
- Gagné, M., Levesque, K., Natile, L., & Locurto, C. (2012). Performance on patterned string problems by common marmosets (*Callithrix jacchus*). *Animal Cognition*, 15, 1021-1030.
- Girndt, A., Meier, T., & Call, J. (2008). Task constraints mask great apes' ability to solve the trap-table task. *Journal of Experimental Psychology: Animal Behavior Processes*, 34, 54 – 62.
- Halsey, L. G., Bezerra, B. M., & Souto, A. S. (2006). Can wild common marmosets (*Callithrix jacchus*) solve the parallel strings task? *Animal Cognition*, 9, 229-233.
- Hare, B., & Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology*, 113, 1-5.

- Harlow, H. F., & Settlage, P. H. (1934). Comparative behavior of primates VII. Capacity of monkeys to solve patterned string tests. *Journal of Comparative Psychology*, 18, 423-435.
- Heinrich, B. (1995). An experimental investigation of insight in common ravens (*Corvus corax*). *Auk*, 112, 994-1003.
- Heinrich, B., & Bugnyar, T. (2005). Testing problem solving in ravens: String-pulling to reach food. *Ethology*, 111, 962-976.
- Herrmann, E., Wobber, V., & Call, J. (2008). Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology*, 122, 220-230.
- Huber, L., & Gajdon, G. K. (2006). Technical intelligence in animals: the kea model. *Animal Cognition*, 9, 295-305.
- Lea, S.E.G., Goto, K., Osthaus, B., Ryan, C.M.E. (2006). The logic of the stimulus. *Animal Cognition* 9, 247–256.
- Lockman, J.J. (2000). A perception–action perspective on tool use development. *Child Development*, 71, 137-144.
- Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2005). Exploring by doing: How young chimpanzees discover surfaces through actions with objects. *Infant Behavior and Development*, 28, 316-328.
- McGreevy, P., Grassi, T.D., & Harman, A.M. (2004) A strong correlation exists between the distribution of retinal ganglion cells and nose length in the dog. *Brain, Behavior and Evolution*, 63, 13-22.
- Miller, P.E., & Murphy, C.J. (1995) Vision in dogs. *Journal of the American Veterinary Medical Association*, 207, 1623-34.
- Mulcahy, N.J., & Call, J. (2006). How great apes perform on a modified trap-tube task. *Animal Cognition*, 9, 193-199.
- Mulcahy, N. J., Schubiger, M. N., & Suddendorf, T. (2013). Orangutans (*Pongo pygmaeus* and *Pongo abelii*) understand connectivity in the skewered grape tool task. *Journal of Comparative Psychology*, 127, 109-113.

- Okanoya, K., Tokimoto, N., Kumazawa, N., Hihara, S., & Iriki, A. (2008). Tool-use training in a species of rodent: the emergence of an optimal motor strategy and functional understanding. *PLoS One*, 3, e1860.
- Osthaus, B., Lea, S. E. G., & Slater, A. M. (2005). Dogs (*Canis lupus familiaris*) fail to show understanding of means-end connections in a string-pulling task. *Animal Cognition*, 8, 37-47.
- Pepperberg, I.M. (2004). “Insightful” string-pulling in grey parrots (*Psittacus erithacus*) is affected by vocal competence. *Animal Cognition*, 7, 263–266.
- Povinelli, D. (2000). *Folk physics for apes: The chimpanzee's theory of how the world works*. Oxford: Oxford University Press.
- Range, F., Hentrup, M., & Virányi, Z. (2011). Dogs are able to solve a means-end task. *Animal Cognition*, 14, 575-583.
- Range, F., Möslinger, H., & Virányi, Z. (2012). Domestication has not affected the understanding of means-end connections in dogs. *Animal Cognition*, 15, 597-607.
- Santos, L. R., Pearson, H.M., Spaepen, G.M., Tsao, F., & Hauser, M.D. (2006). Probing the limits of tool competence: experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). *Animal Cognition*, 9, 94-109.
- Schmidt, G. F., & Cook, R. G. (2006). Mind the gap: means-end discrimination by pigeons. *Animal Behaviour*, 71, 599-608.
- Schuck-Paim, C., Borsari, A., & Ottoni, E. B. (2009). Means to an end: Neotropical parrots manage to pull strings to meet their goals. *Animal Cognition*, 12, 287-301.
- Seed, A. M., Tebbich, S., Emery, N.J., & Clayton, N. S. (2006). Investigating physical cognition in rooks, *Corvus frugilegus*, *Current Biology*, 16, 697-701.
- Seed, A. M., Call, J., Emery, N.J., & Clayton, N.S. (2009). Chimpanzees solve the trap problem when the confound of tool use is removed. *Journal of Experimental Psychology: Animal Behavior Processes*, 35, 23-34.
- Seibt, U., & Wickler, W. (2006). Individuality in problem solving: String pulling in two *Carduelis* species (Aves: Passeriformes). *Ethology*, 112, 493-502.

- Sommerville, J. A., Hildebrand, E. A., & Crane, C. C. (2008). Experience matters: The impact of doing versus watching on infants' subsequent perception of tool use events. *Developmental Psychology*, 44, 1249-1256.
- Spaulding, B., & Hauser, M. (2005). What experience is required for acquiring tool competence? Experiments with two Callitrichids. *Animal Behaviour*, 70, 517–526.
- Takeshita, H., Frigaszy, D., Mizuno, Y., Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2005). Exploring by doing: How young chimpanzees discover surfaces through actions with objects. *Infant Behavior & Development*, 28, 316-328.
- Taylor, A. H., Medina, F. S., Holzhaider, J. C., Hearne, L. J., Hunt, G. R., & Gray, R. D. (2010). An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. *Plos One*, 5, e9345.
- Tebbich, S., Seed, A., Emery, N., & Clayton, N. (2007) Non-tool-using rooks (*Corvus frugilegus*) solve the trap-tube task. *Animal Cognition*, 10, 225-231.
- Werdenich, D., & Huber, L. (2006). A case of quick problem solving in birds: String pulling in keas. *Nestor notabilis*. *Animal Behaviour*, 71, 855–863.

CHAPTER 6

6. GENERAL DISCUSSION

This thesis investigated individual differences in behaviour and cognitive performance of domestic dogs. Study 1 indicates that behavioural assessments of neonate and 6-7-week-old puppies have very limited validity for predicting specific behavioural traits in adult dogs, possibly because of the young age of the puppies and the effects of maturation and environmental influences between tests. Study 2 explores relationships between puppies' behaviour in conflict situations and in other contexts. The results show that highly sociable puppies tend to adopt an interactive conflict resolution strategy whereas less sociable puppies tend to behave passively, paralleling findings from humans (Graziano et al., 1996; Park and Antonioni, 2007; Wood and Bell, 2008) and goats (Miranda de la Lama et al., 2011). Study 3 is the first long-term study on impulsivity in non-human animals and demonstrates high stability of impulsivity in dogs, as measured by performance in a delayed reward choice test and owner questionnaires, over six years. Study 4 investigates how dogs solve a string pulling task and shows that individual dogs may use different problem solving strategies, including attending to connectivity, but that they preferentially choose the simpler rule in ambiguous cases and do not appear to demonstrate true means-end understanding.

6.1. Individual behaviour differences

Study 1 showed that puppies' behaviour in the neonate test was not predictive of the behaviour of the same dogs at the age of 6-7 weeks or as adults. Furthermore only one of ten investigated behaviours was significantly related between the puppy test conducted at 6-7 weeks of age and the adult test. This lack of relations between earlier and later behaviours could reflect (1) significant behaviour change, (2) an artefact of the testing procedure or analysis, or (3) a combination of both.

While behavioural consistency between young puppies and adults generally appears to be low (reviewed in Study 1), studies on older dogs have shown higher temporal consistency (reviewed in Fratkin et al., 2013; see also results of Study 3). Nonetheless, even when tested repeatedly in identical test situations, an individual will not always show identical responses. While “systematic behavioural variation as a function of time or variation in external stimuli” is termed

“contextual plasticity” (Biro and Adriaenssens, 2013, p.622), intraindividual variability is defined as “the variation that remains after accounting for systematic changes over time or across a contextual gradient and any other factors that could affect behavioural variation within individuals” (Biro and Adriaenssens, 2013, p. 622). Test-retest reliability of the neonate, puppy and adult test over short time scales would be informative to what degree the diverging test results may reflect age related changes or other sources of variability (clearly, habituation effects would have to be taken into account). Test-retest assessments were not included in the present studies because of temporal constraints; however, a full validation of the adult test is in progress and will include assessments of test-retest reliability and external validity (correlation with owner questionnaires). Assessing test-retest reliability of neonate and puppy tests over short time intervals would be a worthwhile topic for future studies.

It is conceivable that reliability of these early tests may be low even over shorter timescales (see also Beaudet et al., 1994). Wilsson and Sundgren (1998), who tested puppies that were slightly older than in our study (8 weeks), point out that puppies are maturing rapidly at this age. If level of maturation affects behaviour in the test, then this will have a major effect on the puppy test results (Wilsson and Sundgren, 1998). Degree of maturation might be a factor common to the litter, and so this may have contributed to the fact that litter effects were significant in the puppy test, but less so in the adult test (c.f. Wilsson and Sundgren, 1998). A further, non-exclusive explanation for the lack of litter effects in the adult dogs is that experiences of litter mates at the time of testing were very similar, whereas their experiences varied widely after the transition to their new families, thus emphasising the role of individual experiences on behavioural development.

While the importance of experience early in life has been of interest to researchers for a very long time (e.g. Beach and Jaynes, 1954; King, 1958), it is now recognised that personality can be influenced by salient experiences throughout the lifetime (Bell and Sih, 2007). As the period of maturation is a particularly sensitive phase, it is expected that behavioural consistency assessed before and after maturation would be lower than when test and retest are performed at the same test interval when the animals are adults (e.g. Bell and Sih, 2007; Herde and Eccard, 2013), which may explain the lack of correspondence of behaviour in the puppy and the adult test in our study.

Studies on rodents have shown that stressful and social experiences during the adolescent phase (the gradual transition from childhood to adulthood) have long-lasting effects on later levels of anxiety, aggressiveness and stress responses, which can be measured both behaviourally and physiologically (reviewed in Sachser et al., 2013). For instance, depending on the timing of encounters with aggressive males in juvenile golden hamsters (*Mesocricetus auratus*), later aggressiveness may be either enhanced or inhibited (Delville et al., 2003). In guinea pigs (*Cavia porcellus*), males' ability to integrate with unfamiliar males depends on whether they are housed with other males during early adolescence. While males from mixed sex colonies adapt rapidly to encountering new unfamiliar males, males that were housed with a single female show high levels of aggressive behaviour, frequent escalated fights and strong physiological stress responses (Sachser and Lick, 1991). Furthermore it has been demonstrated in rats that social play in juveniles is crucial for the adequate development of coping with social challenges (van den Bergh et al., 1999). In short, numerous factors, including hormonal and neuronal changes, new habitats and the social environment contribute to behavioural changes through ontogeny (Herde and Eccard, 2013), and all of these factors apply also to the dogs in our study. Not only did they attain sexual maturity, with associated physiological changes, between the puppy test and the adult test, but the change of social and non-social environment following rehoming may also account for the diverging results from the puppy and the adult test.

This lack of correspondence between puppies' and adults' behaviour is also of relevance in relation to Study 2. The results showed that puppies with high sociability scores had a higher tendency to diffuse potential conflicts through active, social-communicative behaviours while less sociable puppies reacted passively, indicating that highly sociable individuals may be better equipped to employ interactive yet nonaggressive conflict resolution strategies. However, the major behavioural changes over time observed in Study 1 indicate that a highly sociable puppy does not necessarily grow into a highly sociable adult. Thus the question arises which measures can be taken to create optimally socialised dogs that are capable of adopting 'constructive' conflict resolution strategies when in a perceived conflict situation. No doubt the sensitive period for socialisation in young puppies is of great importance for shaping later behaviour (e.g. Freedman et al. 1961; Lord, 2013), with good socialisation at an early age appearing to be protective of developing fear or aggression related problems as adults. However, as in the rodent examples above, environmental influences can have crucial effects also during other developmental stages, particularly the adolescence period, and possibly even throughout the

lifetime (reviewed in Sachser et al., 2013). Indeed, a questionnaire study has demonstrated the importance of environmental influences beyond the “sensitive period” in dogs by showing that aggressive and avoidance behaviour in pet dogs was related to puppies’ experiences between the ages of three and six months (Appleby et al., 2002).

Moreover, while Study 2 indicates that conflict behaviour is influenced by individual predispositions, another point to consider is that dogs will learn which strategies ‘work’ for them (e.g. aggressive behaviour causing a conspecific to withdraw; see also Walker et al., 1997) and which do not. Depending on the owners’ skills in managing situations or environmental circumstances, the dogs may thus learn either desirable or undesirable behaviour. It would therefore be interesting to assess whether the link between sociability and conflict resolution strategies in the puppies is maintained in adulthood, or whether initial tendencies may be overshadowed by learning effects.

Trillmich and Hudson, 2011 (p. 506) propose 5 major questions about behavioural development in animals, including

1. How are differences in individual behavioural phenotypes established during development and how do they relate to social and ecological circumstances?
2. Are personality traits stable or instable over a lifetime?
3. If personality changes, at what stage of the life history or under what circumstances do such changes occur?
4. What are the (neuro-)physiological substrates underlying these differences?
5. How are personality differences related to the genotype and how do genes and environment interact to establish personality during ontogeny?

In the case of dogs, question 1 has been addressed by retrospective questionnaire studies on effects of rearing conditions, early experiences, and life circumstances on later behaviour (Appleby et al., 2002; McMillan et al., 2013; Casey et al., 2013). Experimental studies on behavioural consistency in dogs contribute to answering question 2 (reviewed in Fratkin et al., 2013). Several studies on the physiological and genetic underpinnings of personality in dogs have attempted to answer question 4 (e.g. Spady and Ostrander, 2008; Takeuchi et al., 2009; Hall and Wynne, 2012; Kubinyi et al., 2012; Wan et al., 2013), while question 5 has been addressed by studies on the inheritance of behavioural traits, maternal and other environmental effects in

dogs (e.g. Goddard and Beilharz, 1982; Ruefenacht et al., 2002; Strandberg et al., 2005; Wilsson and Sundgren, 1998, 1997). Nonetheless, findings are currently not conclusive with regard to behavioural consistency and the genetic basis of behaviour in dogs.

Study 1 of this thesis contributes to our understanding of question 2 by indicating that assessments of neonates and 6-7 week-old puppies are too early to predict future behaviour traits in pet dogs. However, we still know very little about question 3, or from what age or developmental stage meaningful predictions about later behaviour can be made. In conjunction with Study 1, I made a starting point by conducting a longitudinal questionnaire study on 72 Border collies (Riemer et al in prep.; Riemer et al., 2013a+b). The dogs' owners filled in questionnaires on their dogs' behaviour at three points in time (when the dogs were 6, 12 and 18-24 months old). The results suggested that individual behaviour differences were quite stable already at the age of six months, as the owners' assessments for all 15 investigated behaviour traits at this age were highly correlated with their later assessments. At the group level some changes occurred as the dogs matured, such as increases in controllability and decreases in energy with age, as would be expected. Furthermore, both fearful and aggressive behaviour increased significantly between the ages of 6 and 12 months and/or 12 and 18-24 months (Riemer et al., 2013a+b). This is in line with findings that the onset of generalized anxiety/fear, noise phobia, and aggression towards humans or conspecifics often occurs during the social maturity period (Overall et al., 2006). To my knowledge, there are currently no studies that have specially investigated effects of experiences during adolescence on adult behaviour in dogs, but the evidence from other species (see above) suggests that these are relevant when investigating causes of 'problematic' behaviour, or inappropriate conflict strategies, in domestic dogs, and this is a highly relevant topic for future investigations.

Despite the behavioural changes observed at group level, the rank order of individuals in our questionnaire study remained stable over time, indicating that individual differences in behaviour are already clearly discernible at 6 months and remain relatively stable until 1.5 to 2 years (Riemer et al., in prep.; Riemer et al., 2013a+b). In line with these results, Duffy & Serpell (2009) demonstrated that puppy raisers' assessments (according to a validated behavioural survey, the C-BARQ) could discriminate between successful and released dogs when the dogs were six months old, as well as at 12 months. However, since in both studies the first

questionnaire was administered when the dogs were already six months old, we currently do not know to what extent behavioural stability exists prior to that age.

Thus, to follow up the questionnaire study and to determine when individual behavioural differences stabilise, questionnaires could be administered repeatedly between rehoming of the young puppies and the age of six months, or even starting when the puppies still live at the breeders. Additionally, given some shortcomings of questionnaire studies, such as biased perceptions of the owners, it would be worthwhile to perform behavioural tests repeatedly between the age of six weeks and 1.5 years (or beyond), as well as obtaining assessments from other persons that know the dogs well, such as dog trainers, as is commonly done with studies on personality in captive nonhuman species (e.g. Carlstead et al., 1999; Gosling, 1998; Weiss et al., 2006). This would not only be of high practical value, but may also enhance our understanding of behavioural development in general.

Domestic dogs are well suited for investigating questions of behavioural development as we can follow up their life histories closely, identify breed-specific behavioural tendencies and have extensive genetic information from pedigrees (Saetre and Strandberg, 2006). Moreover, given that (contrary to expectations) repeatability of behaviour was found to be higher in the field compared to the laboratory (Bell et al., 2009), studying dogs has the advantage that they are not kept in sterile laboratory conditions, but live in equally diverse environments as humans do, and so findings from dogs can be applied to real life settings.

6.2. Impulsivity

The impulsivity trait in dogs is particularly promising for modelling conditions and outcomes in humans and is highly relevant to dog-human interactions. Study 3 demonstrated high temporal stability of this trait in adult dogs as both maximum delay reached in the delayed reward choice test (indicative of cognitive impulsivity) and owner-reported impulsivity remained highly stable over six years. However, in agreement with results by Bray et al. (2013), motor impulsivity or inhibitory control, as measured by the number of redundant paw presses, appears to be less consistent. This is in line with the notion that delay aversion and motor impulsivity are separate processes, with different underlying mechanisms (van den Bergh et al., 2006). For example, hyperactivity in human children was found to be associated with tolerance to delay, but not inhibition, and this is in agreement with our finding that owners' assessments of dogs'

impulsivity and maximum delay reached (i.e. delay tolerance) are consistent but paw pressing rate (i.e. inhibitory control) is not (Kuntsi et al., 2001).

Our findings give the first evidence, to my knowledge, of long term consistency of impulsivity in a nonhuman species. Furthermore, the results have implications from a practical viewpoint, as impulsivity may be associated with a range of behaviours that are of relevance in humans' interactions with both family pets and working dogs. For instance, the number one factor that emerged in a survey of what Australians consider to be the ideal family dog was labelled "calm/compliant", with high loadings for questions such as "walks calmly on leash", "is not overly excitable" and "behaves calmly most of the time" (King et al., 2009). An even higher level of impulse control than for pet dogs may be required for working dogs, such as guide dogs that need to walk at a slow pace with their blind owners and bypass distractions by food or prey items, or police dogs required to remain calm in highly arousing situations and act only upon command in very specific contexts.

A significant factor in the dog-human relationship is aggressive behaviour, some forms of which have been linked to impulsivity in dogs (Fatjó et al., 2005; Reisner et al., 1996; Wright et al., 2012) and other species, including humans (Cherek et al., 1997; Odum, 2011a; Reynolds, 2006; Solanto et al., 2001; Winstanley et al., 2006), rats (van den Bergh et al., 2006) and hamsters (Cervantes and Delville, 2009). While effects of impulsivity on trainability have to my knowledge not yet been directly investigated in dogs (see Vas et al., 2007, for an assessment of the effects of training on impulsivity), it is likely that trainability is linked to impulsivity. The attribution of reinforcer value is controlled by those neural systems that are also responsible for decisions in a delayed reward choice tasks (limbic and paralimbic areas and lateral prefrontal brain regions; Koffarnus et al., 2013). Accordingly, there is evidence from both human children and rats that sensitivity to reward, extinction responding and tolerance to delayed rewards are related (van den Bergh et al., 2006; Johansen and Sagvolden, 2004; Sagvolden et al., 1998), and these characteristics will likely influence trainability also in domestic dogs. Thus, impulsivity is related to many characteristics that have implications for our life with pet and working dogs. Considering the high stability of impulsivity in dogs, compared to most other traits (reviewed in Fratkin et al., 2013), assessing this characteristic might be valuable to aid in the selection of individuals suitable as working dogs or stud dogs for breeding of both pet and working dogs.

There are several explanations why impulsivity in Study 3 showed higher consistency compared to sociability, boldness, playfulness and behaviour in conflict situations assessed in Study 1. Firstly, most dogs were already adults when tested for the first time in Study 3, and so less behavioural change can be expected than in those dogs tested for the first time when only 6-7 weeks old. Secondly, despite the longer time gap between tests, environmental circumstances remained relatively stable for the dogs in Study 3 whereas dogs in Study 1 were adopted by their new families after having been tested at the breeders' homes. There are furthermore major methodological differences between the two studies. In Study 3, exactly the same assessments of impulsivity were used on both occasions, whereas in Study 1 the tests were adapted to the ages of the subjects and therefore differed. However, different tests may not measure exactly the same trait and so there may be less correspondence than when using the same test twice (see also Fratkin et al., 2013).

Considering the extremely long term stability of impulsivity in humans (Casey et al., 2011; Mischel et al., 1988), it is conceivable that impulsivity is one of the most consistent personality traits also in domestic dogs. This is also in line with Taylor and Mills' (2006) suggestion that we find higher consistency for traits with a stronger physiological basis. In dogs, there is now good evidence from both genetic and physiological measurements that the dopaminergic system (Hejjas et al., 2007, 2009; Wan et al., 2013; Wright et al., 2012) and the serotonergic system (Hejjas et al. 2007, 2009; Peremans et al., 2003; Wright et al., 2012) are involved in impulsivity or impulsive aggression in dogs. Additionally, polymorphisms in a dopaminergic gene and in tyrosine hydroxylase genes were found to be associated with levels of activity, impulsivity and inattention in German shepherd dogs and huskies, respectively (Kubinyi et al., 2012; Wan et al., 2013). Furthermore, a glutamate transporter gene and a COMT gene (involved in the metabolism of catecholamines) were associated with activity levels in Labrador retrievers (Takeuchi et al., 2009).

Thus, while the physiological and genetic basis of impulsivity, and to some extent activity, are well established, for other behavioural traits in dogs, success in the identification of candidate genes has so far been rather limited (reviewed in Spady and Ostrander, 2008, and Hall and Wynne, 2012). Accordingly, the high stability of impulsivity in Study 3 and of exploratory activity in Study 1 supports the notion by Taylor and Mills' (2006) that traits with a clearer biological basis are more consistent. Impulsivity is known to be highly consistent in humans (e.g.

Casey et al., 2011), and activity and/ or exploration have demonstrated high consistency across maturation or even metamorphosis also in species from other taxa (common voles, *Microtus arvalis*, Herde and Eccard, 2013; frog, *Rana ridibunda*, Wilson and Krause, 2012).

As activity/ exploration component in Study 1 was the only trait that was significantly related between puppies and adults, these findings suggest that activity is one of the more temporally consistent traits also in dogs. However, previous studies on dogs do not confirm this result: According to a recent meta-analysis (Fratkin et al., 2013), consistency of activity in young dogs (less than one year old when tested for the first time) was only moderate ($r = 0.26$) compared to a higher consistency of aggression ($r = 0.51$) and submissiveness ($r = 0.43$; but note that only 2-3 studies were included in the two latter estimates, compared to 7 studies for activity, and that the consistency estimate of submissiveness in dogs tested first above the age of one year was only 0.13). In the older age group, activity showed similar consistency as the other investigated traits (all in the range of 0.47 to 0.51 with the exception of submissiveness).

Taylor and Mills (2006) point out that specificity of the test and the described behaviour is likely to increase the predictive validity of the test. For example, they suggested that tests for working dogs may be more valid than those for pet dogs because they are clearer in their requirements, using specific tests for measuring specific traits needed in a working context (Taylor and Mills, 2006, but see Fratkin et al., 2013). In contrast, tests for companion dogs (such as the one we used in our study) will often tend to seek more general information on the dog's personality and so may include a range of (very different) subtests to cover a range of characteristics (Taylor and Mills, 2006). Following this argument, the higher reliability of impulsivity measures in Study 3 compared to the various variables measured in Study 1 may in part reflect differences in sensitivity of the tests used.

Although the current study demonstrates high consistency of individual impulsivity, this does not mean that it is completely invariant. For example, it has been demonstrated that a fading procedure (i.e. gradually increasing the delay) leads to increased tolerance to delay in pigeons (Mazur and Logue, 1978). Also rats could sustain longer delays when they had been exposed to delayed reinforcers prior to delayed reward testing in a different context, either via long fixed intervals of reinforcement (Eisenberger et al., 1982) or a fixed ratio schedule of reinforcement (Eisenberger et al., 1989; but see Eisenberger et al., 1982). Similarly, progressive delay

procedures have been successfully used to enhance self-control capabilities in pre-school children, identified by their teachers as impulsive (Dixon and Holcomb, 2000), and in adults affected with mental disorders and substance abuse problems (Dixon and Holcomb, 2000).

Importantly, there are suggestions that interventions that decrease delay discounting in one domain could provide beneficial reductions in impulsive behaviours in other domains that may not be as amenable to direct intervention in humans (Odum, 2011a), and the same may hold true for dogs. At a physiological level, there is evidence that decision making in intertemporal choice tasks is governed by two interacting neurobiological systems (Koffarnus et al., 2013). Parts of the limbic and paralimbic system (the amygdala, nucleus accumbens, ventral pallidum, and related structures) are responsible for impulsive choice, favouring immediate reinforcers. In contrast, the prefrontal cortex is involved in executive control and thus inhibition of impulsive behaviour. Accordingly, strengthening of the prefrontal cortices would be associated with improved delay tolerance (Koffarnus et al., 2013). Despite suggestions in the literature that interventions to reduce delay discounting may be beneficial also in real-life situations (Odum, 2011a), surprisingly few studies have attempted to test this.

As delay discounting shows good cross-species generality (Odum 2011a) and domestic dogs have been suggested as a model species for personality (Gosling et al., 2003), social behaviour (Topál et al., 2009), and ADHD (Vas et al., 2007, Lit et al., 2010), dogs may represent a suitable model for investigating to what extent training on impulse control in one domain may have beneficial effects also in other domains. Future studies should furthermore investigate whether individual impulsivity levels can already be predicted in puppies or young dogs. This would not only help us to elucidate the development of impulsivity from a general process perspective, but if such predisposition can be assessed more reliably than other traits at an early age, this could aid in the selection of working and pet dogs. Given the associations of impulsivity with behaviour problems and the high stability observed, tests of impulsivity may furthermore be valuable for shelters for predicting potential problem behaviour and evaluating training needs.

6.3. Individuality in problem solving - unravelling cognitive processes

Impulsivity is not only relevant for various life outcomes and dog-human interactions, but may also have major effects on performance in cognitive tasks and so may have contributed to the variation observed in our string pulling study. For example, Range et al. (2012) suggested that

committing the proximity error in string pulling tasks does not necessarily imply the absence of means-end understanding (Range et al., 2012); alternatively, “inherited predispositions to go for food directly may overshadow the recognition of means-end connections, and in combination with the inability to inhibit this response, could lead to the proximity bias of dogs” (Range et al., 2012, p. 598). The observed performance differences might furthermore reflect differences in ‘general intelligence’, abilities in the physical domain, or task-specific solutions learned individually by the dogs.

The existence of a ‘general intelligence’ versus several separate intelligence factors has been debated for humans as well as for non-human animals (reviewed in Detterman, 2002). While there is some evidence for the existence of a g factor in non-human animals (e.g. Banerjee et al., 2009; Matzel et al., 2003), proponents of the modular approach argue that much of this evidence stems from tests that are based on a restricted range of tasks and point out that inclusion of less traditional tasks leads to emergence of several different factors (e.g. Herrmann and Call, 2012; Herrmann et al., 2010; Vonk and Povinelli, 2011). Our subjects were not tested in cognitive domains other than physical cognition; however, we tested a subset of the dogs from the string pulling study in a second means-end task, the support problem (Müller et al., 2014), and their performance can shed some light on the question whether good performance in the string pulling task reflects physical cognitive ability, superior learning ability in general, or rather a task-specific solution.

The support problem required the dogs to select the baited one of two boards, one with a reward placed on top of it and the other with a reward placed next to it (Müller et al., 2014) and can thus be considered to be functionally related to the string pulling task. However, those dogs that performed best in the string pulling task did not show superior performance in the support problem and vice versa (personal observation). Also, as a group, dogs with string pulling experience did not perform better in the support problem than those without (Müller et al., 2014). Although both tasks gauge abilities in the physical domain related to connectivity, these results imply that dogs’ solutions to these problems are task-specific and have to be learned for each task separately. Possibly this reflects a low ecological validity of such tasks for domestic dogs. As Miklósi (2009) pointed out, a genetic preparedness for understanding of physical rules is more likely in species that use objects in a complex way. Moreover, as suggested by Lea et al. (2006), canids’ ecological niche as cursorial predators may in fact have been associated with

strong selection for a predisposition to approach prey directly when it is very close, thus predisposing the animals to a proximity error.

By scrutinising individual subjects' behaviour in the four-string task, the curved string task and the transfer tasks, we can draw some inferences about the extent to which dogs possess means-end understanding or which rules they were following to solve the tasks. Studies on dogs and other species have shown that animals may follow a set of hierarchical rules to solve physical problems, preferentially pursuing one strategy but switching to a different one if their preferred strategy was unavailable. For instance in an object permanence task (Topál et al., 2009) and in an object choice task requiring inference by exclusion (Erdőhegyi et al., 2007), domestic dogs preferentially seemed to follow human rather than causal cues but showed improved performance when no human-given cues were available, suggesting that they paid more attention to the causal cues when human cues were absent (Erdőhegyi et al., 2007; Topál et al., 2009). Orangutans (*Pongo pygmaeus*) appeared to solve a puzzle tube task by using any one of three combinations of strategies (Tecwyn et al., 2012). In all cases, the successful subjects initially attempted to move the reward towards the open end of the tube but if this was not applicable, they followed any one of three alternative strategies and subsequently solved the task successfully (Tecwyn et al., 2012). Also, New Caledonian crows (*Corvus moneduloides*) seemed to use a two-stage heuristic strategy in a problem requiring them to select or make the correct tools (Hunt et al., 2006). Initially, the birds seemed to pick a tool without much regard to its properties. When unsuccessful (because the selected tool was too short), they seemed to resort to either a previously developed associative learning rule such as “if a tool fails make a longer one” or causal inference (Hunt et al., 2006). As the tested birds did not appear to pay much attention to the tool characteristics required, Hunt et al. (2006) conclude that their performance can be explained by the simpler heuristic rule combination.

Similarly, some dogs in our study appeared to use two-stage strategies in the string pulling task. A few individuals would start pulling one string and – when the reward did not move closer – they switched to a different string (note that switching was not allowed when a string had been pulled out more than halfway). Others would initially paw near where they perceived the reward (i.e., in the case of the curved string task, at the fence where there was no string) and subsequently start pulling on one of the strings. One dog committed the proximity error in the curved string task several times but subsequently chose the correct string significantly above

chance level, thus apparently resorting to a default behaviour first and scrutinising the problem more closely only in case of failure – a strategy common to other species as well (humans: Betsch et al., 2004; New Caledonian crows: Hunt et al., 2006). Such a strategy would not longer be successful, however, in the gap condition where this individual's performance was at chance level. Conversely, the other two subjects that had performed above chance in the curved string task never committed a proximity error and thus appeared to pay attention to the relevant properties of the strings and the reward before making their choice. These two dogs also performed well in the gap task (one of them reached criterion on the first attempt), indicating that they traced the connection between the reward and the string from the outset.

Nonetheless, when proximity and connectivity cues were conflicting in the parallel diagonal string task, proximity appeared to be the more potent choice rule even for these dogs. This implies that their successful performance does not reflect a true understanding of connectivity, but that the dogs had simply learned a perceptual rule, as has been found for great apes in similar setups (Herrmann et al., 2008; Povinelli et al., 2000). Along similar lines, our recent study on the support problem suggested that dogs rely on perceptual cues to solve this task (Müller et al., 2014). The finding by Range et al. (2011) that dogs spontaneously solved this task could not be replicated by Müller et al. (2014), which could possibly be explained by the different shaping procedures applied in training the dogs to pull out the boards. In the study by Range et al. (2011), the dogs were trained to pull out single boards that had a reward resting visibly on top of them, and so the dogs might have learned the correct choice rule already during the shaping trials. In the study by Müller et al. (2014), shaping to pull out the board was performed with a barrier so that the dogs were not exposed to the sight of the reward on the board until they received the test trials. It seems that the dogs in this study needed some exposure to this setup to learn the choice rule appropriate for this particular task (Müller et al., 2014). Thus, methodological differences appear to be responsible for the different findings by Range et al. (2011) and Müller et al. (2014).

The importance of methodological details is also demonstrated by our string pulling study, where relatively small alterations of the experimental setup (introduction of the curved string task, which precluded the use of the proximity strategy to solve the task) affected performance: Unlike in previous studies, some dogs demonstrated attention to connectivity, but only in setups where no proximity cue was available. Similarly, common marmosets (*Callithrix jacchus*), which like dogs are prone to a proximity bias, were able overcome this bias with novel setups and

succeeded in the new tasks (Gagné et al., 2012). The importance of test setup on cognitive performance has furthermore been demonstrated in other species. Chimpanzees showed much improved performance in the trap tube task when they could rake the reward towards them instead of having to push it away from them (Mulcahy and Call, 2006), or in a setup requiring no tool use at all (Seed et al., 2009). Similarly, in a trap table task, performance was poor when chimpanzees were required to select one of two pre-positioned rakes, but it improved when they could position a tool themselves (Girndt et al., 2008). Orangutans were previously found to lack an understanding of connectivity involving physical attachment but succeeded when ecologically valid tools were presented (Mulcahy et al., 2013). In a task where objects were dropped down a chimney connected by an opaque tube to one of three containers, cotton-top tamarins (*Saguinus oedipus*) typically showed a gravity bias, searching in the container underneath the chimney where the food was dropped, even though aligned chimneys and containers were never connected (Hood et al., 1999). However, when the same task was presented in a horizontal way, eliminating the gravity cue, performance was much improved (Hauser et al., 2001). Our study likewise emphasises the importance of paying attention to details in the test setup when inferring cognitive capabilities from experiments, and our new variant of a means-end test may aid in assessing animals' rule choices in such tasks.

To conclude, dogs and other animals seem to adopt various choice rules to solve physical cognition tasks. Some of these may be simple rules of thumb, while others may be more cognitively demanding. Performance in cognitive tasks can be influenced to a large degree by the test setup, and small alterations may explain why different labs sometimes fail to replicate findings or lead to different conclusions regarding a species' cognitive abilities. Since individual performance differences may reflect cognitive differences, preferences for certain choice rules, but also motivational effects or personality differences, future studies should attempt to disentangle these possibilities.

6.4. Implications

Study 1 assessed the validity of early behavioural tests for predicting behavioural tendencies in domestic dogs. This longitudinal study is – to my knowledge – the first peer-reviewed study on the predictive value of neonate assessments. The results imply that such early predictions of behavioural traits are unreliable. By critically reviewing the previous literature I offer an explanation for the diverging results of previous studies on the predictive value of puppy tests. I point out that while puppy tests may have the potential of predicting outcomes (successful qualification as police dogs, Slabbert and Odendaal, 1999; Svobodova et al., 2008, or guide dogs, Goddard and Beilharz, 1984; Scott & Beilfelt, 1976) to some extent (but see Asher et al., 2013; Wilsson and Sundgren, 1998b), there is little evidence that specific behaviour traits can be predicted in young puppies (Beaudet et al., 1994; Goddard and Beilharz, 1986; Wilsson and Sundgren, 1997b).

Study 2 investigated links between sociability, boldness and conflict resolution strategies in dog puppies. This study contributes to our understanding of animals' conflict behaviour by focusing on non-aggressive conflict resolution strategies, which have been somewhat neglected in the animal behaviour literature compared to the more commonly investigated topic of aggressive interactions. Our results imply parallels with humans and add to our understanding of social behaviour in nonhuman animals by showing relationships between behaviours in an affiliative context and conflict situations. While presenting basic research, this study has possible implications for behavioural problems and their prevention e.g. via measures to improve socialisation in dogs.

Study 3 investigated the stability of two measures of impulsivity over a six-year period, using performance in a delayed reward choice test and owners' reports. We found that both of these measures show high consistency in domestic dogs over a time span of six years. While evidence from human studies has suggested that impulsivity is a stable trait (e.g. Casey et al. 2011), to my knowledge this is the first long-term study on impulsivity in non-human animals. Tests of individual impulsivity have the potential to be valuable tools for assessing puppies' or adult dogs' suitability for pet homes or working environments. Based on our findings, further studies of impulsivity in dogs may help us to elucidate development of impulsivity from a general process perspective, behavioural and physiological correlates of impulsivity, and effects of interventions to reduce individual impulsivity.

In Study 4, we re-investigated dogs' ability to consider means-end connections in string-pulling tasks by providing a novel task where proximity was not a confound. We found that some dogs were able to trace the connection between string and reward when the option of choosing by proximity (a preferred strategy) was not available. This study adds to our knowledge of animals' strategy preferences in solving physical cognition tasks by investigating which features they attend to. The study also highlights the effects of task design on performance in cognitive tasks and yields further insights into testing of mental processes employed by animals when faced with physical problems.

6.6. References

- Appleby, D.L., Bradshaw, J.W.S., Casey, R.A., 2002. Relationship between aggressive and avoidance behaviour by dogs and their experience in the first six months of life. *Vet. Rec.* 150, 434–8.
- Asher, L., Blythe, S., Roberts, R., Toothill, L., Craigon, P.J., Evans, K.M., Green, M.J., England, G.C.W., 2013. A standardized behavior test for potential guide dog puppies: Methods and association with subsequent success in guide dog training. *J. Vet. Behav. Clin. Appl. Res.* 8, 431–438.
- Banerjee, K., Chabris, C.F., Johnson, V.E., Lee, J.J., Tsao, F., Hauser, M.D., 2009. General intelligence in another primate: individual differences across cognitive task performance in a New World monkey (*Saguinus oedipus*). *PLoS One* 4, e5883.
- Beach, F.A., Jaynes, J., 1954. Effects of early experience upon the behavior of animals. *Psychol. Bull.* 51, 239.
- Beaudet, R., Chalifoux, A., Dallaire, A., 1994. Predictive value of activity level and behavioral evaluation on future dominance in puppies. *Appl. Anim. Behav. Sci.* 40, 273–284.
- Bell, A.M., Hankison, S.J., Laskowski, K.L., 2009. The repeatability of behaviour: a meta-analysis. *Anim. Behav.* 77, 771–783.
- Bell, A.M., Sih, A., 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecol. Lett.* 10, 828–834.
- Bensky, M.K., Gosling, S.D., Sinn, D.L., 2013. The World from a Dog's Point of View: A Review and Synthesis of Dog Cognition Research. *Adv. Study Behav.* 45, 209–406.
- Betsch, T., Haberstroh, S., Molter, B., Glöckner, A., 2004. Oops, I did it again—Relapse errors in routinized decision making. *Organ. Behav. Hum. Decis. Process.* 93, 62–74.
- Biro, P.A., Adriaenssens, B., 2013. Predictability as a personality trait: consistent differences in intraindividual behavioral variation. *Am. Nat.* 182, 621–629.
- Bray, E.E., MacLean, E.L., Hare, B.A., 2013. Context specificity of inhibitory control in dogs. *Anim. Cogn.* 1–17.
- Carlstead, K., Mellen, J., Kleiman, D.G., 1999. Black rhinoceros (*Diceros bicornis*) in US zoos: I. Individual behavior profiles and their relationship to breeding success. *Zoo Biol.* 18, 17–34.
- Casey, B.J., Somerville, L.H., Gotlib, I.H., Ayduk, O., Franklin, N.T., Askren, M.K., Jonides, J., Berman, M.G., Wilson, N.L., Teslovich, T., others, 2011. Behavioral and neural correlates of delay of gratification 40 years later. *Proc. Natl. Acad. Sci.* 108, 14998–15003.

- Casey, R. A., Loftus, B., Bolster, C., Richards, G. J., & Blackwell, E. J., 2013. Human directed aggression in domestic dogs (*Canis familiaris*): Occurrence in different contexts and risk factors. *Appl. Anim. Behav. Sci.* 152, 52–63.
- Cervantes, M.C., Delville, Y., 2009. Serotonin 5-HT_{1A} and 5-HT₃ receptors in an impulsive--aggressive phenotype. *Behav. Neurosci.* 123, 589.
- Cherek, D.R., Moeller, F.G., Dougherty, D.M., Rhoades, H., 1997. Studies of violent and nonviolent male parolees: II. Laboratory and psychometric measurements of impulsivity. *Biol. Psychiatry* 41, 523–529.
- Delville, Y., David, J.T., Taravosh-Lahn, K., Wommack, J.C., 2003. Stress and the development of agonistic behavior in golden hamsters. *Horm. Behav.* 44, 263–270.
- Den Berg, C.L., Hol, T., Van Ree, J.M., Spruijt, B.M., Everts, H., Koolhaas, J.M., 1999. Play is indispensable for an adequate development of coping with social challenges in the rat. *Dev. Psychobiol.* 34, 129–138.
- Detterman, D.K., 2002. General intelligence: Cognitive and biological explanations. *Gen. factor Intell. How Gen. is it* 223–243.
- Dingemanse, N.J., Kazem, A.J.N., Réale, D., Wright, J., 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* 25, 81–89.
- Dixon, M.R., Holcomb, S., 2000. Teaching self-control to small groups of dually diagnosed adults. *J. Appl. Behav. Anal.* 33, 611–614.
- Doré, F.Y., Fiset, S., Goulet, S., Dumas, M.-C., Gagnon, S., 1996. Search behavior in cats and dogs: interspecific differences in working memory and spatial cognition. *Anim. Learn. Behav.* 24, 142–149.
- Duffy, D. L., Hsu, Y., Serpell, J. A. 2008. Breed differences in canine aggression. *Appl. Anim. Behav. Sci.* 114, 441-460.
- Duffy, D. L., & Serpell, J. A. 2012. Predictive validity of a method for evaluating temperament in young guide and service dogs. *Appl. Anim. Behav. Sci.* 138, 99-109.
- Eisenberger, R., Masterson, F.A., Lowman, K., 1982. Effects of previous delay of reward, generalized effort, and deprivation on impulsiveness. *Learn. Motiv.* 13, 378–389.
- Eisenberger, R., Weier, F., Masterson, F.A., Theis, L.Y., 1989. Fixed-ratio schedules increase generalized self-control: Preference for large rewards despite high effort or punishment. *J. Exp. Psychol. Anim. Behav. Process.* 15, 383.
- Erdőhegyi, Á., Topál, J., Virányi, Z., Miklósi, Á., 2007. Dog-logic: inferential reasoning in a two-way choice task and its restricted use. *Anim. Behav.* 74, 725–737.
- Fatjó, J., Amat, M., Manteca, X., 2005. Aggression and impulsivity in dogs. *Vet. J.* 169, 150.

- Fratkin, J.L., Sinn, D.L., Patall, E.A., Gosling, S.D., 2013. Personality Consistency in Dogs: A Meta-Analysis. *PLoS One* 8, e54907.
- Gagné, M., Levesque, K., Nutile, L., Locurto, C., 2012. Performance on patterned string problems by common marmosets (*Callithrix jacchus*). *Anim. Cogn.* 15, 1021–1030.
- Girndt, A., Meier, T., Call, J., 2008. Task constraints mask great apes' ability to solve the trap-table task. *J. Exp. Psychol. Anim. Behav. Process.* 34, 54.
- Goddard, M.E., Beilharz, R.G., 1982. Genetic and environmental factors affecting the suitability of dogs as Guide Dogs for the Blind. *Theor. Appl. Genet.* 62, 97–102.
- Goddard, M.E., Beilharz, R.G., 1984. A factor analysis of fearfulness in potential guide dogs. *Appl. Anim. Behav. Sci.* 12, 253–265.
- Goddard, M.E., Beilharz, R.G., 1986. Early prediction of adult behaviour in potential guide dogs. *Appl. Anim. Behav. Sci.* 15, 247–260.
- Gosling, S.D., 1998. Personality dimensions in spotted hyenas (*Crocuta crocuta*). *J. Comp. Psychol.* 112, 107.
- Gosling, S.D., Kwan, V.S.Y., John, O.P., 2003. A dog's got personality: a cross-species comparative approach to personality judgments in dogs and humans. *J. Pers. Soc. Psychol.* 85, 1161–9.
- Graziano, W.G., Jensen-Campbell, L.A., Hair, E.C., 1996. Perceiving interpersonal conflict and reacting to it: the case for agreeableness. *J. Pers. Soc. Psychol.* 70, 820.
- Hall, N.J., Wynne, C.D.L., 2012. The canid genome: behavioral geneticists' best friend? *Genes, Brain Behav.* 11, 889–902.
- Hauser, M.D., Williams, T., Kralik, J.D., Moskovitz, D., 2001. What guides a search for food that has disappeared? Experiments on cotton-top tamarins (*Saguinus oedipus*). *J. Comp. Psychol.* 115, 140.
- Hejjas, K., Kubinyi, E., Ronai, Z., Szekely, a, Vas, J., Miklósi, a, Sasvari-Szekely, M., Kereszturi, E., 2009. Molecular and behavioral analysis of the intron 2 repeat polymorphism in the canine dopamine D4 receptor gene. *Genes. Brain. Behav.* 8, 330–6.
- Hejjas, K., Vas, J., Topal, J., Szantai, E., Rónai, Z., Szekely, A., Kubinyi, E., Horváth, Z., Sasvari-Szekely, M., Miklosi, A., 2007. Association of polymorphisms in the dopamine D4 receptor gene and the activity-impulsivity endophenotype in dogs. *Anim. Genet.* 38, 629–633.
- Herde, A., Eccard, J.A., 2013. Consistency in boldness, activity and exploration at different stages of life. *BMC Ecol.* 13, 49.

- Herrmann, E., Call, J., 2012. Are there geniuses among the apes? *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2753–2761.
- Herrmann, E., Hernández-Lloreda, M.V., Call, J., Hare, B., Tomasello, M., 2010. The structure of individual differences in the cognitive abilities of children and chimpanzees. *Psychol. Sci.* 21, 102–110.
- Herrmann, E., Wobber, V., Call, J., 2008. Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *J. Comp. Psychol.* 122, 220.
- Hood, B.M., Hauser, M.D., Anderson, L., Santos, L., 1999. Gravity biases in a non-human primate? *Dev. Sci.* 2, 35–41.
- Hunt, G.R., Rutledge, R.B., Gray, R.D., 2006. The right tool for the job: what strategies do wild New Caledonian crows use? *Anim. Cogn.* 9, 307–316.
- Hunt, G. R., Rutledge, R. B., Gray, R.D., 2006. The right tool for the job: what strategies do wild New Caledonian crows use? *Anim. Cogn.* 9, 307–316.
- Johansen, E.B., Sagvolden, T., 2004. Response disinhibition may be explained as an extinction deficit in an animal model of attention-deficit/hyperactivity disorder (ADHD). *Behav. Brain Res.* 149, 183–196.
- King, J.A., 1958. Parameters relevant to determining the effects of early experience upon the adult behavior of animals. *Psychol. Bull.* 55, 46.
- King, T., Marston, L.C., Bennett, P.C., 2009. Describing the ideal Australian companion dog. *Appl. Anim. Behav. Sci.* 120, 84–93.
- Kis, A., Topál, J., Gácsi, M., Range, F., Huber, L., Miklósi, Á., Virányi, Z., 2012. Does the A-not-B error in adult pet dogs indicate sensitivity to human communication? *Anim. Cogn.* 15, 737–743.
- Koffarnus, M.N., Jarmolowicz, D.P., Mueller, E.T., Bickel, W.K., 2013. Changing delay discounting in the light of the competing neurobehavioral decision systems theory: A review. *J. Exp. Anal. Behav.* 99, 32–57.
- Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M.A.W., Blokhuis, H.J., 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* 23, 925–935.
- Kubinyi, E., Vas, J., Hejjas, K., Ronai, Z., Brúder, I., Turcsán, B., Sasvari-Szekely, M., Miklósi, Á., 2012. Polymorphism in the tyrosine hydroxylase (TH) gene is associated with activity-impulsivity in german shepherd dogs. *PLoS One* 7, e30271.

- Kuntsi, J., Oosterlaan, J., Stevenson, J., 2001. Psychological mechanisms in hyperactivity: I response inhibition deficit, working memory impairment, delay aversion, or something else? *J. Child Psychol. Psychiatry* 42, 199–210.
- Lea, S.E.G., Goto, K., Osthaus, B., Ryan, C.M.E., 2006. The logic of the stimulus. *Anim. Cogn.* 9, 247–256.
- Lindsay, S.R., 2000. *Handbook of Applied Dog Behavior and Training, Vol. 1: Adaptation and Learning*. Iowa State University Press, Ames.
- Madden, G.J., Smith, N.G., Brewer, A.T., Pinkston, J.W., Johnson, P.S., 2008. Steady-state assessment of impulsive choice in Lewis and Fischer 344 rats: between-condition delay manipulations. *J. Exp. Anal. Behav.* 90, 333–344.
- Matzel, L.D., Han, Y.R., Grossman, H., Karnik, M.S., Patel, D., Scott, N., Specht, S.M., Gandhi, C.C., 2003. Individual differences in the expression of a “general” learning ability in mice. *J. Neurosci.* 23, 6423–6433.
- Mazur, J.E., Logue, A.W., 1978. Choice in a “self-control” paradigm: effects of a fading procedure. *J. Exp. Anal. Behav.* 30, 11–17.
- McMillan, F.D., Serpell, J.A., Duffy, D.L., Masaoud, E., Dohoo, I.R., 2013. Differences in behavioral characteristics between dogs obtained as puppies from pet stores and those obtained from noncommercial breeders. *J. Am. Vet. Med. Assoc.* 242, 1359–1363.
- Miklósi, Á., 2009. *Dog Behaviour, Evolution, and Cognition (Oxford Biology)*. Oxford University Press, Oxford.
- Miklósi, Á., Topál, J., Csányi, V., 2007. Big thoughts in small brains? Dogs as a model for understanding human social cognition. *Neuroreport* 18, 467–471.
- Miranda de la Lama, G.C., Sepúlveda, W.S., Montaldo, H.H., María, G.A., Galindo, F., 2011. Social strategies associated with identity profiles in dairy goats. *Appl. Anim. Behav. Sci.* 134, 48–55.
- Mischel, W., Shoda, Y., Peake, P.K., 1988. The nature of adolescent competencies predicted by preschool delay of gratification. *J. Pers. Soc. Psychol.* 54, 687.
- Mulcahy, N.J., Call, J., 2006. How great apes perform on a modified trap-tube task. *Anim. Cogn.* 9, 193–199.
- Mulcahy, N.J., Schubiger, M.N., Suddendorf, T., 2013. Orangutans (*Pongo pygmaeus* and *Pongo abelii*) understand connectivity in the skewered grape tool task. *J. Comp. Psychol.* 127, 109.
- Müller, C.A., Riemer, S., Virányi, Z., Huber, L., Range, F., 2014. Dogs learn to solve the support problem based on perceptual cues. *Anim. Cogn.* 1–10.

- Obozova, T.A., Zorina, Z.A., 2013. Do Great Grey Owls Comprehend Means-end Relationships? *Int. J. Comp. Psychol.* 26.
- Odum, A.L., 2011a. Delay discounting: Trait variable? *Behav. Processes* 87, 1–9.
- Odum, A.L., 2011b. Delay discounting: I'm a k, you're a k. *J. Exp. Anal. Behav.* 96, 427–439.
- Osthaus, B., Lea, S.E.G., Slater, A.M., 2005. Dogs (*Canis lupus familiaris*) fail to show understanding of means-end connections in a string-pulling task. *Anim. Cogn.* 8, 37–47.
- Overall, K.L., Hamilton, S.P., Chang, M.L., 2006. Understanding the genetic basis of canine anxiety: phenotyping dogs for behavioral, neurochemical, and genetic assessment. *J. Vet. Behav. Clin. Appl. Res.* 1, 124–141.
- Park, H., Antonioni, D., 2007. Personality, reciprocity, and strength of conflict resolution strategy. *J. Res. Pers.* 41, 110–125.
- Peremans, K., Audenaert, K., Coopman, F., Blanckaert, P., Jacobs, F., Otte, A., Verschooten, F., van Bree, H., van Heeringen, K., Mertens, J., others, 2003. Estimates of regional cerebral blood flow and 5-HT_{2A} receptor density in impulsive, aggressive dogs with 99mTc-ECD and 123I-5-I-R91150. *Eur. J. Nucl. Med. Mol. Imaging* 30, 1538–1546.
- Povinelli, D.J., Reaux, J.E., Theall, L.A., Giambrone, S., Humphrey, N., 2000. *Folk physics for apes: The chimpanzee's theory of how the world works*. Oxford University Press Oxford.
- Range, F., Hentrup, M., Virányi, Z., 2011. Dogs are able to solve a means-end task. *Anim. Cogn.* 14, 575–583.
- Range, F., Möslinger, H., Virányi, Z., 2012. Domestication has not affected the understanding of means-end connections in dogs. *Anim. Cogn.* 15, 597–607.
- Reisner, I.R., Mann, J.J., Stanley, M., Huang, Y., Houpt, K.A., 1996. Comparison of cerebrospinal fluid monoamine metabolite levels in dominant-aggressive and non-aggressive dogs. *Brain Res.* 714, 57–64.
- Reynolds, B., 2006. A review of delay-discounting research with humans: relations to drug use and gambling. *Behav. Pharmacol.* 17, 651–667.
- Riemer, S., Müller, C., Turcsán, B., Huber, L., Virányi, Zs. & Range, F. 2013a. Personality development in pet dogs from puppyhood to adulthood – a longitudinal study. Oral presentation at Behaviour 2013, Newcastle, August 4-8, 2013.
- Riemer, S., Müller, C., Turcsán, B., Huber, L., Virányi, Zs. & Range, F. 2013b. Pet dogs' personality: consistency and change across time. Oral presentation at the International Veterinary Behavior Meeting, Lisbon, September 26-29, 2013

- Ruefenacht, S., Gebhardt-Henrich, S., Miyake, T., Gaillard, C., 2002. A behaviour test on German Shepherd dogs: heritability of seven different traits. *Appl. Anim. Behav. Sci.* 79, 113–132.
- Sachser, N., Kaiser, S., Hennessy, M.B., 2013. Behavioural profiles are shaped by social experience: when, how and why. *Philos. Trans. R. Soc. B Biol. Sci.* 368, 20120344.
- Sachser, N., Lick, C., 1991. Social experience, behavior, and stress in guinea pigs. *Physiol. Behav.* 50, 83–90.
- Saetre, P., Strandberg, E., 2006. The genetic contribution to canine personality. *Genes, Brain Behav.* 5, 240–248.
- Sagvolden, T., Aase, H., Zeiner, P., Berger, D., 1998. Altered reinforcement mechanisms in attention-deficit/hyperactivity disorder. *Behav. Brain Res.* 94, 61–71.
- Scott, J.P., Beilfelt, S.W., 1976. Analysis of the puppy testing program., in: Pfaffenberger, C.J., Scott, J.P., Fuller, J.L., Ginsburg, B.E., Bielfelt, S.W. (Ed.), *Guide Dogs for the Blind: Their Selection, Development and Training*. pp. 39–75.
- Seed, A.M., Call, J., Emery, N.J., Clayton, N.S., 2009. Chimpanzees solve the trap problem when the confound of tool-use is removed. *J. Exp. Psychol. Anim. Behav. Process.* 35, 23.
- Serpell, J.A. 2005. Effects of breed, sex, and neuter status on trainability in dogs *Anthrozoös* 18, 196–207.
- Slabbert, J.M., Odendaal, J.S.J., 1999. Early prediction of adult police dog efficiency - a longitudinal study. *Appl. Anim. Behav. Sci.* 64, 269–288.
- Solanto, M. V, Abikoff, H., Sonuga-Barke, E., Schachar, R., Logan, G.D., Wigal, T., Hechtman, L., Hinshaw, S., Turkel, E., 2001. The ecological validity of delay aversion and response inhibition as measures of impulsivity in AD/HD: a supplement to the NIMH multimodal treatment study of AD/HD. *J. Abnorm. Child Psychol.* 29, 215–228.
- Spady, T.C., Ostrander, E.A., 2008. Canine behavioral genetics: pointing out the phenotypes and herding up the genes. *Am. J. Hum. Genet.* 82, 10–18.
- Stamps, J.A., Briffa, M., Biro, P.A., 2012. Unpredictable animals: individual differences in intraindividual variability (IIV). *Anim. Behav.* 83, 1325–1334.
- Strandberg, E., Jacobsson, J., Saetre, P., 2005. Direct genetic, maternal and litter effects on behaviour in German shepherd dogs in Sweden. *Livest. Prod. Sci.* 93, 33–42.
- Svartberg, K., Tapper, I., & Temrin, H., 2005. Consistency of personality traits in dogs. *Anim. Behav.* 69, 283–291.
- Svartberg, K., 2005. A comparison of behaviour in test and in everyday life: evidence of three consistent boldness-related personality traits in dogs. *Appl. Anim. Behav. Sci.* 91, 103–128.

- Svartberg, K., Forkman, B., 2002. Personality traits in the domestic dog (*Canis familiaris*). Appl. Anim. Behav. Sci. 79, 133–155.
- Svobodova, I., Vapenik, P., Pinc, L., Bartos, L., 2008. Testing German shepherd puppies to assess their chances of certification. Appl. Anim. Behav. Sci. 113, 139–149.
- Takeuchi, Y., Hashizume, C., Arata, S., Inoue-Murayama, M., Maki, T., Hart, B.L., Mori, Y., 2009. An approach to canine behavioural genetics employing guide dogs for the blind. Anim. Genet. 40, 217–224.
- Taylor, K.D., Mills, D.S., 2006. The development and assessment of temperament tests for adult companion dogs. J. Vet. Behav. - Clin. Appl. Res. 1, 94–108.
- Tecwyn, E.C., Thorpe, S.K.S., Chappell, J., 2012. What cognitive strategies do orangutans (*Pongo pygmaeus*) use to solve a trial-unique puzzle-tube task incorporating multiple obstacles? Anim. Cogn. 15, 121–133.
- Topál, J., Gergely, G., Erdőhegyi, Á., Csibra, G., Miklósi, Á., 2009. Differential sensitivity to human communication in dogs, wolves, and human infants. Science 325, 1269–1272.
- Topál, J., Miklósi, A., Gácsi, M., Dóka, A., Pongrácz, P., Kubinyi, E., Virányi, Z., Csanyi, V., 2009. The dog as a model for understanding human social behavior. Adv. Study Behav. 39, 71–116.
- Trillmich, F., Hudson, R., 2011. The emergence of personality in animals: the need for a developmental approach. Dev. Psychobiol. 53, 505–509.
- Van den Bergh, F., Spronk, M., Ferreira, L., Bloemarts, E., Groenink, L., Olivier, B., Oosting, R., 2006. Relationship of delay aversion and response inhibition to extinction learning, aggression, and sexual behaviour. Behav. Brain Res. 175, 75–81.
- Vas, J., Topál, J., Péch, É., Miklósi, Á., 2007. Measuring attention deficit and activity in dogs: A new application and validation of a human ADHD questionnaire. Appl. Anim. Behav. Sci. 103, 105–117.
- Vonk, J., Povinelli, D., 2011. Individual differences in Long-term cognitive testing in a group of captive chimpanzees. Int. J. Comp. Psychol. 24.
- Walker, R., Fisher, J., Neville, P., 1997. The treatment of phobias in the dog. Appl. Anim. Behav. Sci. 52, 275–289.
- Wallis, L.J., Range, F., Müller, C.A., Serisier, S., Huber, L., Virányi, Z., 2014. Lifespan development of attentiveness in domestic dogs: drawing parallels with humans. Name Front. Psychol. 5, 71.

- Wan, M., Hejjas, K., Ronai, Z., Elek, Z., Sasvari-Szekely, M., Champagne, F.A., Miklósi, Á., Kubinyi, E., 2013. DRD4 and TH gene polymorphisms are associated with activity, impulsivity and inattention in Siberian Husky dogs. *Anim. Genet.*
- Weiss, A., King, J.E., Perkins, L., 2006. Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). *J. Pers. Soc. Psychol.* 90, 501.
- Wilson, A.D.M., Krause, J., 2012. Personality and metamorphosis: is behavioral variation consistent across ontogenetic niche shifts? *Behav. Ecol.* 23, 1316–1323.
- Wilsson, E., Sundgren, P.-E., 1997a. The use of a behaviour test for selection of dogs for service and breeding. II. Heritability for tested parameters and effect of selection based on service dog characteristics. *Appl. Anim. Behav. Sci.* 54, 235–241.
- Wilsson, E., Sundgren, P.-E., 1997b. The use of a behaviour test for the selection of dogs for service and breeding, I: Method of testing and evaluating test results in the adult dog, demands on different kinds of service dogs, sex and breed differences. *Appl. Anim. Behav. Sci.* 53, 279–295.
- Wilsson, E., Sundgren, P.-E., 1998a. Effects of weight, litter size and parity of mother on the behaviour of the puppy and the adult dog. *Appl. Anim. Behav. Sci.* 56, 245–254.
- Wilsson, E., Sundgren, P.-E., 1998b. Behaviour test for eight-week old puppies—heritabilities of tested behaviour traits and its correspondence to later behaviour. *Appl. Anim. Behav. Sci.* 58, 151–162.
- Winstanley, C.A., Eagle, D.M., Robbins, T.W., 2006. Behavioral models of impulsivity in relation to ADHD: translation between clinical and preclinical studies. *Clin. Psychol. Rev.* 26, 379–395.
- Wood, V.F., Bell, P.A., 2008. Predicting interpersonal conflict resolution styles from personality characteristics. *Pers. Individ. Dif.* 45, 126–131.
- Wright, H.F., Mills, D.S., Pollux, P.M.J., 2012. Behavioural and physiological correlates of impulsivity in the domestic dog (*Canis familiaris*). *Physiol. Behav.* 105, 676–682.

SUMMARY

This thesis focuses on individual differences in behaviour and cognition in domestic dogs. Study 1 investigates behavioural development in Border Collies and indicates that tests of puppies in the first days of life or during the socialisation period have low predictive validity for predicting specific behavioural traits in adult dogs (1.5-2 years). The discrepancy observed in previous studies regarding the predictive value of puppy tests can be attributed to different approaches: at a coarse level, early test may indicate suitability for a particular function to some extent; however, specific individual behaviour traits can hardly be predicted from puppy tests.

Study 2 explores relationships between puppies' behaviour in apparent conflict situations and behaviour in other, social and environmental, contexts. The results show that highly sociable puppies tend to adopt an interactive conflict resolution strategy whereas less sociable puppies tend to behave passively. In agreement with studies from other species, this indicates that individual conflict resolution strategies are related to the personality of the individual.

Study 3 assessed the temporal stability of a further cognitive/ behavioural characteristic: different measures of impulsivity in dogs – performance in a delayed reward choice test and owners' questionnaire ratings – demonstrated extremely high stability over a time gap of six years.

Study 4 investigates how dogs solve a cognitive task. The dogs were confronted with a reward that was inaccessible behind a fence and could be pulled towards them with a string. In a task with multiple strings, some individuals apparently attended to the connection between string and reward. Nonetheless this does not imply an understanding of means-end connections. We conclude that dogs may use alternative problem solving strategies and preferentially choose the simpler rule when cues are ambiguous. The results demonstrate individual differences in performance and point out the importance of details such as the test setup on animals' performance in cognitive tasks.

These studies add a puzzle piece to the bigger question of behavioural development and indicate effects of personality on animals' behaviour in social conflict situations. They are furthermore of practical relevance regarding the predictive validity of early puppy tests and the stability of the impulsivity trait in dogs. The latter is not only relevant to human-dog interactions but also of particular interest from a comparative viewpoint, and dogs may serve as models for assessing effectiveness of training to reduce individual impulsivity. The results of the tests of means-end

understanding enhance our understanding of how animals approach physical cognition problems and how individuals may follow alternative rules to solve the task.

ZUSAMMENFASSUNG

Das Thema dieser Dissertation sind individuelle Unterschiede in Verhalten und Kognition bei Haushunden.

Studie 1 befasst sich mit Verhaltensentwicklung von Border Collies und ergibt, dass frühe Tests von Welpen in den ersten Lebenstagen oder der Sozialisationsphase wenig aussagekräftig sind in Bezug auf spezifische Verhaltenseigenschaften der erwachsenen Hunde (1,5-2 Jahre). Die Diskrepanz bisheriger Studien hinsichtlich der Aussagekraft von Welpentests ist möglicherweise auf unterschiedliche Ansätze zurückzuführen: Auf einer gröberen Ebene können frühe Tests evtl. zu einem gewissen Maß eine Eignung für bestimmte Aufgaben vorhersagen; einzelne individuelle Verhaltenseigenschaften scheinen jedoch in Welpentests kaum vorhersagbar zu sein.

Studie 2 untersucht, ob das Verhalten von Welpen in einer scheinbaren Konfliktsituation mit sozialem oder umweltbezogenem Verhalten in anderen Zusammenhängen korreliert. Die Ergebnisse zeigen, dass kontaktfreudige Welpen zu einer interaktiven Konfliktlösungsstrategie tendieren, während weniger kontaktfreudige Welpen eher zu Passivität neigen. Übereinstimmend mit Studien an anderen Arten, deutet dies darauf hin, dass individuelle Konfliktlösungsstrategien mit der Persönlichkeit des Individuums zusammenhängen.

Studie 3 untersucht die zeitliche Stabilität einer weiteren Verhaltens- bzw. kognitiven Eigenschaft: verschiedene Maße für Impulsivität bei Hunden – Verhalten in einem Belohnungsaufschub-Test sowie die Bewertung durch die Besitzer mittels Fragebögen – wiesen eine äußerst hohe Stabilität über einen Zeitraum von sechs Jahren auf.

Studie 4 befasst sich mit Lösungsstrategien in einer kognitiven Aufgabe. Dabei wurden Hunde mit einer unzugänglichen Belohnung hinter einem Zaun konfrontiert, die sie mittels einer Schnur zu sich heran ziehen konnten. In einer Aufgabe, in der die Hunde zwischen mehreren Schnüren die mit der Belohnung verbundene auswählen mussten, verfolgten einige Individuen offenbar die Verbindung zwischen der Belohnung und der Schnur und waren so auch in komplexen Aufgaben erfolgreich. Ein Verständnis von Zusammenhängen kann aus den Ergebnissen dennoch nicht geschlossen werden. Wir schlussfolgern, dass Hunde unterschiedliche Problemlösungsstrategien anwenden und bei uneindeutigen Hinweisen die jeweils einfachere vorziehen. Die Ergebnisse zeigen individuelle Leistungsunterschiede und den Einfluss von Details im Testaufbau auf Leistungen in kognitiven Experimenten auf.

Diese Studien leisten einen Beitrag zu unserem Verständnis von Verhaltensentwicklung und deuten auf den Einfluss von Persönlichkeit auf Verhaltensweisen in sozialen Konfliktsituationen hin. Sie sind weiters von praktischer Relevanz in Bezug auf die Vorhersagekraft früher Welpentests und die Stabilität von Impulsivität bei Hunden. Letztere ist nicht nur in der Mensch-Hund Interaktion relevant, sondern auch aus vergleichender Sicht, und Hunde könnten als Modell für die Effektivität von Maßnahmen zur Reduktion von Impulsivität dienen. Die Ergebnisse der Schnur-Zieh-Experimente tragen zu unserem Verständnis bei, wie Tiere an physikalische Kognitions-Aufgaben herangehen und welche alternativen Lösungswege sie dabei verfolgen können.

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Prizes

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9/2006 **Universities Federation for Animal Welfare (UFAW) Prize** for an outstanding research project in the field of animal welfare (for BSc thesis)
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Selected Work Experience

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- 10 - 11/2008 **Statistical analyses** for the the Austrian Environment Agency (Umweltbundesamt)
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Publications

- Riemer S**, Müller C, Virányi Zs, Huber L &, Range F (2014) The predictive value of early behavioural assessments in pet dogs – a longitudinal study from neonates to adults. *PLoS One*, in press.
- Riemer S**, Müller C, Huber L &, Range F (2014) Dogs can learn to attend to connectivity in string pulling tasks. *Journal of Comparative Psychology* 128(1):31-9.
- Riemer S**, Mills, D & Wright, H (2014) Impulsive for life? The nature of long-term impulsivity in domestic dogs. *Animal Cognition* 17(3): 815-9.
- Riemer S**, Müller C, Virányi Zs, Huber L &, Range F (2013) Choice of conflict resolution strategy is linked to sociability in dog puppies. *Applied Animal Behaviour Science* 149(1), 36-44.
- Müller C, **Riemer S**, Range F & Huber L (2014). The Use of a Displacement Device Negatively Affects the Performance of Dogs (*Canis familiaris*) in Visible Object Displacement Tasks. *Journal of Comparative Psychology*, Mar 10 , 2014,
- Müller, C, **Riemer S**, Virányi Z, Huber L, & Range F (2014). Dogs learn to solve the support problem based on perceptual cues. *Animal Cognition*, 1-10.
- Müller C, **Riemer S**, Range F & Huber L (2013). Dogs' use of the solidity principle: revisited. *Animal cognition*, 1-5.
- Müller C, **Riemer S**, Rosam C, Schöbwendler J, Range F & Huber L (2012) Owner absence does not induce negative judgement bias in pet dogs. *Animal Cognition* 15(5):1031-5.
- Riemer S**, Schulze Ch & Frank G (2011): Densities and habitat use of woodpeckers in the national park Donauauen (Lower Austria). *Egretta* 52: 55–64.
- Riemer S**, Frank G & Schulze CH (2010) Population density and habitat use of the Green Woodpecker *Picus viridis* in Donau-Auen National Park (Lower Austria). *Vogelwarte* 48: 187 – 194.

Published Conference Abstracts

- Riemer S**, Müller C, Virányi Zs, Range F & Huber L (2013) String pulling in dogs revisited: spontaneous performance and learning in novel setups. *Journal of Veterinary Behavior: Clinical Applications and Research* 8(4), e34.
- Müller C, **Riemer S**, Virányi Zs, Huber L & Range F (2013) Effect of inhibitory control on problem solving in dogs. *Journal of Veterinary Behavior: Clinical Applications and Research* 8(4), e35.
- Riemer S**, Müller C, Huber L, Range F, Kersting E & Virányi Zs (2011) Can early temperament tests predict behavioral tendencies in dog puppies? *Journal Of Veterinary Behavior: Clinical Applications And Research* 6(1): 79.

Müller C, Dörrenberg S, Mayer C, **Riemer S**, Huber L, Range F (2011) Understanding of size constancy in dogs: a new approach to account for novelty effects. *Journal of Veterinary Behavior: Clinical Applications and Research* 6(1): 81.

Riemer S, Frank, G & Schulze Ch. (2009) Bestandsdichten und Habitatnutzung von Spechten im Nationalpark Donauauen (Niederösterreich). *Vogelwarte* 47(4): 347 – 348.