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Lisa Wallis, MSc.

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Education

March 2010 – December 2015 – Clever Dog Lab, Department of Cognitive Biology, University of Vienna, Austria, **PhD Candidate**

2005–2008 - Manchester Metropolitan University, Manchester, **MSc Animal Behaviour – Distinction.**

1997–2000 - Anglia Polytechnic University, Cambridge, **BSc Honours Animal Behaviour, Conservation & Ecology. Second Class Honours Upper Degree (2:1)** Thesis – Human influence on captive wolf behaviour, Supervisor Prof. Guy Norton.

Research Experience

- Reproductive Conflict - suppression of subordinate female reproduction in cooperatively breeding meerkats (Suricata suricatta). Analysis project, completed as part of year research assistant position. Studying the behavioural ecology of a number of habituated meerkat groups as a volunteer for Cambridge University.

6th November 2008 – 6th November 2009 – Kalahari Meerkat Project, Van Zylsrus, South Africa
Volunteer Research Assistant

  - ✓ Work involving twice daily observation in the field with adlib data collection, radio tracking, GPS tracking, assisting with captures and experiments.
  - ✓ Skills gained including: habituating meerkats, data entry and analysis, use of Microsoft Access, Microsoft Excel, Cool Edit and Map Source programs.

- Social Interactions in the European Beaver (*Castor fiber*). Studying the behavioural ecology of the Eurasian Beaver, assisting with PhD work of Roo Campbell for the University of Oxford, Wildcru.

29th May – 3rd September 2006, Telemark University College, Bø, Norway,
Research Assistant

  - ✓ Work involved daily nocturnal radio tracking and observation of habituated individuals using continuous behavioural recording, and lodge watches.
  - ✓ Assisting in live trapping of beavers from boats. Data entry and project write up.
  - ✓ Co-ordinating Volunteers. Boat operation and maintenance.

- Behavioural differences in captive European and North American wolves, focusing specifically on communication.

2000 – 2002, UK Wolf Conservation Trust, Reading, **Wolf Curator & Education Coordinator**

- ✓ Public tours, lectures, and seminars, Educational displays. Fundraising and PR work.
- ✓ Supervising and training Volunteers and Work Experience personnel.
- ✓ Project planning and prioritising. Office & Administration work.

- Wolf pup development and socialisation. Onset of howling, social hierarchy development among littermates, and pup integration into the pack. Completed as part of ongoing work at Wolf Park.

Feb-Aug 1997 June-Aug 1998 June-Aug 1999 Wolf Park Battleground, Indiana USA
Six Month Summer Wolf Internship/Volunteer/Assistant Manager

Public Engagement with Science

- Interviews with local news presenters, newspaper journalists and magazine writers.
- Wolf Biographies, newsletters, membership updates, adoption information.
- BBC work – Monarch of the Glen, (Series 4, Part 1), Documentaries, Man Meets Wolf.
- Numerous public talks/seminars on captive wolf behaviour and cognition in domestic dogs.

Memberships

- ASAB (Association for the Study of Animal Behaviour)
- BVBA (British Veterinary Behaviour Association)
- APBC (Association of Pet Behaviour Councellors)
- ISAZ (International Society for Anthrozoology)
- Member of organising committee of Canine Science Forum 2010
- Associate member of DK Cognition and communication PhD Programme (University of Vienna)

Publications

Wallis L, Range F, Müller C, Serisier S, Huber L, & Virányi Z. (2014). Lifespan development of attentiveness in domestic dogs. *Frontiers in Comparative Psychology*. 5:71. Impact factor: 2.6

Wallis L, Range F, Müller C, Serisier S, Huber L, & Virányi Z. (2015). Training for eye contact modulates gaze following in dogs. *Animal Behaviour*. *106*, 27–35. doi:10.1016/j.anbehav.2015.04.020. Impact factor: 3.16

Wallis L, Virányi Z, Müller C, Serisier S, Huber L, & Range F. (2015). Aging effects on discrimination learning, logical reasoning and memory in pet dogs. *AGE*. Accepted. Impact factor: 3.6

Published Conference Abstracts

Wallis L, Range F, Müller C, Virányi Z. (2011). Reversal learning in a social communication task: is there an effect of cue? *Journal of Veterinary Behaviour: Clinical Applications and Research. 6*(1):85-85. Impact factor: 1.653

Wallis L, Range F, Müller C, Serisier S, Huber L, & Virányi Z. (2013). Age effects on interspecific communicative abilities of domestic dogs. *Journal of Veterinary Behaviour: Clinical Applications and Research. 8*(4):31-31. Impact factor: 1.653

Kloesch G, Kemethofer M, Wallis L, Seidel S, and J. P. Dittami. (2014). Sleeping with dogs – results of an internet-based survey. *Journal of Sleep Research* JSR 23 (Suppl. 1), 265

Conference Oral Presentations

Sex-age differences in activity budget and social interactions of Eurasian Beavers (Castor fiber). Konrad Lorenz Graduate Meeting Grünau 17th September 2015, Austria

The Vienna Canine Cognitive Battery: Assessment of cognitive functioning during development and aging in pet dogs. Canine Science Forum (CSF) 15th July 2014, Lincoln, UK

Dogs can follow human gaze despite training to maintain eye contact. International Society for Anthrozoology (ISAZ) 20th July 2014, Vienna, Austria

Cognitive development and aging in pet Border Collies. Invited oral presentation at the Research and Development Center at Royal Canin Head Quarters, 13th June 2014, Aimargues, France

Developing tools to assess cognitive functioning in pet Border collies during development and aging using a computer-automated touchscreen battery. Invited Speaker at Cognitive and neurobiological aging in the dog (Satellite Meeting of Society for Neuroscience (SFN)). San Diego, CA, USA, November 8, 2013.

Age effects on interspecific communicative abilities of domestic dogs. Canine Science Forum (CSF) 25th July 2012, Barcelona, Spain

Awards

Best student oral presentation at ISAZ 2014; University of Vienna PhD completion grant for Life Sciences 2014

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“It is not the most intellectual of the species that survives; it is not the strongest that survives; but the species that survives is the one that is able to adapt to and to adjust best to the changing environment in which it finds itself......”

Charles Darwin (1859), “The Origin of Species.”

"There is in every child at every stage a new miracle of vigorous unfolding."

Erik Erikson (1902-1994)

“Anyone who stops learning is old, whether at twenty or eighty. Anyone who keeps learning stays young. The greatest thing in life is to keep your mind young.”

Henry Ford (1863 – 1947)

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AUTHOR CONTRIBUTIONS

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Chapter 2: Aging effects on discrimination learning, logical reasoning and memory (Study 1)
Friederike Range designed this study with input from Zsófia Virányi and Ludwig Huber. Angela Gaigg, Teresa Marmota and I collected the data, and I analysed it with help from Corsin Müller and wrote the paper. Corsin Müller, Friederike Range, Zsófia Virányi, Samuel Serisier and Ludwig Huber were involved in editing and revising the paper.

Chapter 3: Training for eye contact modulates gaze following (Study 2)
This study was part of the main cognitive battery, which was designed by Zsófia Virányi, Friederike Range and I. I collected and analysed the data with statistical help from Corsin Müller. I wrote the paper, and Corsin Müller, Friederike Range, Zsófia Virányi, Samuel Serisier and Ludwig Huber were involved in editing and revising the paper.

Chapter 4: Lifespan development of attentiveness in domestic dogs: drawing parallels with humans (Study 3)
This study was also part of the main cognitive battery. I collected the data, and analysed it with help from Corsin Müller and wrote the paper. Corsin Müller, Friederike Range, Zsófia Virányi, Samuel Serisier and Ludwig Huber were involved in editing and revising the paper.

Chapter 5: General discussion
Lisa Wallis

1. General introduction

1.1 Cognitive development and aging

Cognition, broadly defined, refers to ways in which animals (including humans) retain, process, and act on information taken in through the senses (Shettleworth, 2001; Dukas 2004) and includes processes such as perception, learning, memory, and problem solving. Such processes play an important role in how animals make decisions in dealing with their physical and social environments (Shettleworth 2001). Cognitive abilities in humans (for example memory and problem solving) increase rapidly from infancy to young adulthood and then, depending on the specific ability, are either maintained (such as verbal learning and general knowledge (Ardila, 2007)), or decline (Baltes, 1987) (such as the ability to acquire new information (Small, Stern, Tang, & Mayeux, 1999), remember specific events (Levine et al., 2002; Spencer and Raz, 1995), and to deploy executive control (Albert, 1993)).

Cognitive change cannot be linked to any one function in the developing and aging brain. Until the late 1960's it was commonly believed that brain development ceased during early childhood, as brain volume during this time reached stable levels. Subsequent histological studies on humans and monkeys have revealed that some brain areas, in particular the prefrontal cortex continue to develop well into adulthood. During childhood there is a proliferation of synapses, and again at puberty, followed by a plateau phase, and finally after puberty, synaptic elimination and reorganization of the synaptic connections (Blakemore & Choudhury, 2006). Adolescence is a critical period for the maturation of the prefrontal cortex, and its development is paralleled by increased abilities in executive control including reasoning, attention, response inhibition, reward evaluation, goal directed behaviour and emotional processing (Yurgelun-Todd, 2007). Changes in cognitive performance with age are linked to dissociations in the development and decline in white matter (myelination of nerve fibers) and grey matter (synaptic connections between neurons), combined with dissociations in the maturity and functioning of specific brain regions and networks (Craik & Bialystok, 2006).

The trajectories of maturational and aging effects have been found to vary considerably over the cortex in healthy normally developing humans (i.e. different regions of the brain mature and age at different rates). Sowell et al., (2003) used magnetic resonance imaging (MRI) and cortical matching algorithms to map the effects of aging on brain morphology across the lifespan from childhood through senescence. Regions which are known to myelinate early such as the visual, auditory and limbic cortices show a more linear pattern of aging, but the frontal cortices, and posterior temporal lobes mature later, and show a quadratic relationship with age. Sowell et al., (2003) suggest that these differences in patterns of development and aging reflect differences in the underlying cellular architecture, which may contribute to the variability in cognitive functions associated with aging.

There are remarkably few studies detailing the behavioural consequences of these biological changes, that is, the course of lifespan changes in cognitive abilities. Lifespan development is the “constancy and change in behaviour throughout the life course (ontogenesis), from conception to death” (Baltes 1987). Historically there have been many theories of human development, which initially were only concerned with infants and children, but since have been expanded to include the whole lifespan. Craik and Bialystok (2006) have highlighted the need for an integration of the processes involved in development and aging to provide a framework to account for the lifespan structure of cognition, and the factors which influence cognitive performance. Cognitive development and aging depends on interactions among genetic, environmental and social factors, and have almost exclusively been studied in humans (Baltes 1987, Craik and Bialystok 2006, Li and Baltes 2006). Unique developmental outcomes emerge as a consequence of the interaction and mutually influencing effect of cognitive and social developmental capacities (Moore, Oates, Hobson, & Goodwin, 2002). Studies on young children with Down syndrome show a delay in the development of cognitive capacities as the primary consequence. However Down syndrome children can be empathic, affectionate and engaging despite this cognitive delay (Wishart & Pitcairn, 2000). Such evidence suggests that there are pre-specified, relatively independent, “domain specific” pathways for some aspects of social and cognitive development (Moore et al 2002). The notion of “environment” as static, and development (both normal and abnormal) as dynamic is well known and accepted in the scientific literature. However a child’s way of processing environmental stimuli may change repeatedly as a function of development, starting with a more domain-relevant mechanism and leading to the progressive formation of domain-specific representations (Karmiloff-Smith, 1998).

The analyses of lifespan development of cognitive abilities becomes even more complicated due to the fact that intelligent thought and action are governed by two factors, representation (an individual’s accumulated knowledge of the world) and control (an individual's ability to use that knowledge flexibly and adaptively). These systems are dependent on each other and their interaction across the lifespan determines cognitive abilities. Representational knowledge increases strikingly during childhood, continues to accumulate at a reduced pace throughout adulthood, but remains moderately stable in old age. However some information is either lost (especially due to lack of practice) or becomes inaccessible. In comparison, executive control, or basic control processes, develops at different ages, increases in power, speed and complexity from infancy to young adulthood, and declines differentially (depending on the brain area involved) from then onwards (Craik and Bialystok 2006; Figure 1).

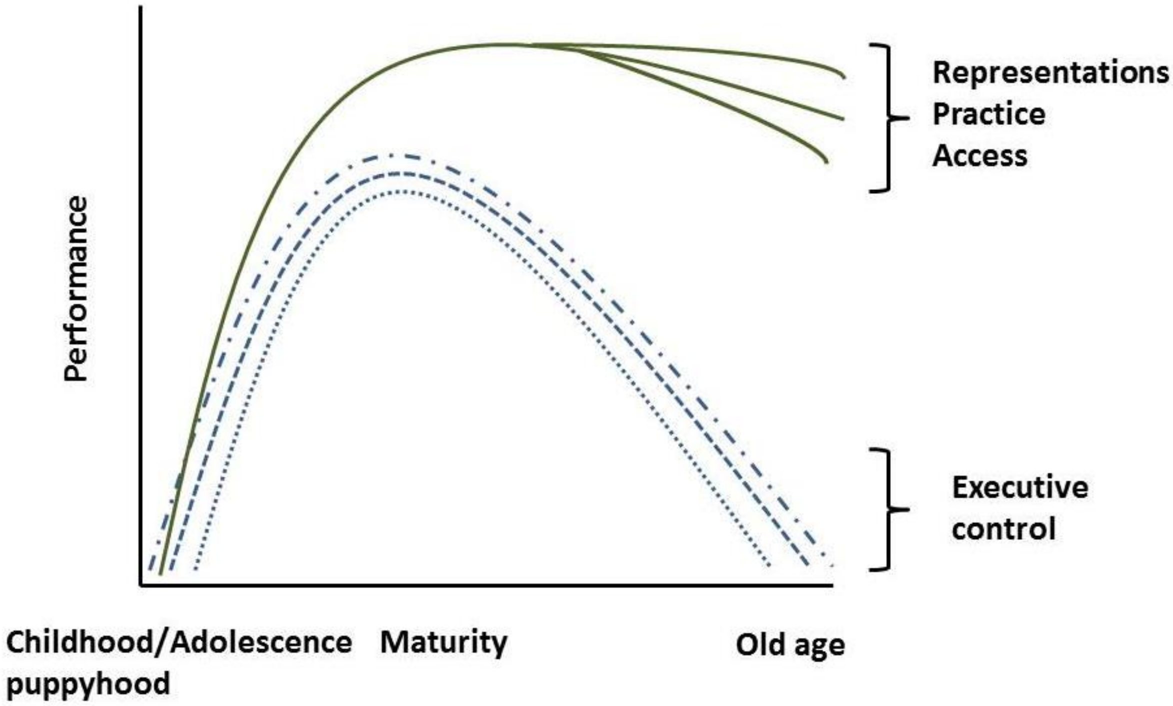

Figure 1: Speculative model of cognitive change across the lifespan (adapted from Craik & Bialystok, 2006).

Both representational knowledge and executive control are central to development; however, they cannot easily be separated at the level of performance, unless they are dissociated through their differential response to experience. The level of executive control displayed by an individual is dependent on the representational system in which the control is normally implemented (Overton, 2010). For example, bilinguals of all ages demonstrate superior executive control than monolinguals matched for age and background (Bialystok, Craik, & Luk, 2012). Therefore, control is greater when the system in question is a highly practiced and "expert" one. Executive control is a set of cognitive skills including attention, inhibition, and working memory, which are limited by an individual's cognitive resources. Executive control allows us to control and coordinate our thoughts and behaviour (Luria 1966). It develops throughout childhood and young adulthood and declines early in aging. An individual's level of executive control can influence cognitive ability and limit cognitive performance in classical tests of cognitive function. Increased abilities in executive control occur in parallel to the maturation of the prefrontal cortex. During late childhood and early adulthood structural and functional re-organisation of the specific brain regions which regulate attention, reward evaluation, affective discrimination, response inhibition and goal directed behaviour are associated with improvements in executive control capacities (Yurgelun-Todd, 2007). In humans, a high level of executive control is essential for academic success, which in turn predicts long-term health and well-being (Hertzman & Wiens, 1996).

There is considerable controversy over the age at which cognitive decline begins in humans. Evidence from cross-sectional studies utilizing tests of cognitive functioning, and a variety of neurobiological variables (such as regional brain volume, myelin integrity, cortical thickness, and accumulation of neurofibrillary tangles), suggests that age-related cognitive declines begin relatively early in adulthood, in the 20s (Fotenos, Snyder, Girton, Morris, & Buckner, 2005; Schroeder & Salthouse, 2004; Sowell et al., 2003). However, when examining the evidence from within-person comparisons, or longitudinal studies, age-related cognitive decline is not detectable until 60 years of age (Aartsen, Smits, van Tilburg, Knipscheer, & Deeg, 2002; Schaie, 2000). Longitudinal studies are influenced by non-maturational factors, such as test-retest effects. This is the difference in performance between the first and the second measurement that can be attributed to the prior experience gained from the previous assessment. Since cross-sectional comparisons do not involve testing the same individual again, test-retest effects are not present. Cross-sectional studies in humans are often criticised due to the fact that they suffer from cohort effects. These are possible influences on cognitive functioning associated with changes in the social and cultural environment (for instance differing quality and quantity of education and medical care). Evidence from studies utilizing non-human laboratory animals argues against the cohort effect interpretation. Since lab animals are kept in near constant environments, cross sectional studies do not suffer from cohort effects, and therefore any age differences in cognitive functioning can be attributed to aging effects. Numerous studies have found age-related declines in memory and cognition in lab animals, for example non-human primates (Herndon, Moss, Rosene, & Killiany, 1997; Lacreuse, Espinosa, & Herndon, 2006; Nagahara, Bernot, & Tuszynski, 2010; Verdier et al., 2015), flies (Fresquet & Médioni, 1993; Le Bourg, 2004), rats (Bizon, Lee, & Gallagher, 2004), and dogs (Adams, 2000; Siwak-Tapp, Head, Muggenburg, Milgram, & Cotman, 2007; Tapp, Siwak, Estrada, Head, et al., 2003).

1.2 The dog as a model for human aging

Animals, like humans, possess a number of mental or cognitive processes that are used during decision making or behavioural regulation, which collectively contribute to an animal's cognitive capacity. To permit the comparison of human and animals, cognitive development in animals can be based on a human model. Although evolution has resulted in animals possessing very different characteristics, many species share the same methods to solve common problems they may be confronted with in their daily lives; for example in the social domain (cooperating with conspecifics in order to hunt large prey) or physical domain (when navigating back to the den site, or to find food). Therefore it can be predicted that there may be a degree of similarity in the cognitive processes of different species (Pearce 2008), and the general patterns of development and decline of cognitive functions, such as those present in representation and control systems mentioned earlier. Closely related species which share a common ancestor may evolve similar cognitive abilities through homology. Additionally, distantly related species may also evolve similar traits through convergence. Similarities in life history traits and environmental conditions may apply similar selection pressures, and result in the development of analogous traits in unrelated species (van Horik & Emery, 2011). Therefore, species which inhabit similar environments may develop similar cognitive abilities, which can enable them to survive in those specific habitats. Cognition is therefore thought to be adaptive and domain specific (Pinker, 2010). Cognitive domains in animals (such as social and physical cognition), similarly to humans, may have relatively independent "domain specific" pathways, and also differing rates of development.

Comparative studies of non-human species mostly ignore the developmental aspect of cognition (e.g. Pack and Herman 2004, Santos and Hauser 2002, Tomasello et al 1999), or take it into account only to the extent of matching subjects' chronological ages across groups. A full understanding of cognitive skills however, requires examining the interplay of phylogenetic and ontogenetic avenues of adaptation, which can be achieved only by combining developmental and evolutionary approaches in comparative developmental studies (Gomez 2005, Parker and McKinney 1999). Therefore, there is a need to examine cognitive development and aging over the whole lifespan of members of a species that grow up in variable environments to gain a better understanding of their capabilities, relate them to their evolutionary significance and enable comparisons across taxonomic groups.

Evidence suggests that dogs are emerging as an alternative model system for human aging, replacing the more traditional flies, worms and mice. The dog is a primary candidate for comparative studies as it shares an evolutionary and developmental history with humans, through a shared living environment. Partly due to the striking physiological similarities between humans and dogs (Waters 2011), the dog has been used to model human social development (Topál et al., 2009), healthspan and longevity, aging and associated diseases such as Alzheimer's disease (Opii et al., 2008), and psychiatric disorders, such as human Obsessive-Compulsive Disorder (OCD) (Rapaport et al 1992) and Attention Deficit Hyperactive Disorder (ADHD) (Lit, Schweitzer, Iosif, & Oberbauer, 2010). Analogies between humans and dogs have also been suggested for social-communicative skills (Hare & Tomasello, 2005) and personality models (Jones & Gosling, 2005). Two factors make the dog especially useful – in dogs it is possible to accurately measure an array of phenotypic domains (such as sensory, cognitive, reproductive, metabolic, and immune function), and secondly, the availability of a wealth of canine medical data amassed by practicing veterinarians around the world.

For example, previous studies have revealed the beagle dog as a useful model for cognitive aging in humans. Measures of learning, memory, and executive control also decline with increasing age in the beagle dog as in humans (Adams et al 2000a, Head et al 1995, Landsberg et al., 2003, Milgram et al 1994, Tapp et al 2003a and b). Aged dogs, like humans, display a wide range of individual variability in cognitive functioning (i.e., different cognitive functions decline at different rates in aged dogs). Gross, Garcia-tapia, Riedesel, Ellinwood, & Jens, (2011) used MRI to examine normal canine brain maturation. Results indicated that canine brain maturation parallels that in humans, albeit at an accelerated rate. However, the authors only examined dogs up to the age of 8 months, and a previous study indicated that brain maturation can gradually increase up to one year (Fox, 1971). To date there has been no study on brain morphology over the lifespan of the domestic dog. Siwak-Tapp, Head, Muggenburg, Milgram, & Cotman, (2007) examined neurogenesis in the hippocampus of five middle aged, and five geriatric laboratory Beagles. The middle aged dogs showed evidence of neurogenesis, but the geriatric dogs showed a 90 – 96% reduction in neurogenesis compared to the middle aged dogs. Siwak-Tapp et al., (2007) additionally correlated inidividual hippocampal neurogenesis with cognitive performance in a black/white discrimination reversal learning task, and spatial memory task. They found that the number of errors comitted in the tasks correlated negatively with neurogensis, such that dogs that performed fewer errors had higher levels of neurogenesis. Indicating that neurogenesis occurs in domestic dogs during middle age, and perhaps throughout life, and neurogenesis is present in the hipcampus after learning and memory tasks, in the same way as has been found in humans (Deng, Aimone, & Gage, 2010; Eriksson et al., 1998).

Development can be divided into several aspects including physical growth, motor development, cognitive development and social-emotional development (Patterson 2008). Just as humans go through stages of development, dogs are also known to go through similar stages including - puppyhood or “juvenile period” (ends between six and 18 months of age), adolescence (starts between six and 18 months of age), adulthood (starts between 12 months and three years of age), the senior years (begin between six and 10 years of age), and geriatric (eight to ten years depending on the breed size – the larger the breed the lower the age of onset) (Siegal 1995). By six months most advanced puppies are similar to adults in size and motor capacities, but continue to develop physically until about two years of age. Sexual maturity varies according to the speed of development of the animal, and is reached between six and 18 months of age depending on the breed (Miklosi 2009). Behavioural maturation in the dog does not occur at this time: although capable of mating, dogs do not display fully adult behaviour until around two to three years of age. Cognitive dysfunction syndrome (CDS) is a major disease affecting mainly geriatric pets, and is equivalent to dementia in humans (Osella et al., 2007). Cognitive decline may occur as early as 7 years of age in some dogs. Hardly anything is known, however, about the earlier development of cognition in dogs.

Lebeau (1953) used life-stage markers (such as puberty, adulthood, old age, and maximum lifespan) to calculate a series of coefficients by which to multiply dogs’ ages to determine their equivalent age in human years. These calculations were not based on cognitive abilities, but rather focused on physical development. Patronek, Waters, & Glickman, (1997) also developed a method to standardise the chronological age of dogs in terms of physiological time using human year equivalents, but included the influence of breed and body weight. For example – the first eight months of a Collies life roughly equals 13 years in human terms (birth to puberty). At one year the dog is equivalent to a

16-year-old human (a teenager to use human terms). After the age of two, when a dog is around 23, every dog year equals approximately 5 human ones. In summary, the relationship between human age and dog age and development cannot be described accurately with a simple linear relationship, as development is not constant over a dog's life span. A polynomial relationship allows for the human year equivalents for dogs' ages to be larger during growth and smaller during maturity (Patronek et al 1997). Selective breeding of dogs has changed the duration of developmental and socialization periods, the sequence of how behaviours emerge, and the level of interaction between breed and environment (Miklosi 2009), for example breed sensitivity to interaction with humans (Freedman 1958). Breed differences in cognitive development are likely to be present; therefore studies using only one breed of dog are necessary to obtain a complete and accurate picture of lifespan cognition in dogs. There is an urgent need for research to examine the changes in development at each life stage in the dog, and document any distinct differences in cognition, personality, socioemotional, and behavioural levels, and whether there is a link between each type of development, and physical growth, which can also vary greatly between breeds.

1.3 The welfare of dogs living with human companions

Aged dogs which display normal aging show considerable deterioration in activity and play levels, response to commands, and an increase in fears and phobias over a six month period (Salvin, McGreevy, Sachdev, & Valenzuela, 2011). Therefore, cognitive changes caused by normal aging can affect quality of life, trainability, learning and problem solving abilities, and the human - animal relationship, through a decrease in the ability of the dog to communicate and interact with its owner. Dogs' welfare and quality of life can be improved by identifying behavioural changes which are a result of normal aging, and which might suggest a clinical pathology. This knowledge may help to provide guidelines for owners, trainers, and veterinarians to flag potential problems and instigate interventions to prevent further cognitive decline (Salvin et al., 2011).

There is considerable variation in behaviour, longevity, physiology and disease in domestic dogs, depending on breed, type and body size (Creevy, Austad, Hoffman, O'Neill, & Promislow, 2016; Fleming, Creevy, & Promislow, 2011; O'Neill, Church, McGreevy, Thomson, & Brodbelt, 2013). Salvin, McGreevy, Sachdev, & Valenzuela 's, (2012) research on the effect of breed on normally aging older pet dogs suggested that there is also considerable variation in the cognitive aging process, particularly between breeds of different sizes. However, no significant differences in the prevalence of cognitive dysfunction between breeds of different size or longevity group has been found (Salvin, McGreevy, Sachdev, & Valenzuela, 2010).

Increasingly, the physical, mental and natural aspects of animal welfare are taken into account when assessing and attempting to enhance the quality of life of animals in captivity. The state of the animal's body and mind, and the extent to which its nature (expressed in breed and temperament) is satisfied can be measured in animal welfare science using various measures such as behaviour, longevity, physiology, and disease (Hewson, 2003). In order to understand the changing needs of non-human animal species over their lifespan, the primary tool utilised by researchers is the observation of animal behaviour. Behaviour is readily visible and measurable through non-invasive means. Behavioural changes are the first biological response to changes in internal and external environments. Both proximate (functional) and ultimate (evolutionary) causes of a behaviour need to be taken into consideration during interpretation. Individual behaviour can be a result of genetic predispositions, can be influenced by experience through learning and memory, and finally can be modified by context, such as emotional state and the surrounding physical and social environment. By measuring behavioural changes in response to challenges in the environment, and taking into account age differences, training history, breed, body condition, and medical history, we can begin to tease apart the influences of genetics and environment on cognition in dogs.

In order to address the practical issues of the welfare of dogs living in human families, and the impact of aging on the human dog bond, the main domains which were examined in this study included general cognition (dogs learning, trainability, memory, and individual problem solving and reasoning skills), and social cognition (interspecific communication). Additionally, since the basic control process of attention is pivotal to cognition (and therefore changes in attention over the lifespan are likely to influence the development and aging of general cognition), the developmental trajectories associated with the separate components of attention were scrutinized. The role of the basic control processes of motivation, perseveration, flexibility and inhibition and their possible influence on cognition is discussed (a subject of which currently there is little reference in the scientific literature in dogs).

To achieve these goals, the first step was to develop tests to detect and analyse age related cognitive changes. Dogs participated in a behavioural test battery and some were also trained to use a touchscreen paradigm in order to examine the development and aging of general and social cognition as well as attention. These methods were designed to provide accurate measures of normal canine cognitive development and aging, which can in the future be used to develop a predictive model to assist with treatments for typical family dogs to enhance cognitive development, delay cognitive decline or diagnose and treat cognitive related problems.

1.4 General Experimental Design

Seven age groups were recruited from six months to old ages (> 10 years). To control for any breed differences, only Border collies were tested. The Border collie is a breed that is currently popular as a pet in Austria, and as such is the best represented in the Clever Dog Lab database. Each age group was counterbalanced for sex, and details about the individual's training history, health and reproductive status were assessed using questionnaires.

The dogs participated in a test battery (the Vienna Canine Cognitive Battery (VCCB)) that was designed to investigate the development and aging of various cognitive functions in the pet dog including general cognition (dogs learning, memory, and individual problem solving and reasoning skills; section 1.6.1), social cognition (section 1.6.2), basic control processes (e.g. attention and motivation – see section 1.6.3), and sensorimotor control (section 1.6.4). Each test was designed to focus on different cognitive domains. Tests which might have been perceptually similar to the dog were separated within the battery so not to cause confusion. Please refer to Table 1 for more details on each specific task in the cognitive battery.

In addition to the VCCB some dogs were also tested in abstract learning tasks on a touchscreen using a computer-controlled two-choice procedure developed to enable comparative testing across species, and examine individual learning abilities without any human interference (utilising the Vienna Comparative Cognition Technology (VCCT)). The great advantage of this method is that the same study tests for three different cognitive functions: learning abilities, strategies (logical reasoning, preference or avoidance of novelty) the dogs use, and memory effects after the dogs were retested six months later.

Test	Sub-test	Description	Variable	Basic control processes				General cognition				Social cognition
				Individual and social features								
				Motivation	Attentiveness	Perseveration/ flexibility	Inhibition	Learning	Trainability	Memory	Problem solving and reasoning	Communication
Touchscreen discrimination	Geometric forms	Two shape discrimination	No. of correction trials			+	+					
			No. of sessions to criterion					+				
	Underwater photos & drawings	Six picture discrimination	No. of correction trials			+	+					
			No. of sessions to criterion					+				
	Clip art pictures	Eight picture discrimination	No. of correction trials			+	+					
			No. of sessions to criterion					+		+		
		Test 1 & 2	No. of times chose by exclusion			+					+	
		Retesting	No. correct choices in session 1							+		
Attention	Event 1:Social	Human painting wall	Latency to orientation, duration of gaze, & average gaze bout		+							
	Event 2:Non-social	Flying object			+							
Spontaneous gaze following, and gaze following after training	Phase 1& Phase 3	Test – control	First look to door within 2 seconds	+			+					+
		Test & control	Frequency of looks to the door		+		+					
			Percentage duration of gaze to experimenter's face		+							+
Clicker training for eye contact with experimenter	Phase 2:Group eye	Selective attention	Clicker training for eye contact: Average first three trials		+		+					+
			Learning over 20 trials (5mins)		+		+		+			
		Sensorimotor control	Latency to find food: Average first three trials	+	+							
			Learning over 20 trials (5mins)	+	+							

Table 1: Detailed breakdown of the tests performed on the touchscreen and in the VCCB with description of variables measured, and related domains and basic control processes related to each variable.

Test	Sub-test/s	Description	Domains and basic control processes measured	Predicted relationship with age
Study 1 Discrimination	Geometric forms, Underwater photos & drawings, Clip art pictures	2, 6 and 8 stimuli discrimination	Flexibility (Perseveration)	Decrease (Increase)
			Learning and working memory	Decrease
	Clip art pictures	Test 1 & 2	Problem solving and reasoning: Inference by exclusion	Quadratic
		Retesting	Long-term memory	No change
Study 3 Attention	Event 1 and 2	Orientation to door and object	Attentional capture	No change
	Event 1: Social	Human painting wall	Sustained attention	Decrease
	Event 2: Non-social	Flying object	Sustained attention	Decrease
Gaze following	Phase 1 and 3	Test – control	Communication	Dependent on hypothesis (see study 2: Table 3)
		Distractibility (frequency of looks to the door)	Attention and inhibition	Quadratic
		Sustained attention experimenter's face	Attention and communication	Quadratic
Study 3 Clicker training for eye contact	Phase 2:Group eye	Selective attention	Attention and communication	Quadratic
		Sensorimotor control	Attention/motivation	Quadratic
		Selective attention over 20 trials	Learning/trainability	Decrease
		Sensorimotor control over 20 trials	Learning/trainability	No change

Table 2: Predicted relationships with age for the different domains and basic control processes measured using the VCCT and the VCCB.

1.5 Objectives

Since pet dogs, (and Border collies in particular) have been selectively bred for human-like skills such as cooperation and communication (Hare & Tomasello, 2005; McConnell & Baylis, 2010), selective pressures have also acted on interspecific communication, which is primarily relevant for the dog human relationship. Therefore, we examined some of the methods dogs use to flexibly adjust to the human environment in which they live, and in some cases work, by utilizing tasks which closely represent challenges in the dogs normal day to day living situation (for example attention towards social and non-social events in the environment, following human given cues, and participating in training exercises). By replacing the beagle model of human cognition, with a pet dog model, we are better able to examine how factors such as training, learning, attentiveness and communication influence how dogs perform in cognitive tests in their natural environment that they share with humans. Our objectives were to examine the different cognitive domains, including general and social cognition, as well as basic control processes of the pet dog, and investigate the degree to which age affects the dogs' cognitive abilities. Specifically I aimed to: -

A. Examine the development of different cognitive functions over the lifespan of pet Border collies from 6 months to old age.
B. Determine when the dogs cognitively mature and when the effect of aging begins.
C. Pin point which cognitive functions change with age and to develop tools to follow these changes, e.g. to detect early signs of cognitive decline.

1.6 Cognitive domains investigated

1.6.1 General cognition

General cognition refers to dogs learning, trainability, memory, and individual problem solving and reasoning skills.

Learning

Learning is a relatively permanent change in a behaviour or a behavioural potentiality, which occurs as a result of reinforcement (experience), cannot be influenced by temporary body states (such as hunger or thirst) (Hergenhahn and Olson 1997), and is controlled by a set of complex ontogenetic processes that allows animals to acquire, store, and subsequently use information about the environment (Galef & Laland, 2005). Motivation is a core component of learning; learning cannot take place without motivation. Knowledge and skill acquisition is dependent on learning, and learning in turn depends on individual differences in other acquired skills, cognitive abilities and development of basic control processes.

Learning ability is often measured in human and animal studies using one specific type of learning called discrimination learning. Discrimination learning proto- cols generally utilise a two-choice procedure, where two stimuli are presented, but only one of them leads to a reward. Since the stimuli are presented simultaneously, parallel processing is necessary. The subject is required to attend to a target stimulus, while ignoring or avoiding 'distractor' information (Julesz & Schumer, 1981). Selection of the target stimulus results in positive reinforcement, which causes an increase in the frequency of the choice of this stimulus (Mell et al., 2005). Deficits in simultaneous processing of stimuli increase with age in humans and animals, due to decreases in processing speed, reduced cognitive resources and an inability to ignore distracting information (Baddeley, Baddeley, Bucks, & Wilcock, 2001; Costello, Madden, Mitroff, & Whiting, 2010; Lavie, 1995; Snigdha et al., 2012).

Discrimination learning and has been extensively studied in laboratory and in some cases pet dogs. For example, spatial learning (Adams et al., 2000; Chan et al., 2002; Christie et al., 2005; Head et al., 1995; Mongillo et al., 2013; Studzinski et al., 2006), visual discrimination learning (including size (Tapp et al., 2003, 2004), landmark (Milgram et al., 2002), contrast (Rivera et al., 2005), object discrimination (Head, Callahan, Muggenburg, Cotman, & Milgram, 1998)), and reversal learning (Christie et al., 2005; Milgram et al., 1994; Tapp et al., 2003), have been found to be age sensitive in the domestic dog. However, procedural and discrimination learning are not consistently affected by age (Adams et al., 2000; Milgram et al., 1994). Increasing task difficulty in discrimination learning tasks produced pronounced age effects in monkeys (Rapp, 1990) and laboratory dogs (Head et al., 1998; Milgram et al., 1994, 2002; Adams et al., 2000).

The dogs' individual learning curves were obtained using the touchscreen procedure and discrimination learning tests (Table 1). Subjects were trained to discriminate between positive (S+) and negative (S-) pictures. Three different discriminations were implemented, and once learning criteria was reached, the next discrimination was executed in order of increasing difficulty. The number of trials to criterion was compared across age groups. A preliminary study (Range et al., pers. comm.) revealed a strong age effect in the initial training - dogs younger than 2 years learned significantly faster than adult dogs. Therefore learning ability was expected to decrease with age (Table 2 and Figure 2).

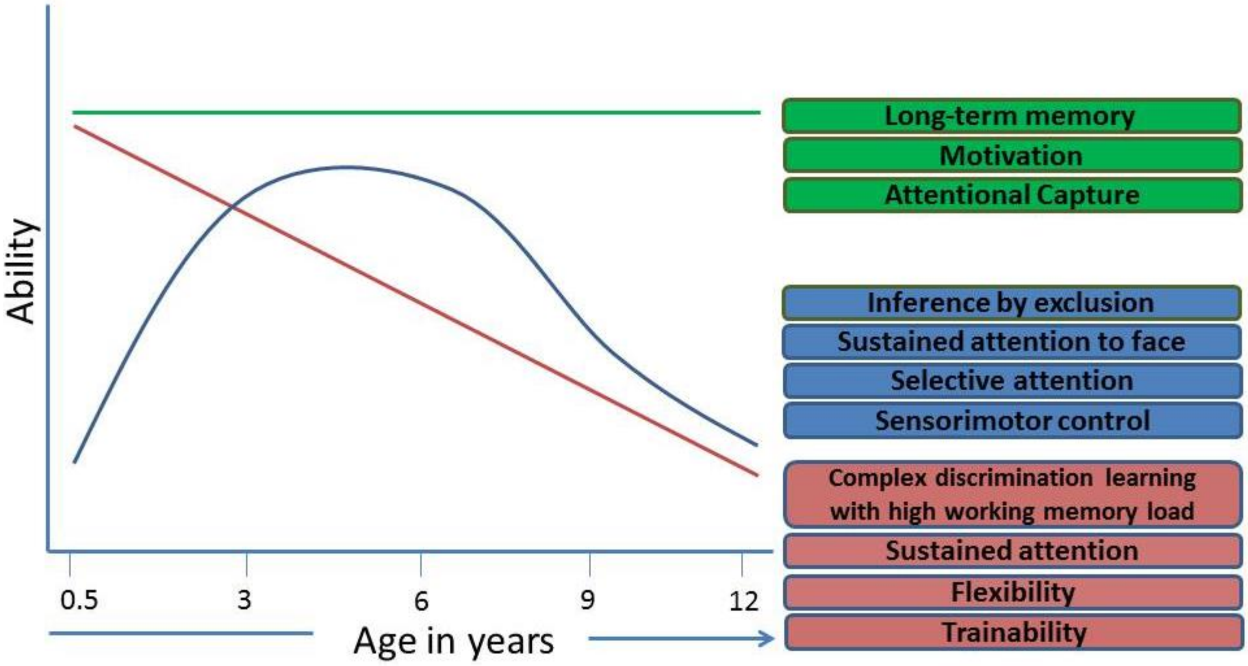

Figure 2: Predicted relationships with age for general cognition (learning, trainability, memory, and inference by exclusion), social cognition (sustained attention to face, and selective attention), and basic control processes (motivation, attention, and flexibility).

Trainability and training experience

The ability to learn and trainability (or training readiness), are related but distinct learning mechanisms (Dierdorff & Surface, 2004). Training is the act of teaching a person or animal a particular skill or type of behaviour. In humans, an individual's level of cognitive ability can predict their trainability (the ability to learn a new task) (Colquitt et al 2000). Historically, dogs' trainability has been equated to their performance in obedience training (Coren, 2006), where the dogs must immediate respond correctly to previously learned commands or directions given by their owner or handler. However, obedience training is just one of many specific types of training in which dogs can participate. An increasing number of training options are available for the modern dog owner. All of which involve learning new tasks/commands/hand signals from the owner/trainer and as such fulfill the criteria of "training".

Additionally, trainability has often been included in the personality assessment of dogs, usually through owner questionnaires (Gosling, Kwan, & John, 2003; Kubinyi, Turscán, & Miklósi, 2009; Turcsán, Kubinyi, & Miklósi, 2011). Available scientific evidence suggests that measures of trainability obtained through owner questionnaires such as the C-Barq are not necessarily correlated with the dogs' actual performance in different training situations, since the questionnaires tend to focus more on response to specific commands used only in obedience training, and or fetching exercises (Miklósi, 2008; Serpell, 2005). Neither do the trainability scores from the questionnaires correlate with the training types the dog participates in (trained dogs vs. untrained dogs; Marshall-Pescini et al., 2008). Therefore, it is necessary to make the distinction between trainability, as measured via questionnaires, trainability in real life situations (measured in test batteries) and training experience over the dogs' lifespan. Taking only one example of training, such as obedience training, can give a misleading indication of trainability, and therefore, also the degree to which training might influence cognitive ability. While obedience is not necessarily correlated with cognitive ability (Fox, 2015), a dogs' level of trainability as measured through training history, has been found to influence cognitive ability (Lindsay 2000), for example in problem solving manipulative tasks (Marshall-Pescini, Valsecchi, Petak, Accorsi, & Previde, 2008; Range et al., 2009), and in a spatial detour task (Marshall-Pescini, Frazzi, & Valsecchi, 2016). Training experience has also been found to strongly affect human-directed communicative abilities (Marshall-Pescini, Passalacqua, Barnard, Valsecchi, & Prato-Previde, 2009).

Trainability in dogs involves a combination of willingness to attend to the trainer (attentiveness/motivation), ability to understand what the trainer wants (general cognitive ability) and ability to remember the tasks being taught (memory). Therefore trainability involves cognitive and non-cognitive aspects. Personality including playfulness, positive and negative affectivity, dominance level, and competitiveness can influence training motivation (e.g. anxiety has been linked to reduced levels of training motivation - Webster, (1993)), and training can affect the general behaviour of the animals (e.g. increases attention to owner/trainer, and improves dogs' problem solving ability – Marshall-Pescini et al (2008)). To date, there have been no studies examining how trainability as measured via behavioural tests changes with age in dogs. However, using owner questionnaires, significant negative correlations between age and the personality trait score for trainability (Kubinyi, Turcsán and Miklósi, 2009), boldness (Kubinyi et al., 2009; Starling, Branson, Thomson & McGreevy, 2013), and sociability (Wahlgren and Lester, 2003) were found.

Extensive training through shaping (successive approximations) when learning a novel response or behaviour pattern (within a dogs behavioural capability) encourages a more proactive and independent approach to learning (Lindsay, 2001, Pryor 1984, Marshall-Pescini et al. 2008, 2016). Clicker training has become a common dog training tool which utilises shaping and uses a conditioned reinforcer as a marker to signal when food is coming. Osthaus, Lea, & Slater, (2003), found that dogs that had been clicker trained were faster in solving a string pulling problem solving task, than non-clicker trained dogs. Therefore clicker training may promote independent problem solving abilities in domestic dogs.

The dog's training level over their lifespan and clicker training status were determined using owner report in an extensive questionnaire completed prior to participation in the cognitive battery. Details of their dog's training experience including 13 different training types: puppy school (83% participated), basic obedience (68%), high level obedience (49%), Protection training (3%), agility (70%), search and rescue training (6%), companion dog training (31%), dog dancing/trick training (54%), dummy training (11%), nosework (27%), sheep dog training (52%), therapy dog (13%) and other (22%). On average, dogs participated in five different training types. Dogs scored according to attendance: no experience = 0, sporadic training = 1, once or twice a month = 2, once or twice a week = 3, and completed training (with or without an exam) = 4. Individual scores in each type of training were added up to a maximum of 52 points. Training score was correlated with age in months (Spearman's rho=0.458, p=<0.001).

Trainability was assessed in the clicker training for eye contact test (measuring latency to eye contact with the experimenter) over 20 trials (Table 1). All age groups were predicted to show learning over the 20 trials, reflected in a decreased latency to eye contact with the experimenter. However, trainability was predicted to decrease with age, as per results from owner questionnaires scoring statement such as "willingness to pay attention to and obey the owner, and the dogs' ability to learn new tasks and to ignore distracting stimuli" (Table 2 and Figure 2).

Memory

Short term memory refers to the capacity for holding small amounts of information in an accessible state over a short period of time, whereas information can remain in long-term memory indefinitely (Cowan, 2008). Short-term memory is just one component of a framework of processes used for the temporary storage and manipulation of information, termed working memory. Working memory tasks involve executive control, which serves to maintain the activation of information relevant to the task, and prevent interference from internal and external events (Engle, Tuholski, Laughlin, & Conway, 1999). Short-term memory and working memory are separate but highly correlated constructs. Working memory shows a strong correlation with cognitive abilities, however, short-term memory does not (Cowan, 2008; Engle et al., 1999; Kyllonen & Christal, 1990). The categories that have been developed to analyze human memory (short term memory, long term memory, and working memory), have been applied to the study of animal memory, and some of the phenomena characteristic of human memory have been detected in animals, including monkeys (McGonigle & Chalmers, 1977), pigeons (von Fersen, Wynne, Delius, & Staddon, 1991), and baboons (Cook & Fagot, 2009). However most progress has been made in the analysis of spatial memory, the part of memory responsible for recording information about the environment and its spatial orientation. Spatial memory has been found to be age-sensitive in the domestic dog (Adams et al 2000; Studzinski et al., 2006). Additionally, some dogs have shown that they are capable of remarkable learning and memory capacities. For instance, “Chaser” a Border collie owned by Professor Pilley, has learned the names of over 1,000 objects, and is highly successful in retrieving each object on command utilizing long-term memory (Pilley & Reid, 2011). This level of word learning is comparable to the vocabulary production of three year old human infants (Fenson et al., 1994).

The dogs’ visual working and long-term memory capabilities were tested using the touchscreen paradigm. Using this method allows the examination of working memory during testing, and for long-term memory, by retesting the dogs 6 months after completing the last test, and investigating to what extent the dogs remember the specific stimuli used in the task (Table 1). Dogs’ working memory ability was expected to decrease in aged animals, but long term memory was expected to remain intact (Table 2 and Figure 2).

Individual problem solving and reasoning abilities

An individual’s reasoning ability can be measured by problem solving tests (such as the human IQ test). ‘Reasoning’ is the power of the mind to think, understand, and form judgments by a process of logic. Inference (in the field of logic) is the act of passing from one proposition, statement, or judgment considered as true to another whose truth is believed to follow from that of the former. Vigo & Allen, (2009) have argued against the popular belief that the process of drawing inferences is language driven and therefore a uniquely human ability. The fundamental processes of similarity assessment, discrimination and categorisation underlie reasoning and associative learning. For example Kaminski, Call, & Fischer, (2004) found that a Border Collie called Rico had the ability to acquire the relation between a word and the object that the word refers to (the referent), and he could also infer the referent of new words by exclusion learning, and retain this knowledge over time. This evidence was later supported by Pilley and Reid's (2011) study on another Border collie called Chaser. Inference by exclusion is defined as the choice of an undefined stimulus (i.e., a stimulus that does not already have a learned association with a category) over a defined one (i.e., a stimulus that is already associated) by excluding (logically rejecting) the latter, which leads to the emergence of an untrained association (see above) between the undefined stimulus and the category (Hurley and Nudds 2006, Premack and Premack 2008). Call's (2006) study showed that Great Apes also have the ability to make inferences by exclusion and results suggested a positive relationship between age and inferential ability.

Dogs' logical reasoning abilities were tested using the touch screen procedure applied by Aust et al. (2008). Subjects were trained to discriminate between 4 positive (S+) and 4 negative (S-) pictures and then presented with the known negative picture in combination with new, unknown pictures (S'). If subjects correctly chose the new pictures, to determine which strategy (inference by exclusion or preference for novelty) they use, they then undertook a further test. Here the displays consisted of one of the (S')-stimuli and one of four novel stimuli (S"). If choosing by novelty, the subject would choose the (S") whereas if reasoning by exclusion the preference for (S') would be maintained (for details please refer to Figure 3 below). Dogs problem solving and reasoning skills were predicted to show a quadratic relationship with age (see Table 2 and Figure 2).

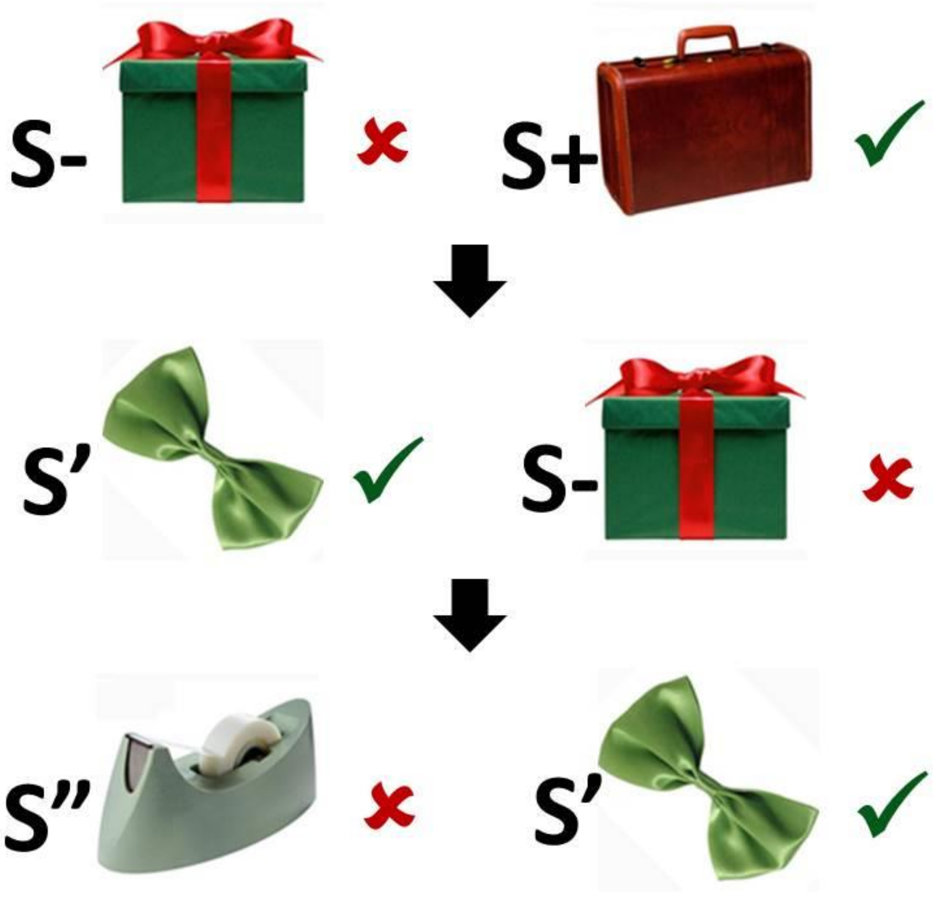

Figure 3: Example of abstract pictures presented to dogs on the touchscreen and the correct positive and negative associations. The first set of pictures show two of the eight original stimuli (one positive (S+) and one negative (S-)), which the dogs learnt. The second and third sets display an example of the inference by exclusion test stimuli. Dogs were presented the images without text (i.e. S-,S+,S'and S").

1.6.2 Social Cognition

Social cognition refers to skills and abilities helping the animals to deal with their conspecifics, and in the case of domestic animals, their human companions. Animals living in highly social environments may have evolved sophisticated general problem solving capacities due to the challenges of group living (Byrne & Whiten 1988, Bond et al. 2003, Emery et al. 2007). Research on social cognition in dogs has focused on emotional recognition, recognition and categorization of conspecifics and humans, the development of attachment and affiliation bonds, social learning, and inter- and intra-specific communication (Prato-Previde & Marshall-Pescini, 2014). The development of social cognition, in particular inter-specific communication, is of significant importance to the human dog relationship.

Dogs possess a factor of key importance for all social interactions; the ability to pay attention to other individuals. The capacity of dogs to form joint attention with humans is a critical precursor to the development of theory of mind (Baron-Cohen, 1991). As a consequence of living in close proximity to humans, and the acceptance of dogs as social companions, dogs have learned to remain predominantly in the visual field of the human, so the direction or object which is the focus of attention for the human, also may become significant for the dog (Miklósi, Topál, & Csányi, 2007). This might have had adaptive significance for dogs that have benefitted from an innate ability to cooperate with humans, which has been enhanced by selective breeding during domestication, and can be modified by training (Naderi, Miklósi, Dóka, & Csányi, 2002).

The dogs' special domestication history, which includes adaptive specialisation, and developmental socialisation within the human environment, may lead to more flexible and "human-like" skills, than features of species which are phylogenetically more closely related to humans (e.g. apes and monkeys) (Topál et al., 2009). For example dogs are more skilled at using human communicative gestures (e.g. pointing and gaze following) to find hidden food, than chimpanzees (Hare, Brown, Williamson, & Tomasello, 2002; Miklósi, Polgárdi, Topál, & Csányi, 1998). The key to the dog's success as a domesticated animal living in human households is the degree to which they are able to form bonds with humans. Evidence suggests that dogs are capable of forming attachment relationships with their owner/s (Palmer & Custance, 2008; Topál, Miklósi, Csányi, & Dóka, 1998), similarly to the way human infants are bonded to their mothers (Ainsworth, 1969). In contrast, socialized wolf puppies also regarded their human handlers as attachment figures up to the age of 7 weeks (Hall et al., 2015), but showed no attachment at 16 weeks of age (Topál et al., 2005). The bond between dog and owner ensures that dogs regard certain humans as sources of protection and help, as well as potentially important information. Through synchronized collaborative activities with their owners, dogs can develop a complex system of interspecific communication (Miklósi & Topál, 2013). This system is mediated by humans' tendency to initialize and maintain communication through the use of ostensive cues, such as direct gaze, addressing the animal by name, and motherese (the use of simple repetitive exaggerated speech, often at a higher pitch than normal). Differences in dogs' relationships to humans, and in the use of ostensive cues by owners, may influence the dogs' learning and training capabilities, through persistency and attention parameters (Range 2009a).

Eye contact is the most important of ostensive cues, and is a crucial feature of social life and communication, that plays a central role in social cognition. However, most canids view direct and sustained eye gaze from a conspecific as a threat (Fox, 1972; Schenkel, 1967). They can learn to tolerate and even seek out eye contact through the use of training (Barrera, Mustaca, & Bentosela, 2011; Bentosela, Barrera, Jakovcevic, Elgier, & Mustaca, 2008; Marshall-Pescini et al., 2009), and when exposed to different living conditions and life experiences (Aniello & Scandurra, 2016; Barrera et al., 2011). Additionally, human directed gazing behaviour may be related to personality traits in dogs (Jakovcevic, Mustaca, & Bentosela, 2012), with more social dogs utilizing gaze to obtain out of reach food in comparison to less social dogs. Finally, several studies have demonstrated breed differences (Jakovcevic, Elgier, Mustaca, & Bentosela, 2010; Passalacqua et al., 2011), and age differences (Passalacqua et al., 2011; Udell & Wynne, 2009) in gazing behaviour. There is some evidence that dogs' ability to utilise eye gaze in humans and to use attention getting signals increases with age in dogs, however further research is necessary (for a review see Udell, & Wynne, 2009).

According to Emery, Lorincz, Perrett, Oram, & Baker, (1997), gaze following and joint attention are different yet intimately related abilities with differing developmental trajectories. Gaze following may be a precursor to joint attention and the ability to infer the mental significance of another's gaze (Baron-Cohen 1994; Perrett & Emery 1994; Povinelli & Eddy 1996). The ability to attend to the same target as another individual provides the foundation for more complex social skills, such as a theory of mind (Gómez, 2009). Three different contexts have been identified where human and non-humans animals may follow the gaze of conspecifics or indeed heterospecifics: 1) gaze following to distant space, 2) around barriers, and 3) to specific a target stimulus/object. Many animal species share these basic gaze following behaviours which suggests that non-human animals also possess the foundations of human social cognition, which could pave the way to the possibility of a theory of mind (Shepherd, 2010).

An early developing automatic component of gaze following explains the basic gaze following response to distant space, but a later developing more controlled component, is needed to take into account the referential information of the gaze. Agnetta, Hare, and Tomasello (2000) found no indication that dogs follow human gaze into distant space, which is considered the most basic of the three different gaze following contexts. Even when dogs' performance in following gaze to a specific object is considered, evidence is mixed. For example, Kaminski, Schulz, & Tomasello, (2012) examined how dogs know when human communication is intended for them, utilizing a pointing and gazing cue in an object choice task. When the experimenter gave an intentional gaze cue (the experimenter established eye contact with the dog and then gaze alternated between the dog and correct location), there was only a trend for dogs to select the correct cup above chance levels. However, when additional ostensive cues were added (calling the dog by name, or the use of another name), the dog performed above chance level. Interestingly, puppies (<11 weeks of age) were not able to follow the gaze cue of the experimenter, indicating that additional experience is necessary for dogs to display this behaviour.

Aging can have additional effects on social cognition in dogs. As dogs age, they may suffer from impairments in their ability to interact socially with others. For example there may be a decrease in greeting behaviour to owners, a decline in soliciting attention or an increase or decrease in following owners around the house. Dogs' relationships with other animals in the household may also change (Landsberg et al 2003). Genetic changes which occurred during domestication and artificial selection, and ontogenetic and environmental factors combine to jointly influence interspecific gazing and effective communication in dogs.

Dogs' interspecific communication abilities were measured using the clicker training for eye contact test (latency to eye contact with experimenter average of first three trials: a measure of selective attention), and the gaze following test (duration of gaze to the experimenters face during distraction) (Table 1). Both measures were predicted to show a quadratic relationship with age (Table 2 and Figure 2).

Dogs' interspecific communication abilities were also measured during the gaze following study. The propensity to follow human gaze may be affected by lifelong learning, long-term habituation to directional gaze cues and/or training to focus their attention on humans. As such, three different hypotheses are proposed to explain possible age and training effects on following human gaze in dogs.

Long-term habituation hypothesis: dogs may lose their reflexive responding to human gaze cues through long-term habituation over an individual's lifetime living with human companions.

Formal training hypothesis: formal training may increase the dog's frequency and duration of fixations to the owner (while waiting for the next cue typical for the given training context), which may then interfere with the dog's response when humans present directional gaze cues that are not part of the formal training.

Lifelong learning hypothesis: dogs are repeatedly asked to look at humans in many different situations over their lives; therefore they have the opportunity to learn about gaze cues and to generalise them to different contexts, and may need more flexibility in detecting the relevant communicative cues of their human partners.

1.6.3 Basic Control Processes

The term "basic control processes" has been attributed to neuronal mechanisms of animals that are not cognitive in its pure sense, but can strongly influence their behaviour and cognitive performance; for example – motivation, attentiveness, perseveration, inhibition and flexibility.

Motivation

Motivation is the activation of goal-oriented behaviour (Dickinson & Balleine, 1994). Motivation facilitates learning and according to the information processing view, involves anticipation and attention – and reduces uncertainty about psychologically significant events through information seeking behaviour (Anselme, 2010). Motivation increases the availability of cognitive resources in problem solving situations. Therefore a lack of motivation can constrain cognitive performance (so an animal's performance may not necessarily reflect the animal's cognitive capacity). Boutet et al., (2005) found that motivation influenced the performance of younger adult dogs in a cognitive task. Motivation was generally higher in older adults than in younger adults.

Motivation was assessed in the clicker training for eye contact test (measuring latency to find dropped food on the floor) over 20 trials (Table 1). Motivation was expected to remain stable with age, as has been found in previous studies in laboratory beagles (Milgram, Head, Weiner, & Thomas, 1994) (Table 2 and Figure 2). Factors which may have influenced dogs' goal orientated behaviour within the discrimination learning, gaze following, and clicker training for eye contact are discussed.

Attentiveness

Attention is dependent on sex, age, and focus of attention as well as on several aspects of the social structure and life history of a species. The focus of attention as well as attention parameters in themselves (for example percentage observation time, and frequency and duration of looks), may vary considerably among individuals and even species (Range et al 2009). Cognitive development in children includes improvements in selective attention (McAvinue et al., 2012), the ability to focus on pertinent information and not to succumb to mental or physical distractions in the environment (Harnishfeger, 1995).

Attentiveness was measured using the attention test and the clicker training for eye contact test within the VCCB (Table 1). Dogs' attentional capture was measured by their latency to orientation; their sustained attention by their duration of gaze to a human and flying object; and finally selective attention, by the average latency to eye contact with the experimenter. Attentional capture was predicted to show no changes with age, sustained attention was predicted to decrease with age, and selective attention would show a quadratic distribution when correlated with age (Table 2 and Figure 2).

Perseveration, inhibition and flexibility

Perseveration is the repetition of a particular response, such as a word, or action, despite the absence or cessation of a stimulus (without learning from repeated negative experience). Several researchers have tried to connect perseveration in human children with a lack of inhibition; however, this connection could not be found, or was weak (Sharon & DeLoache, 2003; Zelazo et al., 2003). Age-related impairments include an increase in perseverative responding. Raz et al. (1998) reported increased perseverative responding and concept abstraction failures in healthy aged adults. Older animals also tend to perseverate on old task sets (Bartus, Dean, & Fleming, 1979; Tapp, Siwak, Estrada, Head, et al., 2003; Voytko, 1999). Increased perseveration in aged human adults has been linked to an inability to suppress a no longer relevant task set due to deficiencies in inhibition (Ridderinkhof, Span, & van der Molen, 2002).

Cognitive inhibition is a mental ability that enables individuals to suppress task-irrelevant information once it has been activated in working memory (Harnishfeger, 1995). Research on brain development suggests that cognitive inhibition is biologically related to the frontal lobes of the brain. This portion of the brain is responsible for executing various cognitive processes, such as planning and concentrating on tasks. Neuropsychological research in humans has determined that the frontal lobes are one of the last areas of the brain to develop, requiring anywhere between 13 to 18 years to fully mature (Harnishfeger & Bjorklund, 1994). Tapp et al (2003) measured inhibitory control in young, middle aged, old and senior Beagle dogs in a size discrimination and reversal learning task. Senior dogs were found to be impaired in their ability to inhibit perseverative behaviours.

Cognitive flexibility is defined as the ability to shift between problem-solving strategies. Reductions in cognitive flexibility occur with advanced age in humans (Botwinick, 1978; Daigneault, Braun, & Whitaker, 1992), rats (Stephens, Weidmann, Quartermain, & Sarter, 1985), and primates (Lai, Moss, Killiany, Rosene, & Herndon, 1995; Voytko, 1993, 1999). Cognitive flexibility is generally thought to depend on the integrity of the prefrontal cortex (Daigneault et al., 1992; Dias et al 1996). Chan et al (2002) interpret the persistent use of inefficient strategies by aged dogs as evidence of an age-dependent decline in cognitive flexibility using a delayed non-matching-to-position task to compare visuospatial learning and memory in young and aged beagle dogs.

Perseveration, inhibition and behavioural flexibility were measured using the touchscreen procedure, specifically the number of correction trials the dogs required (perseveration/inhibition) and the degree to which the dogs are able to apply previously learned rules to new paradigms (flexibility). Behavioural flexibility was predicted to decrease with age, and should correspond to an increase in perseverative responding in aged subjects (Figure 2). Additionally, dogs' ability to inhibit distractions during gaze following and clicker training for eye contact tasks will be discussed (see Table 1 and 2).

1.6.4 Sensorimotor control

One other important component of development which could affect cognitive abilities in dogs is age-related changes in sensory and motor processes. In a cross-sectional lifespan study, Clark et al., (2006) found that two measures of sensorimotor abilities of humans followed quadratic age trends, with performance peaking at the 20–39 years middle age range. Previous studies examining sensorimotor control in non-human animals, have found a significant decline with age, as in human studies. In their study of normative behavioural changes associated with "successful aging" in dogs, Salvin et al., (2011) found that difficulty in finding food increased significantly with age. This could reflect alterations in the cognitive processing of sensory information, or could be a result of physical deterioration of the visual, audio, or olfactory organs.

Therefore it is necessary to exclude physical degeneration as the cause of apparent changes in cognition.

To be included in the current study, dogs were required to meet specific criteria. Owners filled in information about their dogs' recent medical care, disease history, and whether their dogs were currently on any medication. Dogs which were not medically fit [including dogs which suffered from eye abnormalities or second stage (visible) cataracts] were excluded, or testing was postponed until they were in normal health. Owners of dogs older than 6 years also filled in a CCD questionnaire [translated into German, based on Salvin et al. (2011)]. None of the dogs showed significant behavioural signs of CCD (according to the CCD rating scale; all scored under 50 points). Only three dogs had to be excluded: one because of video recording malfunction, and two because of medical problems.

Dog's sensorimotor abilities were assessed during the clicker training for eye contact test, using the latency to find dropped food (Table 1). Sensorimotor ability was predicted to show a quadratic relationship with age (Table 2 and Figure 2).

1.7 Research questions – Chapter outline

This thesis explores cognitive development and aging in pet dogs at the level of both behaviour and cognition. The first study examines general cognition using a touchscreen paradigm, the second study investigates one aspect of social communication - gaze following, and the third study looks at the basic process of attentiveness over the lifespan of pet dogs. Chapters 2 – 4 represent original studies, which have been published in peer-reviewed scientific journals. The results are discussed and conclusions are drawn in Chapter 5.

Chapter 2: Aging effects on discrimination learning, logical reasoning and memory (Study 1, accepted for publication in AGE)

The majority of research on general cognition (learning and memory), has been conducted on laboratory animals such as Beagles, which are considered to be a good animal model for human aging and Alzheimer's disease, since they develop similar age related neuropathologies as humans, as well as a similar decline in their measures of learning, short-term memory, and executive control with age (Adams et al., 2000; Head et al., 1995; Head, Cotman, & Milgram, 2000; Landsberg, Hunthausen, & Ackerman, 2013; Milgram, Head, Weiner, & Thomas, 1994; Tapp, Siwak, Estrada, Holowachuk, et al., 2003b; Tapp, Siwak, Estrada, Head, et al., 2003a; Wallis et al., 2014). Much less is known about cognitive aging in pet dogs living in human families. The use of the touchscreen apparatus allows the design and implementation of non-verbal standardized tasks which can be utilised to examine cognitive functioning in non-human animals (Spinelli et al., 2004; Steurer, Aust, & Huber, 2012). Previous studies in laboratory dogs, have shown that dogs' learning ability decreases with age and perseverative responding increases (Milgram et al., 2002; Snigdha et al., 2012; Tapp, Siwak, Estrada, Head, et al., 2003a). Long-term memory remains stable with age (Araujo, Studzinski, & Milgram, 2005), and studies have shown that some dogs are able to make inferences by exclusion (Aust, Range, Steurer, & Huber, 2008; Kaminski, 2004; Pilley & Reid, 2011). Study 1 reports on a cross-sectional sample of pet Border collies aged from five months to thirteen years. The dogs were given tasks on the touchscreen that were designed to test the effect of aging on three cognitive abilities: visual discrimination learning, logical reasoning, and memory, to determine when dogs cognitively mature and when cognitive decline begins. The results are discussed in reference to previous studies in laboratory and pet dogs, and explanations for the diverging results from the study’s predictions are offered.

Chapter 3: Training for eye contact modulates gaze following (Study 2, published in Animal Behaviour)

In humans, a crucial feature of social life and communication is eye gaze, which plays a central role in social cognition. Gaze following, the ability to monitor and match another's head and eye orientation by following gaze direction into distant space, has been extensively studied in human infants. Although several studies have highlighted the importance of investigating age differences in social cognition, especially in elderly humans, for whom reduced social communication and interaction skills have been found in comparison to middle-aged subjects (Henry, von Hippel, & Baynes, 2009; Slessor, Laird, Phillips, Bull, & Filippou, 2010), there are few lifespan studies of gaze following. Despite their similarities to human infants, and extensive skills in reading human cues in foraging contexts, no evidence that dogs follow gaze into distant space has been found. Study 2 explores the question whether dogs are capable of following human gaze into distant space and, if so, to investigate through age effects whether the propensity to follow gaze is affected by long-term habituation to directional gaze cues and/or training to focus their attention on humans.

Chapter 4: Lifespan development of attentiveness in domestic dogs: drawing parallels with humans (Study 3, published in Frontiers in Psychology)

One of the most intensely studied cognitive processes in humans and animals is attention: the ability to selectively process one aspect of the environment over others. Attention is pivotal to consciousness, perception, cognition, and working memory in all mammals, and therefore changes in attention over the lifespan are likely to influence development and aging of all of these functions (Washburn and Taglialatela, 2006). Non-human mammals have the same general patterns of development and decline of cognitive functions as humans (Pearce, 2008) and can provide good models for the development and aging of specific cognitive domains. Study 3 utilised attention tests, to examine the effects of development and aging, by adapting simplified versions of tests from the human literature, and investigating the normal rate of attention development and decline in a cross-sectional sample of pet dogs ranging in age from 6 months to old age. The resulting basic developmental trajectories of the different sub-processes of attention and sensorimotor control were compared to those of humans using results from previous studies.

Chapter 5: General Discussion

The main findings and implications of the thesis are discussed.

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2. Aging effects on discrimination learning, logical reasoning and memory in pet dogs

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Abstract

In laboratory dogs, aging leads to a decline in various cognitive domains such as learning, memory and behavioural flexibility. However, much less is known about aging in pet dogs, i.e. dogs that are exposed to different home environments by their caregivers. We used tasks on a touch-screen apparatus to detect differences in various cognitive functions across pet Border collies aged from five months to thirteen years. Ninety-five dogs were divided into five age groups, and tested in four tasks: 1) underwater photos vs. drawings discrimination, 2) clip art picture discrimination, 3) inferential reasoning by exclusion and 4) a memory test with a retention interval of six months. The tasks were designed to test three cognitive abilities: visual discrimination learning, logical reasoning, and memory. The total number of sessions to reach criterion and the number of correction trials needed in the two discrimination tasks were compared across age groups. The results showed that both measures increased linearly with age, with dogs aged over three years displaying slower learning and reduced flexibility in comparison to younger dogs. Inferential reasoning ability increased with age, but less than 10% of dogs showed patterns of choice consistent with inference by exclusion. No age effect was found in the long-term memory test. In conclusion, the discrimination learning tests used are suitable to detect cognitive aging in pet dogs, which can serve as a basis for comparison to help diagnose cognition-related problems and as a tool to assist with the development of treatments to delay cognitive decline.

Introduction

The development and aging of cognitive processes such as learning, memory and logical reasoning, and their interactions with genetic, environmental and social factors have so far almost exclusively been studied in humans (Baltes, 1987; Craik & Bialystok, 2006). Learning and memory are basic processes, which are essential for the acquisition of knowledge, and furthermore allow an individual to apply knowledge in novel situations through logical reasoning. These basic cognitive abilities are known to change over the lifespan, increasing rapidly from infancy to young adulthood and then, depending on the specific ability, are either improved (as is the case for knowledge formation), maintained or decline in old age (Baltes, 1987; Pearce, 2008).

Cognitive processes are regulated by executive functions comprising selective attention, working memory, flexibility and inhibition, some of which have also been found to be particularly sensitive to aging (Cepeda, Kramer, & Gonzalez de Sather, 2001; Clark et al., 2006; Manrique & Call, 2015; Rapp, 1990; Tapp, Siwak, Estrada, Holowachuk, & Milgram, 2003b; Tapp, Siwak, Estrada, Head, et al., 2003a; Wallis et al., 2014). There are remarkably few studies in humans or animals which detail the changes in these specific cognitive processes and their regulation by executive processes over the course of the entire lifespan, as cognitive development and aging are frequently disassociated. Previous studies in humans using cognitive batteries showed that learning and logical reasoning increase rapidly from infancy to young adulthood and then decline steadily (Craik & Bialystok, 2006; Moshman, 2004), and that long-term memory increases into the fifth and sixth decade of life, and only shows very gradual decline thereafter (Brickman & Stern, 2010).

Learning ability is often measured in human and animal studies using one specific type of learning called discrimination learning. Discrimination learning protocols generally utilise a two choice procedure, where two stimuli are presented, but only one of them leads to a reward. Since the stimuli are presented simultaneously, parallel processing is necessary. The subject is required to attend to a target stimulus, while ignoring or avoiding "distractor" information (Julesz & Schumer, 1981). Selection of the target stimulus results in positive reinforcement, which causes an increase in the frequency of the choice of this stimulus (Mell et al., 2005). Deficits in simultaneous processing of stimuli increase with age in humans and animals, due to decreases in processing speed, reduced cognitive resources, and an inability to ignore distracting information (Baddeley, Baddeley, Bucks, & Wilcock, 2001; Costello, Madden, Mitroff, & Whiting, 2010; Lavie, 1995; Snigdha et al., 2012). Age-related impairments in learning are shown by an increase in the number of trials necessary to reach a learning criterion, and an increase in perseverative responding, which is defined as the repetition of a particular response, such as selection of a particular stimulus, due to an inability to adapt to external feedback of right and wrong. Perseverative responding may be a sign of reduced cognitive flexibility, which is the ability to adjust thinking or attention in response to changing goals and/or environmental stimuli (Scott, 1962).

Another form of learning is learning by exclusion, a type of logical reasoning defined as the selection of the correct alternative by logically excluding other potential alternatives (Call, 2006). Human children are known to learn by exclusion, which develops from the age of two years (Heibeck & Markman, 1987; Horst & Samuelson, 2008; Spiegel & Halberda, 2011). Since children as young as two years old are able to make simple inferences by exclusion, this ability likely depends on simple associative learning mechanisms, and therefore can also be found in animals, based on previous positive findings (Aust, Range, Steurer, & Huber, 2008; Call, 2006; Herman, Richards, & Wolz, 1984; Kaminski, 2004; Kastak & Schusterman, 2002; Pilley & Reid, 2011). For example, Aust et al. (2008) found evidence of reasoning by exclusion in pet dogs using a touchscreen procedure. Additionally, Kaminski, Call, & Fischer, (2004) found that a Border Collie had the ability to acquire the relation between a word and the object that the word refers to (the referent), and it could also infer the referent of new words by exclusion learning, and retain this knowledge over time. However dogs' preference for novelty could also explain Kaminski et al.'s results (see Kaulfuss & Mills, (2008)). Pilley & Reid's (2011) study on another Border Collie ruled out any influence of novelty preference, by including baseline novelty preference measurements (but see Griebel & Oller, (2012) for an alternative conclusion on the dogs' performance).

Currently there are no studies in non-human animals detailing how the ability to reason by exclusion changes with age over the lifespan. Studies in humans, however, have demonstrated that logical reasoning ability is closely related to an individual's working memory capacity, which is limited in complex tasks (Kyllonen & Christal, 1990; Süß, Oberauer, Wittmann, Wilhelm, & Schulze, 2002). Working memory capacity can severely limit reasoning abilities particularly in tasks where time limits are implemented (Chuderski, 2013). Moreover, in order to reach learning criterions in complex discriminations and learning by exclusion tasks, long-term memory is required to store information such as positive and negative stimulus associations in discrimination learning or the correct labelling of a new word or object in exclusion tasks. While working memory and logical reasoning ability decline with old age (Borella, Carretti, & De Beni, 2008; Brockmole & Logie, 2013; De Luca et al., 2003; Lee et al., 2005; Sander, Lindenberger, & Werkle-Bergner, 2012), long-term memory shows very little decline when comparing younger and older adults (Brickman & Stern, 2010).

Learning and memory have been extensively studied in laboratory dogs which are considered to be a good animal model for human aging and Alzheimer's disease, since they develop similar age related neuropathologies as humans, as well as a similar decline in their measures of sensorimotor ability, selective attention, learning, short-term memory, and executive function with age (Adams et al., 2000; Head et al., 1995; Head, Cotman, & Milgram, 2000; Landsberg, Hunthausen, & Ackerman, 2013; Milgram, Head, Weiner, & Thomas, 1994; Tapp, Siwak, Estrada, Holowachuk, et al., 2003b; Tapp, Siwak, Estrada, Head, et al., 2003a; Wallis et al., 2014). For example, like humans, dogs' selective visual attention and discrimination learning is sensitive to aging in some tasks (Milgram et al., 2002; Snigdha et al., 2012), whereas in other tasks discrimination learning was not affected by age (egocentric spatial discrimination, Christie et al., 2005; object discrimination learning, Milgram et al., 1994). This inconsistency in laboratory dogs is likely explained by the level of difficulty of the task which influences whether an age effect is detected or not (Adams et al., 2000; Head, Callahan, Muggenburg, Cotman, & Milgram, 1998; Milgram et al., 1994). Previous research has also shown that older dogs tend to show perseverative responding in complex discrimination learning tasks similarly to humans (Grant & Berg, 1948; Mell et al., 2005; Tapp, Siwak, Estrada, Holowachuk, et al., 2003b).

Few studies have addressed how long dogs are able to remember previously learnt discriminations, a measure of long-term memory. Araujo, Studzinski, & Milgram, (2005) tested laboratory beagles in a working memory task and found a significant decline with age. In contrast, their performance remained stable after a two-year break period in previously learned discriminations. Therefore working memory capacity in dogs' declines with age, whereas long term memories are more resistant to aging, which reflects similarities to humans (Adams et al., 2000; Fiset, Beaulieu, & Landry, 2003; Fiset, 2007; Salvin et al., 2011; Tapp, Siwak, Estrada, Holowachuk, et al., 2003b).

Most research projects have relied on laboratory kept Beagles to examine age-related cognitive changes. One advantage of utilising pet dogs living with human families is that we are able to examine the development and aging of cognition under the influence of the human living environment. This environment is likely to be more enriching and stimulating than that found in laboratory housed Beagles, and thus may provide a greater level of resistance to the effects of aging (Milgram et al., 2005).

The use of the touchscreen apparatus allows the design and implementation of non-verbal standardized tasks which can be utilised to examine cognitive functioning such as individual learning abilities, memory, and logical reasoning in non-human animals, and permits comparisons with humans and across species (Spinelli et al., 2004; Steurer et al., 2012). Computerization results in the elimination of social cuing, and increases/maintains the motivation to work in the subjects (Range et al. 2008). The touchscreen can be used to establish baseline measures of cognitive aging associated with normal aging, which has so far only been utilised in humans (Clark et al., 2006), laboratory housed non-human primates (Joly, Ammersdörfer, Schmidtke, & Zimmermann, 2014; Nagahara, Bernot, & Tuszynski, 2010), and rodents (Bussey et al., 2008).

Accordingly, the goals of the present study were to test the effect of aging on discrimination learning, reasoning by exclusion and memory in a cross-sectional sample of pet dogs ranging in age from 5 months to 13 years, in order to determine when dogs cognitively mature and when cognitive decline begins. After receiving pre-training on how to work on a touchscreen, the dogs were tested in four tasks: 1) underwater photos vs. drawings discrimination consisting of 6 stimuli, 2) clip art picture discrimination consisting of 8 stimuli (which were also used as a training for the next task on inferential reasoning by exclusion), 3) inferential reasoning by exclusion testing, and 4) a memory test on the clip art picture discrimination (task 2) performed after a six month's break from the touchscreen. Two discrimination tasks were utilised which differed not only in the types and number of stimuli used, but in their difficulty level. In the first discrimination (underwater photos vs. drawings), the positive and negative class was composed of highly similar members with large inter-class and small intra-class differences, whereas the more difficult second discrimination (clip art pictures) had equal inter-class and intra-class differences. Based on previous studies in laboratory dogs, we predicted that dogs' learning ability will decrease with age and perseverative responding will increase (Milgram et al., 2002; Snigdha et al., 2012; Tapp, Siwak, Estrada, Head, et al., 2003a). Long-term memory was predicted to remain stable with age (Araujo et al., 2005), and finally, based on information from the human literature, the ability to make inferences by exclusion was predicted to peak in young adulthood and decline thereafter

(Moshman, 2004), in conjunction with dogs' working memory ability (Tapp, Siwak, Estrada, Holowachuk, et al., 2003b).

Methods

Subjects

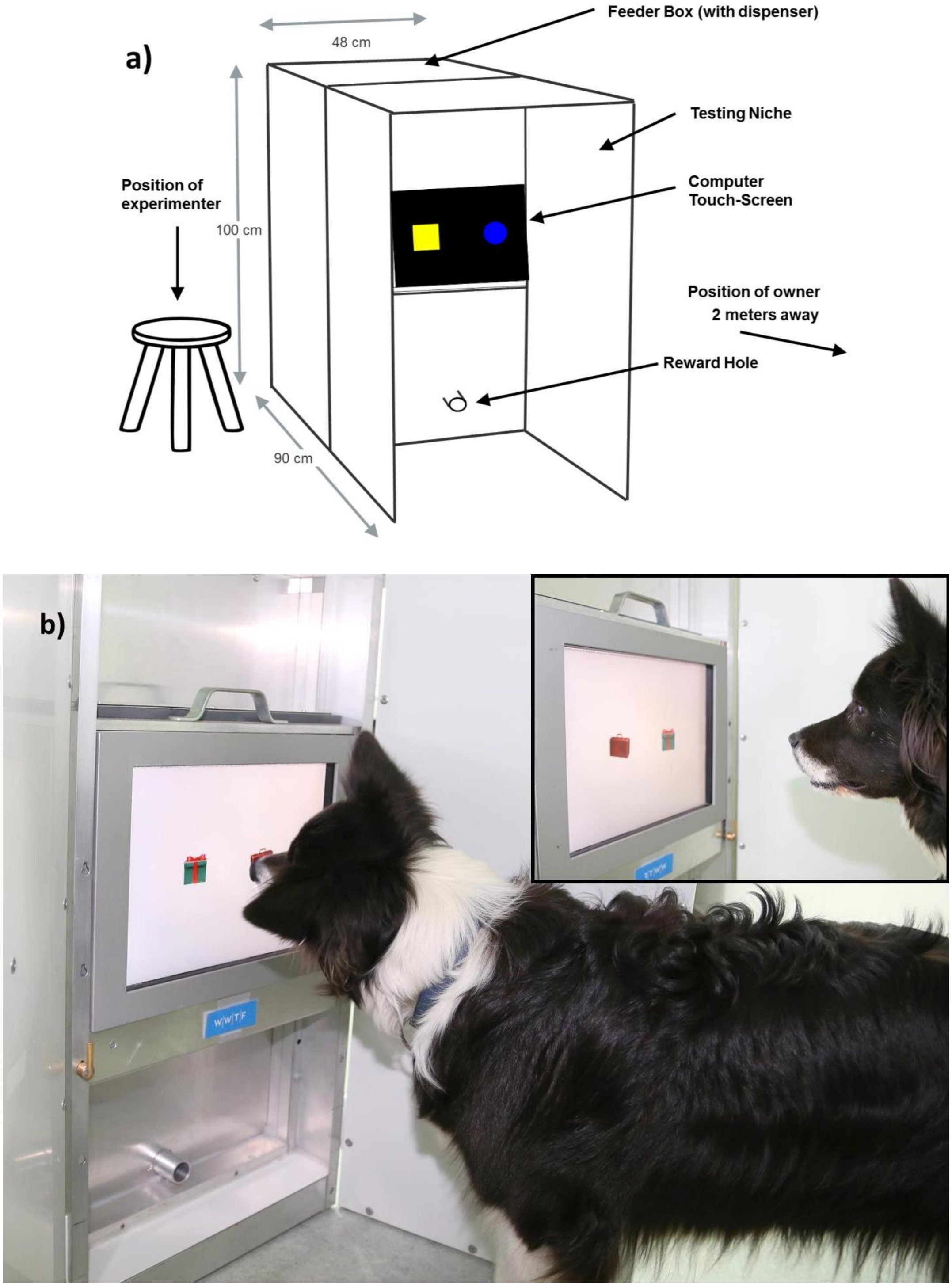
Ninety-five pet dogs ranging in age from 5 months to 13 years and 10 months were recruited to participate in the study (Table 1). All dogs were from one breed, the Border Collie, in order to exclude the effects of different developmental and aging speeds of different breeds. The subjects were split into five age groups according to Siegal & Barlough, (1995), which aimed to reflect the developmental periods in the Border Collie (late puppyhood, adolescence, early adulthood, middle age, and late adulthood (which included senior and geriatric).

Age group	Life stage	Age in months	Mean + SD age in years	Male (neutered)	Female (neutered)	Total
Group 1	Late puppyhood	5 - 12	0.68 + 0.16	7 (0)	13 (1)	20
Group 2	Adolescence	> 12 – 24	1.39 + 0.24	10 (1)	12 (2)	22
Group 3	Early adulthood	> 24 – 36	2.42 + 0.30	7 (3)	14 (5)	21
Group 4	Middle age	> 36 – 72	4.41 + 0.89	5 (2)	13 (6)	18
Group 5	Late adulthood	> 72	8.61 + 2.10	5 (3)	9 (9)	14
Total				34 (9)	61 (23)	95

Table 1: Age, sex and neuter status of subjects

Apparatus

Testing was conducted in a room (3 x 4 meters) at the Clever Dog Lab in Vienna, Austria. The test apparatus consisted of a closed rectangular box containing the food pellet dispenser (feeder box; 48 x 100 x 60 cm (w x h x d)), and an adjacent testing niche (48 x 100 x 30 cm) where the touchscreen was located along the top back wall (Figure 1). Dogs were tested in the testing niche, which allowed subjects to reach the touchscreen whilst their vision was shielded to avoid potential distractions from the side or above, thus minimizing human influence on the dogs' performance. Inside the testing niche a 15" TFT 600 x 800 pixel resolution computer screen was mounted behind an infrared touchframe (Carroll Touch, Round Rock, TX, USA; 32 vertical x 42 horizontal resolution (Aust et al., 2008; Huber, Apfalter, Steurer, & Prossinger, 2005; Range, Aust, Steurer, & Huber, 2008; Steurer et al., 2012)). A small hole beneath the touchscreen allowed commercial dog food pellets to be automatically dispensed in order to administer reinforcement for correct choices. The presentation of the stimuli and the release of the reward were controlled by a microcomputer interfaced through a digital input-output board. The owner and the experimenter were present during the testing, but were prevented from viewing the stimuli by the walls of the testing niche (see Figure 1a for owner and experimenter locations).



Photographs © Lisa Wallis, Clever Dog Lab

Figure 1: a) Schematic drawing of the apparatus, and b) photograph of a dog working in the testing niche with one side open.

Procedure

The touchscreen training and testing procedures consisted of two pre-training steps (an approach training, and a simple geometric form discrimination), and four tasks: a 'categorical' discrimination (underwater photographs and drawings; Task 1), a clip art picture discrimination (the training phase of the inferential reasoning by exclusion tests; Task 2), inferential reasoning by exclusion testing (previously reported in Aust et al., 2008; Task 3), and finally Task 4; a memory test after a six month's break from the touchscreen consisting of a repetition of Task 2 (clip art picture discrimination/inference by exclusion training).

Touchscreen pre-training

Approach training

Dogs visited the lab once a week and participated in three to four sessions (each session consisted of 30 to 32 individual trials), over a half hour period, with short breaks in between sessions. Dogs were trained to touch the monitor with their nose using a clicker aided shaping procedure. A stimulus, either a circle or a square appeared in random locations on a black screen. If the dogs touched the stimulus with their nose, the infrared light grid was interrupted, which triggered an acoustic signal and delivery of a food treat. After the dog became familiar with the action of touching the stimulus and receiving the food reward via the automatic feeder (without help from the experimenter), the simple geometrical form discrimination was initiated.

Geometric form discrimination

In this task, the subjects were shown a square and a circle side by side. Both stimuli were varied in colour between trials (red, yellow or blue, Figure 2a). The dogs were assigned to two groups balanced for age group and sex. Group '*square*' was rewarded for touching the square, group '*circle*' was rewarded for touching the circle. A forced two choice procedure was utilised, where the two shapes were presented simultaneously on a black background in fixed positions on the screen (at the animal's eye-level, one appearing left of the middle, and the other right, Figure 1). Each trial was comprised of one positive stimulus (S+) and one negative stimulus (S-), which were positioned randomly from trial to trial (left/right). Each session consisted of 30 trials. When the positive stimulus was selected, both stimuli disappeared, a short tone was emitted by the computer, and a food reward was provided. If the wrong stimulus was touched (S-), both stimuli disappeared, a short buzz sounded, and a red screen was presented for three seconds. In this case, a correction trial was immediately initiated: the stimuli of the previous trial were presented again in the same positions. A correct choice terminated the trial and resulted in reward and presentation of a new trial. After each trial (except correction trials) an inter trial interval of 2 seconds was initiated (an empty black background was presented). The learning criterion was set at ≥ 20 correct first choices in 30 trials (66.7%) in four out of five consecutive sessions. At this early stage in the training the experimenter often needed to give dogs extra help in sessions, for example verbal encouragement to approach the screen and touch, and occasional pointing. Therefore, the results from this test are presented only in the supplementary materials (Table S1).

Touchscreen testing

Task 1) Underwater photos and drawings discrimination

Once the criterion for the geometric forms task was reached the dogs were transferred to a second discrimination training, involving three underwater photographs, which had to be distinguished from three drawings (two of which were taken from posters by Toulouse-Lautrec; Figure 2b). The dogs were assigned to two groups balanced for age group and sex. Group ‘*drawing’* was rewarded for touching the drawing and group ‘*underwater’* was rewarded for touching the underwater photograph. In each trial one of the three S+ was randomly coupled side by side with one of the three S- .

The procedure and learning criterion were the same as for the geometric forms discrimination.

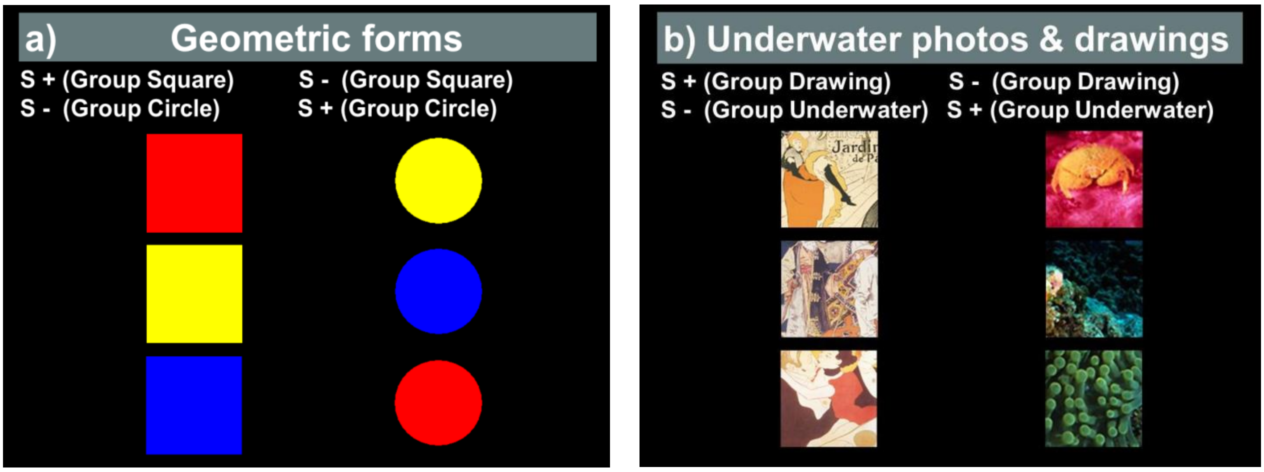


Figure 2: Training stimuli for the a) geometric forms, and b) underwater photos and drawings discriminations.

Task 2) Clip art picture discrimination (training for Task 3: Inferential reasoning by exclusion)

Once the dogs had completed the underwater photos and drawings discrimination, they began the training for the inference by exlusion tests. Dogs were again split into two groups (Group *'A'* and Group *'B'*) balanced for age group and sex. The dogs were trained to discriminate four S+ and four S- stimuli (Figure 3a), this time presented on a white background. Once again the forced two choice procedure was utilisied. The stimuli were colour clip art pictures obtained from the internet, and were grouped within the two sets by avoiding similarities in colour, form or function. The clip art stimuli were the same as those used by Aust et al. in the 2008 study. Each session consisted of 32 trials and contained each of the 16 possible S+/S- pairings twice per session. All dogs were required to reach two learning criteria: a first learning criterion of ≥ 28 correct first choices (87.5%) in two consecutive sessions and a final learning criterion of ≥ 28 correct first choices in five of seven consecutive sessions before beginning testing. Thirteen dogs which were tested prior to 2010 were trained on a 100% reward ratio. For the remaining 72 dogs, the reward ratio was reduced stepwise to 75% (for explanations of the rationale for a change in methodology please see supplementary material: Reward ratio reduction). The unrewarded trials in the training served to familiarise the dogs with the testing procedure, which included up to eight unrewarded test trials in each session. Initially, training sessions for these dogs included four trials that were not rewarded, i.e. the first choice of any of the two stimuli terminated the trial without any acoustic or visual feedback, correction trial or reward. The first learning criterion was utilised (≥ 28 correct first choices in two consecutive sessions), and once dogs reached this criterion, the reward ratio was further reduced to six unrewarded trials per session. The same learning criterion was applied again, after which a final training phase with a 75% reward ratio (eight unrewarded trials) was applied. The final learning criterion was used for this phase (≥ 28 correct first choices in five of seven consecutive sessions), the same criterion as was used for the 13 dogs originally tested with the 100% reward ratio.

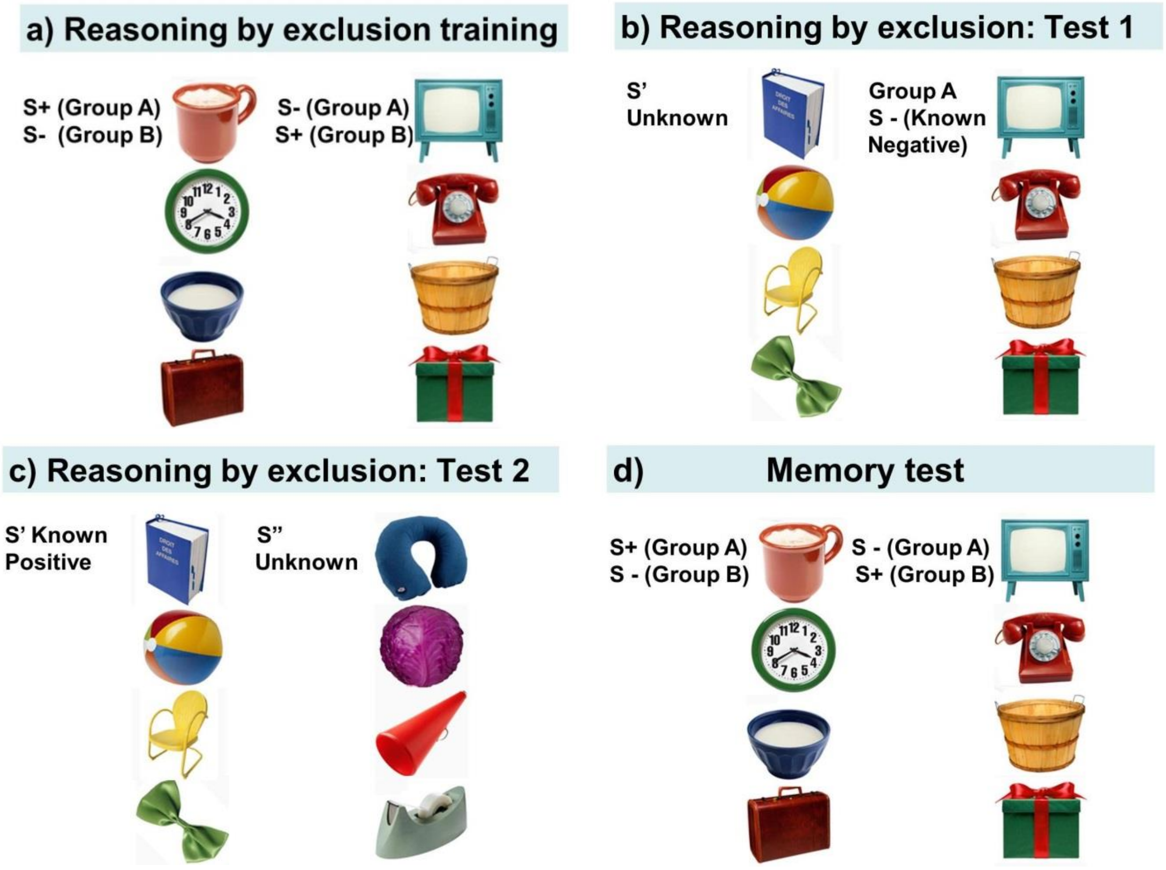


Figure 3: a) Reason by exclusion training stimuli, b) Test 1 stimuli, c) Test 2 stimuli, and d) memory test stimuli

Task 3) Inferential reasoning by exclusion

Test 1:Test sessions consisted of 28 training trials with four randomly interspersed test trials (a total of 32 trials per session). The test trials contained four known S- from the training trials, which were paired with four novel stimuli (Figure 3b). The new stimuli (S') replaced the S+ from the training. Each of the 16 test combinations were shown twice, once in Cycle 1 (sessions 1 – 4), and once in Cycle 2 (sessions 5 – 8).

Subjects which choose by exclusion should choose S’ due to inference of positive class membership; i.e. by assuming there is always a member of the positive class and by excluding S- due to its formed association with the negative class. But dogs which choose according to novelty (neophilia) or avoidance of S- should also choose S’. In contrast, subjects which choose by familiarity should prefer S-. Dogs which chose S’ in ≥ 22 out of a total 32 test trials proceded directly to Test 2.

Test 2: In order to confirm that dogs chose by exclusion an additional test was run to exclude that dogs chose based on novelty or avoidance of S-. The subjects were again tested with one of the four S’ paired with a known S- (same as Test 1, Figure 3b, hereafter known as the Test 1 refresher) to refresh their memory, and then in one of the next two to three trials, they were presented with the same S’ paired with one of four novel alternative stimuli S” (Figure 3c). If dogs chose by inference by exclusion they would choose S’ when paired with the known negative (in Test 1 and 2 (in the Test 1 refresher)), and also choose S’ when S’ was paired with the novel S”. Subjects which showed a preference for S’ in Test 1 due to neophilia, would now prefer the more novel S” over S’ (novelty preference). Subjects which avoided S- in Test 1 without making any inferences about the possitive association of S’, would choose randomly in Test 2, showing no preferences.

In each session in Test 2, there were eight non-rewarded trials (four Test 1 refresher and four Test 2 trials) interspersed within 24 training trials (32 trials in total per session). Each of the 16 test combinations (four known S’ from Test 1, paired with four novel stimuli (S”)) were again shown twice, once in Cycle 1 (sessions 1 – 4), and once in Cycle 2 (sessions 5 – 8).

For each Test 2 trial, dogs were scored as choosing by inference by exclusion if they firstly chose S’ when paired with the known negative (Test 1 refresher), and also chose S’ in the subsequent trial when S’ was paired with the novel S” (Test 2 trial). Over the entire Test 2, dogs were scored as choosing by inference by exclusion above chance if they chose by exclusion in 13 or more out of the possible 32 test trials (Binomial test, chance level = 0.25, p = 0.016 (chance level reflects the four possible choice combinations of Test 1 refresher, and Test 2 trial; S’and S’, S’ and S”, S- and S’, and finaly S- and S”)).

Task 4) Memory test

After completing the tests, all dogs had a minimum of a six months break before they were invited back to participate in a memory test consisting of a repetition of Task 2 (clip art picture discrimination/inference by exclusion training), up to the final criterion of ≥ 28 correct first choices (87.5%) in five of seven consecutive sessions (Figure 3d). Dogs which had been trained on the 75% reward ratio repeated the task at the 75% reward ratio, and dogs, which were trained on the 100% reward ratio, repeated the task at the 100% reward ratio. The total number of correct choices in the first session of the memory test was used as a measure of memory ability.

Data Analysis

Statistical analyses were performed in R 3.0.1 (R Core Team, 2013). Separate statistical models were calculated first with age as a continuous variable (we tested for linear and quadratic relationships), and then with age as a categorical variable to look for specific differences between age groups. Results are presented as mean ± standard deviation unless otherwise indicated.

In the geometric forms, underwater photos and drawings discrimination and the clip art picture discrimination, we used the total number of sessions needed to reach criterion minus the minimum number of sessions needed to reach the criterion of each discrimination (in order to fullfil the assumptions for poisson distribution), and the total number of correction trials as measures of learning speed and behavioural flexibility. In the clip art picture discrimination, the number of sessions needed to reach the first criterion of ≥ 28 correct first choices in two consecutive sessions in both the 100% rewarded and the reduced reward groups was used to allow learning speed to be assessed for the different reward ratios. The proportion of test trial choices of S' in Test 1, and the proportion of test trials where dogs chose based on inference by exclusion (in the repetition of S' paired with S-, and the new S" paired with S') in Test 2 were calculated as two separate variables to describe the logical reasoning strategies of the dogs. Finally, the total number of correct choices in the first session of the memory test was used as a measure of memory ability.

Data were analysed using generalised linear models and generalised linear mixed models, with age, stimulus group, sex, and neuter status included as fixed effects. In the inference by exclusion training and Test 1, we also examined the effect of the type of reward ratio (100% reward or reduced reward). We included the two-way interaction between stimulus group and age to test whether age effects differed between stimulus groups. When examining the proportion of test trial choices of S' in Test 1 and proportion of test trials where dogs chose based on inference by exclusion in Test 2, we also checked whether the dogs performance changed from cycle 1 to cycle 2. The full models can be found in the supplementary materials (geometric forms discrimination (Table S1), underwater photos and drawings discrimination (Table S2), clip art picture discrimination (Table S3), inferential reasoning by exclusion Test 1 (Table S4), inferential reasoning by exclusion Test 2 (Table S5), and memory test (Table S6)). Non-significant predictors ($p > 0.05$) were then removed from the models, and are not reported in the results section. According to the distribution of the response variables, models with negative binomial error structure and log link function (Venables & Ripley, 2002) were used for the number of sessions to criterion and the total number of correction trials, and models with binomial error structure and logit link function for the proportion of choices of S' in Test 1 and Test 2, and the proportion of correct first choices in the memory test. When analysing data including multiple data points per subject, dog identity was included as a random factor in the model. Plots of residuals and Cook's distance were examined for outliers. Since none of the data points exceeded Cook's distance of 1, no outliers needed to be excluded.

Results

Task 1) Underwater photo and drawing discrimination

Of the 95 dogs which began testing with the geometric forms discrimination, 93 passed the learning criterion for the underwater photos and drawings discrimination within 35 sessions. The number of sessions to criterion increased linearly with age in months (Table 2: Model 1, Figure 4a). The subsequent age-group analysis revealed that age groups 4 and 5 took significantly more sessions to reach criterion compared to age group 1 (Model 2). Dogs in the drawing group completed the task in significantly fewer sessions than dogs in the underwater group, reflecting a difference in task difficulty (Figure 4a).

The total number of correction trials also increased linearly with age in months (Table 2: Model 3, Figure 4b). Age group 5 needed significantly more correction trials compared to age group 1 (Model 4). Dogs in the underwater group had significantly more correction trials than dogs in the drawing group, furthermore supporting the difference in task difficulty (Figure 4b).

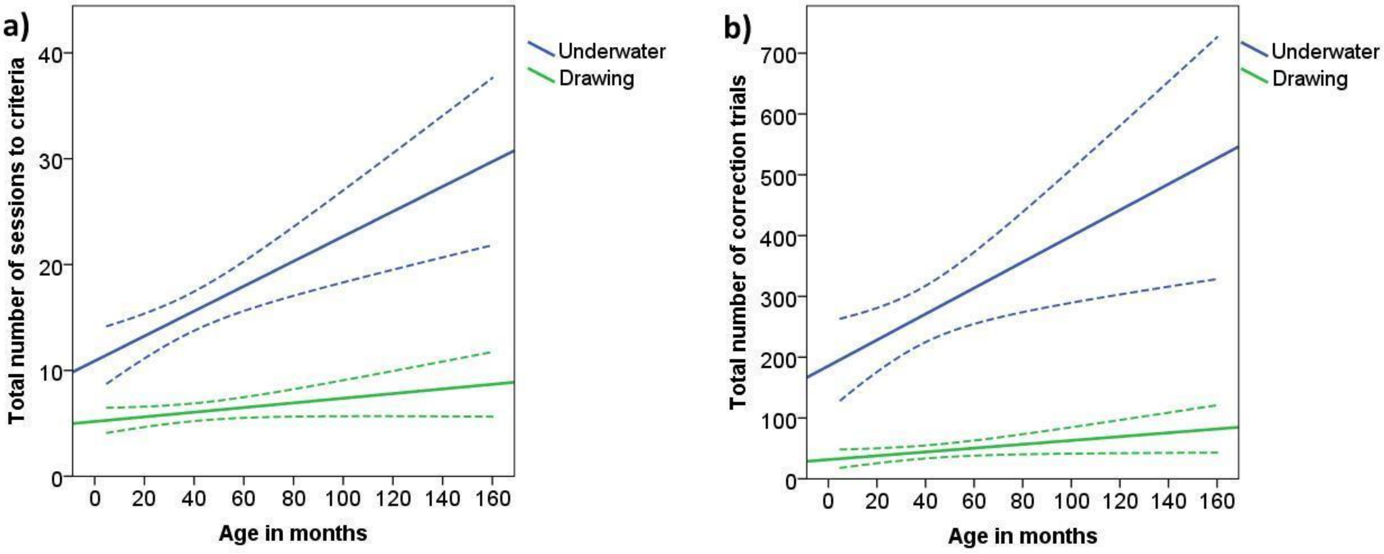


Figure 4: Line graph showing the linear relationship between age in months and a) number of sessions to criterion, and b) number of correction trials, shown separately for dogs that were rewarded for choosing the underwater pictures and for dogs rewarded for choosing the drawings (with 95% confidence intervals (dotted lines)).

Response variable	Model	Minimal model	Average effect	SE	Wald statistic	z	P
Number of sessions to criterion	Model 1	Stimulus group:Underwater	1.3841	0.1389	68.704		**<0.001**
		Age in months	0.0072	0.0018	14.224		**<0.001**
	Model 2	Age group			14.627		**0.006**
		Age group 2	0.0109	0.1969		0.055	0.956
		Age group 3	0.1200	0.2025		0.593	0.553
		Age group 4	0.4832	0.1937		2.495	**0.013**
		Age group 5	0.6104	0.2121		2.877	**0.004**
Number of correction trials	Model 3	Stimulus group:Underwater	1.7887	0.1470	88.076		**<0.001**
		Age in months	0.0067	0.0022	9.584		**0.002**
	Model 4	Age group			11.181		**0.025**
		Age group 2	-0.0631	0.2135		-0.295	0.768
		Age group 3	0.3723	0.2155		1.728	0.084
		Age group 4	0.4144	0.2151		1.927	0.054
		Age group 5	0.5741	0.2412		2.383	**0.017**

Table 2: Negative binomial generalised linear models showing the direction of effects and the significance level of the terms in the underwater photos and drawings dis-

crimination. Z tests indicate which age groups differ from age group 1 in the respective analysis. Bold numbers indicate significant values at p =≤ 0.05.

Task 2) Clip art picture discrimination (training for Task 3: inferential reasoning by exclusion)

Of the 90 dogs which began the training, 85 passed the first learning criterion of 28 or more correct choices in two consecutive sessions within 7 to 113 sessions. The five dogs (all in age groups 4 and 5), which did not reach the learning criterion, dropped out of the study due to motivation problems. The number of sessions to criterion increased linearly with age in months (Table 3: Model 5, Figure 5a). Age groups 4 and 5 took significantly more sessions to reach criterion compared to age group 1 (Model 6). Dogs in Group A completed the task in significantly fewer sessions than dogs in Group B, reflecting a difference in task difficulty depending on the set of pictures the dogs were rewarded for (Table 3: Model 5, Figure 5a). Male dogs needed more sessions to reach criterion than female dogs (Males: 29.03 ± 22.70, N = 31, Females: 23.48 ± 16.26, N = 54; Table 3: Model 5). For further results and a discussion of these sex differences please see supplementary materials. Dogs which participated in the reduced reward ratio training, took significantly longer to reach the first learning criterion than dogs in the 100% rewarded group (reduced reward: 26.79 ± 18.85, N = 72, 100% rewarded: 18.38 ± 18.42, N = 13; Table 3: Model 5). Please refer to supplementary materials for additional results and a discussion of the reward ratio reduction.

The total number of correction trials increased linearly with age in months (Table 3: Model 7, Figure 5b). Age group 4 and 5 had significantly more correction trials compared to age group 1 (Model 8). Dogs in Group B had significantly more correction trials than dogs Group A, (Table 3: Model 7, Figure 5b). Male dogs needed more correction trials than female dogs (Males = 217.26 ± 159.46, Females = 198.52 ± 200.80; Table 3: Model 7).

Response variable	Model	Minimal model	Average effect	SE	Wald statistic	Z	P
Number of sessions to Criterion	Model 5	Age in months	0.0100	0.0017	32.326		**<0.001**
		Stimulus group: B	0.2707	0.1095	5.908		**0.015**
		Sex: Male	0.3507	0.1169	8.710		**0.003**
		Reward ratio: 90%	0.3486	0.1545	4.877		**0.027**
	Model 6	Age group			29.633		**<0.001**
		Age group 2	0.0612	0.2046		0.2990	0.765
		Age group 3	0.1162	0.2088		0.5570	0.578
		Age group 4	0.6525	0.2193		2.9750	**0.003**
		Age group 5	0.8879	0.2215		4.0090	**<0.001**
Number of Correction Trials	Model 7	Age in months	0.0118	0.0019	37.953		**<0.001**
		Stimulus group: B	0.4313	0.1250	11.169		**<0.001**
		Sex: Male	0.3184	0.1253	6.296		**0.012**
	Model 8	Age group			32.130		**<0.001**
		Age group 2	0.3174	0.2287		1.388	0.165
		Age group 3	0.2992	0.2338		1.280	0.201
		Age group 4	0.6798	0.2490		2.730	**0.006**
		Age group 5	1.2756	0.2525		5.053	**<0.001**

Table 3: Negative binomial generalised linear models showing the direction of effects and the significance level of the terms in the clip art picture discrimination (training for Task 3: inferential reasoning by exclusion). Z tests indicate which age groups differ from age group 1 in the respective analysis. Bold numbers indicate significant values at p =≤ 0.05.

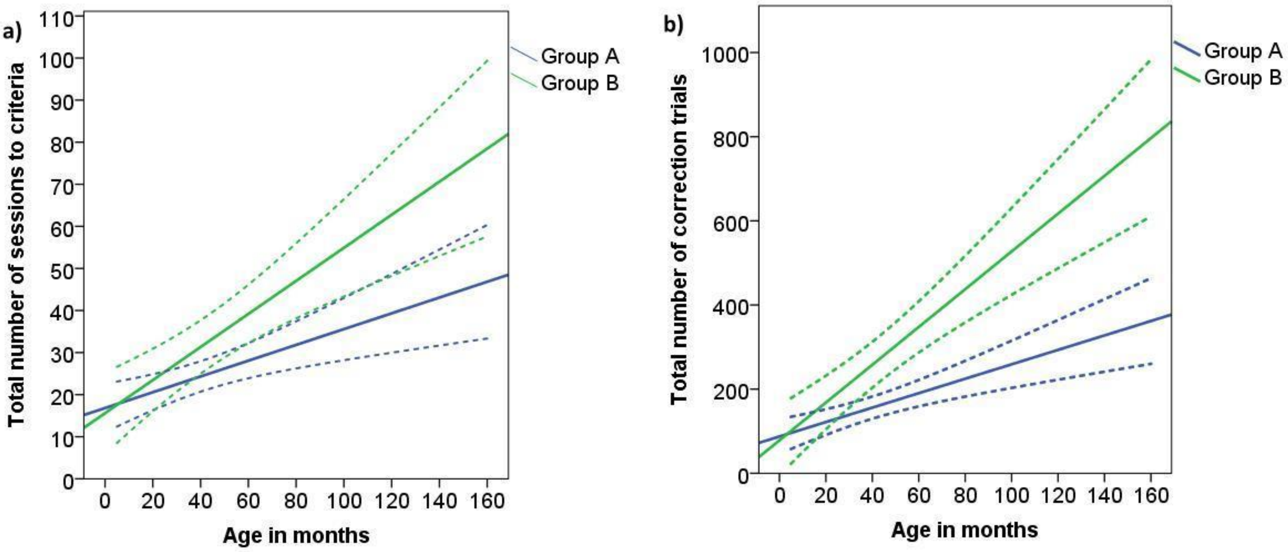


Figure 5: Line graph showing the linear relationship between age in months and a) number of sessions to criterion, and b) number of correction trials, separately for Groups A and B (with 95% confidence intervals (dotted lines)).

Task 3) Inferential reasoning by exclusion

Test 1: Of the 85 dogs which passed the first learning criterion (≥ 28 correct first choices (87.5%) in two consecutive sessions), 82 passed the final learning criterion of 28 or more correct choices in five out of seven consecutive sessions and participated in Test 1.

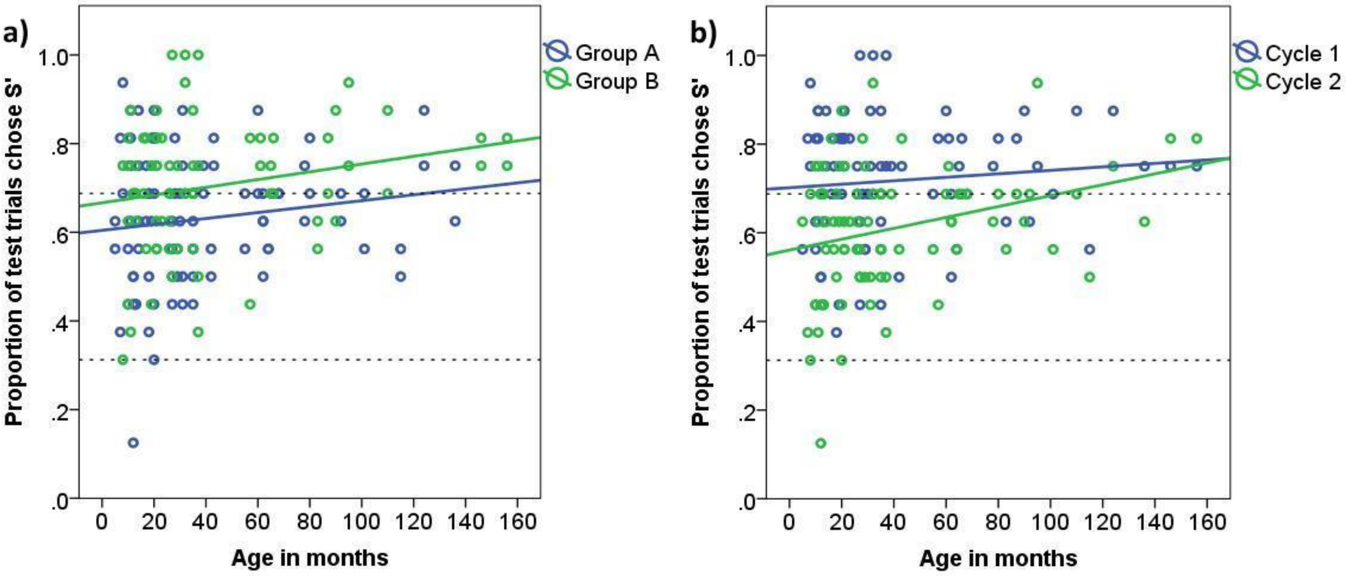


Figure 6: The proportion of test trials in Test 1 in which the dog chose S'; a) Group A and Group B, and b) Cycle 1 (session 1 to 4) and Cycle 2 (session 5 to 8), and age in months. The *upper dashed line* indicates the levels of performance beyond which preference for S' was inferred (68.75%; choice by novelty, avoidance of S-, or reasoning by exclusion). The *lower dashed line* indicates the level of performance below which preference for S- was inferred (31.25%; choice by familiarity).

The proportion of test trials in which dogs chose S' showed a significant increase with age in months (Table 4, Figure 6). No significant differences between the age groups were detected, however. Dogs in Group B chose S' in significantly more test trials than dogs in Group A (Table 4, Figure 6a). Male dogs showed a tendency to choose S' more often than females (Males: N = 30: 0.69 ± 0.02, Females: N = 52, 0.65 ± 0.01; Table 4). Dogs chose S' more often in Cycle 1 compared to Cycle 2 (Table 4, Figure 6b). When results from Cycles 1 and 2 were pooled 42 (51 %) dogs preferred S' (choose S' in 22 or more test trials out of a total of 32), and thus chose based on exclusion (rejection of S- due to its association with the negative class), novelty (selection of S' due to neophilia), or avoidance of the known negative stimulus (S-), and proceeded to Test 2 (apart from one dog which left the study at this stage). The remaining dogs chose at chance level, apart from one individual, which chose based on familiarity.

Response variable	Model	Minimal model	Average effect	SE	Wald statistic /Deviance	P
Proportion of Trials chose S'	Model 9	Cycle: Cycle 2	-0.4943	0.0839	34.723	**<0.001**
		Stimulus: Group B	0.3478	0.1007	11.136	**<0.001**
		Age in months	0.0037	0.0014	6.567	**0.010**
		Sex:Male	0.1919	0.0988	3.693	0.055

Table 4: Generalised linear mixed model on the proportion of trials chose S' when paired with a known negative (S-) in Test 1 of the inference by exclusion task, showing the direction of effects and the significance level of the terms. Bold numbers indicate significant values at p =≤ 0.05.

Test 2: There was no significant difference between the number of times the dogs chose based on inference by exclusion in Cycle 1 and Cycle 2, so data were pooled and generalised linear models were applied (see supplementary material Table S5: Model 11). Seven individuals (17%) scored above chance, and six of these seven were in Group B (Figure 7). The proportion of test trials in which the dogs chose based on inference by exclusion showed a significant increase with age in months (Table 5: Model 12, Figure 7). Age groups 3, 4, and 5 chose S' significantly more often compared to age group 1 (Model 13). Dogs in Group B chose by inference by exclusion in significantly more test trials than dogs in Group A (Table 5: Model 12, Figure 7).

The proportion of test trials in which dogs chose by exclusion showed a significant increase with the total number of correction trials in the inference by exclusion training (Table 5, Model 15) after controlling for age in months. Therefore, regardless of age, dogs which needed more correction trials in the training chose more often using inference by exclusion in Test 2.

Response variable	Model	Minimal model	Average effect	SE	Wald statistic /Deviance	z	P
Proportion of times chose S' in both Test 1 refresher trial and Test 2 trial	Model 12	Age in months	0.0099	0.0014	45.538		**<0.001**
		Stimulus: Group B	0.7027	0.1367	27.739		**<0.001**
	Model 13	Age group			54.570		**<0.001**
		Age group 2	0.4654	0.2816		1.653	0.094
		Age group 3	0.6387	0.2989		2.137	**0.033**
		Age group 4	1.2223	0.2900		4.215	**<0.001**
		Age group 5	1.3916	0.2788		4.992	**<0.001**
	Model 14	Sessions to criterion	0.0008	0.0029	0.082		0.775
	Model 15	Total no. of correction trials	0.0006	0.0003	4.103		**0.043**

Table 5: Generalised linear model on the proportion of times the dogs' chose S' when paired with the known negative (Test 1 refresher), and also chose S' in the subsequent trial when S' was paired with the novel S" (Test 2 trial) in the inference by exclusion task, showing the direction of effects and the significance level of the terms. Z tests indicate which age groups differ from age group 1 in the respective analysis. Age in months was included in Models 12 and 13 to control for age effects. Bold numbers indicate significant values at p =≤ 0.05.

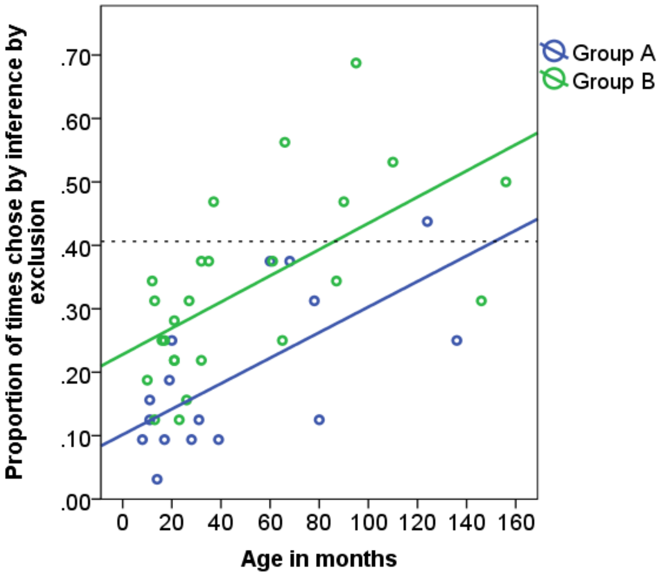


Figure 7: The proportion of times in which the dog chose based on inference by exclusion in Group A and Group B and age in months in Test 2 (cycles 1 and 2 pooled). The *dashed line* indicates the levels of performance beyond which preference for S' was inferred (40.625%; reasoning by exclusion).

Task 4) Memory test

Of the 82 dogs which completed the final learning criterion of the inference training, 46 participated in the memory test after a break of at least six months. Forty-two of these dogs scored significantly above chance level in the first session (22 or more out of the possible 32 first corect choices (Binomial test: 22/32 = 0.6875, chance level = 0.5, p = 0.050; 81.52% ± 10.10). There were no significant effects of age or stimulus group on the proportion of correct first choices in the first session of the memory test (Supplementary Table S6).

Discussion

The aim of the present study was to examine age effects on visual discrimination learning, inferential reasoning by exclusion and long-term memory in domestic dogs kept as pets. We found a significant effect of age on the number of trials needed to reach criterion (as age increased, discrimination learning ability decreased), and degree of perseveration (the number of correction trials) in the two visual discrimination learning tasks. In contrast, older dogs chose more often by exclusion than younger dogs in the crucial (second) reasoning by exclusion test. Finally, dogs' long-term memory was maintained into old age, with no difference in performance in any of the age groups after a six month's break from the touchscreen.

The ability to learn new visual stimulus associations decreased with age as predicted. The youngest dogs aged from 5 months to 1 year needed the lowest number of sessions to complete the criteria, indicating that this age group was already performing at peak performance, and from this age onward, dogs' learning abilities began to decline. In contrast to the present study, previous studies in non-human animals have found no effect of aging on associative learning in simple object discrimination tasks neither in the rhesus macaque (aged from 3 to 34 years: Bachevalier et al., 1991) nor laboratory dogs (aged from 1.5 to 11 years: Milgram et al., 1994). One possible reason for this discrepancy is that, by utilizing a higher number of stimuli to be discriminated, we sufficiently increased the difficulty level, and thus facilitated the appearance of age effects. This interpretation is also supported by the difference we find between the two stimuli groups both in the drawings and underwater photos discrimination and in the clip-art discrimination: If the discrimination seems to be easier for the dogs ('*drawing*'; group '*B*'), the age differences, although still apparent, are not as pronounced as in the more difficult groups ('*underwater*'; group '*A*'). However, although age effects were more apparent in the groups with the less preferred stimuli as positive (that is, in the more difficult version of each task), we found no evidence for an interaction between age and stimulus group in any of the discrimination tasks. For a discussion of stimulus preferences in two choice discriminations please refer to the supplementary materials; Stimulus preferences.

Age differences were more pronounced in the clip art picture discrimination than in the drawings and underwater photos discrimination. This difference in effect size may be explained firstly in terms of the number of stimuli to be discriminated (six in the drawings and underwater discrimination and eight in the picture discrimination), and additionally by the fact that the drawings discrimination could be solved more easily by learning a perceptual discrimination rule. All the drawings looked perceptually similar to each other, as did the underwater photographs, but the clip art picture discrimination required that all the stimuli were encoded into memory individually, as there were no perceptual commonalities in the positive or the negative stimuli. Our results are in line with the findings from human studies; age effects can be better detected by more complex tasks (Alvarez & Emory, 2006; Mell et al., 2005).

The poorer performance of dogs aged over three years in our study could be explained by several possibilities. First, older dogs may suffer from attentional deficits due to reduced processing resources (Snigdha et al., 2012). Additionally, older dogs may use ineffectual strategies in an attempt to solve the discriminations, for example a stimulus response strategy (such as stimulus preferences or avoidance, as seen when dogs repeatedly make incorrect choices), and/or a positional strategy (side bias), before finally switching to a cognitive strategy. Both stimulus response and positional strategies require less working memory, and are therefore less costly than a cognitive strategy (Chan et al., 2002). Unfortunately, we were unable to analyse positional strategies due to limitations in the software program.

Second, younger dogs may have been quicker to utilise the cognitive strategy of forming reward associations for the positive stimuli by utilising working memory, and swift encoding to long-term memory. These younger dogs, assuming that their working memory abilities were good, might have shown more focused selective attention allowing them to quickly pick out the correct stimuli and ignore the negative stimuli (Mongillo, Bono, Regolin, & Marinelli, 2010; Snigdha et al., 2012; Wallis et al., 2014). In contrast, older dogs have a reduced capacity for working memory (Chan et al., 2002; Tapp, Siwak, Estrada, Holowachuk, et al., 2003b), similarly to other species including humans (Cowan, 2001; Matzel & Kolata, 2010). Evidence in humans suggests that older individuals with lower working memory capacity may also need to cope with the processing of negative (or “distractor”) stimuli, which leads to slower learning and the storage of more information in memory than younger individuals with high working memory capacity (Konstantinou, Beal, King, & Lavie, 2014; Vogel, McCollough, & Machizawa, 2005).

Third, an important non-cognitive factor, which could have influenced the results, is age differences in sensory ability (namely eyesight). However, all older dogs in our study were able to pass the criteria in three visual discrimination tasks, and in the geometric forms task, we found no age differences in the number of sessions to criteria (see supplementary materials, Table S1). Additionally, we tested many of the subjects in behavioural tests, and found little evidence that visual impairments influenced the dogs’ performance (Wallis et al., 2015; Wallis et al., 2014).

The total number of correction trials increased with age in all discrimination tasks possibly due to a lack of attention, persistency, and/or side bias in the older dogs, resulting in an inability to adjust thinking or attention in response to feedback. Similarly to earlier findings in dogs (Chan et al. 2002), the oldest age group displayed the most perseverative errors and thus displayed reduced flexibility. Aged members of other species have also shown reduced flexibility reflected in an inability to suppress and/or change behaviour on the basis of negative feedback; for example rats (Stephens, Weidmann, Quartermain, & Sarter, 1985), non-human primates (Lai, Moss, Killiany, Rosene, & Herndon, 1995; Manrique & Call, 2015; Voytko, 1999; Voytko, 1993) and humans (Botwinick, 1978; Daigneault, Braun, & Whitaker, 1992).

The proportion of test trials in which the dogs chose based on novelty, avoidance, or exclusion in Test 1 of the inference by exclusion task increased with age. However, no significant differences between the age groups were found. The proportion of test trials in which the dogs’ chose based on exclusion in Test 2 also increased with age, but with most dogs choosing at chance levels. Less than 10% of dogs in the current study showed patterns of choice consistent with inference by exclusion, indicating that inference by exclusion was not the predominant strategy used by the dogs. In Aust et al.’s (2008) study by comparison 3 out of 6 dogs were found to display this ability.

In contrast to our prediction of a peak in inference by exclusion ability in young adult dogs, seven dogs in middle to late adulthood were found to perform above chance, suggesting that they used reasoning by exclusion. Similarly, in non-human primates one study by Call et al. (2006) found that the ability to reason by exclusion increases with age. Our results are superficially similar to the primate study; however, after looking into the data more carefully, our results seem to reflect a learning rather than a reasoning effect. This learning effect was strongest in younger individuals: In the test trials, the dogs were not rewarded for choosing based on exclusion (choosing S'), which might have made them switch to choosing randomly due to the missing feedback.

A similar effect might explain why in Test 1 choosing S' (based on novelty, avoidance, or exclusion) declined from the first to the second cycle. In the tests, younger dogs might have reacted to the lack of feedback sooner/more often than the older dogs, reflecting their more flexible problem solving style. This interpretation is further supported by the impact of the degree of perseverative responding in the training on performance in the inference by exclusion Test 2. After controlling for age, our results indicated that a higher amount of perseverative responding increases the likelihood of finding response patterns consistent with choosing by exclusion. Conversely, the higher degree of flexibility of the younger dogs may have led to a lower probability of choices following the inference by exclusion pattern in this particular paradigm, where test trials were not rewarded. We suggest that older dogs, especially those that were in the more difficult to learn Group B, were more likely to stick with their initial choice of S’ due to the fact that they showed greater levels of perseverative responding in the training and consequently had more chance to learn about the negative stimuli. These dogs may have persisted in their choice of S’ in the test trials in Test 1, did not alter their strategy in response to the lack of feedback, and may have been able to encode S’ to working memory to enable them to choose S’ when paired with S” a few trials later in Test 2. In Aust et al.’s (2008) study all three dogs, which chose by inference by exclusion, were also in Group B, needed more sessions to reach criteria in the training, and therefore had more experience with correction trials, similarly to dogs in our study. Results from studies on aged humans show similar findings of reduced flexibility (shown in difficulties in switching task sets), and deficiencies in adaptation to external feedback (Kray & Lindenberger, 2000; Mell et al., 2005), supporting the findings of the current study.

Finally, there was no effect of age or stimulus group on the performance of dogs in the memory test six months later. However, the six month break was likely too short a time period to enable the detection of age effects. The lack of age effects on long-term memory confirm previous results in laboratory dogs by Araujo et al., (2005). Nearly all the dogs tested in the current study scored above chance in the very first session suggesting that long-term memory for specific stimuli on the touchscreen is longer than 6 months in dogs. Recently, we re-tested five dogs of different breeds, which had undergone inference by exclusion training between 3 and 5 years previously, and these individuals performed at over 80% correct first choices on the first day of re-training, which is comparable to the performance of dogs in the memory test of the current study. Therefore, domestic dogs' long-term memory for picture stimuli may exceed 5 years, similarly to baboons and pigeons (Fagot & Cook, 2006).

In conclusion, older dogs showed slower learning and reduced flexibility, which may have contributed to an increase in choosing by inference by exclusion in the tests in comparison to young dogs, which were more sensitive to the lack of feedback in test trials, and subsequently flexibly changed their response pattern and used strategies other than inference by exclusion. Dogs' long-term memory for the clip art picture discrimination was well maintained into old age. Our results in the visual discrimination learning tasks show clear age differences confirming that the tests used are suitable to detect cognitive aging in pet dogs, and provide additional evidence of the suitability of the dog as a model for aging. The baseline measures associated with normal cognitive aging in the pet Border collie found in the current study, can serve as a basis for comparison to help diagnose cognition-related problems, and as a tool to assist with the development of treatments to delay cognitive decline. Moreover, the touchscreen apparatus offers a standardized procedure, which can be applied across different dog breeds, other non-human animals, and even humans. Utilizing this method, future studies could investigate the development and aging of cognitive processes and disorders, and their interactions with genetic, environmental and social factors.

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Supplementary Materials

Full models are presented for each of the different tasks: geometric forms discrimination, underwater photos and drawings discrimination, clip art picture discrimination, and inferential reasoning by exclusion Test 1 and Test 2. Stepwise removal of non-significant terms in order of decreasing significant was utilised. In case of non-significant effects, the average effect and SE are given at the point of their removal.

Geometric forms discrimination

The geometric form discrimination was run in order for the dogs to become familiar with the two choice discrimination procedure, and to allow dogs to experience for the first time the consequence of touching a negative stimulus (S-). Results indicate that in a simple discrimination of two geometric forms no age differences were detected, however, the dogs had a preference for the '*circle'* stimuli, which resulted in a significant difference between the stimulus groups.

Table S1: Negative binomial generalised linear models showing the direction of effects and the significance level of the terms in the geometric forms discrimination.

Response variable	Full model	Average effect	SE	Wald statistic	P
Number of sessions to criterion	Stimulus group: Square	1.2751	0.1681	46.5038	**<0.001**
	Sex: Male	0.2294	0.1677	1.8688	0.1716
	Age in months	0.0021	0.0025	0.6764	0.4108
	Neuter: Neutered	-0.1522	0.2082	0.5090	0.4756
	Age*Stimulus group	-0.0018	0.0050	0.1194	0.7296
Number of correction trials	Stimulus group: Square	2.086	0.196	70.3193	**<0.001**
	Sex: Male	0.1966	0.2046	0.9368	0.3331
	Neuter: Neutered	-0.0945	0.2095	0.1971	0.6571
	Age in months	0.00212	0.0036	0.3024	0.5824
	Age*Stimulus group	-0.0029	0.0061	0.2127	0.6446

Table S2: Negative binomial generalised linear models showing the direction of effects and the significance level of the terms in the underwater photos and drawings discrimination. Z tests indicate which age groups differ from age group 1 in the respective analysis.

Response variable	Model	Minimal model	Average effect	SE	Wald statistic	z	P
Number of sessions to criterion	Model 1	Stimulus group:Underwater	1.3841	0.1389	68.7041		**<0.001**
		Age in months	0.0072	0.0018	14.2237		**<0.001**
		Sex: Male	0.1566	0.1289	1.4654		0.2261
		Neuter: Neutered	-0.1453	0.1636	0.7659		0.3815
		Age*Stimulus group	0.0023	0.0037	0.3812		0.5370
	Model 2	Stimulus group:Underwater	1.3841	0.1389	68.7041		**<0.001**
		Age group			14.6271		**0.0055**
		Age group 2	0.0109	0.1969		0.055	0.9559
		Age group 3	0.1200	0.2025		0.593	0.5534
		Age group 4	0.4832	0.1937		2.495	**0.0126**
		Age group 5	0.6104	0.2121		2.877	**0.0040**
Number of correction Trials	Model 3	Stimulus group:Underwater	1.7887	0.1470	88.0760		**<0.001**
		Age in months	0.0067	0.0022	9.5844		**0.0019**
		Neuter: Neutered	0.0866	0.1798	0.2124		0.6449
		Sex: Male	-0.0176	0.1467	0.0142		0.9050
		Age*Stimulus group	0.0004	0.0045	0.0097		0.9217
	Model 4	Stimulus group:Underwater	1.7887	0.1470	88.0760		**<0.001**
		Age group			11.1809		**0.0246**
		Age group 2	-0.0631	0.2135		-0.295	0.7677
		Age group 3	0.3723	0.2155		1.728	0.0841
		Age group 4	0.4144	0.2151		1.927	0.0540
		Age group 5	0.5741	0.2412		2.383	**0.0172**

Table S3: Negative binomial generalised linear models showing the direction of effects and the significance level of the terms in the inferential reasoning by exclusion training. Z tests indicate which age groups differ from age group 1 in the respective analysis.

Response variable	Model	Minimal model	Average effect	SE	Wald statistic	z	P
Number of sessions to Criterion	Model 5	Age in months	0.0100	0.0017	32.3262		<**0.001**
		Sex: Male	0.3507	0.1169	8.7099		**0.0032**
		Stimulus group: B	0.2707	0.1095	5.9078		**0.0151**
		Reward ratio: 90%	0.3486	0.1545	4.8773		**0.0272**
		Age*Stimulus	0.0035	0.0030	1.2236		0.2686
		Neuter: Neutered	0.1298	0.1372	0.8820		0.3476
	Model 6	Age group			29.6328		<**0.001**
		Age group 2	0.0612	0.2046		0.2990	0.7647
		Age group 3	0.1162	0.2088		0.5570	0.5778
		Age group 4	0.6525	0.2193		2.9750	**0.0029**
		Age group 5	0.8879	0.2215		4.0090	<**0.001**
Number of correction Trials	Model 7	Age in months	0.0118	0.0019	37.9526		<**0.001**
		Stimulus group: B	0.4313	0.1250	11.1686		<**0.001**
		Sex: Male	0.3184	0.1253	6.2962		**0.0121**
		Neuter: Neutered	0.2500	0.1524	2.7396		0.0979
		Reward ratio: 90%	0.1845	0.1667	1.1281		0.2882
		Age*Stimulus	0.0038	0.0035	1.1777		0.2778
	Model 8	Age group			32.1295		<**0.001**
		Age group 2	0.3174	0.2287		1.388	0.1652
		Age group 3	0.2992	0.2338		1.280	0.2007
		Age group 4	0.6798	0.2490		2.730	**0.0063**
		Age group 5	1.2756	0.2525		5.053	<**0.001**

Sex differences

Results from the inference by exclusion training indicate a sex difference in learning ability and rate of perseveration. Male dogs needed more sessions to reach criterion, and more correction trials than females. Sex differences in cognitive abilities are widespread in humans (Andreano & Cahill, 2009; Halpern, 2013; Healy, Bacon, Haggis, Harris, & Kelley, 2009; Mann, Sasanuma, Sakuma, & Masaki, 1990), but sex differences in cognition in areas other than spatial cognition are less well known in non-human mammals. Duranton, Rödel, Bedossa, & Belkhir, (2015) reported differences between male and female dogs in problem solving abilities. Male dogs initially outperformed females, but when successful individuals were retested, females performed better than males. The authors propose that this effect was due to differences in the ability to remember the successful strategy of problem solving, probably due to sex-specific effects on brain differentiation in early life. Also in humans females seem to remember precise object features better than males (Voyer, Postma, Brake, & Imperato-McGinley, 2007). Such a sex difference may help to explain the superior performance of female subjects in our study. Alternatively or additionally, the male dogs' poorer performance in our study could be explained by the fact that male individuals show a greater tendency to perseverate, as seen in humans (Boone, Ghaffarian, Lesser, Hill-Gutierrez, & Berman, 1993; Davis & Nolen-Hoeksema, 2000), rhesus monkeys (Herman & Wallen, 2007), and rats (Guillamón, Valencia, Calés, & Segovia, 1986), suggesting that in some contexts males are cognitively less flexible.

Reward ratio reduction

Thirteen dogs which were tested prior to 2010 were trained on a 100% reward ratio in the inferential reasoning by exclusion training picture discrimination. During the inference by exclusion testing, the dogs experienced unrewarded test trials for the first time. Therefore, their performance may have been influenced by expectancy violation, and they may have been more likely to change their initial choice of stimuli, in response to the fact that the reward was withheld. In effect, they may have interpreted the fact that no food reward was received as negative feedback for an incorrect choice (even though no red screen was presented). Since their performance in the test was likely to have been negatively influenced, for the remaining 72 dogs, the reward ratio in the training was reduced stepwise to allow them to experience unrewarded trials.

Reducing the reward ratio from 100% (as used in Aust et al. (2008)) to 90% resulted in an increase in the number of sessions needed to reach criteria in the training in the current study (see Table S3, Model 5). Previous studies on partial reinforcement and learning rate in humans and animals have discovered that response strength is built up more rapidly when a 100% reinforcement schedule is utilised (Jenkins & Stanley, 1950). However, in the inference by exclusion Test 1, we did not find any effect of partial reinforcement (see Table S4, Model 9). The strong learning effect found from Cycle 1 to Cycle 2 likely overshadowed any positive effects of the reduced reward training.

Since only 3 dogs from the 100% reward group passed Test 1 and went onto Test 2, it was not possible to examine the effect of reward ratio on Test 2. Future studies should aim to develop new methodologies which could allow feedback during test trials to prevent the dogs from switching to a different problem solving strategy.

Stimulus preferences

Stimulus preferences were noted in the geometric forms, the underwater photos and drawings, and inferential reasoning by exclusion training discriminations. Preferences for certain stimulus groups resulted in a decreased number of sessions to criteria, and a decrease in the number of correction trials in comparison to the non-preferred stimulus group. In the geometric forms discrimination we noted that dogs showed a preference for the circle stimuli, in the underwater drawing discrimination, the dogs preferred the drawings over the underwater photographs, and finally in the inferential reasoning by exclusion training, the dogs preferred stimuli in Group '*A*'. We can speculate that dogs tend to prefer round stimuli, as many positive objects in their everyday lives are circle shaped (including for instance toys, balls, food bowls, dried dog kibble, and collars). In the inferential reasoning by exclusion training discrimination, the dogs preference for group '*A*' could be due to the fact that in that group there were three stimuli which had a round shape (mug, clock and bowl), compared to only two stimuli in group B (telephone and basket). Dogs' preference for the drawings in the underwater photos and drawings discrimination may be explained by a preference for greater contrast in the drawings, and/or an aversion to the comparably darker colouration of the underwater photographs.

Object preferences have been previously documented in laboratory dogs and primates (B Adams, Chan, Callahan, & Milgram, 2000; Brush, Mishkin, & Rosvold, 1961). Animals tested in two choice discriminations with their preferred object as positive showed significantly more rapid learning than those tested with their non-preferred object. Using the touchscreen paradigm, O'Hara, Auersperg, Bugnyar, & Huber, (2015) tested inference by exclusion in Goffin's cockatoos, and found that stimulus preferences was one of several strategies employed by the birds to solve the task. Therefore, preferences for real life objects and two dimensional images on the touchscreen are possible in mammals, and appear to be relatively common during object choice discriminations.

Table S4: Generalised linear mixed model on the proportion of trials chose S’ when paired with a known negative in Test 1, showing the direction of effects and the significance level of the terms. Z tests indicate which age groups differ from age group 1 in the respective analysis.

Response variable	Model	Minimal model	Average effect	SE	Wald statistic /Deviance	z	P
Proportion of trials chose S’	Model 9	Cycle: Cycle 2	-0.4943	0.0839	34.723		<**0.001**
		Stimulus: Group B	0.3478	0.1007	11.136		<**0.001**
		Age in months	0.0037	0.0014	6.567		**0.0104**
		Sex:Male	0.1919	0.0988	3.693		0.0546
		Neuter: Neutered	0.0953	0.1191	0.637		0.4246
		Age*Stimulus	0.0015	0.0028	0.299		0.5845
		Reward ratio: 90%	0.0562	0.1361	0.169		0.6805
	Model 10	Age group			5.358		0.2524

Table S5: Generalised linear mixed model on the number of times dogs’ chose by inference by exclusion in Test 2, showing the direction of effects and the significance level of the terms. Since there was no significant difference between the number of times dogs’ chose by inference by exclusion in cycle 1 and cycle 2 (model 10), the data was pooled and generalised linear models were applied (Model 10a, 11, 12 and 13). Z tests indicate which age groups differ from age group 1 in the respective analysis.

Response variable	Model	Minimal model	Average effect	SE	Wald statistic /Deviance	z	P
Proportion of times chose by inference by exclusion	Model 11	Cycle	0.0165	0.1279	0.016		0.8977
	Model 12	Age in months	0.0099	0.0014	45.538		<**0.001**
		Stimulus: Group B	0.7027	0.1367	27.739		<**0.001**
		Sex:Male	0.1112	0.1329	0.701		0.4026
		Age*Stimulus	-0.0028	0.0032	0.765		0.3819
		Neuter: Neutered	0.1344	0.1771	0.573		0.4490
	Model 13	Age group			54.570		<**0.001**
		Age group 2	0.4654	0.2816		1.653	0.0984
		Age group 3	0.6387	0.2989		2.137	0.0326
		Age group 4	1.2223	0.2900		4.215	<**0.001**
		Age group 5	1.3916	0.2788		4.992	<**0.001**
		Stimulus: Group B	0.7474	0.1413	29.420		<**0.001**
	Model 14	Age in months	0.0096	0.0017	45.538		<**0.001**
		Sessions to criterion	0.0008	0.0029	0.082		0.7749
	Model 15	Age in months	0.0096	0.0017	45.538		<**0.001**
		Total no. of correction trials	0.0006	0.0003	4.103		**0.0428**

Table S6: Generalised linear model on the proportion of correct trials in the first session of the memory test, showing the direction of effects and the significance level of the terms.

Response variable	Full model	Average effect	SE	Deviance	P
Number of correct first choices in Session 1	Neuter: Neutered	-0.1458	0.1397	1.0824	0.2982
	Age in months	0.0031	0.0030	1.0745	0.2999
	Sex: Male	-0.0956	0.1509	0.3984	0.5279
	Stimulus group: Group B	0.0562	0.1423	0.1560	0.6929
	Age*Stimulus group	0.0043	0.0046	0.8595	0.3539

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3. Training for eye contact modulates gaze following in dogs

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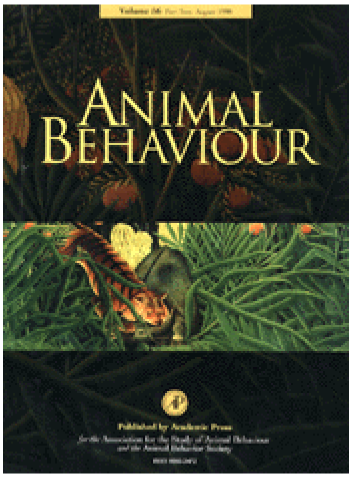

Abstract

Following human gaze in dogs and human infants can be considered a socially facilitated orientation response, which in object choice tasks is modulated by human-given ostensive cues. Despite their similarities to human infants, and extensive skills in reading human cues in foraging contexts, no evidence that dogs follow gaze into distant space has been found. We re-examined this question, and additionally whether dogs' propensity to follow gaze was affected by age and/or training to pay attention to humans. We tested a cross-sectional sample of 145 border collies aged 6 months to 14 years with different amounts of training over their lives. The dogs' gaze-following response in test and control conditions before and after training for initiating eye contact with the experimenter was compared with that of a second group of 13 border collies trained to touch a ball with their paw. Our results provide the first evidence that dogs can follow human gaze into distant space. Although we found no age effect on gaze following, the youngest and oldest age groups were more distractible, which resulted in a higher number of looks in the test and control conditions. Extensive lifelong formal training as well as short-term training for eye contact decreased dogs' tendency to follow gaze and increased their duration of gaze to the face. The reduction in gaze following after training for eye contact cannot be explained by fatigue or short-term habituation, as in the second group gaze following increased after a different training of the same length. Training for eye contact created a competing tendency to fixate the face, which prevented the dogs from following the directional cues. We conclude that following human gaze into distant space in dogs is modulated by training, which may explain why dogs perform poorly in comparison to other species in this task.

Introduction

In humans, a crucial feature of social life and communication is eye gaze, which plays a central role in social cognition. Gaze following, the ability to monitor and match another's head and eye orientation by following gaze direction into distant space, has been extensively studied in human infants. The first such study by Scaife and Bruner (1975) tested infants (of different ages) seated across from an adult experimenter who addressed the infant before turning to look to the side of the room for a few seconds. This and many subsequent studies indicate that the ability to follow gaze improves as the infant develops. This process is influenced by various factors such as perceptual skills and preferences, habituation, reward-driven learning, social environment and spatial layout (Moore, 2008 and Triesch et al., 2006).

Although several studies have highlighted the importance of investigating age differences in social cognition, especially in elderly humans, for whom reduced social communication and interaction skills have been found in comparison to middle-aged subjects (Henry et al., 2009 and Slessor et al., 2010), there are few life span studies of gaze following. The human literature has focused almost entirely on infants in their first 18 months of life, but also studies testing gaze following in chimpanzees, *Pan troglodytes*, have focused mostly on juvenile or adult animals (Teufel, Gutmann, Pirow, & Fischer, 2010).

Comparative studies in nonhuman animal species can help to shed some light on the evolutionary origins and mechanisms of gaze following (Gómez, 2005). A species of particular interest for comparative studies is the domestic dog, *Canis familiaris*. Dogs share an evolutionary and developmental history with humans as a result of their domestication, and there is ample evidence that dogs have specialized skills in reading human-given cues (Kaminski, 2009). Dogs outperform nonhuman primates in following human gaze in object choice tasks (Cooper et al., 2003 and Hare et al., 2002), and their gaze following, as is that of preverbal infants, is modulated by ostensive cuing such as direct gaze and addressing by the person, who then indicates with her gaze one of two objects or which of two containers is baited with food (Téglás, Gergely, Kupán, Miklósi, & Topál, 2012).

However, despite the human-like performance of dogs in following human-given cues in object choice tasks, there is conflicting evidence of whether dogs follow human gaze in nonforaging contexts. Recently, Met, Miklósi, and Lakatos (2014) found evidence that some dogs follow gaze to and around a barrier, even in nonforaging situations; however, as a group, dogs performed below chance. Additionally Agnetta, Hare, and Tomasello (2000) found no indication that dogs follow human gaze into distant space.

Since gaze following into distant space has been documented in many species such as apes (Bräuer et al., 2005 and Povinelli and Eddy, 1997), domesticated goats, *Capra aegagrus hircus* (Kaminski, Riedel, Call, & Tomasello, 2005), several bird species (Kehmeier et al., 2011 and Loretto et al., 2010), the red-footed tortoise, *Chelonoidis carbonaria* (Wilkinson, Mandl, Bugnyar, & Huber, 2010) and wolves, *Canis lupus* (Range & Virányi, 2011), we would expect the gaze-following response to be present also in dogs. So why do we find so little evidence that dogs follow gaze outside of object choice situations?

First, we can hypothesize that as gaze following is likely to be a product of both reflexive and learnt mechanisms (Ricciardelli, Carcagno, Vallar, & Bricolo, 2013), one explanation could be that dogs may lose their reflexive responding to human gaze cues through long-term habituation over an individual's lifetime living with human companions (the long-term habituation hypothesis). Owners often turn and gaze at objects and stimuli that are irrelevant to dogs in their daily lives, which may lead to a gradual loss of the dogs' gaze-following response. Thus we could expect young dogs' gaze-following response to be more automatic and therefore more frequent than in adult dogs, which have been affected more strongly by learnt gaze responses.

Second, dogs' lack of response to human gaze to distant space may be explained by their training. One of the first training exercises recommended for owners when getting a puppy is to condition the dog's name as an orienting cue, and to develop eye contact with the owner (Howell & Bennett, 2011). Dogs receive this training in various forms of formal training, such as in puppy school, and during obedience, agility and trick training. After giving relevant ostensive cues, which encourages the dog to pay attention, the owner then gives the next specific verbal command or visual signal usual for that training context (e.g. ‘Muffin’ and ‘come’). Dogs may pay attention to the whole of the owner's body, hand or face when anticipating the next cue (for example body orientation (used in agility), specific hand signals (used in obedience tasks) and so on). Therefore, the effects of such formal training may increase the dog's frequency and duration of fixations to the owner (while waiting for the next cue typical for the given training context), which may then interfere with the dog's response when humans present directional gaze cues that are not part of the formal training. Hereafter we refer to this explanation as the formal training hypothesis.

On the other hand, in their daily lives dogs are repeatedly asked to look at humans in many different situations in which dogs may need more flexibility in detecting the relevant communicative cues of their human partners. Such informal training for increased attention to humans is, therefore, likely to increase the chances that dogs will be able to detect human cues, such as gaze cues, and thus may increase the likelihood that the dog may follow human gaze. Since dogs have the opportunity to learn about these cues and to generalise them to different contexts over their lives, we refer to this explanation as the lifelong learning hypothesis.

There is experimental evidence that even short-term training can affect dogs' human-directed attention (Bentosela et al., 2008 and Wallis et al., 2014). Short-term training for initiating eye contact (depending on the details and the context of the training) may have a two-fold effect on gaze following: either facilitating it, as proposed by the lifelong learning hypothesis, or hindering it, according to the formal training hypothesis. To examine how such short-term training affects dogs' readiness to follow human gaze cues, we tested the dogs' gaze-following response twice, before and after training to initiate eye contact with the experimenter. On the one hand this training may serve to increase the dogs' attention to the experimenter and thus may confirm the lifelong learning hypothesis, if we find that after such training, the dogs' gaze-following propensity increases. Or, on the other hand, since our short-term training to initiate eye contact follows a specific sequence of events (dog looks up at the experimenter's face, the experimenter uses a clicker to mark the behaviour and then rewards the dog with food), the effect of this training may support the formal training hypothesis, where we would expect that the dogs would follow gaze less after than before the training.

The aims of this study were to re-examine the question whether dogs are capable of following human gaze into distant space and, if so, to investigate through age effects whether the propensity to follow gaze is affected by long-term habituation to directional gaze cues and/or training to focus their attention on humans. Thus, we tested dogs of different ages that had a shorter or longer time to habituate to human gaze cues or to learn to pay attention to relevant human-given cues. We also addressed the potential effect of formal training by examining the influence of lifelong training of different intensity. Finally, we aimed to experimentally test the effects of formal training and of learning to pay attention to humans, by comparing the gaze-following propensity of the dogs before and after training to initiate eye contact with the experimenter. To examine the effects of fatigue and/or short-term habituation during repeated testing, an additional group of dogs was tested using the same procedure, but without being trained for eye contact (instead they were trained to touch a tennis ball with their paw). Our predictions were that if long-term habituation was a key factor, older dogs would follow the gaze of the experimenter less than younger dogs. If, however, lifelong learning to pay attention to humans was important, older dogs would follow gaze more than younger ones, and also short-term training for initiating eye contact would increase gaze following. And finally, if formal training had an influence, highly trained dogs would follow gaze less than dogs with little training experience, and also short-term training for initiating eye contact would decrease the propensity of the dogs to follow gaze (see Table 1 for summary).

	Before short-term training		**After short-term training**	
Age of dog	**Young**	**Old**	**Young**	**Old**
Long-term habituation	✓	✗	✓	✗
Formal training	✓ Low training ✗ High training	✓ Low training ✗ High training	✗	✗
Lifelong learning	✗	✓	✗	✓

Table 1.
The three proposed hypotheses that could affect dogs' propensity to follow gaze and their predictions of performance in young and old dogs, before and after training.

Methods

Subjects

One hundred and forty-five dogs ranging in age from 6 months to 13 years and 10 months were divided into seven groups according to age (Table 2). All recruited dogs were border collies kept as family pets to exclude effects of different developmental and ageing speeds of different breeds. The age groups were chosen according to the timing of the main life span developmental stages in the Border collie (late puppyhood, adolescence, early adulthood, middle age, late adulthood, senior and geriatric, Siegal & Barlough, 1995). Dogs that were reported by the owner (via questionnaire) as suffering from any detrimental behavioural or cognitive effects of old age consistent with a diagnosis of canine cognitive dysfunction were excluded from the sample. Also excluded were dogs that were not medically fit, including dogs with eye abnormalities.

Age group	Life stage	Age (years)	Male	Female	Total
Group 1	Late puppyhood	0.5 to 1	10	13	23
Group 2	Adolescence	>1–2	10	13	23
Group 3	Early adulthood	>2–3	9	10	19
Group 4	Middle age	>3–6	9	12	21
Group 5	Late adulthood	>6–8	13	8	21
Group 6	Senior	>8–10	10	9	19
Group 7	Geriatric	>10	8	11	19
Total			69	76	145

Table 2.
Age and sex of subjects

The gaze-following test was part of an extensive two-part cognitive battery ('Vienna Canine Cognitive Battery', Wallis et al., n.d.), in which all dogs participated. Dogs had prior experience of working with the experimenter, and had visited the lab on a minimum of three occasions before the gaze-following test.

A lifelong formal training score was calculated for each dog using the results from an extensive demographic questionnaire filled in by the owners during the cognitive battery testing. Thirteen different training types were specified and are listed here from highest to lowest participation: puppy school, agility, basic obedience, dancing/trick training, sheep dog training, high-level obedience, companion dog training, nose work, other (including participation in other tests at the lab), therapy dog, dummy training, search-and-rescue training and protection training. Owners reported their dogs' past and current training attendance, and dogs were scored as follows: no experience = 0, sporadic training = 1, once or twice a month = 2, once or twice a week = 3 and completed training (with or without an exam) = 4. Scores for each individual for each training type were calculated up to a maximum score of 52 points. Dogs participated in an average of five different training types. Since training score was correlated with age (Spearman correlation: $r_S = 0.458, P = 0.001$), training score and age were analysed separately in all models.

An additional 13 dogs (five females, eight males; average age 48 months; range 11–112 months) were recruited separately in order to test a second group that did not receive training for initiating eye contact. These dogs did not participate in the cognitive battery, but were familiar with the lab and had been tested previously in other studies. Neither the 145 dogs in the main sample nor the additional 13 dogs in the control had been tested previously in gaze-following tasks.

Ethical Note

This study was discussed and approved by the institutional ethics and animal welfare committee at the University of Veterinary Medicine Vienna in accordance with Good Scientific Practice guidelines and national legislation (http://www.vetmeduni.ac.at/fileadmin/v/z/forschung/GoodScientificPractice_English.pdf). All subjects that participated in the study were family pets, and reward-based training was utilised in all tests conducted, with no potentially harmful experimental manipulations.

Test Setting and Procedure

The same experimenter (L.W.) conducted all the tests in an experimental room measuring 5 m × 6 m at the Clever Dog Lab. Along one 6 m wall in the test room there were two doors located approximately 2 m apart. The room was empty apart from a small table standing next to the side wall and a chair for the owner.

Phase 1

At the beginning of the experiment, the owners entered the experimental room with their dog, released it from the leash, and then sat positioned at the back wall of the experimental room and filled in a questionnaire on an iPad. Owners were instructed to ignore their dog and the actions of the experimenter, and to be as quiet and still as possible. All owners followed these guidelines, and did not attempt to interact with their dogs. The experimenter stood in the centre of the room facing either the windows or the table. She lured the dog into position in the centre of the room sitting in front of her by calling its name and using a small piece of sausage, and then obtained the dog's attention using the ‘watch’ command if necessary. If possible, she held her hands behind her back, but on some occasions it was necessary to point to her face when the dog did not take up eye contact. Looking into the experimenter's eyes in the presence of potential distracters, such as the owner and the food (placed out of reach of the dogs on a table) was the first task dogs needed to fulfil and a precondition of being tested on gaze following. As soon as the dog looked up into her face, the experimenter gave a surprised expression (raised eyebrows, wide eyes, open mouth and intake of breath, see Fig. 1a, b) and either turned her head swiftly and looked to the door for 10 s (test condition Fig 1c) or looked down at her feet for 10 s (control condition Fig. 1d). The cue was presented for a total of 10 s to enable the recording of the first detectable head turn of the dog away from the experimenter, in line with previous studies on gaze following in mammals (Bräuer et al., 2005, Call et al., 1998, Kaminski et al., 2005 and Range and Virányi, 2011). The order of presentation (test/control) was counterbalanced, as was the direction of looking at the door (right/left). In the first session of gaze following two test and two control trials were performed (see the Supplementary Material for a video of the test and control conditions).

Photographs © Clever Dog Lab

Figure 1.

(a) The experimenter centred the dog in the room and gained its attention by calling its name and the command ‘watch’. (b) As soon as the dog looked into her face she immediately made a surprised expression. The gaze cue was then delivered to the dogs in the (c) test and (d) control conditions.

Phase 2

Group eye

After the first gaze-following session, 145 dogs received an intensive training session to initiate eye contact with the experimenter. The experimenter used a secondary reinforcer (clicker) to mark the correct behaviour of looking up into her face, and immediately rewarded the dog after each occasion by throwing onto the floor a small piece of sausage obtained from a food pouch on her back. To initially attract the dog's attention, the experimenter first threw food onto the floor, and then remained motionless waiting for eye contact. No commands were given by the experimenter, and if the dog wandered more than 2 m away from her, she rustled the bag containing the sausage to attract the dog's attention. Importantly, during this training the experimenter never looked to the side; thus the dogs were not trained on gaze following but to look up into her face and establish eye contact. There was no criterion required in the training; each dog participated for a total of 5 min, during which over 95% of the sample achieved a minimum of 20 clicks and rewards.

Group ball

The additional 13 dogs participated in a 5 min long training session with the same experimenter that did not include training for initiating eye contact. After a short ball play session with the experimenter (the ball was rolled across the floor three times and the dog was encouraged to retrieve it), the dog was trained initially to touch the ball held in the experimenter's hand with its paw and once successful, to touch the ball with the paw when the ball was on the ground. First, the ball was removed, and then the experimenter kneeled on the floor in front of the dog, gained the dog's attention, and asked the dog to ‘shake’ paws with her using a verbal command and hand signal (presentation of the palm of the hand in front of the dog). When the dog touched the experimenter's hand with its paw, she clicked the clicker and the dog received a small piece of sausage as a reward. Once the dog successfully completed six clicks, the experimenter hid the ball in her hand, gave the ‘shake’ command and at the last instant turned the ball face up, and clicked and rewarded the dog for touching the ball with its paw. At all times the experimenter ensured that the dog was paying attention by calling the dog's name and gaining eye contact with the dog, before giving the verbal command and hand signal. When the dog responded correctly on a further six occasions, the experimenter placed the ball on the floor and encouraged the dog to touch it with its paw. If the dog did not respond to the command, or attempted to take the ball in the mouth, the experimenter went back to the previous successful step. This training lasted for a total of 5 min.

Phase 3

Immediately after being trained by the experimenter, dogs were tested in a second session of gaze following. Methods were exactly the same as in session 1, except that for the eye group, sausage was no longer needed to centre the dog in a sitting position in front of the experimenter, and the command ‘watch’ was no longer necessary, as dogs were highly motivated to attend to the experimenter after the clicker training for initiating eye contact. Again two test and two control trials were performed, which amounted to a total of four test and four control trials per dog over the two sessions.

Data Collection and Statistical Analysis

Four digital video cameras connected to a video-recording station outside the test room were used to videotape the tests. The video-coding software Solomon Coder beta 12.09.04 (http://solomoncoder.com) was utilised to analyse the videos with a continuous sampling technique. All statistical analyses were performed in R 3.0.1 (R Core Team, 2013).

Clicker training for initiating eye contact

Throughout clicker training for initiating eye contact we measured the latencies until the dogs gained eye contact with the experimenter in order to investigate whether dogs differed by age in their ability to establish eye contact. The methods and results from this experiment have been reported elsewhere (Wallis et al., 2014). Since we previously showed that performance peaked in age group 4, we decided to take this group as a baseline to compare with the other age groups. Other than a short summary of the dogs' performance in this test, there is no overlap between the data sets utilised in this paper and in Wallis et al. (2014).

Gaze following

We measured whether or not the dog's first detectable head turn was towards the door within 2 s of the experimenter cue (first look door: yes/no). In line with previous studies analysing gaze patterns (Miklósi, Polgárdi, Topál, & Csányi, 2000;Range & Virányi, 2011;Russell, Bard, & Adamson, 1997), gaze-following ability was determined at the group level by the presence of a significant difference between the probability of looking at the door first within 2 s of the cue, in the test and the control trials.

Percentage time gaze experimenter face

We also measured the percentage of time the dog gazed at the experimenter's face in each of the four 10 s trials (in test and control).

Interobserver reliability

A randomly chosen set of 20 dogs was double coded independently by two coders, and interobserver reliability was good for percentage gaze experimenter face ($r > 0.73, P < 0.001$) and excellent for first look door (Cohen's Kappa = 0.91, $P < 0.001$).

Statistical models

We analysed the results using generalised mixed models (GLMMs, Pinheiro & Bates 2000) with a binary response term for first look door and linear mixed-effects models (LME, Davidian & Giltinan, 2003) for percentage gaze experimenter face, which was square-root transformed in order to obtain a normal distribution. Condition (test versus control), session (before versus after training), age (continuous), experiment order (test first versus control first) and direction of the cue given (left versus right) were included as fixed effects and dog identity was included as a random factor in the models. Additionally, the potentially confounding variables clicker experience, sex, neuter status and training score were included as fixed effects. Statistical models were calculated first for age as a continuous variable; we tested for linear and/or quadratic relationships. If an age effect was found, separate models were calculated with age as a categorical variable to look for specific differences between age groups. We included the two-way interactions between (1) condition and age and condition and training score to test for any age or training effects that may be restricted to one condition, and (2) session and age and session and training score to test for the effect of short-term training. Additionally, we examined the two-way interaction between group (Ball or Eye) and session, to determine whether first look door and percentage gaze experimenter face differed between the groups after training.

Normality and homoscedasticity were assessed via residual distribution plots. The terms in the models were tested using likelihood ratio tests, comparing the model containing the new term with a model excluding the new term. Nonsignificant terms ($P > 0.05$) were removed stepwise from the models. Results are presented as mean ± SD unless otherwise indicated.

Results

Clicker Training for Initiating Eye Contact

The results of the clicker training for initiating eye contact have been reported previously (Wallis et al., 2014). All age groups were able to improve their initial performance in latency to eye contact over the first 20 trials within the 5 min period. Group averages in trial 20 ranged from 2 to 4.2 s, compared to 4.5–8 s in trial 1. Therefore this task was effective in training the dogs to gain eye contact with the experimenter.

First Look Door

The proportion of dogs that first looked towards the door within 2 s was significantly higher in the test condition (the experimenter looked to the door) than in the control condition (the experimenter looked at her feet; Table 2, Fig. 2), providing evidence for a propensity to follow the gaze of the experimenter. Overall, 48% of the sample followed the gaze of the experimenter to the door (first look within 2 s) in at least one of the four test trials, but did not look towards the door in the control. The relationship between age and first look door was best described by a quadratic function (Table 3, Fig. 2a). We did not find any significant interactions. Dogs looked significantly more to the door in session 1 (before training) than in session 2 (after training).

Fixed effects	Estimate	SE	Wald χ^2	*P*
Condition: test	1.914	0.262	74.412	<0.001
Age in months: linear	−7.271	4.094	2.861	0.091
Age in months: quadratic	13.361	4.071	10.339	<0.001
Session: session1	0.708	0.214	11.560	<0.001

Table 3: Factors affecting whether the dogs first look within 2 s was to the door

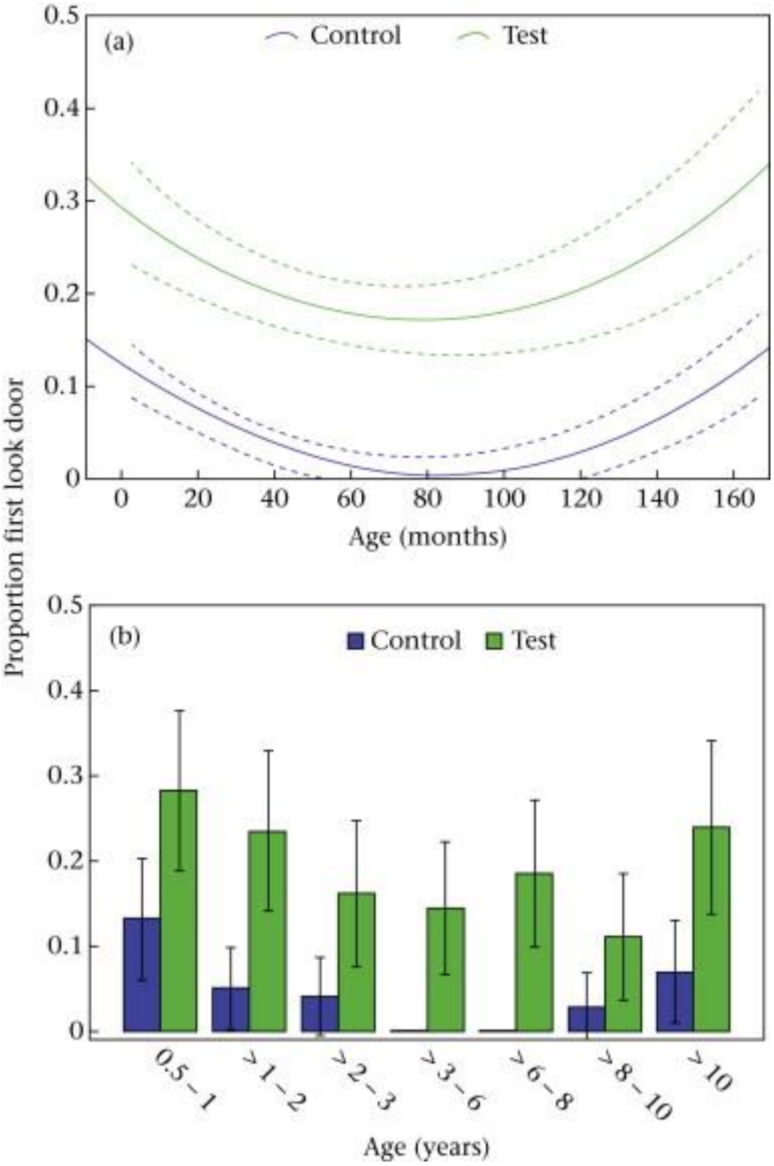

Figure 2.

(a) Relationship between age in months and the mean proportion of dogs that first looked to the door within 2 s in the test and control conditions (with 95% confidence intervals; dotted lines). (b) The mean proportion of dogs in each age group that first looked to the door within 2 s in the test and control conditions (error bars represent SEs).

When comparing the age groups, we found a significant difference in the propensity of dogs to look to the door ($\chi^2 = 16.928$, $P = 0.009$; Fig. 2b). Age group 1 differed significantly from the baseline (age group 4; $z = 3.309$, $P = 0.001$). That is, dogs in late puppyhood looked significantly more often towards the door within 2 s in both conditions than middle-aged dogs.

When comparing the two groups with or without training for initiating eye contact with the experimenter, we found that dogs in Group Eye looked significantly less often to the door within 2 s than dogs in Group Ball (estimate = −1.996, $\chi^2 = 12.538$, $P < 0.001$). There was a significant interaction between group and session (estimate = 1.279, $\chi^2 = 5.495$,$P = 0.019$; Fig. 3a): the number of looks to the door increased in Group Ball after training, but decreased in Group Eye.

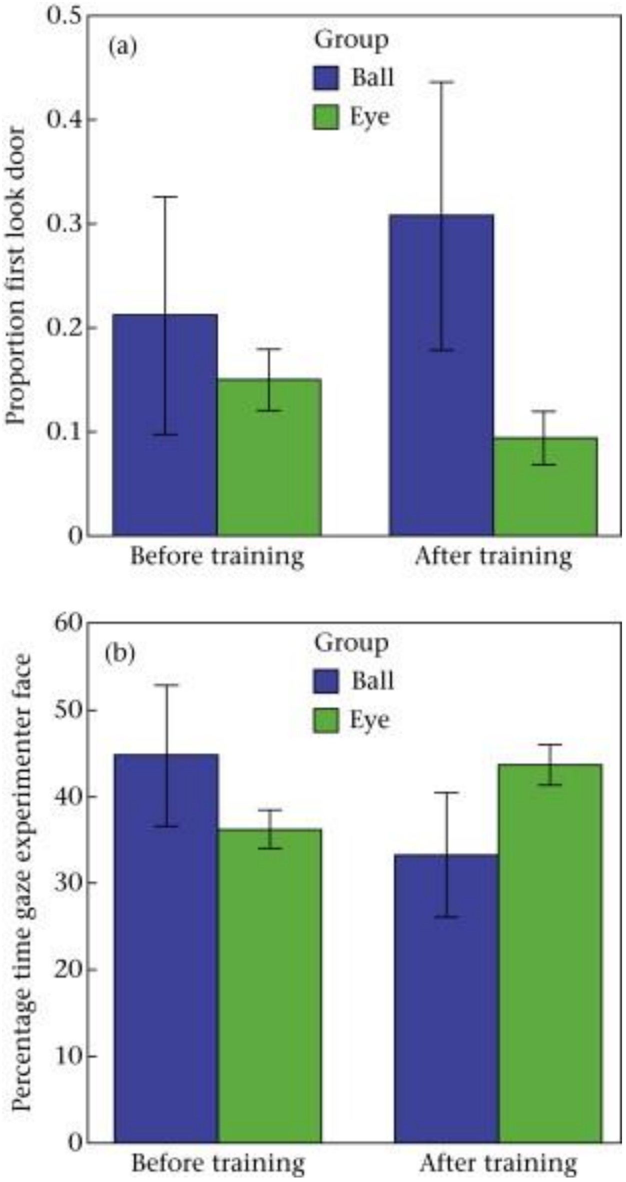

Figure 3.
Results from Group Ball and Group Eye before and after training in (a) the mean proportion of dogs that first looked to the door within 2 s and (b) the mean percentage of time dogs gazed at the experimenter's face (error bars represent SEs).

In a separate model, the effect of lifelong training score was examined. A significant negative linear relationship between the training score and the proportion of the first look towards the door was found (estimate = −0.05, $\chi^2 = 6.198$, $P = 0.013$; Fig. 4). In both conditions, dogs with more formal training experience looked significantly less to the door than dogs with little or no training experience.

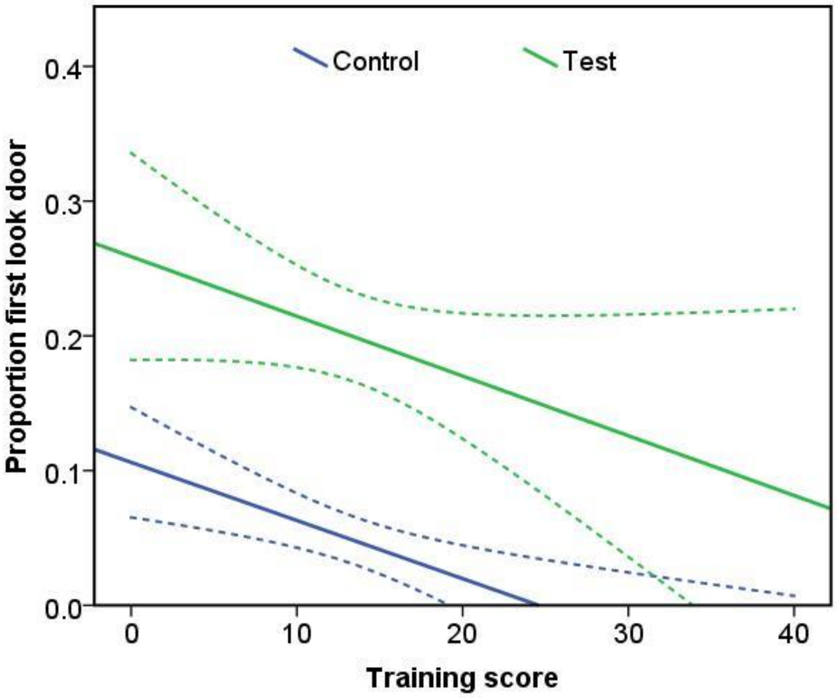

Figure 4.
Long-term formal training-related changes in the proportion of dogs that first looked at the door within 2 s in test and control conditions (with 95% confidence intervals; dotted lines).

Time Spent Gazing at Experimenter's Face

On average the dogs gazed at the experimenter's face for 39.7 ± 26.9% over all trials (or around 4 s per 10 s trial). There was no significant difference between percentage gaze experimenter face in the test condition and the control. The relationship between age and percentage gaze experimenter face was best described by a quadratic function (Table 4). Dogs looked for significantly less time at the experimenter's face in session 1 (36.20 ± 26.56%; before eye contact training) than in session 2 (43.62 ± 26.76%; after training; Table 4). There was a significant interaction between session and age. Percentage gaze experimenter face increased after training particularly in middle-aged dogs (Fig. 5).

Model term	Value	SE	*F*	*P*
Session: before training	−0.674	0.123	30.782	<0.001
Age in months: quadratic	−16.096	4.477	4.490	0.011
Session: age in months: quadratic	11.283	4.155	3.753	0.024

Table 4.
Factors affecting dogs' mean percentage of duration of gaze to the experimenter's face over the eight trials (four control trials and four test trials) each of 10 s duration

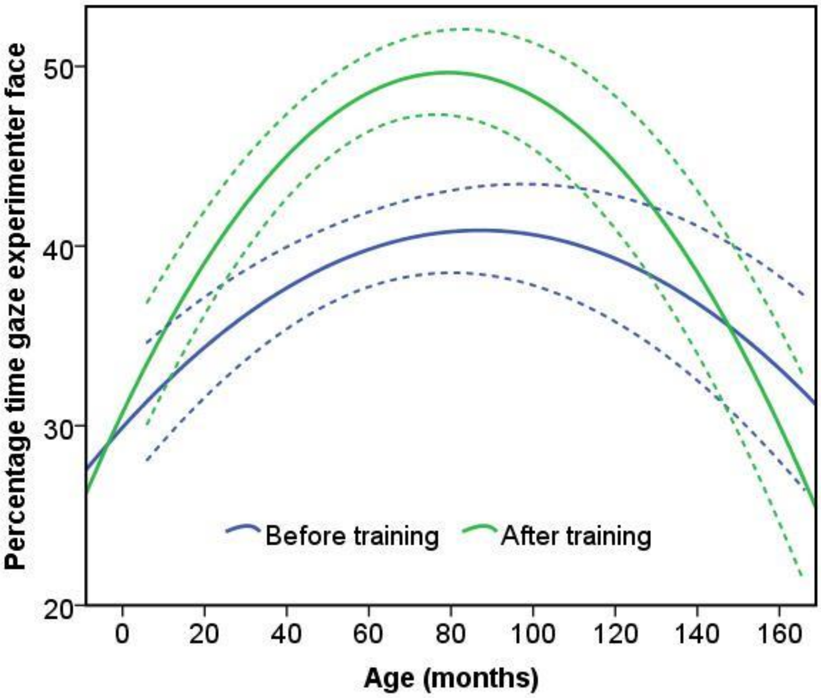

Figure 5.
Age-related changes in the percentage of time the dogs gazed at the experimenter's face before and after clicker training for initiating eye contact (with 95% confidence intervals; dotted lines).

When comparing the age groups, we found a significant difference in the tendency to gaze at the experimenter's face (LME: $F_{6,138} = 2.663$, $P = 0.018$). Percentage gaze experimenter face was significantly lower in age groups 1, 2 and 3 than in age group 4 ($t > 2.52$, $P = 0.013$).

When comparing Group Eye with Group Ball, we found a significant interaction between group and session (LME: $F_{1,1043} = 17.733$, $P < 0.001$; Fig. 3b). The percentage of time the dogs gazed at the experimenter's face increased after training in the eye group, but decreased in the ball group.

In a separate model, the effect of lifelong training score was examined. A significant interaction between condition and training score in the percentage gaze experimenter face was found (LME: $F_{1,956} = 5.297$, $P = 0.021$; Fig. 6). Dogs with more formal training experience looked significantly longer at the experimenter's face than dogs with less training experience, but only in the test condition.

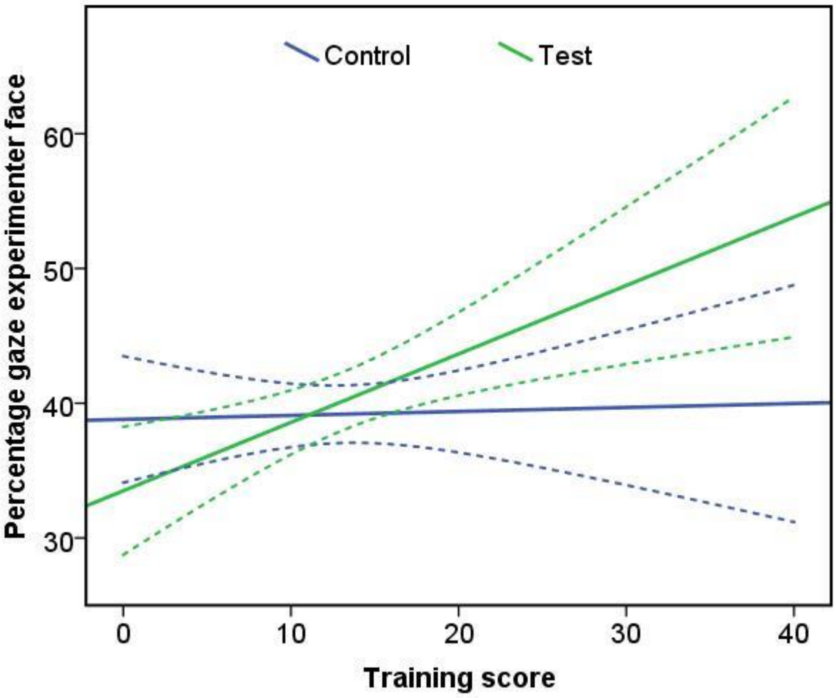

Figure 6.

Age-related changes in the average percentage of time the dogs gazed at the experimenter's face in the test and control conditions (with 95% confidence intervals; dotted lines).

Discussion

The aims of the current study were to examine whether domestic dogs follow human gaze into distant space, and if so, whether their performance changes over their lives due to the effects of either long-term habituation or long-term learning to pay attention to humans, and finally, to determine the effects of short-term training for initiating eye contact and long-term formal training on gaze-following behaviour. Taken together, our results provide the first evidence that the domestic dog is able to follow the gaze of a human into distant space using the traditional test paradigm utilised for human infants (Scaife & Bruner, 1975), and emphasizes the effects of both lifelong formal training as well as short-term training for initiating eye contact on the propensity of dogs to follow gaze.

Our results confirm that border collie dogs show gaze-following behaviour at least when a communicatively relevant pattern of ostensive and referential signals is presented, and, additionally, that they do so outside an object choice context. All age groups were able to follow human gaze, and the propensity to follow gaze did not differ between groups. Around 50% of dogs followed gaze in at least one of the four test trials but did not look towards the door in the control. However, when all test trials were considered dogs followed gaze within 2 s in only 20% of trials. But when we removed the 2 s restriction and examined whether dogs followed gaze within 10 s, this figure jumped to 40%. Previous studies on gaze following into distant space in other species have described similar gaze-following rates between 37% and 80% (Bräuer et al., 2005, Kaminski et al., 2005, Kehmeier et al., 2011, Met et al., 2014 and Range and Virányi, 2011).

Our results indicate that age (including lifelong habituation to gaze cues from humans or learning to attend to relevant human-given cues) had no effect on the gaze-following rates of dogs. However, the frequency of looks to the door showed a quadratic developmental trajectory over the dogs' lifetime, with dogs in late puppyhood and geriatric dogs showing the greatest tendency to look to the door in both test and control trials, and middle-aged dogs the lowest. As the peaks were reflected in both test and control conditions, the actual gaze-following ability of the dogs did not change over their lifetime. One explanation for the differences in the age groups could be that the youngest and oldest dogs were unable to inhibit following the salient head turn of the experimenter, and displayed greater distractibility in general, which resulted in an increased frequency of gazing to the door in the control trials and less time gazing at the experimenter's face over the 10 s trials in both conditions. There is evidence that younger and older dogs are less able to inhibit their behaviour in multiple contexts, although the reasons for decreased inhibition may be different at the different ages (Bray et al., 2014 and Tapp et al., 2003). In the youngest dogs' case, this could, for instance, be due to greater general activity levels, and a higher sensitivity to external environmental stimuli (see Wallis et al., 2014). The higher distractibility of young and old dogs may have masked any potential effects of lifelong learning influences on gaze following in dogs. Perhaps for this reason, we found no evidence that during their lifelong interactions with humans, dogs would learn to pay attention to them and learn when and which of their visual cues are relevant for them.

Despite the age effects on the gazing pattern of dogs described above, across the entire sample, dogs with more formal training experience looked significantly less often to the door irrespective of condition, and in the test trials looked significantly longer into the experimenter's face than dogs with little or no training. These results provide additional evidence that dogs' human-directed behaviours are significantly influenced by their individual training experiences (Marshall-Pescini, Passalacqua, Barnard, Valsecchi, & Prato-Previde, 2009). Prior to the start of our study, the subjects had undergone several different types of formal training over their lives, all of which involved paying attention to humans and receiving subsequent verbal and visual signals from them, which seems to have inhibited their automatic gaze-following response in a social context. Since the different types of formal training the dogs engaged in may have contributed differentially to their gaze-following performance (e.g. by training them on sustained attention to humans or on anticipating a set of signals), future studies should aim to disentangle these effects by examining each training type individually (Scandurra, Prato-Previde, Valsecchi, Aria, & D'Aniello, 2015).

Surprisingly, after just 5 min of clicker training for initiating eye contact, dogs of all ages were less likely to follow gaze and spent more time watching the experimenter's face (in test and control trials). Even though the Group Eye dogs were trained to only briefly orient to the experimenter's face, in the subsequent gaze-following trials the dogs sustained their gaze to the face and ignored the gaze cue. Short-term training was most effective in dogs in early to late adulthood. Importantly, we did not find the same effect of short-term training in a second group, Group Ball, which was trained to touch a ball with their paw. In the absence of training for initiating eye contact with the experimenter, the number of looks to the door increased from session 1 to session 2, indicating that the decrease in gaze following in dogs trained for eye contact cannot be explained by a fatigue effect, or by a short-term habituation to the gaze cue. One explanation for the difference in performance between the groups is that dogs in Group Eye might have perceived the clicker training for initiating eye contact and the gaze following after the training as the same training situation, and as such, they might have simply been waiting for the experimenter to click and reward them. However, the training the dogs received in Group Ball might have been sufficiently different from the gaze-following setup, in that the dogs did not anticipate a click or reward in the gaze-following trials, and therefore were more likely to follow the experimenter's gaze cue.

In sum, our findings do not support the hypothesis that training to pay attention to humans (either during lifelong experiences with them or during formal training) would increase the propensity of dogs to follow gaze. On the contrary, both lifelong formal training and our short experimental training for initiating eye contact created a strong tendency for dogs to sustain their gaze to the human face, and thus prevented them from following the experimenter's gaze to the door. The most likely explanation for this is that training in general creates a competing tendency to fixate on the face, which interferes with the dog's response to the referential cue given by the experimenter. It is possible that the dogs' expectation of certain verbal commands and visual signals specific for the context of their training (such as waiting for the click and treat in the clicker training for initiating eye contact) explains why they did not respond to another cue, the referential gaze of the experimenter.

There are multiple possibilities that could explain why gaze following to distant space was present in this study, but was absent in the Agnetta et al. (2000) study. Positive results found in this study may be due to the motivational effect of positive training exercises the dogs participated in with the experimenter. On at least two preceding visits, the dogs in Group Eye in our study received high-value food rewards (sausage) from the experimenter in training contexts, which is known to increase attention to humans in domestic dogs (Lindsay, 2001).

In light of the recent results from Téglás et al. (2012), who found that communicative context influenced dogs' gaze-following rates, perhaps the absence of sufficient ostensive cuing (for example addressing the individual by name) caused the dogs in Agnetta et al.'s study to ignore the actions of the experimenter. Cue saliency could also have affected dogs' performance in the current study. Ostensive cues directed towards the dog just before giving the gaze cue may have increased the saliency of the cue, and helped to maintain the dog's attention on the face long enough for it to perceive the cue direction. The fact that we used border collies as our test subjects might have influenced our results. Border collies have been selectively bred for generations as a herding dog to work cooperatively with humans, and as a consequence are particularly sensitive to human visual and acoustic stimuli (Gácsi et al., 2009, McConnell and Baylis, 2010 and Passalacqua et al., 2011).

Finally, studies in humans confirm that gaze following occurs more often when the other individual's gaze is oriented towards an object that is of particular relevance to the observer (Ricciardelli et al., 2013). Doors may hold particular social relevance to dogs, as even dogs as young as 6 months already have ample experience with doors, and the possibility that an individual may enter at any time. Gaze cues towards areas of particular relevance for dogs, such as the door in this case, might have facilitated the gaze-following response by providing contextual relevance.

Conclusion

Our results provide the first scientific evidence that the domestic dog is able to follow the gaze of a human into distant space outside an object choice or barrier task context. Of the three hypotheses suggested as possible modulators of gaze following in dogs, long-term habituation, lifelong learning and formal training, only formal training was found to directly influence (decrease) gaze following. This effect was further confirmed by finding a similar, hindering, effect of short-term training for initiating eye contact on the propensity to follow gaze.

Although we found no age effect on gaze following in dogs, developmental effects on distractibility might have influenced the dogs' response. Future studies should aim to test dogs younger than 6 months, in order to more closely study the ontogeny of gaze following. An experimental investigation of long-term and short-term habituation to human gaze cues would provide essential developmental information.

In the current study, an extensive history of formal training as well as short-term training for initiating eye contact decreased the dogs' tendency to follow gaze and increased dogs' duration of gaze to the experimenter's face. We conclude that in dogs, following human gaze to distant space is modulated by training in different contexts. Our results may explain why previous studies on dogs have failed to find a gaze-following response when cues to distant space have been used, and also why dogs perform relatively poorly in comparison to other species in this task.

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4. Lifespan development of attentiveness in domestic dogs: drawing parallels with humans

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Abstract

Attention is pivotal to consciousness, perception, cognition, and working memory in all mammals, and therefore changes in attention over the lifespan are likely to influence development and aging of all of these functions. Due to their evolutionary and developmental history, the dog is being recognized as an important species for modeling human healthspan, aging and associated diseases. In this study, we investigated the normal lifespan development of attentiveness of pet dogs in naturalistic situations, and compared the resulting cross-sectional developmental trajectories with data from previous studies in humans. We tested a sample of 145 Border collies (6 months to 14 years) with humans and objects or food as attention attractors, in order to assess their attentional capture, sustained and selective attention, and sensorimotor abilities. Our results reveal differences in task relevance in sustained attentional performance when watching a human or a moving object, which may be explained by life-long learning processes involving such stimuli. During task switching we found that dogs' selective attention and sensorimotor abilities showed differences between age groups, with performance peaking at middle age. Dogs' sensorimotor abilities showed a quadratic distribution with age and were correlated with selective attention performance. Our results support the hypothesis that the development and senescence of sensorimotor and attentional control may be fundamentally interrelated. Additionally, attentional capture, sustained attention, and sensorimotor control developmental trajectories paralleled those found in humans. Given that the development of attention is similar across humans and dogs, we propose that the same regulatory mechanisms are likely to be present in both species. Finally, this cross-sectional study provides the first description of age group changes in attention over the lifespan of pet dogs.

Introduction

One of the most intensely studied cognitive processes in humans and animals is attention: the ability to selectively process one aspect of the environment over others. Attention is pivotal to perception, consciousness and will (Washburn and Taglialatela, 2006). In humans the different components of executive control (including attentional control) develop at different ages, and follow a quadratic relationship with age over the lifespan; increasing in power, speed and complexity from infancy to young adults, and declining differentially in old age depending in part on the brain areas involved (Craik and Bialystok, 2006).

Attention has been proposed to consist of multiple components that interact during cognitive functioning (Cornish et al., 2006). One model, which clearly delineates the separate components of attention, is Sohlberg and Mateer's (2001)hierarchical clinical model of attention. The model was originally based on the recovery of attentional processes of brain damaged patients after coma, and details five components of attention recruited in tasks of increasing difficulty: focused, sustained, selective, alternating, and divided attention. Each separate component of attention has been extensively studied in humans, which has led to the discovery of different effects of age on the development of attention. For example, age has little influence on orienting to a single location (Enns and Cameron, 1987), and adult efficiency is already reached at 5–7 years of age (Michael et al., 2013). There was also little influence of age on simple sustained attention measures over short periods (Giambra and Quilter, 1988; Berardi et al., 2001). Performance in alternating attention (task switching) and selective attention tests depends on an individual's level of executive attentional control, and crucially involves active inhibition (Cepeda et al., 2001). Both have been found to follow a U shaped developmental trajectory in humans, with abilities peaking in the 20- to 30-year-old age groups (Cepeda et al., 2001; Clark et al., 2006). One other important additional component of cognitive development and decline which could affect attentional abilities is age-related changes in sensory and motor processes. In a cross-sectional lifespan study, Clark et al. (2006) found that two measures of sensorimotor abilities of humans followed quadratic age trends, with performance peaking at the 20–39 years middle age range.

Except in humans, rats and some non-human primates, studies that incorporate measurements of the separate components of attention and sensorimotor control over the lifespan are lacking in mammals and birds. Since attention is a complex cognitive process, and the effect of aging varies with the different aspects of attention investigated, comparative lifespan studies can help to clarify and confirm the main findings in the human literature (Macphail, 1987). Non-human mammals have the same general patterns of development and decline of cognitive functions as humans (Pearce, 2008) and can provide good models for the development and aging of specific cognitive domains. From previous studies we know that attention operates in non-human mammals in much the same way as it does in humans (Blough, 2006). However, the few studies on the development of attention in non-human mammals provide limited knowledge for four reasons: (1) they have focused solely on tests that require extensive training amounting to weeks, months, or even years of testing: such as selective attention performance and response latencies in discrimination learning or matching tests, and thus did not attempt to measure the array of components which constitute attention. (2) Many have failed to provide an adequate sensorimotor control. (3) They tested only lab animals, and of those, (4) small sample sizes with only few age groups were used (Bartus et al., 1979; Presty et al., 1987; Rapp, 1990; Adams et al., 2000; Schoenbaum et al., 2002). Despite of these limitations, the laboratory beagle, on which the majority of studies examining age differences in dogs have focused, has been recognized as a useful animal model, since their measures of learning, memory, and executive function decline with age, similarly to humans (Tapp et al., 2003).

On the other hand, the classic paradigms originally developed for examining attention in humans have so far rarely been used on pet dogs (selective attention: Mongillo et al., 2010; sustained attention: Range et al., 2009b), though this would allow for better comparisons with humans over the lifespan. Even fewer studies have carried out direct comparisons between laboratory dogs and humans in tasks involving attention, and their results are not conclusive. For instance, in the study ofBoutet et al. (2005), dogs showed significant age-dependent deficits, but results from the human sample revealed no age effects.

In contrast to dogs, rodents and primates kept in laboratories, pet dogs present useful subjects for several reasons. Pet dogs are not only available in a great numbers, but they also share an evolutionary and developmental history with humans due to domestication. Dogs can be tested in their natural environment that they share with humans, often using the same observations and experimental protocols (Miklósi et al., 2004). Increasingly the dog is being recognized as an important species for modeling healthspan and longevity, aging and associated diseases such as Alzheimer's disease (Opii et al., 2008), and psychiatric disorders, such as human obsessive–compulsive disorder (Rapoport et al., 1992) and attention deficit hyperactive disorder (Lit et al., 2010) due to the fact that dogs share the same challenges in their daily lives as humans. Despite being distantly related genetically, the fact that pet dogs have evolved in a human-dominated environment may have led to the development of similar social behaviour to humans (Hare and Tomasello, 2005), which increases the probability that dogs and humans may share some of the same brain mechanisms (Miklósi et al., 2007). The high genetic variability and differing environmental experiences found in pet dogs provides the foundation for individual differences and personality (Jones and Gosling, 2005), and can contribute to a more realistic picture of development and aging of cognition. In contrast, animals kept in standardized laboratory conditions are often from highly inbred lines, with limited social and environmental experience.

Finally, from an applied perspective, studying lifespan development of attentiveness is particularly relevant for dogs, since a large proportion of the general public lives and interacts with dogs on a daily basis (Coren, 2012). The extent to which a dog can concentrate selectively on specific aspects of the environment and to exclude others is of utmost importance for effective training, social learning, and communication; all of which rely crucially on a dogs' ability to maintain attention toward humans (Lindsay, 2001; Range et al., 2009a).

The majority of studies examining cognitive abilities in pet dogs have used cross-sectional designs, by examining just a few age groups. Such studies give little information on how task performance develops with age. Cross-sectional studies can be used to indicate developmental change by allowing trajectories to be mapped from individuals at different developmental stages (Thomas et al., 2009). They cannot replace longitudinal studies however; one major concern is that there is no guarantee that behaviour on the same test is being driven by the same processes at different ages. Nevertheless, cross-sectional studies provide valuable information as they can form the basis to design subsequent efficient longitudinal studies (Kraemer et al., 2000). The importance of robust methods when using developmental trajectories in cross-sectional studies has been recently emphasized (Thomas et al., 2009). The use of the trajectory method to study developmental relations is possible wherever there is a wide age range in the sample, and as long as the influence of outliers, or the presence or absence of ceiling and floor effects are checked. The cross-sectional method commonly used begins by constructing a trajectory for each attentional measure across normally aging individuals at different ages. In subsequent studies, the trajectories of groups suffering from canine cognitive dysfunction (CCD) or attention deficits can be compared to this reference by linking changes in performance to chronological age, and establishing whether impairments exist (Annaz et al., 2010), and the cross-sectional studies can be followed up by longitudinal studies to corroborate the data.

The goals of the present study were to (1) develop attention tests, which can be used to examine the effects of development and aging (but do not require extensive training), by adapting simplified versions of tests from the human literature, (2) investigate the normal rate of attention development and decline in a cross-sectional sample of pet dogs ranging in age from 6 months to old age, (3) compare the basic developmental trajectories of the different sub-processes of attention and sensorimotor control in humans using results from previous studies, with the present results found in pet dogs. Compiling cross-sectional data from the majority of the dogs' life course will allow us to examine normative change, which occurs when individuals change in a similar way during a specific period within the life course (McCrae et al., 2000). For these purposes we tested dogs with humans and with objects or food as attention attractors in two separate experiments in order to assess their attentional capture, sustained attention, selective attention, and their sensorimotor abilities.

General Methods

Subjects

One hundred and forty five dog-owner dyads participated in this study. Dog ages ranged from 6 months to 13 years and 10 months (Table 1). All recruited dogs were Border collies to exclude effects of breed differences. Owners could participate with more than one dog, therefore there were more dogs than owners (*N* = 122). There were more female than male owners, (*F* = 108, *M* = 14) and owners were aged between 12 and 72 years. Recruitment was concluded on the completion of seven age groups (Table 1). The choice of the age groups aimed to reflect the developmental periods in the Border collie [late puppyhood, adolescence, early adulthood, middle age, late adulthood, senior, and geriatric (Siegal and Barlough, 1995)].

Age group	Life stage	Age in years	Mean + SD age in years	Male (neutered)	Female (neutered)	Total
Group 1	Late puppyhood	0.5 to 1	0.83 + 0.11	10 (0)	13 (1)	23
Group 2	Adolescence	> 1 – 2	1.51 + 0.32	10 (2)	13 (2)	23
Group 3	Early adulthood	> 2 – 3	2.54 + 0.32	9 (4)	10 (3)	19
Group 4	Middle age	> 3 – 6	4.62 + 0.89	9 (4)	12 (5)	21
Group 5	Late adulthood	> 6 – 8	7.13 + 0.63	13 (7)	8 (8)	21
Group 6	Senior	> 8 – 10	8.88 + 0.57	10 (5)	9 (9)	19
Group 7	Geriatric	> 10	11.61 + 1.03	8 (6)	11 (11)	19
Total				69 (28)	76 (39)	145

TABLE 1. Age, sex, and reproductive status of subjects.

All dogs were tested in the “Vienna Canine Cognitive Battery” (Wallis et al., in preparation), of which the attention tests used for this study were a part. The dogs had visited the lab on a minimum of three occasions before the attention testing, and all had prior experience of working with the experimenter.

Owners filled in an extensive demographic questionnaire to obtain details on their dog’s training experience including 13 different training types. Puppy school (83% participated), basic obedience (68%), high level obedience (49%), Protection training (3%), agility (70%), search and rescue training (6%), companion dog training (31%), dog dancing/trick training (54%), dummy training (11%), nose work (27%), sheep dog training (52%), therapy dog (13%) and other (22%). On average, dogs participated in five different training types. Dogs scored according to attendance: no experience = 0, sporadic training = 1, once or twice a month = 2, once or twice a week = 3, and completed training (with or without an exam) = 4. Individual scores in each type of training were added up to a maximum of 52 points. Training score was correlated with age in months (Spearman's *rho* = 0.458, *p* = < 0.001), therefore in all models, training score and age were analyzed separately. To take into account the dogs' current training participation, the average number of training hours per week was calculated for each dog. This calculation was made based on its current training schedule when the cognitive battery was performed. Mean training hours per week was 5.6 ± 4.49, (range from 0 to 25 h) and was negatively correlated with age in months (Spearman's *rho* = -0.272, *p* = 0.001). However, training score and current training hours were not correlated (Spearman's *rho* = 0.016, *p* = 0.394).

Criteria for Exclusion of Subjects

To be included in the study, dogs were required to meet specific criteria. Owners filled in information about their dogs' recent medical care, disease history, and whether their dogs were currently on any medication. Dogs which were not medically fit [including dogs which suffered from eye abnormalities or second stage (visible) cataracts] were excluded, or testing was postponed until they were in normal health (testing of one dog was postponed due to false pregnancy, another due to actual pregnancy). Owners of dogs older than 6 years also filled in a CCD questionnaire [translated into German, based on Salvin et al. (2011a)]. None of the dogs showed significant behavioural signs of CCD (according to the CCD rating scale; all scored under 50 points). Only three dogs had to be excluded: one because of video recording malfunction, and two because of medical problems.

Test Setting

All tests were conducted in an experimental room (5 m × 6 m) by the same experimenter who was blind to the age of the subjects. In the testing room two doors were located approximately 2 m apart on one wall. The only furniture present was a small table standing next to the side wall and a chair for the owner.

Data Collection and Statistical Analysis

Tests were videotaped using a set-up of four digital video cameras, which were connected to a video station outside of the testing room. Videos were analyzed with Solomon Coder beta 12.09.04 (Copyright © 2013 by András Péter) using a continuous sampling technique. Statistical analyses were performed in R 3.0.1 (R Core Team, 2013). Separate statistical models were calculated first with age as a continuous variable (we tested for linear and/or quadratic relationships), and then with age as a categorical variable to look for specific differences between age groups. Separate models were also calculated to assess the effects of training score and current training hours. Normality and homoscedasticity were assessed via residuals' distribution charts and plots of residuals against fitted values. Non-significant predictors ($p > 0.05$) were removed from the model, and are not reported in the results. Results are presented as mean ± standard deviation unless otherwise indicated. To analyze the effect of outliers, variables were converted to standard *z* scores, any outliers of *z* scores of greater than ±3 were removed from the analysis, and the models re-run.

Experiment 1: Attentional Capture and Sustained Attention

In experiment 1 we tested whether dogs' attentional capture and their sustained attention differed by age in two different contexts, Event 1 comprised of a moving object, and Event 2 a moving human and object. Previous research on attention in monkeys using a touch screen by Baxter and Voytko (1996) determined that attentional capture was preserved in aged rhesus monkeys. Zeamer et al. (2011) compared sustained attention in healthy young and aged rhesus monkeys, using a continuous performance task (individuals were trained to respond to one of three stimuli by touching a screen). Results showed that aged animals made significantly more errors than young animals. This task took many trials to learn before testing could take place. Therefore, for this experiment we simplified the sustained attention test by removing the need for a trained behavioural response to indicate attention. Instead we measured dogs' attention to two stimuli, as indicated by time spent with the head (used as a proxy for gaze direction) directed toward the stimuli.

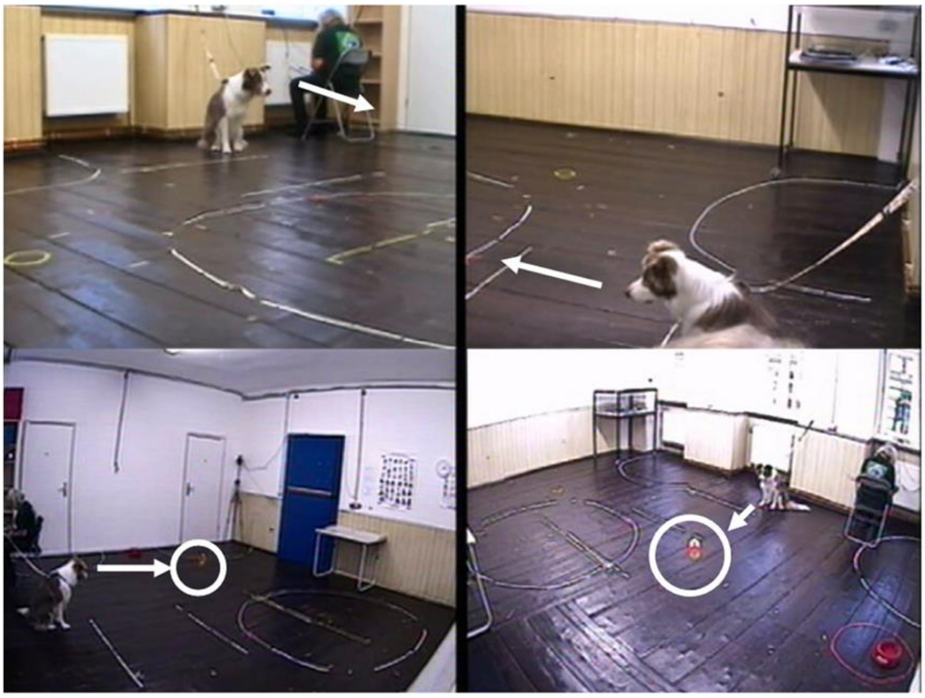
Previous studies focusing on measures of attention to novelty in dogs and rats found that exploratory behaviour varied significantly with age; with older subjects showing the lowest levels of sustained attention (Soffié et al., 1992; Handa et al., 1996; Siwak et al., 2001; Rosado et al., 2012). Therefore, based on the previous research cited above, we predicted that dogs would show no age differences in attentional capture, and sustained attention to the two stimuli was expected to decline with age.

Methods

Test setting and procedure

At the beginning of the experiment, the owners entered the experimental room with their dog on a leash. A hook on the wall next to a window allowed dogs to be tethered in one location. The owners attached their dogs to the 1.5 m leash on the hook, and sat down on a chair facing away from the dog toward the window. They started to fill in a questionnaire on an iPad. Owners were instructed to ignore their dog and the actions of the experimenter, and to be quiet and still. All owners followed guidelines, and did not attempt to interact with their dogs. Two conditions were presented in a counterbalanced order to each dog, Events 1 and 2.

Event 1: After the dog and owner were in position, the experimenter pulled a fishing line, which was attached to a small orange plastic watering can (child's toy) placed in the center of the experimental room. The line ran through a metal hoop in the ceiling in the testing room, allowing the object to be manipulated by the experimenter from outside the room. The object was moved up and down in front of the dog (but the dog was prevented from approaching it by the leash) for approximately 1 min (Figure 1). After this time the experimenter fixed the toy to the ceiling and a tone indicated that the owner and dog should leave the room.



Photographs © Lisa Wallis, Clever Dog Lab

FIGURE 1. Still video frame from set-up of experiment 1 – Event 1 condition.

Event 2: After the dog and owner were in position, the experimenter entered the testing room, closed the door, walked to the wall opposite the dog, and proceeded to walk up and down the length of the wall (6 m) pretending to paint the wall with a roller with her back to the dog. The experimenter removed her shoes before the test, and walked as quietly as possible. At no point did the experimenter gain eye contact with the dog. After 1 min the experimenter left the room, and a tone indicated that the owner and dog should leave the room.

Data collection and statistical analysis

We used the latency to orientation [LO; measured from the first detectable movement of the toy/door handle up to the point where the dogs gaze (head and nose) was centered upon the stimulus (toy/door opening/human entering)] as a measure of attentional capture, and the average gaze (AG)-bout duration (total duration looking time divided by frequency of looks), and the percentage of total looking time (PTLT) as measures of sustained attention. Dogs that were already orientated to the stimuli when the stimuli were first presented, were excluded from the LO analysis (Event 1: $N = 24$, Event 2: $N = 13$). A randomly chosen set of 20 dogs were double coded independently by two coders, and inter-observer reliability for LO, AG, and PTLT was excellent ($r > 0.89$, $p < 0.001$ for each variable).

Latency to orientation was inverse-transformed, AG was log-transformed, and PTLT was square-transformed to attain homogeneity of variances, and additionally we fitted a variance structure which allowed for variance to differ between the two conditions (constant variance). Data was analyzed using linear mixed effects models (LMMs; Pinheiro and Bates, 2000) with condition (Event 1 vs. Event 2), age and experiment order (Event 1 first vs. Event 2 first) as fixed effects and dog identity as a random factor. Additionally, the potentially confounding variables sex and neuter status were included as fixed effects. After testing for age effects we then re-ran the model with training score and current training hours as fixed effects and dog identity as a random factor. We included the two-way interaction between condition and age, training score or current training hours respectively to test whether any effects may be restricted to one condition.

To examine whether dogs attentional performance was consistent across different contexts the relationship between PTLT at Event 1 stimulus and PTLT at Event 2 stimulus was calculated, using a Spearman's rank correlation test.

Results

Dogs' LO to the stimulus was on average 0.57 s (range = 0.1–3.5 s, SD = 0.38 s). The relationship between age and LO was best described by a quadratic function [LMM, $F(1,141) = 4.97$, $p = 0.01$, Figure 2]. When using age group as a predictor no significant age differences or interactions were found ($p = 0.28$). There was no significant difference in LO to Event 1 vs. Event 2 stimuli. The removal of two outliers did not change the results.

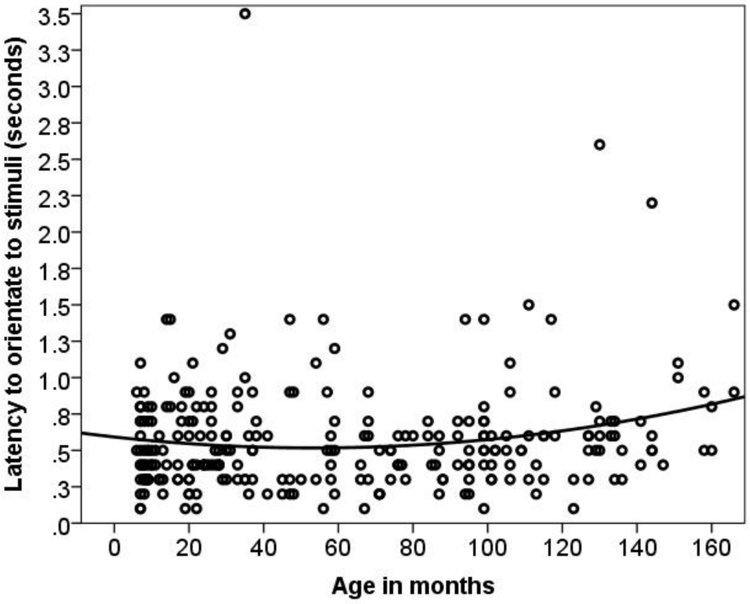


FIGURE 2. The quadratic relationship between latency to orient and age in months.

Percentage total looking time was significantly higher for Event 2 than for Event 1 (Event 1 = 66.17 ± 22.13; Event 2 = 90.43 ± 10.86; LMM, F(1,140) = 221.01, p <0.001). There was a significant interaction between condition and age in months [LMM, F(1,140) = 5.35, p = 0.02, Figure 3]. PTLT decreased with age in Event 1 (Spearman's rho = -1.98, p = 0.02) but not in Event 2 (Spearman's rho = 0.042, p = 0.62). When comparing age groups no significant age differences or interactions were found. When three outliers were removed all reported results remained significant.

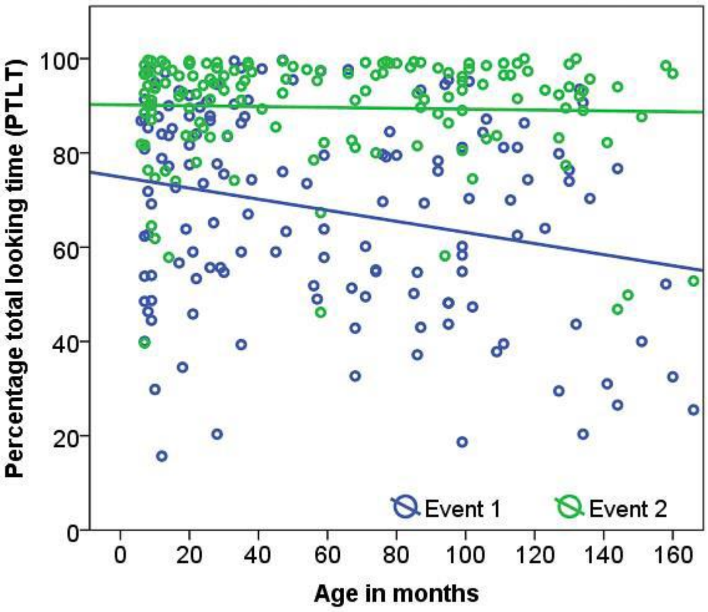


FIGURE 3. Age related changes in percentage total looking time (PTLT) to Event 1 and Event 2 stimuli.

Average gaze-bout length was longer in Event 2 than in Event 1 [Event 1 = 12.51 ± 11.70; Event 2 = 42.82 ± 30.89; LMM, F(1,141) = 289.03, $p < 0.001$]. There were no significant effects of age on AG.

With both variables (PTLT and AG), attention paid to Event 1 was significantly positively correlated with attention paid to Event 2 (PTLT: Spearman's rho = 0.224, $p = 0.010$; AG: Spearman's rho = 0.270, $p = 0.001$). These results remained significant after removing outliers.

Training score and current training hours had no significant effects on any of the variables measured.

Discussion

When examining dogs' attentional capture abilities across age a significant quadratic relationship was found. Age differences can possibly be explained by a slight sensory motor decline in the aged dogs, and a heightened sensitivity to sound/movement in the middle aged dogs. However since latencies to orientation did not differ in Event 1 and Event 2 conditions, and response latencies in the senior age group were not significantly different from the other age groups, the observed relationship was minimally effected by age. Regardless of the original orientation of the dog, all dogs very quickly orientated to the stimuli in Event 1 and 2, and we conclude that the physiological condition of the dog minimally affected its ability to orientate its gaze to the stimuli.

Measures of sustained attention were expected to decline with age in both conditions. However, only attention to the Event 1 stimulus showed a significant reduction with age in accordance with our predictions. The novel stimulus and strange movement of the inanimate object generally caused a startle response in the dogs, and an increase in frequency of looks to the stimulus compared to Event 2. The older dogs showed a decrease in overall looking time compared to young dogs, which could be explained by a life-long learning process to reduce reaction to novel external stimuli, such as moving objects (children, cars, bicycles, etc.). Dogs learn to attend selectively, which helps them to focus their attention on relevant stimuli (for example the owner), whilst ignoring irrelevant occurrences (Lindsay, 2001). We found no age effect on attention paid to Event 2, which may be due a ceiling effect (almost half of the dogs paid attention to the stimuli for over 95% of the time). Therefore, the interaction found between age and stimulus type may be an artifact of the ceiling effect. Future studies will need to determine whether sustained attention toward a social type stimulus might also decrease with age, for example by increasing the duration of presentation of the stimulus in Event 2. Here we can conclude that even senior dogs are capable of high levels of sustained attention over 1 min if the stimulus is of high relevance to them.

Percentage total looking time and AG-bout duration was found to be higher in Event 2 (experimenter painting the wall) than in Event 1 (moving plastic watering can). One possible explanation for this difference is that the size of the stimuli caused a bias in attentional allocation. The type of movement (vertical vs. lateral), the distance of the stimuli from the dog, and the novelty of the stimulus could also have influenced the dogs' attention. Previous studies have indicated that dogs prefer to attend to novel objects over familiar ones (Kaulfuss and Mills, 2008) and also to novel human faces when compared to familiar faces (Racca et al., 2010), therefore we might have expected dogs to attend to Event 1 and 2 similarly. A main difference between the two event situations was that Event 1 contained a non-social stimulus and Event 2 a social stimulus. It seems likely that positive experiences with the experimenter gained in the previous tests of the test battery could have motivated the dogs to attend to her, over the novel non-social object. Horn et al. (2013) found that the nature of past interactions with a human specifies the dogs' relationship with them, and increases attention to that person. Positive reinforcement during previous training experiences has been found to be highly correlated with levels of attention (Lindsay, 2001). Therefore reinforcement of attention in one situation should improve attending to the same stimulus in different contexts.

In sum, by the age of 6 months, Border collie attentional capture and sustained attentional abilities were already at adult levels, which is comparable to the finding of similar tests in human subjects (Berardi et al., 2001; Michael et al., 2013). Nevertheless, individual differences occurred consistently across the different contexts (i.e., dogs which looked longer at the Event 1 stimulus also looked longer at the Event 2 stimulus) which could be a consequence of an underlying personality trait.

Experiment 2: Selective Attention

In experiment 1 we found minimal age effects on attentional capture and sustained attention in pet dogs. Previous studies have established that increasing task difficulty enhances the likelihood of finding age related differences in humans (McDowd and Craik, 1988), therefore we performed a second experiment, where we measured whether dogs selective attention and sensorimotor abilities differed by age during task switching.

One common method widely used to assess selective attention is the visual search task, which requires participants to attend to a target stimulus while disregarding irrelevant "distracter" information. Previous studies have shown that senior dogs are significantly impaired in accuracy and reaction time compared to younger animals in a visual search task with distracters (Snigdha et al., 2012). In a social version of this task, Mongillo et al. (2010) simultaneously presented the owner and a stranger to the dog, forcing it to be selective as to whom it observed. Older dogs discriminated between the owner and the stranger to a lesser extent, because they oriented longer to the stranger compared to adult dogs. Similarly, age and stimulus relevance have a strong influence on selective attention also in humans (Hommel et al., 2004) and non-human primates (Zeamer et al., 2011).

Previous studies examining sensorimotor control in non-human animals, have found a significant decline with age, as in human studies. For example, Wallace et al. (1980) discovered that tasks requiring coordinated control of motor and reflexive responses in rats (such as descent of a wire mesh pole) showed significant declines with age in four age groups (6, 12, 18, and 24 months). In their study of normative behavioural changes associated with "successful aging" in dogs, Salvin et al. (2011b) found that difficulty in finding food increased significantly across three age groups (<10, 10–12, >12 years). This could reflect alterations in the cognitive processing of sensory information, or could be a result of physical deterioration of the visual, audio, or olfactory organs. Therefore it is necessary to exclude physical degeneration as the cause of apparent changes in cognition.

In Experiment 2 we investigated whether dogs differ by age in their selective attention when switching between two tasks: finding food on the floor, and gaining eye contact with the experimenter. Additionally we examined whether dogs differed by age in their ability to find dropped food (sensorimotor performance). Based on human and animal studies, we predicted that younger and older dogs would show an impaired performance in selective attention and sensorimotor control, producing a quadratic effect with age.

Methods

Test setting and procedure

For this experiment, the owner sat positioned at the back wall of the experimental room and filled in a questionnaire. The experimenter stood in the center of the room facing the owner, holding a clicker in her right hand, and the other hand was free. Both hands were positioned in a relaxed posture by her sides. The experimenter had a food pouch on her belt, positioned at her back. Sausage, which had been cut into <1 cm3, was used as a food reward. For the first trial, the experimenter called the dog to her, and threw a piece of sausage on the floor in front of her for the dog to find. She then remained motionless until the dog established eye contact with her, whereupon she immediately clicked the clicker, took a piece of food from a pouch on her belt, tossed the food on the floor to the left or the right of the dog, and then waited for the dog to establish eye contact again after it found and ate the food. The sausage was always thrown so that the dog had to move out of its current position to obtain the food. If the dog wandered further than 2 m from the experimenter, and no longer showed interest, the experimenter rustled the plastic bag containing the sausage, and then returned to her position, with arms and hands at her sides. The experimenter continued this task for a total of 5 min.

We considered this experiment to be demonstrative of dogs' selective attention abilities, as the dogs had to change their focus of attention in the presence of competing stimuli: the experimenter's hand which moments ago threw a piece of sausage, the floor where food could be found, and the face of the experimenter (for which the dog was rewarded when looking at). Thus in this task the dog had to disregard (inhibit) irrelevant "distracter" information in order to receive the food reward.

Data collection and statistical analysis

We used two parameters as measures of attention in this task: the latency to eye contact (LEC) with the experimenter (measured from the moment the dog had taken the food into its mouth until the dog looked up into the face of the experimenter, which was marked by a click from the clicker), and the latency to find food (LFF; measured from the moment the piece of sausage left the experimenters hand, until the dog found the food, and took it into the mouth). The dogs' initial performance in the task was measured by taking the average of the first three trials in both LEC and LFF. A randomly chosen set of 20 dogs was double coded independently by two coders and inter-observer reliability for LEC and LFF was excellent ($r > 0.87$, $p < 0.001$ for each variable). LEC was log-transformed, and LFF was inverse-cube transformed to attain homogeneity of variances. The data was analyzed using linear models (LMs; Chambers, 1991), with age and previous clicker experience (yes/no) as fixed effects. Forty three percent of the subjects were clicker trained, the proportion of clicker trained dogs was highest in age group 1, lowest in age group 7, and clicker training was weakly correlated with age in months (Spearman's rho = -0.191, $p = 0.021$). Additionally, the potentially confounding variables sex and neuter status were included as fixed effects. Age group comparisons were analyzed using LMs with generalised least squares (GLS; Davidian and Giltinan, 1995) and a variance structure which allowed for variance to differ between age groups was fitted. After testing for age effects we then re-ran the models with training score and current training hours as fixed effects.

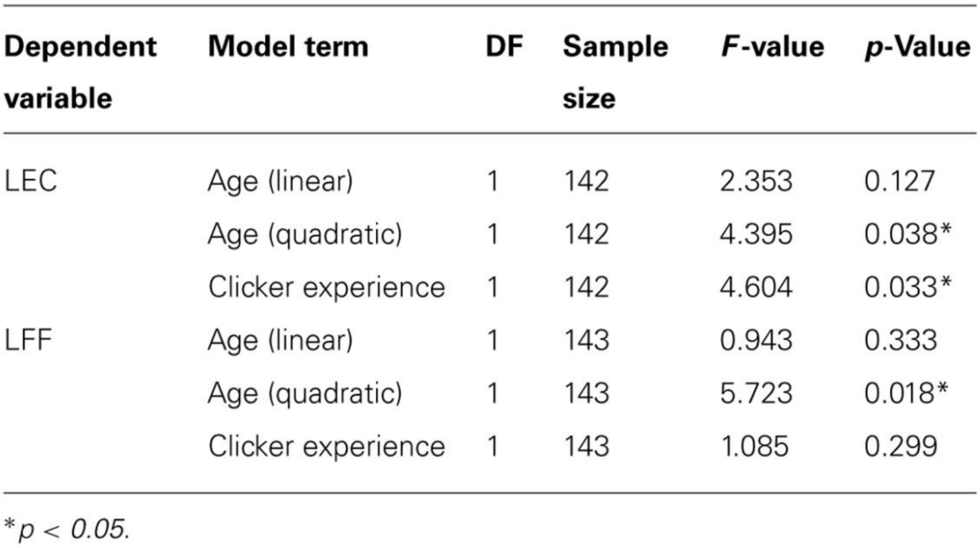
Learning across trials was examined by taking the first 20 trials of LEC and LFF for all dogs (seven dogs were removed from the analysis as they did not complete 20 trials within the 5-min period). LEC learning data was inverse square-root transformed, and LFF data inverse log transformed. To obtain homoscedasticity of data, we also fitted a variance structure which allowed for variance to differ with trial number (exponential variance), and between age groups (constant variance). Data was analyzed using LMM (Pinheiro and Bates, 2000), with age as categorical variable (seven age groups), trial number, previous clicker experience (yes/no), sex, and neuter status, included as fixed effects. We then re-ran the models with training score and current training hours instead of age as fixed effects. We included the two-way interaction between trial number and age, clicker experience, training score or current training hours respectively to test whether learning differed between age groups, or with clicker experience, training score or current training hours.

Finally, to examine whether dogs attentional performance was consistent across different contexts, the relationship between LEC and LFF was analyzed using a Spearman's rank correlation test.

Results

Initial latencies

Dogs' LEC with the experimenter was on average 6.82 s (range = 1.37–29.57 s, SD = 5.34 s). The relationship between age in months and LEC was best described by a quadratic function (Figure 4; Table 2). Previously clicker trained dogs were faster to gain eye contact than non-clicker trained dogs (Table 2). When comparing the latencies in the age groups, performance peaked in group four (middle aged: 3- to 6-year-olds). Therefore, we compared all other age groups to group four to look for differences in performance. There was a significant difference found between the age groups [GLS, $F(6,145) = 3.99$, $p = 0.001$]. LEC was significantly higher in age groups two, three and seven compared to age group four ($t > 2.04$, $p = <0.05$). However, when three outliers were removed, the quadratic relationship between age in months and LEC was no longer significant, and LEC was significantly higher only in age groups two and seven, when compared to age group four.



Dependent variable	Model term	DF	Sample size	*F*-value	*p*-Value
LEC	Age (linear)	1	142	2.353	0.127
	Age (quadratic)	1	142	4.395	0.038*
	Clicker experience	1	142	4.604	0.033*
LFF	Age (linear)	1	143	0.943	0.333
	Age (quadratic)	1	143	5.723	0.018*
	Clicker experience	1	143	1.085	0.299

*$p < 0.05$.

TABLE 2. Factors affecting initial latency to eye contact (LEC) and latency to find food (LFF).

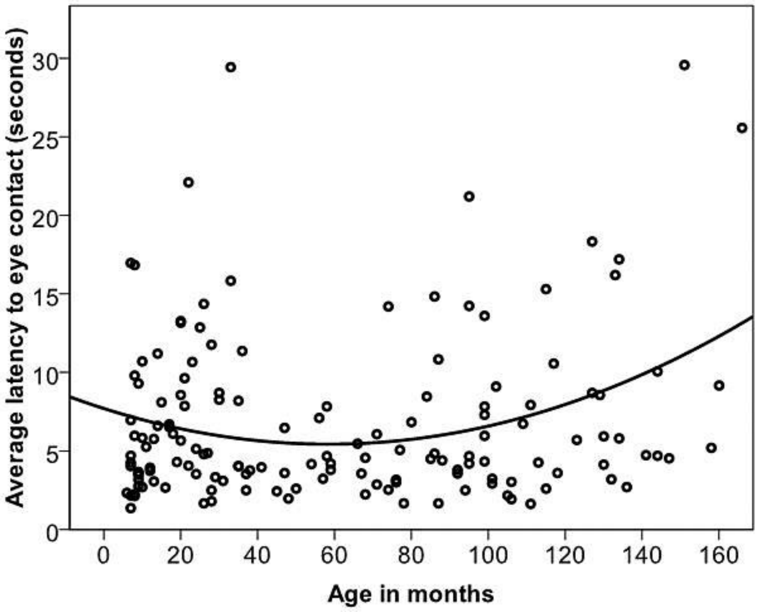


FIGURE 4. The quadratic relationship between the average latency of the first three trials of individual dogs to gain eye contact with the experimenter and age in months.

Dogs' LFF was on average 1.45 s (range = 0.73–5.2 s, and SD = 0.65 s). The relationship between age in months and LFF was best described by a quadratic function (Table 2; Figure 5). When comparing the latencies in the age groups, performance again peaked in group four (middle aged). We compared all other age groups to age group four and found that there was a significant difference between age groups [GLS, F(6,145) = 5.53, p = <0.001]. LFF in age groups one, two, three and seven was significantly higher than LFF in age group four (t <-2.63, p = <0.01). After removing five outliers, all effects found remained significant.

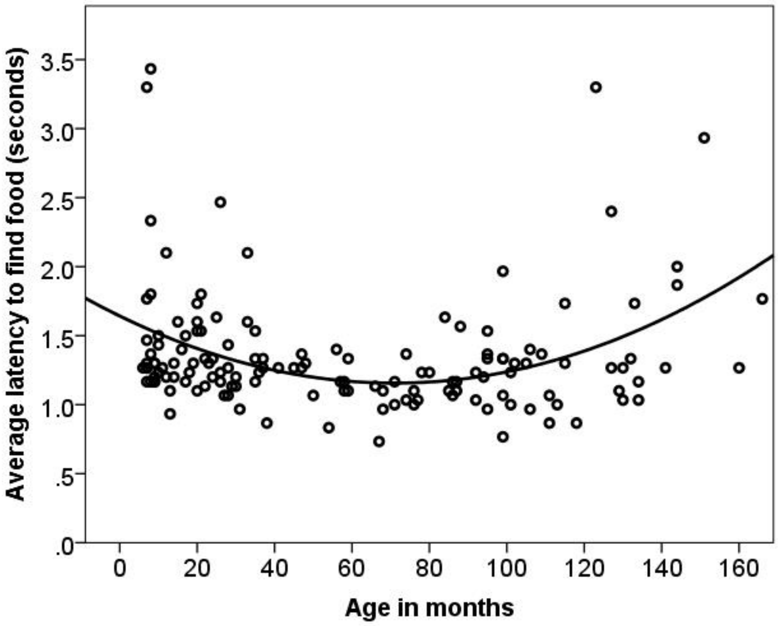
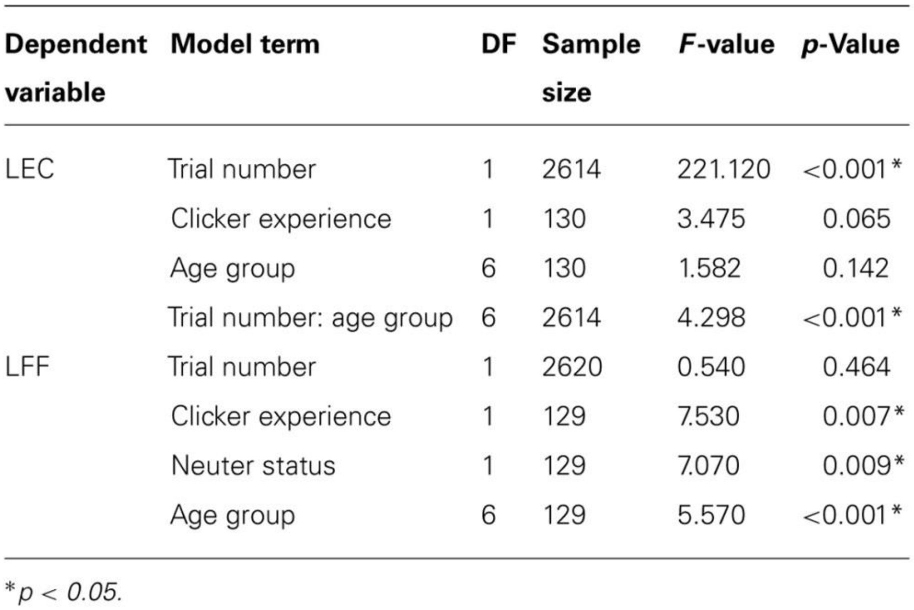


FIGURE 5. The quadratic relationship between the average latency of the first three trials of individual dogs to find food and age in months.

Latency to eye contact was significantly positively correlated with LFF (Spearman’s rho = 0.232, p = 0.005). Training score and current training hours had no significant effects on any of the variables measured.

Learning across trials

Results from the learning across trials analysis produced a significant effect of trial number on LEC, indicating that individuals improved in gaining eye contact over trials (Table 3). There was also a significant trial number by age group interaction (Table 3). When compared with the top performing age group in the initial trials (group four), group two (1- to 2-year-olds) showed a significantly steeper learning curve. Clicker experienced dogs showed a tendency toward shorter latencies to eye contact than dogs with no clicker experience.



Dependent variable	Model term	DF	Sample size	*F*-value	*p*-Value
LEC	Trial number	1	2614	221.120	<0.001*
	Clicker experience	1	130	3.475	0.065
	Age group	6	130	1.582	0.142
	Trial number: age group	6	2614	4.298	<0.001*
LFF	Trial number	1	2620	0.540	0.464
	Clicker experience	1	129	7.530	0.007*
	Neuter status	1	129	7.070	0.009*
	Age group	6	129	5.570	<0.001*

*$p < 0.05$.

TABLE 3. Linear mixed effects models factors affecting learning across trials in latency to eye contact (LEC) and latency to find food (LFF).

As we found a significant interaction between age and trial number, we then controlled for dogs initial performance in this task, which could influence the rate of learning, by running LM using LEC as the response variable and trial number as a fixed effect, to obtain regression slopes for each individual. We then ran LMs with regression slope as the response variable, initial performance (intercept of the regression) as a predictor in addition to age (seven age groups), clicker (previous experience: yes/no), sex, neuter status, training score and current training hours. Results from the model showed a highly significant effect of intercept [LM, F(1,128) = 67.59, p = < 0.001] and a tendency toward a significant difference between the age groups [LM, F(6,128) = 2.13, p = 0.054]. When comparing the age groups, the only significant result was that group two showed significantly steeper learning curves compared to group one (t = -2.71, p = 0.007; Figure 6).

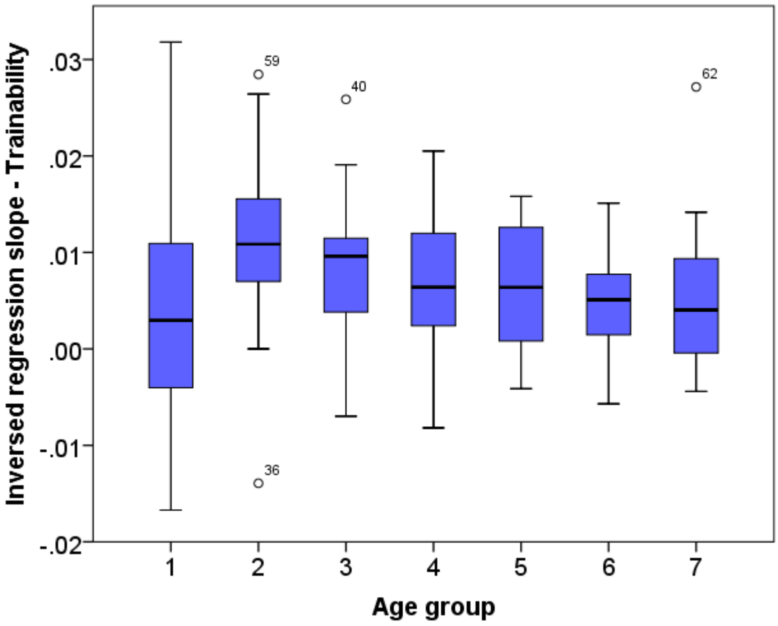


FIGURE 6. The relationship between the rates of learning (trainability) as measured in the latency to orientate to the experimenter's face and age over the 20 clicker training trials.

Results from the LFF model revealed that dogs' performance differed significantly among the age groups (Table 3). Age groups one, two, three, five, six, and seven had significantly higher LFF than group four ($t > 2.00$, $p = <0.05$). There was no significant effect of trial number; therefore the dogs did not significantly improve in their ability to find food over the 20 trials. However, clicker experienced dogs showed a shorter LFF than dogs with no clicker experience, and additionally, neutered dogs were quicker to find the food than intact dogs (Table 3).

Training score and mean number of hours spent in training per week had no significant effects on any of the variables measured.

Discussion

The dogs' selective attention and sensorimotor abilities showed differences between cross-sectional age group means which peaked at middle age (3–6 years), when their LEC and to find food was the lowest. LFF showed a quadratic distribution with age in months, and was highly correlated with LEC. Deficiencies in LEC present in the younger (adolescent) and oldest age groups could be due to: (1) lower motivation, (2) reduced sensorimotor capability, or (3) deficiencies in attentional control. Motivational differences to attend to the experimenter in the age groups are unlikely, since in experiment 1 we found no age differences in sustained attention duration in Event 2 which included a social component, indicating that all of the age groups were equally motivated to attend to the experimenter. Also food motivation did not vary with age, as dogs' performance in LFF over the 20 trials remained stable over time. Therefore we suggest that, due to the low range of LFF values, dogs were equally motivated to find the food and to participate in the trials.

However, there was evidence that the LFF was affected by the dogs' sensorimotor capability. Age differences in the dogs' initial performance were found, and remained consistent over the 20 trials. LFF provided an effective sensory and motor control, which is comparable to similar tests in humans and rats (Wallace et al., 1980; Clark et al., 2006). Given the very short latencies for finding food (mean 1.45 s), and also the LO in experiment 1 (mean 0.57 s), it is unlikely that sensorimotor deficiency explain all of the differences we found in the age groups concerning the LEC. The differences found in the adolescent and oldest age groups were most likely due to deficiencies in attentional control abilities, or increased distractibility. The results from this study complement previous research on selective attention in dogs, which point to a reduced capacity of older dogs to inhibit distracting stimuli (Tapp et al., 2003; Mongillo et al., 2010; Snigdha et al., 2012). With our experimental design we were not able to determine whether reduced visual processing speed, reduced cognitive resources (impairments in other cognitive and learning abilities), and/or an inability to ignore distracting information (decrease in performance accuracy) or a combination of these factors was responsible for the observed results. Future studies should try to separate these three functions to determine to what extent they effect development and aging of attentional processes in the dog. It is also important to note that, despite of its practical importance and relevance for social behaviour, measuring social attentiveness through eye contact has an inherent constraint. Since the experimenter with whom the dogs are required to establish eye contact cannot be prevented from seeing the dogs and some of their characteristics, such as age, it is impossible to make sure that she/he treats all subjects in the same way. In our experiment, the experimenter could easily discriminate the 6 month from the 12-year-old dogs. During the clicker training for eye contact, although the task required that the experimenter remain motionless whilst waiting for the dog to take up eye contact, unconscious subtle movements by the experimenter may have inadvertently captured the dogs attention. Potentially, this effect might have contributed to some of the differences we found. Future studies should attempt to find other measurements of social attention that can control for such effects but at the same time can be as informative as mutual gaze.

In order to fully examine the lifespan development of attention, puppies as young as 2 months of age would need to be tested. Using a similar method, in a study carried out by Passalacqua et al. (2011) over 50% of puppies at 2 months of age looked at the experimenter within 1 min in an “unsolvable task” paradigm. Adult dogs (average age 4.4 years) were significantly faster to look at the experimenter when compared to 4.5 and 2 months old puppies, which suggests that human directed gazing behaviour improves with age, possibly through a history of positively rewarded human interactions. In the present study only adolescent and geriatric dogs showed slower latencies. The onset of sexual maturity varies according to the speed of development of the animal, and is reached between 6 and 18 months of age depending on the breed (Miklósi, 2008). Behavioural maturation in the dog does not occur at this time: although capable of mating, dogs do not display fully adult behaviour until around 2–3 years of age. Our results suggest that the maturation of selective attention may coincide with behavioural maturation in the dog. Adolescent dogs go through a hormonal surge which often affects their behaviour, including their ability to pay attention and respond to previously learned cues (Lindsay, 2001). During this period an imbalance between attention and affective and motivational networks cause emotional and motivational distractors to have a detrimental effect on attentional control, which explains why adolescent behaviour is often erratic (Crone, 2009).

Dogs’ selective attentional performance improved across the 20 training trials in all age groups; therefore dogs from 6 months to 14 years all showed the ability to learn, consistent with previous studies in dogs (Lillard and Erisir, 2011). In this task, even though older and adolescent dogs showed deficiencies initially, they were able to significantly reduce their latencies with training. Dogs aged from 1 to 2 years show a significantly steeper group learning curve when compared to middle aged dogs after controlling for individual initial performance. There are numerous studies suggesting that younger dogs show greater learning ability than aged dogs; however, to date there has been no lifespan studies of learning abilities in domestic dogs. Adolescence may reflect a sensitive period when quick and efficient learning to focus on task demands occurs in normal development in the domestic dog (Scott, 1958).

The dogs' initial LEC and LFF across the first 20 trials were affected by dogs' clicker training status, with dogs having previous experience being faster in gaining eye contact with the experimenter in the first three trials and also quicker in finding the food over the first 20 trials. The simplest explanation for this result is that clicker trained dogs were already familiar with this type of task, and that overall clicker training can improve human directed looking behaviour in dogs. Alternatively, it could indicate heightened motivation (anticipation of food reward) in clicker trained dogs, rather than an overall difference in sensorimotor capabilities. Non-clicker trained dogs could have been confused and/or distracted by the presence of the clicker, which could have resulted in longer latencies to eye contact. Since the oldest age group of geriatric dogs was also the age group with the lowest number of clicker trained dogs, it could be argued that had more of these individuals been in clicker training, the observed difference between middle aged dogs and geriatric dogs may disappear. However, adolescent dogs had a similar proportion of clicker trained dogs to middle aged dogs but a higher LEC, so clicker experience cannot explain all the variation which was present. The youngest age group had the highest proportion of clicker trained dogs (around 70%); therefore we can speculate that current clicker training for eye contact in this age group could also have contributed to faster latencies to eye contact with the experimenter, and younger clicker naïve dogs may show a reduced performance in the alternating attention task.

Dogs' reproductive status influenced their performance in LFF. Neutered dogs were faster to find dropped food over 20 trials than intact dogs. Neutering increases food motivation and decreases metabolic rate, which can lead to lower energy levels and increased risk of obesity (Duffy and Serpell, 2006; German, 2006). Therefore, it is possible that neutered dogs had a greater motivation to obtain the food than intact dogs. However, the reproductive status of the dog had no effect on selective attention, which suggests that for general measures of attention and trainability there are no differences between hormonally intact and neutered dogs.

General Discussion

We investigated the lifespan development of attentiveness of pet dogs in naturalistic situations, by developing several short simple tasks designed specifically to examine possible age effects and by measuring specific components of attention. We examined the normal rate of attention development and decline in a cross-sectional sample of pet dogs from 6 months to old age, and finally, we compared the cross-sectional developmental trajectories of the different attentional components found in dogs to the existing literature in humans. The results from experiment 1 when compared to the human literature, show a similar lack of age effects on attentional capture abilities in humans and dogs, but also reveal differences in task relevance in sustained attentional performance. In experiment 2 we found that selective attention performance in adolescent and geriatric dogs was weaker than in middle aged dogs. We suggest that a U shaped developmental pathway of selective attention may be present, if younger age groups were also examined, and based on our initial results before outliers were removed. Younger and older dogs' performance can be explained by greater levels of distractibility, which has been attributed to weakened inhibitory control (Duchek et al., 1998).

In order to help draw comparisons across the lifespan of humans and dogs, it is necessary to establish the relationship between chronological and physiological age in both species. Patronek et al. (1997) developed a method to standardize the chronological age of dogs in terms of physiological time using human year equivalents. The relationship between human age and dog age and development cannot be described accurately with a simple linear relationship, as development is not constant over a dog's life span. A polynomial relationship allows for the human year equivalents for dogs' ages to be larger during growth and smaller during maturity. Using Patronek's method, the human equivalent age ranges of the dogs in this study was 10–83 years. Thus, regarding simpler forms of attention, a rather crucial developmental stage may have been missed by only testing dogs from 6 months onward. For example, in humans, attentional capture abilities reach adult levels by age 5–7 years. In order to test this in the dogs we would have needed to test them before 3 months of age. The quadratic relationship between selective attention and age (found before outliers were removed) may have been strengthened, had we tested younger dogs. Dogs' selective attentional and sensorimotor abilities peaked at the human equivalent of roughly 28–38 years old, which is around the same time as in human studies (20–30 years old). However, from 15 to 39 years, performance in humans was similar, with few if any differences between these age groups (Clark et al., 2006). A quadratic effect of age in dogs' attentional control could reflect improving capabilities over the years of development followed by decline during old age. Given that the development of attentional control may be similar across humans and dogs, we can speculate that the same mechanism regulates control in both species. Indeed, recent behavioural and physiological research on impulsivity in dogs indicates this might well be the case (Miller et al., 2010; Wright et al., 2012). However, longitudinal studies are needed to validate these suggestions.

The fact that dogs of all age groups were able to improve their selective attention performance in the alternating attention task is of particular importance. Even dogs which had been previously trained to gain eye contact with their owner benefited from the training with the experimenter. This improvement may be explained by the fact that dogs do not automatically transfer training exercises/cues/commands to new trainers (strangers) and to new contexts, unless they have been specifically trained to do so (Hilliard, 2003). There are two possible explanations for the dogs performance in the selective attention measure: (1) dogs were able to improve their level of attentional control over the 20 trials through an increased ability to inhibit prepotent responses, and (2) simple conditioning led to an increased relevance of the stimulus (the experimenters face) over the repeated trials. Most likely both explanations contributed to the dogs' performance. Instrumental conditioning can explain why previous training allowed clicker trained dogs to outperform non-clicker trained dogs in the initial three trials.

Dogs with the equivalent human age of 16–23 years (1–2 in chronological years) benefited more from eye contact training with the experimenter than middle aged dogs. Human research also points to the teenage and adolescent years as a highly important transitional phase marked by significant physical, social, cognitive, and emotional changes (Crone, 2009). Just as in humans, dogs of all ages, including dogs which were clicker trained were able to benefit from a practice period. However, it remains to be seen whether training in just one area can lead to improvements across multiple domains (emotional, intellectual and physical) as has been observed in humans (Oaten and Cheng, 2006a,b), and also whether selective attention across different contexts is correlated. A recent study on dogs discovered that individual scores were not correlated between tasks of executive control (inhibition); suggesting context has a large effect on performance in these tasks (Bray et al., 2014).

Results from experiment 2 suggest that fine sensorimotor ability and attentional control may follow similar developmental pathways. Correlational evidence from cross-sectional and longitudinal studies in humans suggests a close connection between cognitive, sensory, and sensorimotor aging (Baltes and Lindenberger, 1997; Diamond, 2000; Li and Lindenberger, 2002; Li et al., 2004; Ghisletta and Lindenberger, 2005). These factors may be influenced by a common cause, an increase in resource overlap, or a combination of both (Lindenberger et al., 2000). Future research should aim to pinpoint the relative importance of these possibilities using divided attentional tasks in dogs and other species.

Other important aspects to consider when studying attention and cognition in humans and animals include the influence of gender, educational level, and current training. In humans, studies have found that specific training and educational interventions targeted at influencing the development and improvement of attentional abilities has been successful at all life stages including children and older adults (Rueda et al., 2005; Oaten and Cheng, 2006a; Tang and Posner, 2009; Mozolic et al., 2011; O'Brien et al., 2013). The training score used in this study was intended as a measure of the dogs overall educational level, and the mean number of hours spent in training per week was used to reflect dogs' current educational participation. However, the only type of training which influenced LEC and find food was clicker training experience. Two possible explanations for clicker trained dogs' enhanced performance when compared to non-clicker trained dogs include: (1) clicker trained dogs were already familiar with the specific training method (and perhaps the task used), and therefore were better able to generalise to new contexts and trainers (Hilliard, 2003); and (2) clicker training may help to prolong and/or improve behaviour such as eye contact through increased resistance to extinction (Smith and Davis, 2008). In the current study we did not find any effects of gender on any of the components of attention or sensorimotor ability.

Finally, we need to acknowledge the limitations of a cross-sectional design as a means to examine lifespan differences in attention in dogs. Schaie (2000) emphasized the potential susceptibility of cross-sectional designs to cohort differences. In the population of pet dog Border collies used for this study there were few selection pressures, and little problems with inbreeding. Most breeding dogs were chosen on either working ability (working line) sport/agility ability (sport line), or for looks or showing ability (show line). Dogs were recruited from many different breeders, pet owners, and dog schools and care was taken that individuals tested were from as diverse a sampling population as possible. However, we cannot completely rule out the possibility that the correlations and age group means we measured may not accurately reflect true developmental trajectories. Additional research using longitudinal designs would be important to confirm our findings.

Conclusion

Our study provides the first cross-sectional lifespan overview of the development and aging of attention in the pet dog. Our results reveal differences in task relevance in sustained attentional performance when watching a human or a moving object, which may be explained by different life-long learning processes about such stimuli. During the attention alternation task, we found that dogs' selective attention and sensorimotor abilities showed differences between age group means which peaked at middle age for both, indicating some association between the two processes. The differences found in selective attention in the younger adolescent and oldest age group when compared to the middle aged could be due to greater levels of distractibility, which could indicate deficiencies in attentional control abilities. When comparing sensorimotor control in previous studies in humans and the present results found in dogs, a similar quadratic effect of age was discovered. Dogs' attentional capture and sustained attention results also paralleled those found in humans.

The importance of taking into account the dogs' current training status in reference to examining human directed gazing behaviour should be emphasized. Clicker training experience had a significant effect on dogs' performance in the attention alternation task. Dogs of all ages significantly improved their selective attention performance over trials, with the adolescents showing a particularly enhanced learning performance in comparison to the other age groups.

Our results complement the existing research using laboratory beagles, emphasizing the importance of the domestic dog as a model species for comparative study. Finally, this study lends support to the possibility that the development of sensorimotor and attentional control and senescence may be fundamentally interrelated in dogs as proposed in humans.

Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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5. General Discussion

5. 1 Cognitive development and aging in dogs

Over the three studies we investigated cognitive development and aging of the different cognitive domains, including general and social cognition, as well as the influence of basic control processes, in a cross-sectional sample of pet Border collies from 5 months to old age. Below is a brief summary of the results from the three studies and the relationships with age that were found. Additionally, we state whether the results confirmed or contradicted the predictions stated in the introduction (please refer to Table 3 below).

All predicted relationships with age were confirmed in the results from Study 1; older dogs showed decreased visual discrimination learning and reduced working memory ability and flexibility utilising the touchscreen paradigm. Dogs' long-term memory was well maintained into old age as predicted. However, when examining the results from the inference by exclusion tests, a significant positive linear relationship was found between age and inference ability, which was in contrast to the predicted quadratic relationship with age. Older dogs chose by inference by exclusion more often than younger dogs, which flexibly changed their response pattern due to a lack of feedback, and used strategies other than inference by exclusion. A strong learning effect over the test trials in the younger dogs is suggested to explain their reduced performance. Additionally, older dogs showed a higher amount of perseverative responding in the training, which increased the likelihood of finding response patterns consistent with choosing by exclusion.

Study 2 provided the first scientific evidence that the domestic dog is able to follow the gaze of a human into distant space outside an object choice or barrier task context. No relationship between the ability to follow human gaze cues and age was found, thus supporting the formal training hypothesis. However, the frequency of looks to the door showed a quadratic developmental trajectory over the dogs' lifetime, with dogs in late puppyhood and geriatric dogs showing the greatest tendency to look to the door in both test and control trials, and middle-aged dogs the lowest. The youngest and oldest dogs were unable to inhibit following the salient head turn of the experimenter, and displayed greater distractibility in general, which resulted in an increased frequency of gazing to the door in the control trials and less time gazing at the experimenter's face over the 10 s trials in both conditions. During the test and control trials, dogs in late adulthood sustained gaze to the experimenter's face longer than all other age groups, such that a quadratic relationship with age was found.

Study 3 provides the first cross-sectional lifespan overview of the development and aging of attention in the pet dog. The basic developmental trajectories of the different sub-processes of attention all followed the predicted relationships with age including no changes with age in attentional capture, a decrease in sustained attention to non-social stimuli, and a quadratic relationship between selective attention and age, and sensorimotor control and age. However, contrary to prediction, no reduction of sustained attention to a social stimulus with age was found. All age groups showed high sustained attention to the experimenter, with almost half of the dogs gazing at the stimulus for over 95% of the time.

In order to better visualize the results found during the three studies, the different cross-sectional trajectories were plotted on a single graph (please refer to Figure 4). From the graph it is clear to see that the different cognitive domains and basic control processes measured have relatively independent, "domain specific" pathways for some aspects cognitive development, which include differences between social and non-social contexts. We suggest that Border collie dogs seem to have an accelerated rate of development of some executive functions (including attention, working memory, and cognitive flexibility), through to late puppyhood and early adulthood, and experience progressive decline from then onwards. However, when the task measured included an interspecific social context such as during the selective attention tests, and sustained gaze to the face in the gaze following task, the trajectories showed delayed development into adulthood. This might point to the fact that additional life experience may be necessary for these skills to emerge and additionally to generalise to new situations and to people other than the owner.

It is important to note that the trajectories represent in some cases only single measurements of that domain or basic process. Future studies should attempt to obtain multiple measures for each domain and process in both social and non-social contexts. Whether our results can be generalised to other breeds is another topic for future study. However, when compared to the existing studies on the laboratory Beagle we find a very similar pattern of results, which also closely mirror the development and aging of cognition in humans, thus, adding to the growing evidence that the pet dog is a suitable model for human cognitive aging.

Test	Sub-test/s	Description	Domains and basic control processes measured	Predicted relationship with age	Relationship found	Age of maturation
Study 1 Discrimination	Geometric forms, Underwater photos & drawings, Clip art pictures	2, 6 and 8 stimuli discrimination	Flexibility (Perseveration)	Decrease (Increase)	✓	≤ 6 months Late puppyhood
			Learning and working memory	Decrease	✓	≤ 6 months Late puppyhood
	Clip art pictures	Test 1 & 2	Problem solving and reasoning: Inference by exclusion	Quadratic	✗ Increase	≥ 6 years Late adulthood
		Retesting	Long-term memory	No change	✓	≤ 6 months Late puppyhood
Study 3 Attention test	Event 1 and 2	Orientation to door and object	Attentional capture	No change	✓	≤ 6 months Late puppyhood
	Event 1: Social	Human painting wall	Sustained attention	Decrease	✗ No change	≤ 6 months Late puppyhood
	Event 2: Non-social	Flying object	Sustained attention	Decrease	✓	≤ 6 months Late puppyhood
Study 2 Gaze following	Phase 1 and 3	Test – control	Communication	Dependent on hypothesis (see study 2)	Formal training hypothesis – no change	≤ 6 months Late puppyhood
		Distractibility (frequency of looks door)	Attention and inhibition	Quadratic	✓	3years old Middle aged
		Sustained attention experimenter's face	Attention and communication	Quadratic	✓	6 years Late adulthood
Study 3 Clicker training for eye contact	Phase 2:Group eye	Selective attention to experimenters face	Attention and communication	Quadratic	✓	3 years old Middle aged
		Sensorimotor control	Attention/motivation	Quadratic	✓	3 years old Middle aged
		Selective attention over 20 trials	Trainability	Decrease	✓	1 year Increased trainability in Adolescence
		Sensorimotor control - 20 trials	Motivation	No change	✓	≤ 6 months Late puppyhood.

Table 3: Relationships with age, including age of maturation for the different domains and basic control processes measured using the touchscreen and the VCCB.

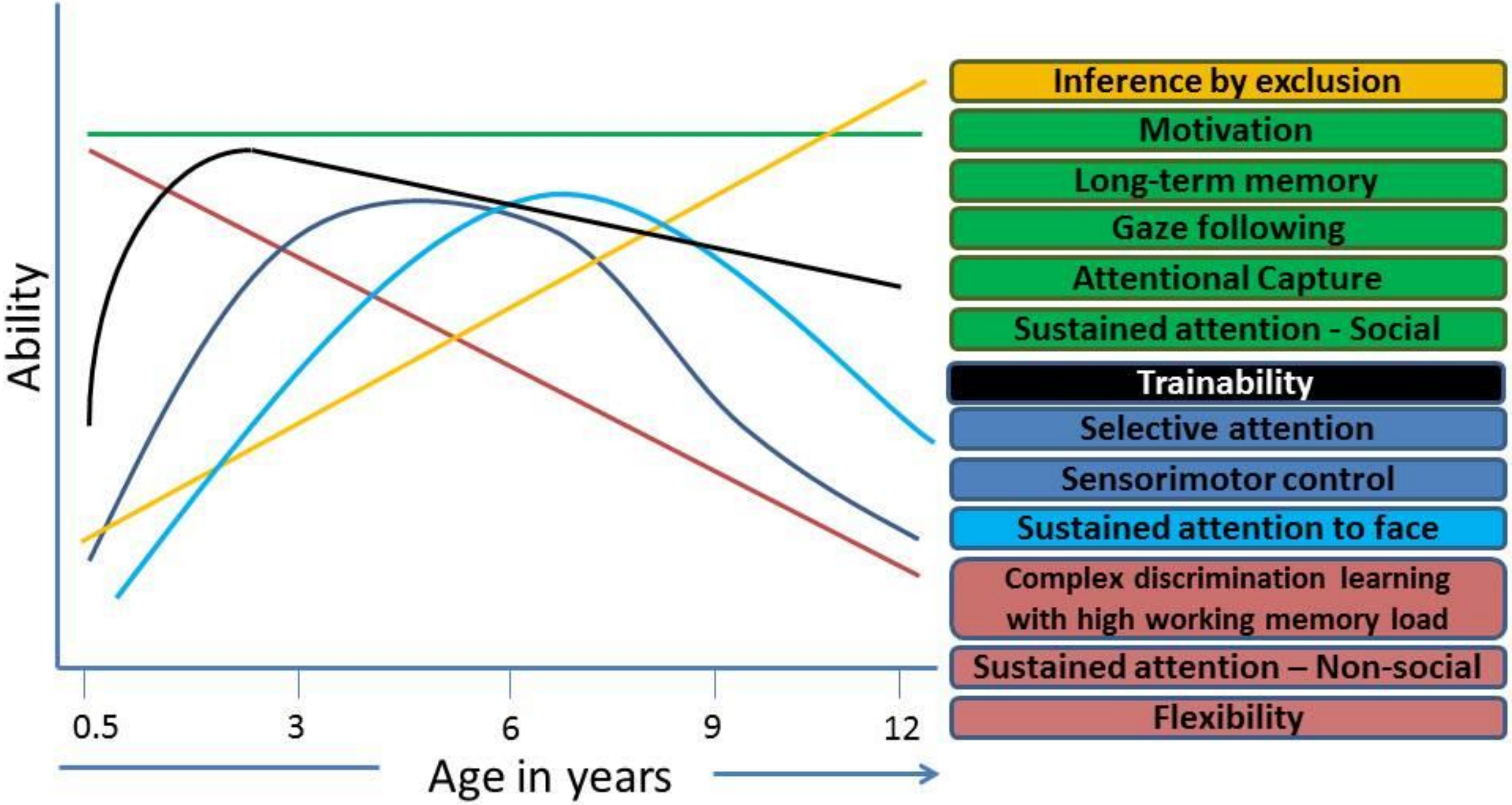

Figure 4: Cross-sectional developmental trajectories of the different domains and basic control processes measured using the touchscreen and the VCCB.

5.1.1 When do dogs cognitively mature?

Since there are differeing trajectories of maturational and aging effects found in different regions of the cortex, and the fact that we expect pre-specified, relatively independent, “domain specific” pathways for some aspects of social and cognitive development (Moore, Oates, Hobson, & Goodwin, 2002), there will be no absolute age at which dogs become cognitively mature. Instead, the different domains and basic control process will also follow differeing developmental trajectories, and ages of maturation. For example, by 6 months of age, pet Border collies displayed adult levels of visual discrimination learning, working memory, long-term memory, attentional capture, sustained attention, gaze following, motivation and flexibility. However, the adolescent period corresponded to a peak in trainability, and the maturation of selective attention and sensorimotor control did not occur until three years of age. Finally, sustained attention to the human face peaked at six years, and the ability to choose by inference by exclusion increased into old age (tested in dogs up to the age of 12). Please refer to Table 3 for ages of maturation for the different domains and processes measured.

Both selective attention and sustained gaze to the face variables were measured during social attention tasks, and involved the individual’s ability to inhibit distractors, which may explain why similar results were found. The maturation of sustained attention to social stimuli differed as regards to whether the dog attended to any part of the human and her movements, or if the dog sustained gaze to the experimenter’s face, and disregarded her gaze cues. The longer period of maturation for sustained gaze to the human face, might indicate that this ability requires additional experience, and the development of a strong preference to attempt to maintain eye contact regardless as to where the experimenter was looking. The age at which the ability to choose by inference by exclusion peaked corresponded to a zenith in perseverative responding. Thus indicating, that in the current test used to measure inference by exclusion, older dogs that displayed inflexible responding outperformed younger individuals.

In order to better examine how the different measures of cognition and basic control processes change with age, and how they may influence each other, each measure was standardized into Zscores and plotted against age in months using the loess function, which allows the non-linear plotting of relationships (Figure 5). Loess lines can be fitted to scatterplots in order to visualize the relationship between age and each of the variables by tracing the trend of the data, without any prior assumptions regarding the form of the underlying relationship (Cohen, Cohen, West and Aiken, 2003). Using this method some interesting fluctuations with age become apparent, which were not detected by linear or quadratic modelling. Firstly, several peaks occur during adolescence and early adulthood, including sustained social and non-social attention, flexibility, and trainability, which also correspond to a decline in gaze following (first look away from experimenter to door in 10 seconds) and selective attention. From about four years onwards, a relatively stable plateau phase occurs where little fluctuation in measures is observed until the dogs are around 7 to 8 years old. Therefore, the data suggest that this corresponds to a period of maturation in the Border collie. However, it is worth noting that during this stable period, the dogs' discrimination learning ability, flexibility, trainability and sustained non-social attention continue to decline.

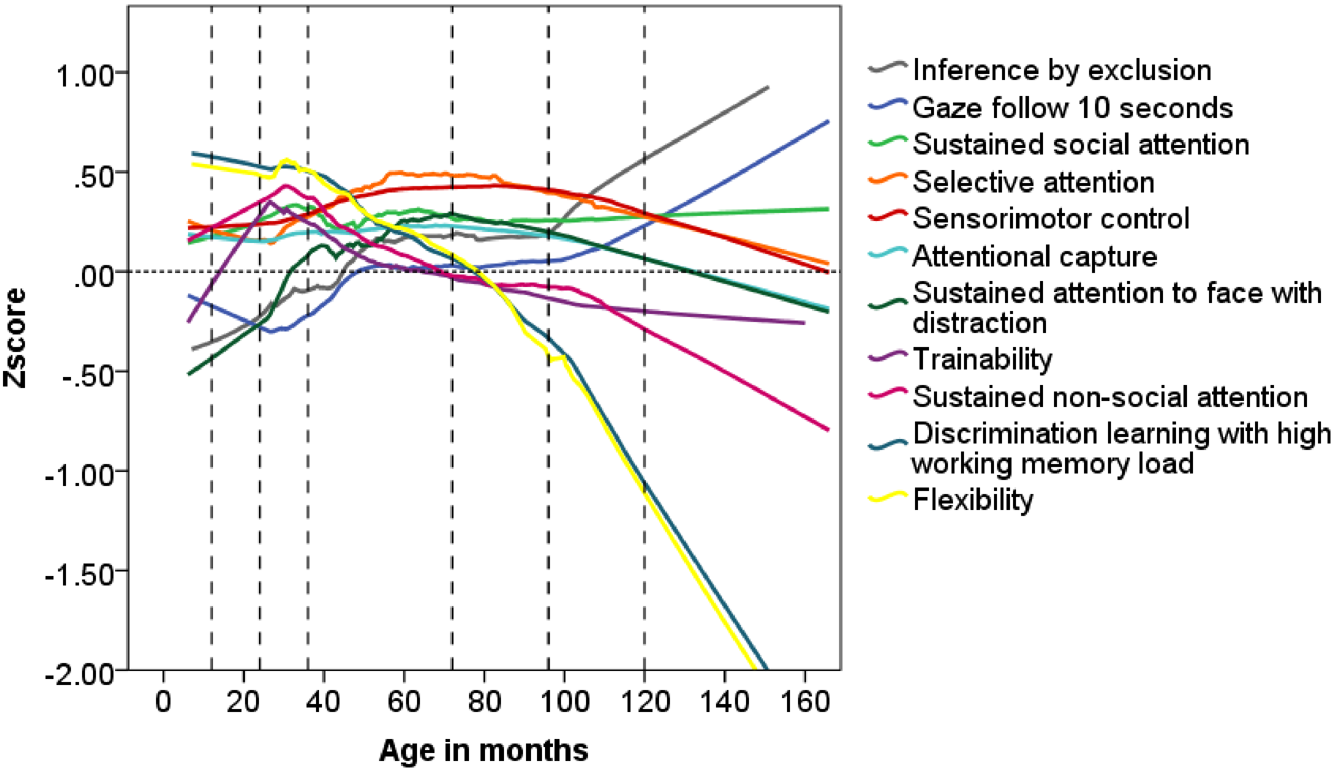

Figure 5: The relationships with age of general cognition: discrimination learning, trainability, memory, and inference by exclusion. Social cognition: sustained social attention, sustained attention to face, selective attention, and gaze follow 2 seconds).

Basic control processes: attention, and flexibility, and finally, sensorimotor control. All raw variables were transformed to z scores and cross-sectional developmental trajectories plotted utilising the loess function (50% of points fitted; kernel: Epanechnikov; statistical software:SPSS). The vertical dividers correspond to the different age groups tested in the cognitive battery (age group 1: 6 – 12 months; 2: 12 – 24 months; 3: 24 – 36 months; 4: 36 – 72 months; 5: 72 – 96 months; 6: 96 – 120 months, and 7: >120 months).

5.1.2 When does aging begin in dogs?

There is a huge variation in mean life span across the different breeds of dogs living in human households (O'Neill, Church, McGreevy, Thomson, & Brodbelt, 2013), therefore the age at which aging begins is likely to change depending on breed, size and weight, as well as the prevalence of hereditary diseases (Szabó, Gee, & Miklósi, 2016). According to O'Neill et al., (2013) Border collies have a median lifespan of 13.5 years, which is very similar to the Beagle at 13.3 years (Michell, 1999). Therefore, when comparing the results from cognitive tests on laboratory Beagles, and pet Border collies, we can assume that they go through the different stages of cognitive development at a similar rate. Studzinski et al., (2006) divided the Beagle adult life into similar periods, as those we utilised in the cognitive battery with the Border collies (puppies (<1 year), young adult (1-3 years) (here we split this group into 1 – <2 years (adolescence) and 2 – <3 years (early adulthood)), adult (3-<6 years) (which we termed middle age), middle aged (6-<8 years) (which we called late adulthood), old (8-<10 years) (here, senior), and senior (>10 years) (Geriatric)). Additionally, different authors have defined the threshold of old age at different intervals, for example Golini, Colangeli, Tranquillo, & Mariscoli, (2009) set the threshold at 7 years, and Neilson, Hart, Cliff, & Ruehl,(2001) at 11 years.

Since we already established that there is no absolute age at which dogs become cognitively mature, but instead, the different domains and basic control process follow differeing developmental trajectories and ages of maturation; it follows that the age at which aging begins in the Border collie will also depend on the domain or process measured. Results from study 1 for visual discrimination learning (the most difficult discrimination which entails a high working memory load - clip art picture discrimination 8 stimuli), indicate that the earliest age group difference is found in middle aged dogs, whose performance is significantly worse than dogs in late puppyhood. The age in month's analysis revealed that there is a linear relationship between age and number of sessions needed to reach criteria, such that from the age of six months onward the number of sessions required increases (please refer to Figure 5). This indicates that performance already begins to decline after adolescence, but only becomes significant in dogs of middle age (3 - <6 years). The same results are found for perseveration (flexibility). In test 2 of task 3 inferential reasoning by exclusion, the age in month's analysis displayed a positive linear relationship between age and choosing by exclusion, But, when we refer to the Zscores graph (Figure 5) we find that inference by exclusion ability starts to increase after a plateau at the age of around 9 years. At this point, discrimination learning and flexibility continue to decline sharply. Finally, long-term memory showed no relationship with age, indicating that all ages were able to retain the discrimination once learned over the six month period. If the time interval between testing was lengthened then it is possible that age differences would appear in long-term memory retention.

Study 2 found no age differences in dogs' propensity to follow human gaze, therefore this ability seems to remain intact in old age. However, when we examine gaze following over the full ten seconds (first look away within 10 seconds), we find that around 9 years of age, gaze following increased after the stable plateau period (Figure 5). No significant differences were found between the older age groups and the middle aged dogs in the amount of time the dogs sustained their gaze to the experimenter's face, even though the age in month's analysis indicated a quadratic trajectory (which shows that old dogs looked for longer into the experimenter's face than middle aged dogs). According to Figure 5, sustained attention to the face during distraction declines slowly from around 7.5 years of age.

Attentional capture was measured in Study 3 and although a quadratic trajectory was found for age in months, no age group differences emerged. When we examine Figure 5, attentional capture begins to decline from aged 8 onwards, and closely mirrors the reduction in sustained attention to the face with distraction. Social sustained attention was not affected by aging, and non-social sustained attention declined with age in months, however, again no age group differences were found. According to the Z scores graph (Figure 5) around 9 years of age sustained non-social attention started to decline sharply. Geriatric dogs (aged > 10 years) were impaired in their selective attention and sensorimotor control in comparison to middle aged dogs.

Therefore we can be confident to report that by 10 years of age dogs show significant declines in selection attention and sensorimotor control. Puppies showed a huge variation in trainability (regression slope of the 20 clicker training for eye contact trials), if these dogs are removed, then a significant linear relationship between age and trainability emerges (r=-.269, p = 0.003) with aged dogs showing declines in trainability in comparison to adolescent dogs. No age effects were found in the measure of motivation (latency to find food on the floor over 20 trials).

In conclusion, we were able to confidently detect the onset of aging through significant differences between the age groups for visual discrimination learning with high working memory load, and flexibility from three years onwards. Selective attention and sensorimotor control declined from 10 years onwards, and trainability from 3 years onwards. However, it is worth noting that the dogs from 3 to 6 years may have already been performing at peak levels from the start of the 20 training trials, therefore additional measures are needed for trainability in order to confirm these results. When also considering quadratic relationships with age in months, there is some indication that the frequency of looks to the door (a measure of distractibility), increases from 6 years, and the amount of time the dogs sustained their gaze to the experimenter's face declines from 7.5 years. Finally, attentional capture declines from 8 years and non-social sustained attention declines sharply from 9 years onwards after a more stable plateau period.

5.1.3 What is the practical relevance of the results?

The results from the three studies can be useful to inform current and future dog owners/trainers and researchers on the normal development of behaviour and cognition over the lifespan of pet dogs from 6 months to old age. Previously, most owners could only refer to books with anecdotal observations, or rely on other dog owners with previous experience or dog trainers, for details of what is normal and abnormal. Most published research only explores limited age groups within laboratory dogs. Although there is a large variation in individual behaviour in the different age groups, it is still possible to map the "normal" development of cognition and basic control processes in the Border collie. For instance the puppy period and adolescence is characterized by large fluctuations in abilities, and corresponds to a time when many behavioural problems occur. During the adolescent period the individual becomes more sensitive to environmental stimuli. Social experience and stressful events in adolescence may increase levels of anxiety, aggressiveness and stress responses. Sachser, Kaiser, & Hennessy, (2013) argue that this phase may represent an additional sensitive period, where an individual’s behavioural profile (including personality and temperament) is profoundly shaped by external events, social events in particular. This assumption would perfectly explain our results, including the peaks in attention to social and non-social stimuli and trainability.

The adolescent period of behavioural and cognitive change extends beyond the pre-defined life stage that we labelled adolescence in Border collies (age group 2: 12 to 24 months). Even though the dog may have gone through the physical development necessary in order to be ready to reproduce, the behavioural and cognitive development continues after this period into early adulthood (24 to 36 months, please refer to Figure 5), before stabilizing at around 3 to 4 years of age. Therefore, we propose that just as in humans, the dog adolescence period extends beyond pure reproductive readiness, and follows the onset of puberty, during which time a young dog develops from a puppy into an adult individual. Adolescence is a period of considerable maturational change in the brain, according to neurobiological and psychological research in humans (Luna & Sweeney, 2001). During adolescence humans are particularly vulnerable to the onset of mental illness such as depression, anxiety, bipolar disorder, and schizophrenia. Correspondingly, this period also coincides with the most behavioural problems reported in dogs, and the subsequent abandonment and euthanasia of animals at shelters and humane societies (Scarlett, Salman, New, & Kass, 2002). By better informing new and potential dog owners of the types of behaviours to expect during adolescence, and the fact that the dogs behaviour will normalise after this period may go a long way in reducing the number of animals released to shelters during this time.

The predictive value of puppy tests has also recently been called into question by Riemer et al., (2014), who found that early behavioural tests yield poor predictability regarding future behaviour in pet dogs. There is no doubt that early socialisation and training during puppyhood and throughout the adolescence period can provide a stable basis for adult dog behaviour (Kutsumi, Nagasawa, Ohta, & Ohtani, 2013), particularly in those behaviours which will help dogs to integrate into human families, such as socialisation (response to strangers), and response to commands (general obedience). There is some speculation if events that occur during adolescence may influence the individual's later adult behaviour (Riemer et al., 2014). Whether behaviour and cognitive performance during adolescence can be predictive of future adult measures has yet to be tested. However, according to our cross-sectional analysis this appears unlikely, as adult individuals tended to show an increase, or reduction in the variables measured in comparison to dogs in the adolescent period. This is good news for dog owners, as the more challenging behaviours they experience from their dogs during adolescence will (in most cases) no longer be an issue once the dogs reach behavioural maturation around 3 years of age. To reduce the possible influence of cohort effects, future studies should investigate longitudinal developmental trajectories by repeated testing dogs at different ages.

Based on the Z scores graph (Figure 5) we can be confident to suggest that cognitive and behavioural maturation occurs around 3 to 4 years of age, and aging effects will start to occur around 9 to 10 years of age in the Border collie. Information on the normal decline of the various cognitive domains and basic processes is important for dog owners, in order for them to understand what the normal process of aging is. If a dog presents signs of cognitive decline at an earlier time period, or in an accelerated manner, there is cause for concern, medical intervention should be implemented, as it is likely that the dog is suffering from canine cognitive dysfunction. The fact that short-term training and training experience over the lifetime can help to boost performance in some domains is also good news for dog owners, and implies that "old" dogs can benefit from some gentle training exercises, and the popular belief that they should be retired, or "put out to pasture" can be debunked. According to studies in laboratory dogs, pet dogs' welfare may also be improved additionally through physical exercise, which could help to delay the onset of aging (Cotman & Berchtold, 2007; Head et al., 2009; Nippak, Mendelson, Muggenburg, & Milgram, 2007). Therefore, owners of aged dogs should be advised to keep their dogs as active as possible, whilst controlling for any pain or arthritis issues.

5.2 The Border collie as a model for human cognition

The development and aging of cognitive abilities and basic control processes in pet Border collies show striking similarities to results found in test with laboratory dogs and humans. In fact, in all measures the predicted relationship with age (based on previous studies in humans and laboratory dogs) was found, except for inference by exclusion, and sustained social attention (please refer to Table 3). However, when alternative testing paradigms are utilised, we may find a different trajectory for inference by exclusion (by allowing rewarded test trials), and for sustained attention to social stimuli (by increasing the difficulty of the task by tested for longer time intervals). Therefore we can be confident to suggest that the pet Border collie is a suitable model for human cognition. We cannot answer the question of whether pet dogs are a better model than laboratory dogs, as no direct comparison has been made here.

The first detectable sign of cognitive decline in laboratory Beagles occurs at 6 years of age (Studzinski et al., 2006). Yet different studies have determined the onset of aging in pet dogs to commence at different ages, at 7 years (Golini et al., 2009), 8 years (Salvin, McGreevy, Sachdev, & Valenzuela, 2010), 9 years (Practice et al., 2009), and finally 10 years (Neilson et al., 2001) utilising aging questionnaires. Since the median age at death for Border collies is around 13.5 years, and larger breeds tend to have a shorter median lifespan (for example 8 years in the Rottweiler (O'Neill et al., 2013)), we can speculate that different breeds will have different ages of maturation, and onset of cognitive decline. In order to utilise multiple breeds of dogs as a model for human cognition, it would be necessary to correct for the lifespan of each breed. Szabó et al., (2016) proposed a simple calculation of dividing the actual age of the dog by the mean or median lifespan for its breed. Since weight has been found to significantly influence lifespan in dogs, the equation used by Greer, Canterberry, & Murphy, (2007) life span/years = 13.620 + (0.027638 x height/cm) - (0.118609 x weight/kg) would also be appropriate. However, both methods do not take into account that the onset of life stages in different dog breeds may vary, and the transition from one life stage to the next is not linear.

By utilising the pet dog as a model for human cognition we are able to generalise the findings from the laboratory setting, into real life environmental settings, provide valuable information relevant for the multitude of dog owners around the world, and potentially benefit both canines and humans, by utilising cognitive testing to assist with the development of treatments to delay cognitive decline. By replacing the beagle model of human cognition, with a pet dog model, we were better able to examine how factors such as training, learning, attentiveness and communication influence how dogs perform in cognitive tests in their natural environment that they share with humans. Many of the tests used in the cognitive battery were included in order to examine some of the methods dogs use to flexibly adjust to the human environment in which they live, and in some cases work, by utilizing tasks which closely represent challenges in the dogs' normal day to day living situation. Thus, we can argue that the methods used are practically more relevant to examine cognitive development and decline, than those used in laboratory Beagle studies.

5.3 Selecting tests to detect cognitive change over the lifespan of pet dogs

The three studies aimed to provide a baseline for the normal development of cognition and basic control processes over the lifespan of pet dogs from 6 months to old age. The resulting developmental trajectories of the various measures obtained from the cognitive battery and the touchscreen paradigm demonstrate that the effects of aging are not only observable, but are also measurable. When the aim is to examine lifespan development in one breed of the pet dog, then the methods used in the three studies are appropriate. The tests in the cognitive battery can be completed in a very short time period, only around 15 minutes, need only few props (moving novel object, clicker, and food pouch), and the analysis limited to a few select variables to cut down on video coding time. Therefore, for instance, due to the short testing and analysis time, they can be used on a large sample of pet dogs to accurately assess breed differences in cognitive development and aging, either in a laboratory environment, or even in the home, or shelter setting.

The discrimination learning tasks on the touchscreen in particular show clear age differences confirming that the tests used are suitable to detect cognitive aging in pet dogs. However, the touchscreen paradigm is much more time and labour intensive and requires specialist equipment. Touchscreen technology is slowly becoming cheaper, and before long, the average dog owner might afford to buy a system including automatic feeder, so that their dog might be trained at home, and the owner carries out the cognitive testing themselves. Online applications with tests designed to engage the dog and the owner could be implemented and a citizen science approach adopted, similar to the already existing Dognition.com website, which utilises a series of 10 simple cognitive tests carried out in the dogs home (Stewart et al., 2015). A subscription and profile service would ensure that all data collected by the application would be available online via a cloud server and fully downloadable. The data collected could then be used to examine the effect of age, personality, and training, test experience, sex and breed differences, by additionally collecting demographic, dog personality and training questionnaires.

The selection of tests to detect cognitive change in pet dogs depends on the specific aim in question, the life stage that will be examined, and whether a baseline should be used, as a basis for comparison.

Future studies can answer the questions of -

1) Whether the cognitive battery has reliability and validity, which are crucial requirements to consider a measurement relevant and accurate. This could include the additional of questionnaires which could be correlated with the results from the cognitive battery. For example, reliability and validity has already been determined for some tests designed to measure personality in dogs (Túrcsan et al. 2016, in prep).
2) Whether the developmental trajectories from the cognitive battery and touchscreen paradigm found in the Border collies are generalizable to other dog breeds. I.e. do other breeds show the same patterns of development and aging in the different domains and processes?
3) Whether the tests are sensitive enough to detect changes in dogs of 6 years and over, in order to more closely examine the normal aging process.
4) Whether dogs that have been diagnosed with canine cognitive dysfunction are able to participate in the tests in order to compare normal aging to pathological aging.
5) Are the different trajectories found dependent on each other? For example can the measures for attention predict performance in tests designed to measure cognitive ability (such as trainability and discrimination learning) and other basic control processes (such as flexibility and inhibition).
6) Is there a general intelligence factor in dogs as found in humans? (For details of statistical analysis please refer to Arden & Adams, (2016)).
7) To what extent does personality play a role in shaping the development of cognitive abilities in pet dogs?
8) Whether the dependency of the dog on the owner, otherwise known as the attachment bond, or type of attachment influences dogs' cognitive performance in the cognitive battery?

5.4 Cognitive domains investigated

In the next section we will examine the different cognitive domains and basic control process individually and discuss the results from the three studies in comparison to those found in non-human lab animals, and in normal human development and aging over the lifespan. Additionally, we will examine existing studies which detail neural correlates with cognition, and provide suggestions for futures studies where data is lacking.

5.4.1 General cognition

Learning

Dog's visual discrimination learning ability was assessed using a touchscreen apparatus, and baseline measures associated with normal aging were established using one dog breed, the Border collie. This study provides the first large scale touchscreen based dataset on general cognitive skills and age-related dysfunction in the canine aging model. Dogs' learning ability decreased with age in line with previous studies in laboratory dogs (Milgram et al., 2002; Snigdha et al., 2012; Tapp, Siwak, Estrada, Head, et al., 2003a). Age differences increased with task difficulty caused by stimuli preferences, and a larger number of stimuli which needed to be encoded into long-term memory. In human studies, age effects are also better detected by utilizing more complex tasks (Alvarez & Emory, 2006; Mell et al., 2005). Middle aged dogs performed significantly worse than dogs in late puppyhood, possibly due to decreases in processing speed, reduced cognitive resources, an inability to ignore distracting information (Baddeley, Baddeley, Bucks, & Wilcock, 2001; Costello, Madden, Mitroff, & Whiting, 2010; N Lavie, 1995; Snigdha et al., 2012), and the use of ineffectual problem solving strategies, such as stimulus response strategies (stimulus preferences or avoidance) and positional strategies (side bias). Similar results were found in smaller scale touchscreen discrimination studies in mouse lemurs (Joly, Ammersdörfer, Schmidtke, & Zimmermann, 2014), rats and mice (Bussey et al., 2008; Creer, Romberg, Saksida, van Praag, & Bussey, 2010), rhesus monkeys (Nagahara, Bernot, & Tuszynski, 2010; Voytko, 1999; Zeamer, Decamp, Clark, & Schneider, 2011), and larger scale studies in humans (Clark et al., 2006).

Younger dogs superior learning ability was also reflected in their performance in the inference by exclusion test trials. These dogs were quick to react to the lack of external feedback in the unrewarded test trials, quickly learnt that a “correct” response did not result in a food reward, and subsequently changed their response pattern and tried other strategies to obtain the reward. Decision making behaviour is driven by reward prediction errors generated in dopaminergic neurons, which encode the magnitude of the discrepancy between the expected and the experienced reward, and is the neural basis for learning (Schultz & Dickinson, 2000). When rewards are omitted, activity in anterior cingulate, dorsolateral prefrontal, and orbitofrontal cortex is increased (Niki & Watanabe, 1979; Tremblay & Schultz, 2000) which allows behavioural adaptations to changing situations, thus enabling subjects to form new predictions and obtain the desired rewards.

Dog’s trainability was examined in study 3 during the first twenty trials of clicker training for eye contact with the experimenter. This task fits the definition of trainability, as the dog must be willing to attend to the trainer (the experimenter), and to understand what the trainer wants (eye contact without a command), and finally to remember the task which is being taught (to look up into the face after finding food). The dogs’ performance improved across the training trials, proving that all age groups showed the ability to learn in this task. Older dogs showed deficiencies initially in this task, as was predicted, but they were able to significantly reduce their latencies with training similarly to the other age groups. Adolescent dogs also displayed initial deficiencies in the clicker training for eye contact task. However, this age group showed the highest learning rates of all the age groups. Indicating that during adolescence, dogs may experience an increase in attention as a result of goal directed behaviour, and thus show improved learning ability in this task. The regulation of attention and goal directed behaviour in human adolescents’ has also found to improve during this period (Yurgelun-Todd, 2007). Our results confirm Bentosela, Barrera, Jakovcevic, Elgier, & Mustaca's, (2008) assertion that the gaze response involves instrumental learning processes, and does not require complex cognition. Even very short training sessions result in a significant increase in the dog’s gaze to the human face. Aged dogs can benefit from such training sessions, to help counteract the effects of aging on dogs’ interspecific communicative abilities.

Our results confirm that complex discrimination learning tasks that require extensive cognitive control are sensitive to aging in domestic dogs. Future studies should aim to test simple discrimination tasks, for example those that only require two picture stimuli to be encoded (a task which may not involve a strong load on working memory), to examine whether age effects are still present. The influence of previous touchscreen discrimination experience on dogs' performance needs to be investigated, as well as their' reaction speed, and whether reaction speed predicts learning, perseveration, and/or test performance. Future studies utilizing the touchscreen and behavioural tests could also examine the effects of repeated cognitive and attentional training, and the retention and improvement of general cognitive abilities in dogs. Neuroprotective nutraceuticals are now available to treat Canine cognitive dysfunction (CCD), such as Senilife®, which can markedly improve signs of CCD after three months as measured by owner report (Osella et al., 2007; Osella, Re, Badino, Bergamasco, & Miolo, 2008). Touchscreen studies and cognitive batteries could also provide accurate measures of the effects of dietary and nutraceutical interventions to preserve cognitive abilities in dogs.

Memory

Some of the phenomena characteristic of human memory have been detected in animals, including working memory in monkeys (McGonigle & Chalmers, 1977; Rapp, Kansky, & Eichenbaum, 1996; Spinelli et al., 2004; Treichler & Raghanti, 2010), pigeons (von Fersen, Wynne, Delius, & Staddon, 1991), baboons (Cook & Fagot, 2009), and dogs (Fiset, Beaulieu, & Landry, 2003; Fiset, 2007; Salvin, McGreevy, Sachdev, & Valenzuela, 2011; Tapp, Siwak, Estrada, Holowachuk, & Milgram, 2003). Working memory capacity has been measured using a progressive delay modification of the delayed non-matching to position task. Some exceptional young dogs are capable of delays up to 110 seconds, and aged dogs up to 30 seconds (Adams, 2000; Chan et al., 2002), and in an object permanence task, dogs' were able to find hidden objects above chance at delays of 4 minutes (Fiset et al., 2003). In comparison, age dependent working memory deficits can already be detected in rhesus monkeys at delay intervals of 5 seconds (Presty et al., 1987) using a delayed matching to sample task. Performance decreased much more rapidly in non-human primates, than it did in dogs, which could be due to differences in testing protocols (matching versus non-matching). Working memory in humans shows a gradual increase over childhood and a decline in old age (Borella, Carretti, & De Beni, 2008; Sander, Lindenberger, & Werkle-Bergner, 2012). Changes in frontal subcortical white matter occur in conjunction with age-related decline in executive capacity in humans (Craick et al., 2000; Sander et al., 2012), and in animals (Bizon & Woods, 2008; Peters, Leahu, Moss, & McNally; Tapp et al., 2006).

Although dogs are able to learn to categorise and memorise two dimensional pictures on the touchscreen, their performance is well below that of pigeons, rats, birds, humans and non-human primates (Aust, Range, Steurer, & Huber, 2008; Bussey et al., 2008; Joly et al., 2014; Laude, Pattison, Rayburn-Reeves, Michler, & Zentall, 2015). Perhaps the fact that the dogs needed to remember abstract two dimensional images on a screen, which have little meaning to the dogs in their everyday lives, caused them to use strategies other than working memory to attempt to solve the tests. In our inference by exclusion tests, dogs were only required to remember new stimuli for a maximum of approximately 30 seconds, which should be well within the capabilities of dogs, according to tests of working memory.

Zanghi, Araujo, & Milgram, (2015) examined whether working memory ability (as measured using a variable delay non-matching to position task) could predict performance on two-choice discrimination learning, selective attention, and motor learning tasks. Although significant age effects were found for discrimination learning, working memory ability in aged dogs was found to be independent from learning and attentional domains. However, the authors point out that the dogs had extensive experience in the working memory task, but not in the discrimination or attention tasks. Results suggested that tasks which are designed to independently measure cognitive domains and basic control processes may not be directly comparable, due to differences in testing paradigms. Evidence from previous studies confirms that after learning specific tasks, dogs do not generalise their performance when the context, location, apparatus, and/or stimuli are changed (Bray, MacLean, & Hare, 2014; Müller, Riemer, Virányi, Huber, & Range, 2016). Additional tests to examine working memory in dogs utilizing the touchscreen paradigm, compared to other paradigms will help to determine whether dogs working ability is generally poor when multiple stimuli/locations need to be remembered, or if the context of the tests affect dogs working memory performance.

Working memory capacities in dogs can be improved in subjects through training, however, rates of learning are faster in younger than aged subjects (Adams, 2000). Working memory can also be improved by nutraceutical supplements (Araujo, Landsberg, Milgram, & Miolo, 2008), and exercise (Snigdha, de Rivera, Milgram, &

Cotman, 2014). Future studies could utilise the touchscreen paradigm to examine the effects of breed, training, exercise, supplements, and diet on working memory and long term memory in dogs.

Few studies have addressed long-term memory capacity in animals. One study examined long-term memory for 320 picture stimuli in pigeons after a two year interval. The pigeons performed above chance when discriminating between the two categories of pictures (Vaughan & Greene, 1984). In a study by (Fagot & Cook, 2006) both baboons and pigeons demonstrated evidence for large long-term memory capacities, recalling over 5900, and 1900 picture – response associations respectively, over a 3 to 5 year period. Araujo, Studzinski, & Milgram, (2005) tested laboratory beagles in a memory task, and found significant declines in working memory with age, however, long term memory remained stable (memory for previously learned discriminations after a two year break period). Our results from study 1 replicate these findings using the touchscreen paradigm (but with a 6 month break period), providing additional evidence that long term memory and procedural memory are more resistant to aging, mirroring the development of memory in humans. The limits of dogs' long-term memory, both in terms of the capacity and length before decay, and the effects of aging on these abilities, have yet to be tested.

Individual problem solving and reasoning abilities

Inference by exclusion

The capacity for logical reasoning such as learning by exclusion is well documented in non-human animals (Watanabe & Huber, 2006), and has been studied in nonhuman primates, sea lions, dolphins, dogs, goats, ravens, crows, African grey parrots, Kea and Goffin cockatoos and dolphins, using an inference by exclusion paradigm (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Call, 2006; Erdőhegyi, Topál, Virányi, & Miklósi, 2007; Herman, Richards, & Wolz, 1984; Mikolasch, Kotrschal, & Schloegl, 2011, 2012; Nawroth, von Borell, & Langbein, 2014; O'Hara, Auersperg, Bugnyar, & Huber, 2015; O'Hara, Schwing, Federspiel, Gajdon, & Huber, 2016; Schloegl et al., 2009; Schusterman, Gisiner, Grimm, & Hanggi, 1993). However, there have been very few studies to examine whether logical reasoning is also affected by aging in non-human animals (Call, 2006). Call's (2006) study showed that Great Apes have the ability to make inferences by exclusion and results suggested a positive relationship between age and inferential ability. Study 1 examined dogs' ability to reason by exclusion, which was predicted to peak in young adults, and then steadily decline, based on studies in human literature, and dogs' working memory capacity. Although we found that a small percentage of the subjects were able to use inference by exclusion as one strategy utilizing the touchscreen paradigm, due to a learning effect or a violation of expectancy in the younger subjects (owing to lack of a reward after logically selecting the "correct" stimulus), we were unable to confirm the relationship between inference by exclusion and age. Patterns of choice consistent with inference by exclusion were found in some individuals, but this strategy was not the predominant one utilised by the dogs. Inference by exclusion, one trial learning, stimulus and novelty preference and avoidance, and novelty rule abolishment/reversal are all theoretical response patterns, which could be displayed by dogs.

Currently, we are conducting a new study based on the methods developed by O'Hara et al., (2015), which allows feedback in test trials to examine dogs' inference by exclusion abilities and how they may change with age. This study will also measure the neophilic tendencies of dogs and how age affects neophilia. Results from test 1 in study 1 showed an initial preference for novel stimuli regardless of age. However, previous studies in dogs have indicated that preference for novelty shows a decline with age (Handa, George, Gordon, Campbell, & Lorens, 1996; Rosado et al., 2012; Siwak, Tapp, & Milgram, 2001; Soffié, Buhot, & Poucet, 1992). Indeed, in study 3, we found that older dogs showed decrease sustained attention to a novel flying object compared to young dogs. In the touchscreen study, an initial avoidance of the known negative (S-) in test 1, and a subsequent novelty avoidance in test 2 (when paired with S") can explain the performance of the older dogs which showed inference by exclusion above chance. Our follow up study will examine the predominant strategies used on an individual as well as age group level, and will also confirm whether levels of neophilia, and/or increased experience with negative stimuli (as found in study 1, when dogs repeatedly chose S- during training), results in a higher likelihood of finding response patterns consistent with choosing by exclusion.

Our findings add to the increasing amount of evidence for the existence of inference by exclusion ability in nonhuman animals, and argue against the suggestion that it is a uniquely human trait (Ogawa, Yamazaki, Ueno, Cheng, & Iriki, 2010). Neural correlates of inference by exclusion could help to establish whether the mechanism, which is utilised during exclusion tasks by humans and nonhuman animals are similar. However, neural correlates have so far only been investigated in humans using functional magnetic resonance imaging. When the subjects were utilizing exclusion, significant activation in the prefrontal cortex and inferior parietal lobule (IPL) was observed (Ogawa et al. 2010), which indicates that executive functions such as working memory are utilised during tasks involving inference by exclusion. Specific regions in the human IPL are activated when detecting new salient items and when maintaining or controlling attention over time (Husain & Nachev, 2007). Parts of the human IPL are thought to be similar to Macaque IPL; however, further studies are necessary to elucidate species similarities, and whether there are new functional subregions within the human IPL which are not present in nonhuman primates or other animals.

5.4.2 Social Cognition

Dogs are uniquely suited for investigating the evolution and development of social cognition, given their special domestication history, living in the human environment and engaging in communicative interactions with humans for more than 10,000 years (Cooper et al., 2003; Huber et al., 2009; Miklósi, Topál, & Csányi, 2004). One crucial feature of the human – dog relationship is communication utilising visual signals. Eye contact is an essential feature of attention, and is fundamental in communicative situations (Gómez 1991). Dogs can sense the attentional state of their owners and can flexibly adapt their behaviour in response to signals such as eye contact, and eye, head and body orientation (Schwab & Huber, 2006). Dogs have been found to excel at interspecific communication tasks, and studies have shown that associative learning is one of the most important contributors to dogs performance (Bentosela et al., 2008; Elgier et al., 2009; Marshall-Pescini, Passalacqua, Barnard, Valsecchi, & Prato-Previde, 2009; Wynne, Udell, & Lord, 2008). Indicating that age at testing and the amount of training experience the dog has been exposed to could have a significant effect on dogs' abilities in tasks involving interspecific communication.

Our results from study 2 and 3 support both the effects of training experience on dogs' gaze following abilities, and age on dogs' gaze orientation to the experimenter in the clicker training for eye contact test. We predicted that dogs' interspecific communication abilities would follow a quadratic distribution with age, which we found in the clicker training for eye contact test, however dogs' gaze following tendencies were not affected by age. This may have been due to the fact that the dogs had a conflicting goal of attending to the experimenter and waiting for a clear vocal command or hand cue, rather than following the experimenter's gaze direction, due to past training experiences. But we did find a quadratic effect of age on the number of times the dogs looked towards the door in both test and control trials, with the youngest and oldest dogs showing the highest tendency. We suggest that these dogs displayed greater distractibility, resulting in an increased frequency of gazing to the door in the gaze following test, and an increase in latency to orientate to the experimenter in the clicker training for eye contact test; indicating that dogs in late puppyhood and geriatric dogs are less able to inhibit their behaviour in multiple contexts. Our results lend support to Gómez (2005) assertion that gaze following develops in interaction with other cognitive and motivational systems such as selective attention. Our results also highlight the importance of taking into account methodology, testing and motivational contexts when examining interspecific social cognition in dogs (Gómez, 2005; Met, Miklósi, & Lakatos, 2014; Prato-Previde & Marshall-Pescini, 2014).

Human directed gazing behaviour has been found to be influenced by both genetic factors and life experiences. Persson, Roth, Johnsson, Wright, & Jensen, (2015) tested 437 laboratory Beagles to investigate within-breed variation in human-directed contact seeking in an unsolvable problem task, to estimate its genetic basis. They found that older dogs (up to six years of age) looked at the experimenter earlier, more frequently, and for longer durations than younger dogs (from 8 months to 2.4 years). Heritability was estimated for social interactions during the test (including physical contact with the experimenter and eye contact), as 0.23, revealing a significant genetic contribution. However, it is important to note that these dogs were laboratory animals with limited experience of human interactions, and very different rearing conditions from normal household pet dogs. Additionally, specific breeds have been selectively bred for their understanding of human communicative signals, and for their enhanced cooperative ability, such as herding and gun dogs. These breeds stay in continuous visual contact with their human partner, and this enduring or sustained attention to humans may facilitate performance in interspecific tasks, due to the fact that it increases the chance that subjects might detect and recognize human gestural signals (Gácsi, McGreevy, Kara, Miklósi, & Miklósi, 2009; Jakovcevic, Elgier, Mustaca, & Bentosela, 2010; Wobber, Hare, Koler-Matznick, Wrangham, & Tomasello, 2009). When compared to mix breeds and independent workers, dog that were bred as cooperative workers were significantly more successful in utilizing human pointing gestures, providing evidence that phenotypic traits affect the ability of dogs to rely on human cues (Gácsi et al., 2009).

Dogs that spend a significant amount of time in a shelter environment tend to have less experience with human visual cues. Barrera, Mustaca, & Bentosela, (2011) tested shelter dogs and pet dogs' gaze to a human face during acquisition and extinction phases, when a food reward was out of reach. Shelter dogs gaze duration decreased more quickly during the extinction phase than pet dogs, highlighting the importance of learning experiences during ontogeny on dogs' communicative responses. Human-directed gazing behaviour improves not only with age, but also with both short-term, and long-term training (Bentosela et al., 2008; Passalacqua et al., 2011; Wallis et al., 2014). Dogs with different types of training display differing amounts of human directed communicative behaviours. Compared to trained dogs, untrained dogs spend more time looking at humans when faced with an unsolvable problem (Marshall-Pescini, Valsecchi, Petak, Accorsi, & Previde, 2008), and agility trained dogs gazed for longer at their owners, than search and rescue and untrained dogs (Marshall-Pescini et al., 2009). Finally, more sociable dogs gazed for longer at the experimenter than less sociable dogs (Jakovcevic, Mustaca, & Bentosela, 2012). All of the evidence so far presented indicates that several factors modulate interspecific communication in dogs. The communicative mechanisms between dogs and humans involve the interaction of environment, learning, personality, genetics and differential selection of traits in the different breeds.

There is evidence that oxytocin can increase gaze to the eye region in dogs, as there is for humans (Graustella & MacLeod, 2012), which indicates that it could be involved in the modulation of eye contact seeking, for example in clicker training for eye contact and gaze following in dogs. Future studies are necessary to find genes and polymorphisms associated with interspecific social skills in dogs, and the effects of age and experience on eye contact seeking. Dogs may prove to be important translational models to enable the understanding of the genetic basis of reduced eye contact and communication caused by dementia, Alzheimer's, and autism spectrum disorders (Sturm et al., 2011; Yamasue et al., 2012).

5.4.3 Basic Control Processes

Motivation

Learning and problem solving cannot take place without motivation. Lack of motivation can constrain cognitive performance, such that true values of individual cognitive abilities are not expressed. Therefore, measures of motivation in cognitive batteries are necessary to rule out any constraints. There are two measures of motivation which may affect performance; extrinsic (the value of the reward obtained, e.g. food) and intrinsic (the value the individual obtains for engaging in the task itself) (Herrmann & Call, 2012).

Study 1 utilises the touchscreen paradigm to examine general cognitive abilities in the dogs, by eliminating the influence of social cuing. Firstly extrinsic motivation is triggered through the use of high value food rewards, which are easily obtainable and triggered immediately upon a correct nose touch on the screen. Initially, obtaining rewards was very easy for the dogs, and task difficulty was increased only after individuals mastered that particular level. By removing social cuing, frustration towards the owner or experimenter was virtually eliminated; however, dogs did show a degree of frustration towards the touchscreen itself, if task difficulty was increased too quickly. Secondly, intrinsic motivation steadily increased throughout touchscreen training, to the point that some dogs preferred to touch the stimuli, and forgot to search for the food reward. Additionally, in the rare cases when the touchscreen feeder malfunctioned, and no food reward was received, the dogs carried on working, and the lack of food reward did not unduly affect performance in subsequent sessions. However, it is worth noting that reducing the reward ratio by 10% from the beginning of the training in the clip art discrimination resulted in an increase in the number of sessions needed for the dogs to complete the learning criterion. This increase was unlikely to have been caused by reduced motivation, for the reasons stated above, but likely reflects a reduction in response strength caused by the partial reinforcement (Jenkins & Stanley, 1950).

In study 2, one reason why dogs may have followed the experimenter's gaze, but not in the study of Agnetta, Hare, & Tomasello, (2000), may have been due to increased motivation to attend to the experimenter, caused by the motivational effect of previous positive training exercises. Extrinsic and by default, intrinsic motivation was increased by two preceding visits where dogs received high value food items (sausage) from the experimenter in training contexts. Indeed, in study 3, dogs' were motivated to sustained high levels of attention towards the experimenter, on average over 95% of the time, providing evidence that positive reinforcement during previous training experiences in multiple situations increases motivation, and results in improvements in attention in different contexts (Horn, Range, & Huber, 2013; Lindsay, 2001).

Study 3 confirmed that sensorimotor ability (as measured by dogs' latency to find dropped food) varied with age, and was lowest in the youngest and oldest age groups. Since high value food items were used, extrinsic motivation likely remained high in all age groups. Over a series of 20 trials, dogs did not show an increase in their latencies to find dropped food, which might have been expected when motivation is lacking. During the clicker training for eye contact, all age groups significantly reduced latencies to eye contact with the experimenter, thus indicating they were motivated to learn this simple social task. Additionally, previously clicker trained dogs out performed non-clicker trained dogs in this task, possibly due to heightened motivation. Dogs can be more motivated by the anticipation of a food reward, than by the food itself. Berns, Brooks, & Spivak, (2012) investigated brain function using fMRI in fully awake unrestrained dogs. They used hand signals, which were associated with either a food reward, or the absence of a reward. The reward prediction error hypothesis of the dopamine system indicates that brain activity should be found in the ventral caudate of the dog, when anticipating a food reward. Berns et al. results confirmed this prediction, and found striking similarities between dogs and humans in both the structure and function of the caudate nucleus. Future studies could examine the influence of aging on reward prediction and intrinsic and extrinsic motivation in dogs using fMRI and visual, odor and auditory stimuli.

Attentiveness

Dogs' attention to social stimuli was measured in study 2 and 3, and additionally their attention to non-social stimuli were measured in study 1 and 3. Dogs attentional capture abilities showed very little change with age, similarly to humans (Enns & Cameron, 1987). There is also little influence of age on sustained attention for short periods in humans (Berardi, Parasuraman, & Haxby, 2001). The youngest age group of dogs tested was already capable of adult levels of sustained attention. Future studies should test dogs aged below 6 months to determine when this ability reaches maturation. Human infants are capable of sustained attention for short periods by the age of four to six months and can even learn to delay orientation to distracter targets (Colombo, 2001). Therefore we may expect that this ability develops early also in the domestic dog. Study 3 provides the first cross-sectional lifespan overview of the development and aging of attention in the pet dog. The basic developmental trajectories of the different sub-processes of attention were found to parallel those of humans. Dogs' selective attention and sensorimotor abilities showed differences between age group means which peaked at middle age for both, indicating that they may be fundamentally interrelated in dogs as proposed in humans (Diamond, 2000). Our results complement the existing research using laboratory beagles, emphasizing the importance of the domestic dog as a model species for comparative study.

Results from study 3 suggest that there appears to be different developmental trajectories of sustained attention to social and non-social stimuli. We found a strong preference for social stimuli over non-social in the dogs. In humans, a similar preference for social stimuli over non-social stimuli is also observed, particularly in young adults and children (Hess, Popham, Dennis, & Emery, 2013; Stavropoulos & Carver, 2014). Our results add to evidence which suggests that social stimuli are processed differently than non-social stimuli, with social stimuli receiving additional attentional resources (Humphrey & Underwood, 2010). Indeed, in an event-related functional magnetic resonance imaging (fMRI) study by Harvey, Fossati, & Lepage, (2007), adult humans who viewed social pictures had brain activation located in the dorsal and ventral medial prefrontal cortex (mPFC). This area was not activated during the viewing of nonsocial pictures. The mPFC has a dual role in both inferring the mental states of others (theory of mind) and performing tasks that require people to examine their own thoughts or feelings (self-referential processing) (Kelley et al., 2002). The position and connections of the orbital and medial areas of the prefrontal cortex are similar across species (rats, primates and humans) (Uylings & van Eden, 1991), and function to link sensory and visceromotor activity, as well as guiding emotional and social behaviour (Ongur, 2000). When animals experience diminished mPFC activity their ability to selectively focus attention and to regulate impulses is compromised (Lindsay, 2001).

Preference for social stimuli over non-social may be mediated by the valence of the stimuli. For example, younger adult humans show greater sustained attention to negative pictures than older adults, but no age differences when pictures were positive or neutral (Rösler et al., 2005). Dogs' attention towards non-social stimuli showed a reduction with age, as reflected in selective attention performance in discrimination learning (study 1), and sustained attention to Event 2 (non-social stimuli (study 3)), however, we did not detect a reduction in attention to social stimuli with age (no age differences in gaze following (study 2), or sustained attention to Event 1 (social stimuli (study 3)). We propose that the dogs perceived the non-social event 2 stimulus (the flying object) as negative, which caused a heightened reaction in younger dogs, and may explain why we found age differences in this condition. The dogs are also likely to have perceived the social event 1 (human) as positive due to previous positive social experiences with humans in general, and with that specific human in previous tests. Dogs were highly motivated to attend to the experimenter and were not distracted by other external visual or auditory stimuli. Goal directed control processes help the dogs to select which information to attend to and which to ignore. Younger dogs were more distracted by non-social stimuli, which caused increased vigilance behaviour. However, older dogs were better able to ignore the potentially threatening or negative stimuli. There is evidence that older adult humans are better able to focus on emotional regulation than younger adults, and they also utilise cognitive control mechanisms that enhance positive and diminish negative information (Mather & Carstensen, 2005), which may be true also for dogs.

When we examine dogs' sustained gaze to the experimenter's face during the gaze following trials (study 2), we find that dogs aged below 3 years spent significantly less time gazing than dogs aged between 3 and 6 years. This difference was apparent before and after clicker training for eye contact, where middle aged dogs showed even greater sustained gaze to the face after training than the other age groups. Since we measured dogs' gaze to the experimenters face during the test (experimenter looked to the door) and control cues (looked to the floor), we could consider this measure to be representative of dogs' sustained attention abilities in the presence of distractors (the experimenter's salient head movement). Here we speculate that for the dogs, the aim may have been to maintain their gaze to the face in order to receive a treat, and not to be distracted by external stimuli, such as when the experimenter turned her head to look away perhaps to an interesting event in the environment. The resulting quadratic cross-sectional developmental trajectory then closely mirrors the results which we obtained in study 3 for the selective attention measure (latency to eye contact with the experimenter after finding dropped food). However, essentially two different measurements were analysed (percentage duration gaze to face, and latency to orientate to the face), so we must be cautious when interpreting these results. It is likely that both the measurements in the two tests involved various degrees of external distraction, which is known to cause problems for very young and elderly human subjects, who are less able to ignore task-irrelevant information (Baddeley et al., 2001; Costello et al., 2010; Guerreiro, Murphy, & Van Gerven, 2010).

Maturation of the prefrontal cortex function during development and alterations during aging can cause increased distractibility and impaired selective attention (Chao & Knight, 2000). Our results corroborates previous research on selective attention in laboratory and pet dogs, which indicates that older dogs have a reduced capacity to inhibit distracting stimuli (Mongillo, Bono, Regolin, & Marinelli, 2010; Snigdha et al., 2012; Tapp, Siwak, Estrada, Head, et al., 2003). In study 2 and 3, younger animals were particularly impaired in their selective attention ability. Lifespan data from humans suggest a developmental pattern of increasing control over selective attention throughout young adulthood (Plude, Enns, & Brodeur, 1994), which corresponds to the maturation of the prefrontal cortex (Luna & Sweeney, 2001). We suggest that human and dog prefrontal cortical maturation and the development of selective attention seems to follow a similar pattern. Previous studies have already found a close link between human and non-human primate cortical maturation (Goldman-Rakic, 2011).

In study 1 we suggested that younger dogs may have shown more focused selective attention, which allowed them to quickly pick out the correct stimuli on the touchscreen, and to ignore/avoid the negative stimuli. According to our lifespan prediction, we would have expected middle aged dogs (from 3 to 6 years) to perform better than younger dogs in this task, due to the fact that their selective attention abilities are at their peak at this age. However, our results indicate that dogs' attention towards non-social stimuli reduces with age, and may cause middle aged dogs to pay less attention to the discrimination stimuli and their contingencies, even though their selective attention abilities in less complex social tasks is higher than younger animals. Additionally, the discrimination learning tasks require working memory in order to memorise each individual stimuli, but the selective and sustained attention measurements in study 2 and 3 do not require the dog to remember multiple stimuli. Thus indicating that when working memory load is increased dogs' selective attention ability may be compromised, especially in middle aged and older age groups. There is evidence that visual selective attention is also impaired in humans when increasing demands are placed on working memory (Han & Kim, 2004; Lavie, 2005; Pratt, Willoughby, & Swick, 2011).

Perseveration, inhibition and flexibility

Animals live in dynamic environments and therefore need to quickly adapt to changes by suppressing and/or changing their behaviour in response to negative feedback. This ability is known as cognitive flexibility and is controlled through executive function, which depends on the integrity of the prefrontal cortex (Miller, 2000). Perseverative errors can indicate lack of inhibitory control, an inability to respond to negative feedback and consequently low cognitive flexibility. Numerous studies have found that older human and non-human animals tend to show perseverative responding in complex discrimination learning tasks (Grant & Berg, 1948; Joly et al., 2014; Laude et al., 2015; Manrique & Call, 2015; Mell et al., 2005; Picq, 2007; Ridderinkhof, Span, & van der Molen, 2002; Tapp, Siwak, Estrada, Head, et al., 2003). Very young individuals may also show perseverative tendencies and low inhibitory control (Manrique & Call, 2015; Vegas & Dempster, 1992; Weed, Bryant, & Perry, 2008; Zelazo et al., 2003). Evidence that executive system dysfunction can occur as early as middle-age was found in the Rhesus monkey using a set-shifting task on the touchscreen (Moore, Killiany, Herndon, Rosene, & Moss, 2006). This task required superior working memory, selective attention, abstraction and shifting of stimulus set abilities. The youngest age group (5 – 10 years) outperformed middle aged and old monkeys in all tasks. A strong linear relationship between age and perseverative errors was found, similarly to the results from study 1.

Traditionally perseveration is measured in reversal learning tasks, and older dogs are known to perform poorly making many perseverative errors once stimulus contingencies are reversed (Laude et al., 2015; Tapp, Siwak, Estrada, Head, et al., 2003). Poor working memory and inhibitory control are suggested as contributing factors to reduced performance in comparison to other species, such as birds, rats and primates (Macpherson & Roberts, 2010; Osthaus, Marlow, & Ducat, 2010). In study 1, perseveration was measured during complex discrimination learning. A larger number of stimuli which needed to be encoded into working and long-term memory resulted in an increased load on working memory, selective attention, and performance monitoring. The fact that learning is impaired in older dogs during the discrimination, and perseveration occurs despite the fact that the stimulus associations have not yet been established, indicates that these dogs show a greater degree of cognitive inflexibility in performance. Ineffectual strategies were used by dogs over 3 years of age when attempting to solve the discriminations. For example, stimulus response strategies such as stimulus preferences or avoidance, and/or a positional strategy (side bias), can result in the dogs repeatedly making incorrect choices. Failure to respond to negative feedback could also be due to a lack of attention and/or increased persistency. Habitual motor responses can overrule sensory input and demonstrates the strength of conditioned stimulus response behaviour in domestic dogs (Osthaus et al., 2010).

One reason that younger dogs were not impaired could be due to the fact that they have a higher sensitivity to non-social stimuli, in comparison to older dogs, and their working memory abilities may be at a peak at that age. Future studies should determine if there may be different developmental trajectories for selective attention and inhibitory control measured using social and non-social paradigms in dogs. Working memory is at optimal efficiency in young adults in humans at around 16 to 18 years old (Diamond, 2006), which would correspond to dogs aged from one to two years (age group 2). Perhaps working memory ability, attention to non-social stimuli and superior inhibitory control all combine in dogs aged 6 to 12 months, to produce superior performance in discrimination tasks on the touchscreen. A recent study on dogs discovered that context has a large effect on performance in tasks which measure inhibitory control (Bray et al., 2014). Suggesting that the testing paradigm has a strong influence on dogs' performance, and factors other than inhibitory control may cause age effects in dogs.

Recently, Cook, Spivak, & Berns, (2016) tested 11 dogs in a go/no-go task whilst in an fMRI scanner and additionally an out-of-scanner A-not-B task, to investigate the relationship between brain regions underlying response inhibition and behavioural measures of cognitive control. Their results parallel evidence in humans, that individual differences in control correlate with structural and functional measures in frontal brain regions (Forstmann et al., 2008). The brain region which showed the greatest activation was in the cortex along the pre-sylvian sulcus, and overlapped with the proreal and orbital cortex. The dog proreal cortex includes granular layer IV, which is also found in the primate prefrontal cortex, and therefore may be comparable to frontal regions activated during inhibition in humans and other primates. Additionally, there was a trend towards a negative correlation of age and false alarm rate in the go/no-go task (*p*=0.07 unpublished), which would imply that older dogs were better able to inhibit responding to no-go trials. This result contradicts the general assumption that older dogs show impaired inhibition. Perhaps performance in the go/no-go task is dependent on the degree of behavioural flexibility of the dogs. Older dogs show highly inflexible behaviour, therefore as long as they are able to recognize the “no-go” signal, they have ample time to execute the correct response, which had been extensively trained, and younger dogs, being more flexible, may have tended to try out responding to “no-go” trials more often. Alternatively, the older dogs may have benefitted more than younger dogs from the extensive training needed to allow non-invasive awake brain scanning utilizing fMRI, which could have resulted in superior inhibition ability in this task.

Hauser, (1999) differentiated between affective and paradigmatic perseveration. During affective perseveration, individuals fail to inhibit prepotent emotions or motivational drives. For example, some dogs, especially older dogs may fail to inhibit their emotions and motivations when working on the touchscreen, which gets in the way of their reasoning, causing them to make the same error over and over again. Another type of error which dogs may be susceptible to, due to a result of an impoverished conceptual system, is paradigmatic perseveration. Throughout development, animals, like humans, are susceptible to paradigmatic perseveration, which may be caused by factors other than weak inhibitory control. For example, during discrimination training, the computer randomly allocated stimuli positions to the left and right of the screen. This random allocation occasionally resulted in the positive stimuli being presented on one side of the screen for six or more trials in a row. Since dogs are known to be highly egocentric and influenced by spatial positional cues (Chan et al., 2002; Christie et al., 2005; Fiset, Landry, & Ouellette, 2006), repeated presentation of the stimuli on one side may have caused the dogs to develop a positional strategy in an attempt to solve the task, which resulted in perseverative responding. Unfortunately, we are not able to distinguish between the two types of perseverative responding. However, future studies could examine the strategies used by the dogs by measuring the occurrence of side bias, and additionally take physiological measurements such as heart rate, heart rate variability, and breathing rate. This would allow us to distinguish between affective arousal, caused by an inability to inhibit prepotent responses, and the use of ineffectual strategies, which are highly resistant to change, such as side bias. However, cognitive differences between individuals are probably caused by the degree to which inhibition can prevent both affective and paradigmatic perseveration (Hauser, 1999). Therefore, inhibitory control is necessary in order for the dogs to switch to a new strategy and break the cycle of perseverative behaviour.

The dogs' cognitive flexibility was additionally measured in the inference by exclusion tests on the touchscreen. Younger dogs performed in a more flexible manner, switching their strategy in response to lack of feedback in the test trials, providing additional evidence of the more flexible behaviour of juvenile dogs. Dogs' flexibility has also been measured in a social version of the reversal task. Elgier, Jakovcevic, Barrera, Mustaca, & Bentosela, (2009) examined reversal learning using a pointing gesture in an object choice task. Dogs were able to learn to inhibit their response to go to the pointed container when food was no longer available during extinction. They could also learn to choose the non-pointed container during the reversal, however, leash corrections and a verbal reprimand ("no") was necessary to indicate when the dogs had made an incorrect choice. Just withdrawal of the food was not sufficiently aversive enough for the dogs change their behaviour. These corrections are similar to the incorrect trials on the touchscreen, where not only the food is withheld, but the dogs must wait during a delay period, before they are able to choose again. Although dogs between the ages of 2 and 9 were tested, no age effects were reported. In a pilot study we conducted to determine whether cue type affected the reversal learning ability of dogs, four dogs were successfully able to reach criteria in the reversal, to go to the non-pointed container when the experimenter performed a momentary distal point (Wallis, Range, Müller, & Virányi, 2011). But, dogs that had learnt to go to the container that the experimenter touched were unable to inhibit their prepotent response to the strong locally enhanced cue. Therefore the saliency of cue type has a significant effect on the ability of dogs to perform in a flexible manner in this social task.

The age effects found in study 2 (increased number of looks to the door in test and control trials), and study 3 (decreased selective attention ability) can be explained by greater levels of distractibility, which has been attributed to weakened inhibitory control (Duchek, Hunt, Ball, Buckles, & Morris, 1998). Distractibility has already been discussed in the basic control section of attention. There is evidence that younger and older dogs are less able to inhibit their behaviour in multiple contexts, although the reasons for decreased inhibition may be different at the different ages

(Bray et al., 2014 and Tapp et al., 2003). In the youngest dogs' case, this could, for instance, be due to greater general activity levels, and a higher sensitivity to external environmental stimuli (see Wallis et al., 2014). In the older dogs' case, it is more likely due to decreased ability to inhibit prepotent responses. Dogs' performance in the selective attention task (study 3) improved with practice over the 20 trials either through an increased ability to inhibit prepotent responses, or through simple associative conditioning, which led to an increased relevance of the stimulus. Additional studies are necessary to examine the effects of aging and training on dogs' inhibitory control utilizing multiple contexts/paradigms.

5.4.4 Sensorimotor control

The cognitive battery contained only one test which was designed to measure the dogs' level of sensorimotor control. Although the results from the latency to find food on the floor analysis produced the predicted quadratic relationship with age, additional measures should be implemented in future studies, in order to more fully examine the impact of aging on sensorimotor control in dogs. A score could be assigned to each individual corresponding to their performance in these tests, and this score could then be used in future analysis to determine whether the dogs' degree of sensorimotor control influences any of the measures taken in the other tests within the cognitive battery. The score could also be correlated with owner questionnaires regarding the dogs' daily life activities, and the degree to which aging has impacted their dog's life. Finally, a thorough veterinary examination could also provide an index of sensorimotor ability, which could also be correlated with the sensorimotor control measures within the cognitive battery. In this way, future studies can validate measures of sensorimotor control, and additionally control for an individual's level of sensorimotor control within the cognitive battery.

5.5 Conclusion

We examined different cognitive domains, including general and social cognition, as well as basic control processes of the pet dog, and investigated the degree to which age affects the dogs' cognitive abilities utilising the Vienna Canine Cognitive Battery (VCCB), and the Vienna comparative cognition technology (VCCT). By exploring the development of different cognitive functions over the lifespan of pet Border collies from 6 months to old age, we were able to determine when the dogs cognitively matured and when the effect of aging began. We found differeing trajectories of maturational and aging effects for the different domains and processes measured. Additional analysis revealed that a plateau in cognitive ability and basic control processes is found from four to 7 years, marking a period of stability, which could be considered the maturation point for the majority of measures of the cognitive battery. We were able to confidently detect the onset of aging through significant differences between the age groups for visual discrimination learning with high working memory load, trainability and flexibility from three years onwards, sustained gaze to the experimenter's face from 7.5 years, attentional capture from 8 years, non-social sustained attention from 9 years, and selective attention and sensorimotor control from 10 years. Therefore we suggest that cognitive and behavioural maturation occurs around 3 to 4 years of age, and most aging effects will start to occur around 9 to 10 years of age in the Border collie.

When comparing our findings to the existing studies on the laboratory Beagle we find a very similar pattern of results, which also closely mirror the development and aging of cognition in humans, thus, adding to the growing evidence that the pet dog is a suitable model for human cognitive aging. Our study also provides important practical relevance. Dogs' welfare and quality of life can be improved by informing dog owners/trainers and researchers, of cognitive and behavioural changes which are a result of normal aging, and which might suggest a clinical pathology. If the Vienna Canine Cognitive Battery is found to produce the same trajectories in other dog breeds as those found in the Border collie, the measures of normal canine cognitive development and aging can be used to develop a predictive model to assist with treatments for typical family dogs to enhance cognitive development, delay cognitive decline or diagnose and treat cognitive related problems.

To reduce the possible influence of cohort effects, future studies should investigate longitudinal developmental trajectories by repeated testing dogs at different ages. Additionally, future studies should aim to determine: - whether the developmental trajectories found in the Border collie are generalizable to other dog breeds, whether the cognitive battery has reliability and validity, and is sensitive enough to detect changes in aged dogs, and dogs suffering from pathological aging. Additionally, if there is a general intelligence factor in dogs, and whether dog personality and attachment to the owner influences cognitive abilities. Finally, the effects of sex and neuter status, individual differences in performance in cognitive tests, and common patterns in cognitive and behavioural development need to be addressed.

5.6 Implications

Study 1 assessed aging effects on discrimination learning, logical reasoning and memory in pet Border collies. To my knowledge this is the first peer reviewed study on the influence of age on general cognition over the lifespan of a non-human animal utilising the touchscreen procedure. Based on previous discrimination studies in laboratory dogs, we predicted that dogs' learning ability will decrease with age and perseverative responding will increase (Milgram et al., 2002; Snigdha et al., 2012; Tapp, Siwak, Estrada, Head, et al., 2003a). Long-term memory was predicted to remain stable with age (Araujo, Studzinski, & Milgram, 2005), and finally, based on information from the human literature, the ability to make inferences by exclusion was predicted to peak in young adulthood and decline thereafter (Moshman, 2004). All predicted relationships with age were confirmed. However, when examining the results from the inference by exclusion tests, a significant positive linear relationship was found between age and inference ability, which was in contrast to the predicted quadratic relationship with age. The discrimination learning tasks on the touchscreen in particular show clear age differences confirming that the tests used are suitable to detect cognitive aging in pet dogs.

Study 2 provided the first scientific evidence that the domestic dog is able to follow the gaze of a human into distant space outside an object choice or barrier task context. In dogs, following human gaze to distant space is modulated by training in different contexts. Formal training over the lifespan and short-term training for initiating eye contact was found to directly influence (decrease) gaze following. Our results may explain why previous studies on dogs have failed to find a gaze-following response when cues to distant space have been used, and also why dogs perform relatively poorly in comparison to other species in this task.

Study 3 provides the first cross-sectional lifespan overview of the development and aging of attention in the pet dog. Based on previous research in humans a non-human animals, we predicted that dogs would show no age differences in attentional capture, sustained attention was expected to decline with age, and younger and older dogs would show an impaired performance in selective attention and sensorimotor control, producing a quadratic effect with age. The basic developmental trajectories of the different sub-processes of attention and sensorimotor control were found to parallel those of humans. Dogs' selective attention and sensorimotor abilities showed differences between age group means which peaked at middle age for both, indicating that they may be fundamentally interrelated in dogs as proposed in humans. Dogs' attentional capture and sustained attention results also paralleled those found in humans. Our results complement the existing research using laboratory beagles, emphasizing the importance of the domestic dog as a model species for comparative study.

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SUMMARY (ENGLISH)

Age related changes of cognitive abilities, including accelerated early and slower later development, as well as cognitive decline in the senior years are well reported in humans. Non-human research however, mostly focuses on evolutionary questions and often ignores the role of developmental processes in species comparisons. In dogs our understanding of age-related cognitive changes is limited to the study of aging in laboratory kept beagles that have been recognised as a useful animal model for cognitive aging in humans. However there have been very few studies examining cognitive development and aging in pet dogs living in variable environments provided by human families over their lives. Such studies would not only contribute to our better understanding of animal as well as human cognition but have important practical relevance as well. Cognitive changes can affect quality of life, trainability, learning and problem solving abilities, and the human - animal relationship, through a decrease in the ability of the dog to communicate and interact with its owner. We investigated the development and aging of various cognitive functions in pet dogs including: general cognition (learning, memory and logical reasoning) using the touchscreen paradigm (study 1); social cognition (gaze following and communication – study 2), as well as basic control processes such as attention (study 3), motivation, inhibition, and flexibility (studies 1 - 3) using a cognitive battery of tests. This thesis is one of the first to address lifespan cognition in a social species which shares our living environment, and will enable a better understanding of the life stages of pet dogs and the role of basic processes and their possible influence on cognition. These measures of normal canine cognitive development and aging can then be used to develop a predictive model to assist with treatments for typical family dogs to enhance cognitive development, delay cognitive decline or diagnose and treat cognitive related problems.

Zusammenfassung

Altersbezogene Veränderungen der kognitiven Fähigkeiten, wie frühe erhöhte und späte langsame Entwicklung, so wie kognitiver Abbau bei Senioren sind bei Menschen bereits gut dokumentiert. Forschung, die sich nicht mit dem Menschen beschäftigt, fokussiert hingegen hauptsächlich auf evolutionäre Fragen und ignoriert oft die Rolle der Entwicklungsprozesse beim Vergleich verschiedener Arten. Bei Hunden ist unser Verständnis für altersabhängige kognitive Veränderungen ausschließlich auf Studien zum Altern von Beagles, welche im Labor gehaltenen wurden beschränkt. Dies ist ein brauchbares Tiermodel für kognitives Altern beim Menschen. Jedoch gibt es nur sehr wenige Studien zur kognitiven Entwicklung und dem Altern von Haushunden, in denen die Tiere im Laufe ihres Lebens in verschiedenen Umgebungen mit menschlichen Familien zusammenleben. Diese Studien würden nicht nur zu unserem besseren Verständnis von Kognition bei Tieren und Menschen beitragen, sondern hätten auch eine wichtige praktische Bedeutung. Kognitive Veränderungen können die Lebensqualität, die Trainierbarkeit, das Lernen und die Fähigkeit, Probleme zu lösen, sowie die Mensch-Tier Beziehung beeinflussen, indem sich die Fähigkeit mit dem Besitzer zu kommunizieren und zu interagieren verschlechtert. Wir untersuchten die Entwicklung und das Altern von verschiedenen kognitiven Funktionen bei Haushunden, einschließlich sozialer (Blick verfolgen und Kommunikation) und allgemeiner Kognition (Lernen, Gedächtnis und logisches Denken), so wie grundlegende Kontrollprozesse (Motivation, Inhibition, Flexibilität und Aufmerksamkeit). Diese Studie ist eine der ersten, die sich mit der lebenslangen Kognition von sozialen Arten, welche eng mit dem Menschen zusammenleben, beschäftigt. Sie soll zu einem besseren Verständnis für die Lebensabschnitte von Haushunden und die Rolle und dem möglichen Einfluss von Grundprozessen auf Kognition führen. Diese Messungen der normalen kognitiven Entwicklungen und dem Altern von Caniden können zur Entwicklung eines vorausschauenden Modells verwendet werden. Dieses soll helfen Verfahren für die Verbesserung der kognitiven Entwicklung typischer Familienhunde zu finden, den kognitiven Verfall hinauszuzögern oder kognitive Probleme zu diagnostizieren und zu behandeln.