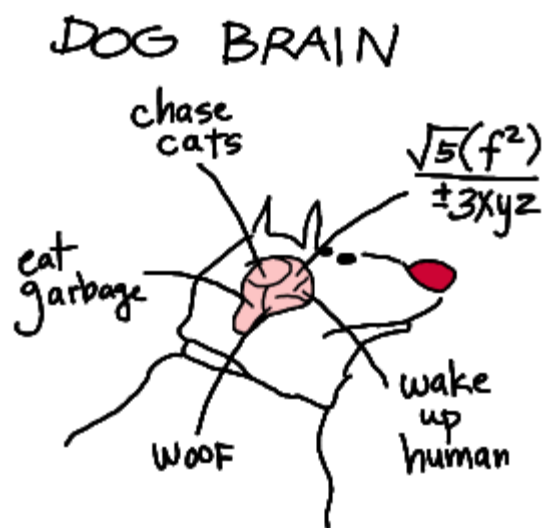# Coping strategies, paw preferences and cognition in dogs

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Abstract

Individual variation in behaviour that is consistent over time and across different contexts is assumed to reflect traits. In humans, traits like high impulsivity, low sociality and low flexibility have been associated with aggression and possibly also in dogs traits exist that facilitate or even predispose individuals to express unwanted behaviour. The latter is of public concern as, for example, it leads to bite incidences or relinquishment of the dogs. So far, little is known about associations between individuals' traits in dogs. This study investigated the relationship between coping strategies and lateralization, and their possible associations with cognitive abilities and fear-aggressive tendencies in dogs. Hundred dogs were tested in a reversal learning test and a memory test using either spatial or object cues. The memory test involved three subtests and we recorded percentages of success (i.e. choosing the baited object) and behaviours like attention and curved runs to the targeted object. The reversal learning test consisted of a T-maze, and performance was scored based on the number of errors made and the number of trials needed to switch in arms after the rewarding one had been reversed. Coping scores were based on an adapted version of the CBARQ and the latter also provided information on a number of (owner-reported) behaviour traits, including ones related to fear-aggression. The direction and strength of lateralization were derived from paw preferences as dogs showed during a puzzle test. Results were analysed using Spearman's rank correlations or IRClass procedures for ordinal values. Coping score was not significantly correlated to paw preference or paw preference strength. However, paw preference strength was positively correlated with the CBARQ factors Trainability and Stranger-directed aggression, and negatively correlated with Separation anxiety. Further research on the relationship between lateralization and temperament should focus on the strength instead of the direction of lateralization, as no correlations were found between the direction and CBARQ factors. It is suggested that dogs that are more strongly lateralized are more internally driven (aggression) and less externally driven (anxious). Also, bolder dogs are said to be better at learning which could be reflected by the higher Trainability found in more lateralized dogs. Therefore, it is suggested that dogs with a higher paw preference strength are more bold. Coping strategy had no influence on cognitive functioning of the tested dogs as measured during reversal learning and memory tests. Similarly, no effects of paw preference and paw preference strength on cognitive functioning were found. The dogs' behaviour during tests were associated with paw preference and dogs with a stronger paw preference strength showed more contact with their owner. Possibly, paw preference strength predicts dogs' temperament and performances in different training tasks or programs.

Contents

Introduction

Coping strategies

Individual variation in animals is found in a variety of species. If this variation is consistent over time and different contexts it is often referred to as personality or temperament. Other terms which are used to describe these differences in coherently organized behaviours include coping strategies, behavioural syndromes, predispositions, individualities, profiles, or axes (Gosling, 2001; Sih et al., 2004; Carere & Locurto, 2011).

Coping strategies do not refer only to behaviour, but can be defined as a set of behavioural *and* physiological responses to stress which is consistent over time (Koolhaas et al., 1999). In rodent research these are often termed the reactive and proactive coping strategy, while in other animals such as fish, birds and dogs the terms 'fast and slow explorers' and 'shy and bold' are often used (Groothuis & Carere, 2005; Coppens et al., 2010; Svartberg, 2002). Koolhaas et al. (1999) showed that proactive rodents are relatively active, bold and aggressive and seem to have a flight-fight mentality. These animals are actively trying to manipulate their environment to deal with stressors, they are rigid in their behaviour and tend to develop routines (Carere & Locurto, 2011; Koolhaas et al., 1999). In contrast, the reactive animals are characterized by a conservation-withdrawal response which involves immobility and low aggression. These animals are sensitive to environmental changes and flexible in their behaviour (Carere & Locurto, 2011; Koolhaas et al., 1999). It is assumed that proactive animals are more adapted to stable environments while reactive animals are more adapted to deal with changing environments. There are also physiological and neuroendocrine differences between the two coping strategies. Proactive animals show a low hypothalamus–pituitary–adrenal (HPA) axis response and low levels of corticosterone, and a high sympathetic reactivity leading to higher levels of (nor)adrenaline. The reactive coping animals show a higher HPA-axis response and high levels of corticosterone and high parasympathetic reactivity (Koolhaas et al., 1999). For a summary of the different characteristics of the coping strategies see Table 1. Similar coping strategies and characteristics have also been reported in other species such as great tit, trout, lizard, pig and chicken (Carere et al., 2005; Øverli et al, 2007; Ruis et al., 2000; Korte et al., 1997).

In recent years there has been a growing interest in animal personality or temperament in different species including the dog. These studies often aim to determine the suitability of the dogs for guide-type work and police work, or assessing fearfulness in potential pet dogs (Jones & Gosling, 2005). Pavlov, in the beginning of the 20th century has defined four types of personality in dogs: Excitable, Lively, Quiet and Inhibited (cited by Carere & Locurto, 2011). Further research in dog personality focused on traits related to the bold-shy dimension such as reactivity (e.g.

approach/avoidance novel objects, behaviour in new situations), fearfulness (e.g. avoid novel objects, shaking), activity (e.g. general/locomotor activity), sociability (e.g. initiating friendly contacts), responsiveness to training (e.g. working with people, learning quickly in new situations), submissiveness (e.g. moving out of a person's path) and aggression (e.g. biting, growling) (Jones & Gosling, 2005; Svartberg, 2002). A main problem in the research field of dog personality is that there is no clear vocabulary to describe which traits are considered. Different traits can by indexed by the same behaviour. For example, a dog that friendly approaches strangers was scored high on confidence, while in other cases this behaviour gave a high score for friendliness (Jones & Gosling, 2005). Hsu and Serpell (2003) developed a CBARQ questionnaire that measures dog temperament along 11 factors, focussed on unwanted behaviours. Research showed that the behaviours reported in the questionnaire are correlated to outcomes of behaviour problem diagnosis and behavioural tests suggesting that the questionnaire is a reliable method to obtain information on dogs' personality (Hsu & Serpell, 2003; Svartberg, 2005). Another study identified three coping strategies in police dogs exposed to a social threatening situation (Horváth et al., 2007). They argued that one group of dogs was more active, had a shorter attack latency, had a lower HPA-axis reactivity and showed more aggressive behaviour compared to the other groups and that this was in line with the proactive coping strategy. The other group was less active, had a longer attack latency, had a moderate HPA-axis reactivity and showed more fearful behaviour which resembled the reactive coping strategy. The third category of dogs was said to be ambivalent, they did not chose a strategy but showed signs of acute stress like paw lifting and mouth licking. Also in these dogs the HPA-axis reactivity was moderate (Horváth et al., 2007). These results seem to imply that more fearful dogs use a reactive coping strategy, but it should be kept in mind that fearful dogs can both flee (proactive) or stay immobile (reactive).

Table 1 Behavioural, physiological and neuroendocrine characteristics of the proactive and reactive coping strategy (adapted from Koolhaas et al., 1999).

	Proactive	Reactive
Behavioural characteristics		
Attack latency	Low	High
Active avoidance	High	Low
Defensive burying	High	Low
Risk taking	High	Low
Nest-building	High	Low
Routine formation	High	Low
Cue dependency	Low	High

	Proactive	Reactive
Conditioned immobility	Low	High
Flexibility	Low	High
Physiological and neuroendocrine characteristics		
HPA axis activity (baseline)	Low	Normal
HPA axis reactivity (corticosterone)	Low	High
Sympathetic reactivity (noradrenaline, adrenaline)	High	Low
Parasympathetic reactivity (heart rate)	Low	High
Testosterone activity (testosterone)	High	Low

Coping strategy and cognition

Pavlov suggested that there was an association between the different personality types and cognition. For example, a dog of the Excitable type was supposed to respond well to excitatory conditioning but was limited in its learning when inhibitory processes were involved (cited by Carere & Locurto, 2011). In excitatory conditioning the conditioned stimulus indicates the occurrence of the unconditioned stimulus, while in inhibitory conditioning the conditioned stimulus indicates the absence of the unconditioned stimulus (Bernard, 2004). According to Pavlov the Excitable type seemed to have more difficulty establishing inhibitory connections. Pavlov assumed there was an association between personalities and cognitive functions but there has been relatively little work done on this topic in dogs (cited by Carere & Locurto, 2011). Research in other animals also points towards a link between coping strategies and cognitive abilities. For example, rats with a high innate anxiety that seem to adopt a more reactive coping strategy have been shown to make less errors in a modified hole board paradigm. In this experiment rats were tested on a board with 23 holes of which four holes were baited. The lids of the baited holes were marked and these lids moved back over the hole after a visit. The fact that reactive rats made fewer errors would indicate that they have a better recollection of learned information (Ohl et al., 2002) suggesting that reactive animals are better in memory tasks. In a T-maze reversal learning task pigs with different responses to a backtest performed differently. Pigs that were low resistant in a backtest (reactive) made significantly less errors when the previously rewarding arm became unrewarding from the fifth reversal trial. The high resistant (proactive) pigs had more trouble inhibiting their previous behaviour and thus made more errors (Bolhuis et al., 2004). Similar results have been found in birds, where slow-exploring birds were better at the reversal learning of acoustic cues (Guillette et al., 2011). Recent research on rainbow trout showed no difference between lines selected for low (proactive) and high (reactive) post stress plasma cortisol levels in learning the location of food (de Lourdes Ruiz-Gomez et al.,

2011). When the food was relocated to the other arm of the T-maze there was no difference between the lines in the time it took to find the food. However, differences did appear when the food was relocated to an open area before the maze. All proactive fish ignored the food and went to the previously rewarded arm while all reactive fish found the food before entering the maze. Another manipulation involved placing a novel object in the open area. In this situation the reactive fish took longer to find the food (de Lourdes Ruiz-Gomez et al., 2011). This is in agreement to the earlier described differences between the reactive and proactive coping strategy, with reactive animals being more sensitive to environmental changes and proactive animals more rigid and routine-like in their response.

Other animal characteristics can also influence learning processes. A study on beagles showed no effect of age in the learning of an object visual discrimination task in which dogs had to discriminate between a blue Lego block and an orange plastic coffee jar top, but a significant effect of age was found in the reversal learning task with young dogs performing better than the old dogs (Milgram et al., 1994). In a size-discrimination task, where the objects were the same except for their height, old and senior dogs made more errors and needed more trials to reach the set criterion than young dogs (Tapp et al., 2003). In the reversal learning both young and senior dogs made more errors than in the initial discrimination task, and old and senior dogs made more errors compared to the young dogs (Tapp et al., 2003). The absence of age effects in the initial discrimination learning could be explained by the conspicuous differences between the used objects. Perhaps older dogs perform better when the differences between the objects are striking as in the study of Milgram et al. (1994). Also breed differences have been found in maze performance, with beagles performing best and shelties the poorest (Elliot and Scott, 1965). Behavioural differences between dog breeds have been interpreted as differences in breed-specific coping strategies (e.g. Corson 1971) and possibly coping strategies are related to cognitive functions. Shy or reactive animals appear more focused on their surroundings compared to bold or proactive animals and therefore may be better at reversal learning and memory tasks, though other factors as age and breed can also play a role.

Where shy individuals may do relatively well in some tasks bolder animals may have the advantage in other tasks. A study of cooperative string pulling in rooks showed that bolder individuals were more willing to perform and that pairs were more successful if one of them was bold (Scheid & Noë, 2010). Studies in birds showed that fast explorers were faster at learning an acoustic discrimination task (Guillette et al., 2009), however a later study by the same group found no evidence to support this earlier finding (Guillette et al., 2011). Another study on blue tits showed that risk taking influenced their performance in a spatial memory task (Arnold et al., 2007). Birds which showed extreme risk taking failed the spatial learning task while risk aversive birds avoided the learning apparatus and therefore also failed the learning task. Birds which showed intermediate risk

taking were most successful at the spatial learning task. This suggests that animals which are too bold/proactive and animals which are too shy/reactive have more difficulty learning spatial tasks (Arnold et al., 2007). In dogs it has been shown that bolder dogs reached higher levels of performance in trials of searching, tracking, delivering a message, and owner protection (Svartberg, 2002). It was shown that dogs with a proactive coping strategy, which had a higher HPA-axis activity, learned new tasks more rapidly, while the more fearful and reactive animals showed impaired learning (Blackwell et al., 2010). This finding of proactive copers showing a higher HPA-axis is in contrast with earlier findings which state that a higher HPA-axis activation is characteristic for reactive copers (Koolhaas et al., 1999). Blackwell et al. (2010) also caution that cortisol is produced in response to positive and negative events and thus it could be that the higher HPA-axis reactivity may be a result of excitement and activity (Blackwell et al., 2010). The performance is in line with the idea that proactive animals might be better at learning novel tasks as they are more active and exploratory.

Coping strategy and lateralization
Findings from research seem to indicate that animals with a preference for the right paw show responses that are consistent with characteristics of the proactive coping strategy, while left pawed animals appear to have a reactive coping strategy (Rogers, 2009). In human infants and adults it has been shown that arousal of positive, approach-related emotions are associated with higher activity of the left hemisphere, while arousal of negative, withdrawal-related emotions are associated with higher activity of the right hemisphere (Davidson, 1992). Several studies in primates have shown that right-handed chimpanzees, common marmosets, and Geoffroy's marmosets were faster to explore novel surroundings and actively engaged with novel objects (Hopkins & Bennet, 1994; Cameron & Rogers, 1999; Braccini & Caine, 2009). Left-handed marmosets did show the same number of head turns, suggesting they were exploring their new surrounding but more in a visual manner (Cameron & Rogers, 1999). It was also shown that left-handed marmosets froze longer after hearing calls of a predator (Braccini & Caine, 2009). This preference for a paw/hand is an indicator for lateralization of the brain, where the contralateral brain hemisphere is dominant. This would mean that in left-handed animals the right hemisphere is dominant which is associated with the expression of emotions, especially negative emotions as fear and withdrawal. Assumingly, reactive copers show a higher HPA-axis response and evidence indicates that this is similar for left-handed primates. Left-handed marmosets had higher levels of cortisol following return to their home-cage after spending time in an unfamiliar cage (Rogers, 2009). In regards to aggression results are less clear. Aggression has been shown to be under control of the right hemisphere (left-handedness) (Rogers, 2009). However, research has shown that left handed male rhesus macaques were more often on the

receiving end of aggressive interactions and were more likely to be submissive (Westergaard et al., 2003), while the opposite was found in females (Westergaard et al., 2004). In the case of right-handed animals there is a dominant left hemisphere which suppresses fear and enhances approach behaviour (Rogers, 2009). This data suggest that there could be a relation between hand preferences and coping strategy, though it is unclear how strong this association is.

Lateralization in dogs

In dogs evidence has been found for paw preferences. Wells (2003) examined the paw preference of 53 dogs across three different tasks, namely paw lifting, blanket removal and food retrieval. The number of times a dog used its right or left paw during these tasks were recorded and a directional handedness index was calculated after which animals were categorized in ambilateral or right- or left-pawed. She found a significant effect of the animals' sex with female dogs preferring their right paw while male dogs preferred their left paw (Wells, 2003). This difference was also found in further research on dogs (Quaranta et al., 2004, McGreevy et al., 2010). Other research found no significant association between sex and paw preference (Branson & Rogers, 2006; van Alphen et al., 2005). It has been suggested that these differences could be related to hormonal differences, studies where a sex-dependent effect was found all tested intact dogs (Wells, 2003; Quaranta et al., 2004; McGreevy et al., 2010) while Branson and Rogers (2006) tested neutered dogs. Paw preference strength, the absolute value of the handedness index which indicates how strongly lateralised an animal is, was not affected by sex (Wells, 2003; McGreevy et al., 2010; Branson & Rogers, 2006). Other factors as age and breed were also not associated with paw preference and paw preference strength (McGreevy et al., 2010) but only four breeds were investigated. Another study on 113 potential guide dogs (Labrador retrievers, golden retrievers and Labrador-golden retrievers) did reveal a significant effect of breed on paw preference strength in a food retrieval task (Tomkins et al., 2010b). They also found significant interactions between age and breed, and breed and sex on the direction of laterality. A near significant effect of sex on paw preference was found when dogs were categorized in ambilateral, right- or left-pawed dogs. Again, males were suggested to be less right-pawed that females (Tomkins et al., 2010b).

Little research has been done on the relationship between lateralization, behaviour and cortisol concentrations in dogs (Batt et al., 2009). Dogs were tested in several temperament tests and for paw preference using a tape removal test and food retrieval test. They found that latency to approach a strange human was positively correlated to right paw preference and negatively correlated with paw preference strength. Also the latency to catch a moving object and latency to rest were negatively correlated with paw preference strength. This seems to indicate that dogs with a higher paw preference strength are more bold as they are faster to approach a strange human

(Human Contact Test) or object (Chase Test) and faster to settle in new environments (Passive Test). No interaction between lateralization and cortisol concentrations was found but it has been suggested that this was because of the stress of entering the kennel (Batt et al., 2009). A study on 114 potential guide dogs showed that lateralization index and paw preference measured by a food retrieval task were predictors for a successful completion of a Guide Dog Training Programme. Each unit increase in the lateralization index and thus to right directional bias, the odds of the dog being successful increased with 1.7%. Dogs that preferred the left paw were less successful in completing the programme (38%) compared to right preferring (68%) and ambidextrous dogs (64%) (Tomkins et al., 2011).

Dogs also appear to respond to acoustic signals in a lateralized manner, with conspecific calls usually being processed by the left hemisphere while the sound of a thunderstorm was processed by the right hemisphere (Siniscalchi et al., 2008). In this research the investigators looked at the direction of head turns of a dog that was feeding in the middle of a room with one speaker on its right and one on its left at equal distant. They assumed that if the dog turned to the speaker on the right the sound would by processed by the left hemisphere and vice versa, at least for the initial attention to the sound. They found no significant association with paw preference, which indicates that these asymmetries are unrelated (Siniscalchi et al., 2008). Other research found that dogs without a clear paw preference showed a greater reactivity to sounds of thunderstorms and firework (Branson & Rogers, 2006). It has been stated that conspecific calls could also be processed by the right hemisphere if they elicit strong emotions as fear (Siniscalchi et al., 2008). During feeding 30 dogs were presented with silhouettes of a snake, cat and dog on both the right and left side (Siniscalchi et al., 2010). It was found that dogs preferred to turn their head to the left when presented with the snake and cat silhouette. This initial turn to analyse visual information implies the use of the right hemisphere when confronted with threatening or alarming stimuli (Siniscalchi et al., 2010). In a study that investigated sensory lateralization dogs wore modified halters so that dogs could either use both eyes, or only their left or right eye during a jump. Monocular dogs had less successful jumps than binocular dogs as measured by the jump bar remaining in place but improved over time. Dogs that could use their left eye had less successful jumps than dogs which could use their right eye which indicates a left hemisphere dominance for the initial navigation of the jump (Tomkins et al., 2010c). Dogs also show asymmetry in tail wagging (Quaranta et al., 2007). Thirty dogs were presented with different stimuli; the owner, an unknown person, a dominant unfamiliar dog and a cat. Tail position was scored every ten seconds on video and the angle was measured to determine the amplitude of the tail wagging. They found that the tail-wagging movements occurred more to the right (left hemisphere) when there was a familiar person while the tail moved more to the left (right hemisphere) when confronted with the unfamiliar dog. This is in accordance with the

idea that the left hemisphere is associated with approach while right hemisphere is associated with fear response and withdrawal (Quaranta et al., 2007).

Lateralization and cognition
Lateralization also can have an effect on the performance during different tasks. Visual lateralization in an intact animal was first demonstrated in the chick (review Vallortigara, 2000). By temporarily covering one eye it was shown that chicks that used the right eye were better at visual discrimination while chicks that used the left eye were more reactive to stimuli which elicited an emotional response. For example, when exposed to predator alarm calls hens were more likely to use their left eye to look up (Vallortigara, 2000). Detour experiments also showed that chicks which used their right eye to look at an imprinting object took the detour to the left and reached the target faster, while chicks which used their left eye took the detour to the right (Vallortigara, 2000). In an experiment by Diekamp et al. (1999) there was a slight advantage for pigeons which used their right eye when learning a colour discrimination task although this was not significant. Later, reversal learning was applied and only in later reversal blocks did the right-eyed birds seem to have an advantage (Diekamp et al., 1999). As this experiment was based on colour discrimination and thus on object specific cues it could be that this set up was more favourable for right-eyed pigeons which could explain why they performed better later on. However, these results based on eye use should be interpreted with caution. Though in birds the primary visual projections ascend to the contralateral side of the brain there are also ipsilateral projections. This means that one can never be certain that only the contralateral hemisphere is involved. But because sustained viewing in birds is often monocular it could be that after initial recognition, the choice for using their right or left eye for viewing might be influenced by lateralization of function (Vallortigara, 2000). In mammals with frontally placed eyes each eye also relays information to both brain hemispheres but it has been suggested that the crossed fibers may dominate the uncrossed fibers because they are larger and conduct neural signals faster (Vallortigara, 2000). In dogs it has been estimated that 75% of the optic fibers cross though it has been suggested that this is an overestimation (Tomkins et al., 2010). Another study looked at the effect of hippocampal lesions on discrimination learning and reversal learning in cats (Teitelbaum, 1964). It was shown that a hippocampal lesion in the right hemisphere had no effect on the acquisition of a tactile discrimination task but it did impair reversal learning to the same degree as with bilateral lesions (Teitelbaum, 1964), suggesting that the right hemisphere is more important in reversal learning than the left hemisphere. It can be suggested that reversal learning is under a more dominant control of the right hemisphere and that would imply that left-handed animals should be more successful at reversal learning.

In different memory tasks in which reference memory and working memory were tested, chicks which could only use their left eye traced a food reward using spatial cues (Vallortigara, 2000). In the reference memory test they continued to search for food in the center of the arena while the landmark, which indicated the food location, had been moved. In contrast, right-eyed chicks did search near the landmark (Vallortigara, 2000). The working memory task involved finding a food reward which was hidden behind one of two different screens. The screen was moved so that the correct screen was in the incorrect position to determine whether the chicks used spatial or object-specific cues. Left-eyed chicks approached the wrong screen which was on the correct position and thus used more spatial cues, while the right-eyed chicks approached the right screen on the incorrect position and thus used more object-specific cues (Vallortigara, 2000). Similar results have been found in other experiments. Tests of object discrimination seemed to favour right-eyed birds, while spatial position seemed to be remembered better by left-eyed birds (Clayton & Krebs, 1993; 1994). This system is described by Andrews (1991) which suggest that the left eye/right hemisphere holds detailed information about the spatial context of the stimulus while the right eye/left hemisphere is more focused on conspicuous cues and consequences of reacting to the stimulus (cited by Clayton & Krebs, 1993). Prior and Güntürkün (2001) tested pigeons on a task where they had to remember spatial location and food-related object cues. They found that right-eyed birds made more correct choices in the object discrimination task than left-eyed birds and that there was no difference when birds could use both eyes. This suggests that object discrimination is under control of the left hemisphere and independent of interaction with the right hemisphere. In the spatial memory task left and right-eyed birds performed equally well and both poorer than when both eyes could be used. This suggested that maximum performance based on spatial information is dependent on interaction between both hemispheres (Prior & Güntürkün, 2001). However, based on the literature (Vallortigara, 2000; Clayton & Krebs, 1993, 1994; Andrews, 1991) it is suggested that left handed (reactive) animals are better at memory tasks when using spatial cues while right-handed (proactive) perform better when object cues can be used. An overview of the specialization of the left and right hemisphere is provided in Table 2. Briefly summarizing this common pattern of lateralization implies that the left hemisphere is specialized to attend to similarities, creates categories and follows rules based on experience. It performs routine functions and established patterns of behaviour. The right hemisphere notices small differences and responds to novel stimuli. It plays a role in emergency situations and expresses strong negative emotions (Rogers, 2011).

Table 2 Complementary specializations of the hemispheres *Characteristics of left and right hemisphere (adapted from Rogers, 2010).*

Left hemisphere	Right hemisphere
Proactive	Reactive
Approach	Withdrawal
Controls routine behaviour (uses learnt templates)	Controls emergency responses (escape, fear, aggression)
Focused attention (not easily distracted)	Global attention (easily distracted)
Object-specific cues	Spatial cues
Positive cognitive bias	Negative cognitive bias
Recognition familiar species-typical vocalizations (right hemisphere also used when strong emotions as fear are provoked)	Controls physiological stress responses (heart rate, hypothalamic–pituitary–adrenal axis)

Identifying which hemisphere is being used could reflect the animals' emotional state. Animals which are more fearful or aggressive use the right hemisphere more and this can be identified by use of their left eye, left ear, right nostril or tail-wagging to the left in dogs (Rogers, 2011). Rogers also suggests an interesting application of the laterality in the ear used by dogs in response to human voices. The dog-human relationship which is characterized by use of the left ear and thus right hemisphere could be a fearful relationship, while a relationship which is characterized by the use of the right ear (left hemisphere) would be a more positive relationship (Rogers, 2011). Also tail-wagging is suggested to take into account to see how dogs respond to persons (e.g. in rescue shelters) with tail movement to the left indicating negative emotions in the dog (Rogers, 2011).

Visible displacement in dogs

Research in dogs has shown that dogs are successful in locating hidden foods in visible displacement tasks (Fiset et al., 2003; Miller et al., 2009; Triana & Pasnak, 1981). Understanding of visible displacement problems, where animals can see objects being hidden, seems to emerge already in the 5th week and appear to be developed in full around 8 weeks in domestic pups (Gagnon & Doré, 1992). Further research from this group and others showed that olfactory cues did not play a role in the successful completion of displacement tasks. This was shown by masking the scents by spraying rose water, hiding treats somewhere else in the room, or hiding treats in all covers (Gagnon & Doré, 1992; Triana & Pasnak, 1981; Miller et al., 2009). Dogs are also successful in solving visible displacement task when a delay is introduced (Fiset et al., 2003). For example, Miller et al. (2009) found that dogs had a success percentage of 96% and 83% when there was no delay and a 5 second delay, respectively. Others showed that dogs still performed above chance in a visible displacement

task when there was a delay of 240 seconds, even though the success did decrease (Fiset et al., 2003). It has been indicated that dogs could also solve invisible displacement tasks, in which a target is hidden under a displacement device which is then moved and the target is hidden in another location and the empty device is shown to the subject (Collier-Baker et al., 2004). They used a number of experiments which suggested that the dogs' ability to solve this task is based on associative cues such as the location of the displacement device rather than the dogs' ability to form a mental representation of the target objects' trajectory (Collier-Baker et al., 2004; Watson & Gergely, 2001). This research also showed that when they controlled for cues from the experimenter, by hiding the upper part of the experimenters' body behind a curtain, the dogs still performed above chance (Collier-Baker et al., 2004). This implies that cueing by the experimenter did not have a major influence on the dogs performance. Dogs have been shown to use human cueing to find hidden food (Agnetta et al., 2000) and Szetei et al. (2003) showed that dogs performed worse in an two-object choice task when a human pointed to the wrong box, with this effect being more pronounced when they only had olfactory cues than when they had visual cues (e.g. they saw the reward get hidden). It has further been suggested that dogs more readily make use of spatial cues than object specific cues (Dumas, 1998; Doré et al., 1996; Head et al., 1995), but influences of paw preference or coping strategy were not investigated in these studies. In experiments by Dumas (1998) dogs were successful in 49% of the trials based on object-specific cues while 78% of the trials were successfully solved when based on spatial cues. The object was hidden behind one of two different screens. In the figurative condition, where dogs had to use object-specific cues, objects were always hidden behind the same screen. The screen was either moved to the left or right with the other screen on the opposite place. In the spatial condition the object was hidden behind both screens for half of the trials and the target screen was always moved to the same side (Dumas, 1998). Dogs can solve spatial tasks using egocentric cues based on body position or allocentric cues based on positions of landmarks in the environment (Christie et al., 2005). Egocentric information is used when an observer uses their own body position as a reference for spatial navigation. Allocentric information is used when the observer navigates to a location by use of landmarks (Christie et al., 2005). Beagles were tested in a egocentric spatial discrimination task where a food reward was always hidden under one of two identical blocks at the same side of the dog and in a allocentric spatial discrimination task where the food reward was always hidden under the block that was indicated by a thin, yellow wooden peg as a landmark (Christie et al., 2005). It was found that dogs mostly use egocentric cues in spatial location task (Christie et al., 2005; Fiset & Gagnon, 2000), though allocentric cues can also be used (Milgram et al., 1999).

Summary and research questions

Thus it appears two theories could be formed for the cognitive functioning based on either coping strategy or lateralization (Table 3). It is found that reactive and proactive animals show different behavioural and physiological characteristics. These differences have an effect on the cognitive functioning in different tasks over different species though literature on dogs is limited. This study aims to investigate the relationship between coping strategies and cognition in dogs. Findings from this study could help in understanding the learning abilities of dogs and training methods could be adapted accordingly. Based on literature on coping strategies it is hypothesized that reactive animals are more sensitive to their environment and therefore will perform better in a reversal learning task, spatial memory task and objective memory task compared to the more rigid proactive animals. Proactive animals in turn are expected to perform better in the objective memory task than in the spatial memory task because the differences in the environment are more present and less subtle than in the spatial memory task. Furthermore, this study attempts to investigate the link between paw preference (brain lateralization) and coping strategies. This is to the authors' knowledge the first study to investigate the association of paw preference and coping strategies in dogs. Based on literature on lateralization it would be expected that left pawed dogs are more reactive and that they perform better in the reversal learning task and the spatial memory task while right pawed dogs are more proactive and perform better in the objective memory task. This paw preference could be an easily measured indicator to select dogs which are suited for different training programs.

Table 3 Hypothetical framework Associations made between lateralization, coping strategies and cognitive functions. The expected success in reversal learning, spatial memory and object memory task is indicated. * Proactive dogs are expected to have a lower success than reactive animals, but a higher success compared to their own performance in the spatial memory task.

Theory		Cognition		
		Reversal learning	*Spatial memory*	*Object memory*
Lateralization	Left paw (right hemisphere)	High	High	Low
	Right paw (left hemisphere)	Low	Low	High
Coping strategies	Reactive	High	High	High
	Proactive	Low	Low	Low*

The aim of this study is to investigate if there is a difference in cognitive functioning in dogs with different coping strategies and if this is linked to paw preferences. Therefore the following questions will be asked:

- *Is there an association between coping strategies and paw preference?*
- *Do dogs with different coping strategies or paw preferences perform differently*
  - *In a reversal learning task?*
  - *In a visible displacement task using either spatial or object cues?*

Material and methods

Owners were invited to participate in testing with the only selection criterion that the dog had to be at least two years old to ensure that the personality of the dog had been developed and that the dog could readily perform the battery of tests. Testing took a maximum of 2 hours per dog and was done at facilities of the Wageningen University (FMD building, Haarweg). Owners could stop the tests at any given time. Food rewards consisted of a quarter of a Frolic unless otherwise indicated by the owner. The owner was present during all tests and accompanied by an instructor and where necessary an experimenter. Three video cameras recorded the behaviour of the dog for further analysis.

Coping strategies

In order to determine the dogs' coping strategy owners had to fill in an adapted version of the CBARQ-questionnaire (Hsu & Serpell, 2003). Additional questions were asked regarding the behaviour of the dog in novel and threatening situations to determine their coping strategy. Also, some questions related to the opinion of the owner on the dogs' personality (Appendix I). Based on the answers scores were assigned to dogs with a high score indicating a more proactive coping strategy.

Paw preference (puzzle test)

Apparatus

Paw preference was determined by a food retrieval task using a puzzle. Paw use was defined as *the dog makes a sweeping motion with its paw that comes in contact with the puzzle.* The puzzle consisted of a wooden DogBrick puzzle (DogBrick by Nina Ottosson; http://www.nina-ottosson.com/Dogbrickwood.php) with two sliding squares where a treat could be hidden underneath. The puzzle was fastened to a 1 x 1 m wooden plate so that the puzzle would remain in place during testing. The puzzle (40 x 26 cm) was sealed off with a small wooden plate to ensure only one column (12 cm width) remained for the dogs to search. During the test the instructor and experimenter avoided cueing the dog by looking straight ahead and keeping their arms neutral.

Procedure

The puzzle test consisted of three levels of difficulty and each level was tested in three trials that lasted a maximum of 30 seconds each. The levels increased the amount of work the dog had to perform to get to the treat; dogs either had to move one square (level 1), two squares (level 2) or lift one peg and move two squares (level 3). The dog sat about 1 m from the puzzle on the leash while the experimenter hid the treat. The treat was always hidden under the same square. After the

experimenter returned to her place the owner gave the 'search' command and released the dog. Owners were allowed to point to the puzzle and repeat the command to search. Before testing the owner was instructed to hide two treats and play the puzzle with the dog for one minute to let the dog get used to the puzzle. If the dog showed no interest in the puzzle for three trials in a row the test was stopped.

Measurements

The number of times the dog used its right or left paw was recorded and a directional handedness index (HI) was calculated. The index was calculated by $HI = (L - R)/(L + R)$ where L is the number times the animal used its left paw and R the number of times the animal used its right paw. This gives a value of +1 for a left pawed to -1 for right pawed preference. A value of 0 will be calculated for animals without clear preference and these animals are considered ambilateral (Wells, 2003). When animals used their muzzle and not their paws no score could be given and these animals were not included in analysis. Paw preference strength was calculated by taking the absolute value of the handedness index.

Reversal learning (T-maze)

Apparatus

Dogs were tested for their ability to reverse a previously rewarding action by use of a T-maze (Figure 1). The T-maze is built of wooden screens which could be disconnected to move the separate parts. The blocking screen (80 x 80 cm) was only present during the first phase. During the test only the owner and instructor were present in the room.

Procedure

Before testing the dog was familiarized to the T-maze by six trials where during each trial one of the arms was blocked by a screen (alternately the right and left arm). Dogs had to reach their owner at the end of the maze to receive a food reward. The owner stood in the middle of the apparatus with their back towards their dog looking straight ahead to prevent cueing. The startbox was opened by the instructor and the owner was allowed to call the dog. The dog was rewarded each time when it reached the owner, this to ensure that the dog learnt that both sides of the maze could be used to reach the owner. The owner always walked in a straight line through the doors from the startbox to the end of the maze, i.e. without entering the arms of the maze, so that their path could not influence the dog in its choice.

This was followed by a training phase to learn the dogs that one of the arms was rewarding. The same procedure was followed as described above only now the screen was removed meaning that both arms could be used to reach the owner.
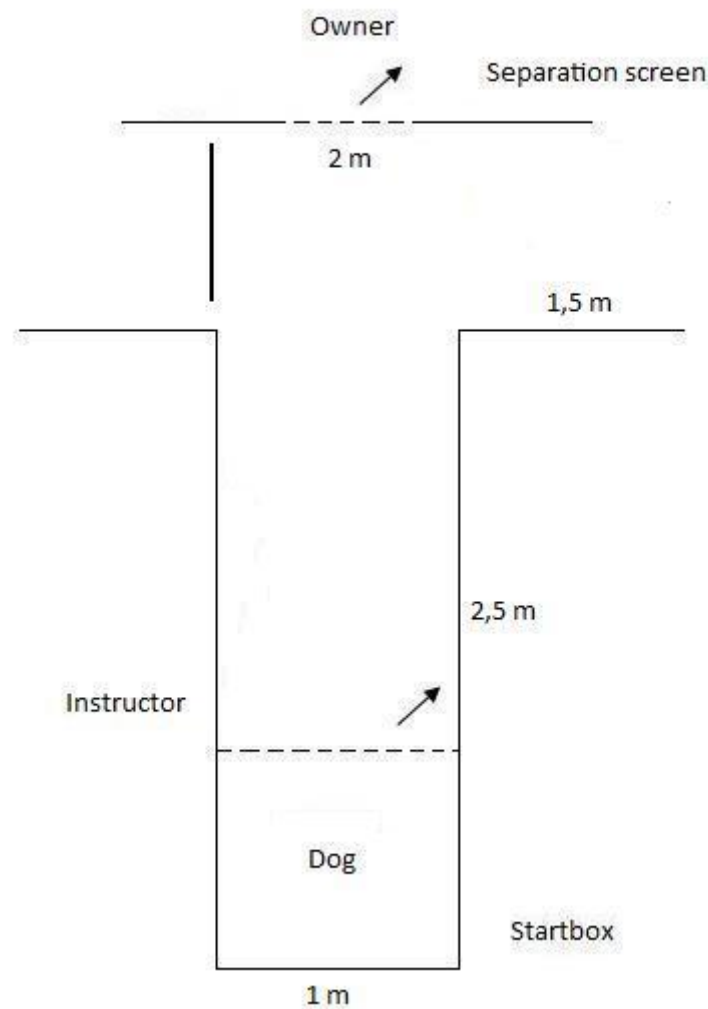

Figure 1 Schematic overview of the T-maze *Dogs are located in startbox which is opened when the trial starts. Owners stand facing the wall with their back towards the dog. Dotted lines (- - -) represent doors used during the test, bold line (▬) represents the block.*

The choice was recorded as the side which the dog used to reach the owner. The choice made by the dog in the first trial was set as the rewarding (correct) side. In following trials the owner only rewarded the dog when it chose the correct arm to reach the end of the maze. If the wrong arm was chosen the owner ignored the dog and brought it straight back to the startbox. These trials were repeated eight times with after the first four trials a break of 60 seconds during which the owner was instructed to give attention to the dog, to prevent the dog from becoming uninterested.

During the reversal phase a reversal of the previously rewarding action was implemented. Procedures were the same as during the learning phase but now owners only rewarded the dog if it chose the opposite arm than taught in the learning phase. Trials were again done eight times with a break after four trials. Dogs were allowed to search the maze for a maximum of 30 seconds, if the dog failed to reach the owner in this time it was scored as an error.
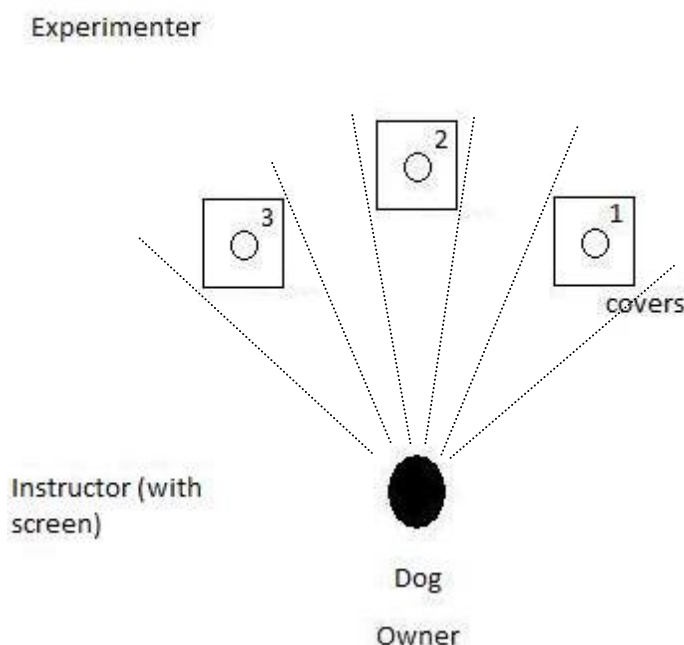
Measurements

The percentage of success and the direction preference as indicated by the first chosen arm during the training phase were recorded. In the reversal phase the number of errors and the number of trials needed till the dog made a switch in arms were recorded.

Memory tests

Apparatus

The memory test contained three subtests of visible displacement to investigate the effect of spatial and object cues; 1) spatial task without screen, 2) spatial task with screen, and 3) object task with screen. The order of the three tests was randomized over dogs to prevent the tests from influencing each other (e.g. by experience). The screen was introduced to avoid the dogs succeeding by tracking the correct cover by gazing. The screen temporarily blocked the dogs' vision forcing the dog to recall the right cover from memory. Three covers were placed in a semi-circle in front of the dog at a distance of 1 m between each cover and a 2 m distance from the dog (Figure 2). In the spatial memory task three identical covers (blue plastic cups) were used. In the objective memory task three different covers were used (a red plastic cup, white square box and green bowl). The covers were placed in the middle of taped squares (60 x 60 cm) to score the choice of the dog. In total nine trials were performed, three for each subtest.

Figure 2 Schematic overview of the experimental set up *Dog is positioned approximately 2 m from each cover. Distance between cups is approximately 1 m. Dotted lines represent the area of a straight path.*

Procedure

Before testing the dog was allowed to sniff each set of covers for approximately 30 seconds. During testing all dogs started at the same start-point. The owner held the dog in place by the collar and the leash which was attached to a safety hook. The experimenter showed the dog the treat and moved the treat in front of each cover for approximately one second. The treat was then randomly hidden under one of the covers. Treats were hidden randomly while making sure that treats were not hidden under the same cover in more than two consecutive trials. After the experimenter returned to its place, the instructor told the owner when to release the dog. In the task where no screen was used the dog was released after six seconds. In case the screen was used, the instructor placed the screen in front of the dog for three seconds and after an additional three seconds the dog was released. This to make sure approximately the same amount of time passed between hiding the treat and allowing the dog to search in all tests. The owner was allowed to give a search command and instructed not to direct the dog in the right direction.

The dog succeeded when it entered the square around the cover. After the dog had made a choice the owner prevented the dog from searching the other covers and removed the chosen cover after which the dog was allowed the treat. When the dog chose a wrong cover the same procedure was followed to allow the dog to see that there was no treat under the chosen cover. If the animal made no choice within five seconds, no reinforcement was given and the dog was positioned by the owner at the start-point.

Measurements

The number of successes was recorded to see if the dog performed above chance level (33% chance at success) and to investigate difference in success percentage for each subtest. Also, some behavioural aspects were scored from the moment the experiment showed to treat until the dog found the treat or the trial was terminated. No observations were made when the screen was in front of the dog and between trials. Behaviour aspects included where the dog paid attention to and if the dog approached the cover in a straight line (Appendix II).

Data analysis

All statistical procedures were conducted using GenStat 14th edition and MatMan. Significance levels were set on the standard 0.05 level and trend levels on 0.05 to 0.1. Values are presented as calculated means ± SE, unless stated otherwise.

Coping score and paw preference

To determine the relationship between coping score and paw preference (strength) Spearman's rank correlations were calculated. Additionally, correlations to the CBARQ factors were investigated. Also

the effects of sex (male, female) and state (intact, neutered) on the dependent variables coping score, paw preference and paw preference strength were examined using ANOVA tests. The following model was used: $y_{hi} = \mu + Sex_h + State_i + Sex_h.State_i + e_{hi}$ with y representing the dependent variable, μ the intercept and e the residual error variance.

Reversal learning T-maze

Spearman's rank correlations were calculated to determine the relationship between the percentage of training success, number of errors, and number of trials till reversal and either coping score or paw preference (strength). ANOVA tests were used to examine the effects of paw preference (strength) and coping strategy separately on the direction preference (left, right) in the first free trial.

Memory test

The percentage of success and frequency of curved runs in the memory test were analysed using the IRClass procedure for ordinal values. The main model was $y_{hij} = \mu + Test_h + Coping\ score_i + Test_h.Coping\ score_i + Dog_j + e_{hij}$ with test (spatial no screen, spatial screen, object screen), coping score and their interaction as fixed effects and the dog as random effect. In order to answer the research questions coping score was replaced by paw preference and paw preference strength while test always remained in the model. Additionally, coping score was replaced by age in the model for the percentage of success.

 Video observations were analysed in the Observer 5 program. Intra-observer reliability was assessed by a random extra observation revealing a kappa of 0.74 for duration and 0.98 for frequencies. A principal component analysis was done on the behavioural scores for the purpose of data reduction. The PCA tests for interrelationships between parameters and underlying correlation matrices in sets of parameters are represented by components as linear combinations of behaviour scores. The components identify parameters that co-vary in the same or opposite direction as indicated by relatively high absolute loadings. Based on the outcomes component scores are calculated from an individual dog's behaviour scores, using loadings as weighing factors, integrating multiple behaviours by giving most weight to those with high loadings. Component scores or scores for separate behaviours were analysed using Restricted Maximum Likelihood (REML) applying the same model as described for the IRClass procedure. Again a same routine was followed by replacing coping score with paw preference (strength) to determine the effects of test, coping score, and paw preference (strength) on the measured behaviours. When the assumption of equal variances was not met a log transformation of the original data was analysed. Further correlations between behaviours were investigated. Finally another principal component analysis was done to investigate possible relationships between coping score, paw preference (strength) and cognitive parameters from the reversal learning test and the memory test.

Results

Subjects

In total 96 owners participated in testing a total of 100 dogs but not all dogs completed all tests. A high response rate for the participant questionnaire was acquired (96%). In total 49 male dogs (n neutered = 15) and 51 female dogs (n neutered = 36) were tested. The age of the dogs ranged from 1.5 – 13 years with an average age of 5.2 years. The mean values obtained from the questionnaire for the QBARC factors and the coping score are presented in Table 4.

Table 4 Mean values CBARQ factors and coping score The mean values and range for the percentages obtained for each CBARQ factor and coping score as determined by the questionnaire for 96 dogs.

	Mean (%)	Range
Proactive coping score	64.1	44 – 90
Pain sensitivity	13.7	0 – 69
Separation anxiety	6.2	0 – 56
Excitability	45.8	4 – 96
Attachment	46.7	12 – 96
Chase	47.4	0 – 100
Trainability	59.9	25 – 88
Stranger directed aggression	11.4	0 – 62
Owner directed aggression	3.4	0 – 62
Dog directed aggression	27.3	0 – 93
Non-social fear	15.5	0 – 75
Social fear	12	0 – 88
Dog directed fear	10.2	0 – 82

Coping score

The coping scores of the dogs determined by the questionnaire ranged from 44 to 90% with a higher score indicating a more proactive animal. The average coping score was 64.1 ± 1.1. In order to account for the effect of sex (male, female) and state (intact, neutered) of the dogs on their coping score an ANOVA model was run with Sex, State and Sex x State interaction. No significant interaction effect of sex and status on coping score was found (ANOVA $F_{91,1}$ = 0.024; P > 0.05). Likewise, no main effect of sex (ANOVA $F_{92,1}$ = 0.226; P > 0.05) and state (ANOVA $F_{92,1}$ = 0.980; P > 0.05) was found. No significant correlation between coping score and age was found (r = 0.133; df = 93; P > 0.05). Correlations between coping score and the CBARQ factors determined by the questionnaire were calculated (Appendix III). Coping score was (near) significantly correlated with Trainability (r = 0.207; df = 80; P = 0.062), Social fear (r = -0.362; df = 80; P = 0.001) and Dog-directed fear (r = -0.407; df =

80; P < 0.001). Thus, proactive type of dogs scored relatively low for fear (social and dog directed) and tended to be trainable.

Paw preference (puzzle test)

In order to determine the paw preference direction and strength, dogs' paw use was measured over the total puzzle test. Fifteen dogs were excluded from the puzzle test for reasons of not using their paw, signs of fear/aggression and technical problems with the puzzle. Paw preference was calculated by $HI = (L - R)/(L + R)$ with L representing the number of times the left paw was used and R the number of times the right paw was used. A score ranging from -1 for right to +1 for left-pawed dogs was obtained and the absolute value of this score was used to determine the paw preference strength. Two dogs scored a paw preference of zero and were considered ambilateral (2.4%). Of the remaining dogs 51.8% was right-pawed and 45.9% was left-pawed. The average paw preference direction was -0.01 ± 0.06 (n = 85) and the average paw preference strength was 0.40 ± 0.03 (n = 85).

First, the effects of sex (male, female) and state (intact, neutered) on paw preference were analysed using two ANOVA models for paw preference direction and strength. No interaction effect was found on paw preference direction (ANOVA $F_{80,1}$ = 0.053; P > 0.05), though intact animals seemed to have a lower paw preference indicating a preference for their right paw (Figure 3). Also no main effects of sex (ANOVA $F_{91,1}$ = 0.038; P > 0.05) or state ANOVA $F_{91,1}$ = 0.930; P > 0.05 were found. Paw preference strength also was not significantly influenced by interaction (ANOVA $F_{80,1}$ = 0.076; P > 0.05) and main effects of sex (ANOVA $F_{81,1}$ = 0.033; P > 0.05) and state (ANOVA $F_{81,1}$ = 0.517; P > 0.05). Paw preference and preference strength were both not significantly correlated to age (r = -0.053; df = 82; P > 0.05, and r = 0.111; df = 82; P > 0.05, respectively).
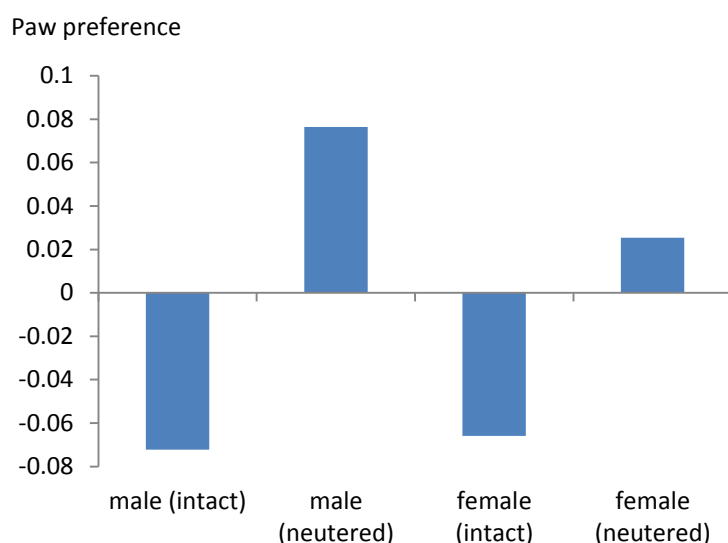

Figure 3 Average paw preference in female (intact n = 12, neutered n = 33) and male dogs (intact n = 26, neutered n = 13) Paw preference was measured over nine food retrieval trials with a negative value indicating right-pawedness and a positive value left-pawedness.

Finally, the relationship between coping score and paw preference characteristics were examined. Spearman's rank correlation showed no significant correlation between coping score and paw preference (r = 0.153; df = 81; P > 0.05) (Figure 4). Paw preference strength was also not significantly correlated to coping score (r = -0.006; df = 81; P > 0.05). However, significant correlations were found between paw preference strength and Trainability (r = 0.225; df = 80; P = 0.042) and Separation anxiety (r = -0.227; df = 80; P = 0.04), while a near significant correlation was found with Stranger-directed aggression (r = 0.19; df = 80; P = 0.088, see Appendix III). The results indicate that coping strategy was not related to paw preference (strength), but strongly lateralized individuals were readily trainable and prone to show aggression towards strangers but rarely exhibited separation anxiety.
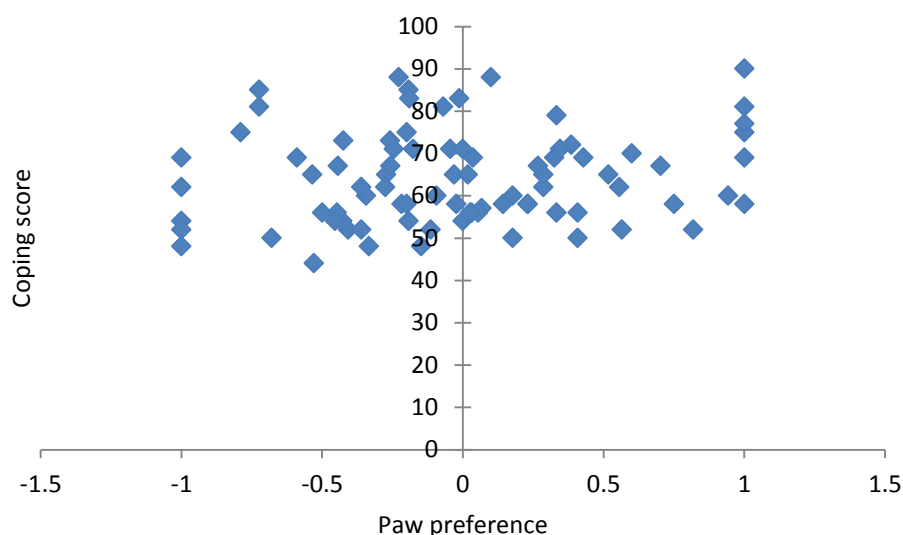

Figure 4 Correlation between coping score and paw preference Coping score (%) was determined by the questionnaire with a higher score representing more proactive individuals. Paw preference was measured over nine food retrieval trials with a negative value indicating right-pawedness and a positive value left-pawedness.

Reversal learning (T-maze)

Ninety-eight dogs completed the T-maze test used to investigate effects of coping score and paw preference on reversal learning. Overall, most dogs were relatively successful in the training phase by making many correct choices, i.e. they went to the first chosen arm in 86.9% of the trails (Table 5). The left arm was chosen first by the majority of the animals. It was hypothesized that the block used in the introduction phase could influence the dogs' decision in the first free trial. If at the start of the test the block would be in the right arm and the dog would continue to alternate the arms then the dog would be expected to go left in the first free trial. However, no significant effect of the first blocked arm was found (Chi-square = 0.002; df = 1; P > 0.05, see Appendix IV). Further associations

between the first choice and paw preference or coping score were investigated by running ANOVA models with either paw preference or coping score as the dependent variable and first choice as fixed effect. Paw preference had no significant association with the first choice (ANOVA $F_{81,1} = 0.554$; $P > 0.05$) but there was a trend with coping score (ANOVA $F_{92,1} = 3.437$; $P = 0.067$). The coping score of dogs that chose the right arm tended to be higher than the coping score of dogs that went left (predicted means 66.4 ± 1.8 and 62.2 ± 1.4, respectively).

After the training phase of 8 trials in which dogs were reinforced to approach the owner by the first selected arm, the reversal phase was started. During the reversal phase in which dogs had to go through the opposite arm, dogs made an average of 6.3 errors and needed 5.2 trials before they made a first switch in arm used. Positive correlations were found between the percentage of training success (percentage of correct choices in the training phase) and the number of errors in the reversal phase ($r = 0.602$; df = 96; $P < 0.001$) and the needed trials before reversal ($r = 0.589$; df = 96; $P < 0.001$). No significant correlations were found between the percentage of training success, the number of errors, the number of trials and either coping score (all $P > 0.05$), paw preference (all $P > 0.05$), or age (all $P > 0.05$).

Table 5 Results T-maze per coping strategy and paw preference Dogs were classified as reactive or proactive based on their coping score (reactive = 40 – 64; proactive = 65 – 90) and as left-pawed or right-pawed based on their paw preference (left > 0; right < 0).

	Total	Reactive	Proactive	Left-pawed	Right-pawed
First choice					
Left	61 (62.2%)	34 (66.7%)	25 (58.1%)	23 (60.5%)	25(58.1%)
Right	37 (37.8%)	17 (33.3%)	18 (41.9%)	15 (39.5%)	18(41.9%)
Training success (%)	86.9	90.2	83.1	87.2	86.3
Errors (#)	6.3	6.6	6.0	6.2	6.3
Trials till reversal (#)	5.2	5.5	5.1	5.1	5.5

Memory tests

Memory testing was performed based on spatial or object-specific cues and effects of coping score and paw preference were investigated. Dogs had to pick one of three covers under which a treat had been hidden in 3 trials per subtest and an average success percentage for each subtest was calculated. In total 92 dogs were tested in the memory test. Dogs performed above chance (>33% successful choices) in the three visible displacement subtests (all one-sample t tests; $P < 0.001$). Dogs performed better in the spatial task without screen (68.8 ± 3.3) than in spatial task with screen (66.3 ± 3.4). The average success percentage in the object task was the lowest (63.8 ± 3.3) (Figure 5).
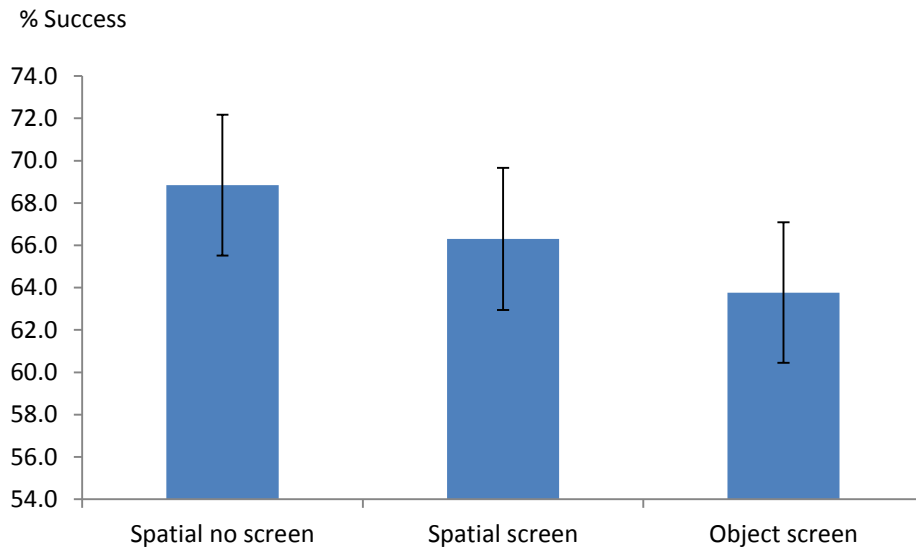
% Success

Figure 5 Percentage of success per memory task Error bars represent standard errors of the mean.

Because the percentage of success is an ordinal variable, with four possible options (0%, 33%, 67% or 100%), the IRclass procedure for repeated measures was used in GenStat. The model showed no significant difference between the success percentages of the different tasks and no effect of coping score was found (IRClass procedure, Fixed effect: Test + Coping score + Test.Coping score, Random effect: Dog; $P > 0.05$). Also, when replacing the variable coping score for age, sex, paw preference, and paw preference strength no significant effects were found ($P > 0.05$) (Table 6).

Table 6 Percentage of success per memory task (mean ± SE) according to age, coping strategy, paw preference and sex

	Spatial no screen	Spatial screen	Object screen
Age			
Young (< 6 yr)	71.2 ± 4.2	67.8 ± 4.5	62.7 ± 4.1
Old (≥ 6 yr)	65.6 ± 5.5	63.5 ± 5.0	64.6 ± 6.0
Coping strategy			
Reactive	66.0 ± 4.7	66.0 ± 5.0	59.9 ± 4.6
Proactive	70.8 ± 4.9	66.7 ± 4.6	66.7 ± 5.1
Paw preference			
Left	63.9 ± 4.7	61.1 ± 5.8	63.9 ± 5.6
Right	75.4 ± 5.1	70.6 ± 4.6	65.1 ± 4.3
Sex			
Male	70.5 ± 4.4	69.8 ± 4.9	64.3 ± 4.6
Female	67.3 ± 5.1	63.3 ± 4.9	63.3 ± 4.9

A similar model was run for the number of times the dog approached the cover in a curved line. Again the ordinal data (four options: 0, 1, 2, 3) was analysed by an IRClass procedure for repeated measures with test, coping score and their interaction as fixed effects and dog as random effect. There was a significant difference between the tasks (IRClass procedure; P = 0.011) with a higher frequency of curved runs in the object memory task (Figure 6).
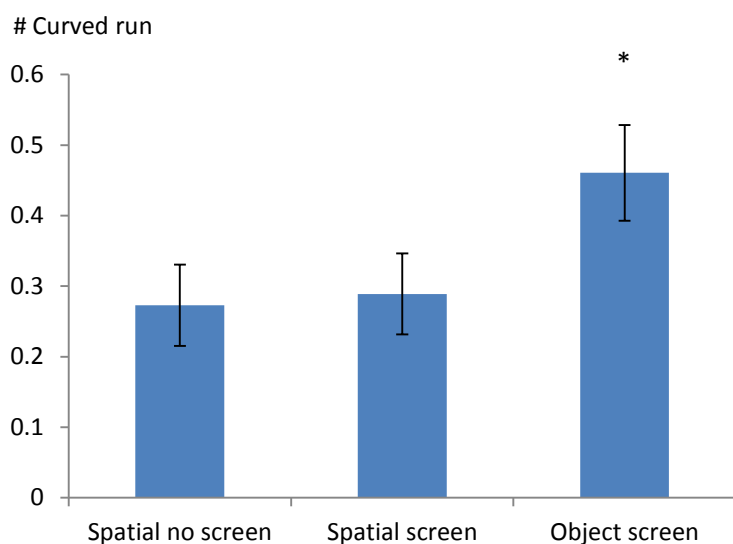
Figure 6 Number of curved runs per memory task Error bars represent standard errors of the mean. Asterisk indicates a significant difference.

No association between the number of times dogs showed a curved run and coping score or paw preference and their interaction with test was found (IRClass procedure; P > 0.05). When running the model with paw preference strength an almost significant interaction effect of test and paw preference strength was found (IRClass procedure; P = 0.053). Because of the transformation used in the IRClass procedure, the frequency of curved runs changed to negative values. Transformed values that approach zero indicate a higher frequency of curved runs while a more negative value indicates that less curved runs were observed. A trend was found for dogs with higher paw preference strength to show more curved runs in the object screen and less in the spatial no screen task. Across the paw preference strength the number of curved runs remained more or less similar for the spatial screen task (Figure 7).

Curved runs

Figure 7 Predicted number of curved runs per memory task and paw preference strength A more negative value for the number of curved runs indicates less curved runs while a more positive value indicates more curved runs.
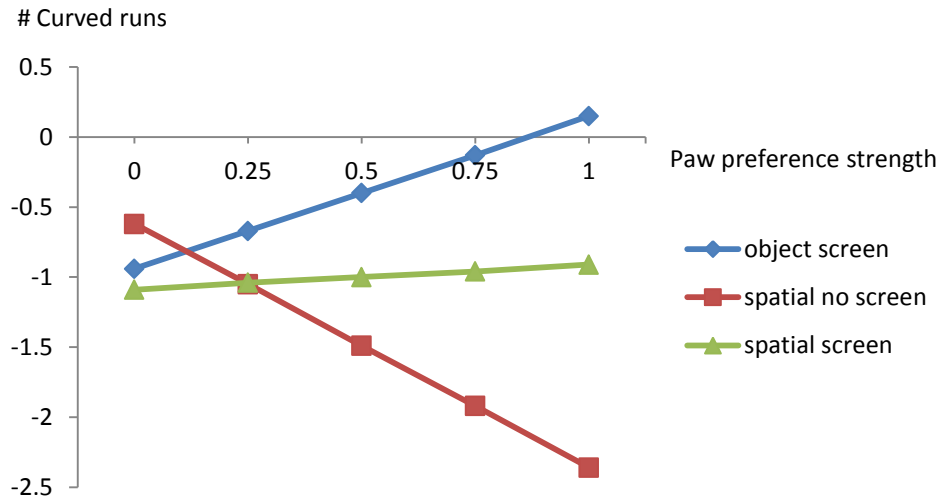
The behaviours scored during the memory test are summarized in Table 7. Behaviours that were scored in less than 10% of the records were omitted. These included percentage tail low, attack intention, tilting head, scratching/grooming, playing bow, barking, high barking, and growling. Because of the small variation in shaking, yawning, oral behaviours and paw lifting these behaviours were taken together in the total stress signals.

Table 7 Average values of behaviours observed during the memory test Values are presented as means (range)

Behaviour	Mean (range)	Behaviour	Mean (range)
Exploration (%)	0.4 (0 – 10.3)	Standing (%)	30.6 (0 – 100)
Task performance (%)	71.8 (41.0 – 97.0)	Sitting (%)	57.0 (0 – 96.9)
Contact owner (%)	2.6 (0 – 34.6)	Lying (%)	5.6 (0 – 97.2)
Contact experimenter (%)	24.5 (1.1 – 57.0)	Panting on (%)	28.8 (0 – 100)
Do nothing (%)	0.7 (0 – 37.6)	Panting off (%)	71.2 (0 – 100)
Ears high (%)	18.0 (0 – 100)	Tail wagging (%)	41.8 (0 – 100)
Ears neutral (%)	80.0 (0 – 100)	Tail wagging off (%)	58.2 (0 – 100)
Ears low (%)	2.1 (0 – 100)	Sniffing	0.3 (0 – 4)
Tail high (%)	41.2 (0 – 100)	Stress signals	1.0 (0 – 7)
Tail neutral (%)	57.4 (0 – 100)	High vocalizations	0.5 (0 – 12)
Move/walking (%)	6.8 (0 – 29.9)		

Spearman's rank correlations were calculated between behaviours. Task performance was negatively correlated with contact with owner (r = -0.549; P < 0.001), contact with the experimenter (r = -0.800; P < 0.001), panting (r = -0.221; P = 0.001), and stress signals (r = -0.143; P = 0.032). Contact with the

owner was positively correlated to contact with the experimenter (r = 0.145; P = 0.030). Positive correlations were found for both contact with the owner and experimenter, with panting (r = 0.216; P = 0.001, and r = 0.129; P = 0.055, respectively), and stress signals (r = 0.124; P = 0.065, and r = 0.112; P = 0.094, respectively). A high ear posture was positively correlated to panting (r = 0.229; P = 0.001) and negatively correlated to normal tail wagging (r = -0.162; P = 0.015). In contrast, a low ear posture was positively correlated to stress signals (r = 0.153; P = 0.023) and high vocalizations (r = 0.134; P = 0.046). High vocalizations were shown more when dogs showed more normal tail wagging (r = 0.239; P < 0.001). Dogs that moved/walked more and lay down more tended to show less stress signals (r = -0.120; P = 0.073, and r = -0.145; P = 0.031, respectively). Stress signals were also positively correlated with panting (r = 0.359; P < 0.001). Thus, it appears that dogs show two behavioural response patterns. Dogs either focus on the task showing little signs of stress and panting or they focus on people.

A principal component analysis on the scored behaviours was done as to establish data reduction. The analysis revealed one factor which explained 12.1% of the variance. The percentage of task performance and contact experimenter loaded on this factor which was labelled people orientation (loading > |0.4|, Table 8).

The different behaviours scored were analysed using REML mixed models for the factors test (spatial no screen, spatial screen, object screen), coping score (covariate), paw preference (covariate) and paw preference strength (covariate). The main model consisted of test, coping score and their interaction as fixed effects with dog as random effect. For the other models coping score was replaced by the other covariates one at a time (Table 9).

Differences were found in the attention of the dogs. Dogs with a higher paw preference spent significantly more time exploring their environment (F = 13.66; P < 0.001). This result indicates that left pawed dogs explore their environment more than right-pawed dogs. A higher paw preference strength also was associated

Table 8 Results of the principal component analysis for behaviours scored during the memory test. Bold values indicate behaviours that loaded on the factor.

	People orientation
% Exploration	0.0542
% Task performance	**-0.5743**
% Contact owner	0.3913
% Contact experimenter	**0.4411**
% Ears High	0.1621
% Ears Low	0.1656
% Tail Neutral	0.2008
% Tail High	-0.1857
% Move/Walking	-0.1035
% Sitting	-0.0458
% Lying	0.1386
% Panting On	0.2181
% Panting Off	-0.0105
% Wagging Off	0.119
% Normal Tail Wagging	-0.1597
Sniffing	-0.1437
Stress signals	0.2171
High vocalizations	-0.063

with more exploration (F = 8.53; P = 0.005), but this effect disappeared after log transformation. When transforming data to log-values to correct for a normal distribution a trend in test became apparent (P = 0.063). Animals seemed to show less exploration in the object screen task than in the spatial no screen task. The score for people orientation was also significantly influenced by test (F = 3.62; P = 0.029). Higher scores for people orientation were found in the spatial no screen task compared to the spatial screen task. Thus, it appears that dogs focus on people when no changes are made in the environment.

Table 9 P-values of measured behaviours for test, coping score, paw preference, and paw preference strength. Bold values indicate significance, cursive values indicate trends.

	Model 1			Model 2		Model 3	
	Test	Coping score	Test.Coping score	Paw Preference	Test.Paw Preference	Paw Strength	Test.Paw Strength
Attention							
% Exploration	0.302	0.908	0.745	**<0.001**	0.132	**0.005**	0.420
% Contact owner	*0.090*	*0.070*	**0.005**	0.128	**0.050**	**0.044**	0.671
% Do nothing	0.221	0.300	0.701	0.135	0.176	0.774	0.139
People orientation	**0.029**	0.532	0.525	0.137	0.513	0.943	0.582
Posture							
% Ears high	0.424	*0.082*	0.810	0.867	0.952	0.596	0.910
% Ears neutral	0.315	0.236	0.411	0.795	0.742	0.898	0.787
% Ears low	0.733	0.131	0.135	0.785	0.666	0.272	0.871
% Tail neutral	0.801	0.678	0.390	0.760	0.120	0.921	0.217
% Tail high	0.599	0.681	0.362	0.708	0.144	0.858	0.196
% Tail wagging	0.635	0.795	0.198	0.656	*0.052*	0.571	0.430
Locomotion							
%Move/walking	**0.011**	0.108	0.789	0.379	0.844	*0.067*	0.543
% Standing	0.555	0.787	0.168	0.883	0.151	0.443	0.996
% Sitting	0.458	0.384	*0.082*	0.616	0.349	0.187	0.739
% Lying	0.978	0.263	0.280	0.295	0.488	*0.075*	0.312
Sniffing	0.292	0.392	0.762	0.651	*0.077*	0.816	0.365
% Panting	0.158	**0.044**	0.749	0.128	0.182	0.128	0.111
Stress signals	**0.043**	0.610	0.585	0.208	0.157	0.473	*0.081*
High vocalization	**0.050**	**<0.001**	0.628	0.828	0.933	*0.08*	0.149

Contact with the owner was significantly affected by the interaction between test and coping score (F = 5.45; P = 0.005) and the interaction between test and paw preference (F = 3.05; P = 0.050). Contact with the owner remained quite stable across coping scores for the spatial no screen task. With the object screen and spatial screen task the percentage of contact with the owner decreased as coping score increased (Figure 8A). When paw preference increased contact with the owner also increased in the spatial no screen and spatial screen task while in the object screen task the percentage of contact remained similar (Figure 8B). Contact with the owner was also effected by paw preference strength (F = 4.19; P = 0.044). Dogs with a higher paw preference strength spent more time in contact with their owner. More proactive dogs are seeking less contact with their owner in a situation which can be seen as threatening (i.e. tasks with screen) and thus appear more independent than more reactive dogs.
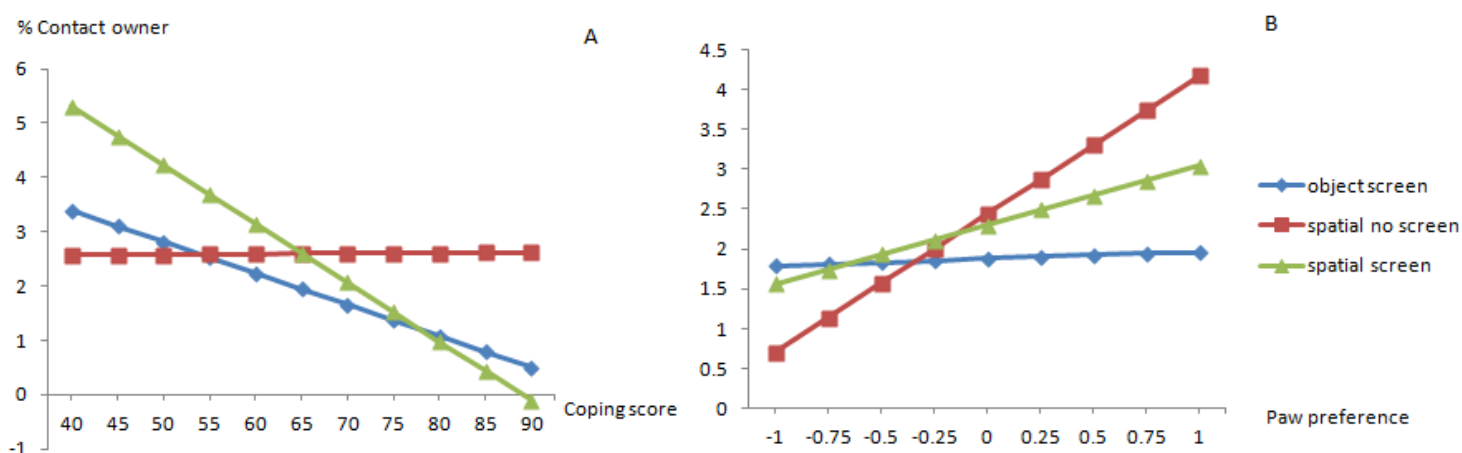

Figure 8 Predicted percentage of contact with the owner per memory task A) Percentage of contact with the owner according to coping score. A higher coping score indicates a more proactive strategy. B) Percentage of contact with the owner according to paw preference. A negative paw preference indicates a preference for the right paw while a positive value indicates a preference for the left paw.

No differences were found in ear and tail postures between tasks (all P > 0.05). There was a trend for dogs with a higher coping score to spent a higher percentage of time with their ears in a high position (F = 3.12; P = 0.082). Normal tail wagging tended to occur more in dogs with a higher paw preference in the spatial screen and object screen task than dogs with a lower paw preference. Dogs with a lower paw preference tended to show more normal tail wagging in the spatial no screen (F = 3.02; P = 0.052). This suggests that in this test situation differences in coping strategies or paw preference (strength) are not expressed through differences in these postures.

The percentage of moving or walking was significantly lower in the spatial no screen task compared to the spatial screen and object screen task (F = 4.65; P = 0.011). A trend showed that dogs with a higher paw preference strength spent more time moving or walking (F = 3.45; P = 0.067). Another trend involved the interaction effect for test and coping score on sitting (F = 2.54; P = 0.082). Dogs with a higher coping score tended to spent more time sitting in all tasks than dogs with a lower

coping score, though this effect was more pronounced in the spatial no screen and spatial screen task. Log transformation for the percentage of lying showed dogs with a higher paw preference to spent less time lying (F = 3.97; P = 0.050). At the same time, the log transformation cancelled out the earlier found effect of paw preference strength on lying (F = 3.25; P = 0.075). The only significant effect in locomotion behaviours (i.e. more moving/walking in both screen tasks) is probably due to the structure of the test with the introduction of the screen evoking a response in the dog.

While an almost significant interaction was found between paw preference and test for the frequency sniffing (F = 2.61; P = 0.077) this became not significant after the log transformation. Panting was significantly affected by coping score (F = 4.19; P = 0.044). More proactive dogs showed more panting during the test. The total stress signals (shaking, yawning, oral behaviours, and paw lifting) were significantly more observed during the spatial no screen task than the spatial screen task (F = 3.22; P = 0.043) (Figure 9A). The difference between the object screen task and the spatial no screen task was almost significant (difference between means was only slightly higher than two times the standard error of difference, data not shown). A trend for an interaction effect of test and paw preference strength was also found (F = 2.54; P = 0.081) which showed that dogs with a stronger paw preference strength performed more stress signals in both spatial tasks than dogs with a weaker paw preference strength. In contrast, in the object screen task dogs with a weaker paw preference strength showed more stress signals than dogs with a stronger paw preference strength. It appears that the frequency of stress signals is mostly associated with the difference in tasks. The use of the screen is related to a lower number of stress signals. Similar results were found for the frequency of high vocalizations (F = 3.04; P = 0.050) with significantly more high vocalizations in the spatial no screen task than the object screen task (Figure 9B).
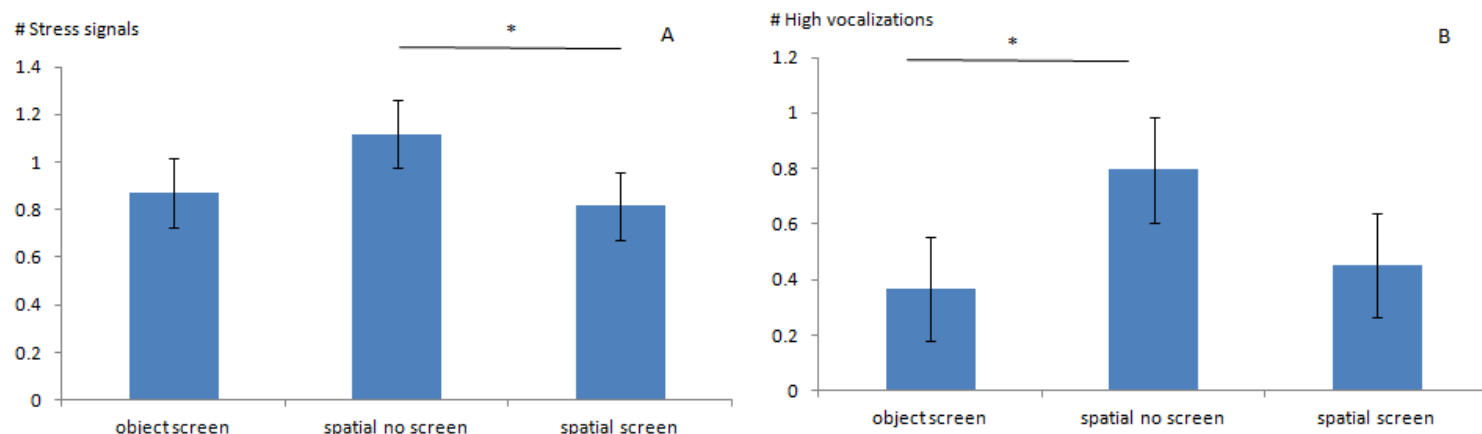

Figure 9 A) Predicted number of stress signals per task B) Predicted number of high vocalizations per task. Error bars represent standard errors of the mean. Asterisk indicates a significant difference.

Again, the difference between the spatial screen task and the spatial no screen task was approaching significance (difference between means was only slightly higher than two times the standard error of difference, data not shown). Dogs with a higher coping score showed more high vocalizations ($F = 11.64$; $P < 0.001$). A trend was also found for dogs with a higher paw preference strength to show less high vocalizations ($F = 3.15$; $P = 0.080$). The occurrence of stress signals and high vocalization appear influenced by the structure of the task; the absence of a screen is associated with a higher number of stress signals and high vocalizations. Dog characteristics as coping strategy and paw preference did not appear to influence stress signals shown by dogs. However, more proactive dogs did show more high vocalizations than more reactive dogs.

A principal component analysis was done to investigate if different cognitive parameters from the T-maze and memory test could be linked to the dog characteristics coping score, paw preference and paw preference strength. Parameters from the T-maze included the training success percentage and the number of errors, while parameters from the memory test included the total success percentage over the three subtests and the absolute difference in success percentage between the object screen and spatial screen task. Three relevant factors were found (Table 10). The number of errors and training success percentage loaded both negatively on Factor 1. Both total success of the memory test and the difference between the object and spatial screen task loaded on the second factor. Also coping score was moderately correlated to this factor. Finally, paw preference and paw preference strength both loaded positively on Factor 3. Another principal component analysis was run to include the factors measured in the CBARQ, however this is beyond the scope of this paper and will not be discussed further (Appendix V and VI).

Table 10 Principal component analysis of cognitive parameters and coping score, paw preference and paw preference strength. Bold values indicate behaviours that loaded on the factor (loading > |0.4|).

	Factor 1	Factor 2	Factor 3
% Variation	23.83	18.69	15.53
% Total success memory	0.1871	**0.5509**	-0.0495
% Difference success object and spatial screen task	0.0194	**-0.6502**	-0.0893
Paw preference	0.0559	-0.1226	**0.7028**
Paw preference strenght	0.1438	-0.087	**0.6579**
Coping score	0.2069	**0.4655**	0.1817
# Errors	**-0.6774**	0.0866	0.1441
% Success training	**-0.6627**	0.1642	0.0949

Discussion

The cognitive abilities of dogs have been tested in relation to coping strategies and paw preference. Coping strategies are a set of behavioural and physiological responses to stress which are consistent over time (Koolhaas et al., 1999). Two main coping strategies exist, the proactive and reactive strategy, each with different characteristics. Proactive animals are said to be more bold, aggressive and tend to develop routines while reactive animals are more flexible, less aggressive and more sensitive to their environment (Carere & Locurto, 2011; Koolhaas et al., 1999) (see Table 1 for overview). These coping strategies have also been found in dogs (Horváth et al., 2007) and it has been suggested that differences in coping strategies could lead to differences in cognitive abilities (Pavlov cited by Carere & Locurto, 2011). Reactive animals are expected to be more flexible and sensitive to their environment and this could provide an advantage during a reversal learning (which requires flexibility in behavioural reponses) and a memory test (which requires sensitivity to the environment). Additionaly, lateralization of the brain where one hemisphere is more dominant during certain tasks can also influence the cognitive performance. Reversal learning is thought to be under more dominant control of the right hemisphere (Teitelbaum, 1964). It has been indicated that spatial cues are more readily processed by the right hemisphere, while use of the left hemisphere is suggested to be more dominant when using object-specific cues (Vallortigara, 2000; Clayton & Krebs, 1993, 1994; Andrews, 1991). Finally, there have been some indications that coping strategies and lateralization are linked. Right-handed primates showed behaviours which were consistent with a proactive coping strategy (faster to explore, routine behaviour) while left-handed primates appeared to adopt a more reactive coping strategy (withdrawal, sensitive to the environment) (review Rogers, 2009). The main aim of this study was to examine the effect of coping strategy or lateralization on cognitive performance in a reversal learning task and memory task. Further, this study attempted to investigate the relationship between coping strategy and lateralization (see Table 3 for hypothetical framework).

Coping score and paw preference

The aim of this study was to investigate the influence of coping strategies and paw preference on cognitive functions. Dogs were given a score for coping strategy with a higher score indicating a more proactive coping strategy. These scores were based on an owner reported questionnaire and are assumed to be a useful proxy for a dog's coping strategy. The dogs' coping scores were negatively correlated with owner-reported scores for the CBARQ factors Social fear and Dog-directed fear suggesting that more proactive dogs show less social and dog-directed fear and that coping strategy scores indeed reflected more boldness. When classifying the dogs in either having a reactive or proactive coping strategy (reactive = 40 − 64; proactive = 65 − 90) it was found that 51 dogs were

reactive (53%) while 45 dogs were proactive (47%). This means that the test population had a good variation in coping scores, though very reactive dogs were not a part of the study population. A slightly more skewed distribution was found in earlier research where dogs were threateningly approached by a strange person with 60% reactive dogs and 40% proactive dogs (Horváth et al., 2007). A principal component analysis of the behaviours they scored revealed the factors fearfulness and aggressiveness which were then used to group the dogs into different coping strategies using hierarchical cluster analysis (Horváth et al., 2007). Present coping scores were not affected by sex or state of the animals and no significant correlation with age was found. This implies that coping score is not associated with basic animal characteristics. Coping strategies in dogs have been demonstrated to contain the same differences in behavioural and physiological characteristics as reported in rodents (Koolhaas et al., 1999). Proactive dogs were more active, had a shorter attack latency, a tendency for aggression, and low HPA-axis reactivity. The reactive dogs were less active, had a longer attack latency, reacted with passivity and submission, and showed a higher HPA-axis reactivity (Horváth et al., 2007). In the current study individual differences in dogs' coping strategies were also found with a more or less equal representation of proactive and reactive dogs.

Apart from coping strategies our interest also went out to brain lateralization in order to determine the relationship between lateralization and coping strategy and its influence on cognitive abilities. Paw preference was used as indicator of brain lateralization where the hemisphere contralateral to the preferred paw is dominant (Rogers, 2009). In primates hand preference is often determined by which hand they use to reach for food (Rogers, 2009). It could be that primates have developed a stronger hand preference because they use their hands more to manipulate their environment than dogs do with their paws. The average paw preference score in this study was close to zero indicating an equal distribution of right and left-paw preferring dogs as dogs that did not use their paws were excluded from analysis. Wells (2003) found that in a food retrieval task 41.5% of the dogs used their right paw more while 39.6% used their left and 18.9% were ambilateral. This study had a lower percentage of ambilateral dogs (2.4%) and therefore a higher percentage of right and left pawed dogs (51.8% and 45.9%, respectively). This difference stemmed from the difference in classification; Wells (2003) based her classification on binomial z-scores. Dogs that had scores greater than +1.96 were left preferring, scores lower than -1.96 were right preferring, and scores between -1.96 and +1.96 were ambilateral. In this study dogs with a score of zero were ambilateral, a score greater than zero were left preferring, and a score lower than zero were right preferring. Still, the ratio of right and left pawed dogs in both studies are similar. The average paw preference strength found was 0.40 ± 0.03 which shows that there is lateralization in the paw use of dogs. This score is similar to the found absolute handedness score in another food retrieval task in dogs (0.39 ± 0.03,

Wells, 2003) though others have also found lower scores in dogs (0.30 ± 0.04 Batt et al., 2008; 0.25 ± 0.019 McGreevy et al., 2010).

No significant correlation was found between coping score and paw preference of the 83 dogs in the present study population. On forehand, it was expected that with an increasing coping score (more proactive) the paw preference score would decrease (more right-pawed). In fact, the coping score was positively correlated with paw preference, but the correlation was not strong ($r = 0.153$). This is in contrast with findings in primates that indicate that left-handed animals have a more reactive coping strategy and right-handed animals have a more proactive coping strategy (Rogers, 2009). The difference in coping strategies between left and right-handed primates was based on a few behaviours such as exploration and freezing (Hopkins & Bennet, 1994; Cameron & Rogers, 1999; Braccini & Caine, 2009). In these studies primates were tested for hand preference by investigating which hand was used to reach for food. Behavioural measures included latency to leave the nestbox, latency to approach novel objects, the number of novel objects touched, latency to taste novel foods, the number of vocalizations, the duration of freezing and the number of head movements. The results from these studies showed that right-handed primates had a lower latency to leave the nestbox, to approach or touch novel objects, to taste novel foods, and had a shorter duration of freezing than left-handed primates (Hopkins & Bennet, 1994; Cameron & Rogers, 1999; Braccini & Caine, 2009). These behavioural responses led to the suggestion that right-handed animals adopt a more proactive coping strategy (Rogers, 2009). While the questionnaire used to determine coping strategy in this study queried about exploration of new environments and the dogs' reaction to a threat, a wide variety of responses could be scored by the owners which aimed to give complete overview of the dogs coping strategy. Interestingly, findings from one study on dogs did indicate that temperament is related to paw preference (Batt et al., 2009). Dogs with a higher paw preference strength were suggested to be more bold as they were faster to chase objects, approach strange humans and settle in a strange environment. This seems to indicate that paw preference strength is more important than the direction in relationship to the behaviour. Rogers and Branson (2006) reported that dogs with a lower paw preference strength were more reactive to thunderstorms and fireworks. Interestingly, others found no association in latency to resume play after a sudden loud noise and paw preference (Batt et al., 2009). In this study also no significant correlation was found between paw preference strength and non-social fear which includes items as the dogs' reaction to thunderstorms and sudden noises. However, the other items in this factor affect the dogs' score because it also includes items with both visual and auditory stimuli (e.g. exposure to heavy traffic). It has been suggested that dogs are more reactive to auditory cues only because they are less able to assess the threat than when both visual and auditory cues can be used (Schneider, 2011). This would mean that scores for the factor non-social fear are lower than those for reactivity to sudden noises.

Rogers and Branson (2006) noted similarity between high reactivity to thunderstorms and fireworks in less lateralized dogs and higher anxiety in less lateralized humans. In this study a significant negative correlation was found between paw preference strength and Separation anxiety indicating that dogs with a stronger paw preference strength show less separation anxiety. There was also a trend for a higher Stranger-directed aggression in dogs with a higher paw preference strength. So, though paw preference strength was not significantly correlated to coping score in this study it appears that it is correlated with different aspects of dog temperament including separation anxiety and stranger-directed aggression. Dogs with a higher paw preference strength are suggested to be more bold as they appear to be more internally driven (aggression) and less externally driven (anxious).

Paw preference and sex/state

Three theories have been reported on the role of prenatal testosterone to differences in lateralization (review Grimshaw & Bryden, 1995). In brief, the sexual differentiation theory implies that increased testosterone concentrations may be associated with the more masculine pattern of left-handedness, however no mechanism is proposed. The Geschwind hypothesis states that increased levels of prenatal testosterone is associated with left handedness either because testosterone is thought to slow the growth of the left hemisphere or enhanced growth of the right hemisphere. The final callosal hypothesis proposes that lateralization is a result of the pruning of callosal axons (review Grimshaw & Bryden, 1995). Post-mortem investigation of human brains has shown differences in brain structures between sexes and left- and right-handed people. It was shown that left-handed humans had a larger corpus callosum and it was suggested that in men lower testosterone leads to less regressive neural events, and thus a larger corpus callosum, and increased left-handedness. A different mechanism may be involved in females (Witelson, 1991). This theory could also explain the fact that left-handed primates were more often on the receiving end of aggressive interactions and more submissive because the low testosterone levels associated with left-handedness could be responsible for the lower aggression observed (Westergaard et al., 2003). Experimental evidence showed that girls with high levels of prenatal testosterone showed more right-handedness and had stronger left hemisphere representation for speech at the age of 10. For boys no relationship was found between prenatal testosterone levels and handedness, but higher testosterone levels were associated with stronger right hemisphere specialization for recognition of emotion (Grimshaw & Bryden, 1995). These findings are most consistent with the callosal hypothesis that higher levels of prenatal testosterone lead to greater lateralization of function (Grimshaw & Bryden, 1995; Witelson, 1991). Literature on non-human primates gives conflicting results; some report a tendency for female primates to be more right-handed (Hopkins & Leavens, 1998) while

others could not find a significant effect of sex on hand preference (Hopkins & Bennett, 1994). A genetic aspect to the direction of hand preference has been suggested because of evidence for lateralization in neonates and young infants, stronger correlations found between handedness of children and their biological parents than adoptive parents, and lack of reliable evidence of environmental correlates (review McManus et al., 1988).

This study could not find a sex effect on paw preference as reported in earlier research with males preferring their left paw and females preferring their right paw (Wells, 2003; Quaranta et al., 2004; McGreevy et al., 2010). No significant effect of sex was found when paw preference was based on the first stepping paw in a search task (van Alphen et al., 2005) or when only neutered dogs were tested (Branson & Rogers, 2006; Tomkins et al., 2010b). It was suggested that this difference in paw preference between males (left) and females (right) could be related to sex asymmetries in the brain and the hormonal influence of testosterone as found in humans (Wells, 2003; Quaranta et al., 2004; see previous section). A main difference between this study and the studies by Wells (2003), Quaranta et al., (2004), and McGreevy et al. (2010) is that in the latter studies only intact dogs were tested while this study tested both intact and neutered dogs. It was expected in this study that the intact males would show less left paw use than the neutered males, and while the intact animals indeed seemed to prefer their right paw this was not significant. Batt et al. (2008) investigated lateralization in dogs over time measuring before and after neutering. Forty-three dogs were tested in a food retrieval task and a tape task where dogs had to remove a piece of tape from their nose. They found no effect of sex on paw preference and paw preference strength in both the food retrieval task and the tape removal task (Batt et al., 2008). Another issue is that most studies categorize their animals on a one-zero scale while only a few look at the continuous lateralization index which is suggested to provide more statistical power (Tomkins et al., 2010a). Similarly to this study no significant effect of sex on paw preference or paw preference strength was found in these studies that used a continuous lateralization index (Batt et al., 2008; Branson & Rogers, 2006; Tomkins et al., 2010b), though a significant interaction effect of sex and breed was found on paw preference direction (Tomkins et al., 2010b). They found that golden retriever males were more likely to prefer their right paw than golden retriever females. However, because this effect interacted with breed and only a small sample of this breed was tested (n = 9) it is possible that this was a chance effect (Tomkins et al., 2010b). To be able to compare data, Batt et al. (2008) also examined categorical paw preferences and found that during the tape task there was a significant interaction effect of breed, sex and test. Golden retriever females were more left-pawed than golden retriever males during the last test and black Labrador retriever females were more right-pawed during the last test than the first test. This final result could indicate that after neutering dogs become more lateralized but because of only 5 female black Labrador retrievers were tested authors believe that

paw preference is a stable trait over time and not affected by maturation (Batt et al., 2008). A possible explanation for the fact that no sex or status effect was found could be that paw use in dogs is a learned trait. Dogs are often trained to 'give paw' and rewarded for this action; this could lead to a preference for a certain paw (Wells, 2003). For this reason it was decided to use a food retrieval task instead of the paw command. One could argue that in case the dog was successful in getting the treat, it was rewarded and this could have influenced which paw the dog would use in the following trials. However, if this would have been the case stronger paw preferences would have been expected than currently found. If paw use in the puzzle test was affected by learning experience then it would have been expected that a paw preference strength similar to the 'give paw' task would have been found (0.80 ± 0.04, Wells, 2003).

Overall, paw preference appears to be present in dogs and this is not determined by sex or neuter status. It appears that other genetic factors may play a role in determining paw preference. Further research could investigate the relationship between hand preference of the owner as right-handed owners may train their dogs to use their right paw more and this could carry over to paw preference in different tasks.

Paw preference and age

A relationship between age and handedness has been suggested in humans. In children the direction of handedness appears to be stable around 3 years of age while strength of preference seems to increase with age (McManus et al., 1988). This increase in preference strength could be seen as a self-reinforcing loop where the same hand is used more often over time. Research on chimpanzees indicated that older individuals were more right-handed (Westergaard et al., 1993; Hopkins & Leavens, 1998) but it has been cautioned that age could be confounding with rearing history as the subjects with unknown rearing history were probably wild caught (Hopkins & Leavens, 1998). Besides direction, age was also correlated to a stronger hand preference (Westergaard et al., 1993; Hopkins & Leavens, 1998). Other research found no significant effect of age on hand preference (Hopkins & Bennett, 1994).

Dogs in this study had an average age of 5.2 years with the youngest dog being 1.5 and the oldest 13 years of age. The dog of 1.5 years was taken up in the study because the owner brought two dogs to the test day, no indication was found that the dog could not finish the test procedures. In order to investigate possible effects of age on lateralization the correlations between age and paw preference and paw preference strength were determined. Results from this study found no significant correlation between age and paw preference and paw preference strength. This is also found in other research (McGreevy et al., 2010), though a significant interaction between age and breed on paw preference was found (Tomkins et al., 2010b). Golden retriever dogs older than 15 months used

their left paw more than Golden retriever dogs of younger age. They suggest that factors like age, sex, and breed influence the outcome of lateralization variables in a food retrieval task and that future studies should measure motor lateralization with a first stepping test where these factors did not play a significant role (Tomkins et al., 2010b). However, in this study no evidence was found that paw preference as measured by a food retrieval task is influenced by factors as age or sex. The influence of breed could not be investigated in this study due to the low numbers of dogs per breed.

Reversal learning

To investigate the role of coping strategy and paw preference on cognitive abilities dogs were tested for their reversal learning abilities using a T-maze. Earlier research had shown that reactive animals made less errors than proactive animals following a reversal of the food location (Bolhuis et al., 2004) or relocation of food to an open area in front of the maze (de Lourdes Ruiz-Gomez et al., 2011). Regarding lateralization and reversal learning very little to no literature was found. One study indicated that a lesion in the right hemisphere impaired performance of cats in a tactile reversal learning task to the same degree as bilateral lesions. This suggested that the right hemisphere is more dominant during reversal learning but because of the invasive aspect of the study only 2 animals were tested (Teitelbaum, 1964). However, because no other indication was found it was hypothesized that left-pawed dog would perform better than right-pawed dogs in the reversal learning task. Also, the associations between the first choice for the left or right arm and paw preference and coping score were investigated.

The first choice the dogs made for either the left or right arm was not associated with paw preference, as had been hypothesized, but it was associated with coping score. Dogs that went right on the first trial had a higher coping score meaning that they were more proactive. This is the only finding that supports the idea that proactive animals are more right-orientated (Rogers, 2009). Dogs were successful in learning that one arm was the rewarded arm as evident by a high success percentage during the training phase (86.9%) though no significant relationships with coping score or paw preference were found. It was hypothesized that dogs with a higher coping score might be faster in learning to consistently choose the rewarding arm during the training phase because proactive animals seem to learn new tasks more readily (Svartberg, 2002; Blackwell et al., 2010). Thirty-two dogs were tested on a classical conditioning and two operant conditioning tasks where dogs were trained to associate the sound of a clicker with a food reward and they had to touch a toy and a bucket with their nose (Blackwell et al., 2010). Dogs with a more proactive strategy reached the criterion for these tasks faster which could be a consequence of their more bold and exploratory tendencies. Svartberg (2002) analysed data of 2655 working dogs and found that dogs that reached higher levels of the working dog tests had higher boldness scores. They also suggested that because

there was no difference in boldness score over the different working dog tests (tracking, searching, delivering messages, handler protection), that the boldness score was related to general trainability. In other species also no difference in learning a food location in T-maze (as measured by the number of trials and time needed to find the food) between reactive or proactive animals was found (Bolhuis et al., 2004; de Lourdes Ruiz-Gomez et al., 2011). It is probable that going to the owner is a common task for most dogs so in principle the task is not new. While coping score was not significantly correlated with the training success percentage in the learning phase, it was almost significantly correlated with owner-reported scores for the CBARQ factor Trainability. This showed that dogs were more trainable when they had a more proactive coping score as suggested by Svartberg (2002). Also, a significant positive correlation between paw preference strength and Trainability was found. Perhaps proactive dogs are more trainable because they are more active and exploratory making it more likely to accomplish the novel task and because of routine formation the training pattern holds better than in reactive dogs which are more flexible and attentive to their surroundings and thus more easily distracted. Another option could be that proactive dogs are less susceptible to stress-related impairments in learning.

Reversal learning of the dogs was measured as the number of errors made in the reversal phase, where dogs had to switch their conditioned response of going through the first chosen arm. On average the dogs made 6.3 errors over the 8 trials, which indicates that dogs had trouble learning the reversal. Dogs also went through an average of 5.2 trials before they made a switch in arms. This is in line with the finding that approximately 50% of the tested pigs went to the correct arm faultlessly in the sixth reversal trial (Bolhuis et al., 2004). Unfortunately, the sixth trial was the last reversal trial for the pigs so it is unsure if these animals also continued to go through the correct arm. This shows that both dogs and pigs went to the wrong arm approximately 80% of the trials. However, pigs were free to walk from one arm to another until they found the food or the maximum 300 seconds were up. This means that pigs with an incorrect performance could also have made a switch in arms because they could have gone to the correct arm first but then turn around to the other arm. This suggests that the percentage of pigs that made a first switch in arms is higher than 50% in the sixth trial. Pigs were also directed to the food if they failed to find it in time (Bolhuis et al., 2004). Despite these opportunities to learn about the right location the pigs still only performed correctly in the sixth trial. In our study dogs only had one chance to make a correct choice and were immediately returned for the next trial without reward if incorrect. This suggests that dogs were faster to switch arms on their own accord than pigs in reversal learning. Another issue could be that reaching the owner is already a reward in itself (Elliot & Scott, 1965) for the dogs and that this explains why dogs make many errors in the reversal phase and wait long to switch arms. No significant correlations were found between the number of errors made or the number of trials needed till the first switch in arms and the coping

score or paw preference. It had been expected that dogs with a lower coping score (i.e. reactive individuals) would make less errors as found for pigs (Bolhuis et al., 2004) and fish (de Lourdes Ruiz-Gomez et al., 2011) and that they would make a switch in arms faster, because proactive animals are expected to be more rigid (Koolhaas et al., 1999). Also, no correlations were found between age and training success percentage, the number of errors or the number of trials till first switch. It had previously been described that older dogs made more errors in a reversal task based on size discrimination and that they needed more trials to reach the learning criterion (Tapp et al., 2003). An explanation could be the difference in reversal tasks (T-maze and size discrimination), with size discrimination in general being more difficult for older dogs than making a distinction in their own behaviour (going left/right).

It appears that in dogs reversal learning is not associated with coping strategy or paw preference. In general, dogs had a high number of errors and a high number of trials before a first switch in arms in the reversal task. This suggests that the training phase was effective and that the extinction of a previously rewarding action was slow. Owner presence could be a reward in its own right and therefore further testing should be done without owner and only with a food reward. A high paw preference strength is suggested to be an indicator of a more bold dog and these are more trainable according to their owners. This can be explained by the fact that bold dogs are more active and exploratory and therefore more likely to accomplish the novel task and because of routine formation the training pattern holds better than in less bold dogs.

Memory test

The memory test was used to investigate if dogs with a different coping strategy or paw preference are better at finding food using spatial or object-specific cues. Dogs were allowed to see a treat being hidden under one of three cover in different subtests: 1) spatial task without screen, 2) spatial task with screen, and 3) object task with screen. The screen was used to prevent dogs from succeeding because they could keep their attention on the right cover and forcing the dogs to recall the cover from memory. During the spatial task identical covers were used so that dogs could only use spatial cues such as position or orientation in the room. During the object task three covers differing in shape and colour were used so that dogs could use both spatial and object-specific cues making this test relatively more easy compared to the spatial screen task. Dogs were relatively successful in the three subtests (spatial no screen, spatial screen, and object screen) making a correct choice in more than 66% of the trials. This supports the idea that dogs are successful in visible displacement tests were they can see the object being hidden (Fiset et al., 2003; Miller et al., 2009; Triana & Pasnak, 1981). Miller et al. (2009) found that after a delay of 10 seconds dogs still showed an average success of 75% which is somewhat higher but could be explained by the fact that they only tested 6 dogs and

used two covers. Though a decline in success percentages was found from the spatial no screen (68.8%), spatial screen (66.3%) to object screen task (63.8%), no significant differences in success percentages were found between tasks. This means there was no difference between the spatial no screen and spatial screen task suggesting that dogs perform equally well when they can keep their attention on the covers or when a screen temporarily blocks their view. This could suggest that the time the screen was in front of the dog was not long enough to ensure dogs really had to use their memory. Interestingly, the non-significant decline in success over the subtests is in the direction of earlier findings that dogs are more adapted to use spatial cues than object cues (Dumas, 1998; Doré et al., 1996; Head et al., 1995). Doré et al. (1996) tested 20 dogs on visible and invisible displacement using either identical or non-identical screens behind which an object was hidden. During the invisible displacement the object was hidden behind one of the screens and the screens were then manipulated. They used a control for delay (no screen manipulation but a time delay), a control for movement (target screen remained in place but another screen was relocated), single transposition (target screen moved one position), double transposition (target and adjacent screen both moved one position leaving the original target position open), substitution transposition (target and adjacent screen both moved on one position placing the adjacent screen on the original target position), and switch transposition (target and adjacent screen switched positions). While they found no significant difference in the percentage of success between the group with identical or non-identical screen, it was found that dogs performed significantly worse in the substitution and switch transposition. These were the only manipulations that put a screen on the original target position suggesting that spatial cues are more readily used than object-specific cues (Doré et al., 1996). Dumas (1998) tested eight dogs in a figurative and spatial condition where the original target position was always left empty. Two different screens were used and in the figurative condition the target screen was always the same and then moved either to the left or right position. In the spatial condition the target screen differed for half of the trials and the screen was always moved to the same side. They found that dogs found the target in 78% of the trials in the spatial condition and in 49% of the trials in the figurative condition (Dumas, 1998). Similarly, in a study on beagles it was found that they made less errors in a spatial visual discrimination test where they were trained to find a treat that was always hidden under one of two identical red Lego blocks than when it was always hidden under either a blue Lego block or an orange plastic coffee jar top (Head et al., 1995; Milgram et al., 1994). This suggests that dogs more readily use spatial cues than object cues and could possibly be the reason why there is a small decline in success percentage from the spatial to the object screen task.

It has been suggested that reactive animals are better at memory tests than proactive animals because they are more sensitive to their environment (Ohl et al., 2002; Carere & Locurto, 2011;

Koolhaas et al., 1999). Reactive mice have been shown to make less errors on a modified hole board where mice were trained to find baited holes that were marked (Ohl et al., 2002). Further, left-pawed dogs were expected to do better in the spatial screen task while right-pawed dogs were expected to do better in the object screen task (Clayton & Krebs, 1993; 1994; Rogers, 2011; Vallortigara, 2000). Analysis showed no significant effects of coping score, paw preference, paw preference strength and their interaction with the different tests on the percentage of success. Also, when averaging the success percentages over the three tasks no significant correlations were found with coping score and paw preference (data not shown). Therefore, based on these results it appears that memory is not associated with coping strategy or paw preference. Also, no significant effect of age, including its interaction with the type of task, was found. On forehand it was assumed that older dogs would have more trouble remembering the right location and that they would have more success in the object screen task where the differences between the objects were larger and better recognizable. Older dogs have been shown to take longer to reach a learning criterion compared to young dogs when the objects only differ in size (Tapp et al., 2003) but that this was not the case when the objects differed in shape and colour (Milgram et al., 1994). In this study no association was found between coping strategy or paw preference and memory in dogs regardless of the use of spatial or object cues. This suggests that both proactive and reactive dogs both pay enough attention to the environment and are capable of storing this information to succeed in a visible displacement test with a 6 second delay. Paw preference for either the left or right paw was not associated with a higher success in the spatial or object task, respectively. This indicates that the theory that the right hemisphere uses more spatial cues and the left hemisphere uses more object cues is not proven in dogs.

The frequency of curved runs, i.e. as opposed to walking in a straight line, to the cover of choice was significantly affected by the type of test. Dogs made more curved runs in the object screen task than in the other spatial tasks. This could be because the different covers are more distracting to the dogs despite the short familiarization period of 30 seconds with the covers before testing. Though the object screen task is associated with significantly higher curved runs the overall effect is small as the difference between the tasks is lower than 0.2 curved runs. The maximum number of runs per task was 3 runs and in the object task the average number of curved runs was 0.5 while in the spatial no screen and spatial screen task the average number of curved runs was 0.2. Still, this could explain why the percentage of success is somewhat lower, though not significantly, in the object screen task compared to the other spatial tasks. The number of curved runs which was taken as a sign of distraction was not influenced by coping score or paw preference, but there was a trend for the interaction between test and paw preference strength. Dogs with a low paw preference strength showed little difference in the number of curved runs per task. Differences were present in dogs with

a high paw preference strength, which showed more curved runs in the object screen task and less in the spatial no screen task compared to the dogs with low paw preference strength. If low paw preference strength is associated with more reactive animals (Branson & Rogers, 2006) and a high strength with bolder animals (Batt et al., 2009) it could be that dogs with a low paw preference strength are more cautious when approaching the cover while those with a strong preference simply go straight toward the cover. However, this does not explain why more curved runs are observed in dogs with a high paw preference in the object screen task. The higher frequency of curved runs during the object screen task by dogs that are more bold (high paw preference strength) suggest that internally regulated animals are more distracted by a larger alteration in the test (the use of non-identical compared to identical covers).

A principal component analysis on the behaviours shown in the memory test led to the factor 'people-orientation' (12.1% of variance). Dogs that scored high on this factor showed a low percentage task performance and a high percentage contact with the experimenter. This was significantly affected by the test; dogs showed this more during the spatial no screen task than the spatial screen task. Reasons for this can be found in the different procedures of the tasks; in the spatial no screen task no screen is introduced and dogs tended to follow the experimenter that hid the treat. When the screen was used dogs were distracted from the experimenter and remained more focused on the covers. So, it seems that the dogs focused more on where they last saw movement (experimenter returning to position or the cover being lifted). Following this reasoning it was expected that this difference would also be found between the spatial no screen and object screen task. While it was not found for the factor people-orientation (though it came close to significance), when the percentage task performance and contact with experimenter were investigated separately this was the case (data not shown). Exploration was significantly affected by paw preference. Dogs with a higher paw preference, meaning they use their left paw more, spent more time exploring. This would confirm that left-pawed dogs are more sensitive to their environment (Rogers, 2010) despite the fact that no relationship has been found between paw preference and coping score. Contact with the owner seemed to decrease when dogs became more proactive in the object and spatial screen task. This could mean that dogs that are more reactive rely more on social cues from their owner when a change is made in the environment (i.e. introduction of the screen). The percentage of contact with the owner remained almost constant for the spatial no screen task and this could be explained by dogs focusing on the experimenter during this test. Contact with the owner increased in the spatial no screen and spatial screen task for dogs with a higher paw preference. This would mean that in this aspect the more left-pawed dogs behave similar to the more reactive dogs, though the behaviour was shown in different tasks. Also this could be an indication that left-pawed dogs seek more reassurance from their owner when spatial cues are

available which goes against the idea that animals with left paw preference are better at using spatial cues. Dogs with a higher paw preference strength were found to have more contact with the owner. If we assume that dogs with a high paw preference strength are more bold it would be expected that they would need less reassurance from their owner. It could be that these animals are more eager to start as they were also faster to chase an unknown object (Batt et al., 2009). Therefore they could contact their owner more to be given the cue to go.

Stress signals (including shaking, yawning, oral behaviours and paw lifting) and high vocalizations were observed more in the spatial no screen task compared to the spatial screen and object screen task, respectively. These behaviours were almost significantly more observed in the spatial no screen task compared to both other tasks, probably because of the wait in the spatial no screen task. It is assumed that during the wait dogs are most aroused and that the screen in the other tasks distracts the dogs from the wait. Dogs with higher paw preference strength also tended to show more stress signals in both spatial tasks but less in the object screen task compared to the dogs with a lower paw preference strength. This would suggest that dogs with a high paw preference strength are less equipped to deal with spatial cues. Also, a trend was found with the number of high vocalizations decreasing when paw preference strength increased. This can be comparable to the lower reactivity found in more lateralized dogs (Branson & Rogers, 2006). However, significantly more high vocalizations were observed in dogs with a higher coping score. This shows that dogs with a high paw preference strength cannot be seen as bolder animals in all contexts (Batt et al., 2009).

Dogs that were focussed on the task were logically in less contact with the experimenter or owner. They also showed less panting and stress signals, while dogs that were focussing more on the people in the room tended to show these behaviours more. This indicates that stress and focus are related but cause and effect can't be untangled (e.g. are dogs unable to focus because they are stressed or are dogs unable to focus on the task and so become more stressed).

The principal component analysis on the cognitive parameters (memory test: percentage success, difference between success percentage object and spatial task; reversal task: number of errors, percentage success during training) and the coping score, paw preference and paw preference strength of a 100 dogs revealed three relevant factors. The percentage of success during training and the number of errors in the T-maze both loaded negatively on Factor 1 (24% of variance). This makes sense because dogs that were successful in training are expected to make more errors. Indeed, a positive correlation between these two parameters was found. Paw preference and paw preference strength both loaded positively on Factor 3 (16% of variance), meaning that a high paw preference was associated with a high paw preference strength. While this is correct, a high paw preference +1 gives a high paw preference strength 1, it is also the case for a low paw preference of -1 making this factor difficult to interpret. It is also unlikely that a high paw preference strength is found for left-

pawed dogs compared to right-pawed dogs as the average strength was similar (0.43 and 0.40, respectively). Factor 2 (19% of variance) was loaded with the total success percentage in the memory test (positively), the absolute difference in success percentage between the object screen and spatial screen task (negatively), and coping score (positively). This indicates that a high success percentage over all memory tasks is associated with a small difference in success percentage between the object and spatial screen task. This is understandable, considering that on average dogs performed well in all tasks and a large difference between the object and spatial screen task would lower the average total success percentage. The interesting part here is that this is also associated with a higher coping score while earlier no significant correlation between coping score and the total success percentage was found.

Overall, the results suggest that paw preference strength is a possible indicator for dog temperament. Paw preference strength was associated with Trainability, Stranger-directed aggression and Separation anxiety and dogs with a higher paw preference strength are suggested to be more bold. Paw preference strength can easily be measured and used in selection programmes for potential guide dogs. No associations were found between coping score and paw preference on cognitive abilities as measured in a reversal learning and memory tasks.

Conclusions

This study aimed to investigate the effects of coping strategies and lateralization on cognition in dogs. Hundred dogs were tested with an equal distribution of male and female dogs. Coping scores were determined based on an owner-reported questionnaire after which paw preference was determined by a food retrieval task in the form of a dog puzzle. Cognitive abilities were tested in a reversal learning task in a T-maze and a memory test using spatial and object-specific cues. The study population showed equal distribution for both coping score and paw preference. First, the relationship between paw preference and coping score was examined. The direction preference in a T-maze was almost significantly associated with coping score; dogs that went right on the first trial were more proactive. Further, more left-pawed dogs had more contact with their owners and this was also found in more reactive dogs. These were the only indications that supported the hypothesis that proactive animals are more right-oriented and reactive animals are more left-oriented. However, coping score was not correlated to paw preference or paw preference strength. Paw preference strength was positively correlated with the CBARQ factors Trainability and Stranger-directed aggression and negatively with Separation anxiety. This suggests that the strength of lateralization is more important than the direction in relation to temperament as no associations were found between paw preference direction and CBARQ factors. Based on the correlations between paw preference strength and the CBARQ factors it is suggested that more strongly lateralized dogs are bolder because bolder animals are more internally driven as shown by the higher Stranger directed aggression and less externally driven as shown by the lower Separation anxiety. Also, bolder dogs are said to be better at learning tasks and this corresponds with the finding that higher lateralization is associated with higher Trainability.

No effects of coping score and paw preference were found on the cognitive abilities of the dogs. It was hypothesized that reactive dogs would perform better in a reversal learning and memory test. No significant differences were found in the performance of reactive and proactive dogs in both the reversal learning and the memory test. Similarly, no effect of paw preference or paw preference strength was found on the performance of the dogs in the reversal learning and memory test. It is concluded that coping strategy has no influence on cognitive functioning of the tested dogs during a reversal learning and memory test. Coping strategy is also not significantly correlated to paw preference or paw preference strength. However, paw preference strength is associated with temperament and further research should focus on the strength instead of the direction of lateralization. Possibly, paw preference strength predicts dogs' temperament and performances in different training tasks or programs.

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Appendix I – Questionnaire coping strategies

Reactiestijlen

Honden kunnen verschillend reageren op stressvolle situaties, dit worden reactiestijlen genoemd. Deze reacties kunnen worden ingedeeld in een vecht-vluchtreactie of een bevriesreactie. De volgende vragen zijn bedoeld om te onderzoeken welke strategie u hond het meest gebruikt.

Wilt u, door het aanklikken van een nummer op de onderstaande 5-puntsschaal, aangeven in hoeverre u hond de volgende gedragingen vertoont in bepaalde situaties (1 = nooit, 2 = zelden, 3 = soms, 4 = meestal, 5 = altijd).

In een nieuwe situatie (bv. binnenkomen van een nieuwe ruimte) zal mijn hond

zich hetzelfde gedragen als daarvoor (toont geen interesse) ☐1 ☐2 ☐3 ☐4 ☐5

blijven stilstaan zonder tekenen van angst ☐1 ☐2 ☐3 ☐4 ☐5

blijven stilstaan met tekenen van angst ☐1 ☐2 ☐3 ☐4 ☐5
(bv. lage staart, bevriezen)

(proberen) weg te lopen en tekenen van angst vertonen ☐1 ☐2 ☐3 ☐4 ☐5
(bv. lage staart, vluchten)

(proberen) weg te lopen en de omgeving te verkennen ☐1 ☐2 ☐3 ☐4 ☐5
(bv. door snuffelen)

In een dreigende situatie (bv. tegenkomen van een agressieve hond) zal mijn hond

zich hetzelfde gedragen als daarvoor (toont geen interesse) ☐1 ☐2 ☐3 ☐4 ☐5

blijven stilstaan zonder tekenen van angst ☐1 ☐2 ☐3 ☐4 ☐5

blijven stilstaan met tekenen van angst ☐1 ☐2 ☐3 ☐4 ☐5
(bv. lage staart, bevriezen)

(proberen) weg te lopen en tekenen van angst vertonen ☐1 ☐2 ☐3 ☐4 ☐5
(bv. lage staart, vluchten)

dreigen naar de bedreiging (bv. hond) of aanvallen ☐1 ☐2 ☐3 ☐4 ☐5
(bv. grommen, tanden ontbloten, happen)

Wilt u, door het aanklikken van een nummer op de onderstaande 5-puntsschaal, aangeven in hoeverre u het eens bent met de volgende stellingen over u hond (1 = heel erg mee oneens, 2 = mee oneens, 3 = neutraal, 4 = mee eens, 5 = heel erg mee eens).

Mijn hond is zelfverzekerd	☐1	☐2	☐3	☐4	☐5
Mijn hond vormt routines	☐1	☐2	☐3	☐4	☐5
Mijn hond is actief	☐1	☐2	☐3	☐4	☐5
Mijn hond is bezig met zijn omgeving	☐1	☐2	☐3	☐4	☐5
Mijn hond is speels	☐1	☐2	☐3	☐4	☐5
Mijn hond is sociaal	☐1	☐2	☐3	☐4	☐5
Mijn hond is nieuwsgierig	☐1	☐2	☐3	☐4	☐5

Appendix II – Ethogram dog behaviour memory tests

Behaviour	Description
Attention	
Task performance	Dog is focused on task e.g. by looking at, approaching or manipulating test-objects
Contact owner	Dog seeks contact with its owner e.g. by looking at or approaching owner
Contact experimenter	Dog seeks contact with experimenter e.g. by looking at or approaching experimenter
Explore environment	Dog explores environment other than test-objects, owner or experimenters
Do nothing	Dog stands still without performing any of the previously mentioned general behaviours
Ear position	
Ears high	Ears are pointed forward
Ears neutral	Ears are in natural position
Ears low	Ears are lower than in neutral position or in neck
Ears out of sight	Ears are out of sight of the camera
Tail position	
Tail high	Higher position of the tail than in 'neutral' or upright position of the tail
Tail neutral	Natural position of the tail according to breed standards (www.fci.be)
Tail low	Lower position of the tail than in 'neutral' or tail between hind legs
Tail out of sight	Tail is out of sight of the camera
Locomotion	
Moving (walking)	Walking at least one step with all four paws
Standing	All four paws on ground with legs upright and extended supporting the body, the dog may move two steps from its original position
Sitting	Hind quarters on ground and forelegs supporting the body
Lying	In ventral or lateral position, all four legs make contact with ground (belly on ground)

Panting	
Panting on	Breathing in high frequency, which is often accompanied by the protrusion of the tongue
Panting off	No panting
Mouth not visible	Mouth is out of sight of the camera
Tail wagging	
Wagging off	No tail wagging
Normal tail wag	Regular sideward movements of the tail
Stiff tail wag	Stiff movement of the tail, without excessive removal
Tail not visible	Tail is out of sight of the camera
Miscellaneous	
Freezing	General rigidity of the body without staring at the stimulus
Crouching	Rapid and pronounced lowering of posture without large movement. 1-2 steps from the stimulus, the dog completely withdraws its head and legs
Trembling	Shaking of all or part of body
Lifting lip/Baring teeth	Tension of the upper lip muscles, so it is lifted (teeth not shown) may be accompanied by wrinkle of the nose. Uncover the whole or part of the upper teeth, the corner of the mouth can be drawn back or shortened, it may be accompanied by wrinkle of the nose
Attack intention	Fast movement toward the stimulus with signs of aggression
Jumping owner	Jumping up at the owner
Press nose owner	Dog presses the owner using its nose
Sniffing	Sniffing the ground or stimulus within 3 cm
Tilting head	The head is directed towards the stimulus and is held bent
Paw lifting	Lifting one of the fore paws, the wrist is bent up at an angle of 45 degrees (not meant to stand for the hunting dogs)
Biting leash	The upper and lower teeth make physical contact, pressuring the leash
Piloerection	Erection of hairs, e.g. neck, shoulder, back, legs, and/or tail
Yawning	An involuntary intake of breath through a wide open mouth
Teeth clapping	Multiple, fast and continue movements, open and close of the jaws, may be accompanied by bare teeth
Scratching/grooming	With one of the rear legs the dog scrapes its own body (usually head and neck)
Shaking	Fast sideward movements with the body and/or head
Sneezing	An involuntary, sudden, intense, and audible expulsion of air through the mouth and nose

Stretching	Mechanical lengthening of the body, when it is at maximum length the forelegs are lowered it creates a hollow back (similar to play bow)
Playing bow	Characteristic form of challenging to play, the dog falls on its fore legs and the hind legs are kept high, is often accompanied by tail wagging and a relaxed open-mouth smile
Circling	Movement roughly in a circular pattern, returning to the same spot at least once
Oral behaviour	Behaviours as licking mouth (with the tongue on the upper lip, the dog moves the tongue to one of the corners of the mouth) and tongue flicking (briefly shows the tip of the tongue straight ahead towards the nose, possible even up to the nose)
Vocalization	
Repeat bark	Loud and regular barking
Bark	One single short bark
High barking	Low barking with a higher pitched intonation than normal barking (the vocal chords are pressed together due to stress)
High vocalization	Peeping, whining, yelling or howling
Intention bark	Low bark while the mouth is partly closed, it is less louder than normal barking
Growling	Low buzzing sound
Run	
Straight run	Dog runs in a straight line towards a cover, meaning that two legs are within the imaginary path at all times
Curved run	Dog runs in a curved line towards a cover, meaning that at least three legs are outside the imaginary path
Testphase	
Not observing	Not observing
Spatial no screen	Observing trials with spatial cues without screen
Spatial with screen	Observing trials with spatial cues with screen
Objects with screen	Observing trials with objective cues with screen
Trial	
Trial 1	First trial
Trial 2	Second trial
Trial 3	Third trial

Appendix III – Correlations coping score, paw preference, paw preference strength and all CBARQ factors

Spearman's rank correlation coefficient

Sample size 82
Degrees of freedom 80

Correlation matrix (adjusted for ties)

		1	2	3
PawPreference	1	1		
PawPreferenceStrenght	2	0.011	1	
ProactiveCopingScorePerc	3	0.122	0.021	1
TrainabilityPerc	4	-0.077	**0.225**	*0.207*
StrangerDirAggrPerc	5	0.145	*0.19*	-0.072
OwnerDirAggrPerc	6	0.048	0.028	0.1
DogDirAggrPerc	7	0.106	-0.014	0.063
NonSocialFearPerc	8	0.056	-0.056	-0.131
SocialFearPerc	9	-0.103	0.014	**-0.362**
PainSensitivityPerc	10	-0.066	-0.101	-0.064
DogDirFearPerc	11	0.038	-0.038	**-0.407**
SeparationAnxietyPerc	12	0.052	**-0.227**	0.034
ExcitabilityPerc	13	0.042	-0.081	-0.026
AttachmentPerc	14	-0.032	0.014	0.213
ChasePerc	15	0.118	-0.039	0.107
		1	2	3

Appendix IV – Chi-square test first blocked arm on first choice

		First Choice		
		Left	Right	Grand Total
First Blocked Arm	Left	30	17	47
	Right	27	15	42
	Grand Total	57	32	89

	Left	**Right**
Left	-0.02	0.02
Right	0.02	-0.03

Standardized Residuals of Matrix: Sheet3

Chi Square:	**0.002002**
Degrees of Freedom:	**1**
Likelihood Ratio Statistic G:	**0.002002**
Adjusted Likelihood Ratio Statistic Gadj:	**0.001965**

Appendix V – Principal component analysis including CBARQ factors

Percentage variation	16.73	12.58	12.29	9.17	8.68
Loadings :	ev1	ev2	ev3	ev4	ev5
PercSuccessTotal	0.152	0.0075	0.3909	0.1773	**-0.4449**
DiffObjectSpatial	0.0798	-0.139	-0.2724	-0.3362	0.1646
PawPreference	0.0455	-0.0331	0.0597	-0.2398	**0.4391**
PawPreferenceStrenght	0.0692	-0.039	0.2096	0.2936	**0.6147**
ProactiveCopingScorePerc	-0.3125	0.0389	**0.4754**	0.0197	0.0124
Errors	-0.0314	**0.6123**	-0.2332	0.062	0.0295
PercSuccessTraining	-0.0054	**0.6429**	-0.1632	0.0299	0.0032
TrainabilityPerc	0.2127	0.1662	0.2495	**0.4998**	0.0599
StrangerDirAggrPerc	0.3296	0.1377	0.3623	-0.1322	0.2802
OwnerDirAggrPerc	0.0463	0.0467	0.3579	-0.3412	-0.2257
DogDirAggrPerc	0.2304	0.2813	0.241	**-0.5477**	0.0284
NonSocialFearPerc	0.3861	-0.2417	-0.0861	-0.0293	-0.0289
SocialFearPerc	**0.5153**	-0.0353	-0.1372	0.1461	0.0617
DogDirFearPerc	**0.4912**	0.0261	-0.1123	0.0286	-0.2546

Appendix VI – Principal component analysis including all CBARQ factors

Percentage variation	14.94	11.79	9.44	8.32	6.5

Loadings :

	ev1	ev2	ev3	ev4	ev5
PercSuccessTotal	0.1469	0.0836	0.1242	0.2778	-0.2859
PercDiffObjectSpatial	0.1261	-0.1058	-0.1126	-0.1979	-0.071
PawPreference	0.056	0.0579	0.0299	-0.0484	**0.4934**
PawPreferenceStrenght	-0.0172	-0.0308	0.1439	**0.4446**	**0.4977**
ProactiveCopingScorePerc	-0.112	**0.4241**	0.0617	0.2807	-0.1741
Errors	-0.0392	-0.061	**-0.632**	0.0501	0.0155
PercSuccessTraining	-0.0161	-0.0629	**-0.6329**	0.1106	0.0091
TrainabilityPerc	0.1522	-0.0898	-0.0325	**0.5855**	-0.1917
StrangerDirAggrPerc	0.3374	0.0773	-0.0416	0.2168	0.3761
OwnerDirAggrPerc	0.1772	0.3017	0.0187	0.0303	-0.1639
DogDirAggrPerc	0.304	0.2245	-0.2401	-0.0087	0.2105
NonSocialFearPerc	0.3081	-0.181	0.2235	-0.1617	0.0836
SocialFearPerc	0.3674	-0.3683	0.0406	0.0444	0.0469
PainSensitivityPerc	0.346	-0.1636	0.0333	-0.0407	-0.2396
DogDirFearPerc	0.3472	-0.3087	-0.0122	0.0291	-0.1431
SeparationAnxietyPerc	0.2554	0.2082	-0.1302	-0.1965	-0.1296
ExcitabilityPerc	0.2782	0.3475	-0.0854	-0.1505	0.043
AttachmentPerc	0.2262	0.3306	0.0576	0.155	-0.1275
ChasePerc	0.1413	0.2657	0.0726	-0.2887	0.1417