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

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

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

the age groups were detected, however. Dogs in group B chose S' in significantly more test trials than dogs in group A (Table 4, Fig. 6a). Male dogs showed a tendency to choose S' more often than females (males, $N = 30$, 0.69 ± 0.02, females, $N = 52$, 0.65 ± 0.01; Table 4). Dogs chose S' more often in cycle 1 compared to cycle 2 (Table 4, Fig. 6b). When results from cycles 1 and 2 were pooled, 42 (51 %) dogs preferred S' (choose S' in 22 or more test trials out of a total of 32) and thus chose based on exclusion (rejection of S− due to its association with the negative class), novelty (selection of S' due to neophilia) or avoidance of the known negative stimulus (S−) and proceeded to test 2 (apart from one dog which left the study at this stage). The remaining dogs chose at chance level, apart from one individual, which chose based on familiarity.

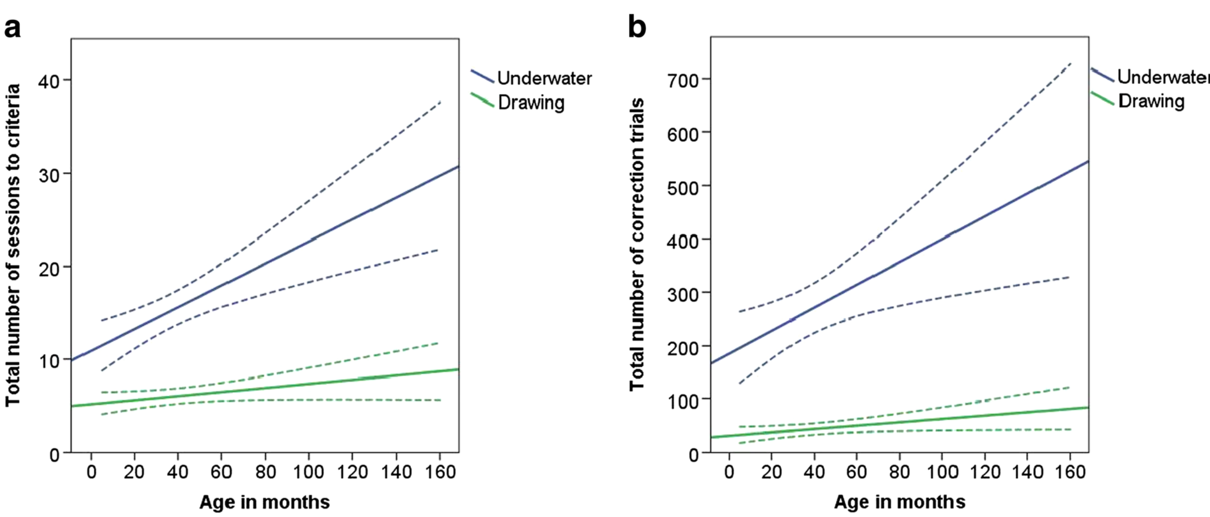

Fig. 4 *Line graph* showing the linear relationship between age in months and **a** number of sessions to criterion and **b** number of correction trials, shown separately for dogs that were rewarded for choosing the underwater pictures and for dogs rewarded for choosing the drawings (with 95 % confidence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

Table 3 Negative binomial generalised linear models showing the direction of effects and the significance level of the terms in the clip art picture discrimination (training for task 3: inferential reasoning by exclusion)

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

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

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

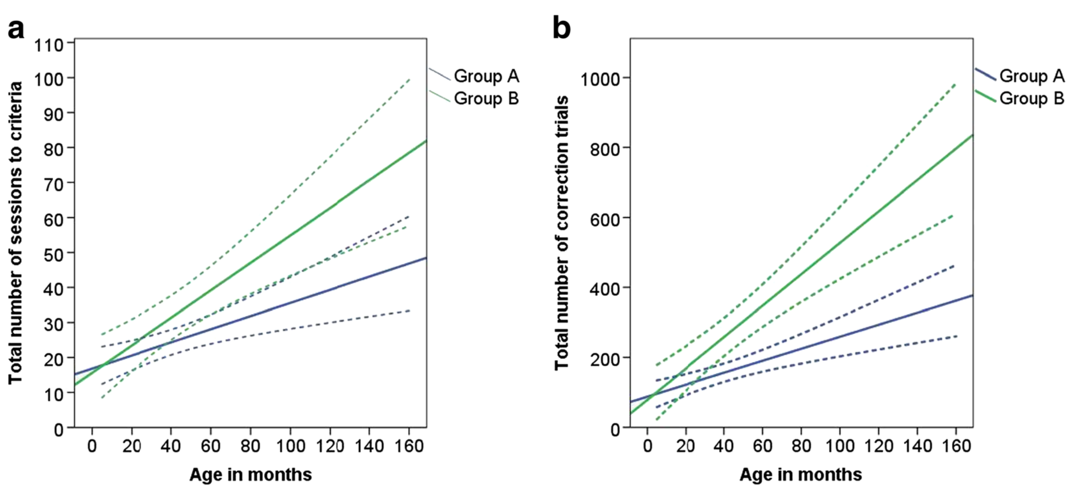

Fig. 5 *Line graph* showing the linear relationship between age in months and **a** number of sessions to criterion and **b** number of correction trials, separately for groups A and B (with 95 % confidence intervals (*dotted lines*))

Table 4 Generalised linear mixed model on the proportion of trials chose S' when paired with a known negative (S−) in test 1 of the inference by exclusion task, showing the direction of effects and the significance level of the terms

Response variable	Model	Minimal model	Average effect	SE	Wald statistic /deviance	*p* value
Proportion of trials chose S'	Model 9	Cycle: cycle 2	−0.4943	0.0839	34.723	**<0.001**
		Stimulus: group B	0.3478	0.1007	11.136	**<0.001**
		Age in months	0.0037	0.0014	6.567	**0.010**
		Sex: male	0.1919	0.0988	3.693	0.055

Bold numbers indicate significant values at $p = \leq 0.05$

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

Task 4: memory test

Of the 82 dogs which completed the final learning criterion of the inference training, 46 participated in the memory test after a break of at least 6 months. Forty-two of these dogs scored significantly above chance level in the first session (22 or more out of the possible 32 first correct choices (binomial test 22/32 = 0.6875, chance level = 0.5, $p = 0.050$; 81.52 ± 10.10 %). There were no significant effects of age or stimulus group on the proportion of correct first choices in the first session of the memory test (Supplementary Table S6).

Discussion

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

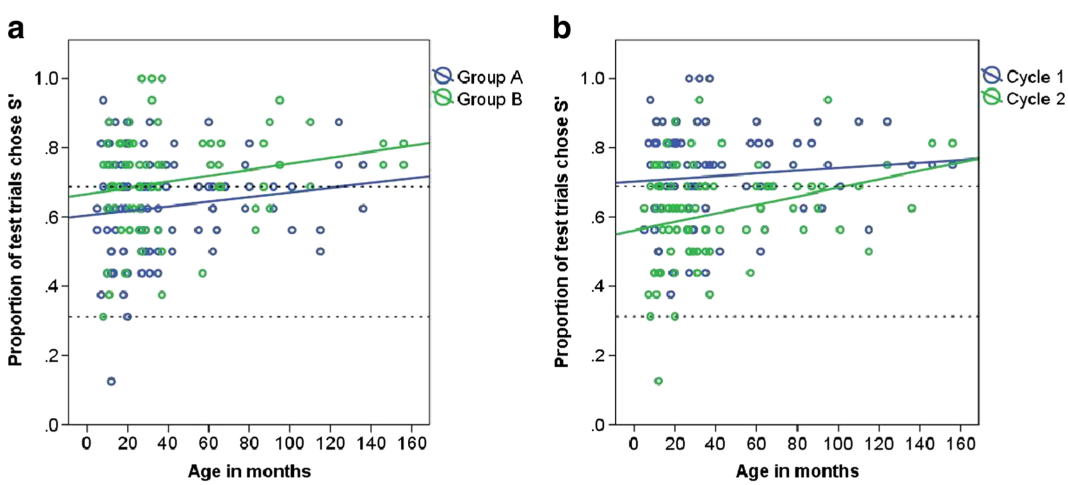

Fig. 6 The proportion of test trials in test 1 in which the dog chose S'; **a** group A and group B, and **b** cycle 1 (sessions 1 to 4) and cycle 2 (sessions 5 to 8), and age in months. The *upper dashed line* indicates the levels of performance beyond which preference for S' was inferred (68.75 %;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

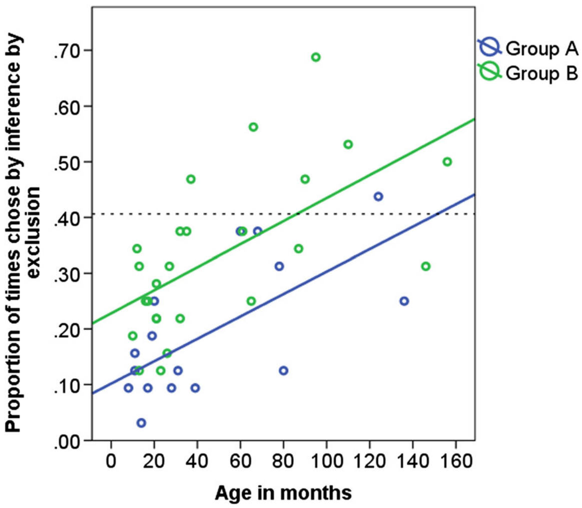

Fig. 7 The proportion of times in which the dog chose based on inference by exclusion in group A and group B and age in months in test 2 (cycles 1 and 2 pooled). The *dashed line* indicates the levels of performance beyond which preference for S' was inferred (40.625 %; reasoning by exclusion)

any of the age groups after a 6-month break from the touchscreen.

The ability to learn new visual stimulus associations decreased with age as predicted. The youngest dogs aged from 5 months to 1 year needed the lowest number of sessions to complete the criteria, indicating that this age group was already performing at peak performance, and from this age onward, dogs' learning abilities began to decline. In contrast to the present study, previous studies in non-human animals have found no effect of aging on associative learning in simple object discrimination tasks either in the rhesus macaque (aged from 3 to 34 years; Bachevalier et al. 1991) or in laboratory dogs (aged from 1.5 to 11 years; Milgram et al. 1994). One possible reason for this discrepancy is that, by utilising a higher number of stimuli to be discriminated, we sufficiently increased the difficulty level and thus facilitated the appearance of age effects. This interpretation is also supported by the difference we find between the two stimuli groups both in the drawing and underwater photo discrimination and in the clip art discrimination: If the discrimination seems to be easier for the dogs ('drawing'; group B), the age differences, although still apparent, are not as pronounced as in the more difficult groups ('underwater'; group A). However, although age effects were more apparent in the groups with the less preferred stimuli as positive (that is, in the more difficult version of each task), we found no evidence for an interaction between age and stimulus group in any of the discrimination tasks. For a discussion of stimulus preferences in two choice discriminations, please refer to the Supplementary Materials: Stimulus preferences.

Age differences were more pronounced in the clip art picture discrimination than in the drawing and underwater photo discrimination. This difference in effect size may be explained firstly in terms of the number of stimuli to be discriminated (six in the drawing and underwater discrimination and eight in the picture discrimination) and additionally by the fact that the drawing discrimination could be solved more easily by

Table 5 Generalised linear model on the proportion of times the dogs' chose S' when paired with the known negative (test 1 refresher) and also chose S' in the subsequent trial when S' was paired with the novel S" (test 2 trial) in the inference by exclusion task, showing the direction of effects and the significance level of the terms

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

Z tests indicate which age groups differ from age group 1 in the respective analysis. Age in months was included in models 12 and 13 to control for age effects. Bold numbers indicate significant values at $p = \leq 0.05$

learning a perceptual discrimination rule. All the drawings looked perceptually similar to each other, as did the underwater photographs, but the clip art picture discrimination required that all the stimuli be encoded into memory individually, as there were no perceptual commonalities in the positive or the negative stimuli. Our results are in line with the findings from human studies; age effects can be better detected by more complex tasks (Alvarez and Emory 2006; Mell et al. 2005).

The poorer performance of dogs aged over 3 years in our study could be explained by several possibilities. First, older dogs may suffer from attentional deficits due to reduced processing resources (Snigdha et al. 2012). Additionally, older dogs may use ineffectual strategies in an attempt to solve the discriminations, for example, a stimulus response strategy (such as stimulus preferences or avoidance, as seen when dogs repeatedly make incorrect choices) and/or a positional strategy (side bias), before finally switching to a cognitive strategy. Both stimulus response and positional strategies require less working memory and are therefore less costly than a cognitive strategy (Chan et al. 2002). Unfortunately, we were unable to analyse positional strategies due to limitations in the software program.

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

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

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

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

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

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

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

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

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