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Age-associated cognitive deficits in humans and dogs: A comparative neuropsychological approach

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Abstract

We compared performance of younger and older human participants to that of younger and older dogs on tasks that evaluate object discrimination, egocentric spatial ability, object recognition, spatial memory, and cognitive flexibility. Our goal was to determine whether (i) tasks sensitive to advanced age in dogs are also age-sensitive in humans; (ii) the pattern of task difficulty observed in dogs mirrors that observed in humans; (iii) dogs and humans use similar strategies to solve equivalent tasks. Dogs performed more poorly than humans on reversal tasks that evaluate cognitive flexibility. We suggest that dogs, most notably older dogs, use different strategies than healthy humans when solving these tasks. Humans appear to test a priori hypotheses to solve the task at hand. As a consequence, expectations about the complexity of the task being tested can impair human performance. By contrast, dogs appear to rely more heavily on either simpler hypotheses, or associative trial and error learning, which probably accounts for their difficulty in learning non-matching tasks. Dogs also show perseverative responding, which hinders the acquisition of reversal tasks.

Keywords: Aging; Delayed non-matching; Discrimination; Reversal; Species differences

1. Introduction

Human aging is associated with significant changes in cognitive functions, including impairments in the ability to remember specific events (Levine et al., 2002; Spencer and Raz, 1995), to acquire new information (Small et al., 1999), and to deploy executive functions (Albert, 1993). Investigating the relationship between neural changes and behavioral impairments in humans is limited by the inability to collect combined behavioral and anatomical data within a short period of time. To overcome this limitation, researchers are increasingly relying on animal models. These models have been particularly valuable for studying the relationship between neural changes and age-associated behavioral impairments as well as for exploring interventions that can arrest these impairments. However, results obtained using animals cannot always be extended to humans because the tasks employed differ in their ability to evaluate cognitive functions such as perceptual discrimination, storage, retrieval, and cognitive flexibility.

A recent line of research, termed comparative neuropsychology, uses a modified version of the Wisconsin General Test Apparatus (WGTA) developed for use with

Abbreviations: DNMP, delayed non-matching to position; DNMS, delayed non-matching to sample; EDL, egocentric discrimination learning; EDR, egocentric discrimination reversal; M, mean; MMSE, mini-mental status examination; OA, older adults; ODL, object discrimination learning; ODR, object discrimination reversal; SE, standard error; SD, standard deviation; WGTA, Wisconsin General Test Apparatus; YA, younger adults.

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primates to evaluate cognition in humans (Freedman and Oscar-Berman, 1986, 1987, 1989; Oscar-Berman and Zola-Morgan, 1980). This approach allows researchers to compare humans and animals on the same tasks. Because the tasks are non-verbal, individuals with severely limited cognitive abilities can be evaluated. Moreover, researchers can make inferences about neuropathology because the neural substrates underlying the ability to perform these tasks have been delineated. Animal-based tasks have been successfully employed in a variety of populations including infants (Overman, 1990; Overman et al., 1992, 1993, 1996) and patients with Down syndrome (Nelson et al., unpublished data), Alzheimer disease (Irle et al., 1987), Parkinson disease (Freedman and Oscar-Berman, 1986, 1987, 1989; Sahakian et al., 1988), and Korsakoff syndrome (Oscar-Berman and Zola-Morgan, 1980). However, animal models do not always display the same behavioral impairments on a given task as humans with comparable brain damage (Kessler et al., 1986), suggesting that different psychological constructs may be triggered when animals and humans perform these tasks.

In the present study, we obtained data from a sample of younger and older human participants on tasks for which data had previously been collected with dogs. Our goals were threefold. First, we compared the effect of age in humans on tasks that are sensitive to advanced age in dogs. In particular, older dogs have been shown to have more difficulties than younger dogs in tasks that evaluate object recognition (Milgram et al., 1994) and spatial memory (Head et al., 1995; Adams et al., 2000a). There is also some evidence that older dogs need more trials to acquire reversed stimulus–reward associations than the original association (Milgram et al., 1994; Tapp et al., 2003). Second, we examined whether the pattern of task difficulty found in dogs is comparable to humans. Previous research has shown that in dogs, more extensive training is required to acquire memory tasks that involve delayed responses and reversal tasks that involve switching a previously learned stimulus–reward contingency than simple discrimination tasks (Adams et al., 2000a; Milgram et al., 1994). Finally, we examined whether dogs and humans employ similar strategies when solving equivalent tasks. In dogs, aging seems to affect the type of strategy employed to solve discrimination learning and reversal tasks with older dogs relying more heavily on associative learning than younger dogs, and younger dogs relying more heavily on concept learning than older dogs (Milgram, 2004; Tapp et al., 2003).

2. Method

2.1. Human participants

Seventeen older adults (11 females, 6 males) and 30 younger adults (22 females, 8 males) were tested in this study. All participants provided informed consent. Older adults had a mean age of 73 years (range 58 to 83). They were recruited from a registry of volunteers at the Baycrest Centre for Geriatric Care, Toronto, Canada. Participants suffering from mood disorders, psychosis, obsessive compulsive disorder, panic disorder, severe systemic disease, poor vision or hearing, inadequate English, or neurological disorders were excluded. The Mini-Mental State Examination (MMSE) was used to provide an independent measure of cognitive status. One older male participant obtained a score of 24 on the MMSE. Considering that this participant displayed motivational problems throughout the study, we felt that this low score was not indicative of a cognitive deficit and excluded the data from the analysis.

Younger adults had a mean age of 21 (range 19 to 24). They were recruited from the student population at the University of Toronto at Scarborough. All younger participants obtained a score of 27 or more on the MMSE (M: 29.34; SD: 0.86) except for one participant who obtained 26, which is the cut-off score for mild cognitive impairment in older adults. We consequently excluded this participant's data from the analyses.

2.2. Apparatus

Human participants were tested using a modified version of the WGTA similar to the apparatus devised by Oscar-Berman and Zola-Morgan (1980) (Fig. 1). The apparatus consists of a vertical panel and a horizontal box with a sliding tray. The tray contains three reinforcement wells. The bottom of the vertical panel consists of hinged door that can be opened and closed to allow the investigator to move the tray towards and away from the participant. When the door is closed, the participant cannot see the tray or the investigator. The vertical panel has a one-way mirror

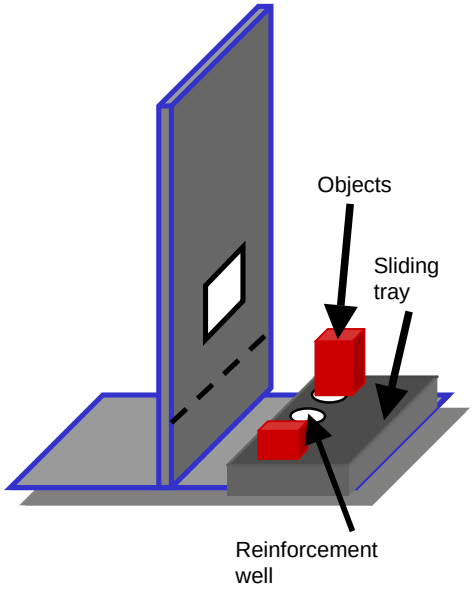

Fig. 1. A schematic illustration of the apparatus used in this study.

window that allows the investigator to see the participant and that can be opened to allow the investigator and participant to communicate. The apparatus was placed on a table and the investigator and the participant sat on each side of the apparatus. All objects were glued on white coasters that fitted tightly over the well to ensure that the well was not uncovered when the tray was moved.

2.3. Procedure

Participants were asked some general questions about their health and administered the MMSE prior to starting the experiment. Participants were then read the following instructions:

"This is a game and your job is to find a nickel hidden under an object. I am going to show you one or two objects. If I show you one object, simply pick the nickel under it. If I show you two objects, there is a nickel under only one of them. I want you to try to get the nickel every time the tray is presented to you. All right. Remember, your task is to get the nickel every time the tray is presented. Any questions?"

Participants were told "Remember, you want to get a nickel every time" prior to beginning each task and they were provided with positive verbal reinforcement such as "That's great" or "Good job" on every successful trial. Participants were tested on a given task until they obtained 9 correct answers in a block of 10 trials (criterion) or until a maximum of 50 trials were administered. Participants were tested on the following six tasks.

2.3.1. Object discrimination learning (ODL)

During ODL, participants were presented with two different objects, one of which was deemed positive and associated with the reward. The two objects consisted of a stack of three Lego blocks arranged in similar configurations that differed with respect to height and block orientation. On the first trial, no object was rewarded and participants were free to choose their preferred object. For the remaining trials, the nickel was always placed under their initially non-preferred object. Participants were tested until they either achieved the learning criterion or until a total of 50 trials were administered.

This task evaluates the ability to form an association between a stimulus and a reward as well as the ability to discriminate between two objects on the basis of visual attributes.

2.3.2. Object discrimination reversal (ODR)

Participants who achieved criterion on the ODL were immediately tested on an ODR. For the ODR, the same two objects were used but the reward contingencies were reversed. Otherwise, the procedure was identical to ODL.

Because ODR requires inhibiting a previously learned association and shifting to a new strategy, it is considered a measure of executive function or cognitive flexibility (e.g., Lai et al., 1995).

2.3.3. Egocentric discrimination learning (EDL)

Participants were repeatedly shown two identical red Lego blocks covering all combinations of two of the three wells. The rewarded spatial location was determined by reference to the participant's body position, or according to an egocentric frame of reference. Participants were rewarded for selecting the object closest to the right side of their body, or the object closest to the left side of their body. If the rule was to select the object closest to the right side of the body, a nickel was placed under the rightmost object on the tray (e.g., nickel under the center well and no nickel under the left well). On the first trial, no well was reinforced and participants were free to choose their preferred side. For the remaining trials, the nickel was always placed in the well corresponding to the non-preferred side. Participants were tested until they either passed criterion or had completed a maximum of 50 trials.

2.3.4. Egocentric discrimination reversal (EDR)

Participants who achieved criterion on the EDL were next tested on an EDR task. For the EDR, the reward contingency was reversed so that the rewarded spatial location was switched from left to right or vice versa. Otherwise, the procedure was identical to EDL.

EDL and EDR are comparable to the ODL and ODR tasks except that a rule based on visuo-spatial egocentric coordinates had to be employed to solve the EDL and EDR tasks.

2.3.5. Delayed-non-matching-to-sample (DNMS)

For the DNMS task, participants were presented with a sample object in the center well. This object was removed and following a 20-s delay, participants were presented with the sample object plus a novel object, one over the right well and one over the left well. The sample and new object were randomly chosen from a pool of 100 common household items. Participants were tested until they either passed criterion or had completed a maximum of 50 trials.

The DNMS task was used to evaluate object recognition. Moreover, correct performance on the DNMS required the acquisition of the abstract rule of 'novelty,' that is to pick an object that *does not match* the sample (Irle et al., 1987; Overman, 1990).

2.3.6. Delayed-non-matching-to-position (DNMP)

The DNMP task is similar to the DNMS task in that it too involves a non-matching strategy. It differs from the DNMS in that the successful strategy for solving the task is based on a spatial location rather than an object identity. The same red Lego blocks as those used for the EDL and EDR tasks were used for the DNMP. One object was presented over one of the wells. The tray was subsequently removed and after a 20-s delay, two objects were shown, one over at the

same well and one over a new well. The object presented at the new well was rewarded. Participants were tested until they either passed criterion or had completed a maximum of 50 trials.

The DNMP task serves as a spatial counterpart to the DNMS. It is used to evaluate spatial memory as well as the acquisition of a novelty rule.

For all tasks, object position was determined using a semi-random sequence in which all thee well positions occurred equally often over a 50 trial sequence. All participants were first tested on the ODL and ODR, half of the participants were then tested on the DNMS and then on the DNMP, followed by DNMS and DNMP in counterbalanced order. The EDL and EDR tasks were administered last. Younger and older adults were tested in one continuous session with a break between the two delayed non-matching tasks. Testing lasted approximately one hour and a half.

2.4. Canines

Methodological details for the canine work have been previously published (DNMP task: Chan et al., 2002; ODL, ODR, and DNMS tasks: Milgram et al., 1994; EDL and EDR: Christie et al., in press). The following methodological differences between dogs and humans are worth noting. First, for the ODL and ODR tasks, dogs were tested with only two wells. Second, dogs were tested on multiple daily sessions of 10 (ODL, ODR, and DNMS) or 12 (EDL, EDR, and DNMP) trials. Third, different criteria for determining successful acquisition of the tasks were used in dogs. For the ODL, ODR, and DNMS tasks, dogs were tested until one of two criteria was met: 9/10 correct responses on one session or 8/10 correct on two consecutive sessions. Dogs were tested for a maximum of 40 sessions. For the EDL and EDR tasks, dogs were tested until they obtained 90% correct over three consecutive sessions to a maximum of 25 sessions. For the DNMP task, dogs were tested until they obtained 11/12 correct responses on one session, or 10/12 correct responses on two consecutive sessions, or a cumulative score of 26/36 in three sessions. They then had to respond with an accuracy of at least 70% over the next three sessions. Dogs were tested on a maximum of 50 sessions. Finally, the delay used in the DNMS and DNMP tasks was 10 s.

2.5. Statistical analysis

Percent errors and number of trials necessary to reach criterion or end the task were recorded. All statistical analyses reported pertain to the data collected with the younger adults and older adults. Considering that the dog data were previously published, we retrieved the relevant results and graphed them in the same format as the human data to facilitate a qualitative comparison.

3. Results

3.1. Age effects: comparison between dogs and humans

Fig. 2 illustrates number of trials and number of errors to learn the visuo-perceptual task (ODL, ODR, and DNMS) as a function of subgroup for both humans and dogs. Fig. 3 illustrates the same results but for the visuo-spatial tasks

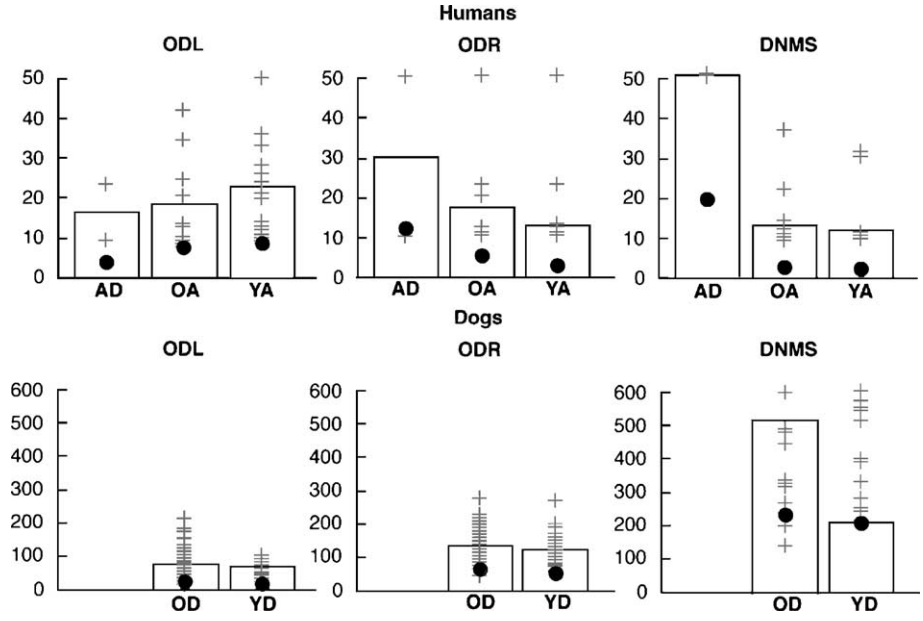

Fig. 2. Mean trials (bars) and errors (●) to learn the three visuo-perceptual tasks for humans and dogs as a function of age. Gray crosses represent individual trial scores. ODL—object discrimination learning; ODR—object discrimination reversal; DNMS—delayed non-matching to sample; OA—older adults; YA—younger adults; OD—older dogs; YD—younger dogs.

(EDL, EDR, and DNMP). For the humans, there were no statistically significant differences in performance between old and young on any of the tasks but there was considerable variability in the data as illustrated in Figs. 2 and 3.

Human data were analyzed quantitatively using a 2×6 mixed-design ANOVA with Group (older adults, younger adults) as the independent-group variable and Task (ODL, ODR, EDL, EDR, DNMS, and DNMP) as the repeated-measures variable. For percent errors, there was a significant main effect of Task [$F(5,185)=4.39$, $p<0.01$]. The main effect of Group was not significant [$F(1,37)<1$], nor was the Group×Task interaction [$F(5,185)<1$].

For number of trials, the main effect of Group was not significant [$F(1,37)<1$]. The main effect of Task was significant [$F(5,185)=2.57$, $p=0.03$]. The Group×Task interaction was marginally significant [$F(5,185)$, $N=2.11$, $p=0.07$]. The significant Group×Task interaction was further examined using multiple t-tests with a Bonferroni corrected alpha level to compare younger and older adults for each task tested. Only the comparison for the DNMP task was marginally significant ($t(44)=1.74$, $p=0.09$]. Surprisingly, younger adults performed more poorly than older adults on this task with two younger adults never passing criterion. This result is responsible for the interaction effect we obtained as older adults tended to perform more poorly than younger adults on the other tasks.

The significant main effects of task obtained with percent errors and number of trials were further examined using paired t-tests with a Bonferroni corrected alpha level. For percent errors, performance on the DNMS was significantly better than on the ODL [$t(45)=5.26$, $p<0.003$], EDL [$t(45)=3.06$, $p<0.003$], EDR [$t(43)=3.18$, $p=0.003$], and DNMP [$t(45)=3.79$, $p<0.003$]. None of the other comparisons were significant. A similar pattern of results was obtained with number of trials. Performance on the DNMS was significantly better than on the ODL [$t(45)=4.92$, $p<0.003$], EDL [$t(45)=3.50$, $p<0.003$], and DNMP [$t(45)=3.30$, $p=0.003$].

The canine data are presented for comparative purposes. Note in Figs. 2 and 3 that differences between older dogs and younger dogs were generally more pronounced than differences between older adults and younger adults, and as we have previously reported, significant age differences were found on the ODR (Milgram et al., 1994; Tapp et al., 2003), EDR (Christie et al., in press), DNMS (Milgram et al., 1994), and DNMP (Head et al., 1995; Adams et al., 2000a) tasks.

3.2. Task difficulty

Figs. 2 and 3 further reveals differences between dogs and humans with respect to the relative difficulty of the various tasks. First, dogs had more difficulties on reversal learning than on original learning, as indicated by differences between ODR and ODL as well as between EDR and EDL. Opposite results were found in humans who performed better in the ODR than the ODL as well as in the EDR than in the EDL. Second, humans performed better on the visuo-perceptual tasks (ODL, ODR, DNMS) than on visuo-spatial tasks (EDL, EDR, DNMP), while dogs showed an opposite pattern of results. This difference was particularly pronounced in the EDL where 3% of the younger adults and 6% of the older adults failed to learn the task within the 50 trials administered. By contrast, all of the

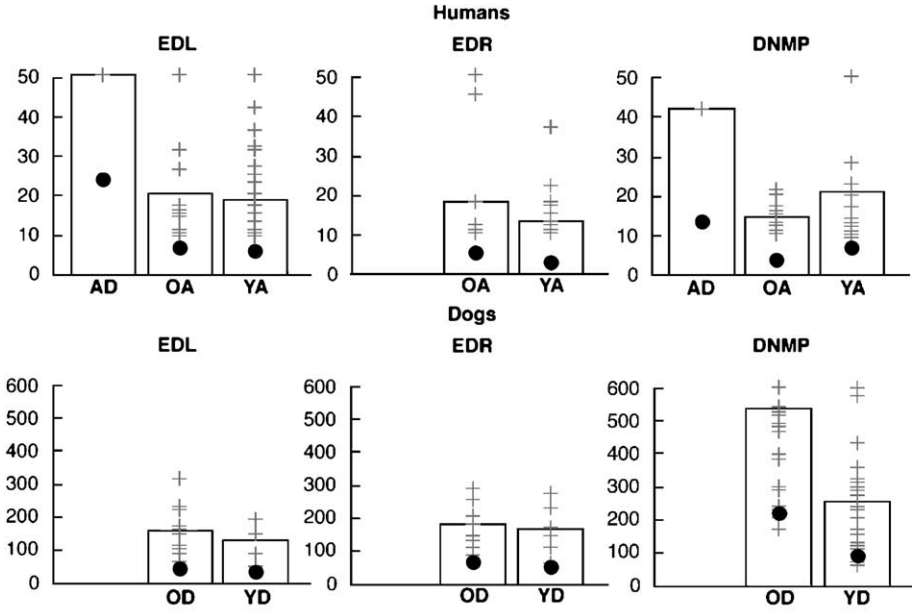

Fig. 3. Mean trials (bars) and errors (●) to learn the three visuo-spatial tasks for humans and dogs as a function of age. Gray crosses represent individual trial scores. EDL—egocentric discrimination learning; EDR—egocentric discrimination reversal; DNMP—delayed non-matching to position; OA—older adults; YA—younger adults; OD—older dogs; YD—younger dogs.

Table 1
Percentage of dogs and humans who failed to pass criterion on the different tasks tested

	Dogs		Humans	
	Younger	Older	Younger	Older
ODL	0	0	14	12
ODR	0	0	4	13
EDL	0	0	3	6
EDR	0	0	0	6
DNMS	47	74	0	0
DNMP	0	69	21	6

ODL—object discrimination learning; ODR—object discrimination reversal; EDL—egocentric discrimination learning; EDR—egocentric discrimination reversal; DNMS—delayed non matching to sample; DNMP—delayed non matching to position.

dogs tested reached criterion in less than 30 sessions (i.e., 360 trials). The DNMP task also proved to be relatively more difficult for humans than for dogs in the younger groups where 21% of the younger adults vs. 0% of the younger dogs failed to reach criterion (Table 1). Third, dogs had greater difficulty than humans on both delayed non-matching tasks with several older dogs failing to pass criterion on both tasks despite the use of a shorter delay than in humans and a much larger number of trials. Finally, more human participants failed to reach criterion on the object and egocentric discrimination and reversal tasks than dogs despite the relatively simple nature of these tasks.

3.3. Stage analysis

We characterized the pattern of errors in the object and egocentric discrimination reversal tasks according to the three stages described by Jones and Mishkin (1972). The trials required to learn each reversal task were divided into blocks of ten trials. We defined Stage I as the occurrence of seven or more errors in a block of ten trials. This provided a measure of perseverative responding or in other words an inability to inhibit responses to a previously reinforced stimulus. Stage II represented chance performance with four to six errors in a block of ten trials. Stage III was characterized as an above chance level of performance with zero to three errors occurring in a block of ten trials. Fig. 4 illustrates the percent number of errors for each stage for the younger and older adults. As can be seen in Fig. 4, above chance performance dominated learning in the reversal tasks for both groups.

A 2×3 mixed-design ANOVA with Group (younger adults, older adults) and Stage (I, II, III) was performed on the ODR and EDR data separately. For the ODR task, the main effect of Group was not significant [$F(1,39)<1$], nor was the Group×Stage interaction [$F(1,78)=1.37$, $p=0.26$]. The main effect of Stage was significant [$F(2,78)=105.11$, $p<0.01$] with Stage III errors occurring more often than either Stage II or Stage I errors.

For the EDR task, the main effect of Group was not significant [$F(1,41)<1$], nor was the Group×Stage interaction [$F(1,82)<1$]. The main effect of Stage was significant [$F(2,82)=55.25$, $p<0.01$] with Stage III errors occurring more often than either Stage II or Stage I errors.

3.4. Transfer effects

We also examined whether experience learning one non-matching task improved performance on the subsequently tested non-matching task. A 2×2 mixed-design ANOVA with Task (DNMS, DNMP) as the repeated-measures variable and Order (DNMS first, DNMP first) as the independent-groups variable was performed. For percent errors, the main effects of Task was significant [$F(1,43)=14.28$, $p<0.01$] with performance on the DNMS task being better overall than performance on the DNMP task. None of the other effects were significant. For number of trials, the main effect of Task was significant [$F(1,43)=8.85$, $p=0.01$] with fewer trials being required to

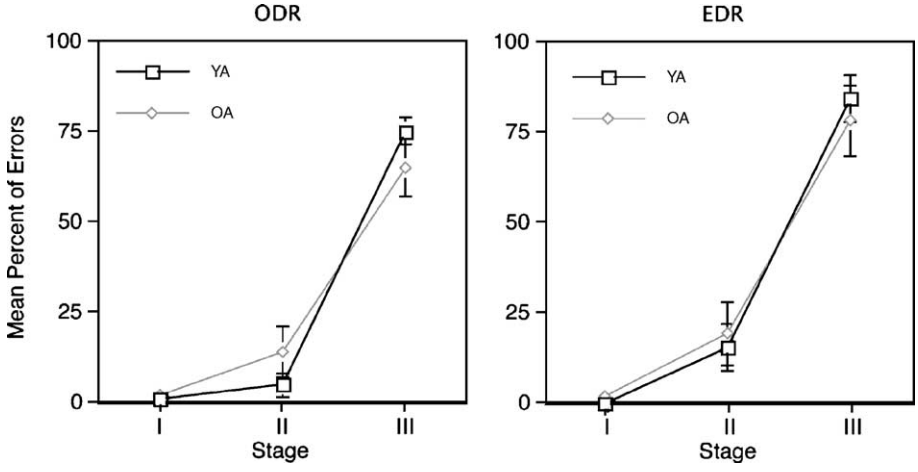

Fig. 4. Mean percent errors for older adults (OA) and younger adults (YA) for three different stages in the acquisition of the object discrimination reversal (ODR) and egocentric discrimination reversal (EDR) tasks. Stage I represents perseverative errors; Stage II is a chance performance; Stage II is above chance performance. Error bars represent ±1 S.E.

learn the DNMS task as compared to the DNMP task. None of the other effects were significant.

Although the effect of practice was not significant, inspection of individual data suggests that training on the DNMP improved performance on the DNMS. For example, 71% of the participants who had previously been tested in the DNMP solved the DNMS with one error or less. However, the transfer effect was much less pronounced for the DNMP as only 32% of the participants who had previously been tested in the DNMS solved the DNMP with one error or less. This finding further highlights the difficult nature of the DNMP task in humans. Practice effects were not observed in dogs that were trained on the DNMS immediately after being trained on the DNMP task or vice versa.

4. Discussion

This study compared the performance of dogs and humans on a battery of comparable tasks that evaluated visual discrimination learning, reversal learning, egocentric spatial abilities, spatial memory, object recognition, and cognitive flexibility. Our goal was threefold: (1) to examine whether tasks that show age effects in dogs are also sensitive to aging in humans, (2) to determine whether the pattern of task difficulty observed in dogs mirrors that observed in humans, and (3) to compare strategies used by dogs and humans to solve these tasks.

As previously reported, dogs showed significant age-dependent deficits on the object reversal learning (Milgram et al., 1994; Tapp et al., 2003), egocentric reversal learning (Christie et al., in press), DNMS (Callahan et al., 2000; Milgram et al., 1994), and DNMP (Adams et al., 2000a) tasks. None of these tasks revealed significant age-associated impairments in humans. The discrepancy between the ability of these tasks to pick-up age differences in dogs but not in humans may be attributable to a number of factors. First, the tasks may have been too easy to reveal normal age differences in humans. For example, the ODR task was learned with a single error in 65% of the participants tested, providing an obvious ceiling effect. Nonetheless, tendencies for older adults to perform more poorly than younger adults were observed in the EDL and EDR tasks. Considering that these tasks were the most difficult in the set, we predict that these tasks would be sufficiently sensitive to detect age differences if task difficulty was increased. Possible ways to achieve this goal include adding an extra well, repeating the object presentations in the DNMS task, and using a list learning paradigm to increase the memory load of the delayed tasks.

Second, the younger adults' data were quite variable, with some of them performing as poorly as the most impaired older adults. The variability in the younger adults may reflect more heterogeneity in their expectations about the task at hand. As discussed below, we believe that expectations about task complexity can significantly influence performance in these tasks. Another possibility is that low levels of motivation influenced the performance of younger adults. Indeed, it is our experience that motivation is generally higher in older adults than in younger adults. Consistent with this interpretation is the finding that some younger adults obtained lower than expected scores on the MSSE, with six out of 30 individuals obtaining a score of 28 or lower. However, low MMSE scores were not associated with poor performance on the experimental tasks. Whereas it is difficult to determine what role motivation may have played in the results we obtained, it is likely an important factor that warrants further consideration.

Finally, differences in sampling procedures may also account for the finding that age effects were more pronounced in dogs than in humans. Our sample of older adults was selected to be representative of normative aging and all participants were of good health and cognitive status as determined by the MMSE and a screening questionnaire. The canine data, by contrast, were based on the entire population of dogs tested, which includes successful agers, dogs showing restricted cognitive impairments, and dogs showing more general and severe impairments or dementia (Adams et al., 2000b). This inconsistency highlights the difficulties inherent in comparing age effects in animals and humans. A future avenue of research currently being pursued in our laboratory focuses on developing standard behavioural or physiological screening measures to dissociate healthy from pathological aging in dogs.

Dogs and humans also differed in the relative difficulty experienced in acquiring the various tasks. Overall, dogs had more difficulty solving visuo-perceptual tasks than visuo-spatial tasks, with the reverse being true for humans. For example, the DNMS task was the easiest task for humans to acquire; but the most difficult task for dogs. Dogs may perform better on visuo-spatial tasks that do not require high spatial resolution, because performance on these tasks is not dependent on good visual acuity (Miller and Murphy, 1995). In contrast, the human visual system is wired to analyze fine details and can easily discriminate between visually similar objects.

The ease with which humans learned the reversal tasks was striking when contrasted with the difficulties experienced by dogs on the same tasks. Whereas dogs had more difficulty learning the reversal tasks than the original discrimination tasks, the reverse was true in humans who performed at ceiling in the reversal tasks. Previous studies that have employed similar tasks with normal older adults as well as patients suffering form various forms of dementia (Freedman and Oscar-Berman, 1989; Oscar-Berman and Zola-Morgan, 1980) have reported similar results with fewer errors being made on visual and spatial reversal tasks than original learning. Furthermore, like dogs, monkeys have more difficulties acquiring reversal tasks than original learning tasks (e.g., Lai et al., 1995; Rapp, 1990; Voytko, 1999).

One possible interpretation for the difference between the ability to acquire reversal tasks in animals and humans is

that they employ different strategies to solve tasks in the WGTA. According to Levine (1971), humans and animals possess both associative and cognitive systems for processing information and depending on the situation, one system can dominate responding to the exclusion of the other. It may be that humans rely more heavily on cognitive strategies than on associative strategies. As such, humans may formulate a priori hypotheses to solve the rule governing the task at hand. Once they become aware of the relevant stimulus–reward association in the original discrimination tasks (i.e., that the correct response depends on selecting one of the two objects), they can easily switch to the opposite association in the reversal task.

In contrast, dogs and monkeys (e.g., Lai et al., 1995; Rapp, 1990; Voytko, 1999) show slower learning on reversal than on original discrimination tasks. Animals' poor performance in reversal tasks is largely attributable to perseverative responding, which was not seen in the healthy human participants. Whereas associative strategies may dominate responses in dogs, we have found evidence for transfer of knowledge from one discrimination task to another, suggesting that cognitive strategies can also be used in this species (Milgram, 2004; Tapp et al., 2003). It may also be that dogs use a hypothesis testing strategy when performing these tasks but that perseverative responding prevents them from switching to a more appropriate response set when they are performing poorly.

The hypothesis that humans rely heavily on cognitive strategies to solve the task at hand could also explain why they performed poorly on tasks that are governed by simple rules that are relatively easy to solve for dogs. Indeed, if a participant's hypothesis set is large or only contains complex hypotheses, then numerous trials will be required until all the hypotheses in the participant's set are sampled and new hypotheses are formulated. The hypothesis that humans formulated a priori hypotheses to solve the rule governing the task at hand could also explain why humans performed particularly poorly in the ODL task. Because this was the first task tested, participants' expectations about the complexity of the tasks had not yet been confirmed. Finally, the high variability observed in the human data may reflect individual differences in hypothesis set. Participants who entered the experiment with complex or large hypothesis sets were more likely to perform poorly on the tasks than participants who had no expectations. Although we have no quantitative data to support this hypothesis, comments such as 'the rule could not be that simple' or 'this is not following the pattern I had guessed' suggest that several participants did in fact employ a hypothesis testing strategy to arrive to solve the task at hand.

In animals, poor performance in reversal tasks is largely attributable to perseverative errors where an individual fails to inhibit a previously learned stimulus–reward association (e.g., Lai et al., 1995; Milgram et al., 1994; Rapp, 1990; Tapp et al., 2003; Voytko, 1999). In contrast, most human participants acquired the reversal tasks with only one or two errors, indicating that perseverative responding does not hinder performance in this population. Furthermore, older animals tend to persevere for a longer number of sessions than younger ones, a finding that was not replicated with the healthy older adults we tested. Our exclusion criteria, together with the absence of very old individuals in our sample, probably accounts for the absence of age differences in this study. Previous research indicates that analysis of perseverative responding in reversal tasks reveals significant differences when healthy older adults are compared to patients suffering from a variety of age-associated dementias (Freedman and Oscar-Berman, 1989; Oscar-Berman and Zola-Morgan, 1980). Stage analysis of reversal tasks may therefore be particularly promising to detect early changes in neuronal health status in older adults.

5. Conclusions

We have used a comparative approach to examine whether age-associated impairments in dogs parallel those found in humans. Our results suggest that humans use different strategies to solve tasks that evaluate object discrimination, egocentric spatial ability, object recognition, spatial memory, and cognitive flexibility. Humans appear to test a priori hypotheses to solve the task at hand. In contrast, dogs mainly rely on associative learning to solve these tasks. Furthermore, whereas dogs perform optimally on visuo-spatial tasks, humans perform optimally on visuo-perceptual tasks. These differences highlight the limitations inherent to directly applying the results obtained with animal models to the study of human aging. Future efforts should be devoted to testing participants with mild cognitive impairments to determine whether or not these tasks are sufficiently sensitive to detect subtle changes in cognitive decline in the early stages of AD.

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