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Cognitive and motor aging in female chimpanzees

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Abstract

We present the first longitudinal data on cognitive and motor aging in the chimpanzee (*Pan troglodytes*). Thirty-eight adult female chimpanzees (10–54 years old) were studied. The apes were tested longitudinally for 3 years in a modified Primate Cognition Test Battery (Herrmann et al., 2007, *Science* 317,1360–1366), which comprised 12 tests of physical and social cognition. The chimpanzees were also administered a fine motor task requiring them to remove a steel nut from rods of various complexity. There was little evidence for an age-related decline in tasks of Physical Cognition: for most tasks, performance was either stable or improved with repeated testing across age groups. An exception was Spatial Memory, for which 4 individuals over 50 years old experienced a significant performance decline across the 3 years of testing. Poorer performance with age was found in two tasks of Social Cognition, an attention getting task and a gaze-following task. A slight motor impairment was also observed, with old chimpanzees improving less than younger animals with repeated testing on the simplest rod. Hormonal status effects were restricted to spatial memory, with non-cycling females outperforming cycling females independently of age. Unexpectedly, older chimpanzees were better than younger individuals in understanding causality relationships based on sound.

Keywords

Ape; Cognition; Cognitive Decline; Hormonal Status; Menstrual Cycle; Motor function

1. Introduction

Cognitive impairment affects a large portion of the older population in the United States. Recent estimates provided by the Aging, Demographics, and Memory Study (ADAMS) indicate that as much as 22% of adults 71 years and older suffer from cognitive impairment without dementia (Plassman et al., 2008). About 12% of these people progress annually to dementia. Cognitive impairment, which is associated with decreased quality of life,

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increased disability, and increased neuropsychiatric disorders, greatly impacts patients, families, and society as a whole. As the number of older people continues to increase rapidly, there is an urgent need for new interventions to slow or prevent cognitive aging and dementia.

The pattern of aging in humans is unique among primates in a number of ways. The most obvious of these is that the human is the longest living of all primates, with a maximum lifespan of more than 100 years, nearly double that of our nearest evolutionary relative, the chimpanzee. Another human-exclusive trait is the long period of healthy post-reproductive life of women, in stark contrast to other primates that usually die before menopause (Walker and Herndon, 2008). Humans are also susceptible to such age-related diseases as Alzheimer's disease and Parkinson's disease, which are absent in all other primates (Finch and Austad, 2012; Heuer et al., 2012). Because this unique human aging phenotype emerged during the 6 million years since the human line diverged from that of the chimpanzee and bonobo, it must result from a relatively small number of genetic changes. In view of these evolutionary changes, we have argued that the pattern of aging in the chimpanzee must be studied in order to shed light upon our own pattern of aging including the neuropathological burdens that accompany it (Herndon and Walker, 2010).

Yet, only three studies have examined age-related cognitive decline in chimpanzees (see for review, Lacreuse and Herndon, 2009). Bernstein, (1961) studied the rate of learning, memory, and response variability in 8 young (11 to 19 y) and 8 old (28 to 40 y) chimpanzees of unspecified sex in object discrimination tasks and a wheel-rotating task. No differences between the age groups were revealed in any of the tasks. Similar results were obtained in another study in 19 chimpanzees of unspecified sex (7 to 41 y) that were tested on 2 object discrimination tasks (Riopelle and Rogers, 1965). However, poorer performance with age was observed in a version of the Delayed Response task, in which the chimpanzees had to remember the location of a reward after various delays. Unexpectedly, compared to young chimpanzees, older chimpanzees were impaired for short delays of 0 or 5 s, but not for the longer delay of 10 s. A significant decline with age was also found in a four-choice oddity task, in which chimpanzees were required to select one odd stimulus among four stimuli. The third study was an attempt to replicate these findings and revealed no difference in performance as a function of age (Bloomstrand and Maple, 1985). The results from these three early studies must be replicated in larger samples, wider age ranges, and broader cognitive domains. Such investigations are pressing, as the permanent funding moratorium on chimpanzee breeding (Cohen, 2007; Knight, 2008), along with the recent implementation of strict limitations on chimpanzee research (Altevogt et al., 2011) will necessarily result in a major decline in laboratory chimpanzee numbers over the next decades. These increased restrictions will not eliminate all chimpanzee research as some of these studies could be conducted in zoos or sanctuaries (see <http://news.sciencemag.org/sciencenow/2013/05/live-chat-should-chimpanzees-be.html> for more on this debate).

Recently, a test battery was developed to study physical and social cognition abilities in a variety of primates. The Primate Cognition Test Battery (PCTB; Herrmann et al., 2007) includes a set of 16 tests that probe Physical and Social cognition. Physical Cognition included 3 scales of Space, Quantity, and Causality. Social Cognition was subdivided into Social Learning, Communication, and Theory of Mind. We used a modified version of this battery (Russell et al., 2011) to assess cognitive abilities across the chimpanzee life span. Our rationale for the use of the PCTB in this study was based on three main factors: (1) the PCTB had already been used to effectively compare chimpanzees and humans in a developmental context (Herrmann et al., 2007); (2) the battery included tests of social cognition in addition to tests of physical cognition; and (3) it could be easily administered to the apes. Female chimpanzees, of ages representing the entire adult life span, were studied

annually for 3 years. We focused on females because they live longer than males (Hill et al., 2001) and because selection related to post-reproductive robustness would be expected to target females more than males (Hawkes et al., 2011; Hawkes et al., 1998).

When considering female cognitive function, it is essential to examine hormonal status which may significantly impact performance on selective tasks. Indeed, many studies on women have reported that low estrogen conditions due to surgical (Nappi et al., 1999; Sherwin, 1988), pharmacological (Craig et al., 2008; Sherwin and Tulandi, 1996) or natural menopause (Berent-Spillson et al., 2012) led to impaired performance, most consistently on tasks of verbal memory and verbal fluency. Such hormone-dependent fluctuations in cognitive performance have also been found across the menstrual cycle, with verbal memory being better and spatial ability worse when estrogen levels were elevated, and spatial memory best and verbal memory lowest when estrogen levels were low (Hampson, 1990). Changes in cognition according to the menstrual cycle (Lacreuse et al., 2001), natural menopause (Roberts et al., 1997) or surgical menopause (Lacreuse et al., 2000) have also been observed in female rhesus monkeys. In the present study, we included hormonal status (cycling vs. non-cycling) to examine its possible influence on cognitive performance. Finally, rearing history has been found to greatly influence performance on the PCTB in chimpanzees (Russell et al., 2011), in that extended contact to humans led to better understanding of rotation, quantities and of causal relationships inferred from sound and better understanding of social cues, better production of gestures to a hidden reward and better modality-appropriate communication. To control for the potential effect of rearing on these tasks, rearing history was included as a factor in the analysis.

2. Methods

2.1. Subjects

Thirty-eight adult female chimpanzees (*Pan troglodytes*) were studied; they ranged in age from 10 to 54 y (Table 1), covering nearly the entire adult life span. Subjects lived in social groups of 2 to 6 compatible individuals at the Yerkes National Primate Research Center (YNPRC) of Emory University. Five groups consisted only of females, and 9 groups included a male as part of the social group. The chimpanzees were part of a larger project investigating the effects of aging on cognition and the brain. Because ovarian hormones may influence cognition, the chimpanzees were removed from all forms of hormonal contraception before the onset of the larger project, about 2 years before the present observations began. In addition, anogenital swelling was observed and rated in all chimpanzees 5 days/week. As a part of husbandry practices at YNPRC, some apes were raised in a nursery, rather than by their mothers. In the nursery, human caregivers provide food, sensory stimulation, and play. Eighteen of the 38 chimpanzees studied were nursery reared. For the analyses in this paper, animals were defined as nursery-reared if they entered the nursery within the first 30 days of life.

2.2. Hormonal status

Ovarian cycles can be tracked in chimpanzees by observing and rating anogenital swelling. Swelling was rated on a 5 point scale and menstrual bleeding was recorded if observed. This procedure reliably indicates the occurrence of ovulation (Graham, 1979; Lacreuse et al., 2008), as recently confirmed by urinary hormone levels in a subset of the chimpanzees used in this study (Herndon et al., 2012). These observations allowed us to separate chimpanzees into those who were cycling normally and those who were not (Table 1). Cycling and non-cycling chimpanzees were present in all age groups. The presence of cycling in aged chimpanzees and its absence in some young and middle aged chimpanzees is discussed elsewhere (Herndon et al., 2012; Lacreuse et al., 2008).

2.3. Cognitive and Motor Testing

We used a modified version of the Primate Cognitive Testing Battery (PCTB) which was designed by Herrmann et al. (2007) to assess Physical Cognition (i.e. tasks requiring processing of information about space, quantities, and causality) as well as Social Cognition (tests of communication and Theory of Mind). The modified version of the PCTB was also employed by Russell et al. (2011). Each of the cognitive tasks was presented to each chimpanzee on 3 occasions at intervals of approximately 18 months. We also administered a fine motor task designed after the study done by Gash et al., (1999) in which the chimpanzee was timed as she removed a steel nut from a bent steel rod. Because of the delay in building the stimuli for this task, motor performance was not assessed in Year 1 but was tested in each chimpanzee in Years 2 and 3 at about 12 months apart. The experimenter knew the animals individually and was aware of their age at the time of testing.

Physical Cognition Tasks—Eight tasks were used to assess Physical Cognition (Table 2). Our test differed from the original PCTB in several ways: we excluded the Addition task as well as certain components of the Tool Properties tasks.

Space: Spatial Memory (3 trials): This test assessed the subject's ability to remember the location of food rewards. The subject watched as food was hidden in 2 of 3 possible locations. Each subject received all 3 possible combinations of baited locations. The subject was then allowed to search the locations. The subject was scored as successful if she located both food items without searching the unbaited location.

Space: Object Permanence (9 trials): We tested the chimpanzee's ability to follow a food reward after displacement, not visible to the subject, given 3 different possible displacements. During single displacement trials, only 1 of 3 possible locations was manipulated and thus potentially baited. In the double displacement trials, 2 of 3 possible locations were manipulated. Double displacement trials were further divided into those where the baited locations were adjacent to one another and those where they were not. In order to be considered successful, the subject had to locate the hidden food item without searching in the unmanipulated location.

Space: Rotation (9 trials): We examined the subject's ability to track a food reward as it was spatially rotated either 180 or 360 degrees. The subject watched as one of 3 possible locations was baited and then as the 3 locations were rotated as a unit on a horizontal plane. Three different manipulations were employed. In 180 degree middle trials, the middle location was baited and the platform was turned 180 degrees. In 360 degree side and 180 degree side trials, either the left or right location was baited and the platform was then rotated 360 or 180 degrees, respectively. The subject successfully completed a Rotation trial by tracking and identifying the correct location.

Space: Transposition (9 trials): The subject watched as a food reward was hidden in one of 3 possible locations and then as the baited location was changed in one of 3 ways. In one condition, the baited location was switched with one of the unbaited locations. In the second condition, the baited location was switched with one of the unbaited locations and then the 2 unbaited locations were switched. In the last condition, the baited location was switched with one of the unbaited locations and then with the other unbaited location. To be considered successful on this task, the subject had to track the reward and choose the baited location.

Quantity: Relative Numbers (13 trials): This task tested the ability to discriminate between different quantities by choosing between two plates containing different amounts of

equally sized food pieces. Each subject received 13 different quantity pairings (1:0, 5:1, 6:3, 6:2, 6:4, 4:3, 3:2, 2:1, 4:1, 4:2, 5:2, 3:1 and 5:3). During each trial, the subject was allowed to choose only one plate and received whatever reward was on the chosen plate. A correct response was recorded when the subject chose the plate containing the larger quantity of food. We did not include Addition Numbers of the original PCTB.

Causality: Noise (6 trials): This task assessed the subject's understanding of causal relationships based on sound. The experimenter placed a hard food reward (i.e. peanut) in one of two metal containers such that the container with the food reward made a sound when shaken while the unbaited container did not. In "Full" trials, the metal container containing the food reward was lifted and shaken and then the unbaited container was lifted. In the "Empty" trials, the empty container was lifted and shaken and then the baited container was lifted. The subject was then allowed to choose one of the two containers. A correct choice was recorded when the subject chose the baited container.

Causality: Shape (6 trials): Each subject was tested for her causal understanding of the physical world in the visual domain. Specifically, in one trial type a food reward was placed underneath one of two boards lying flat on the testing table. The food caused the baited board to be tilted while the unbaited board lay flat. In the second trial type, a food reward was placed underneath one of two pieces of cloth lying flat on the testing table. The reward created a visible bump in the baited cloth while the unbaited cloth lay flat. In both trial types, the subject had to choose the baited item to be considered successful.

Causality: Tool Properties (6 trials): This task explored understanding of the physical properties of tools and how those relate to achieving a goal. In each condition, the subject was presented with a choice between two similar tools. One tool could be used to obtain a food reward while the other tool was ineffective. For Side condition, the subject was presented with two identical pieces of paper. One piece of paper had a food reward sitting on top of the far end while the second piece of paper had a food reward sitting beside it. The subject could pull either piece of paper into her cage, but only by pulling the paper with the food on top would she be able to retrieve the food reward. In the Ripped condition, one tool was identical to the effective tool in the first task. The second tool consisted of two smaller pieces of paper with a small gap between them. The food reward was placed on the out-of-reach piece of the two disconnected pieces of paper. The subject could pull in the reward using the effective tool, but pulling the piece of the disconnected paper was ineffective in obtaining the reward. We did not include three tool properties conditions of the original PCTB (Bridge, Broken Wool, and Tray Circle).

Social Cognition Tasks—Four tasks of the PCTB were used (Table 2). The first two were designed to test the ape's ability to understand and to produce communicative signals. The third task assessed her sensitivity to the attentional state of an experimenter and her ability to use appropriate communicative modalities based on this information. The final task was designed to assess rudimentary aspects of Theory of Mind by testing the chimpanzee's ability to follow gaze. We excluded the Social Learning tasks of the original PCTB and made some modifications to several of the other Social Cognition tasks as noted below.

Communication: Comprehension (6 trials): To assess the ape's communicative ability, we used a strategy different from that of Herrmann et al., (2007). We placed a target on the left and right sides of the enclosure while the subject was in the center. The experimenter then used either gaze (3 trials) or gaze combined with manual pointing (3 trials) to direct the subject to one of the two targets. The subject had to move to and touch the designated target

to be considered successful on this task. Successful responses were rewarded with a small piece of fruit. We did not include the “Mark” condition of the original PCTB.

Communication: Production (4 trials): We followed the original PCTB procedure to test the ape’s ability to produce communicative signals to indicate a hidden food item. In this task, the ape watched as an experimenter baited a location on either the far left or far right side of the enclosure. A second experimenter then approached the cage, centered the subject and waited for the subject to indicate which location contained the hidden food. The subject was given 60 s to indicate the correct location by using an overt communicative signal, such as a manual gesture towards the hidden food. If the chimpanzee indicated the correct location, the experimenter gave the subject the piece of food hidden in that location.

Communication: Attentional State (8 trials): We followed the methods outlined by Herrmann et al. (2007), but added an additional test. First, an experimenter placed a piece of food on the ground outside of the subject’s enclosure. Then a second experimenter approached the cage and altered her attentional state in one of four ways, each represented by a separate trial. In the first trial, the experimenter’s face and body were directed towards the food item and the subject. In the second trial, the experimenter’s body faced the subject but her face was turned away. In the third trial, the experimenter stood with her body facing away from the enclosure but then turned her head to look at the subject. In the fourth trial, the experimenter’s body and face were oriented away from the subject. In order to be successful, the subject had to use a communicative signal in the modality appropriate to the experimenter’s attentional state. For example, if the experimenter was looking at the subject, the chimpanzee could use a manual gesture to point to the food. However, if the experimenter was facing away from the subject, the subject had to first use an auditory or tactile signal, such as a cage bang or a spit to get the attention of the experimenter and then, once the experimenter was looking at her, use a visual signal to indicate the food. We added a set of 4 trials using the same basic conditions, but with the trials conducted in a more familiar setting with the experimenter sitting at the testing table, placing a piece of food on the table, and carrying out the 4 variations of attentional state. In all attentional state trials, if the chimpanzee responded correctly, she was given the piece of food. If not, the experimenter removed the food.

Theory of Mind: Gaze Following (3 trials): We examined each ape’s ability to follow gaze. The experimenter sat on a stool approximately one meter from the subject’s enclosure. The experimenter captured the subject’s attention and centered her within the cage by offering a piece of food. Then the experimenter shifted her head and eyes to gaze at a point directly above her head for a period of 10 s. In order to be successful, the subject had to follow the gaze of the experimenter by looking upward. The chimpanzees received a small food reward at the end of the 10 s trial regardless of whether or not they followed gaze. We did not employ two of the gaze following tasks (“Back” and “Eyes”) of the original PCTB.

Fine Motor Task—Each subject participated in 4 sessions of 12 trials each. Three wire shapes were used: straight (9.5" long), question mark (9.5" × 3") and “S” (11" × 4.5"). During each session, the chimpanzee completed 2 left-hand and 2 right-hand trials with each wire type. The order of presentation of the 3 wire types and whether each subject started with the left or right hand was pseudo-counterbalanced across subjects and sessions. At the onset of each trial, the wire (with the nut in place) was inserted inside the cage and the subject was allowed to remove the nut using the target hand. The subject was then reinforced for returning the nut to the experimenter. If at any point during the trial, the subject attempted to use the non-target hand or her mouth to remove the nut, the experimenter retracted the wire. The experimenter recorded the time needed to remove the

nut from the wire for each trial. Time was recorded from the moment the subject grasped the nut until the nut came off the end of the wire.

2.4. Data Analysis

The dependent measure for the cognitive tasks was the proportion of correct responses on each task. Linear mixed effects (LME) modeling was employed to examine the effect of Age and repeated testing on performance. In an initial analysis Age (at the onset of the study rounded to the nearest year), Test Number (the 3 annually repeated tests) and the Age $\times$ Test Number interaction were considered as fixed effects. If p values associated with the regressions terms for Test Number and Age $\times$ Repeated Testing were greater than 0.05, these terms were removed from the final model producing a model with Age as the only predictor. The individual subjects were treated as random variables in the LME models. To assess the effect of social rearing, we performed a subsequent analysis in which NR was added to the final LME model as a factor.

A similar approach was applied to the motor performance, with separate analyses being conducted for each of the shapes of bent rods used in this test. Finally in a separate analysis, we used analysis of variance (ANOVA) to evaluate the effects of hormonal status on spatial tests and motor tests, because these have been hypothesized to be influenced by ovarian hormones. For the ANOVAs we considered Age Group (rather than Age) and the absence or presence of ovarian cyclicity in a factorial analysis for each subject. Age groups and cycling status of the chimpanzees are shown in Table 1.

3. Results

3.1. PCTB: Yearly Changes in Performance

Table 3 summarizes the performance of each age group of chimpanzees on the 3 annual tests on the PCTB. While performance on most tasks neither improved nor declined significantly over the 3 years of testing, Spatial Memory and Object Permanence were exceptions in that performance on these tasks improved significantly over time. For Spatial Memory, but not Object Permanence, a significant Age $\times$ Test Number interaction indicated that the rate of improvement across repeated testing was influenced by age. This differential improvement can be seen in Fig. 1, which indicates greater year-to-year improvement in the Young group than in the Middle-aged and Old groups. Interestingly, in contrast to the other age groups, the 4 chimpanzees over 50 years old experienced a significant decline in spatial memory performance from Year 1 to 3 ($F(2,3)=13.50$, $p < .032$). For Object Permanence (Fig. 1), the year-to-year changes were approximately equal in all 4 age groups, as indicated by the similarity of slopes and by the absence of significant terms for the Age $\times$ Test Number interaction (Table 3). For the remaining tests in the battery, there was no change in performance over successive repetitions, therefore the final LME models did not include terms for Test Number. Graphic representations of the performance on these tasks (Fig. 2) therefore depict average performance over the 3 tests plotted against the age of each chimpanzee at the time of the first test.

3.2. PCTB: Effect of Age

As can be seen from the F and p values in Table 3, Age had no overall effect on performance on the tasks designed to assess spatial functioning (Spatial Memory, Object Permanence, Rotation, and Transposition). Performance on the Relative Numbers task also remained uninfluenced by Age. Within the domain of Causality, the effect of Age was nonsignificant for the Shape, Tool Use, and Tool Properties tasks, but was significant for the Noise task, in which the chimpanzee located a reward based upon sound. Interestingly, a scatterplot of performance on the Causality:Noise task across the age range (Fig. 2)

indicated a slight improvement in performance with age, with the oldest chimpanzee showing the best performance. The influence of Age on performance of the Social Cognition tasks was mixed. While comprehension and production were uninfluenced by age, performance on the Attentional State and Gaze following tasks was significantly influenced by Age (Table 3). Specifically, older chimpanzees were less likely to succeed in using a signal appropriate to the experimenter's apparent attention or to follow a pronounced gaze by the experimenter by looking in the same direction (Fig. 2).

3.3. PCTB: Effects of Nursery Rearing

Because Nursery Rearing (NR) involves extensive interaction with a human caregiver, we wanted to see if this factor might account for the apparent effect of age on Gaze following. When NR was added to the final LME model for this task, the effect of NR itself was not statistically significant. But p value for the effect of age was increased from 0.001 to 0.01. In addition, there was an interaction of borderline significance ($p = 0.07$) between NR and Age. Inspection of the performance of the 5 old animals that had a history of NR revealed that they indeed showed a higher level of Gaze following than did the 8 individuals in the old age group that had not experienced NR. While this effect was not statistically significant, it remains possible that we did not have enough statistical power to detect this influence. LME terms for the NR $\times$ Age interaction were of significance ($p < 0.05$) for 3 additional tests (Space: Transposition, Communication: Comprehension, and Communication: Attentional State), none of which was significantly influenced by age. None of the other behavioral measures were influenced by NR.

3.4. Fine Motor Task

Fig. 3 depicts the average length of time taken to remove the nut from the straight, Question-mark shaped and the S-shaped metal rods. There was significant improvement between year 1 and year 2 on all shapes, as indicated by significant main effect for Test Number (Straight rod: $F = 14.04$; Question-mark: $F = 14.09$; S-shape: $F = 16.30$; for all shapes: $df = 1, 28$, $p < 0.001$). Although there were no significant main effects for age, there was a significant Age $\times$ Year of Testing effect for the Straight rod (Age $\times$ Test, $F = 4.68$, $df = 1, 28$, $p < 0.039$). The Old group of chimpanzees improved on this shape less dramatically than the Young and Middle-Aged groups. In addition, the two chimpanzees over 50 years old tested on the task were the only ones to perform worse on retest with this shape.

3.5. Hormonal Status

Because ovarian hormones have been reported to influence a variety of tasks that require spatial processing, we examined the effect of cycling status on the Spatial Memory, Object Permanence, Rotation, and Transposition tasks. A significant effect of cycling status was observed in the Spatial Memory task ($F = 4.85$, $df = 1, 29$, $p = 0.036$); non-cycling chimpanzees performed better than those who did cycle (Fig. 4). The Cycle $\times$ Age interaction was not significant. The remaining 3 spatial tasks (Object Permanence, Rotation, Transposition) were not affected by cycling status. Hormonal status was also without effect on performance of the tasks involving Quantity, Causality, Communication and Theory of Mind.

4. Discussion

4.1. Overall age differences

This report is the first to assess longitudinal changes in cognitive performance and fine motor skills in a relatively large sample of young adult, middle-aged and aged female chimpanzees. We used tests that had previously detected significant cognitive differences

between apes and children (Herrmann et al., 2007), between enculturated and non-enculturated apes (Russell et al., 2011) as well as between chimpanzees and bonobos (Herrmann et al., 2010). We also employed tests that had previously detected cross-sectional and longitudinal age-related decline in fine motor function in humans and monkeys (Gash et al., 1999). Our investigation yielded unexpected results. First, no age-related decline in Physical Cognition was detected in chimpanzees younger than 50 years old. The 4 chimpanzees in their 50's were the only ones to experience a significant decline in spatial memory from Year 1 to Year 3. Second, age-related decline was evident in two tasks that required sensitivity to the attentional state of the experimenter, one involving the production of appropriate communicative signals to capture the attention of the experimenter, and one requiring following the gaze of the experimenter. Third, there was only modest evidence for a decline in fine motor function: older chimpanzees improved less than the younger ones when retested with the easiest of three shapes; we note that the two 50+ chimpanzees that were tested on the task exhibited a significant decline in motor speed at retest. Fourth, improvements with age were observed in one task requiring selection of a container based on the sound of the reward inside it. Finally we confirmed that hormonal status affected spatial memory performance, with non-cycling females outperforming cycling females.

4.2. Physical cognition

Limited evidence for age-related cognitive decline—The surprising finding from this experiment was that performance on the tasks of Physical Cognition remained either remarkably stable or even improved (spatial memory and object permanence) within and across age groups during the 3 years of testing. The only exception was the task of spatial memory, in which the 4 chimpanzees in their 50s, in contrast to the other age groups, experienced a significant decline from Year 1 to Year 3.

Because only 4 chimpanzees were in the “oldest old” group, these results need to be interpreted with caution. Yet, these 4 females experienced a decline in spatial memory across the 3 years of testing that was not observed in chimpanzees aged 30 to 49 years. Although the possibility that spatial memory drops abruptly in chimpanzees after 50 years of age cannot be ruled out, it is likely that subtle impairments developing at an earlier age were not detected, due to the lack of substantial memory demands in the task, since the retention interval was shorter than 1s.

Despite the lack of delay, we note that the task of spatial memory was the only task among a set of 8 tasks to show a declining pattern of performance (in the oldest old group only). This confirms previous observations in monkeys (e.g., Herndon et al., 1997) and humans (e.g., Park et al, 1982) that spatial memory is a cognitive domain particularly vulnerable to age-related decline.

It would be tempting to conclude that that age-related decline in physical cognition in the chimpanzee is limited to spatial memory and develops only very late in life. However, it is unlikely that chimpanzees in their 30s do not experience cognitive decline, as virtually all other primates, including humans, show significant declines in cognitive abilities with age, starting as early as middle-age (Erwin and Hof, 2002; Lacreuse and Herndon, 2009). Specifically, large declines in speed of processing, working memory, executive function, attention and long-term memory characterize normal cognitive aging in humans (Salthouse, 2010) and monkeys (Herndon et al., 1997; Moore et al., 2006; Nagahara et al., 2010), with some of these changes beginning in the 30s in humans (Salthouse, 2009) and 12 years of age in rhesus monkeys (Moore et al., 2006). As noted in the introduction, prior studies on the effect of aging on cognition in chimpanzees yielded mixed results. Thus, Bernstein (1961) found no evidence for age-related declines in a set of object discrimination tasks. Although the study by Riopelle and Rogers (1965) did detect age-related decrements in performance

for the shorter delays of the DR and for a 4-choice oddity task, these findings were not replicated in a later study (Bloomstrand and Maple, 1985). Given these discordant findings and the results of the current study, we speculate that age-related differences in the chimpanzee would be more likely detected in tasks taxing memory capacity and executive function. Because the PCTB does not include memory tests with retention intervals longer than 1s, it is likely not sensitive to age differences in physical cognition. Thus, despite the fact that the PCTB can detect subtle species differences in physical cognition (Herrmann et al., 2007; Herrmann et al., 2010; Schmitt et al., 2012), we believe that the lack of memory and executive function measures makes this battery relatively insensitive to age-related differences within a species. The clear demonstration of age-related declines in physical cognition in the chimpanzee awaits further testing with tasks assessing executive function and memory capacity.

Improvement in causality understanding (noise condition)—Another unexpected finding was that older chimpanzees were significantly better than younger individuals in selecting a container based on the sound of a reward inside it. It is intriguing that this advantage was only found for understanding of causality based on auditory, not visual input, and was not found for other tasks of causality understanding that involved tool-use and tool properties. Although speculative, one possible explanation is that older chimpanzees may excel at detecting a reward based on sound as to compensate for diminished visual acuity. This hypothesis needs to be tested in future experiments.

4.3. Fine motor function

The task of fine motor function only detected modest impairment in older chimpanzees: the old group displayed less improvement than the two younger age groups when retested with the simplest shape on year 2 but no overall age differences was found in the speed with which animals retrieved the nut from the different wire shapes. Notably, the 2 chimpanzees over 50 years old tested on the task were the only ones showing a slowing of motor function at retest with the simplest shape and the Question Mark shape. The lack of clear age differences was unexpected, as the task previously showed robust age-related slowing in humans and monkeys (Gash et al., 1999; Lacreuse et al., 2005; Zhang et al., 2000). It is possible that age-related changes in motor function are only observed very late in the lifespan of the chimpanzee. Alternatively, the modifications made to the original version of the task may have rendered the nut removal too easy to be sensitive to age differences. Indeed, one of the major differences with the original procedure was that the shapes were presented horizontally rather than vertically, therefore the nut did not have to be lifted upward, but rather pulled horizontally towards the subject. Nevertheless, older chimpanzees did not improve as much as the younger individuals when retested with the simpler shape on year 2. This result can be interpreted as a floor effect, in which older chimpanzees might have been unable to get faster with practice, due to general slowing of motor function related to nigrostriatal dysfunction (Emborg and Kordower, 2002) or constraints caused by arthritis or neuromuscular impairments. The declining performance of the two 50+ chimpanzees is consistent with such an interpretation.

4.4. Social Cognition

Attentional state and gaze following—Producing communicative signals that are appropriate to the attentional state of another individual (i.e. the experimenter) requires the animal to understand what the other can see. Chimpanzees have previously been found to modulate their gestural and vocal signals according to the attentional state of a human partner (Hostetter et al., 2001; Tomasello et al., 1994; Tomasello and Camaioni, 1997) and there is substantial evidence that these signals serve an intentional communicative function (Leavens et al., 2004; Tomasello, 2008). The deficit of older chimpanzees in production of

signals appropriate to the attentional state of the experimenter does not reflect deficits in the production of gestures, since these could be produced effectively by the older apes. Rather, older chimpanzees must have had impaired understanding of the attentional state of the human, which would point to specific deficits in the ability to decode social cues based on face and/or body orientation. Kaminski et al (2004) indeed reported that chimpanzees are minimally sensitive to the eyes and rely instead on the face and body orientation to determine the attentional state of a human observer. In addition to these age-related declines in detecting the attentional state of the human observer, deficits in gaze following were also evident in older chimpanzees. Interestingly, more skillful gaze following in younger than older individuals was also found in chimpanzees aged 5 to 22 years old (Herrmann et al., 2010), suggesting that age-related visual impairment is not likely to mediate these effects. Gaze following is an important social skill that allows individuals to share attention with others by orienting their attention to the same stimulus in the environment. Gaze following does not necessarily require an understanding of what the other individual sees and can be performed in a reflexive manner by many primate species (Rosati and Hare, 2009). Nevertheless, studies in chimpanzees clearly indicate that they understand what others see (Tomasello and Call, 2010). Whether they also understand the psychological states of others, however, remains highly controversial (Vonk and Povinelli, 2006). Conservatively speaking, gaze-following can be understood as a *precursor* of more complex aspects of social cognition such as Theory of Mind (Baron-Cohen, 2005), the ability to represent the mental states of others. It has recently been found that older humans show an age-related decline in their ability to detect gaze direction and follow the gaze of others (Slessor et al, 2007; Slessor et al., 2008). Importantly, these deficits were not explained by changes in visual perception. Rather, age-related deficits in gaze following might have been caused by changes in the superior temporal sulcus (Sowell et al., 2003), a key region involved in gaze processing in humans and other primates (Kamphuis et al., 2009; Shepherd, 2010). Such deficits in basic aspects of social cognition could lead to impairments in more complex processing of social cue decoding such as Theory of Mind. Increasing evidence points to an age-related impairment in Theory of Mind in humans (Kemp et al., 2012; Rakoczy et al., 2012), which has been attributed to a dysfunction of a fronto-subcortical network.

An alternative explanation for the age-related decline in social cognition may be decreased motivation of the older individuals to perform in tasks that did not selectively reinforce correct responses. Indeed, unlike the Physical Cognition tasks that reinforced correct responses only, chimpanzees were rewarded whether or not they performed correctly for their participation in the Gaze following task. This explanation is not entirely satisfactory, however, since the attentional state task, which rewarded correct responses only, was also significantly impaired in older chimpanzees.

4.5. Hormonal effects

The only significant effect related to hormonal status was found in spatial memory: non-cycling females outperformed cycling females, independently of age. Tasks involving spatial cognition have been found to be impaired with high levels of ovarian hormones in a number of species, including humans. For examples, women exhibit poorer spatial skills during the preovulatory and midluteal phases of the menstrual cycle, when estrogen levels are high, than during menstruation, when estrogen levels are low (Hampson, 1990; Hausmann et al., 2000). Some, but not all, rodent studies also indicate impairments in spatial memory in females when estrogen levels are high (Galea et al., 1995; Warren and Juraska, 1997). In rhesus monkeys, we found that spatial working memory was significantly lower during the peri-ovulatory phase than during the follicular and luteal phases of the cycle (Lacreuse et al., 2001). In another study, spatial working memory was compared in intact older females and in females who had been ovariectomized at least 10 years before. Long-

term ovariectomy was associated with better spatial working memory performance, suggesting that the lack of ovarian hormones enhanced spatial cognition (Lacreuse et al., 2000). Similar results were obtained in rats (Bimonte-Nelson et al., 2003) and were shown to be largely due to the removal of progesterone in ovariectomized animals (Bimonte-Nelson et al., 2004). Altogether these results suggest that the lack of ovarian hormone fluctuations can enhance spatial memory in primates and rodents.

The unexpected lack of cyclicity in some of the Young and Middle-aged chimpanzees has previously been addressed elsewhere (Herndon et al., 2012). Whereas the causes of anovulation in these animals remain unknown, it is certainly an abnormal pattern that is worth further study. Independently of the causes of anovulation, the conclusion remains that the lack of cyclicity is associated with better spatial memory across the age groups in female chimpanzees.

4.6. Limitations

In retrospect, our study had a number of limitations, some of which have already been briefly addressed above. The lack of long retention intervals in the PCTB probably made the tasks rather insensitive to age differences. In addition, it would have been desirable to have a longer follow-up period than the 3 years of this study. Furthermore, although we categorized the females as cycling and non-cycling, we did not monitor the hormonal status of the cycling females. It is possible that the phase of the cycle modulated performance on some tasks. Our study also lacked objective assessments of physical and sensory deficits in the older chimpanzees. Physical disability (i.e., arthritis) in the precise manipulation of the fingers could explain the small effect of age that we observed in fine motor function. Potential sensory impairments are also a concern. For example, unknown visual impairments could explain, at least partly, the detrimental effect of age on attentional state and gaze following. This interpretation is unlikely however, because almost all the tasks relied on vision, and only these two tasks showed age-related declines. It is more conceivable that these age-related differences are rooted in a deficit in basic social cognition skills associated with the processing of gaze, face and body orientation cues. However, we speculate that compensatory processes for visual acuity impairments could potentially explain the advantage of the older chimpanzees in detecting a reward based on sound. A comprehensive assessment of sensory impairments in older chimpanzees is needed for a clearer understanding of cognitive aging in our closest relative.

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Figure 1.

Performance of female chimpanzees on the Spatial Memory task and the Object Permanence task in 3 successive annual tests.

Figure 2.

Average proportion of correct responses of female chimpanzees on the Causality: Noise, Attentional State, and Gaze Following tasks over 3 consecutive annual tests. Subject Age at the initial test is shown.

Figure 3.
Time (s) to remove a hardware nut from the 3 rods as a function of testing year.

Figure 4.

Performance of Young, Middle-aged, Old, and Oldest-old female chimpanzees with and without menstrual cycles on the Spatial Memory task. Non-cycling females performed better than those that did cycle ($F = 4.85$, $df = 1, 29$, $p = 0.036$). Numbers of chimpanzees studied are indicated above each column.

Table 1
Number of female chimpanzees studied in each age group, with and without menstrual cycles.

	Young 10 – 16 y	Middle-aged 17 – 29 y	Old 30 – 49 y	Oldest-Old 50 – 54 y	Total
With menstrual cycles	6	9	8	1	24
Without menstrual cycles	6	4	1	3	14
Total	12	13	9	4	38

Table 2

Summary of the cognitive tests administered, as described by Herrmann et al. (2007)

<i>Domain</i>	<i>Scale</i>	<i>Test</i>	<i>No. of Trials</i>	<i>Description</i>
Physical Cognition				
	Space	Spatial Memory	3	Locating a reward
		Object Permanence	9	Tracking a reward after visible displacement
		Rotation	9	Tracking a reward after a rotation
		Transposition	9	Tracking a reward after location changes
	Quantity	Relative Numbers	13	Discriminating quantity
	Causality	Noise	6	Causal understanding of produced noise by hidden rewards
		Shape	6	Causal understanding of appearance change by hidden rewards
		Tool Properties	6	Understanding of functional and non-functional tool properties
	Social Cognition			
	Communication	Comprehension	6	Understanding communicative cue indicating rewards' location
		Production	4	Producing communicative gestures in order to retrieve a hidden reward
		Attentional State	8	Choosing communicative gestures considering the attentional state of the recipient
	Theory of Mind	Gaze Following	3	Following experimenter's gaze direction to a target

Summary of the effects of age on each cognitive measure. F and p values are from the final statistical model. These values are given for Age, and, if applicable, for repeated testing (Test No.) and for its interaction with Age. Significant p values are indicated in bold.

Table 3

Domain	Scale	Test	Age		Test No.		Age x Test	
			F	p	F	p	F	p
Physical Cognition								
Space	Spatial Memory		0.32	0.86	3.58	0.04	3.54	0.04
		Object Permanence	0.26	0.62	4.87	0.01	0.34	0.71
		Rotation	0.29	0.10				
		Transposition	0.30	0.59				
Quantity			1.43	0.24				
Causality	Noise		5.70	0.02				
		Shape	1.50	0.23				
		Tool Properties	0.59	0.45				
Social Cognition								
Communication	Comprehension		1.28	0.27				
		Production	1.37	0.25				
		Attentional State	4.41	0.04				
Theory of Mind			Gaze Following	12.56	0.001			