On the Social Life and Motivational Changes of Aging Monkeys

Julia Fischer

Cognitive Ethology Laboratory, German Primate Center, Göttingen and
Leibniz ScienceCampus “Primate Cognition“, Göttingen

Author Note

Correspondence concerning this article should be addressed to: Julia Fischer, Cognitive
Ethology Laboratory, German Primate Center - Leibniz Institute for Primate Research, Kellnerweg 4,
37077 Göttingen. Germany, Phone: +49 551 3851 375. Fax: +49 551 3851 372, Email:
jfischer@dpz.eu.
Abstract

Although nonhuman primates have been used in biomedical research to develop a better understanding of physiological aging processes, their value as models for studying age-related differences in motivation, cognition, and decision-making has only recently been appreciated. This paper reviews the state of the art, with a focus on a recent study on Barbary macaques. A number of studies reported that with increasing age, Old World monkeys spend more time resting, have fewer social partners and/or spend less time in social interactions, though other studies found no such effects. Less was known about changes in cognitive performance and shifts in interest in the physical and social environment across age. A recent comprehensive study of motivational changes in a large age-heterogeneous population of Barbary macaques (*Macaca sylvanus*) living at “La Forêt des Singes” in Rocamadour explicitly tested predictions from social selectivity theory, which posits that in light of a shrinking future time perspective, humans become increasingly selective in terms of their social interactions. Given that nonhuman primates most likely have no conception of their limited life time, this allowed disentangling the effects of cognitive insights and basal physiological processes that contribute to changes in the valuation of different activities. The Barbary macaques under study revealed marked and differential motivational shifts with age: while they interacted with fewer social partners, they continued to attend to social information. In contrast, they revealed a marked loss of interest in novel objects in early adulthood, unless these were baited with a food reward. Some of the motivational changes observed during human aging may thus be shared with our closest living relatives. The awareness of a limited future time perspective in humans may enhance the effects of these ancestral processes, but does not appear to be the only explanation. Future studies should employ a broader array of different cognitive tests to delineate the trajectories of different cognitive processes such as attention, memory, and behavioral flexibility more clearly. Taken together, an evolutionary developmental psychology perspective that combines a lifespan psychology with evolutionary biology appears to be a promising avenue for investigations of age-related changes in motivation and cognition.
Key Words: Aging, Cognition, Decision-making, Evolution, Lifespan, Nonhuman Primates, Social Relationships
On the Social Life and Cognitive Performance of Aging Monkeys

The increasing life expectancy of humans has spawned a growing research interest in age-related changes not only with regard to health, but also cognitive ability and well-being [1]. Nonhuman primates have long played an important role in research of physiological aging processes, as they reveal similar age-related changes as humans [2–4]. Yet, studies on nonhuman primates may also help to develop a better understanding for the determinants of ‘successful’ aging, i.e. how individuals cope with age-related shifts in the availability of resources [5,6]. Studies of aging in nonhuman primates allow disentangling the influence of physiological processes and top-down cognitive regulation on age-related changes in motivation and social behavior. In addition, such comparative studies may aid to delineate more clearly how both competence and motivation contribute to performance and problem-solving behavior in the social and the non-social domain. In the following, I will briefly summarize the available evidence for age-related changes in cognitive performance and social behavior in nonhuman primates (hereafter: ‘primates’). I will then discuss in more detail the results of a recent study of motivational changes in aging Barbary macaques (Macaca sylvanus), which was explicitly designed to test predictions from psychological theory [7], and will conclude with some ideas for future research.

Macaques as models in research on aging

Most of the studies that examined how age affects social behavior and cognitive performance have been conducted on rhesus monkeys (M. mulatta) and long-tailed macaques (M. fascicularis) [4]. Members of this genus live in ‘female-bonded’ societies where females remain in their natal group and preferentially bond with their female kin, while males typically disperse and immigrate into other groups, in this way avoiding incest and inbreeding depression.

To put the findings of age-related changes in social behavior and cognition for the members of this genus into perspective, a few words on their life-history seems warranted (see [11] for a more detailed account of the diversity of primate societies and life-history). Newborns spend the first six months of their life mostly with the mother, initially carried and held in a ventro-ventral position, and later also transported on the back of the mother or another group. There is considerable variation in care by other group members in the different species. At about six months, the weaning process
begins, which may involve severe tantrums and protests by the infant. Infancy ends at about 1.5 years of age, followed by a juvenile phase characterized by large amounts of play with peers and the initiation of grooming interactions with same aged- but also older group members by the young.

Adolescence commences at about 3.5 years in female macaques (some of which may already conceive at this age) and about 4.5 years in male macaques, although they are only fully grown at an age of about 7-8 years. In terms of life expectancy, the median survival for rhesus monkeys living in captivity was about 26 years of age. Ten percent of the monkeys reached an age of 35 years, and the oldest animal reportedly reached an age of 43 years [8–10]. Comparable data for Barbary macaques are unfortunately lacking. One of the oldest animals in the park where we conducted our studies died at an age of 31 (Ellen Merz, personal communication). In our study, we classified Barbary macaques from an age of 4 years for females and 5 years for males up to an age of 19 years as ‘adult’, between an age of 20 and 25 years as ‘old’, and beyond that age as ‘very old’.

Not surprisingly, the vast majority of studies on old and very old subjects to date are done on captive monkeys, as mortality rates of sick and old animals in the wild are high, making it difficult, if not impossible, to collect data on old and very old subjects. For captive animals, housing conditions may affect interaction rates as well as group composition through the selective removal or replacement of adult males to avoid competition or inbreeding. Although direct comparisons of activity budgets in the wild and in captivity are rare, it is safe to assume that the direction of age-related changes observed in captivity and in the wild is similar, although these changes may show different temporal dynamics due to the striking differences in stress levels and physical demands in the wild and in captivity.

**Changes in activity patterns with age**

Analyses of general activity patterns revealed conflicting results. Some studies found that older monkeys spend more time sleeping and resting than younger ones [12–15]. With increasing age, female Japanese macaques (*M. fuscata*) engaged in fewer social interactions [16], while aged female long-tailed macaques spent less time engaging in social interactions; this effect was more pronounced in low-ranking compared to high-ranking aged females [15]. Rank is of relevance in this context because higher-ranking animals are assumed to be more attractive to others than lower-ranking ones [17]. A study on rhesus macaques on the island of Cayo Santiago, Puerto Rico, was able to compare
the behavior of adult females and adult males. Old females spent less time in affiliative social
behavior, both directed towards others and received by others, and showed a smaller social network
size, while older males had similar numbers of partners as adult males [12]. No effect of rank was
detected in this study [12]. A study on aged female Japanese macaques, finally, found no decrease in
sociability with increasing age [18].

**Testing psychological theories of successful aging**

Studies of changes in social behavior in aging monkeys can also be used to test predictions
from psychological theory. As people age, they typically have fewer social partners (for a review see
[19]), which may impact health and increase mortality risk [20,21]. Different psychological theories
have attempted to explain the diminishing sociability occurring in old age: According to ‘disengagement
theory,’ a voluntary withdrawal from the society is a biologically determined and inevitable process
reflecting waning physical strength, ultimately culminating in death [22]. ‘Activity theory,’ in
contrast, presumes that older humans shift their previously pursued social activities to other behaviors
that are less physically engaging but still socially satisfying [23]. Although disengagement theory is no
longer very influential in psychology [4], it still received attention in studies of nonhuman primate
behavior [18] but see [24].

One of the theories opposing disengagement theory in human aging research is ‘socio-
emotional selectivity theory’ (SST). According to SST, goals shift across the life-span in relation to
perceived future time perspective [25,26]. In younger years, acquisition of skills and the establishment
of new social contacts are deemed beneficial under the assumption that benefits may be reaped at a
later stage. With a shrinking temporal horizon, people shift their attention to emotionally meaningful
partners and well-being. SST posits that the heightened motivation to maintain or increase well-being
in old age leads to a general focus on emotionally positive (over negative) social and non-social
stimuli in the environment. Importantly, changes in cognition (e.g., attention to positive stimuli) and
behavior (e.g., selective focus on familiar social partners) are attributed to underlying changes in
motivation due to a shrinking time extension rather than to age per se [25,26].

Finally, it has been proposed that people become more selective regarding which goals they
set for themselves in order to focus the declining resources on their most important goals (“Selection,
Optimization, Compensation” or “SOC-Model” [27,28]). The SOC-Model posits that across adulthood people shift from a primary gain orientation towards a stronger orientation to compensate losses in resources [27,28]. An interesting question is whether this model could be used to derive predictions regarding the investment into social relationships by the animals. According to the SOC-Model, younger individuals should be more willing to establish additional relationships because these may confer benefits later on, while older individuals are more focused on already existing relationships.

Motivational shifts in aging Barbary macaques

Almeling and colleagues recently set out to test the predictions of socio-emotional selectivity theory in nonhuman primates by comparing variation in age across different social and cognitive domains in large age-heterogeneous population of Barbary macaques [7] living at “La Forêt des Singes” [29]. This enclosure is a 20-ha large tourist attraction in which visitors are confined to a park, while the monkeys roam freely. Thus, the monkeys are extremely well habituated to humans. During the time of the study, 166 animals lived in the park in three different social groups with largely natural dynamics, including male transfer between groups during adolescence. The monkeys are fed fresh fruit, vegetables and grain several times a day and also feed on natural vegetation. Water is available at libitum. There is no predation risk and veterinary procedures are kept to a minimum. About one third of the subjects were older than 20 years; the oldest subject in the park was 30 years old during the time of the study. Females from an age of 4 years and males from an age of 5 years on were included in the study [7].

A combination of field experiments and behavioral observations allowed us to assess the role of motivational shifts in the absence of an awareness of a future time perspective. We were able to contrast changes in social behavior with performance in a variety of cognitive tests that assessed interest in the physical and the social environment, which allowed us to assess whether the subjects became increasingly selective in their activities, and whether these changes were indicative of motivational shifts rather than diminishing competence [7].

We first presented male and female subjects with different types of novel objects: animal toys and a plastic cube, and a tube that was baited with a food reward, allowing us to explore the effect of the food on the eagerness and persistence to explore the novel object [7]. The tube was closed with
soft tissue at both ends, so that the monkeys had to figure out how to retrieve the reward. Already in young adulthood, subjects lost interest in the toys (Fig. 1A), while the animals retained a high interest in the baited tube into old age (Fig. 1B). The time needed to open the tube increased with increasing age of the subjects, however, and none of the subjects older than 20 years was able to retrieve the reward within the time allotted (Fig. 1C). The results suggest that the presence of a food reward strongly influenced their interest in novel objects, although we did not directly compare the attractiveness of an identical object that was either baited or not. Regardless, we concluded that the exploration per se less appears less rewarding once the monkeys had reached adulthood. The increased latency to open the tube points to either motor impairments, or possibly decreasing cognitive flexibility that with increasing age [7].

To assess age-related changes in social interest, we adopted a protocol established by Schell and colleagues [30], which consists of the presentation of portrait photographs of conspecifics and recording their responses using a video camera for later analysis (blind to the condition) of the animals’ responses and looking time on a frame-by-frame basis. This previous study found that monkeys might take a keen interest in photographs and study them intently; it also indicated that older subjects generally showed less interest in the pictures than juveniles. Adults distinguished between pictures of members from a neighboring group compared to pictures from members of their own group (revealing a higher interest in the out-group members), however, while juveniles did not [30]. In the study by Almeling and colleagues on motivational changes in old age [7], male and female subjects were presented with photographs of new-born conspecifics, a close ‘friend’ or a ‘non-friend’, as defined by the frequency of affiliative interactions. The rationale was that in Barbary macaques, females maintain close bonds with both related and unrelated females, so that the ‘friends’ were not necessarily relatives of the subject. Moreover, males interact with infants at high rates [31]. When confronted with the photographs, both males and females showed a higher interest in pictures showing socially important partners (females: friends and infants; males: infants), and this preference was also observed in animals of old age.

We also conducted playback experiments [32] in which we played recruitment screams elicited in agonistic contexts [33] from close partners and non-friends to female subjects. Responses
were recorded on videotape and later analyzed blind to the condition on a frame-by-frame basis.

Females looked significantly longer towards the speaker after playback of screams of their ‘friends’ compared to their ‘non-friends’, but again, there was no significant effect of age on overall response strength. As a final measure to assess to which degree females keep track of the interactions between third parties, we determined how frequently they emitted ‘commentary’ vocalizations [33,34]. These vocalizations are typically given when animals are watching agonistic interactions or infant handling. Notably, we found that into very old age, females continued to vocally comment on interactions in their environments [7]. In summary, these results indicate that the monkeys did not show diminished interest or a lack of differentiation in response to different social stimuli.

Behavioral observation of female monkeys’ social interactions revealed that with increasing age, they spent less time actively grooming others. They also groomed fewer adult partners. In contrast, the time females received grooming and the number of individuals by whom they were groomed did not vary with age. Unfortunately, we were not able to clarify whether females specifically focused on ‘old friends’, as longitudinal data were lacking. We could rule out, however, that they only focused on relatives – instead, the majority of the top two active grooming partners were unrelated [7].

In conclusion, the monkeys lost interest in the non-social environment already in young adulthood and appeared to favor social over non-social stimuli (see Fig. 2 for a summary). Particularly noteworthy is the contrast between the diminished social activity in old age on the one hand, and the continued interest in social information on the other. Thus, the decrease in social activity does not appear to be driven by a loss of social interest. Instead, it may be the case that the monkeys specifically avoid social interactions to minimize the costs associated with aggressive interactions, because injuries are relatively costlier to old or very old subjects than to younger ones. Barbary macaques maintain not only affiliative and agonistic relationships but also ambiguous ones where the quality of the next interaction is rather unpredictable. Possibly, the uncertain outcome of future interactions might deter older monkeys from engaging in interactions with other group members to a greater degree than younger ones, as well. An alternative, but not mutually exclusive explanation might be the ‘positivity effect’ [35], which posits that in old age attention shifts towards positive
stimuli, because negative stimuli are perceived as increasingly aversive. Older humans, for instance, are more likely to remember positive than negative stimuli [35] (but see [36]). A recent experimental study set out to test this effect in nonhuman primates by presenting photographs depicting positive (affiliative) and negative (agonistic) facial expressions of conspecifics to rhesus monkeys on the island of Cayo Santiago [37]. Older monkeys were more attentive to negative signals than to positive ones, raising the question whether the high competition in this species may drive the allocation of attention (for a negativity effect in older humans see [38]). Complicating matters further, another study showed that previous exposition to positive or negative situations may affect attentional biases in captive rhesus monkeys [39]. Thus, the question of whether monkeys show positivity (or rather negativity) effects requires further investigation.

Younger Barbary macaques continued to groom old and very old females [7], although the benefits that groomers may gain appeared rather limited at first sight. One explanation might be that the continued grooming is a byproduct of the intense selection for sociality in monkeys. Indeed, monkeys with strong bonds have a higher reproductive success and live longer [40–42]. Consequently, groomers may value relationships per se, irrespective of the immediate gains they confer. An alternative view is to conceive grooming as a ‘currency’ that is traded in a ‘biological market’ [43]. If this holds true, older subjects should provide some benefits to young, for instance in the form of ‘vocal alliances’ in aggressive interactions. There was no effect of rank of the subject on the likelihood of being groomed, but a trend that higher ranking females had more contact partners than lower ranking females, irrespective of age (see supplementary material in [7]).

Taken together, the study by Almeling and colleagues [7] suggested that even without awareness of a limited lifetime, the monkeys continued to be interested in social stimuli, while losing interest in non-social stimuli (unless they were associated with a food reward). Furthermore, they reduced the number of social partners they actively sought to engage with. These findings imply that shifting preferences and goals in aging humans may be caused by both shared and ancestral changes in motivation, which in turn may be driven by changes in physiology. Specifically, internal reward structures may change across the life-span. Importantly, our results do not discount the idea that the awareness of limited lifetime impacts on preferences and goals in humans [25,26] [44].
At the empirical level, future studies should aim to collect a better understanding of the consequences of aging for the social networks of male primates. The majority of studies focusing on social aging in monkeys (including our own [7]) was restricted to females. While female macaques are bound into their matrilineal social network across lifetime, males are the dispersing sex and leave their natal group after reaching sexual maturity [11]. Their position in the group is not determined by a kin-based hierarchy but rather by their own ability to build up a network of supportive social relationships [45]. Male monkeys thus provide us with the opportunity to assess how aging impacts social bonding patterns under different cost-benefit scenarios.

Species comparisons provide a further avenue to assess how variation in life-history parameters may affect changes in motivation across age. In chacma baboons (Papio ursinus), where males disperse into new groups, they experience a rather short tenure as alpha males at best. During this time, they are able to reap the majority of copulations. In a system with stiff competition and no coalitionary support among males, males past their prime turn to interactions with their offspring, as long as these are still in their infancy [46]. This may be viewed as the best strategy to enhance reproductive success. Guinea baboons (P. papio), in contrast, live in a multi-level society with one-male-units consisting of a primary male and 1-6 females with their young [47]. Dispersal is female-biased. Males maintain strong bonds between each other that may last many years and show much lower levels of aggression than chacma baboons [48]. Older males that to do not have access to sexual reproduction affiliate with prime males and maintain social (but not sexual relationships) with the females associated with that particular male [47]. Although it is difficult to assess well-being in these animals, future studies may use glucocorticoid (GC) levels as a proxy for the physiological stress response and thus an indirect estimation of well-being. GC metabolites can be determined from feces, thus allowing for a non-invasive assessment of the physiological stress response [49].

To understand the variation in cognitive ability with age, further experiments that target different processes that shape cognitive performance are needed. For instance, inhibitory control, flexibility and persistence all shape problem-solving capacities. Whether these follow an inverted U-shaped trajectory, with low inhibitory control in very young and very old age, or another pattern remains a question for further investigation. In specific tasks, older subject may profit from
experience, for instance in pattern recognition, and a higher ability to transfer acquired knowledge
between tasks (generalization). It would be interesting to assess whether and up to which age primates
may be able to compensate the effects of cognitive decline due to physiological aging [5]. Sets of tests
that address these different cognitive components and their development across the life-span,
including the effects of training, would help us to develop a better understanding of cognitive
performance in old age.

At the conceptual level, more cross-talk between the disciplines is needed. For instance,
“goals” in human social psychology vs. animal behavior studies take on an entirely different
connotation. Humans are able to “set” goals such as acquiring a novel skill, advancing their career, or
maintaining close contact with the family; further they are able to reflect upon their ability to reach
them. In the animal literature, “goals” refer to the fulfillment of more or less immediate needs
(satisfying hunger, thirst, sexual interaction, social interaction etc.). The term is also used in the
context of “ultimate goals” at the evolutionary level, namely the maximization of inclusive fitness, i.e.
the number of gene copies pushed into following generations (reproductive success often serves as the
proxy here, but inclusive fitness may also be maximized indirectly by supporting relatives). These
differences in conceptualization of goals reveal the value as well as the limitations of using nonhuman
primates as models in aging research. Nonhuman primates are valuable precisely because they do not
“set goals”, as humans do, so that they allow us to study changes in motivation and cognition in the
absence of such goals; at the same time, they cannot tell us anything about the interaction between
variation in “set goals” and more fundamental physiological processes. To fill this gap in knowledge,
comprehensive studies on aging in different human societies with different conceptions of the passage
of time need to be considered. Furthermore, it is impossible to obtain “self-report” data from primates,
which renders specific research questions moot. For instance, Freund and colleagues [5] suggested to
integrate both subjective and objective criteria to judge the quality of older peoples’ life, i.e. whether
they are aging successfully. With nonhuman primates, we have to rely on indirect measures of their
well-being, as noted above.

In summary, after a trickle of studies on old aged primates in the last decades, there is now a
growing interest in shifts in motivation and cognitive performance with age in nonhuman primates. An
integrative research program that combines the investigation of physiological (including epigenetic) effects with behavioral and experimental studies that tap into variation in social behavior and cognition, respectively, will shed light on the orchestration and interplay that characterize aging in our closest living relatives. This, in turn, will aid aging research in humans to develop a better understanding of the biological basis of cognitive and social aging processes.

Acknowledgements

We are grateful to Ellen Merz and Gilbert and Guillaume de Turckheim for permission to study the Barbary macaques at “La Forêt des Singes” and making crucial demographic data available. I am indebted to Laura Almeling, Alexandra Freund, Kurt Hammerschmidt, Eva-Maria Rathke and Holger Sennhenn-Reulen for collecting data, running the analyses, passionate discussions, and above all, for sharing the endearment with the old ladies and gents residing in the monkey park. Alexandra Freund, Kurt Hammerschmidt and Laura Almeling provided valuable comments on the draft and Rebecca Jürgens helped with the final preparation of the manuscript. Funding from the Deutsche Forschungsgemeinschaft via the German Initiative of Excellence is gratefully acknowledged.
Figure 1. (A) Exploration time of a novel object (toy or a cube with colorful liquid) as a function of age. A permutation test of a linear mixed model [LMM] with N trials = 192, N subjects = 93 revealed a significant interaction between age and novel object type (data for the other objects not shown), p < 0.05, indicating a significant preference for the baited object into old age. (B) Proportion of successes in opening the tube baited with a peanut. Old subjects (> 19 years) failed to retrieve the peanut from the tube. The size of the points corresponds to number of subjects (N = 1-6) tested at a specific age (generalized linear model [GLM]: N subjects and trials = 53; effect of age, $\chi^2 = 11.81$, df = 1, $p < 0.001$. (C) The latency to open the tube steadily increased from young adulthood on (Spearman rank correlation, N subjects and trials = 21, rho = 0.61, p < 0.01). The maximum allotted time until the
experiment was aborted was 2 min., with 1 min. extension if the subject was still handling the tube
unsuccessfully after 2 min, resulting in the exclusion of all old and very old subjects who failed to
open the tube. Modified and reprinted with permission from [7].
Figure 2. (A) Summary of developmental trajectories observed in the study on aging Barbary macaques. “The monkeys lost interest in the physical environment relatively early in adulthood, whereas they maintained an interest in social information into very old age, irrespective of a decrease in social activity” (cited from graphical abstract for [7]). (B) Picture of a female Barbary macaque (age: 25 yrs.) residing at “La Forêt des Singes”.

339 Figure 2. (A) Summary of developmental trajectories observed in the study on aging Barbary macaques. “The monkeys lost interest in the physical environment relatively early in adulthood, whereas they maintained an interest in social information into very old age, irrespective of a decrease in social activity” (cited from graphical abstract for [7]). (B) Picture of a female Barbary macaque (age: 25 yrs.) residing at “La Forêt des Singes”.

344
References


27 Freund AM, Baltes PB: The orchestration of selection, optimization and compensation: An


37 Rosati AG, Santos LR: Changes in social cognition and decision-making across the lifespan in
semi-free ranging rhesus monkeys. IPS Conf Chicago 2016;


