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10 On the Social Life and Motivational Changes of Aging Monkeys

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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.

- 50 *Key Words:* Aging, Cognition, Decision-making, Evolution, Lifespan, Nonhuman Primates, Social
- 51 Relationships

On the Social Life and Cognitive Performance of Aging Monkeys

52
53 The increasing life expectancy of humans has spawned a growing research interest in age-
54 related changes not only with regard to health, but also cognitive ability and well-being [1].
55 Nonhuman primates have long played an important role in research of physiological aging processes,
56 as they reveal similar age-related changes as humans [2–4]. Yet, studies on nonhuman primates may
57 also help to develop a better understanding for the determinants of ‘successful’ aging, i.e. how
58 individuals cope with age-related shifts in the availability of resources [5,6]. Studies of aging in
59 nonhuman primates allow disentangling the influence of physiological processes and top-down
60 cognitive regulation on age-related changes in motivation and social behavior. In addition, such
61 comparative studies may aid to delineate more clearly how both competence and motivation contribute
62 to performance and problem-solving behavior in the social and the non-social domain. In the
63 following, I will briefly summarize the available evidence for age-related changes in cognitive
64 performance and social behavior in nonhuman primates (hereafter: ‘primates’). I will then discuss in
65 more detail the results of a recent study of motivational changes in aging Barbary macaques (*Macaca*
66 *sylvanus*), which was explicitly designed to test predictions from psychological theory [7], and will
67 conclude with some ideas for future research.

68 **Macaques as models in research on aging**

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

74 To put the findings of age-related changes in social behavior and cognition for the members of
75 this genus into perspective, a few words on their life-history seems warranted (see [11] for a more
76 detailed account of the diversity of primate societies and life-history). Newborns spend the first six
77 months of their life mostly with the mother, initially carried and held in a ventro-ventral position, and
78 later also transported on the back of the mother or another group. There is considerable variation in
79 care by other group members in the different species. At about six months, the weaning process

80 begins, which may involve severe tantrums and protests by the infant. Infancy ends at about 1.5 years
81 of age, followed by a juvenile phase characterized by large amounts of play with peers and the
82 initiation of grooming interactions with same aged- but also older group members by the young.
83 Adolescence commences at about 3.5 years in female macaques (some of which may already conceive
84 at this age) and about 4.5 years in male macaques, although they are only fully grown at an age of
85 about 7-8 years. In terms of life expectancy, the median survival for rhesus monkeys living in
86 captivity was about 26 years of age. Ten percent of the monkeys reached an age of 35 years, and the
87 oldest animal reportedly reached an age of 43 years [8–10]. Comparable data for Barbary macaques
88 are unfortunately lacking. One of the oldest animals in the park where we conducted our studies died
89 at an age of 31 (Ellen Merz, personal communication). In our study, we classified Barbary macaques
90 from an age of 4 years for females and 5 years for males up to an age of 19 years as ‘adult’, between
91 an age of 20 and 25 years as ‘old’, and beyond that age as ‘very old’.

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

100 **Changes in activity patterns with age**

101 Analyses of general activity patterns revealed conflicting results. Some studies found that
102 older monkeys spend more time sleeping and resting than younger ones [12–15]. With increasing age,
103 female Japanese macaques (*M. fuscata*) engaged in fewer social interactions [16], while aged female
104 long-tailed macaques spent less time engaging in social interactions; this effect was more pronounced
105 in low-ranking compared to high-ranking aged females [15]. Rank is of relevance in this context
106 because higher-ranking animals are assumed to be more attractive to others than lower-ranking ones
107 [17]. A study on rhesus macaques on the island of Cayo Santiago, Puerto Rico, was able to compare

108 the behavior of adult females and adult males. Old females spent less time in affiliative social
109 behavior, both directed towards others and received by others, and showed a smaller social network
110 size, while older males had similar numbers of partners as adult males [12]. No effect of rank was
111 detected in this study [12]. A study on aged female Japanese macaques, finally, found no decrease in
112 sociability with increasing age [18].

113 **Testing psychological theories of successful aging**

114 Studies of changes in social behavior in aging monkeys can also be used to test predictions
115 from psychological theory. As people age, they typically have fewer social partners (for a review see
116 [19]), which may impact health and increase mortality risk [20,21]. Different psychological theories
117 have attempted to explain the diminishing sociality occurring in old age: According to ‘disengagement
118 theory,’ a voluntary withdrawal from the society is a biologically determined and inevitable process
119 reflecting waning physical strength, ultimately culminating in death [22]. ‘Activity theory,’ in
120 contrast, presumes that older humans shift their previously pursued social activities to other behaviors
121 that are less physically engaging but still socially satisfying [23]. Although disengagement theory is no
122 longer very influential in psychology [4], it still received attention in studies of nonhuman primate
123 behavior [18] but see [24].

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

134 Finally, it has been proposed that people become more selective regarding which goals they
135 set for themselves in order to focus the declining resources on their most important goals (“Selection,

136 Optimization, Compensation” or “SOC-Model” [27,28]). The SOC-Model posits that across adulthood
137 people shift from a primary gain orientation towards a stronger orientation to compensate losses in
138 resources [27,28]. An interesting question is whether this model could be used to derive predictions
139 regarding the investment into social relationships by the animals. According to the SOC-Model,
140 younger individuals should be more willing to establish additional relationships because these may
141 confer benefits later on, while older individuals are more focused on already existing relationships.

142 **Motivational shifts in aging Barbary macaques**

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

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

161 We first presented male and female subjects with different types of novel objects: animal toys
162 and a plastic cube, and a tube that was baited with a food reward, allowing us to explore the effect of
163 the food on the eagerness and persistence to explore the novel object [7]. The tube was closed with

164 soft tissue at both ends, so that the monkeys had to figure out how to retrieve the reward. Already in
165 young adulthood, subjects lost interest in the toys (Fig. 1A), while the animals retained a high interest
166 in the baited tube into old age (Fig. 1B). The time needed to open the tube increased with increasing
167 age of the subjects, however, and none of the subjects older than 20 years was able to retrieve the
168 reward within the time allotted (Fig. 1C). The results suggest that the presence of a food reward
169 strongly influenced their interest in novel objects, although we did not directly compare the
170 attractiveness of an identical object that was either baited or not. Regardless, we concluded that the
171 exploration per se less appears less rewarding once the monkeys had reached adulthood. The increased
172 latency to open the tube points to either motor impairments, or possibly decreasing cognitive
173 flexibility that with increasing age [7].

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

190 We also conducted playback experiments [32] in which we played recruitment screams
191 elicited in agonistic contexts [33] from close partners and non-friends to female subjects. Responses

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

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

208 In conclusion, the monkeys lost interest in the non-social environment already in young
209 adulthood and appeared to favor social over non-social stimuli (see Fig. 2 for a summary). Particularly
210 noteworthy is the contrast between the diminished social activity in old age on the one hand, and the
211 continued interest in social information on the other. Thus, the decrease in social activity does not
212 appear to be driven by a loss of social interest. Instead, it may be the case that the monkeys
213 specifically avoid social interactions to minimize the costs associated with aggressive interactions,
214 because injuries are relatively costlier to old or very old subjects than to younger ones. Barbary
215 macaques maintain not only affiliative and agonistic relationships but also ambiguous ones where the
216 quality of the next interaction is rather unpredictable. Possibly, the uncertain outcome of future
217 interactions might deter older monkeys from engaging in interactions with other group members to a
218 greater degree than younger ones, as well. An alternative, but not mutually exclusive explanation
219 might be the ‘positivity effect’ [35], which posits that in old age attention shifts towards positive

220 stimuli, because negative stimuli are perceived as increasingly aversive. Older humans, for instance,
221 are more likely to remember positive than negative stimuli [35] (but see [36]). A recent experimental
222 study set out to test this effect in nonhuman primates by presenting photographs depicting positive
223 (affiliative) and negative (agonistic) facial expressions of conspecifics to rhesus monkeys on the island
224 of Cayo Santiago [37]. Older monkeys were more attentive to negative signals than to positive ones,
225 raising the question whether the high competition in this species may drive the allocation of attention
226 (for a negativity effect in older humans see [38]). Complicating matters further, another study showed
227 that previous exposition to positive or negative situations may affect attentional biases in captive
228 rhesus monkeys [39]. Thus, the question of whether monkeys show positivity (or rather negativity)
229 effects requires further investigation.

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

240 Taken together, the study by Almeling and colleagues [7] suggested that even without
241 awareness of a limited lifetime, the monkeys continued to be interested in social stimuli, while losing
242 interest in non-social stimuli (unless they were associated with a food reward). Furthermore, they
243 reduced the number of social partners they actively sought to engage with. These findings imply that
244 shifting preferences and goals in aging humans may be caused by both shared and ancestral changes in
245 motivation, which in turn may be driven by changes in physiology. Specifically, internal reward
246 structures may change across the life-span. Importantly, our results do not discount the idea that the
247 awareness of limited lifetime impacts on preferences and goals in humans [25,26][44].

248 At the empirical level, future studies should aim to collect a better understanding of the
249 consequences of aging for the social networks of male primates. The majority of studies focusing on
250 social aging in monkeys (including our own [7]) was restricted to females. While female macaques are
251 bound into their matrilineal social network across lifetime, males are the dispersing sex and leave their
252 natal group after reaching sexual maturity [11]. Their position in the group is not determined by a kin-
253 based hierarchy but rather by their own ability to build up a network of supportive social relationships
254 [45]. Male monkeys thus provide us with the opportunity to assess how aging impacts social bonding
255 patterns under different cost-benefit scenarios.

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

271 To understand the variation in cognitive ability with age, further experiments that target
272 different processes that shape cognitive performance are needed. For instance, inhibitory control,
273 flexibility and persistence all shape problem-solving capacities. Whether these follow an inverted U-
274 shaped trajectory, with low inhibitory control in very young and very old age, or another pattern
275 remains a question for further investigation. In specific tasks, older subject may profit from

276 experience, for instance in pattern recognition, and a higher ability to transfer acquired knowledge
277 between tasks (generalization). It would be interesting to assess whether and up to which age primates
278 may be able to compensate the effects of cognitive decline due to physiological aging [5]. Sets of tests
279 that address these different cognitive components and their development across the life-span,
280 including the effects of training, would help us to develop a better understanding of cognitive
281 performance in old age.

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

302 In summary, after a trickle of studies on old aged primates in the last decades, there is now a
303 growing interest in shifts in motivation and cognitive performance with age in nonhuman primates. An

304 integrative research program that combines the investigation of physiological (including epigenetic)
305 effects with behavioral and experimental studies that tap into variation in social behavior and
306 cognition, respectively, will shed light on the orchestration and interplay that characterize aging in our
307 closest living relatives. This, in turn, will aid aging research in humans to develop a better
308 understanding of the biological basis of cognitive and social aging processes.

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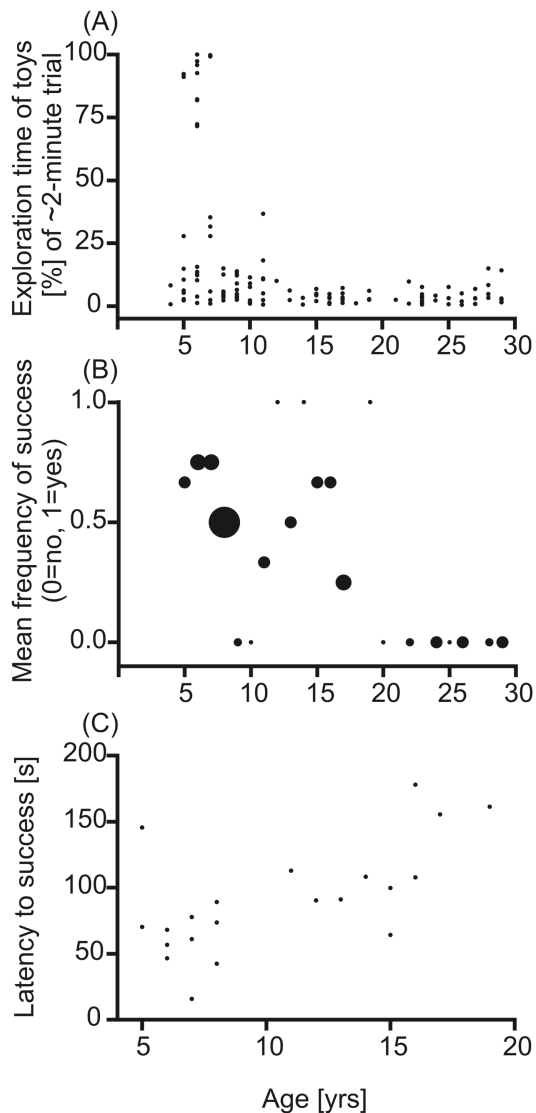
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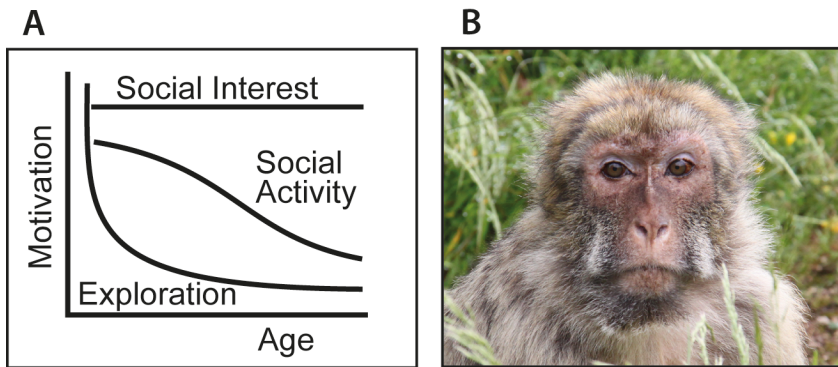
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323 Figure 1. (A) Exploration time of a novel object (toy or a cube with colorful liquid) as a function of
 324 age. A permutation test of a linear mixed model [LMM] with N trials = 192, N subjects = 93 revealed
 325 a significant interaction between age and novel object type (data for the other objects not shown), $p <$
 326 0.05, indicating a significant preference for the baited object into old age. (B) Proportion of successes
 327 in opening the tube baited with a peanut. Old subjects (> 19 years) failed to retrieve the peanut from
 328 the tube. The size of the points corresponds to number of subjects (N = 1-6) tested at a specific age
 329 (generalized linear model [GLM]: N subjects and trials = 53; effect of age, $\chi^2 = 11.81$, $df = 1$, $p <$
 330 0.001. (C) The latency to open the tube steadily increased from young adulthood on (Spearman rank
 331 correlation, N subjects and trials = 21, $\rho = 0.61$, $p < 0.01$). The maximum allotted time until the

332 experiment was aborted was 2 min., with 1 min. extension if the subject was still handling the tube
333 unsuccessfully after 2 min, resulting in the exclusion of all old and very old subjects who failed to
334 open the tube. Modified and reprinted with permission from [7].

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

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