Social information processing across the life-span in Barbary macaques

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Article

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Abstract

According to the Strength-and-Vulnerability-Integration (SAVI) model, older people are more motivated to avoid negative affect and high arousal than younger ones. To explore the biological roots of this effect, we investigated communicative interactions and social information processing in Barbary macaques (*Macaca sylvanus*) living at 'La Forêt des Singes' in Rocamadour, France. The study combined an analysis of the use of (N = 8185 signals, 84 signalers) and responses to communicative signals (N = 3672 events, 84 receivers) with a field experiment (N = 166 trials, 45 subjects). Here we here show that older monkeys were not more likely to specifically ignore negative social information or to employ avoidance strategies in stressful situations, although they were overall less sociable. We suggest that the monkeys have only a limited capacity for self-regulation within social interactions and rather rely on general avoidance strategies to decrease the risk of potentially hazardous social interactions.

Introduction

Older humans report a higher life-satisfaction than persons in mid-adulthood [e.g., 1]. A number of prominent life-span developmental theories have aimed to explain why this is the case. Social Selectivity Theory (SST) focuses on the importance of a limited future time perspective, which drives behaviors that enhance well-being [2]. The Strength-and-Vulnerability-Integration (SAVI) model emphasizes that older humans aim to avoid situations that could potentially lead to adverse outcomes, because they are associated with higher arousal [3]. The SAVI model suggests that older humans avoid interpersonal conflicts and potentially stressful situations by shifting the attention away from the stressor or waiting for the situation to be resolved [4]. Both SST and the SAVI model are empirically well supported [5,6]. The avoidance of negative experience is considered a result of self-regulation processes [7]. Both bodies of theory imply a sophisticated conception of time and may also involve meta-cognitive skills. Yet, changing preferences might also be related to age-related changes in the internal reward system [8], raising the question to which degree age-related changes in such biological processes (senescence) contribute to the observed age-related changes in human preferences.

Studying aging nonhuman primates (hereafter 'primates') allows distinguishing the importance of higher-level cognitive insight from more basic biological processes that contribute to motivational changes during the life-span. Primates undergo similar physiological changes during aging as humans [9,10], but there is no evidence that they are aware of their limited future time [11]. Moreover, their social behavior is not affected by cultural norms [12]. Studies of age-related changes in primate social behavior thus provide the opportunity to put some of the assumptions of life-span psychological theories to a test [13–15].

Here we set out to test hypotheses derived from life-span psychological theories in Barbary macaques (*Macaca sylvanus*). With increasing age, female Barbary macaques have fewer partners. They engage in fewer but more extended affiliative interactions, which has been taken as evidence for an age-related increase in social selectivity [13,16]. Males experience similar changes in sociality as females [17]. But how precisely do older individuals maneuver in their social groups? Is there evidence that older individuals strategically avoid negative affect, similar to humans? We here set out to study how older individuals regulate their social interactions by analyzing how the use and the responses to communicative signals vary with age, combining an analysis of natural signal exchanges with a field experiment.

There are two ways in which communicative behavior may contribute to altered social behavior: signalers may change the propensity with which they use specific signals, and receivers may change the tendency to respond to particular signals. Following the SAVI model, we expected that older Barbary macaques would be less likely to initiate social interactions using communicative signals than younger monkeys and predicted that this effect would be more pronounced for agonistic signals. We further predicted that older monkeys would be less responsive to other monkeys' signals and that the effect would be more pronounced for agonistic signals. Specifically, we expected that older monkeys would be more likely to adopt avoidance or de-escalation strategies such as ignoring others' signals or walking away (study 1). In addition, we conducted a field experiment in which we presented pictures of unknown conspecifics displaying agonistic ('open mouth threat face') or neutral facial expressions (study 2). We predicted that older monkeys would spend less time looking at pictures depicting agonistic facial expressions.

Neither the analysis of the responses to signals nor of the responses in the experiment revealed evidence for a specific avoidance of negative compared to positive or neutral social signals. We suggest that the monkeys have only a limited capacity for self-regulation within social interactions.

General Methods

Study site and subjects

We conducted this study in 2017 and 2018 in the enclosure 'La Forêt des Singes' in Rocamadour, France [18]. During the study period, 170-180 Barbary macaques aged between 0-30 years (see Supplementary Table 1) lived in the park, split into three social groups. Data collection took place in two of the three groups 5 to 6 days a week, from 9 am to 8 pm. Focal observations were balanced across daytime and observer. Animals in the PB group were observed in 2017; animals in the GB group in 2018. We considered monkeys as 'young' up to an age of 9 years, as 'middle-aged' between 10 and 19 years, and as 'old' when they were 20 years and older. Note that in the statistical analyses, age was always entered as a continuous variable.

Study 1

Methods

Data collection

We collected an average of 26.0 observation hours from each of 84 subjects (N = 50 females) (range: 24 h 38’-27 h 25’, except for one male who died and was observed for 12 h 31’, resulting in a total of 2180 observation hours). We conducted 30-min continuous focal protocols [19] using handheld devices (Samsung Galaxy Note 2) with the software program Pendragon Forms (Pendragon Software Cooperation, Libertyville, IL, USA). During focal observations, we recorded all social interactions of focal animal and extracted all instances of the use of agonistic and affiliative signals. Agonistic signals included threat stare, open-mouth threat, head bob, ground slap, silent scream face and scream face; affiliative signals included teeth-chatter and lip-smack, as well as the responses by the interaction partner. We further noted additional agonistic interactions *ad libitum* to establish the dominance hierarchies. To this end, we used all dyadic and decided agonistic interactions (submissive reaction and no counter-aggression). We determined the dominance rank based on the normalized David’s score, implemented in the *EloRating* package in R [20]; for further details see [17].

Statistics and Reproducibility

Signal usage

We conducted all analyses in the R environment (see Supplementary Table 2 for all version numbers). For the analysis of signal use, we used a General Linear Model (GLM) with negative binomial error distribution and logit link function, applying the function *glm.nb* of the R package *MASS*. Model 1 comprised the analysis of the use of agonistic signals; model 2 the analysis of affiliative signals. A Poisson distribution did not provide a good fit as both response variables appeared overdispersed given the model. Age and rank were z-transformed to a mean of zero and a standard deviation of one to ease interpretability of the model estimates. Rank was only included in the analysis of affiliative signals but not used in the analysis of agonistic signals, because the dominance rank was mainly based on the occurrence of agonistic signals. Hence, the inclusion of rank would have created a circular situation. We included focal observation time (log-transformed) as an offset term [21]. We checked the stability of both models using the function *dfbeta* and for potential collinearity issues by determining Variance Inflation factors (VIF) using the function *vif* [22] of the R package *car*.

The analysis of the agonistic signals revealed that a quadratic relationship better predicted age-related variation in the number of signals. However, it should be kept in mind that the inclusion of age squared represents an a-posteriori hypothesis. Hence, caution is required when interpreting such adjusted models.

The sample analyzed for these models comprised a total of 84 signalers (50 female) which produced a total of 5485 agonistic signals (model 1) and 2700 affiliative signals (model 2). None of the two models was overdispersed (dispersion parameters, model 1: 0.942; model 2: 1.032), and collinearity was also not an issue (maximum VIF, model 1: 1.001; model 2: 2.692). Both models also were of good (model 1) or moderate stability (model 2) as assessed by means of DFBeta values.

Probability of showing any response

With model 3, we estimated the extent to which the probability of *showing any response* was influenced by receiver age. We fitted a Generalized Linear Mixed Model (GLMM) [23] with binomial error structure and logit link function [21]. We included receiver age and its interaction with the signal category (agonistic or affiliative) as our key test predictors with fixed effects. We also included the age and the sex of the signaler and also the main effect of signal category as control fixed effects. We included random intercept effects for the identity of the receiver, the signaler, and the receiver-signaler dyad to avoid pseudo-replication. To prevent an overconfident model and keep the type I error at the nominal level of 0.05, we included random slopes [24,25] of receiver age, signal category, and their interaction within signaler and also those of signal category, signaler age, and signaler sex within receiver. We also included parameters for the correlations among random intercepts and slopes. To avoid cryptic multiple testing [26], we compared this full model with a null model that lacked receiver age and its interaction with signal category in the fixed-effects part.

The model was fitted using the function *glmer* of the R package *lme4*. Prior to fitting the model, we z-transformed receiver age and signaler age to achieve easier interpretable estimates and to ease model convergence. We manually dummy coded and then centered signal category and signaler sex before including them as random slopes. We determined confidence intervals of model estimates and fitted values by means of a parametric bootstrap (function *bootMer* of the R package *lme4*; 1000 bootstraps). Significance of individual effects we obtained by dropping them from the full model, one at a time, and comparing the respective reduced models with the full model. All model comparisons were based on likelihood ratio tests [27]. To estimate model stability we excluded signalers, receivers, and dyads one at a time, fitted the full model to each of the subsets and compared the estimates derived with those for the full data set. The model had a good stability in the fixed-effects part and did not suffer from collinearity [22] as indicated by a maximum Variance Inflation Factor of 1.023 (based on a model lacking the interaction).

The sample analyzed for this model comprised a total of 3115 events where we noted the responses of females (N=846 to affiliative and N=2269 to agonistic signals). Signals were given by 83 signalers to 50 receivers, which together formed 1005 signaler-receiver dyads. We observed a total of N = 2238 behavioral reactions and N = 877 ‘no response’. For male receivers, we observed a total of N = 557 events (279 affiliative, 278 agonistic signals). Males showed no responses to signals of others in 85 affiliative signaling events and 158 agonistic signaling events. Due to the smaller sample size and the model complexity, we refrained from further analyses of male receiver behavior.

Type of response

We next addressed which types of response individuals produced after an agonistic signal and how this choice was affected by receiver age (model 4). As above, we included the signaler’s age and sex as control factors. The reason that we did not consider responses after both signal types within one analysis was that most response types occurred exclusively in response to one signal category (‘Lip Smack’ only after affiliative signals; ‘Give Ground’, ‘Make Room’, ‘Present’, and ‘Squeak’ only after agonistic signals).

In the analysis of response types observed following agonistic signals, we included the patterns 'Give Ground', 'Make Room', 'Present', and 'Lip Smack', as these occurred with sufficient frequency (> 25, Supplementary Table 3). The model fitted was identical to the model of 'any response' (model 3; with the exception that it lacked signal category in the fixed as well as random-effects part. Since the response was multinomial and since we were not aware of an option to fit such a model with complex random effects structure in a maximum likelihood framework, we decided to use a Bayesian framework and utilized the function *brm* of the R package *brms*. We fitted the model with a maximum tree depth of 20 and set adapt delta to 0.99. The chains successfully converged as indicated by Rhat values between 1.000 and 1.001. The sample considered for this model comprised a total of 1594 responses by 50 receivers in response to signals of 81 signalers; signalers and receivers formed 654 dyads. We did not conduct a separate analysis for response types after affiliative signals, as the two types that occurred most frequently were relative similar facial expressions ('Lip Smack' and 'Teeth Chatter').

Data availability statement

Data and code for all analyses are available at https://osf.io/vjeb3/?view_only=7de3d702357844739d7a4da6fe5c5759.

Results

Signal usage

The use of agonistic signals varied with age and sex (model 1; Likelihood Ratio test for negative binomial models: LR statistic = 48.89, $df = 3$, $P < 0.001$; Fig. 1a, Supplementary Table 4). The use of agonistic signals was highest in mid-adulthood, and males used such signals more frequently than females. To illustrate the monkeys' behavior, young males used on average 2.43 agonistic signals/h, and young females 1.88 signals/h. In mid-adulthood, males used 4.15 agonistic signals/h and females 2.65 signals/h. For old males, the rate of agonistic signals was 2.55 signals/h, and for old females 1.25 signals/h.

The use of affiliative signals also varied with age, sex, and rank (model 2; Likelihood Ratio test LR statistic = 33.85, $df = 2$, $P < 0.001$; Fig. 1B; Supplementary Table 5). On average, females produced affiliative signals more frequently than males, and young and mid-adult subjects more frequently than old ones. More specifically, young males produced on average 0.99 affiliative signals/h, and young females 2.39 signals/h. In mid-adulthood, males produced 0.43 affiliative signals/h and females 1.21 signals/h. For old monkeys, the rate of affiliative signals was 0.96 signals/h for males and 0.55 signals/h for females.

Responses to signals

There was no evidence that the likelihood to react varied with age and signal category (no significant interaction between age and signal category: model 3, = 0.27, $P = 0.606$). The likelihood to respond to signals by others was not obviously different in older compared to younger females (Fig. 2) and did not vary with signal category. The probability of a response was ca. 0.8 for affiliative as well as agonistic signals (Supplementary Table 6). Concerning the control predictors, we found that the probability to respond clearly varied with signaler age, however: the older the signaler, the less likely it was that the recipient responded to that signal (Fig. 3).

Type of response

Receiver age had no strong effect on the type of response (Fig. 2). With regard to the control predictors, we found that 'Teeth chatter', a low-cost submissive signal, occurred more frequently in response to aggressive signals by females than to aggressive signals by males (the other three response types occurred with roughly comparable frequencies after female and male signals).

A follow-up analysis of the different response types showed that old females were generally more likely to respond to an agonistic signal with 'Teeth chatter'. While receiver age did not strongly affect the likelihood to respond, signaler age did. The likelihood that females responded to a signal was 83% for the youngest monkeys' signals, 72 % for middle-aged monkeys' signals. The response rate to old monkeys' signals was 57% (Supplementary Fig. 1). The likelihood to respond varied neither with signaler sex nor signal category (Supplementary Table 7).

Discussion

Older monkeys used fewer affiliative signals such as teeth chattering and lip-smacking than younger monkeys, and males used affiliative signals less frequently than females. The variation in signal usage corresponds to the variation in affiliative signals involving physical interactions [16,17]. Young females showed the highest rates of affiliative signals, suggesting that they have the highest motivation to establish and consolidate social bonds. In line with previous studies, males used agonistic signals more frequently than females. The age-related trajectory in the use of agonistic signals by males is in line with the peak of their resource holding potential around 15 years of age [28,29].

The social reclusion of older males and females appears to result from two processes, driven by younger individuals on the one hand, and the old individuals on the other. First, older monkeys are less often the targets of interactions and interact with fewer partners [17]. Second, signals produced by older monkeys were more likely to be ignored by other group members, suggesting that older monkeys are perceived both as less threatening and less valuable as social partners. Yet, old individuals may maintain specific relationships with selected partners. Detailed analyses of the long-term development of dyadic relationships will be needed to explore the differentiated use of and responses to signals with regard to the relationship quality of a dyad.

Concerning the responses to other group members' signals, our results did not conform to the predictions of the SAVI model. We did not find the predicted interaction between age and signal type in the responses to group members' signals, as older monkeys were not more likely to ignore or move away from agonistic signals as a strategy to regulate negative affect.

Study 2

Methods

Data collection

We conducted the field experiment in the GB group from April to June 2018. We tested 47 monkeys, including 25 adult females (5 to 30 years old), 13 adult males (7-27 years old), and nine juvenile / sub-adult males (2-6 years old). Following the procedures described in [30], we presented the monkeys with photographs of conspecifics with different types of facial expressions and measured the time spent looking at the picture. Pictures were taken from members of the other groups in the park. As individuals of the social groups rarely interact with one another, we did not need to control for the animals' social relationships in the analysis. We took 26 pairs of pictures (11 from females, 15 from males) of neutral and mildly agonistic facial expressions ('open mouth threat face') using a Nikon E-300 photo camera. We printed the photos on matte DIN-A4 paper in 0.17 m diameter and used each picture two to five times. In total, we presented every subject with up to two pairs of photos (one male and one female pair). The identity of the subject on the photo was constant within a pair. Within each pair, we balanced the order of presentation for the type of facial expression (agonistic/neutral) and randomized the assignment of the picture pairs to the subjects.

For any given trial, the photo was placed in a wooden frame with two plastic rails to keep it in place. The experimenter was blind concerning the type of facial expression. The experimenter sat down approximately three meters away from the test subject with the wooden frame and a photo inside. White cardboard covered the photo before the test started. During the testing procedure, the experimenter wore a baseball cap and sunglasses to avoid eye-contact with the subject. The experimenter began filming the scene using a Panasonic HC-X929 video camera and attracted the subject's attention by tapping against the wooden frame. Once the subject looked up or in the direction of the photo, the experimenter removed the cover and filmed the monkey's response for one minute. When the monkey left the test area (1-m radius around the test setting), the trial ended. After each trial, there had to be at least a break of four days before testing the same subject to avoid habituation to the testing paradigm.

We conducted a total of N = 177 trials with N = 47 subjects. Eleven trials had to be excluded from the analysis, either because the pairwise presentation could not be completed (N = 9 trials) or experimenter error (N = 2 trials), resulting in 166 trials with 45 subjects for analysis. Supplemental movie 1 provides an example of a subject's response.

Statistical Analyses

We assessed looking time by examining the videos frame-by-frame with 25 frames per second with the program Mangold Interact (Version 17). We scored the duration of the 'first look', i.e., the time from looking at the photo until the animal looked away for the first time, to measure initial interest and also scored the total looking time within the first minute as a measure of the overall interest. Additionally, we recorded the occurrence of self-directed behaviors (yawn, scratch, or self-grooming), communicative signals (lifting eye-brows, head bob, lip-smack) and picture manipulation (touch), but used these only for descriptive purposes. The inter-observer reliability was assessed for N = 56 of the video clips using the intra-class reliability correlation coefficient (ICC(1,k) from the R package *irr*. The agreement was excellent [31] for looking time (0.98) and the behavior towards the pictures (1.0).

To estimate the effects of age on the looking time, we fitted Linear Mixed Models [LMM; 23], using the function *lmer* from the package *lme4* [32]. We fitted one model for the initial looking time (model 5a) and one for the total looking time (model 5b). We included subject age, subject sex, picture type (agonistic/neutral), the interaction between subject age and picture type, and sex of the subject shown in the picture as fixed effects, the IDs of the test subject and of the subject shown in the picture as random effects. We included random slopes of picture sex and picture type within signaler ID; and age, picture type, and the interaction between age and picture type within picture ID. We used a likelihood ratio test to compare the full model, including all predictors, with the null model lacking the predictors of interest.

We checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visual inspection of a qq-plot of the residuals and residuals plotted against fitted values. The inspection of the correlation between the predicted values and the residuals were not ideal (slight positive correlations), most likely due to the small number of repeated measures per individual. We accepted this deviation from the assumptions. Given the absence of any strong effects apparent in the data, we do not believe that the deviation affects our conclusions. As above, we determined Variance Inflation Factors using the R package *car*. None of the VIFs exceeded 2.0, thus not raising concerns. We used a likelihood ratio test to compare the full model, including all predictors with the null model lacking the predictors of interest. Estimates for the fixed effects were extracted using the R package *lmerTest*.

Results

Neither the interaction between age and picture type, nor age or picture type were strongly related to variation in initial looking time (Fig. 5) or total looking time. We found no significant differences between the full and the null models (initial looking time: =1.56, P = 0.457; total looking time =1.02, P = 0.60). In the analysis of total looking time, the number of presentation (first or second pair) had a significant effect on looking time, with looking time being significantly shorter for the second pair; see Supplementary Table 8-11 for the model outputs for all analyses of looking time).

Discussion

We did not find the predicted interaction between age and facial expression category, suggesting that older monkeys did not specifically avoid negative social information. We are relatively confident that the lack of distinct responses is not due to issues with the methodology, as this method had been used to reveal differential interest in out-group vs. in-group conspecifics [30]and babies and friends vs. non-friends [13] in this population. The lack of an age effect more generally corroborates previous findings in this study population (Almeling et al., 2016) that the interest in social information remains stable, although the rate of social interactions declines. The results underscore the importance of distinguishing between the motivation to engage in potentially detrimental social interactions and the motivation to obtain in social information.

The pattern observed in the Barbary macaques differed from that reported for rhesus monkeys, *Macaca mulatta.* In this species, a comparable study involving the presentation of photographs showing male and female monkeys with different facial expressions, older monkeys looked less at the pictures than younger ones, but the age-related decrease was attenuated for the threat photo [14]. These results did not conform to the predictions of the SAVI model either.

Rhesus macaques differ from Barbary macaques in terms of their social tolerance and are classified as a rather despotic species [33]. Interestingly, female rhesus macaques showed selective attention to agonistic interactions of third parties compared to affiliative ones [34]. Barbary macaques, in contrast, live in a relatively egalitarian system [35] with a significant share of ambivalent relationships and ambiguous social signals [36]. Coalitionary support by others is a major determinant of conflict outcome [29,37]. Therefore, the agonistic facial expression may elicit less attention in Barbary macaques than in rhesus macaques. Our study lends further support for the notion that differences in social structure, including the quality of relationships and steepness of the rank hierarchy, shape the allocation of social attention [38].

General Discussion

Older monkeys did not specifically avoid negative social information, neither in the behavioral observations nor the field experiment. Thus, the predictions from the SAVI model were not met. In the behavioral observations, we also found no evidence for a 'positivity effect' [39], according to which older persons favor positive information and avoid negative one. Rather than to use signals strategically with the aim to shape the kind of interaction, older monkeys appeared to avoid physical interactions more generally [16,17]. Overall, our results as well as those by Rosati and colleagues [15] suggest that the general motivation to engage in social interactions declines with age in both humans and different nonhuman primate species. So far, the evidence suggests that only humans are able to employ more sophisticated self-regulation strategies in old age. For instance, the model of Selection, Optimization, and Compensation [40] stresses the importance of active goal setting, the use of adaptive strategies to attain these goals, and the switching to alternative strategies when previous ones are no longer efficient [41,42].

Likewise, older adults are assumed to employ cognitive control mechanisms to regulate their emotions [39]. It appears unlikely that nonhuman primates have such control mechanisms at their disposal; instead, they very much “live in the moment”, and age-related changes in sociality or problem-solving are related to changes in motivation [13].

Interestingly, a recent large-scale survey involving 1.7 million respondents in 166 countries observed only small age-related differences in negative affect or life satisfaction in humans across the life-span, but a substantial decrease in positive affect with increasing age [43]. That is, a central tenet in lifespan developmental theories has been called into question. At the same time, substantial differences between different cultural regions were found. The differences between different cultures – but also between humans and nonhuman primates – highlight the need for further research on the question how affective experience, emotion regulation, and emotion perception vary with age, individual experience, and cultural background [44]. Future studies should involve experimental paradigms that can be applied to both humans and nonhuman primates, to develop a comprehensive understanding how evolved biological processes and cognitive evaluation interact and contribute to emotion regulation.

Declarations

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Author contributions

E.M.R. and J.F. developed the study concept and design. E.M.R. collected the data. All authors performed the statistical analysis and prepared the figures. E.M.R. and J.F. drafted the manuscript, and J.F. compiled the final version.

Competing interests

The authors declare no competing interests.

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Figures

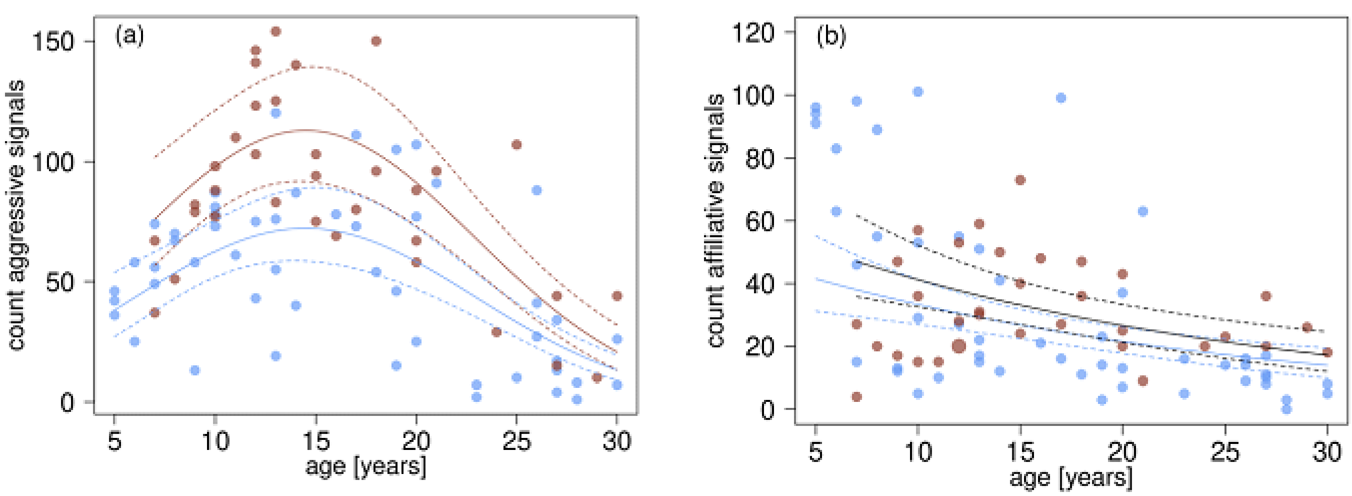

Figure 1

Variation in signal usage in relation to age. a) Total number of agonistic (model 1) and **b)** affiliative (model 2) signals. Females are represented by blue, males by brown points. Point size represents the frequency of a signal at a given age (range 1 to 2). The solid lines depict the fitted model, and the dashed lines indicate their lower (2.5 %) and upper (97.5 %) confidence limits. The model shown in **b)** is for an individual with an average rank (determined separately for females and males).

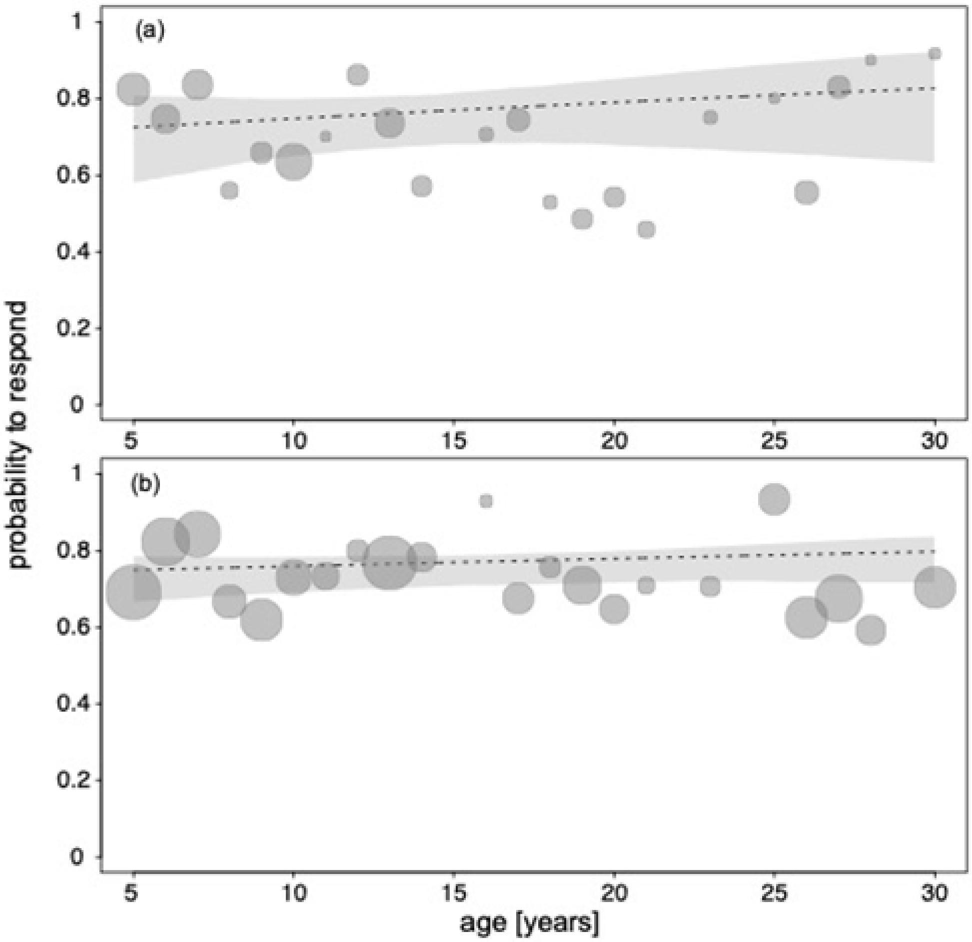

Figure 2

Effect of receiver age on the probability to respond to in relation to signal category. a) affiliative, **b)** agonistic signals. The area of the points represents the number of events per age (range: 10 to 233). Dashed lines and he grey polygons indicate the fitted model and its (2.5 % and 97.5 %) confidence limits (for all other terms in the model being centered to a mean of zero).

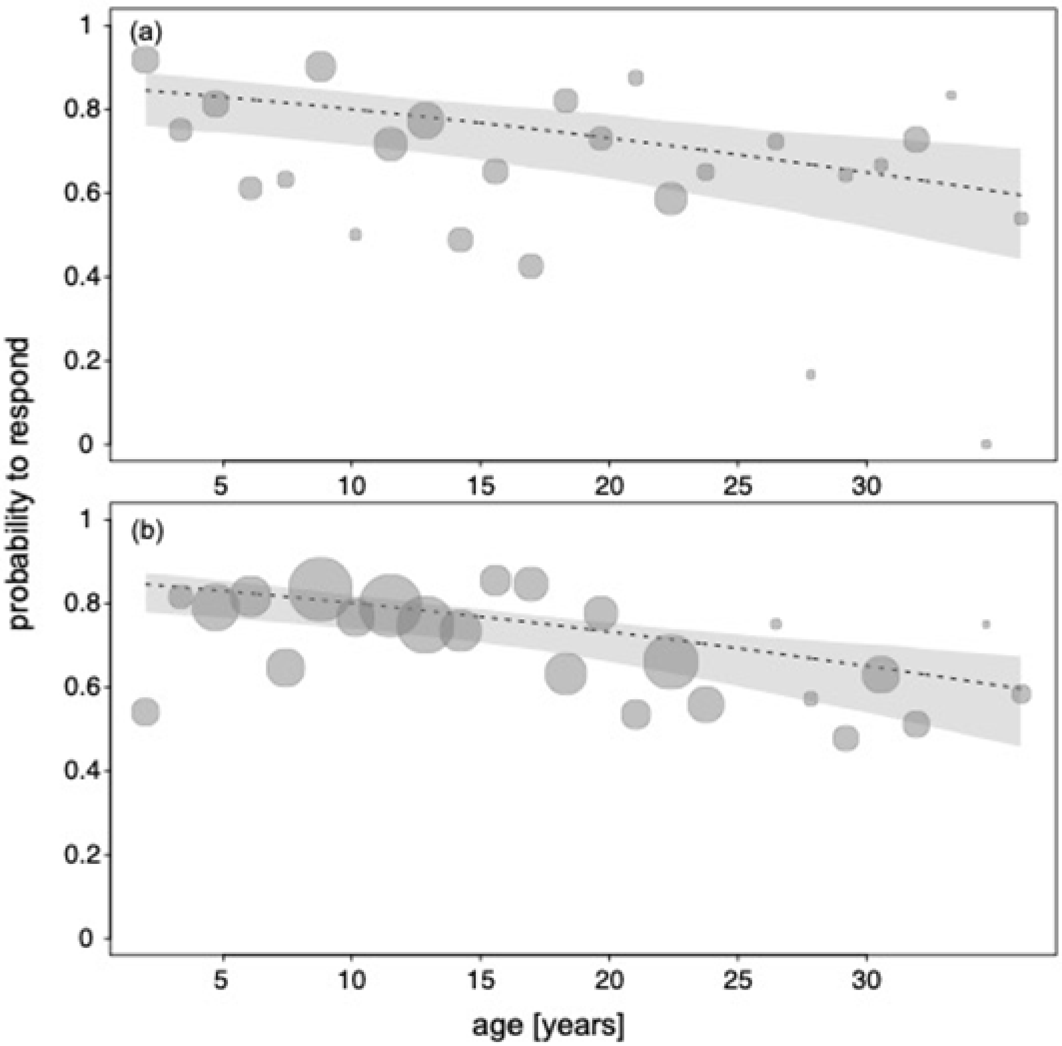

Figure 3

Effect of signaler age on the probability to respond to a signal. a) affiliative, **b)** agonistic signals. The area of the points represents the number of events per age (range: 4 to 264). Dashed lines and the grey polygons indicate the fitted model and its (2.5 % and 97.5 %) confidence limits (for all other terms in the model being centered to a mean of zero).

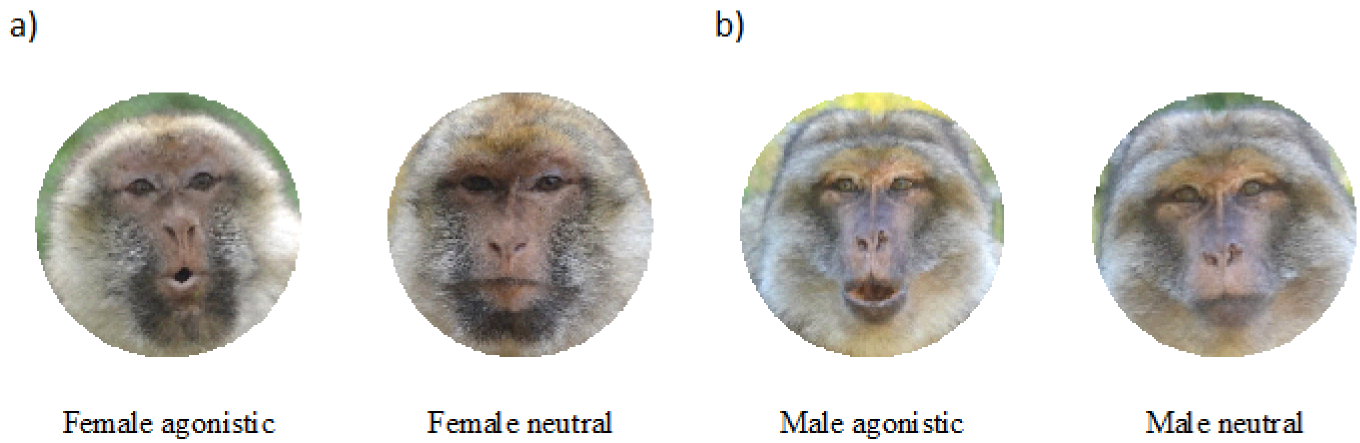

Figure 4

Stimuli used in the experiment. **a)** female agonistic and neutral facial expression; **b)** male agonistic and neutral facial expression.

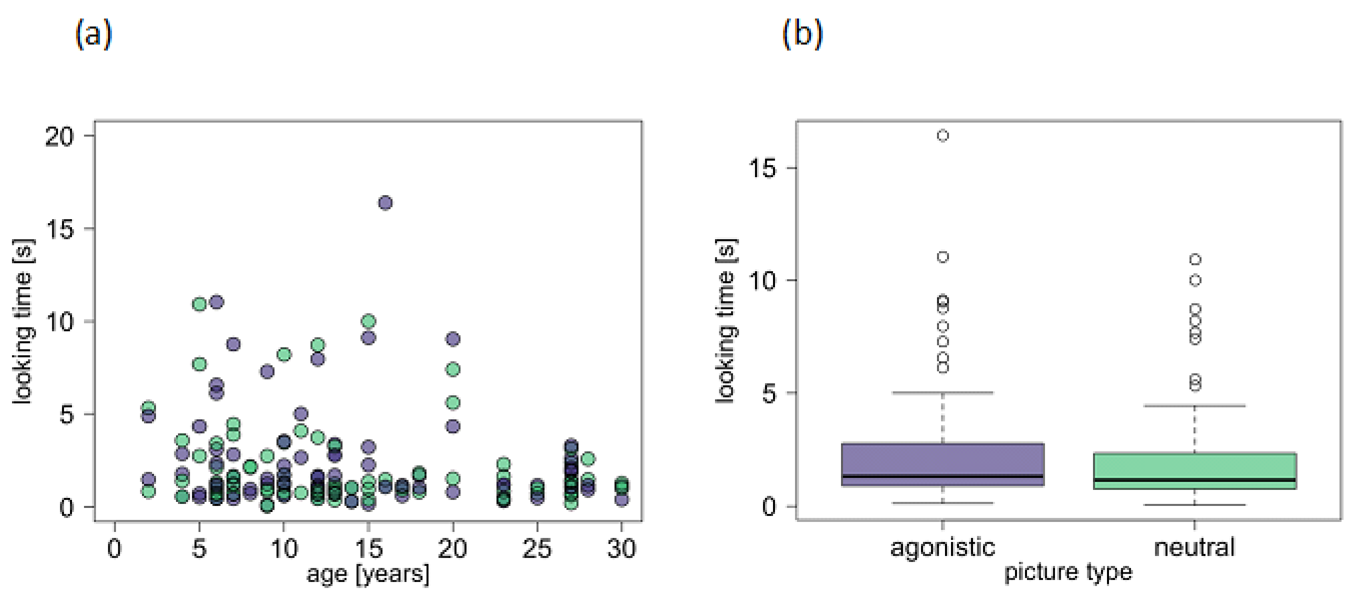

Figure 5

Time spent looking at agonistic and neutral pictures in relation to age and condition. a) Time of the first look in relation to age and picture type (violet=agonistic; green=neutral); **b)** aggregated looking time in relation to picture type (agonistic, neutral).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementalOnlineMaterial220211.docx

- FV7117042018.mov