# Heritability and maternal effects on social attention during an attention bias task in a non-human primate, *Macaca mulatta*.

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## Abstract

Social attention is fundamental to a wide range of behaviours in non-human primates. However, we know very little about the heritability of social attention in non-human primates, and the heritability of attention to social threat has not been assessed. Here, we provide data to begin to fill this gap in knowledge. We tested 67 female rhesus macaques, *Macaca mulatta,* on an attention bias preferential looking task in which they viewed threat-neutral face pairs. We recorded a number of looking time measures of social attention to conspecific faces, and attention to conspecific threat faces specifically. In addition, we recorded levels of vigilant scanning in the social group. We quantified heritability and maternal effects using pedigree information. Repeatabilities for social attention ranged from 11% - 25%. Repeatability for attention to threat faces was 16%, with zero repeatability for attention bias, calculated by subtracting duration of looking towards the neutral face from duration of looking towards the threat face (a common practice in the literature). Heritabilities for social attention were 8% - 14%, with maternal effects 6% - 11%. Heritability for attention to threat was 10%, with maternal effect 4%. This is the first study that we are aware of to test the heritability of attention to threat in a non-human primate. We discuss these findings in light of understanding mechanisms underlying social behaviour in primates, evolutionary pathways of social attention in humans, epidemiology of mental health issues such as anxiety, and potential for improving markers of animal emotion and wellbeing in captivity.

## Keywords

Social attention, attention bias, repeatability, heritability, maternal effects, primate

## Introduction

Social attention underpins a wide range of behaviour in human and non-human primates, allowing individuals to gain rich information about conspecifics – e.g. in relation to their identity, status, behaviour, emotional state and intentions – which then guides decisions about subsequent social interactions (Klein et al., 2009). The importance of social attention in primates' lives is reflected in the expansion of the visual cortex in this lineage (Barton, 1998) and by the existence of evolved brain mechanisms for processing social information (Chang et al., 2013), including areas specialised for processing faces (Adolphs et al., 1996, Chang et al., 2013) and for rapid assessment of threat (LeDoux, 1996). Studies with primates have demonstrated that patterns of social attention vary markedly between individuals (Bethell et al., 2012, Deaner et al., 2005, Watson et al., 2015), but the causes of such variation are not fully understood. Differences between individuals ('personality': Carter et al., 2013, Dall et al., 2012, Dall et al., 2004, Gosling & John, 1999) may be driven by genetic or environmental factors (Dingemanse et al., 2010, Nicolaus et al., 2012) and there is evidence that some of this variation is heritable ( Dochtermann et al. 2015; Drent et al. 2003, Winney et al. 2018).

Work on the heritability of social attention in non-human primates has mostly explored this phenomenon indirectly, for example through gene association studies (Coyne et al., 2015). A small but growing number of non-human primate studies have more directly quantified heritability of social attention by including measures of relatedness between individuals (e.g. Blomquist & Brent, 2014). However, most have not accounted for other potentially confounding causes of variation such as maternal effects (Cheverud & Wolf, 2009, Maestripieri, 2009), and common environmental effects (Blomquist & Brent, 2014, Johnson et al., 2015,). Maternal effects are here defined as influence of the mother on the phenotype of the offspring - prenatal and/or postnatal - aside from those explained by inheritance of genetic material, for example through nutritional, behavioural and epigenetic means (Schroeder et al., 2012, Schroeder et al., 2015). In conjunction with the impact of sharing a common environment during the dependent phase, offspring behaviour might appear to result from heritability, but could also be attributed to maternal behaviour (Ainsworth & Bell, 1970, Maestripieri, 2009, Mandalaywala et al., 2014) or can magnify the apparent magnitude of the heritability that is present.

Heritability of social attention in non-human primates has been little studied. Johnson et al (2015) recorded the time olive and yellow baboons, *Papio anubis* and *P. cynocephalus,* spent watching a human observer during a novel object test. Heritability of this behaviour was in the range 18%-38%, with significant effects of sex and age (females tended to be more watchful of the observer while age effects are not fully reported). Watson et al (2015) measured levels of vigilant scanning by rhesus macaques while drinking from a waterhole. Heritability for scanning was 12%, with significant effects of age and sex (lower vigilance in females and older monkeys). However, neither of these studies reported the contribution of environmental or (non-genetic) maternal effects. To understand more fully the mechanisms underpinning social attention in primates, it is important to explore the consistency (‘repeatability’), narrow-sense heritability (degree of behavioural expression that can be accounted for by an individual’s genes) and influence of non-genetic (including maternal and other socio-environmental) effects on this behaviour.

Here we addressed these goals, using data on general attention to social information and attention specifically to social threat, collected from group-housed female rhesus macaques *Macaca mulatta* for whom pedigree information was available. We recorded levels of vigilant scanning while the monkeys were freely interacting with conspecifics, and also measured patterns of attention in a preferential looking task, during which animals were shown pairs of conspecific faces (one with a threatening expression, the other a neutral expression: after Bethell et al., 2012). We tested the heritability of attention to social information by measuring the extent to which relatedness explains (a) variation between individuals in vigilant scanning rates, and (b) the total time spent looking towards pictures of conspecific faces during the preferential looking task. We tested the heritability of attention to social threat specifically, by measuring the extent to which relatedness explains, during the preferential looking task (a) the time spent looking towards the threat face only, and (b) the bias in attention bias towards to the threat face relative to the neutral face. Finally, we examined the extent to which any heritability may be explained by genetic and non-genetic effects by accounting for variance explained by mother identity, separately. Because the rhesus macaque is a female philopatric species with strong mother-daughter bonds, and due to the controlled environmental conditions of captive housing, we treat maternal and permanent environmental effects as a single ‘non-genetic’ factor labelled here as ‘maternal-environmental’ effects.

## Materials and Methods

### **Animals and housing**

Data were collected from 67 adult female rhesus macaques (*Macaca mulatta*) housed at the Centre for Macaques, MRC Harwell Institute, UK (mean age on first day of testing: 8.8 years, range 2.5 – 18.3 years; Table S1). Monkeys were UK-bred from founders of Indian origin. Information about and a video of the facility can be seen at: https://www.mrc.ac.uk/research/facilities-and-resources-for-researchers/mrc-centre-for-macaques/ and www.nc3rs.org.uk/macaques. Monkeys were housed in social breeding groups comprising 1 adult male and between 3–11 related females, plus infants and juveniles, following best practice guidelines (NC3Rs, 2006). Breeding groups had access to two home areas: a main home room (dimensions 8.04m long x 3.35m wide x 2.8m height) with an adjoining cage room (dimensions 6.12m long x 1.5m wide x 2.8m height); overall floor area 35.19m$^2$, and total volume 98.54m$^3$. The main room had a large shelf c. 2m above the ground and shelves at multiple heights. The floor was covered in deep bedding material, and hanging enrichment included ladders, hoses, tunnels, boxes, swings and visual barriers. The main room was also fitted with adjustable mirrors which the monkeys could control using a handle inside the main room which allowed them to look along the corridor outside their room. The cage room typically contained no enrichment devices and was designed so that staff could feed directly through the bars, and dividers could be used to separate off an individual for veterinary inspection if needed. The main room and cage room were connected by four hatches (one high, two medium and one low) which were kept open at all times during this study, and were only closed at other times during specific husbandry and veterinary protocols. For this study, monkeys were tested in the cage room and all individuals were free to come and go at all times (no dividers were used nor was any monkey separated for testing). For the largest group (n=21 adults, juveniles and infants) the two rooms provided c. 9m$^3$ volume per adult which is above the minimum of 3.5m$^3$ for breeding animals under the UK Home Office Code of Practice (HomeOffice, 2014). All other groups were smaller than this and so had more space per individual. Monkeys were fed a regular diet of primate pellets, and a forage mix and various fruit and vegetables which were scattered in the deep bedding to encourage natural foraging behaviour. Food and water were available *ad libitum* in the main room at all times.

### Pedigree

Pedigree information was available from colony records managed by DF and CW. The full pedigree contained 597 individuals with a maximum depth of 7 generations. Pedigree information was processed in R version 3.4.3 (RCoreTeam, 2018) using the package *MasterBayes* (Hadfield et al., 2006). Summary statistics were calculated using the R package *pedantics* (Morrissey, 2014 ). The full pedigree and informative pedigree are presented in Supplementary materials (Figure S1). Mother identities were assigned from the pedigree.

### Life history measures

For each female, life history information for three factors was collected through direct observation and from colony records (Table S1). Information was compiled for age on day of testing (mean=9.7 years, range 2.5 – 18.1), social rank (high n=27, middle n=27, low n=13) and reproductive status (cycling, pregnant, nursing). We assigned social rank in discussion with facility staff based on our observations of which animals were most likely to attack or displace others from preferred locations or food sources. High rank was assigned to monkeys which displaced most others, low rank was assigned to monkeys who were most likely to be displaced, attacked or to avoid others, and those who were displaced by high ranked individuals but displaced low ranked individuals were assigned mid rank. Reproductive status was in some cases confirmed retrospectively from timings of births, assuming a gestation length of 167 days (Silk et al., 1993).

## Cognitive measures

Attention to social information in general, and social threat specifically, was assessed using an attention bias preferential looking task (Bethell et al., 2012). Monkeys had previously been target-trained, using positive reinforcement, to sit next to individual ‘targets’ in the caged area adjacent to the main enclosure, as detailed in (Kemp et al., 2017). Whilst seated by their unique target, each monkey was familiarised with a freestanding apparatus consisting of two picture holders with occluders on a height-adjustable tripod, and with a digital video camera (Panasonic HCV520) positioned centrally between them. During the initial familiarisation monkeys were encouraged to look towards the apparatus by presenting food rewards centrally in front of the camera. Once oriented centrally, the occluders were manually opened via a sliding mechanism at the back of the apparatus to reveal two pictures which had been pre-loaded, one into each picture holder. Monkeys freely viewed the pictures for 3 seconds until the occluders were closed. During familiarisation, pictures were of food items and conspecific infants, which were considered to be of interest to adult female macaques.

During testing, monkeys underwent the same procedure except that pictures shown were of male conspecific faces (Figure 1) and the monkeys' gaze towards the two images was filmed for each 3 second trial. Studies with humans most commonly use angry, disgust and pain facial expressions as social threat cues (Heathcote et al., 2015, Hommer et al., 2014, Pérez-Edgar, 2010, Perez-Edgar et al., 2011, Schofield et al., 2013,). Here we used images of seven unknown male macaques taken during aggressive encounters and during resting states. Each picture pair contained one frontal view of the unfamiliar male macaque face with direct gaze and mouth open baring teeth in a tense, aggressive expression (threat face) and one frontal view of the same male with the eyes and mouth closed and face relaxed in a presumably neutral expression (neutral face). Pictures were cropped around the face and superimposed on a rectangular grey background. Within each picture pair faces were equated for luminance and contrast energy (full details given in Bethell et al., 2012). Location of the threat face on the left or right of the picture pair was counterbalanced across trials for each monkey. This counterbalancing allowed us to control for the enhanced processing of emotional information in the right hemisphere of the primate brain (i.e. for information presented to the left visual field: Adolphs et al. 1996) in our analyses.

Monkeys took part in one cognitive trial per day for four consecutive days from Tuesday – Friday in a given week. As part of a larger study investigating the relationship between emotion state and attention to social threat, monkeys were tested during weeks in which veterinary health checks took place (presumed to be stressful, referred to here as ‘stress’ condition), and weeks during which no presumed stressors occurred (referred to here as ‘baseline’ condition). During baseline weeks, when unexpected disruptions occurred (e.g. a monkey had given birth, or a fight had occurred that morning) testing was delayed until the next available day; this is because we intended to conduct trials with monkeys in a presumed ‘non-stressed’ state. To control for these potential confounding factors we included condition as a control variable. As reproductive hormone levels may also affect patterns of social attention (Lacreuse & Herndon, 2003) we also included reproductive status as a control variable.

Figure 1. A threat – neutral face pair

Video was coded in JWatcher+ Video V1.0 (Blumstein et al., 2000). Two coders (CK and HT) blind coded video on a frame-by-frame basis for direction of eye gaze towards the left and right picture locations during each trial. Coders achieved good agreement for coding a subsample of the videos (Cohen's *k*=0.87). Once coded for direction of gaze on each frame, trials were matched with records for location of the threat face (left/right). Number of trials each monkey completed was recorded, as was time of day at which testing occurred.

## Behavioural observations

In the afternoon following a monkey's cognitive trial, her levels of vigilant scanning in the social group were recorded for 5 minutes using continuous focal animal sampling (Altmann, 1974). We recorded duration of time engaged in vigilant scanning behaviour, defined here as '*predominant behaviour is observing surrounding environment, moving the eyes and or head actively scanning surroundings'*. We considered vigilant scanning to be a suitable proxy for social vigilance behaviour since social groups were generally highly socially active.

## Data preparation

Five variables functioned as response measures. There were three measures of *social attention*. Duration of vigilant scanning in the social group (VIG), was recorded in seconds/min; duration of time looking at both face pictures during the preferential looking task (SOC), was recorded in ms per trial; and duration of time spent looking at faces presented in the left location (i.e. to the left visual field, LVF), was recorded in ms per trial.

There were two measures of *attention to threat*. Duration of time looking at the threat face (THREAT), was recorded in ms per trial. Attention bias for threat (BIAS), was calculated as [THREAT – NEUT] where NEUT was the time spent looking towards the neutral face during the trial, providing bias scores on a scale from -3000ms to 3000ms.

We visually inspected plots of all response and predictor variables to check for a normal distribution using the R packages 'tidyverse' (Wickham, 2017) and 'car' (Fox & Weisberg, 2011). We transformed variables where this improved the distribution. For the response variables, we square-root transformed THREAT and LVF. For the predictor variables time of day and trial number required log transformation. All covariates were then scaled to a mean of 0 and SD±1 to provide more comparable estimates (Aiken & West, 1991, Schielzeth, 2010).

## Statistical analysis

Statistical analyses were performed in R v. 3.4.3 (RCoreTeam, 2018). We estimated additive genetic and maternal-environmental effects using an 'animal model' (Falconer & Mackay, 1995) with a Bayesian approach (Hadfield, 2010). The animal model is a generalised linear mixed model (GLMM) which includes the pedigree as a random effect. This allows heritability to be estimated and accounts for its effect on the statistical relationships being tested. Specifically, we first calculated repeatability (with individual monkey as a random effect) to establish how much variation in each attention measure was due to between-individual differences. The proportion of variance explained by between-individual differences is the repeatability – typically considered the upper limit for heritability of a trait

(Lynch & Walsh, 1998). Therefore we subsequently only assessed heritability and maternal-environmental effects for measures with a repeatability >0. We built an appropriate model using the function ‘lmer’ in the package ‘lme4’ (version 1.1-15; (Bates et al., 2015). We checked all potential predictor variables for autocorrelation. The three life-history variables (age, rank and reproductive status) showed no evidence of autocorrelation and were retained as fixed effects (all r<0.04).

We controlled for experimental factors expected to contribute to within-individual variation in the measures of attention. Condition (baseline or stress) was included to account for the effects of current emotion state on attention to threat faces (Bethell et al., 2012). Time of day (recorded as 1-hour time blocks between 9am and 1pm) was included to control for possible influence of circadian rhythm on alertness (Foster & Kreitzman, 2014); and trial number (1-12) was included to control for habituation effects following repeated presentations of stimuli over time (Bethell et al., 2019). For analysis of data from the cognitive trials, side on which the threat face was shown (left or right) was included to control for left visual field priority of processing for emotional information. Stimulus ID (seven stimulus pairs were used) was included to account for variation in features of the stimulus monkeys’ faces that might influence attention (Waitt et al., 2003).

**Repeatability**

We ran GLMMs with measurements of the response variable with repeated observations within individuals, one model for each response variable, using the package MCMCglmm

(Hadfield, 2010). To estimate repeatability (R) for each response variable we modelled an identifier for each individual animal as a random factor on the intercept. We then calculated the repeatability as

(1) $R = V_{\mathrm{ID}}/(V_{\mathrm{ID}}+V_{\mathrm{R}})$

where $V_{\mathrm{ID}}$ stands for the variance explained by between-individual differences, and $V_{\mathrm{R}}$ for the residual variance. This approach is common in animal personality research (Nakagawa & Schielzeth 2010).

**Heritability and maternal effects**

For those traits in which we identified non-zero repeatability, we ran animal models to estimate additive genetic variance ($\mathrm{V_A}$), and maternal-environmental ($\mathrm{V_M}$) effects using the MCMCglmm package in R (Hadfield et al., 2006, Hadfield, 2010). Models were structured as for the repeatability, but we added additional random effects. Firstly, we included the inverse relatedness matrix calculated from the pedigree as a random effect to estimate additive genetic variance ($V_{\mathrm{A}}$) (Wilson et al. 2010). Secondly, we added maternal identity as a random effect to estimate maternal effects ($V_{\mathrm{M}}$). In these models (compared to the repeatability models above) variance component estimated by the individual identity was named $V_{\mathrm{PE}}$, because now this part only estimates the variance explained by permanent environment effects estimated through repeated measures on the individual, excluding any additive genetic effects (Kruuk & Hadfield 2007). Note that $\mathrm{V_{PE}}$ also accounts for the pseudoreplication introduced by the repeated measures, and as such we always kept this parameter in the model. We calculated the heritability $h^2$, the proportion of variance explained by permanent environment *PE*, and the proportion of variance explained by maternal effects *M* of each behavioural trait as

(2) $h^2 = V_A/(V_{PE}+V_A+V_M+V_R)$

(3) $PE = V_{PE}/(V_{PE}+V_A+V_M+V_R)$

(4) $M = V_M/(V_{PE}+V_A+V_M+V_R)$.

(Dochtermann et al., 2015) suggested that, to better understand the heritability of behavioural traits, any within-individual variance is not relevant as it is not informative for between-individual differences, which we are interested in. For transparency and to aid meta-analytic approaches, we present both types of quantitative genetic estimates. Hence, following Dochtermann et al. (2015), we also calculated the heritability of our looking measures treated as components of 'personality' differences by assessing the proportion of the variance due to between-individual differences (disregarding $V_R$), and present the proportion of the repeatable variance in contrast to the total variance in equations 2-4 as:

(5) $h_P^2 = V_A/(V_{PE}+V_A+V_M)$

(6) $PEp = V_{PE}/(V_{PE}+V_A+V_M)$

(7) $Mp = V_M/(V_{PE}+V_A+V_M)$

We fitted Bayesian GLMMs using the R package MCMCglmm (Hadfield 2010). We used default priors where possible, and if needed we used proper priors with a low degree of belief. We used visual inspection of plots of posteriors to ensure that the chain converged, and assured empirically that autocorrelation at the specified thinning interval was low (i.e. <0.1).

## Ethical Statement

This work was approved by the CFM Animal Welfare and Ethical Review Body and LJMU ethics panel approval #EB/2014-1. All research was carried out in accordance with ethical guidelines for work with non-human primates (NC3Rs, 2006) and reported following ARRIVE guidelines (Kilkenny et al., 2010). The general health of the animals was monitored daily by the care staff via visual checks, and annually with a full veterinary examination. If during the course of the project a researcher observed an injury or a concerning pattern of behaviour they reported their concerns to the CFM care staff promptly so that any necessary treatment could take place.

## Results

### Data summary

Vigilant scanning

Data on vigilant scanning in the social group were collected from 67 monkeys on 400 occasions over a period of 15 months (mean = 7.01 observations per monkey, range 2-12). Monkeys spent an average of 26.65 seconds/minute engaged in vigilant scanning (range 0 – 59.60 seconds).

Cognitive trials (SOC, LVF, THREAT and BIAS)

A total of 432 cognitive trials were completed by the 67 monkeys (mean = 8.27 trials, range 4-12). We removed data related to cognitive trials as follows: trials involving monkeys which had given birth in the preceding 24 hours, or which had been injured in the last 48 hours (n=6 trials, 1.39% of the data); trials involving monkeys which had experienced a change in group structure in the preceding 7 days (n=15 trials, 3.47% of the data); trials that occurred within 24hours after room cleaning (n=10 trials, 2.31% of the data); and trials that occurred after 13:00hrs (n=29 trials, 6.71% of the data). We also removed data from 10 females which were moved to a non-breeding group at the start of the study period (n=72 trials, 16.67%). This resulted in 371 cognitive trials from 57 monkeys for inclusion in the analysis (mean = 6.50 trials per monkey, range 4-12). Model output for cognitive trials are given in Supplementary Table S2.

### Pedigree

There were 144 individuals in the informative pedigree, with 49 unique mothers for 67 mon keys (Figure S1).

## Repeatability

Repeatabilities are shown in Table 1. Vigilant scanning in the social group was repeatable (VIG, R= 0.11), as was attention to social information during cognitive trials (SOC, R=0.25), duration of looking at faces presented in the left visual field (LVF, R=0.13), and time spent looking towards the threat face (THREAT, R=0.16). There was zero repeatability for attention bias score (BIAS, R=0.00).

Table 1. Repeatability (R), heritability ($h^2$), and maternal-environmental effects (*M*) for behaviour ($_B$) and personality ($_P$) for the four measures of attention for social information and social threat with non-zero repeatability (95% Confidence Intervals shown in brackets). R: repeatability of behaviour within individuals; $h^2$B: heritability of behaviour; MB: maternal effects on behaviour; $h^2$P: heritability of personality; MP: maternal effects on personality. VIG: duration of vigilant scanning in the social group; SOC: duration of time looking at both faces; LVF duration of time looking at both faces when presented to the left visual field only; THREAT: duration of looking towards the threat face; BIAS: attention bias score calculated as [duration of looking towards threat face - duration of looking towards the neutral face]. *Confirmatory analyses revealed zero repeatability (R=0) for duration of looking at faces presented to the right visual field. ‡Confirmatory analysis revealed there was zero repeatability (R=0) for attention towards the NEUT face.

| | | *R* | $h^2$ | $M_B$ | $h^2$ | $M_P$ |
|---|---|---|---|---|---|---|
| Target of attention | Response | *(95CI)* | *Behaviour* | *Maternal effects on Behaviour* | *Personality* | *Maternal effect on Personality* |
| Social information | VIG | 0.11 | 0.09 | 0.06 | 0.55 | 0.32 |
| | | (0.00-0.24) | (0.02–0.18) | (0.02 – 0.16) | (0.19-0.78) | (0.24-0.49) |
| | SOC | 0.25 | 0.14 | 0.11 | 0.59 | 0.38 |
| | | (0.13 - 0.38) | (0.04–0.26) | (0.02 - 0.23) | (0.17-0.83) | (0.08 - 0.61) |
| | LVF* | 0.13 | 0.08 | 0.10 | 0.23 | 0.38 |
| | | (0.06-0.26) | (0.02-0.18) | (0.02 – 0.20) | (0.08-0.60) | (0.11-0.64) |
| Social threat | | 0.16 | 0.10 | 0.04 | 0.63 | 0.30 |
| | THREAT‡ | (0.06–0.30) | (0.04 - 0.23) | (0.02-0.15) | (0.22-0.85) | (0.11 - 0.59) |

## Heritability and Maternal Effects

Heritabilities and maternal-environmental effects for all measures with non-zero repeatability are shown in Table 1. Heritability for attention to social information (VIG, SOC and LVF) and social threat (THREAT) was present but low (VIG, $h^2 = 0.09$; SOC, $h^2 = 0.14$; LVF, $h^2=0.08$; THREAT, $h^2 = 0.10$). Maternal-environmental effects were of comparable magnitude to heritability for all four measures, with highly overlapping confidence intervals (VIG, $M_B = 0.06$; SOC, $M_B = 0.11$; LVF, $M_B =0.10$; THREAT, $M_B = 0.04$).

## Discussion

We tested for heritability of, and maternal-environmental effects on, attention for social information in general, and social threat specifically, in adult female rhesus macaques. Using data on levels of vigilant scanning while animals were in their social group, and their duration of looking towards threat-neutral stimulus pairs presented during an attention bias preferential looking task, we found evidence that both attention for social information in general, and for social threat specifically, are heritable and also shaped by maternal-environmental effects. These findings provide the first measures of both genetic and non-genetic contributions to social attention in a non-human primate.

The heritability of vigilant scanning in the social group in this study, at 9%, is slightly lower than, but generally consistent with values reported in the few other published findings on social attention within social groups: rhesus macaques – 12% (Watson et al., 2015); baboons

16-38% (Johnson et al., 2015). In both of these studies maternal and other permanent environmental effects were not directly accounted for in the analysis. Here we found that vigilant scanning was also partly explained by maternal-environmental effects, which accounted for 6% of the variability in this behaviour. Both genetic and non-genetic factors therefore influence vigilant scanning in the social group. We also found genetic and non-genetic contributions to social attention in the attention bias preferential looking task - heritability and maternal-environmental effects being 14% and 11% respectively for attention to social stimuli overall, 8% and 10% for attention to social stimuli presented to the left visual field and 10% and 4% for attention to threat faces.

Our findings contribute to a growing literature demonstrating heritability of social attention in non-human primates. Hopkins et al. (2014) assessed heritability of joint attention in chimpanzees (*Pan troglodytes*), finding this to be between 22%-25%, and more strongly heritable in males than females. Maternal effects were not tested in that study. Work with rhesus macaques highlights how important maternal effects are and their potential for interaction with genetics: Golub et al. (2012) tested infant male rhesus macaques between 3 -14 months for the effect on several measures of social attention of MAOA genotype and iron deficiency in the mother's diet during the third trimester. Offspring with the low-expressing MAOA genotype whose mothers had the iron deficient diet showed the poorest level of emotion regulation; they were most vigilant towards video of aggressive conspecifics and exhibited the most fearful behaviours during a number of social response tests. Where data are available, the inclusion of mother identity in studies of heritability of behavioural traits will help elucidate the relative contribution and interaction between genotype and environment.

Repeatability values were slightly lower than, but broadly consistent with, the distribution of reported values for a wide range of behaviours in the animal behaviour literature (our range: 0.11-0.25; literature mean=0.37 and mode = 0.2, Bell et al., 2009). In their meta-analysis of animal studies Bell et al (2009) found lower repeatability for behaviours expected to be flexible across contexts, for data collected in the laboratory compared to the field, and for measurements taken further apart in time. They found no relationship between number of repetitions of a measure and repeatability, although the majority of studies in the analysis used only a single or a few repeats of a measure. Our more conservative values for repeatability may be partly explained by our previous work showing attention for threat varies across contexts (Bethell et al., 2012), testing of animals in a captive environment, and the relatively large number of repeated trials (up to 11 repeats) spread across a 10 month period.

There was zero repeatability in our study for attention bias for threat (BIAS). Looking time towards the threat face alone may therefore be a more reliable measure of threat bias than calculating difference scores, as is typical in the human literature (Bar-Haim et al., 2007) and seen in earlier attention bias studies with non-human primates (Bethell et al 2012; Mandalaywala et al. 2014). Indeed, a confirmatory check revealed there was zero repeatability for looking time towards the neutral face (NEUT: result not presented here), indicating that the calculation for BIAS diluted the repeatability for THREAT.

Our finding for non-heritability of attention bias for threat (BIAS) is in line with the few studies that have explored the heritability of attention bias for threat in humans, typically by comparing responses on cognitive tasks between monozygotic and dizygotic twins (Savage et al., 2017). These studies all found no evidence for heritability of attention bias for threat faces. For example, Rijsdijk et al. (2009) tested 125 pairs of female monozygotic and dizygotic twins on an emotion-face dot-probe study (Mogg & Bradley, 1999), in which threat-neutral face pairs were presented for 19ms (i.e. subliminally), and reaction times to subsequently presented probes recorded. Participants showed an overall attention bias for threat (measured as significantly faster responses to probes occurring at the location of previously shown threat versus neutral faces). There was no evidence for heritability of attention bias when data were collapsed across both visual fields ($h^2 = 0$). Brown et al. (2013) conducted an emotion-face dot-probe task with 600 eight-year-old mono- and dizygotic twins, in which threat-neutral face pairs were shown for 1,000ms. Attentional avoidance of threat was evident in the most anxious children, and this was not influenced by either degree of relatedness between twins or shared environment. The authors concluded that attentional processes probably do not mediate the link between genetic risk and the development of anxiety disorders in children, as has been widely proposed in the literature (Macleod et al., 1986, Mogg & Bradley, 1999). Finally, (Elam et al., 2010) conducted a dot-probe task with 22 twins aged five years in which threat-neutral face pairs were shown for 500ms. While monozygotic twins were more similar than were dizygotic twins in their responses to probes, this difference failed to reach significance. Attention bias for threat therefore appears to be a highly plastic behaviour in both human and no-human primates. By calculating attention bias scores we lost any of the repeatability seen for looking towards the threat face on its own. It is interesting to consider that calculating difference scores, as is typically done in human cognitive psychology research, introduces noise that may mask any signal of heritability or maternal effects.

Also in line with the human attention bias literature, we found heritability of attention to social information presented to the left visual field, regardless of emotional content, in the range 2-18%. Rijsdijk et al. (2009) reported heritability for attention to social information among female twins tested on a dot probe task using threat-neutral face pairs. Heritability was only found for reaction times to probes presented to the left visual field, regardless of which face type they followed (41% and 49% for threat and neutral faces respectively). This finding was interpreted as evidence for a right hemisphere sensitivity for subliminal biologically relevant cues under substantial genetic control; response times to probes in the right visual field were driven by environmental effects only (both $h^2 = 0$). Elam et al. (2010) also found evidence for heritability of a bias for responding to probes following faces in the left visual field (~40%), while again heritability was 0% for probes following faces in the right visual field.

Our results will also be of interest to researchers interested in social attention for threat as an underlying mechanism in human mental health conditions (e.g. Savage et al., 2017) from an evolutionary perspective (Tremblay et al., 2017). There has been a paradigm shift in approaches to mental health in the last decade, moving away from categorising phenotypes under the traditional diagnostic categories presented in the DSM (American Psychiatric Association, 2013), and towards an approach informed by genetics, neurobiology and experimentally-derived behavioural measures, including attention bias (see Savage et al., 2017, for a review). As an example, attention bias for positive and negative faces has been proposed to be a heritable mechanism underlying emotional resilience and vulnerability to anxiety in humans, mediated by serotonin transporter (5-HTTLPR) polymorphism (Fox et al., 2009). Attention bias for threat words has been proposed to mediate the link between neurobiology and behavioural pathology in trauma survivors (Pietrzak et al., 2014). The data presented here may be of value for interpreting human data in an evolutionary context (e.g. Green & Phillips, 2004).

Finally, our results will also be of value to animal cognition, behaviour and welfare researchers, trying to unpick the relative contribution of genetic and environmental factors influencing susceptibility to stress. Work with mammals (primates: (Bethell et al., 2012), sheep: (Monk et al., 2018)) and birds (Brilot et al., 2009) has shown that attention bias for threat has potential for tracking changes in affective state (reviewed in (Crump et al., 2018). Providing new and adaptable measures of animal emotion are essential for refinement in animal welfare practice (NC3Rs, 2006, Mendl et al., 2010). We hope the findings presented here will help welfare researchers in these fields to better understand the role of heritable and environmental factors in shaping the development and expression of social attention, and its relationship to wellbeing.

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