Chimpanzee sociability is associated with vasopressin (Avpr1a) but not oxytocin receptor gene (OXTR) variation

Nicky Staes a,b,⁎,1, Sonja E. Koski c,1, Philippe Helsen b,a, Erik Fransen d, Marcel Eens a, Jeroen M.G. Stevens b,a

⁎ Corresponding author at: Koningin Astridplein 20, B-2018 Antwerp, Belgium.
E-mail addresses: Nicky.staes@kmda.org (N. Staes), sonja.koski@helsinki.fi (S.E. Koski), Philippe.Helsen@kmda.org (P. Helsen), erik.fransen@uantwerpen.be (E. Fransen), Marcel.Eens@uantwerpen.be (M. Eens), Jeroen.Stevens@kmda.org (J.M.G. Stevens).

1 Both authors contributed equally to the manuscript and should therefore be considered shared first authors.

Introduction

The field of personality research is flourishing and no longer limited to human psychology. Personality traits have been identified in a wide variety of animal species (Gosling, 2001; Mather and Logue, 2013; Van Oers and Naguib, 2013) and have demonstrated some level of heritability (Van Oers and Sinn, 2013) and influence on fitness (Smith and Blumstein, 2007). Yet, identifying the proximate mechanisms, more specifically the genetic variation that causes such consistent variation in behavioral phenotypes, remains challenging (Munafo and Flint, 2011). Most literature on the genetic architecture of personality traits originates from human research (Balestri et al., 2014; Ebstein et al., 2002). Corresponding studies that link genetics and personality in non-human animals remain scarce, although recently progress has been made in birds and rodents (Van Oers and Mueller, 2010; Van Oers and Sinn, 2013).

In non-human primates, research is increasingly focusing on identifying the genetic variation that underlies phenotypic differences, both within and between species (Bradley and Lawler, 2011). Currently, however, only a few studies have investigated the effects of particular candidate genes on primate personality, respectively. In rhesus macaques (Macaca mulatta), playfulness and aggressiveness are influenced by length variations in the serotonin transporter gene (5-HTTLPR) (Barr et al., 2004) and MAOA gene (Newman et al., 2005). In vervet monkeys (Chlorocebus aethiops), an association between novelty seeking and the dopamine D4 receptor gene (DRD4) has been identified (Bailey et al., 2007), and chimpanzee (Pan troglodytes) neuroticism is associated with variation in the TPH2 gene (Hong et al., 2011). From a comparative perspective, studying chimpanzees offers unique opportunities in revealing more recent patterns in the role of genetics in the evolution of human behavior (Wrangham and Pilbeam, 2001).

Here we focus on two genes that have been shown to contribute to individual differences in social personality traits: the vasopressin receptor gene 1a (Avpr1a) and the oxytocin receptor gene (OXTR). Oxytocin and vasopressin are neuropeptides produced in cell bodies of paraventricular (PVN) and supraoptic nuclei (SON) of the hypothalamus. Oxytocin and vasopressin neurons either project from the PVN or surrounding structures to the pituitary, from where the neuropeptides can be released peripherally or back into the brain, or to brain areas other than the hypothalamus, such as the amygdala, septum, medulla.
oblongata or hippocampus (Buijs et al., 1983). The interaction of the neuropeptides with their receptors in these different brain regions results in the regulation of behavior (Brownstein et al., 1980; Young, r and Gainer, 2003). The vasopressin and oxytocin pathways are present in a variety of taxa and, therefore, are relatively evolutionarily conserved in structure and expression (Donaldson et al., 2008). However, small variations in the genes coding for vasopressin and oxytocin receptors cause species-specific behavioral variation (Hammock and Young, 2005), likely through differences in the brain distribution patterns of these receptors (Donaldson and Young, 2013; Insel and Shapiro, 1992). In humans, genotype variation, for both Avpr1a and OXTR, is linked with prosociality (Israel et al., 2009; Knafo et al., 2008), social cognition (Ebstein et al., 2009) and partner bonding (Walum et al., 2008, 2012). Similar effects have been described in voles (Microtus sp.), where genotype differences for Avpr1a and OXTR are associated with levels of parental care, social engagement and partner bonding (Hammock et al., 2005; Hammock and Young, 2005).

Regarding vasopressin, most studies have focused on length variations in the upstream 5′-region of the Avpr1a gene, finding that individuals with longer Avpr1a alleles show increased sociability (Hammock et al., 2005; Hammock and Young, 2005; Knafo et al., 2008; Meyer-Lindenberg et al., 2009; Walum et al., 2008; Young and Wang, 2004). Within this region humans have three microsatellites that vary in length, STR1, RS1 and RS3 (Thibonniére et al., 2000), with RS3 demonstrating the most notable association with social behavior (Bachner-Melman et al., 2005; Hong et al., 2009; Knafo et al., 2008; Meyer-Lindenberg et al., 2009). The RS3 microsatellite is located in the second part (= DupB) of a larger ~350 bp tandem duplicated region (called DupA and DupB). Interestingly, chimpanzees have a homologous Avpr1a 5′ promoter region, but unlike humans, individuals either have duplicated (containing both DupA and DupB) or single alleles (hence lacking DupB the RS3 microsatellite) (Donaldson et al., 2008; Hammock and Young, 2005; Rosso et al., 2008; Staes et al., 2014). Previous studies on captive chimpanzees have found associations between DupB deletion and a variety of social personality factors. Based on personality data derived from questionnaires, DupB−/− male chimpanzees score higher on dominance and conscientiousness factors compared to females, whereas DupB+ individuals do not differ significantly from females (Hopkins et al., 2012). Furthermore, males with a DupB+ allele score higher on their responsiveness to socio-communicative cues compared to DupB−/− males (Hopkins et al., 2014). Anestis et al. (2014), using behavioral observations to determine personality, found that males without the deletion were more affiliative, and both males and females with a DupB allele received more grooming, play, and coalition support than chimpanzees homozygous for the deletion. The results of these studies suggest that Avpr1a affects chimpanzee personality, particularly in males. However, these studies were biased towards the Western chimpanzee subspecies or to rather young individuals between ages 4 and 10, and differed in the methods used to assess personality.

Endocrinological studies suggest that oxytocin plays a potentially large role in regulating social bonding in chimpanzees (Crockford et al., 2013; Wittig et al., 2014), but little is known about the potential effects of genetic variation in OXTR. In humans, a particular single nucleotide polymorphism (SNP), which indicates a genome position size that if ss1388116472 is of functional importance, and it will have male-specific effects on social traits. Based on previous research that described a link between OXTR and affiliation (Lucht et al., 2009), social bonding (Walum et al., 2012) and prosociality (Israel et al., 2009) in humans, we hypothesized that male chimpanzees will show an effect of OXTR genotype on two previously established personality components: sociability and positive affect (Koski, 2011).

In this study we investigated the effects of Avpr1a and OXTR allelic variation on personality by combining newly available genetic data from chimpanzee populations with previously established individual variation in personality traits. The current assessment of the association of social behavior and Avpr1a expands on previous research by integrating methodology and improving upon limitations found in previous studies. In small sample sizes true effects may not always be found (Ioannidis, 2005), therefore, we utilized a larger sample size, and captured genetic and behavioral data from three subspecies of adult chimpanzees of both sexes. Moreover, the personality assessment was comprehensive and based on a broad study sampling of a large number of behavioral variables, which had been formally assessed for long-term repeatability, contextual consistency and correlational structure (Koski, 2011; Massen and Koski, 2014). Furthermore, this is the first study investigating the effects of the OXTR SNP allelic variation on personality in chimpanzees. We specifically looked for sex differences and their interaction with the SNP variation and predicted a larger effect among male chimpanzees for both neuropeptide receptor genes.

Methods

Personality profiles

Data on individual personality scores were taken from earlier published data on 90 chimpanzees housed in 4 groups: Burger’s Zoo (N = 22), Dierenpark Amersfoort (N = 15) and Beekse Bergen Safaripark (N = 29) in The Netherlands, and Chester Zoo (N = 24) in the UK (Koski, 2011; Massen and Koski, 2014), to these data we added new data on individuals from a different captive group: Antwerp Zoo (N = 7) in Belgium. In total, 97 adult and adolescent captive chimpanzees (69 females and 28 males between 7 and 46 years of age) were used to assess the personality structure. For group compositions see supplementary information Table S1. Personality was determined via behavioral observations (Table 1) by SEK and students. Students involved in data collection were trained for a period of minimum 4 weeks after which inter-observer reliability (IOR) was tested and had to meet the minimum criterion of 90% similarity before data were considered as reliable. IOR was checked for all zoos involved in this study. The methods of observation and data extraction were identical in all zoos. For detailed information on observation methods see Koski, 2011; for more information on the behavioral variables that were extracted to assess personality profiles see Supplementary information Table S2. Behavioral variables used for further personality analysis were first tested for within zoo temporal consistency using intraclass correlation (ICC). Only significantly repeatable variables were retained (Koski, 2011).

Following the methodology of Koski (2011), we repeated the analysis of the underlying correlational structure of the 11 temporally consistent behavioral variables due to the addition of 7 individuals to the previously published data (Massen and Koski, 2014). The resulting four personality dimensions were highly similar to the earlier findings reported by Massen and Koski (2014), indicating the stability of this personality structure. The personality traits formed four orthogonal
factors: Sociability, Positive Affect, Anxiety and Grooming Equity. The characteristic behaviors of each personality factor are shown in Table 1; details of item loadings on the personality dimensions can be found in supplementary information (Table S3).

**DNA extraction and genotyping**

In addition to the genotypic information on 24 unrelated individuals described in Staes et al. (2014), we genotyped an additional set of 38 individuals for whom personality profiles were already available (Table S1). Genotyping was done by NS and PH. To ensure unbiased observations, genotypes were unknown to researchers involved in behavioral data collection. We obtained hair and blood samples from 43 female and 19 male chimpanzees (a total of 62 individuals from the following institutes: the Centre for Research and Conservation at the Royal Zoological Society of Antwerp, Belgium N = 7, the Beekse Bergen, the Netherlands N = 23, Arnhem Zoo, the Netherlands N = 22, Chester Zoo, United Kingdom N = 10). Subspecies status has been assigned to 52 out of 62 of the chimpanzee subjects (Carlssen, 2012; Hvislom et al., 2013). Our sample group consisted of 38 Pan troglodytes verus, two Pan troglodytes schweinfurthii, one Pan troglodytes troglodytes, one labeled as P. t. troglodytes or P. t. schweinfurthii and 13 subspecific hybrids of all mixtures (Table S1). We extracted DNA using a Puregene Core Kit B (QIAGEN). Human DNA from the main investigators and negative control samples were included in all procedures to prevent potential sources of contamination during analysis. For both OXTR and Avpr1a we re-analyzed approximately 20% of the samples at least once. Additionally, we used studybook information to validate inheritance patterns of the alleles.

**Results**

Individuals were genotyped using automated capillary electrophoresis (Macrogen Inc., Korea).

Linear mixed models (LMM)

Linear mixed models were fitted to estimate the effect of sex, age and genotype on each of the four personality dimensions. To account for non-independence of observations within the same zoo, we included zoo as a random intercept in the linear mixed model. We used empirical Bayesian techniques to predict the zoo-specific effect on the outcome, assuming that these effects follow a normal distribution. The differences between an individual’s personality score value and the overall mean of this personality factor, was calculated as a weighted average between the zoo-specific effect and the effect attributable to the genotype (Fitzmaurice et al., 2004). This model enabled us to disentangle the effect of the genotype and the zoo-specific effect, even in the presence of a confound. Genotype and age were entered as fixed effects. The significance of the fixed effects was tested by an F-test with a Kenward–Roger correction for the number of degrees of freedom. Linear mixed models were fitted using the lme4 package in the statistical software program R (www.r-project.org, version 3.1.0). The F-test and post hoc analysis were performed using the add-on packages pbkrtest and multcomp, respectively.

**Ethics statement**

No animals were sacrificed or sedated for the purpose of this study. All DNA samples were provided by existing DNA databanks that collect and store samples following BIAZA guidelines (specifically stating that some material may be obtained opportunistically during health checks or other recognized husbandry procedures). The majority of samples were non-invasively collected hair samples. With regard to blood samples we followed the BIAZA guidelines that state that no more than 10% of samples taken for veterinary purposes can be used for secondary research purpose. Human DNA from the main investigators (NS and JMGS) was acquired non-invasively by use of buccal swabs. As these samples were collected non-invasively, and only for the purpose of methodological validation and with no intent to interpret or publish results regarding these samples, the Scientific Advisory Board of the Royal Zoological Society of Antwerp waived the requirement for human subject approval for human tissue collection and use in this study. This research was approved by the University of Antwerp (Belgium).

**Table 1**

<table>
<thead>
<tr>
<th>Personality Factor</th>
<th>Item</th>
<th>Loadings</th>
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<tbody>
<tr>
<td>Sociability</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grooming density</td>
<td>0.90</td>
<td></td>
</tr>
</tbody>
</table>

**List of Tables**

Table 1: The behavioral contents of the personality dimensions.

- **Sociability**: Frequency of grooming given and received, Grooming density given and received (no. of grooming partners out of all available partners) Average number of individuals sitting in 2 m proximity but not in contact with individual
- **Grooming equity**: Average number of individuals sitting in 2 m proximity but not in contact with individual, Non-aggression, Inactivity
- **Positive affect**: Frequency of affiliative behaviors (hugs, kisses, gentle touches, finger-to-mouth), Frequency of play initiated and joined (including social and individual play)
- **Anxiety**: Self-scratching, Self-grooming

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regarding the s1388116472 (C/T) SNP. Sixteen individuals were heterozygous (CT; 7 males, 9 females) and 48 were homozygous (TT; 14 males, 34 females). Our sample did not contain any CC individuals. Genotype frequencies for this SNP do not deviate from the Hardy–Weinberg equilibrium in our sampled population ($\chi^2 = 1.36 \text{ df} = 1, p = 0.76$).

An overall model including both sexes, and accounting for the effects of age and zoo, did not meet the assumption of homoscedasticity. To address this, we fitted separate models for males and females (Table 2). In the best model, sociability was predicted by the Avpr1a genotypes (males: $F(2,5.84) = 5.91; p = 0.040$; females $F(2,37.35) = 4.00; p = 0.027$) (Fig. 1). Post hoc analysis, using Tukey’s correction for multiple testing, showed that DupB+/−/− males ($M = 2.40$, $SD = 0.65$) were significantly more sociable compared to DupB++/−/− ($M = 0.24$, $SD = 0.43$) ($p = 0.001$; Cohen’s $d = -1.43$) and DupB−−/−/− males ($M = 0.26$, $SD = 0.80$) ($p < 0.001$; Cohen’s $d = -1.10$). In females, post hoc testing showed that DupB+/−/− females ($M = 0.39$, $SD = 1.19$) score significantly higher than DupB++/−/− ($M = 1.01$, $SD = 2$) ($p = 0.029$; Cohen’s $d = 0.60$) and DupB−−/−/− females ($M = -0.40$, $SD = 0.45$) ($p = 0.042$, Cohen’s $d = -0.41$). The models investigating the effect of age and genotype on the three other personality factors also revealed no significant associations with the Avpr1a genotype in either sex (Supplementary information Table S4). OXTR genotype and age were not significant predictors for any of the personality component scores in either sex.

**Discussion**

We hypothesized that individual differences in social personality traits in chimpanzees are associated with variation in two candidate genes: Avpr1a and OXTR. Our study provides further support for the positive association of the vasopressin promoter region in chimpanzees, and sociability. DupB+/−+ male chimpanzees show higher sociability than DupB+/−/− and DupB−−/−/− males, and DupB+/−/− females score higher on sociability compared to DupB+/−/− and DupB+/++ females. In contrast, no significant associations were found for the SNP, which was earlier identified on the oxytocin receptor gene (i.e. ss1388116472), with any of the personality components measured for either sex.

Our results suggest that this SNP is not of functional importance in regulating any of the personality components measured here, despite a potential functional mechanism described for the OXTR SNP ss1388116472 T/C (Staes et al., 2014). We cannot rule out other possible behavioral effects, such as associations between this SNP and stress or social sensitivity as described for rs53576 in humans (Rodrigues et al., 2009). In addition to this third intro, recently other regions have emerged as being potentially interesting for behavioral association studies, such as the 5′ upstream region of OXTR that has been linked with autism in humans (Wang et al., 2009; Wermter et al., 2010). Future studies should focus on understanding the similarities and differences in the role of the oxytocin receptor on behavioral variation across species.

Our study corroborates previous findings on an association between a reduction in sociability and deletion of the DupB region in the Avpr1a gene. DupB++/+- males have higher sociability scores, meaning that they are more frequently involved in grooming interactions with others. Anestis et al. (2014) found that adolescent chimpanzees with a DupB allele scored higher on two personality components, “Smart” and “Affiliative”, each of which include a measure of grooming, with the latter association having been found only in males. “Smart” individuals receive more grooming than they give, have a higher frequency of coalitions when involved in aggressive interactions and display a higher probability to initiate play. “Affiliative” males groomed more often related to total grooming in the group and showed a higher percentage of initiated affiliative interactions (Anestis et al., 2014). We found a similar association of grooming with DupB presence using a slightly different, but more uniform measure of grooming, suggesting that the presence of the DupB allele including the RS3 microsatellite, is an important factor in determining affiliative behavioral tendencies in chimpanzees.

In females, the effect of Avpr1a genotype on sociability was more complex. We found that DupB++/−/− females scored higher than homozygous females, but found no significant difference between the two homozygous genotypes. As there is sexual differentiation in the vasopressin system (De Vries and Panzica, 2006), and as previous studies also primarily report associations with male social behavior, these results are not unexpected (Hopkins et al., 2012; Walum et al., 2008; Winslow et al., 1993). Although we could not test for group effects statistically, we found that females that are housed in groups with DupB++/−/− males (in particular at Antwerp Zoo) scored higher on the sociability component compared to females that were housed with DupB−−/−/− males. This suggests that for females, social factors may strongly influence phenotypic differences. This, in turn, may reflect flexibility in female chimpanzee social behavior in captivity. These results are consistent with our knowledge of how chimpanzees balance their grooming services over repeated interactions (Gomes et al., 2009). When DupB++/−/− males show higher frequencies of grooming interactions with group members, including the females housed in that group, females may reciprocate grooming more frequently compared to females housed with less sociable males.

In contrast to previous studies, we were able to investigate all three genotype combinations: DupB++/+, DupB++/−/− and DupB−−/−/. Until now, results on the behavioral consequences of DupB deletion were only available for captive Western chimpanzees, with low frequencies of DupB++/−/− individuals and where comparisons were only made between individuals having (DupB++/−/− and DupB−−/−/) or lacking (DupB−−/−/) the DupB region (Anestis et al., 2014; Hopkins et al., 2012, 2014). Therefore, these studies could not rule out a possible heterozygous advantage. As we included more DupB++/−/− individuals in our analysis we were able to exclude this as a possibility. However, as all the DupB++/−/− males in

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**Table 2**

Model statistics for Sociability as an outcome variable.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Predictor variable</th>
<th>$p^a$</th>
<th>Condition</th>
<th>Est</th>
<th>SD</th>
<th>Cohen's $d$</th>
<th>$p^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Avpr1a</td>
<td>0.040</td>
<td>DupB++/−/−</td>
<td>−2.10</td>
<td>1.47</td>
<td>−1.430</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>DupB++/−/−</td>
<td>−2.19</td>
<td>2.00</td>
<td>−1.097</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>DupB−−/−/−</td>
<td>−0.09</td>
<td>1.72</td>
<td>−0.054</td>
<td>0.974</td>
</tr>
<tr>
<td>Female</td>
<td></td>
<td>0.762</td>
<td>TT</td>
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<td></td>
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<tr>
<td></td>
<td>OXTR</td>
<td>0.649</td>
<td>Age</td>
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<td></td>
</tr>
<tr>
<td>Female</td>
<td>Avpr1a</td>
<td>0.027</td>
<td>DupB++/−/−</td>
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<td>1.78</td>
<td>0.597</td>
<td>0.029</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>DupB++/−/−</td>
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<td>2.17</td>
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<td>0.534</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>DupB−−/−/−</td>
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<td>1.64</td>
<td>−0.406</td>
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</tr>
<tr>
<td>Female</td>
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</tr>
<tr>
<td></td>
<td>Age</td>
<td>0.114</td>
<td>Age</td>
<td></td>
<td></td>
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</tbody>
</table>

*a* $p$-Value regression.

*b* $p$-Value post-hoc Tukey test.
our study were housed in the same zoo, where no male individuals with DupB<sup>+/−</sup> and DupB<sup>−/−</sup> genotypes were present, the observed differences may partially be due to zoo-specific effects on sociability. To explore this possibility, we corrected for a zoo effect by fitting the linear mixed models with a random intercept for zoo, and showed that the effect was not solely due to the particularities of the Antwerp Zoo group. The differences between an individual’s sociability value and the overall mean sociability was calculated as a weighted average between the zoo-specific effect and the effect attributable to the DupB<sup>+/−</sup> genotype (Fitzmaurice et al., 2004). The model thus enabled us to disentangle the effect of the genotype and the zoo-specific effect, even in the presence of a confound. Therefore we can conclude that the significant differences in sociability scores between the genotypes cannot be attributed solely to the zoo-effects and are, at least partly, attributed to the genotype.

Previous studies showed that frequencies of the presence of DupB differ between subspecies of chimpanzees, with Western chimpanzees (P. t. verus) showing higher frequencies of the deletion and Eastern chimpanzees (P. t. schweinfurthii) showing DupB<sup>−</sup> as the minor allele (Anestis et al., 2014; Donaldson et al., 2008; Staes et al., 2014). Therefore, the question arose whether DupB deletion may be causing subspecific differences in social behavior (Anestis et al., 2014; Donaldson et al., 2008; Staes et al., 2014). A formal investigation of this possibility was, however, difficult as earlier studies only included personality data on Western chimpanzees (Anestis et al., 2014; Hopkins et al., 2012, 2014). Our study included individuals from three subspecies (Eastern, Western and Central (P. t. troglodytes)) and subspecific hybrids, but due to the low number of individuals per subspecies and the high frequency of subspecific hybrids we were not able to formally test subspecies effects. The question, therefore, remains as to whether the bias towards higher sociability scores in DupB<sup>+/−</sup> individuals was solely due to DupB genotype or involves a confound of subspecies effect. The bias towards higher sociability in the Eastern and Central subspecies without the deletion is inconsistent with findings on subspecies differences on sociability levels in the wild. Namely, Western chimpanzees are more sociable and range in larger, bisexually bonded parties (Boesch and Boesch-Acherman, 2000; Lehmann and Boesch, 2005) and yet, they have a higher prevalence of the deletion genotype (thus lower sociability). Based on the length of geographic isolation and evolutionary divergence of the subspecies (Hey, 2010), we cannot rule out the possibility that other subspecific genetic variation is to some extent involved in the regulation of sociability aspects. Unfortunately, the captive chimpanzee population is largely composed of Western chimpanzees making it difficult to address any subspecific effects on behavior or personality. However, there are indications that our results do not merely reflect subspecific genetic variation other than DupB. In our study, one of the three males with very high sociability scores and a DupB<sup>+/−</sup> genotype is a hybrid of Western and Central subspecies, while the other two are hybrids of Central and Eastern subspecies. Secondly, the DupB<sup>−/−</sup> genotype is present in Eastern/Western or Western/Central hybrids, and these all score low on sociability, despite being part Eastern or Central. Lastly, previous studies that found effects of DupB presence on personality in chimpanzees worked solely with Western chimpanzees, but found similar effects on social personality aspects.

These results indicate the importance of ecological and environmental factors on the regulation of social association patterns in chimpanzees. Compared to Western chimpanzees, Eastern chimpanzees experience higher seasonality food availability and periods of food scarcity, which influences levels of gregariousness (Doran et al., 2002; Goodall, 1986). Therefore, the question remains as to what extent behavioral differences can be attributed to ecology, genotype or an interaction of the two. One benefit of captive research is that ecological variation can be minimized, allowing for the assessment of primarily genotypic effects within a specific environmental setting. Despite the fact that DupB behavioral effects may be leveled out by environmental effects in the field when comparing chimpanzee subspecies, it could be interesting to consider them on a population level within subspecies. Allele frequencies may differ between populations of the same subspecies, which could partly account for reported inter-population differences in levels of association and intersexual long-term bonding (Langergraber et al., 2009, 2013). Genotype differences could even be considered on an individual level, as, for example, different alpha males belonging to the same population in Gombe show significant differences in their tendency to groom (Foster et al., 2009).

These predictions could be extended to captive research, where reports of group effects on behavioral variation have been documented and often attributed to environmental effects or group history (Fraser and Aureli, 2008; Fraser et al., 2008; Koski et al., 2007, 2012). With regard to Avpr1a, the conflicting findings on the occurrence of prosociality in different groups of chimpanzees are particularly interesting (for review see Cronin, 2012). As Avpr1a variation has been linked to prosociality in humans (Knafo et al., 2008), and we find evidence here for association of Avpr1a with frequencies of grooming behavior in chimpanzees, a low-cost form of prosocial behavior (Dunbar and Sharman, 1984), these different levels of prosociality reported in chimpanzees could be due to differences in DupB<sup>+/−</sup> frequencies in the tested populations. As test groups are typically small, the addition of an outlier, such as a DupB<sup>+/−</sup> individual, may potentially influence the outcome of the experiments. Future studies in prosocial tendencies of chimpanzees could consider looking into genotypes of the tested individuals.

Interestingly, the deletion of the DupB region is absent in bonobos and humans (Donaldson et al., 2008; Staes et al., 2014). The question remains as to whether this difference could explain reported interspecies differences in prosociality (Hare and Kvetuenda, 2010; Tan and Hare, 2013; but see: Cronin et al., 2015) and social tolerance (Hare et al., 2007; but see Jaeggi et al., 2010) between bonobos and chimpanzees, with bonobos scoring higher than chimpanzees in both aspects. The evolutionary origin of these behavioral differences between the two species is often explained by environmental factors, but we suggest that genetic differences may also play a role. Future research should focus on quantifying bonobo personality using methods similar to those used for chimpanzees, and on comparing these with the results found for chimpanzees.
In conclusion, our study provides more evidence for the regulatory function of the 5′ promoter region of the Avpr1a gene on social behavior and its evolutionary stable effects across species. Our findings highlight the importance of considering genotypic effects, in addition to ecological and demographic factors in the regulation of inter-and intra-group behavioral differences. Furthermore, despite the fact that complex social behavior is known to be regulated by a combination of genes, the environment and their interaction, our findings highlight the importance of candidate genes, like Avpr1a, that have large effects on behavioral variation.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.ybeh.2015.08.006.

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