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The factor structure of the macaque social responsiveness scale-revised predicts social behavior and personality dimensions

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Abstract

Most primate species are highly social. Yet, within species, pronounced individual differences in social functioning are evident. In humans, the Social Responsiveness Scale (SRS) measures variation in social functioning. The SRS provides a quantitative measure of social functioning in natural social settings and can be used as a screening tool for autistic traits. The SRS was previously adapted for use in chimpanzees and recently refined for rhesus macaques, resulting in the macaque Social Responsiveness Scale-Revised (mSRS-R). Here, we performed an exploratory factor analysis on the mSRS-R in a large sample of male rhesus macaques ($N = 233$). We investigated the relationships of the resulting mSRS-R factors to quantitative social behavior (alone, proximity, contact, groom, and play) and to previously-established personality dimensions (Sociability, Confidence, Irritability, and Equability). Factor analysis yielded three mSRS-R factors: Poor Social Motivation, Poor Social Attractiveness, and Inappropriate Behavior. mSRS-R factors mapped closely to social behavior and personality dimensions in rhesus macaques, providing support for this instrument's convergent and discriminant validity. Animals with higher Poor Social Motivation were more likely to be observed alone and less likely to be observed in contact and grooming with conspecifics. Animals with higher Poor Social Attractiveness were less likely to be observed playing but more likely to be observed grooming with conspecifics. Inappropriate Behavior did not predict any behavioral measure. Finally, animals with higher Poor Social Motivation and higher Poor Social Attractiveness had less sociable personalities, whereas animals with more Inappropriate Behavior were more confident and more irritable. These findings

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data analyzed in the current study are available from the corresponding author upon reasonable request.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

suggest that the mSRS-R is a promising, psychometrically robust tool that can be deployed to better understand the psychological factors contributing to individual differences in macaque social functioning and, with relevant species-specific modification, the SRS may hold promise for investigating variation in social functioning across diverse primate taxa.

Keywords

autism spectrum disorder (ASD); factor analysis; personality; rhesus macaque; social behavior; Social Responsiveness Scale (SRS)

1 | INTRODUCTION

Sociality, the preference for living in a community rather than in isolation, is central to human and nonhuman primate social organizational systems (Sussman & Chapman, 2017). Although the structure of social systems varies widely across the primate order from as few as two individuals in a social group to over a hundred, members of every primate species are social for at least part of their life cycle (Sussman & Chapman, 2017). The ability to function in primate society depends, in part, on one's ability to recognize, remember, and garner information about the social relationships between individuals in one's social group (Talbot, 2016). Yet, within primate species, there is wide, natural variation in individual social functioning (Clark & Ehlinger, 1987; Phillips et al., 2014). These individual differences are well documented, but poorly understood. Indeed, there is surprisingly little systematic research on the nature of variation in nonhuman primate social functioning.

In humans, variation in social functioning has been measured using the Social Responsiveness Scale (SRS; Constantino & Gruber, 2005, 2012). The 65-item SRS provides a quantitative measure of social functioning in natural social settings, and has been used cross-culturally as a diagnostic aid in clinical practice and as an autism spectrum disorder (ASD) screening tool (Bölte et al., 2008; Stickley et al., 2017; Wigham et al., 2012). ASD is a poorly understood brain disorder characterized by core social interaction impairments and the presence of restricted, repetitive behaviors (American Psychiatric Association, 2013). The SRS is composed of a total score, as well as five subscale (i.e., social awareness, social cognition, social motivation, social communication, and restricted interests and repetitive behaviors) scores. The SRS total score reflects autistic trait severity, with higher scores indicating greater severity of impairment. However, the SRS subscales were clinically, rather than quantitatively, derived. As a result, studies examining the factor structure of the SRS, and hence the underlying constructs of the scale, do not support these five subscales as separable factors. Rather, many of the earlier studies supported one unidimensional factor (Constantino & Todd, 2000; Constantino et al., 2004, 2007), whereas more recent studies suggest that two (Frazier et al., 2012), four (Nelson et al., 2016; Uljarević et al., 2019), or five (Frazier et al., 2014), factor solutions provide better fit. Thus, while the literature remains mixed on the number of SRS factors and the constructs that the factors represent, understanding the factor structure of the SRS is critical to the discovery and interpretation of causal mechanisms underlying variation in social functioning.

Because nonhuman primates, like humans, are highly social, have complex social cognitive abilities, and display pronounced individual differences in social functioning (Phillips et al., 2014), the human SRS was adapted for use in nonhuman primates. The SRS was first modified for use in chimpanzees (Faughn et al., 2015; Marrus et al., 2011), and more recently, for use in rhesus macaques (Feczko et al., 2016). Like the early studies of the human SRS factor structure, the initial study of the SRS in a sample of $N = 29$ chimpanzees observed a continuous distribution and supported a single factor solution accounting for 27% of the variance. This factor encompassed traits across social, communicative, and repetitive behavioral domains. The authors cross validated this tool by giving it to children with ($N = 10$) and without ASD ($N = 10$) and found that it appropriately distinguished between typical and ASD children (Marrus et al., 2011). Feczko et al. (2016) subsequently found support for a three-factor solution in macaques, with Factor 1 accounting for 30.64% of the variance. Items that loaded on Factor 1 included items associated with social avoidance, social anxiety, and social confidence. However, no items loaded significantly on to Factor 2 or Factor 3, suggesting that the sample size ($N = 105$) was too small to capture the underlying constructs of these factors. Still, these initial findings suggest that variation in social functioning can be quantified in rhesus macaques using the macaque Social Responsiveness Scale (mSRS). We subsequently refined and validated the macaque version of the SRS to yield a 17-item macaque SRS-Revised (mSRS-R; Talbot et al., 2020). Consistent with the human SRS total score (Constantino, 2011), mSRS-R total scores are continuously distributed across the general rhesus monkey population (Talbot et al., 2020). Moreover, mSRS-R total scores robustly and negatively predict two extremes of social behavior (low-social and high-social) of a large study sample with 96% accuracy (Talbot et al., 2020), thereby demonstrating the convergent construct and predictive validity of this scale.

To better understand the psychological factors that contribute to variation in macaque social functioning, in the present investigation we first used a hypothesis-generating approach to evaluate the underlying factor structure of the mSRS-R in a large population of male rhesus macaques. Next, to investigate the convergent validity of the mSRS-R factor structure, we examined whether the resulting mSRS-R factors predicted quantitative social behavior measures obtained by unobtrusive focal observations of monkeys in their outdoor field corrals. In this way, we evaluated whether the mSRS-R factors showed agreement with the construct being modeled, that is, social functioning. Thus, we hypothesized that the mSRS-R factors would predict quantitative social behavior measures. Broadly, we expected higher scores on the resulting mSRS-R factors to be associated with less frequent social behavior. However, given previous mixed results in various primate species on SRS factor number and the constructs that these factors represent, we did not have any further predictions as to whether the resulting mSRS-R factors would predict particular social behavior measures. Finally, we evaluated the relationship between the resulting mSRS-R factors and previously established personality dimensions, including Sociability, obtained from ratings on a standardized instrument (Capitanio & Widaman, 2005). To our knowledge, this is the first study to examine SRS factor scores in relation to personality dimensions. Because higher scores on the mSRS-R indicate greater social impairment, we expected the primary resulting mSRS-R factor (i.e., the factor accounting for the majority of the variance) to negatively predict the personality dimension Sociability. This would establish convergent construct

validity, such that the primary mSRS-R factor measures what it theoretically should measure: one's ability to function socially. We also expected the mSRS-R factors to demonstrate relationships with some, but not all, of the other personality factors, suggesting discriminant validity between the resulting mSRS-R factors. That is, the resulting mSRS-R factors should reflect separate underlying aspects of social functioning and, therefore, should not demonstrate the same relationships with all four macaque personality dimensions.

2 | METHODS

2.1 | Ethical statement

No animals were handled in this study. We collected all data unobtrusively from outside of each animal's home corral. Animal husbandry followed the Guide for the Care and Use of Laboratory Animals. The California National Primate Research Center (CNPRC) is fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care, International. All procedures were ethically reviewed and approved by the Institutional Animal Care and Use Committee of the CNPRC, University of California, Davis, as well as the Administrative Panel on Animal Laboratory Care of Stanford University. All procedures complied with the National Institutes of Health policies on the care and use of animals and the American Society of Primatologists Principles for the Ethical Treatments of Nonhuman Primates.

2.2 | Subjects and housing

Subjects were $N = 233$ male rhesus macaques (*Macaca mulatta*), born and reared at the CNPRC. All subjects lived in mixed age and sex groups of up to 150 individuals in large, outdoor, half-acre (0.19 ha) field corrals (30.5 m wide × 61 m deep × 9 m high). Individuals were housed among 16 field corrals. Soon after birth, monkeys were tattooed and dye-marked before behavioral observation to facilitate easy identification. Because our original interest was in developing the mSRS-R as a translational tool for use in a macaque model of naturally-occurring social impairments with direct relevance to ASD (Parker et al., 2018; Sclafani et al., 2016), and because ASD is an early onset male-biased disorder (Maenner et al., 2020), we focused on young male monkeys in this study. Mean (*SD*) age of subjects was 3.62 (1.12) years with a range of 1.25–6.27 years at the time of study. Monkeys had ad libitum access to Lixit-dispensed water. Primate laboratory chow was provided twice daily and fruit and vegetable supplements were provided weekly. Outdoor field corrals, enhanced with various toys, swinging perches, and other enrichment, provided a stimulating environment for all subjects.

2.3 | Behavioral observations: Quantitative social behavior measures

Behavioral observations were performed over a 2-year period (April–September 2016 and 2017). Before conducting behavioral observations, observers became reliable on data collection with ≥90% agreement (number of agreements divided by the [number of agreements + number of disagreements]) on all behavioral categories. Subjects were observed unobtrusively in their home field corrals by one of five observers. Each observer conducted 10-min focal samples on subjects during two observation periods per day (0830–1030 and 1045–1300), 4 days per week, for 2 weeks, resulting in a total of 16 focal samples

over a period of 160 min for 640 data points per subject. Each observer watched a maximum of nine subjects, residing in one to three corrals, during each 2-week observation period. We used instantaneous sampling (Altmann, 1974) in which we recorded, at 15-s intervals, whether the subject was engaged in any of the following behaviors: alone (subject is not within an arm's reach of any other animal and is not engaged in play), proximity (subject is within an arm's reach of another animal), contact (subject is touching another animal in a nonaggressive manner), groom (subject is engaged in a dyadic interaction with one animal inspecting the fur of another animal using its hands and mouth), or play (subject is involved in chasing, wrestling, slapping, shoving, grabbing, or biting accompanied by a play face [wide eyes and open mouth, without bared teeth] and/or a loose, exaggerated posture and gait; the behavior must have been deemed unaggressive to be scored; Parker et al., 2018). Behavioral data were scored such that an individual could be engaged in more than one behavioral category at the same time (e.g., playing while in proximity to another individual). However, because social functioning, and thus social behavior, was the focus of this study, behavioral data were summarized in a hierarchical fashion based upon the degree of coordination and tolerance required for its display (i.e., play > groom > contact > proximity > alone) such that only one behavior was scored per interval to yield the total frequency observed in each behavioral state. Here, we report on the frequency with which subjects were observed in each behavioral state, which ranged from 0 to 640.

2.4 | Rating instruments: mSRS-R and personality assessment

At the conclusion of each 2-week behavioral observation period (at least 1 h after the final observation was concluded and no more than 24 h after the last observation), observers rated each subject on the original 36-item mSRS (Feczko et al., 2016) and on a 29-item personality instrument (Capitanio & Widaman, 2005). One monkey's personality data were missing, so for analyses including personality dimensions, $N = 232$. Both rating instruments employed a seven-point Likert scale (1 = total absence of the trait, 7 = extreme manifestation of the trait) for each item.

After these ratings were obtained, the mSRS was substantially refined and revised based on psychometric assessments (inter-rater and intra-rater reliabilities), resulting in the more reliable 17-item mSRS-R (Talbot et al., 2020; Supporting Information Material 1). Accordingly, the 17 reliable items of the mSRS-R are used here. Before final summary, questions written in the infrequent direction were reverse scored such that higher scores always indicated greater impairment. Final summed total scores on the mSRS-R could range between 17 and 119. Observed mSRS-R total scores in this sample ranged from 23 to 101 (Talbot et al., 2020).

The personality instrument comprised 29 adjectives derived from several published articles on primate personality (Capitanio & Widaman, 2005; Capitanio, 1999; Stevenson-Hinde & Zunz, 1978; Supporting Information Material 2). Previous exploratory (Maninger et al., 2003) and confirmatory (Capitanio & Widaman, 2005) factor analyses revealed a four factor structure of personality with this instrument. The four dimensions, named for the adjective with the highest factor loading were: (1) Sociability (comprising the positively-loaded adjectives "affiliative" and "warm," and the negatively-loaded "solitary"), (2) Confidence

(comprising the positively-loaded adjectives “confident”, “bold”, and “direct” and the negatively loaded adjectives “timid” and “submissive”), (3) Irritability (comprising the positively-loaded adjectives “irritable” and “reckless”), and (4) Equability (comprising the positively-loaded adjectives “slow” and “calm”). For the present study, scores for the personality dimensions were constructed by z-scoring each adjective across all subjects, reverse-coding the adjectives that had a negative loading, and then summing the resulting values for all adjective items loading on a given dimension using unit weights (see Capitanio & Widaman, 2005, for details). We then checked the reliability of the resulting personality dimensions using Cronbach’s alpha.

2.5 | Statistical analysis

Because we were interested in the aspects underlying separate mSRS-R items, we took a hypothesis-generating approach (Floyd & Widaman, 1995) and ran an exploratory factor analysis on the 17 items comprising the mSRS-R (Talbot et al., 2020; Supporting Information Material 1). Factors were rotated using oblique rotation. Scales for each of the resulting factors were constructed by adding the scores (using unit weights) for each item that loaded ≥ |0.40|. We used Cronbach’s alpha to test the reliability, or the internal consistency, of the resulting factors.

We next tested whether the resulting mSRS-R factors predicted social behavior frequencies (i.e., alone, proximity, contact, groom, and play) using linear regression models. Finally, we used linear regression to evaluate the relationship between mSRS-R factors and the four established dimensions of rhesus macaque personality (i.e., Sociability, Confidence, Irritability, and Equability). We know that age and rank may impact social behavior in nonhuman primates (Vessey, 1984); therefore, we included these variables as covariates in all linear regression models. Rank was assessed in each corral by Behavioral Management personnel on an approximately monthly basis by recording aggressive and submissive interactions following provision of sunflower seeds. Because rank has little meaning when different corrals contain a different number of males, for analyses, rank was calculated as the proportion of males in the group that the focal individual outranked, such that the highest-ranked individual had a value of 1 and the lowest-ranked individual had a value of 0 (Linden et al., 2019). Data were analyzed using SPSS statistical package version 26 (SPSS Inc.).

3 | RESULTS

3.1 | mSRS-R factor structure

We performed an exploratory factor analysis on the 17 mSRS-R items. The scree test (Gorsuch, 1983) supported retaining three factors. These three factors also had eigenvalues greater than 1.0 and explained 50.20%, 11.10%, and 6.83% of the variance, respectively. Ten items loaded significantly on Factor 1. These items related to social avoidance (e.g., item 3, Alone), lack of social motivation (e.g., item 6, [Not] Interactive), and social anxiety (e.g., item 9, Avoidant). Therefore, we refer to Factor 1 as “Poor Social Motivation.” Three items loaded significantly on Factor 2, items 12 (Silly), 13 (Repetitive), and 14 (Disruptive). These items were associated with inappropriate or odd behavior and we therefore refer to Factor 2 as “Inappropriate Behavior.” Four items loaded significantly on Factor 3, including items 7

(Playful [reverse scored]), 8 (Comforting [reverse scored]), 11 (Serious), and 17 ([Not] Likeable). Given that all these items related to negative social attractiveness, we refer to Factor 3 as "Poor Social Attractiveness." All factors demonstrated acceptable internal consistency (Poor Social Motivation: α = .95; Inappropriate Behavior: α = .61; Poor Social Attractiveness: α = .84). Rotated factor loadings and the direction in which each item loads on each of the three factors are presented in Table 1; all items loaded significantly on separate factors. Poor Social Motivation and Poor Social Attractiveness were correlated (r = .72), indicating that they share approximately 52% of their variance. All other factors were not correlated (r < .2).

3.2 | Relationships between mSRS-R factors and age and rank

Age and rank were correlated in this sample of male macaques (r = .668; N = 233; p < .001). We found that neither age (r = .082; N = 233; p = .215) nor rank (r = −0.024; N = 233; p = .711) significantly correlated with Poor Social Motivation. In contrast, both age and rank negatively correlated with Inappropriate Behavior (age: r = −.339, N = 233, p < .001; rank: r = −.263, N = 233, p < .001) and positively correlated with Poor Social Attractiveness (age: r = .328, N = 233, p < .001; rank: r = .286, N = 233, p < .001). Thus, in the following analyses, we included age and rank as covariates in the linear regression models examining the relationship between the mSRS-R factors and social behavior and personality dimensions.

3.3 | Relationships between mSRS-R factors and quantitative social behavior measures

Because the mSRS-R instrument measures raters' impressions of behavioral traits (and not the frequency of specific behaviors), we next evaluated whether mSRS-R factors predicted variation in frequencies of social behavior (i.e., alone, proximity, contact, groom, play) obtained by focal observations of monkeys in their outdoor field corrals. We found that higher scores on Poor Social Motivation positively predicted the frequency of being alone in nonsocial behavior and negatively predicted the frequency of being in contact and grooming with conspecifics. Inappropriate Behavior was not predictive of any social behavior measure. Poor Social Attractiveness positively predicted the frequency of grooming and negatively predicted the frequency of playing (Table 2). Confirming this latter finding, grooming and play behavior exhibited a significant negative relationship (r = −.329; N = 233; p < .001).

3.4 | Relationships between mSRS-R factors and personality dimensions

Finally, we examined whether Poor Social Motivation, Inappropriate Behavior, and Poor Social Attractiveness predicted scores on the established personality dimensions Sociability, Confidence, Irritability, and Equability. Sociability, Confidence, and Irritability demonstrated acceptable internal consistency (Sociability: α = .87; Confidence: α = .88; Irritability: α = .65), whereas Equability had poor internal consistency (α = .53). In accordance with our impressions of the mSRS-R factors identified in our exploratory factor analysis, both Poor Social Motivation and Poor Social Attractiveness negatively predicted scores on the personality dimension Sociability (comprising the positively-loaded personality adjectives "affiliative" and "warm," and the negatively-loaded adjective "solitary"). Specifically, higher scores on these two mSRS-R factors, indicating greater social impairment, were associated with lower Sociability scores. All three mSRS-R factors

were predictive of Confidence scores (comprising the positively-loaded personality adjectives “confident,” “bold,” and “direct” and the negatively loaded personality adjectives “timid” and “submissive”). However, Poor Social Motivation negatively predicted Confidence scores, whereas Inappropriate Behavior and Poor Social Attractiveness positively predicted Confidence scores. Likewise, Poor Social Motivation negatively predicted Irritability scores (comprising the positively-loaded personality adjectives “irritable” and “reckless”); yet, Inappropriate Behavior and Poor Social Attractiveness positively predicted Irritability scores. None of the mSRS-R factors predicted Equability scores (comprising the positively-loaded adjectives “slow” and “calm”; Table 3).

4 | DISCUSSION

In the present study, we determined the underlying factor structure of the psychometrically robust mSRS-R in a large sample of rhesus monkeys ($N = 233$). Further, we evaluated the relationships of the resulting mSRS-R factors to quantitative social behavior measures and scores on established macaque personality dimensions to evaluate the convergent and discriminant validity of the mSRS-R factors, respectively. The three mSRS-R factors identified distinct aspects of social functioning and predicted social behavior measures and scores on personality dimensions as discussed below.

4.1 | The mSRS-R factor structure

Our study was conducted in a large sample of male rhesus monkeys born and reared in large, outdoor social groups. Summed total scores on the mSRS-R could range between 17 and 119. Observed mSRS-R total scores ranged from 23 to 101 in this sample (Talbot et al., 2020), indicating that our study evaluated nearly the full range of social functioning in this species. Exploratory factor analysis enabled us to examine the underlying aspects of the mSRS-R (Floyd & Widaman, 1995). Factor analysis revealed three factors, two of which were related to sociality: Poor Social Motivation and Poor Social Attractiveness. Items that loaded on these factors were associated with social avoidance or a lack of social motivation (i.e., Poor Social Motivation), and with traits low in social attractiveness (i.e., Poor Social Attractiveness), demonstrating sensitivity to behavior similar to ASD (i.e., face validity). These items largely mapped on to two of the five clinically derived subscales of the human SRS (Constantino & Gruber, 2005, 2012), social motivation and social communication. Specifically, seven of the 10 items that loaded on the mSRS-R Poor Social Motivation factor mapped to the human SRS social motivation subscale, two items mapped to the human SRS social communication subscale, and one item mapped to the human SRS restricted interests and repetitive behaviors subscale. All four items that loaded on the mSRS-R Poor Social Attractiveness factor mapped to the human SRS social communication subscale. Our third mSRS-R factor, Inappropriate Behavior, encompassed three items related to odd behavior, all of which mapped to one of the proposed human SRS factors for repetitive mannerisms (Frazier et al., 2014). Given the disparate results reported in the human literature (Constantino & Todd, 2000; Constantino et al., 2004, 2007; Frazier et al., 2014; Nelson et al., 2016; Uljarević et al., 2019), however, we will not speculate further on the translational nature of the mSRS-R factors obtained here.

4.2 | mSRS-R factors and quantitative social behavior measures

We found that the mSRS-R factors, Poor Social Motivation and Poor Social Attractiveness, predicted variation in quantitative social behavior measures obtained by focal observations of monkeys in their outdoor field corrals. Higher scores on Poor Social Motivation (indicating greater social impairment) positively predicted the frequency of being alone, and negatively predicted the frequency of being in contact and grooming with conspecifics, supporting our interpretation that the underlying construct this factor related to Poor Social Motivation. Similarly, Poor Social Attractiveness, which encompassed traits such as (Not) Playful and (Not) Likeable, was predictive of less play with and more grooming with conspecifics. This result was bolstered by the negative relationship we found between grooming and play behavior. Both grooming and play behavior function in the formation and maintenance of social bonds (Kalbitz et al., 2016; Shimada & Sueur, 2018), suggesting that individuals who are not socially attractive partners (and perhaps not well co-ordinated or communicative) may employ a different social strategy and spend more time grooming and less time playing than their more socially attractive peers. Finally, Inappropriate Behavior did not demonstrate a relationship with any of the social behavior measures, supporting our interpretation that this factor was not related to social behavior. However, it is possible that Inappropriate Behavior is related to other behaviors, such as repetitive or stereotyped behavior, which should be evaluated in future work.

These collective findings largely demonstrate the convergent validity of the identified mSRS-R factor structure, such that each of the mSRS-R factors related to social functioning (i.e., Poor Social Motivation and Poor Social Attractiveness) predicted frequencies of social behavior (as expected). These findings also suggest discriminant validity, such that the one mSRS-R factor unrelated to social behavior, Inappropriate Behavior, did not predict any social behavior measure. Additionally, these results suggest discriminant validity, such that each of the mSRS-R factors demonstrated different relationships with different behaviors. Only Poor Social Motivation was associated with more nonsocial behavior and less contact with others, whereas only Poor Social Attractiveness was associated with less play behavior. Furthermore, while both Poor Social Motivation and Poor Social Attractiveness demonstrated a relationship with conspecific grooming, they demonstrated different relationships: Poor Social Motivation was associated with less grooming, whereas Poor Social Attractiveness was associated with more grooming. It is not surprising that Poor Social Motivation, our primary mSRS-R factor associated with a greater frequency of nonsocial behavior, was negatively associated with grooming—the more time one spends alone, the less time one has for social engagement. In contrast, individuals who are socially unattractive (and thus score high on Poor Social Attractiveness) may spend more time cultivating social relationships through social bonding activities like grooming. Thus, these results support the concept that the mSRS-R factors reflect separate underlying aspects of social functioning.

4.3 | mSRS-R factors and personality dimensions

We found that both Poor Social Motivation and Poor Social Attractiveness negatively predicted scores on Sociability: higher scores on these factors, which indicate greater social impairment, were associated with lower Sociability. This result demonstrates convergent

predictive validity such that both mSRS-R factors encompassing social items predicted scores on the well-established personality dimension, Sociability. However, Poor Social Motivation and Poor Social Attractiveness demonstrated different relationships with Confidence and Irritability. Poor Social Motivation was associated with lower Confidence and lower Irritability, whereas Poor Social Attractiveness was associated with higher Confidence and higher Irritability. Thus, individuals who score high on Poor Social Motivation seem to be relatively uninterested in social interaction: they are less social, less confident, and less irritable or reckless. On the other hand, individuals who score high on Poor Social Attractiveness tend to be less social, more confident, and more irritable. It is possible that what makes an animal socially unattractive is an overconfident and irritable personality, which together may result in less social opportunity. Finally, we found the mSRS-R factor, Inappropriate Behavior, was associated with higher Confidence and higher Irritability; this finding aligns with our interpretation of the underlying construct. The fact that the mSRS-R factors demonstrate different relationships with personality dimensions is suggestive that these mSRS-R factors show discriminant validity.

4.4 | mSRS-R factors and age and rank

Previous research has found that higher SRS total scores are associated with lower rank in chimpanzees (Faughn et al., 2015) and macaques (Feczko et al., 2016). Although other population factors may have impacted the relationship between rank and SRS scores, we note that in these studies rank was scored categorically (i.e., high, medium, or low) based on humans' impression of the animal's rank. However, our recent analysis of the relationship between mSRS-R scores and rank found no relationship in rhesus macaques (Talbot et al., 2020). In our prior study and in the current study, rank was calculated as the proportion of individuals the subject outranked within their respective social group and was based on observed behavior rather than humans' impression of subjects' rank. Furthermore, we also found no relationship between mSRS-R scores and age in our previous study (Talbot et al., 2020), suggesting the possibility that the mSRS-R measures intrinsic social traits more accurately than other SRS versions. Our prior results are also consistent with the human literature showing no relationship between the SRS and age (Constantino, Przybeck,, Friesen, et al., 2000). Although other nonhuman primate studies have found small to moderate effects of age, such that SRS total scores are higher in older animals (Faughn et al., 2015; Feczko et al., 2016; but see Marrus et al., 2011), these studies sampled males and females across a broad age range, whereas our previous study specifically focused on young males. Thus, it is possible that rank and age may display different relationships with social functioning (and possibly even with different aspects of social functioning) depending upon one's sex and/or stage of development.

Here, we found that age and rank did not correlate with Poor Social Motivation, whereas both age and rank had small effects on Inappropriate Behavior and Poor Social Attractiveness. Younger and lower-ranking animals were more likely to score high on Inappropriate Behavior, encompassing three items—silly, repetitive odd behavior, and disruptive. This is not surprising given that younger animals are often still learning socially appropriate behavior (Goodall, 1986; Gray, 2019), and tend to exhibit more silly, playful behavior compared to adults (Kulik et al., 2015). Older and higher-ranking animals were

more likely to score high on Poor Social Attractiveness, encompassing four items—Playful (reversed scored), Serious, (Not) Likeable, and Comforting (reverse scored). Note that three of these items relate to not being playful (Supporting Material 1). We know from previous research that macaques, like many primate species, decrease the amount of time they spend playing as they get older (Kulik et al., 2015; Yanagi & Berman, 2019). In addition, high-ranking males tend to decrease their rate of play as they get older, more so than their peers (Kalbitz et al., 2016). We also know that individuals often compete to groom higher-ranking individuals (Colvin, 1983b; Kaufmann, 1967), suggesting that higher-ranking males spend more time grooming with conspecifics which may leave less time for play. Accordingly, we found that individuals who scored high on Poor Social Attractiveness tended to play less and groom more (as discussed above). Although future work should examine whether those who score high on Poor Social Attractiveness are receiving grooming or initiating these interactions, these relationships are consistent with typical male rhesus macaque behavior (Kulik et al., 2015).

4.5 | Limitations and future directions

The present study had several limitations that warrant comment. First, as with the majority of rating studies, the ratings and behavioral observations were not strictly independent of each other. That is, the same raters who conducted the behavioral observations also completed the mSRS-R and personality ratings. However, we attempted to maximize independence by including the criteria that observers must fill out their ratings at least one hour after their final observation (after the observers had returned to their desk from the field corrals) and within 24 h of their final observation. Moreover, the instructions of the ratings specified that their ratings were to be based on their experience with the animal, which was not limited to focal observations. Second, in keeping with our interest in developing a monkey model of ASD, and due to the male-biased prevalence of this disorder, the present study sample was composed of only males. The study composition may have impacted our results in several ways. In rhesus macaques, females are philopatric (Gouzoules & Gouzoules, 1987), and males disperse at puberty (Colvin, 1983a). Because of this, rhesus macaques exhibit sex differences in social behavior, which may change throughout development (Kulik et al., 2015). For instance, adult philopatric females preferentially interact with other females, particularly maternal kin (Kapsalis & Berman, 1996). Thus, sex differences in social behavior may lead to significant sex differences in social functioning throughout ontogeny. Similarly, rhesus macaques exhibit a matrilineal dominance hierarchy, with separate hierarchies for males and females. Therefore, it is possible that rank interacts with social functioning differently in male and female rhesus macaques, a possibility that should be explored in future studies. Although human males are more likely to be diagnosed with ASD, growing evidence supports the notion of gender-specific developmental trajectories of social impairments, with females more likely to experience subtler impairments or a genuinely later onset of social symptoms (Mandy et al., 2018). Further work is needed to evaluate social functioning and autistic-like traits in female rhesus macaques systematically.

5 | CONCLUSION

Determining the factor structure underlying the mSRS-R is a critical step in the discovery and interpretation of causal psychological mechanisms that produce variation in social functioning as well as in social impairments. Findings from the present study suggest that three factors underlie the mSRS-R (Poor Social Motivation, Poor Social Attractiveness, and Inappropriate Behavior), which map closely to quantitative social behavior measures and personality dimensions in rhesus macaques. These findings suggest that the mSRS-R is a promising, psychometrically robust tool that can be deployed to better understand individual differences in macaque social functioning (which might be useful, e.g., in a behavioral management context) as well as the pathogenesis of autistic-like traits. Furthermore, given that the SRS has been used to study variation in social functioning in humans, chimpanzees, and rhesus macaques, the present findings suggest that with relevant species-specific modifications, the SRS may hold promise for investigating and better understanding individual differences in social functioning across diverse primate taxa.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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TABLE 1

Rotated factor loadings from the macaque Social Responsiveness Scale-Revised (mSRS-R) exploratory factor analysis on the 17 mSRS-R items using oblique rotation

	Factor 1	**Factor 2**	**Factor 3**
mSRS-R item	***Poor social motivation***	***Inappropriate behavior***	***Poor social attractiveness***
Alone (3)	**0.654** ↑	−0.043	0.253
Avoidant (9)	**0.735** ↑	0.021	0.211
Awkward (10)	**0.670** ↑	0.143	0.145
Bizarre (4)	**0.699** ↑	0.131	−0.012
***Comforting* (8)**	0.130	0.164	**0.545** ↑
Disruptive (14)	−0.048	**0.575** ↑	0.156
Fidgety (1)	**0.932** ↑	0.064	−0.068
(Not) Interactive (6)	**0.728** ↑	−0.042	0.217
(Not) Likable (17)	0.269	−0.024	**0.566** ↑
Playful (7)	0.247	−0.192	**0.583** ↑
Repetitive (13)	0.033	**0.641** ↑	0.054
***Self-confident* (5)**	**0.936** ↑	−0.118	−0.141
Serious (11)	0.044	0.022	**0.808** ↑
Silly (12)	0.073	**0.636** ↑	−0.292
***Socially confident* (2)**	**0.917** ↑	−0.165	−0.046
Stares (16)	**0.513** ↑	0.180	0.094
Tense (15)	**0.677** ↑	0.051	0.156

Note: Each item is listed with its corresponding mSRS-R item number in parentheses. All loadings appear in the table. Italicized items indicate reverse scoring. The primary factor loading (≥|0.40|) for each item is in bold and arrows indicate the direction in which each item loaded.

TABLE 2

Relationships between macaque Social Responsiveness Scale-Revised (mSRS-R) exploratory factor analysis-derived factors and quantitative social behavior measures

Behavior	*b*	*SE b*	*β*	*p*
Alone				
Constant	308.02	23.33		
Age	10.30	5.71	.15	.072
Rank	−61.64	20.78	−.25	.003
Poor Social Motivation	27.05	6.37	.39	<.001
Inappropriate Behavior	1.19	5.50	.01	.829
Poor Social Attractiveness	1.10	6.56	.02	.867
Proximity				
Constant	113.43	12.95		
Age	−1.55	3.17	−.04	.626
Rank	23.65	11.54	.18	.042
Poor Social Motivation	−5.74	3.53	−.16	.106
Inappropriate Behavior	−0.99	3.05	−.02	.747
Poor Social Attractiveness	−3.24	3.64	−.09	.375
Contact				
Constant	105.55	15.07		
Age	−7.10	3.69	−.17	.056
Rank	39.89	13.43	.26	.003
Poor Social Motivation	−8.67	4.11	−.21	.036
Inappropriate Behavior	−0.03	3.55	.00	.993
Poor Social Attractiveness	−0.75	4.24	−.02	.860
Groom				
Constant	32.09	12.27		
Age	9.62	3.00	.28	.002
Rank	0.42	10.93	.00	.970
Poor Social Motivation	−11.99	3.35	−.34	<.001
Inappropriate Behavior	−0.03	2.89	.00	.991
Poor Social Attractiveness	7.79	3.45	.22	.025
Play				
Constant	80.92	5.75		
Age	−11.27	1.41	−.55	<.001
Rank	−2.32	5.13	−.03	.652
Poor Social Motivation	−0.65	1.57	−.03	.679
Inappropriate Behavior	−0.13	1.36	−.01	.921
Poor Social Attractiveness	−4.90	1.62	−.24	.003

Note: A summary of multiple regression analyses for predictors of the five social behavior measures (alone, proximity, contact, groom, and play) are presented for $N = 233$ male rhesus monkeys. Age and rank are included as covariates in all regression models. Derived factors include Poor Social Motivation, Inappropriate Behavior, and Poor Social Attractiveness. Reported values include unstandardized regression coefficients (*b*) and associated *SE* (*b*), standardized regression coefficient (*β*), and corresponding *p* values.

TABLE 3

Relationships between macaque Social Responsiveness Scale-Revised (mSRS-R) exploratory factor analysis-derived factors and scores on personality dimensions

Personality factor	*b*	*SE b*	*β*	*p*
Sociability				
Constant	2.85	0.16		
Age	−0.07	0.04	−.08	.081
Rank	0.29	0.14	.09	.042
Poor Social Motivation	−0.51	0.04	−.55	<.001
Inappropriate Behavior	0.00	0.04	.00	.940
Poor Social Attractiveness	−0.35	0.05	−.39	<.001
Confidence				
Constant	0.80	0.24		
Age	−0.02	0.06	−.03	.688
Rank	0.63	0.21	.19	.003
Poor Social Motivation	−0.81	0.06	−.88	<.001
Inappropriate Behavior	0.23	0.06	.20	<.001
Poor Social Attractiveness	0.27	0.07	.30	<.001
Irritability				
Constant	−1.24	0.31		
Age	0.02	0.08	.02	.802
Rank	−0.02	0.28	−.01	.940
Poor Social Motivation	−0.22	0.09	−.24	.011
Inappropriate Behavior	0.44	0.07	.39	<.001
Poor Social Attractiveness	0.29	0.09	.32	.001
Equability				
Constant	−0.94	0.32		
Age	0.20	0.08	.22	.012
Rank	0.61	0.29	.18	.036
Poor Social Motivation	0.11	0.09	.12	.214
Inappropriate Behavior	−0.03	0.08	−.03	.691
Poor Social Attractiveness	−0.11	0.09	−.12	.248

Note: A summary of multiple regression analyses for predictors of scores on the four personality dimensions (Sociability, Confidence, Irritability, and Equability) are presented for $N = 232$ male rhesus monkeys. Age and rank are included as covariates in all regression models. Derived factors include Poor Social Motivation, Inappropriate Behavior, and Poor Social Attractiveness. Reported values include unstandardized regression coefficients (b) and associated SE (b), standardized regression coefficient (β), and corresponding p values.