

A neuroanatomical predictor of mirror self-recognition in chimpanzees

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Abstract

The ability to recognize one's own reflection is shared by humans and only a few other species, including chimpanzees. However, this ability is highly variable across individual chimpanzees. In humans, self-recognition involves a distributed, right-lateralized network including frontal and parietal regions involved in the production and perception of action. The superior longitudinal fasciculus (SLF) is a system of white matter tracts linking these frontal and parietal regions. The current study measured mirror self-recognition (MSR) and SLF anatomy in 60 chimpanzees using diffusion tensor imaging. Successful self-recognition was associated with greater rightward asymmetry in the white matter of SLFII and SLFIII, and in SLFIII's gray matter terminations in Broca's area. We observed a visible progression of SLFIII's prefrontal extension in apes that show negative, ambiguous, and compelling evidence of MSR. Notably, SLFIII's terminations in Broca's area are not right-lateralized or particularly pronounced at the population level in chimpanzees, as they are in humans. Thus, chimpanzees with more human-like behavior show more human-like SLFIII connectivity. These results suggest that self-recognition may have co-emerged with adaptations to frontoparietal circuitry.

Key words: self-recognition; chimpanzees; superior longitudinal fasciculus; brain evolution; lateralization

Introduction

A distinguishing feature of human and non-human great ape social cognition is mirror self-recognition (MSR). MSR was first demonstrated by Gallup's (1970) study using the mark test (Gallup, 1970; Anderson and Gallup, 2015). In the mark test, an odorless, non-tactile pigment is placed on a part of the animal's body which cannot be perceived without a mirror, typically the face. As a control, a transparent, non-pigmented mark is also placed in the same area. A mirror is then placed in the animal's proximity. Responses to the mirror follow a distinctive

progression, beginning with species-typical social behavior toward a conspecific (e.g. threat faces), followed by exploration of the area behind the mirror, 'testing' of the reflection's properties and, potentially, exploration of the mark and other regions of the body not visible without the mirror (Gallup, 1970). Since the original report by Gallup (1970), there have been numerous attempts to document MSR abilities in a variety of nonhuman species (Anderson and Gallup, 2015) and the evidence indicates that only a few other species show MSR. Among primates, mirror-self recognition has been reported in chimpanzees and

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other great apes [bonobos (Westergaard and Hyatt, 1994; Walraven et al., 1995), some gorillas (Parker, 1994; Patterson and Cohn, 1994; Posada and Colell, 2007) and orangutans (Suarez and Gallup, 1981; White Miles, 1994)] but not in lesser apes such as gibbons (Hyatt, 1998; Ujhelyi et al., 2000; Suddendorf and Collier-Baker, 2009) or more distantly related Old and New World monkeys (Gallup, 1977; Anderson, 1983; Shaffer and Renner, 2002; Roma et al., 2007; Macellini et al., 2010). There are two reports of Old World monkeys passing the mark test (Rajala et al., 2010; Chang et al., 2015) but some have questioned the methods and interpretation of these findings (Anderson and Gallup, 2015). Beyond primates, there are some reports of MSR abilities in Asian elephants (Plotnik et al., 2006, 2010), magpies (Prior et al., 2008), killer whales (Delfour and Marten, 2001) and bottlenose dolphins (Reiss and Marino, 2001); evidence, however, was limited to a single subject in the elephant and dolphin studies and has yet to be replicated. Furthermore, tactile cues may have been produced by mark application to the magpies, making interpretation of results difficult (Soler et al., 2014).

Though it is generally accepted that great apes demonstrate MSR, considerable individual differences in performance on the mark test within different samples are apparent. For instance, in a study of 105 captive chimpanzees, Povinelli et al. (1993) reported that ~65% of the sample failed to demonstrate compelling evidence of MSR. Similarly, Mahovetz et al. (2016) reported in a sample of 73 chimpanzees that 71% of the individuals failed to show compelling evidence of MSR. The origin of these individual differences in MSR abilities are unclear and the extant data suggest that subject variables, such as age, sex, rearing history and genetic factors account for a relatively modest proportion of variance in performance (De Veer and Van Den Bos, 1999; Heschl and Burkart, 2006).

In this study, we examined whether individual differences in connectivity between gray matter regions may explain some of the variability in MSR performance within chimpanzees. The neural correlates of self-recognition in chimpanzees and other species have not yet been directly experimentally investigated, although neuroanatomical comparisons between species that do vs. do not show MSR have been carried out; see (Butler and Suddendorf, 2014) for a recent detailed review. However, the neural correlates of self-recognition have been extensively studied in humans. Research with split-brain patients indicates that both hemispheres are capable of self-recognition, but there appears to be a right-hemisphere advantage (Sperry et al., 1979). Healthy individuals are faster to recognize their own faces than the faces of other familiar individuals only if the response is made by the left hand (i.e. the right hemisphere; Keenan et al., 1999). Anesthetization or transcranial magnetic stimulation (TMS) impairs visual self-recognition when applied to the right hemisphere, but has no discernable effect when applied to the left hemisphere (Keenan et al., 2001). Human neuroimaging studies of self-recognition generally implicate a rightwardly asymmetric fronto-parietal network, along with some other regions associated with social cognition, social perception and interoception (e.g. Uddin et al., 2005; Sugiura et al., 2015), reviewed in (Devue and Bredart, 2011). One ALE (activation likelihood estimation) meta-analysis compared fMRI studies on self-face recognition to studies on false-belief tasks; this revealed foci for self-face recognition in right superior temporal gyrus, right parahippocampal gyrus, right inferior frontal gyrus/ anterior cingulate cortex, left inferior parietal lobe, superior temporal gyrus and ventromedial prefrontal cortex (van Veluw and Chance, 2014). Another recent ALE meta-analysis compared fMRI activations for self-face recognition, other-face

recognition, and non-visual self- and non-self-referential processing; this also implicated a right-lateralized network of inferior frontal, inferior parietal, and temporal/occipital regions in self-face recognition (Hu et al., 2016).

The proposed self-recognition network in humans involves regions that differ in their anatomy or response properties between modern primate species, suggesting that the functions subserved by these regions have been the focus of recent selection pressure. For instance, compared with macaques, chimpanzees and especially humans show a trend toward increasing elaboration in fronto-parietal and fronto-temporal white matter tracts (Rilling et al., 2008; Hecht et al., 2013). Several of the frontal and parietal regions linked by these tracts show species differences in responses to external stimuli, such as visual perception of objects, extrapolation of 3D form from moving objects, perception of hand-object interactions, and tool use (Vanduffel et al., 2002; Denys et al., 2004; Peeters et al., 2009; Hecht et al., 2013). Further, like humans, chimpanzees show human-like leftward asymmetries associated with gestural communication, tool use, and right-handedness (Tagliabue et al., 2006; Cantalupo et al., 2009; Keller et al., 2009; Schenker et al., 2010; Lyn et al., 2011; Hopkins, 2013), suggesting that chimpanzees may also show human-like asymmetry for the functions that are right-lateralized in humans, including self-recognition. Recently, Hecht et al. (2015) identified species differences in a white matter tract that shows rightward asymmetry in humans, the third branch of the superior longitudinal fasciculus (SLFIII) (Hecht et al., 2015). In chimpanzees, Hecht et al. (2015) observed a modest extension of SLFIII into the anterior aspects of the inferior frontal gyrus (extending beyond area 44 into area 45), a region not reached by this tract in macaques (Petrides and Pandya, 2002, 2009). However, in chimpanzees, neither SLFIII's white matter nor its terminations in the inferior frontal gyrus were right-lateralized. In humans, this prefrontal extension was markedly more pronounced, and both SLFIII's white matter and its terminations in the inferior frontal gyrus were significantly larger in the right hemisphere.

Hecht et al. (2015) proposed that this right-hemisphere prefrontal extension of SLFIII might support increased integration between the higher-order action-representation processing of anterior inferior frontal cortex and the kinematic and proprioceptive processing of anterior inferior parietal cortex, which may have had evolutionary relevance for social learning and tool use. However, this functionality may also be relevant to MSR, because it could link higher-order descending motor commands (e.g. the intention to move one's arm toward the mirror) with the corresponding visual and proprioceptive feedback (e.g. the sight and feeling of one's arm moving). At the same time, right-lateralization of SLFII, which links some of the same frontal and parietal regions as SLFIII, is associated with individual variation in visuospatial attention in humans (Thiebaut de Schotten et al., 2011). This study investigated whether MSR is related to SLF anatomy in chimpanzees. Chimpanzees were administered a mark test and, based on their frequency in mark-directed behavior, classified as passing, failing or showing ambiguous evidence of MSR. We then compared these groups on variation in the volume and asymmetry in SLFII and SLFIII pathways quantified from diffusion tensor images (DTIs). We hypothesized that individual differences in MSR behavior would be linked to variation in the SLF anatomy; specifically, that measures of SLF white and gray matter volume and asymmetry would differ significantly across chimpanzees with different levels of MSR ability.

Methods

Subjects

Behavioral and neuroimaging data were available in 60 adult chimpanzees including 21 males and 39 females housed at the Yerkes National Primate Research Center (YNPRC). Although chimpanzees do show age effects in mirror-self recognition, the ability develops around age 4.5–8 years (Lin et al., 1992; Povinelli et al., 1993; Eddy et al., 1996); all of the animals involved in this study were well beyond this age. In total 11 of the participants in this study had exposure to mirrors 10 years or more in the past (Lin et al., 1992; Bard et al., 2006); we are unaware of any additional mirror exposure, although we cannot definitively say that none occurred. All procedures were carried out in accordance with protocols approved by YNPRC and the Emory University Institutional Animal Care and Use Committee.

Measurement of MSR behaviors

Behavioral assessment and classification in MSR abilities were based on methods and procedures described in detail by Mahovetz et al. (2016). Briefly, each subject received two 10 min test sessions to assess MSR abilities that were separated by at least 1 week. Prior to exposure to the mirror, chimpanzees were orally given sugar-free Kool-Aid that had been mixed with a blue colored non-toxic food dye. This procedure temporarily stained the inside of the chimpanzee's mouth and this served as the mark. Immediately after marking the subject, the experimenter placed the mirror (91.44 × 60.96 cm) ~30 cm away from the subject's home cage, turned on the video camera and walked away for the 10 min test session. From the videos, an ethogram comprising 10 target behaviors was scored, including (i) scratching, (ii) non-mirror-guided self-directed actions, (iii) non-mirror-guided mouth directed actions, (iv) conspecific agonistic behavior, (v) conspecific affiliative behavior, (vi) body-contingent actions, (vii) mouth-contingent actions, (viii) mirror-guided visual self-inspection, (ix) mirror-guided self-directed actions and (x) mirror-guided mark-directed actions. Of specific interest to this study were two classes of behavior, including (i) the number of mirror-guided self-exploration behaviors, and (ii) the number of mirror-guided mark-directed responses produced by each subject. These were the two behavioral categories that have been used in previous studies to characterize MSR abilities in primates. The frequencies in mirror-guided self-exploration and mirror-guided mark-directed behaviors were summed across the two test sessions and were used to classify MSR performance. Following Povinelli et al. (1993), we classified subjects as passing (MSR+), failing (MSR-) or ambiguous (MSR?) based on frequency in mirror-guided mark-directed behaviors. Specifically, subjects that exhibited five or more mirror-guided mark-directed responses across the two test sessions were conservatively classified as MSR+, between one and four as MSR?, and zero as MSR-. Using these criteria, 21 chimpanzees classified as MSR-, 14 as MSR? and 25 as MSR+. Second, we also computed the frequency of body and mouth contingent actions to serve as a covariate variable in the analyses. These behaviors were selected as covariates because previous studies have shown that chimpanzees that typically pass the mark test show significantly higher frequencies of contingent actions in front of the mirror. Therefore, in evaluating the association between MSR and variation in white matter connectivity within the SLF tracts, we sought to statistically control for these behaviors.

Neuroimaging data acquisition

Scans were acquired under propofol anesthesia (10 mg/kg/h) using previously described procedures (Hecht et al., 2013). The DTI scans were 60-direction images at B = 1000 with isotropic 1.8 mm³ voxels and were acquired on a Siemens Trio 3.0 tesla scanner (TR: 5900 ms; TE: 86 ms; 41 slices). Five B0 volumes were acquired with no diffusion weighting. For 37 individuals, T1-weighted images were acquired on the same scanner with isotropic 0.8 mm³ voxels (TR: 2600 ms; TE: 3.06 ms; slice thickness: 0.8 mm). For the remaining 22 chimpanzees, T1-weighted images were collected using a 3D gradient echo sequence (pulse repetition = 2300 ms, echo time = 4.4 ms, number of signals averaged = 3, matrix size = 320 × 320, with 0.6 × 0.6 × 0.6 resolution). Scans will be made available online at the National Chimpanzee Brain Resource, <http://www.chimpanzeebrain.org/>.

Neuroimaging data processing and analysis

The FSL software package was used for image processing and analysis (Smith et al., 2004; Woolrich et al., 2009; Jenkinson et al., 2012). Processing for T1 images included noise reduction using SUSAN (Smith and Brady, 1997) and bias correction using FAST (Zhang et al., 2001). Processing for DTI images included eddy-current correction using EDDY and diffusion tensor fitting using DTIFIT. Both T1 images and the averaged B0 images underwent brain extraction using BET (Smith, 2002). BEDPOSTX (Behrens et al., 2003, 2007) was used to build up a Bayesian distribution of diffusion information in 3D space for each voxel, modeling three fibers at each voxel. BEDPOSTX automatically estimates the number of crossing fibers at each voxel. Diffusion images were aligned to T1 images using rigid-body linear transformations computed with FLIRT, a linear registration algorithm (Jenkinson et al., 2002; Jenkinson and Smith, 2001). T1 images were nonlinearly aligned to a chimpanzee template (Li et al., 2010) or using FNIRT (Andersson et al., 2007). Combined diffusion-to-template transformations were computed by combining the linear and nonlinear registrations. Tractography analyses used PROBTRACKX, a probabilistic algorithm that samples from Bayesian distributions of multiple diffusion directions in order to facilitate tracking through crossing fibers and into gray matter (Behrens et al., 2003, 2007).

Virtual dissection of the SLF was carried out as in (Hecht et al., 2015). SLFI tractography was seeded with regions of interest (ROIs) in the superior frontal gyrus and superior parietal lobule; SLFII was seeded with ROIs in the middle frontal gyrus and posterior inferior parietal lobule (i.e. angular gyrus); SLFIII was seeded with ROIs in the inferior frontal gyrus and anterior inferior parietal lobule (i.e. supramarginal gyrus). Streamlines were only retained if they passed through a large inclusion mask situated in the frontoparietal white matter at the level of the central sulcus, and were excluded if they passed the mid-sagittal plane, temporal cortex, or the temporal-frontal white matter in the vicinity of the extreme/external capsules. Supplementary Figure S1 shows the seed ROIs, exclusion masks and inclusion masks. Symmetric waypoints-mode tractography was carried out using the following parameters: 25 000 samples/voxel, loopchecks enabled, curvature threshold at 0.2, steplength at 0.5, fiber threshold at 0.1, tractography not explicitly constrained by fractional anisotropy (but later steps that measured white matter tract volume did so after white matter/gray matter segmentation). Tractography results were thresholded to 0.1% of the way-total. All quantification occurred in native space, after thresholding. Tract white matter volume was measured as the number of above-threshold voxels within the white matter of

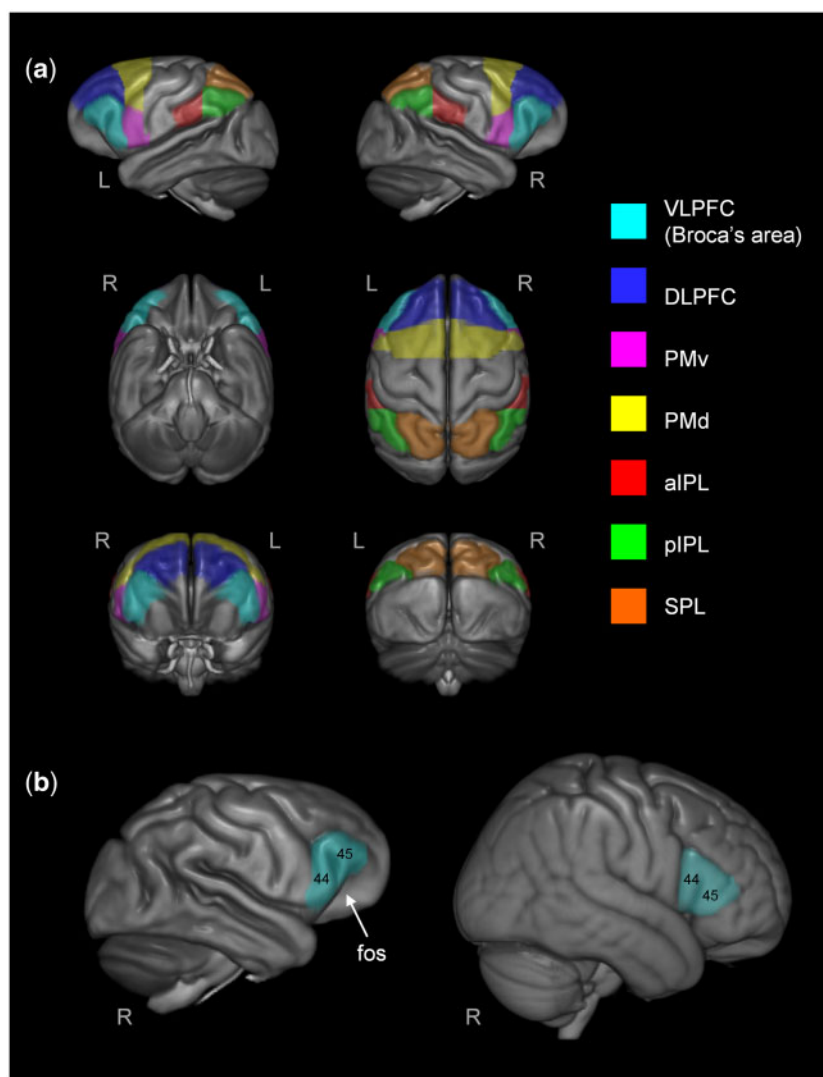


Fig. 1. (a) Regions of interest used for quantifying SLF gray matter terminations. Target regions included ventrolateral prefrontal cortex (VLPFC, Broca's area), DLPFC, PMd, PMv, aIPL, pIPL and SPL. (b) Broca's area in chimpanzees (left) and humans (right), with the approximate locations of Brodmann areas 44 and 45 indicated. It should be noted that while in humans, Broca's area (areas 44 + 45) occupies the pars opercularis and pars triangularis of the inferior frontal gyrus, the sulcal anatomy of inferior frontal cortex differs in chimpanzees and the homologous chimpanzee cytoarchitectonic regions occur surrounding the 'fos' (Schenker et al., 2008, 2010).

each thresholded tract. Connectivity between gray matter regions was measured as the number of gray matter voxels in each target region that received above-threshold tractography streamlines. The chimpanzee ROIs for Broca's area and other gray matter regions are shown in Figure 1. Table 1 lists anatomical boundaries, cytoarchitectonic areas, and human homologs. Group-composite images were created by binarizing and summing individuals' thresholded template-space tracts. These composite images were thresholded a second time, at the group level, to show connectivity common to at least one-third of subjects.

Data analysis

Non-parametric statistics (chi-square) was used for analysis of the MSR classification data. Inferential statistics (i.e. MANOVA, ANOVA) were used to evaluate the influence of MSR performance in the volume and asymmetry data for the SLF regions. For all analyses, alpha was set to $P < 0.05$ (two-tailed) and *post-hoc* tests, when necessary, were performed using Tukey's Honestly Significant Difference. Volumes of the SLF tracts were computed by adding the

right and left hemisphere values while the asymmetry quotients (AQs) were derived by subtracting the right hemisphere values from the left. Thus, positive values indicated a leftward bias while negative values reflected a right hemisphere bias.

Results

Measurement of MSR behaviors

A chi-square test of independence revealed a significant association between sex and the distribution in MSR performance classification [$\chi^2(2, n = 60) = 8.832, P = 0.012$, see Table 2]. As can be seen, the proportion of MSR+ females (70%) was higher than in males (30%).

Virtual dissection of SLF

Figure 2 shows virtual dissection of SLFII and III in the entire group. These images represent group composites of above-threshold connectivity in all 60 chimpanzees.

Table 1. Anatomical descriptions of regions

ROI	Anatomical description in chimpanzee brain	Chimpanzee cytoarchitectonic region(s)	Human cytoarchitectonic homolog(s)
DLPFC	Bordered dorsally by the interhemispheric fissure, posteriorly by the PMd ROI, inferiorly by the Broca's area ROI, and anteriorly by an imaginary line which is an extension of the orbital sulcus drawn past the tip of the middle frontal sulcus.	FDm (BA 9), Fddelta (BA 46)	BA 9, BA 46
VLPFC (Broca's area)	Bordered posteriorly by the inferior precentral sulcus, anteriorly by the small sulcus that extends anteriorly from the fronto-orbital sulcus (fos), and superiorly by the inferior frontal sulcus.	FCBm (BA 44), FDp (BA 45)	BA 44, BA 45
PMd	At its dorsal aspect, it extends anteriorly to an imaginary line drawn from the tip of the inferior pre-central sulcus at a 90 degree angle with the lateral sulcus. The inferior part of the ROI is bordered anteriorly at the inferior frontal sulcus, curving down and back to meet the PMv ROI. The border between PMd and PMv is an imaginary line drawn parallel to the lateral sulcus at the dorsal tip of the fronto-occipital sulcus so that the superior borders of PMv and Broca's area are continuous.	FB (BA 6), FC (BA 8)	BA 6, BA 8
PMv	Bordered posteriorly by anterior edge of M1, superiorly as described above, and anteriorly by the inferior precentral sulcus.	FBA (BA 6)	BA 6
IPL	Its anterior border is the posterior bank of post-central sulcus. Its posterior border is situated at the approximate half-way point of the inferior parietal lobe.	PFD, PF (BA 40/7b),	BA 40
piPL	Its anterior border is the aiPL as described above. Its posterior border is a vertical line drawn up from the termination of the inferior sulcus that extends off the posterior end of the STS.	PG (BA 39/7a)	BA 39
SPL	Its anterior border is the posterior bank of post-central sulcus. Its posterior border is a vertical line drawn up from the termination of the inferior sulcus that extends off the posterior end of the STS.	Pem (BA 5), PEp (BA 5)	BA 5, BA 7

Table 2. Distribution in MSR performance in male and female chimpanzees

	Classification		
	MSR-	MSR?	MSR+
Females	7	13	19
Males	11	2	8
Total	20	14	27

White matter measures within the SLF

To investigate measurement of SLF white matter volumes, we performed a repeated measures ANOVA with a within-subject factor of tract (SLFII, SLFIII) and between-subject factors of sex and MSR classification. No significant main effects or interactions were found in this analysis. A second repeated measures ANOVA investigated the asymmetry of SLF white matter volumes in MSR+, MSR? and MSR- individuals. This revealed a significant two-way interaction between MSR classification and SLF region $F(2, 54) = 6.63, P = 0.003$; see Table 3). *Post-hoc* analysis indicated that for SLFIII, there were no significant differences between the MSR groups. However, for SLFII, MSR+ and MSR? chimpanzees had greater rightward asymmetries than MSR- chimpanzees. No significant differences in AQ scores were found for SLFII between MSR+ and MSR? apes.

Measurement of SLF gray matter terminations

In the next set of analyses, we performed two separate MANCOVA analyses based on the bilateral volume (L + R) and

AQ (L-R) of the gray matter terminations of SLFII and SLFIII into seven cortical gray matter regions: ventrolateral prefrontal cortex (VLPFC), dorsolateral prefrontal cortex (DLPFC), dorsal premotor cortex (PMd), ventral premotor cortex (PMv), anterior inferior parietal cortex (aiPL), posterior inferior parietal cortex (piPL) and superior parietal cortex (SPL). Thus for each analysis, there were 14 dependent variables (2 SLF tracts \times 7 cortical gray matter regions). The independent factors were sex (M, F) and MSR classification (MSR-, MSR?, MSR+) while the covariate included the total number of contingent actions. Table 4 shows the mean volume of the terminations of SLFII and SLFIII in each of these gray matter regions while Table 5 shows AQs for these terminations.

For the MANCOVA analysis on bilateral volume of gray matter terminations, a main effect for sex was found $F(14, 40) = 2.05, P = 0.004$. Subsequent univariate *F*-tests revealed significant differences in SLFIII's terminations in Broca's area $[F(1, 52) = 8.37, P = 0.005]$, PMd $[F(1, 53) = 4.82, P = 0.033]$ and aiPL $[F(1, 53) = 4.84, P = 0.032]$. For SLFII's terminations in Broca's area, PMd and aiPL males had significantly higher values than females.

For the MANCOVA analysis on AQs of gray matter terminations, main effects were found for sex $[F(14, 40) = 2.24, P = 0.023]$ and MSR classification $[F(28, 82) = 2.19, P = 0.003]$. Though the MANOVA was significant, subsequent univariate *F*-tests for the variable of sex failed to reveal significant differences for SLFII's and SLFIII's terminations. Univariate *F*-tests for the variable of MSR classification found significant differences for the asymmetry of Broca's areas terminations from SLFII $[F(2, 53) = 3.55, P = 0.036]$ and SLFIII $[F(2, 52) = 6.59, P = 0.003]$. *Post-hoc* analysis for the SLFII- and SLFIII-Broca's area effect revealed that

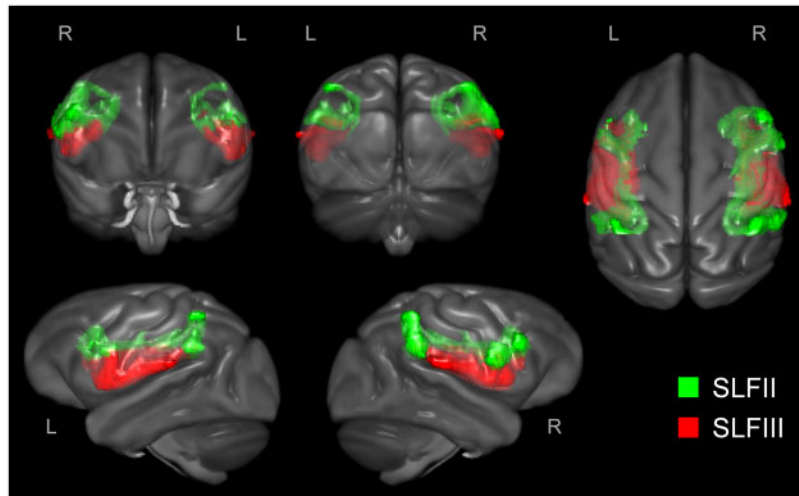


Fig. 2. Group composites of above-threshold SLFII and SLFIII tractography in all 60 chimpanzees.

Table 3. Mean AQ values (+SEM) for SLFII and SLFIII white matter volumes in MSR+, MSR? and MSR– chimpanzees

	SLFII	SLFIII
MSR+	−0.39	−0.04
SEM	0.09	0.06
MSR?	−0.38	0.06
SEM	0.16	0.10
MSR–	0.080	0.07
SEM	0.09	0.06

Table 4. Mean volume of cortical gray matter terminations of SLF II, and III

	Regions						
	Broca	DLPFC	PMd	PMv	aIPL	pIPL	SPL
SLFII							
Females	7.27	20.51	37.43	7.05	11.46	28.94	53.65
SEM	1.75	3.44	4.53	1.92	2.24	4.07	6.19
Males	9.41	8.84	27.72	9.74	10.11	22.97	51.69
SEM	3.03	5.96	7.85	3.33	3.88	7.04	10.72
SLFIII							
Females	17.43	16.55	24.31	19.01	22.67	61.10	21.87
SEM	2.62	3.08	3.84	2.61	2.70	4.45	4.36
Males	33.61	16.95	41.20	22.78	34.56	56.12	22.91
SEM	4.53	5.33	6.66	4.52	4.67	7.71	7.55

Abbreviations: Broca: Broca's area. DLPFC, dorsolateral prefrontal cortex; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; aIPL, anterior inferior parietal lobe; pIPL, posterior inferior parietal lobe; SPL, superior parietal lobe. Bolded values were significant as univariate F-tests at $P < 0.05$.

MSR+ chimpanzees had significantly greater rightward asymmetries than MSR– but not MSR? individuals (see Figure 3).

Regression analysis on SLF measures and MSR behaviors

In the previous analysis, we found that chimpanzees classified as failing, ambiguous or passing the mark test differed in the

Table 5. AQs for cortical gray matter terminations of SLF II and III

	Regions						
	Broca	DLPFC	PMd	PMv	aIPL	pIPL	SPL
SLFII							
Females	−5.54	−5.28	−3.69	−6.13	−6.20	−12.57	−2.72
SEM	3.44	3.21	3.96	2.61	3.33	6.76	4.44
Males	−18.44	−6.25	−16.02	−7.56	−16.54	−16.15	2.79
SEM	5.96	5.56	6.86	4.52	5.77	11.71	7.69
SLFIII							
Females	−0.29	−0.49	−0.35	5.46	−4.44	−1.86	0.16
SEM	1.76	0.61	1.58	3.26	3.95	1.89	0.52
Males	−5.16	−0.14	1.47	11.79	−1.56	0.21	1.11
SEM	3.06	1.06	2.74	5.65	6.84	3.28	0.91

Bolded values were significant as univariate F-tests at $P < 0.05$. Abbreviations: Broca, Broca's area; DLPFC, dorsolateral prefrontal cortex; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; aIPL, anterior inferior parietal lobe; pIPL, posterior inferior parietal lobe; SPL, superior parietal lobe. Bolded values were significant as univariate F-tests at $P < 0.05$.

asymmetry of terminations in the gray matter of Broca's area from SLFII and SLFIII. The previous analyses characterized MSR performance by classifying subjects using cut points based on their frequency in mark-directed behaviors while the total number of contingent actions served as a covariate. In our next analysis, rather than using a MSR classification criteria, we used hierarchical multiple regression analysis to determine if we could predict the frequency in MSR behaviors based on asymmetry measures of SLFII, and SLFIII's terminations in Broca's area after accounting for variation due to sex and frequency of contingent actions. In this analysis, total frequency in MSR behaviors was the outcome variable. The first block of predictor variables included the variable sex and total frequency in contingent actions. The second block included AQs of SLFII and SLFIII's terminations in Broca's area. We calculated changes in R^2 when entering each block to determine the relative contribution of each set of variables to overall variation in the frequency of MSR behaviors.

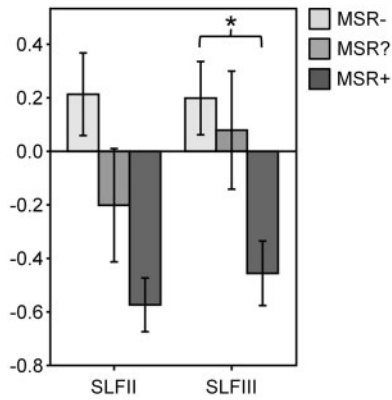


Fig. 3. AQ for SLF terminations in the gray matter of Broca's area. MSR+ chimpanzees showed greater rightward asymmetries compared with MSR? and MSR- apes, but no significant difference was found between MSR? and MSR- individuals. Error bars: ± 1 SEM. * $P < 0.05$.

The first block of variables accounted for a significant proportion of variance in MSR $R^2 = 0.306$, $F(2, 57) = 12.79$, $P = 0.001$. Adding the second block accounted for a significant increase in the proportion of variance in MSR frequency, R^2 change = 0.130, $F(2, 55) = 6.33$, $P = 0.003$. When considering the full model, the overall $R^2 = 0.436$ was significant [$F(4, 55) = 10.63$, $P = 0.001$]. Examination of the partial correlation coefficients showed that frequency of contingency movements ($\beta = 0.481$, $P = 0.001$) and the asymmetry of SLFIII terminations in Broca's area ($\beta = -0.368$, $P = 0.005$) were the significant predictors of MSR frequency. Higher frequencies in contingent actions were associated with higher frequencies in MSR behavior. Further, higher MSR frequencies were associated with greater rightward asymmetries in SLFIII's terminations in Broca's area. Figure 4a and b show the partial correlation scatter plots for the associations between MSR frequency and the total number of contingent actions and the AQs for SLFIII's terminations in the gray matter of Broca's area.

Visualization of SLFIII prefrontal terminations in MSR+, MSR? and MSR- individuals

In order to visualize how SLFIII anatomy covaries with MSR behavior, we produced composite images of thresholded right-hemisphere SLFIII white matter tracts and gray matter terminations in Broca's area, creating separate images for MSR+, MSR? and MSR- (Figure 5). This reveals a gradient in the prefrontal extension of right SLFIII from MSR- to MSR? to MSR+ individuals.

Discussion

This study examined the relationship between individual variation in MSR and the connectivity of the SLF in 60 chimpanzees. Individuals were classified as MSR+ if they showed compelling evidence of self-recognition (more than four instances of self-exploratory behavior while looking at their reflection); MSR? if they showed ambiguous evidence (one to four such instances); and MSR- if they showed negative evidence (0 instances). We also measured body- and mouth-contingent behaviors exhibited while interacting with the mirror. We found an interleaved relationship between SLF anatomy, sex, and successful MSR. Independent of self-recognition behaviors, there were some sex differences in the connectivity of SLFIII. More females than males were classified as MSR+, but independent of sex, MSR was associated with greater rightward asymmetry of the

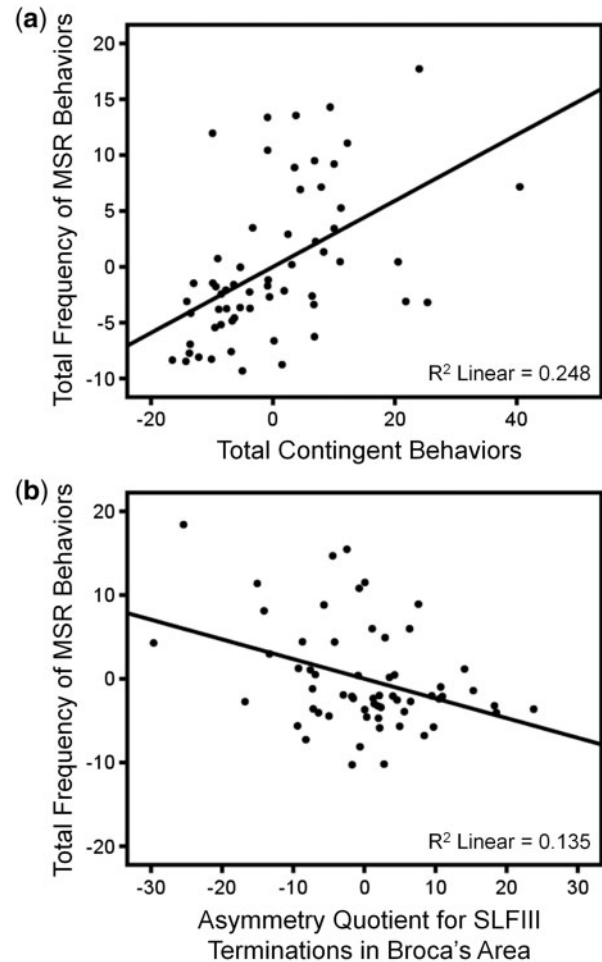


Fig. 4. Partial correlation scatter plots, showing associations between total frequency of MSR behaviors and (a) the total number of contingent behaviors and (b) AQ for SLFIII's terminations in the gray matter of Broca's area. Negative AQ values are more rightwardly asymmetric.

SLFII white matter body and of SLFII and SLFIII's gray matter terminations within Broca's area. To disentangle the interacting contributions of sex, non-MSR contingent behaviors and neuroanatomy, we performed a regression analysis. This revealed that over and above the effects of sex and frequency of contingent behaviors, MSR was associated with greater rightward asymmetry in SLFIII's terminations in the gray matter of Broca's area.

Previously, Hecht et al. (2015) have identified human-specific adaptations to SLFIII. In macaques, this tract terminates in areas 6v, 44 and 9/46v (Petrides and Pandya, 2002, 2009), but has not been found to connect with area 45. In chimpanzees, SLFIII primarily terminated in the precentral gyrus, with some connectivity to the inferior frontal gyrus, including the pars triangularis, which is where Brodmann's area 45 neurons are located; interestingly, these terminations were not asymmetric at the population level. In humans, both the left and right SLFIII made significantly more terminations in inferior frontal gyrus than precentral gyrus, with this effect being significantly stronger in the right hemisphere, where SLFIII showed prominent projections into the pars triangularis (area 45). This agrees with a separate tractography study showing human SLFIII connectivity with the pars triangularis and orbitalis (Thiebaut de

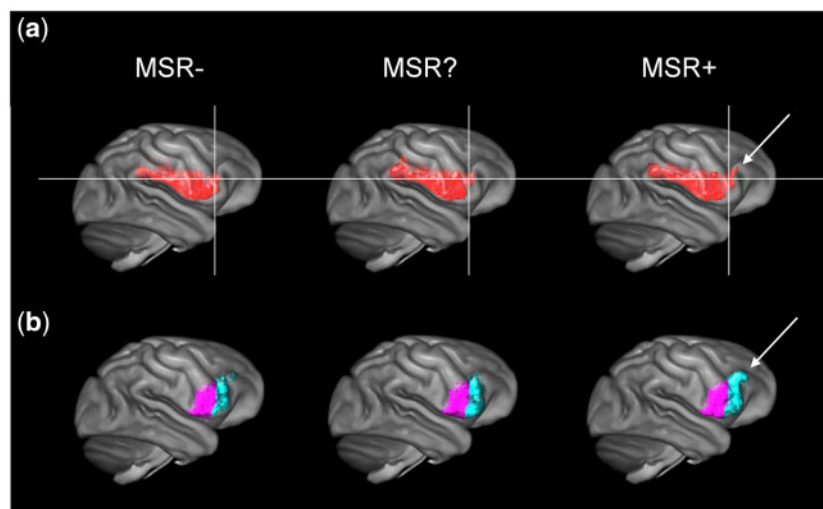


Fig. 5. Right-hemisphere SLFIII in MSR-, MSR? and MSR+ chimpanzees. (a) White matter tract cores. Crosshairs are at the same coordinates in each panel; note the extension into more anterior regions of the white matter beneath the inferior frontal gyrus in MSR+ chimpanzees (white arrow). (b) Gray matter terminations in the cortex of PMv (magenta) and Broca's area (cyan). Note that more anterior regions of the inferior frontal gyrus receive gray matter terminations in MSR+ chimps.

Schotten et al., 2012). Thus, humans show prefrontal extension of SLFIII, particularly in the right hemisphere.

This study found that chimpanzees who show greater extension of SLFIII into the prefrontal regions of the inferior frontal gyrus are more likely to successfully recognize their reflection in a mirror. There is a visible gradient in the degree of prefrontal SLFIII extension, from apes that show no evidence of self-recognition, to those that show questionable evidence, to those that show clear evidence (Figure 5). In other words, chimpanzees with more human-like MSR behavior, at least as measured by the mark test with limited exposure, show more human-like SLFIII anatomy. From these findings, we propose a model by which prefrontal extension of SLFIII might mediate MSR. During behavior in front of a mirror, individuals are both producing and perceiving their own movement. Production of volitional movement involves a descending chain of commands from prefrontal to premotor to primary motor cortex (Badre and D'Esposito, 2009), modulated by ongoing exchange with proprioceptive and visuospatial information from posterior parietal cortex (Milner and Goodale, 1993; Rizzolatti et al., 1997). Observing movement produces ascending visual and proprioceptive input into these same frontal and parietal systems. MSR hinges upon successful realization that the two streams of information (produced and observed movement) in fact correspond to the same entity—that self-generated motor commands correspond with the visual perception of the reflection and proprioceptive feedback. Posterior parietal cortex has access to both the visual and proprioceptive components of this trio, and in fact, rTMS of the right inferior parietal lobe impairs MSR in humans (Uddin et al., 2006). Behaviorally, self-recognition in humans does occur in multiple sensory modalities, and self-recognition is facilitated via cross-modal perception (Platek et al., 2004). SLFIII links inferior parietal regions involved in visual-proprioceptive integration with inferior frontal cortex. Action representation in frontal cortex is hierarchical, with higher-order representations localized more rostrally (Petrides, 2005; Badre and D'Esposito, 2009). Thus greater extension of SLFIII into more-anterior regions of the inferior frontal gyrus might support MSR by facilitating multimodal visual-motor-proprioceptive integration.

This model also suggests an explanation for why macaques, and some chimpanzees, typically fail to demonstrate MSR. Evidence suggests that in macaques, prefrontal cortex is strongly tied to the ventral visual stream and less directly tied to the dorsal visual stream. Macaque VLPC receives strong projections from higher-order temporal visual regions (Petrides and Pandya, 2009). In macaques, these temporal-frontal connections far outweigh dorsal-stream connections between inferior parietal cortex and premotor cortex (Hecht et al., 2015), and in line with this, macaques show stronger prefrontal activation than humans when viewing objects (Denys et al., 2004). Thus when a monkey looks in a mirror, frontal regions involved in the generation of behavioral responses are engaged mainly with ventral-stream, visual-identity aspects of the reflection—i.e. that the reflection is a monkey. Indeed monkeys, and individual chimpanzees who fail the mark test, often respond to their reflection as if it is a conspecific and engage in agonistic or avoidant behaviors. In the case of individuals who fail the MSR tests, the brain is undoubtedly not failing to process proprioceptive feedback about one's own actions, or visual feedback from the reflection; this information may simply fail to integrate with prefrontal descending motor commands, and so the responses to the reflection are generated on a unimodal (visual) basis. To what extent these skills are acquired or develop in chimpanzees with increasing exposure to a mirror or other interventions is not clear and warrants further inquiry.

Several testable predictions follow from the model we have proposed. First, MSR performance should be facilitated by manipulations that attenuate ventral visual stream processing, such as temporary deactivation or lesion, or by manipulations that reduce social-threat processing, such as administration of anxiolytics or oxytocin. Second, MSR performance should also be facilitated by manipulations which increase the salience of visual-proprioceptive correspondence. In humans, when an experimenter strokes the faces of two people who can see each other in a mirror, this induces an 'enfacement illusion', or a feeling of self-recognition of the other's reflection (Tsakiris, 2008; Sforza et al., 2010). Whether a similar paradigm, such as stroking an animal's face while it views its own reflection, might facilitate self-recognition in nonhuman primates is

unknown, but our proposed model suggests that this might be the case. Additionally, given that the mirror system of macaques and chimpanzees seems to be strongly goal- or intention-oriented, we wonder whether MSR performance might be facilitated if the animal is encouraged to perform a goal-directed behavior in front of the mirror, such as eating peanuts out of a bucket or using a stick to extract honey from a well. Interestingly, the two reports to date that have claimed MSR in monkeys have involved manipulations that may mediate the salience of visual-proprioceptive relationships and/or the link between visual-proprioceptive processing and goal-directed behavior (Rajala et al., 2010; Chang et al., 2015) but, as noted earlier, some have questioned the methods and interpretation of these results. The findings from these studies may suggest that monkeys may have some sense of self-agency but not necessarily MSR (Couchman, 2015).

Butler and Suddendorf (2014) suggested that comparisons between species that do or do not show MSR may be used to narrow the search space for the underlying neural correlates. Through a detailed analysis of comparative neuroanatomy and human visual self-recognition research, they postulate that this ability may likely involve spindle cells (also known as von Economo neurons), particularly those in the right anterior insula. Spindle cells integrate information from widespread cortical regions and appear in large-brained species with complex social-cognitive abilities, notably including many of the species capable of self-recognition (Von Economo and Koskinas, 1929; Nimchinsky et al., 1999; Butti et al., 2009; Hakeem et al., 2009). The anterior insula is immediately adjacent to, and shows strong connectivity with, the anterior sectors of the inferior frontal gyrus, where we observed MSR-related SLFIII extension (Ghaziri et al., 2015). More research is needed on this issue. For example, future post mortem examinations of the chimpanzee brains studied here might investigate whether individual variation in spindle cell density, SLFIII extension and MSR ability are all interrelated. Additionally, studies aimed at assessing the functional correlates of MSR through the use of non-invasive psychophysiology or neuroimaging methodologies would provide important insights.

A common interpretation is that MSR equates to self-awareness. However, some have argued that a general capacity to collate visual and somatomotor representations could be sufficient to produce MSR (Mitchell, 1997; Suddendorf and Butler, 2013). Interestingly, self-awareness and visuo-motor coordination are dissociable in humans, as is evidenced by neurological conditions like hemi-neglect. For example, one study performed intracarotid amobarbital inactivation of the non-language-dominant hemisphere in evaluation for epilepsy surgery in 62 patients. During this procedure, 75% of patients failed to identify the contralateral hand as their own, but yet 38% correctly located their arm on the table (Meador et al., 2000). This indicates that the ability to know where one's arm is and to know that it is 'mine' likely rely on at least partially separable neural substrates. Thus, normal human self-awareness is likely not a single unified construct, but the emergent outcome of integration between multiple, separable underlying mechanisms. This integration may rely on recursive processing—i.e. representing different aspects of self-relevant processing as referring to each other. Edelman proposed that reentry, or bidirectional reciprocal exchange along axon fibers linking multiple brain regions, might underlie sensory integration and awareness (Edelman and Tononi, 2000; Edelman and Gally, 2013); similarly, others have proposed recursion as a mechanism for meta-cognition and consciousness (Minsky, 1986). Recursive processing involves the pars opercularis and pars triangularis of the inferior

frontal gyrus (areas 44 and 45) (Friederici et al., 2006; Badre, 2008), so greater SLFIII connectivity with these regions might facilitate recursive representation of the motor, proprioceptive and visual dimensions of one's own behavior.

To the extent that MSR involves integration between visual-somatomotor matching and recursive representation, it may be linked to other recently evolved behaviors which also rely on these processes. Notably, language involves recursion in syntactic structure, a feature thought to be unique to human communication (Hauser et al., 2002). While language involves recursive, hierarchical, multi-component 'symbolic' sequences, other forms of intentional behavior also involve recursive, hierarchical, multi-component 'action' sequences, particularly tool use (Holloway, 1969; Stout and Chaminade, 2012). The ability to observationally acquire these complex action sequences, and contribute modification and improvements to them, may also involve hierarchical integration between higher-order action goals and visual-somatomotor matching (Hecht et al., 2013, 2015). These functions all involve similar, overlapping lateral frontal-parietal-temporal networks which show unique adaptations in humans, suggesting that they may have co-evolved in a mutually reinforcing way. It may be that self-recognition, along with social learning, tool use and communication, are all outcomes of an underlying evolutionary trend toward increased integration between the highest- and lowest-order aspects of action representation.

Supplementary data

Supplementary data are available at SCAN online.

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