

Changes in Frontoparietotemporal Connectivity following Do-As-I-Do Imitation Training in Chimpanzees (*Pan troglodytes*)

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Abstract

■ Human imitation is supported by an underlying “mirror system” principally composed of inferior frontal, inferior parietal, and superior temporal cortical regions. Across primate species, differences in frontoparietotemporal connectivity have been hypothesized to explain phylogenetic variation in imitative abilities. However, if and to what extent these regions are involved in imitation in nonhuman primates is unknown. We hypothesized that “Do As I Do” (DAID) imitation training would enhance white matter integrity within and between frontoparietotemporal regions. To this end, four captive chimpanzees (*Pan troglodytes*) were trained to reproduce 23 demonstrated actions, and four age-/sex-matched controls were trained to produce basic husbandry

behaviors in response to manual cues. Diffusion tensor images were acquired before and after 600 min of training over an average of 112 days. Bilateral and asymmetrical changes in frontoparietotemporal white matter integrity were compared between DAID trained subjects and controls. We found that imitation trained subjects exhibited leftward shifts in both mean fractional anisotropy and tract strength asymmetry measures in brain regions within the mirror system. This is the first report of training-induced changes in white matter integrity in chimpanzees and suggests that frontoparietotemporal connectivity, particularly in the left hemisphere, may have facilitated the emergence of increasingly complex imitation learning abilities. ■

INTRODUCTION

Imitation is defined as the transformation of others' actions into one's own (modified from Thorndike, 1898). Many have hypothesized that learning by imitation plays an important role in social cognition and cultural variation in human behavior. From birth, humans imitate facial expressions (Meltzoff & Moore, 1977), and by 9 months of age, they engage in imitative play (Meltzoff, 1990). Throughout development and adulthood, humans learn about their social and physical environment by observing and imitating others' actions (Heyes, 1993). Imitative abilities are associated with a large suite of human sociocognitive processes such as empathy (Williams, Nicolson, Clephan, de Grauw, & Perrett, 2013; Iacoboni, 2009; Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008; Schulte-Ruther, Markowitsch, Fink, & Piefke, 2007; Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003), joint attention (Charman et al., 1997; Carpenter, Tomasello, & Savagerumbaugh, 1995), mirror self-recognition (Nielsen & Dissanayake, 2004; Asendorpf, Warkentin, & Baudonnière, 1996), and action/intention understanding (Rizzolatti & Fogassi, 2014). Furthermore, imitation's role in human social learning likely underlies cultural transmission of

specific behavior patterns (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009) including language (Corballis, 2010; Iacoboni, 2009; Iacoboni & Wilson, 2006; Rizzolatti & Craighero, 2004; Nadel, 2002). These collective findings have led some to assert that imitation is what distinguishes humans from other species (Meltzoff, 1988).

To what extent imitative abilities are uniquely human is a matter of considerable debate (Buttelmann, Carpenter, Call, & Tomasello, 2013; Tennie, Call, & Tomasello, 2012; Visalberghi & Fragaszy, 2002; see also Galef, 2012, for a review of social learning across animal taxa). Some have suggested that truly imitative behaviors are nonexistent in nonhuman primates (Tennie, Call, & Tomasello, 2009; Tomasello, 1996; Tomasello, Kruger, & Ratner, 1993); however, a large body of evidence indicates considerable similarities between apes' and humans' imitative capacities (see Whiten, 2017, for a review). Like human infants, there is evidence that newborn chimpanzees can imitate some facial expressions (Bard, 2007; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2004), and similar findings have been reported in some macaque species (Paukner, Pedersen, & Simpson, 2017; Paukner, Simpson, Ferrari, Mrozek, & Suomi, 2014). There is also evidence of species differences in imitation recognition and production abilities. For instance, the ability to recognize when one is being imitated is present in all great apes that have been tested to date (Pope,

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Russell, & Hopkins, 2015; Haun & Call, 2008; Nielsen & Dissanayake, 2004; Asendorpf et al., 1996) but is equivocal in Old and New World monkeys (Paukner, Suomi, Visalberghi, & Ferrari, 2009; Paukner, Anderson, Borelli, Visalberghi, & Ferrari, 2005). This imitation recognition likely relies, at least in part, on neural networks that also serve imitation production.

Humans tend to copy the specific actions used during a demonstration, even irrelevant ones (Horner & Whiten, 2005), whereas chimpanzees tend to reproduce the end-state of demonstrations, ignoring the details of the actions (Carpenter & Call, 2009; Buttelmann, Carpenter, Call, & Tomasello, 2007; Tennie, Call, & Tomasello, 2006; Call, Carpenter, & Tomasello, 2005; Myowa-Yamakoshi & Matsuzawa, 2000); yet importantly, they are capable of invoking more specific action-copying (Horner & Whiten, 2005). Indeed, evidence has shown that apes can learn to play a “Do As I Do” (DAID) imitation game, in which they reproduce demonstrated actions during a training period and then continue to imitate when tested with a battery of novel actions (Call, 2001; Custance, Whiten, & Bard, 1995; Hayes & Hayes, 1952). In contrast, attempts to teach monkeys this same imitation game have been largely unsuccessful and seem to suggest that they may favor end-state copying by mimicking the environmental effect of demonstrations, rather than copying others’ specific actions (Fragaszy, Deputte, Cooper, Colbert-White, & Hemery, 2011; Visalberghi & Frigaszy, 2002; Mitchell & Anderson, 1993). In fact, when action-copying is irrelevant, monkeys’ ability to learn an abstract response sequence is facilitated by observing a conspecific; a process termed cognitive imitation (Subiaul, Cantlon, Holloway, & Terrace, 2004). Thus, the extent to which action-versus goal-copying behaviors are utilized varies considerably within the primate lineage.

In the current study, we sought to examine the neural basis of imitation in chimpanzees. If and to what extent the human imitative phenotype relies on the same neural substrates as other primates’ action-copying behaviors is controversial (Hickok, 2009). The discovery of mirror neurons, which fire both when an action is produced and when the same action (produced by another individual) is observed, within the macaque premotor area F5, has been hypothesized to be a critical neuronal mechanism involved in action-copying (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Additional mirror neurons were later found within monkey parietal regions, which innervate the premotor cortex (Gallese, Fadiga, Fogassi, & Rizzolatti, 2002). With the incorporation of superior temporal regions, which are involved in recognizing biological motion (Perrett et al., 1990) and are reciprocally connected to parietal regions, a putative macaque imitation system has emerged (Rizzolatti, Fogassi, & Gallese, 2002; Gallese et al., 1996). However, one significant limitation of the mirror neuron system model of imitation in macaque monkeys is the simple fact that the available data indicate

that the imitative abilities of species within this genus are notably limited (Visalberghi & Frigaszy, 2002).

In humans, imitation also involves frontoparieto-temporal regions. In keeping with the existing nomenclature, we refer to these regions collectively as the putative “mirror system” throughout the text; this should not be taken as an indication that it is necessarily composed of mirror neurons (see Hickok, 2009, for a critical discussion of the “mirror neuron system”). During imitation, an action is observed, translated into a mental representation (including its goal, if known), and then transformed into the observer’s own action. Similar to monkeys, in humans the STS is implicated in the initial observation of bodily motion (Allison, Puce, & McCarthy, 2000), and it is reciprocally connected to the inferior parietal lobule (IPL), which appears to be involved in coding an observed action’s valence and direction (Fabbri-Destro & Rizzolatti, 2008; Halsband et al., 2001; Goldenberg, 1999). The IPL, in turn, is connected to frontal mirror regions, namely within the inferior frontal gyrus (IFG), which functions in goal imitation (Hecht et al., 2013; Koski et al., 2002; Iacoboni et al., 1999).

To explain the spectrum of primate imitative phenotypes, Hecht et al. (2013) compared frontoparietotemporal white matter connectivity among macaques, chimpanzees, and humans. These authors found prominent ventral STS to IPL connections in macaques, pronounced dorsal IPL to IFG connections in humans, and more equivalently proportioned dorsal/ventral connections in chimpanzees. According to Hecht et al. (2013), ventral connections, hypothesized to facilitate the understanding of actions’ goals, underlie macaques’ goal-copying, whereas dorsal connections, hypothesized to facilitate the understanding of action kinematic details, underlie humans’ action-copying abilities. Thus, chimpanzees’ intermediate expression of both dorsal and ventral connections is consistent with their intermediate usage of both goal- and action-copying. Although there appears to be homology between the macaque and human frontoparietotemporal systems, its functional involvement in chimpanzee imitation is entirely speculative. Indeed, there are no data regarding the functional correlates of imitation in chimpanzees or other great apes; thus, the hypothesis that the same frontoparietotemporal regions are involved in ape imitation remains untested.

As a means of examining the potential neural basis of imitation in chimpanzees, the current study utilized diffusion tensor imaging (DTI) before and after DAID imitation training to assess changes in frontoparietotemporal connectivity. DTI has been used in humans to document training-induced cortical changes for numerous motor and cognitive tasks, such as juggling (Scholz, Klein, Behrens, & Johansen-Berg, 2009), second language acquisition (Schlegel, Rudelson, & Tse, 2012), and playing an instrument (Zatorre, Fields, & Johansen-Berg, 2012; Hyde et al., 2009). In addition, chimpanzees are capable of being taught the DAID imitation game and

subsequently apply the “copy this” rule to successfully imitate novel actions (Custance et al., 1995; Hayes & Hayes, 1952). Here, we combined DAID imitation training with DTI scanning to quantify changes in cortical connectivity, specifically within the frontoparietotemporal mirror system. After learning the imitation game, we measured chimpanzees’ imitative abilities on a list of novel actions (i.e., not part of their training). We hypothesized that if IFG, IPL, and STS regions are involved in imitation in chimpanzees, then connectivity between these putative mirror regions would increase following successful DAID imitation game acquisition and participation.

METHODS

Subjects

Eight adult captive chimpanzees, four male and four female, housed at the Yerkes National Primate Research Center (YNPRC) were matched on sex, rearing history, age (within 6 years), and the date of their initial DTI scan. All procedures were approved by the Emory University Institutional Animal Care and Use Committee.

Training Procedure

One member from each matched pair was randomly selected to be taught the DAID imitation game (IM) and the other served as a control (CO). Each IM/CO pair was trained concurrently (i.e., on the same days and during the same times of day) via positive reinforcement training. IM subjects learned to reproduce an experimenter’s (EXP) action from a list of 23 DAID behaviors, whereas CO subjects were rewarded for producing basic husbandry behaviors in response to manual cues. Basic husbandry behaviors included presenting body parts, such as arms, legs, hands, feet, back, etc. All DAID actions are listed in Table 1. For lateralized DAID behaviors, IM subjects were trained to use the corresponding ipsilateral body part as the EXP (i.e., EXP’s left = ape’s right), as if they were looking in a mirror (Bekkering, Wohlschläger, & Gattis, 2000). IM and CO subjects each received 600 min of training (apart from one IM/CO pair, which received 602 and 589 min, respectively, due to experimenter error) and the number of days spent training ranged from 73 to 134 ($M = 112.14$, $SD = 19.24$). The number of days of training varied between subjects because of differences in training motivation from day to day, but there was no significant difference in the number of training days between the IM and CO groups, $t(6) = -.15$, $p = .884$. The number of training sessions ranged from 36 to 43 ($M = 39$, $SD = 2.19$), and the average session length ranged from 13.95 to 16.67 min ($M = 15.39$, $SD = 0.88$).

Two different lists of 23 DAID behaviors were generated (Table 1). IM subjects were trained on one list of 23

Table 1. DAID Behaviors Comprising Lists 1 and 2

<i>List 1</i>	<i>List 2</i>
Protrude lips	Protrude tongue
Open mouth	Lip smack
Teeth chatter	Puff cheeks
Reach to side	Reach across
Foot raise	Hand raise
Pat head	Pat belly
Touch chin	Touch nose
Hand shake	Wipe hands on floor
Grasp wrist	Wipe hands together
Back of hand	Fist
Raised index	Wave
Touch elbow	Touch armpit
Touch knee	Touch thigh
Touch ear	Touch back of head
Both hands raise	Both arms wide
Clap	Palm point
Hands together front	Hands together above head
Peek-a-boo	Wipe face
Foot stomp	Both feet raise
Lay down	180-degree turn
Shake head	Stand up
Cage bang	Slap ground
Hoo	Extended grunt

actions and then tested for generalization in imitation performance on the remaining novel, 23 actions. Lists were composed of similar but distinct actions in an attempt to minimize differences in difficulty between lists. Training and test lists were counterbalanced, such that one male and one female were trained on List 1 and tested on List 2 and vice versa for the remaining two individuals.

Testing Procedure

Following training, all subjects were tested on their generalization in imitative abilities. During each test session, both trained and novel DAID actions were modeled for the subjects; each action was presented on three separate occasions for a total of 138 trials. To start a test session, subjects were engaged by prompting familiar, previously trained DAID (IM subjects) or husbandry (CO subjects) behaviors, followed by random presentations of novel

actions. The novel modeled actions were presented by the experimenter for 10 sec, followed by the delivery of a small food reward, independent of their responses. In other words, no matter how the apes responded to the action modeled by the experimenter, they received a reward, thereby avoiding differential reinforcement of their behaviors. To keep subjects engaged, several familiar, previously trained behaviors (the exact number depended on the subject's motivation but ~ 3) preceded each DAID test behavior. Testing sessions continued as long as the chimpanzees were engaged (i.e., remained proximal and attentive to EXP and produced the trained behaviors in response to cues) or until 46 test trials were administered ($M = 4.5$ sessions, $SD = 1.2$).

Test sessions were video-recorded (Canon HD Vixia HFS21) and later scored based on the following criteria: 3 = Subject used the corresponding ipsilateral body part to produce the demonstrated action. For example, EXP cage banged with right hand and the subject responded by cage banging with their left hand at least once within the 10 sec trial. 2 = Subject used a different or the corresponding contralateral body part to produce the demonstrated action or subject used the corresponding ipsilateral body part to produce a similar action. Using the above example (EXP cage bangs with their right hand), subjects would score a 2 if they (a) cage banged with their right hand or (b) waved their left hand (or any other action similar to cage bang). 1 = Subject used the corresponding ipsilateral body part to produce any action. Thus, if EXP cage banged with right hand, the subject could produce any action with their left hand and receive a score of 1. 0 = Subject did not use the corresponding body part and did not produce the demonstrated action. When subjects produced multiple actions within the 10 sec, the behavior with the highest score was recorded. To ensure that experimenter bias did not factor into scoring, 132 (12% of the total) test behaviors were re-coded by a second observer who was blind to both the subjects' training condition and the hypothesis. A Spearman rank order correlation between the two observers revealed the scoring of the chimpanzees' actions to be reliable ($r_{ho} = .75, p < .05$).

To compute each subject's overall performance, a cumulative imitation score was calculated. For IM subjects, 69 of the 138 behaviors presented during test sessions were from the familiar list that they were trained on and the remaining 69 were novel. However, for CO subjects, none of the 138 behaviors were familiar. Thus, IM subjects' imitation scores were calculated from only novel behaviors and because training occurred in CO/IM pairs, CO subjects' imitation scores were calculated based on the list that was novel to their IM counterpart to control for list difficulty. The three imitation scores for each of the 23 behaviors were summed (69 total scores) to derive a cumulative imitation score for each subject. Performance could vary from 0 to 207 (3 trials \times 23 actions \times a score of 3). Because of EXP error, one CO subject only received

two tests for one of the behaviors (68 total scores); thus, their highest score for that behavior was used again, as a conservative third score.

Scanning Protocol

In vivo MRI and DTI scans were obtained at the same time that the chimpanzees were participating in their annual physical examinations, which was coordinated with the end of their training. Subjects were first immobilized by ketamine (10 mg/kg) or telazol (3–5 mg/kg) and subsequently anaesthetized with propofol (40–60 mg/(kg/hr)) following standard procedures at the YNPRC. Subjects were then transported to the YNPRC MRI facility and were placed in the scanner chamber in a supine position with their head fitted inside the human-head coil. The subjects remained anaesthetized for the duration of the scans as well as the time needed to transport them between their home cage and the imaging facility (total time ~ 1.5 hr). After scanning was completed, the apes were returned to their home cage and allowed to fully recover from the anesthesia before being reunited with their group members. Within pairs of subjects, the time between pre- and post-DTI scans ranged from 0.02 to 0.50 years ($M = 0.22, SD = 0.23$). Time between final training day and post-DTI scan ranged from 6 to 18 days ($M = 11.57, SD = 4.49$); however, there was no difference between IM and CO apes, $t(6) = -2.93, p = .06$.

Subjects were imaged using a 3.0 T Siemens Trio scanner (Siemens Medical Solutions USA, Inc., Malvern, PA). T1-weighted images were collected using a three-dimensional gradient-echo sequence (pulse repetition = 2300 msec, echo time = 4.4 msec, number of signals averaged = 3, matrix size = 320×320). Scanning parameters were slightly different for the first two DTIs (one CO and one IM) than for the remaining 14. For all scans, two whole-brain diffusion-weighted data sets, with a single shot EPI sequence and a b value of 1000 sec/mm^2 with 64 (Scans 1–2 = 60) diffusion directions, along with an additional image without diffusion weighting (b value = 0 sec/mm^2) were acquired. Acquisition occurred transaxially: for Scans 1–2 FOV = 230 and resolution = $1.8 \times 1.8 \times 1.8 \text{ mm}$ for 60 slices; for Scans 3–16 FOV = 243 and resolution = $1.9 \times 1.9 \times 1.9 \text{ mm}$ for 42 slices. Diffusion-weighted data with phase-encoding directions of opposite polarity were averaged (Scans 1–2 = 10 averages; Scans 2–6 = 1 average) to correct for susceptibility to distortion. Preprocessing was performed using The Oxford Center for Functional Magnetic Resonance Imaging (FMRIB) software, FSL (www.fmrib.ox.ac.uk/fsl) and consisted of (1) reorientation, (2) removal of nonbrain tissue using the Brain Extraction Tool, (3) head motion correction, and (4) eddy current distortion correction (FDT toolbox). DTIFIT was used to fit diffusion tensors at each voxel to create fractional anisotropy (FA) maps. Radial diffusivity (RD) maps were then calculated from the DTIFIT output by summing the L2 and L3 volumes

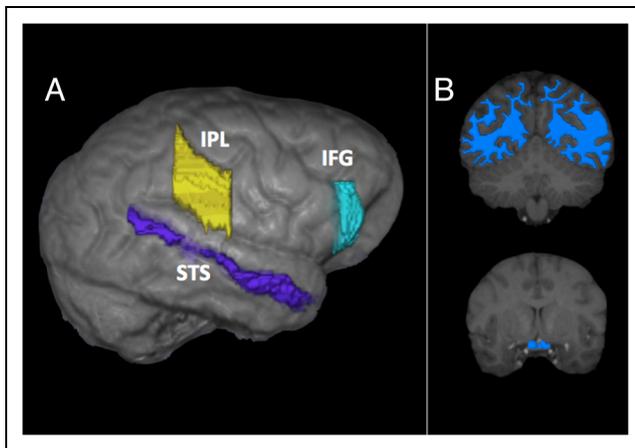


Figure 1. (A) ROIs for the hypothesized chimpanzee mirror system composed of IFG, IPL, and STS regions and (B) ROIs for the geniculostriate control tract composed of an occipital slice and the optic chiasm.

and dividing by 2. To assess probabilistic tractography, diffusion gradient information was reconstructed using FSL's BEDPOSTX tool within the FDT toolkit (Behrens et al., 2007). All image preprocessing followed standard procedures outlined in the FDT userguide.

ROIs

To assess changes within and between frontoparietotemporal regions, bilateral ROIs were manually traced onto each subject's previously collected T1-weighted MRI scans (Autrey et al., 2014). The landmarks used to identify each of the three ROIs are defined below and shown in Figure 1.

Inferior Frontal Gyrus

In the axial plane, the ROI was defined as the area between the fronto-orbital and inferior precentral sulci (PCI) with the medial boundary being a straight line between the medial edges of the two sulci. Following axial tracing, the image was returned to the sagittal plane and the first lateral slice where the insula was no longer visible was located. The ROI was extended from the bottom-left corner of this slice either along PCI if it was still apparent or straight down if it was not. This was repeated for all remaining slices, moving laterally.

Inferior Parietal Lobe

First, the image was placed in the sagittal plane, where the most medial slice in which the insula was not visible was identified. A line was then drawn from the most anterior extension of the postcentral sulcus (PoC) straight down to the lateral sulcus (Lt). This served as the anterior boundary. Next, the dorsal boundary was marked as the point that the PoC was no longer parallel to the Lt. Finally,

a diagonal line was drawn from this dorsal boundary to the Lt, which served as the posterior boundary. The image was then rotated into the axial plane, and the area between the PoC and Lt, within the predefined bounds, was captured.

STS

First, the image was placed in the sagittal plane, where the most medial slice in which the insula is not visible was identified. The gray matter between the superior temporal and the medial-temporal gyri was traced. The dorsal boundary was marked at the intersection with the inferior parietal sulcus. Moving laterally, the area between the superior temporal and medial-temporal gyri was captured in each slice. Next, the image was rotated into the coronal plane where the extreme medial and lateral extensions of the STS were captured for all slices.

FA and RD Methods

Within the putative mirror system, changes in FA, which indicates how uniformly directional diffusivity is within a given voxel as a proxy for tract integrity, and RD, which indicates myelination by measuring the rate of diffusivity in the perpendicular direction, were compared between training conditions. Processed FA and RD maps for both pre- and postscans were linearly registered to subjects' previously collected, T1-weighted MRI scans. Following this registration, subject-specific frontoparietotemporal ROIs and pre/post FA and RD maps were in the same stereotaxic space. Next, ROIs for each hemisphere were placed on the registered FA and RD volume, and the average value within the ROI was calculated. Variation in signal-to-noise ratios between scans was adjusted by dividing the mean FA and mean RD within each ROI by the mean FA and RD, respectively, within that hemisphere or by the mean whole-brain FA and RD, respectively, for bilateral analyses, for each scan. Finally, the pre FA and RD values were subtracted from post FA and RD values to reflect measures of change in white matter integrity within each ROI within the frontoparietotemporal regions for each subject.

Probabilistic Tractography Methods

To assess potential changes in mirror system white matter connectivity, we used FSL's software package for probabilistic tractography, PROBTRACKx (Behrens et al., 2007). First, registration matrices were created and used to place diffusion gradient information for each scan (generated from BEDPOSTx) into the same stereotaxic space as subjects' T1-weighted MRI scan. Probabilistic tractography was then used to assess the connectivity distributions between ROIs. To increase the likelihood that streamlines were generated within ROIs and not underlying white matter tracts passing through the ROI, seed ROIs were masked to only include gray matter.

We chose to use networks mode tractography, which includes bidirectional streamlines passing through all ROIs, and a midline exclusion mask to prevent them crossing into the contralateral hemisphere. Thus, all connectivity maps were intrahemispheric. To account for differences in brain size due to diffusion data being in subjects' native space (rather than template space), we incorporated distance correction into the tractography algorithm. All other default settings were used (5000 samples were generated from each seed voxel, 0.2 curvature threshold, 0.5 mm step length, 2000 maximum number of steps, loopcheck enabled, and waypoints were applied independently to both directions). In this manner, connectivity distribution maps were generated for (1) IFG-IPL, (2) IFG-STG, and (3) IPL-STG. To control for differences in scan quality, connectivity maps were divided by the waytotal (the total number of streamlines within a connectivity map) of a control tract—the geniculostriate—for each hemisphere. The geniculostriate tract was generated by seeding coronal sections of the optic chiasm and occipital white matter (see Figure 1). From these normalized connectivity maps, the mean voxel intensity (a measure of how many streamlines pass through a given voxel) was calculated, which reflects “tract strength.” In addition, the total number of voxels comprising the tract was also calculated, which was defined as “tract volume.” Tract volume values were also normalized by dividing by the geniculostriate waytotal.

We chose not to apply thresholding to connectivity maps for two reasons. First, thresholding is typically used to exclude erroneous streamlines from analysis; however, our inclusion of the control group already addresses this issue (i.e., error should be equally distributed across IM and CO subjects). Second, thresholding would limit analyses to only the most established tracts, which may be less likely to change—due to ceiling effects—following training. In other words, training-induced increases in connectivity may occur less readily in voxels already containing a large proportion of the streamlines.

Data Analysis

We analyzed the data two ways. First, we identified mean FA, mean RD, tract strength, and tract volume when summed across the two hemispheres for each ROI/tract to identify bilateral frontoparietotemporal changes. Second, we tested for changes in lateralization of mean FA, mean RD, tract strength, and tract volume to gain an understanding of any asymmetrical frontoparietotemporal changes. To assess the magnitude and direction of lateralized changes following imitation training, asymmetry quotients (AQ) were calculated following the formula $[AQ = (R - L) / ((R + L) \times .5)]$ where *R* and *L* represented the normalized mean FA and RD and mean strength and volume within each tract for the right and left hemispheres. Negative values indicated leftward asymmetries, whereas positive values indicated rightward biases. Next,

changes in AQ scores (ΔAQ) were calculated by subtracting each subject's prescan AQ score from the postscan AQ score, of which the absolute value indicated the magnitude of the change but not the direction. We then differentiated between leftward and rightward changes by setting these magnitude values to negative and positive, respectively. This was done for IFG, IPL, and STG ROIs and IFG-IPL, IFG-STG, and IPL-STG tracts.

RESULTS

Behavioral Analysis

To determine if DAID imitation training generalized to imitation of novel behaviors, DAID scores were compared between training conditions. IM subjects had significantly higher mean novel imitation scores ($M = 100.5$, $SD = 21.49$) as compared with CO subjects ($M = 52.50$, $SD = 9.75$), $t(6) = 4.069$, $p = .007$. The results were consistent across all four IM/CO pairs, with the IM subjects performing significantly better than their CO match (see Table 2).

FA and RD

As a measure of overall change in frontoparietotemporal white matter integrity, bilateral changes in mean FA and mean RD were calculated. Left and right hemisphere values were summed, and prescan values were subtracted from postscan values, for each ROI. Mixed-model repeated-measures ANOVAs revealed no significant effects of training condition for overall frontoparietotemporal FA or RD values.

Next, lateralized effects of training condition on frontoparietotemporal white matter integrity were assessed. A mixed-model repeated-measures ANOVA, with ΔAQ as the repeated-measure and Training condition as the between subjects variable, revealed a significant between-subject effect of Training condition on mean FA, $F(1, 6) = 6.12$, $p = .048$ (Figure 2). IM subjects showed leftward increases in FA for all frontoparietotemporal ROIs. There

Table 2. Novel DAID Behavior Test Scores for Each IM/CO Subject Pair

<i>IM</i>	<i>Sum</i>	<i>CO</i>	<i>Sum</i>
Carl	84	Fritz	59
Jacqueline	100	Cissie	48
Faye	87	Evelynne	41
Gelb	131	David	62
Average	100.5		52.5
<i>SE</i>	10.74		4.87

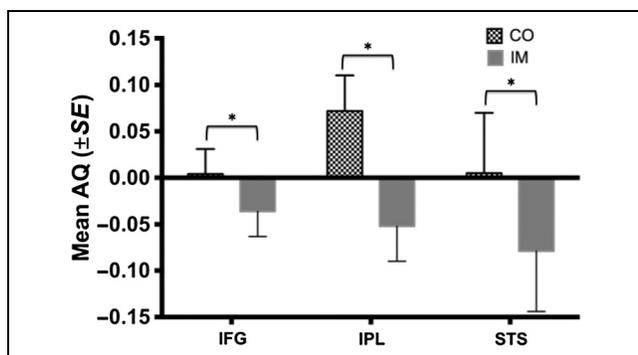


Figure 2. Mean (and *SE*) changes in AQ for FA within mirror system ROIs following training in IM subjects (solid gray) and CO subjects (checker). Positive values indicate increases in the right hemisphere as compared with the left, whereas negative values indicate increases in the left hemisphere as compared with the right.

were no significant changes in Δ AQ for mean RD. Means and standard deviations for all FA and RD measures are presented in Table 3.

Tractography

To assess overall changes in white matter connectivity between frontoparietotemporal ROIs, bilateral tract strength and volume measures were calculated. Values from left and right hemispheres were summed, and pre-scan values were subtracted from postscan values for each tract. Mixed-model repeated-measures ANOVAs revealed no significant changes in overall frontoparietotemporal connectivity.

Next, lateralized effects of training condition on white matter connectivity were determined. Changes in AQ for mean tract strength and volume were assessed using mixed-model repeated-measures ANOVAs, with Δ AQ as the repeated-measure and Training condition as the between-group factor. A significant between-subject effect of Training condition was found for mean tract

Table 3. Means and Standard Deviations (in Parentheses) for the Differences in FA and RD between Pre- and Postscans

	IFG		IPL		STS	
	CO	IM	CO	IM	CO	IM
FA total	0.001 (0.163)	-0.061 (0.071)	-0.064 (0.062)	-0.012 (0.157)	-0.026 (0.245)	0.068 (0.214)
RD total	-0.041 (0.065)	0.027 (0.082)	0.042 (0.057)	-0.003 (0.089)	-0.004 (0.164)	-0.040 (0.132)
FA AQ	0.004 (0.038)	-0.036 (0.066)	0.072 (0.048)	-0.052 (0.096)	0.005 (0.074)	-0.079 (0.168)
RD AQ	0.009 (0.030)	-0.001 (0.020)	-0.015 (0.022)	0.011 (0.044)	0.006 (0.015)	0.018 (0.070)

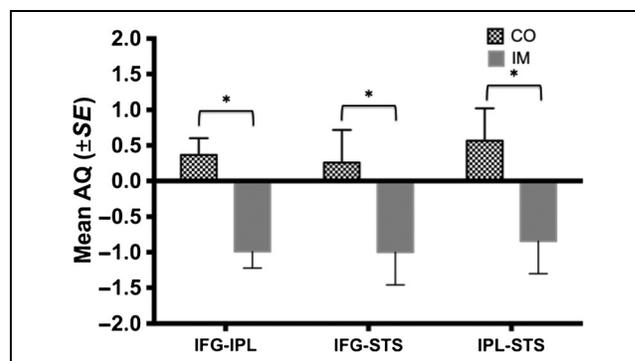


Figure 3. Mean (and *SE*) changes in AQ for MNS tract strength following imitation training in IM subjects (solid gray) and CO subjects (checker). Positive values indicate increases in the right hemisphere as compared with the left, whereas negative values indicate increases in the left hemisphere as compared with the right.

strength, $F(1, 6) = 6.910, p = .039$ (Figure 3). Similar to FA within ROIs, IM subjects showed leftward increases in mean tract strength between all frontoparietotemporal ROIs. No significant changes were found for tract volume Δ AQ. Means and standard deviations for all tract strength and volume measures are presented in Table 4.

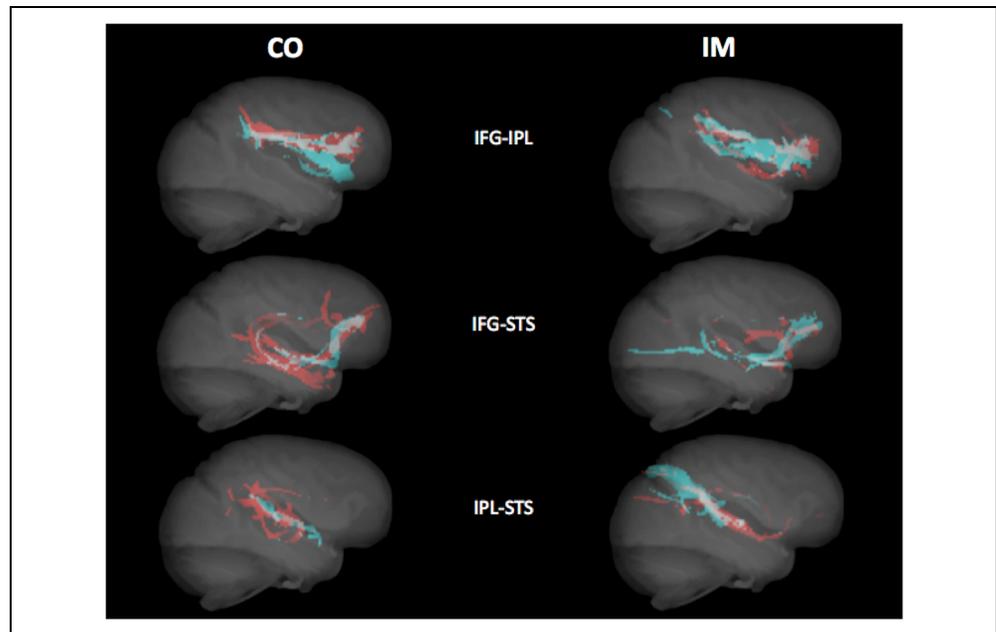
DISCUSSION

The current study reports two main findings. First, adult chimpanzees that were DAID trained were better able to copy novel behaviors than nonimitation trained controls. This generalization from trained imitative behaviors to the imitation of novel actions has been reported in juvenile chimpanzees (Custance et al., 1995). However, this is the first instance in which such transfer occurred in adults, illustrating continued behavioral plasticity for DAID imitation learning past the period of juvenile development in

Table 4. Means and Standard Deviations (in Parentheses) for the Differences in Tract Strength and Volume between Pre- and Postscans

	IFG-IPL		IFG-STG		IPL-STG	
	CO	IM	CO	IM	CO	IM
Strength total	0.242 (0.307)	0.096 (0.277)	0.197 (0.264)	0.016 (0.198)	0.036 (0.297)	0.140 (0.308)
Volume total	-3.72 (4.00)	-7.54 (6.14)	-3.83 (4.85)	-6.18 (3.50)	-4.27 (2.61)	-4.98 (3.33)
Strength AQ	0.366 (0.329)	-0.990 (0.575)	0.258 (0.623)	-1.00 (1.14)	0.565 (0.882)	-0.844 (0.946)
Volume AQ	-0.371 (0.425)	0.022 (0.533)	-0.474 (0.390)	0.052 (0.764)	-0.212 (0.137)	0.127 (0.418)

Figure 4. The average increases (note that this does not depict the decreases in connectivity that are accounted for in the AQ measure) in right (red) and left (green) tract intensity between pre- and postscans in CO and IM subjects' probabilistic tractography maps. Bilateral increases in connectivity were apparent in CO subjects' IFG-IPL tract and rightward increases were seen in IFG-STS and IPL-STS tracts. IM subjects, however, exhibited greater leftward increases across IFG-IPL, IFG-STS, and IPL-STS tracts.



chimpanzees. Second, this study is the first to show imitation related neural plasticity in nonhuman apes. Specifically, following DAID imitation training, significant leftward increases were found in the white matter integrity of frontoparietotemporal regions that make up the putative chimpanzee mirror system (Figure 4).

Our findings provide further evidence that chimpanzees are capable of imitative behaviors (see Whiten, 2017, for a review), which may be honed through DAID training. We suggest that DAID practice strengthened IM subjects' existing frontoparietotemporal imitation system, the presence of which has been indicated by other recent findings showing that juvenile chimpanzees exhibit seemingly automatic motor mimicry while learning nut-cracking behavior (Fuhrmann, Ravignani, Marshall-Pescini, & Whiten, 2014). To clarify, control subjects' decreased propensity toward imitative behaviors during testing should not be taken as evidence that they did not know how to imitate or that imitation itself was trained in IM subjects. DAID training simply provided IM subjects with an environment in which imitation was rewarded and subsequently practiced. Thus, during testing, CO subjects were playing a game for which they did not know the rules.

DAID training and participation induced left lateralized increases in frontoparietotemporal white matter integrity in chimpanzees. These changes were found in mean FA (a measure of tract integrity) within frontoparietotemporal ROIs and in mean tract strength (the number of identified streamlines passing through any given voxel) connecting those ROIs. It is likely that this reflects increased myelination of existing pathways such that they became strong enough for inclusion by the probabilistic tractography algorithm. Furthermore, the significant leftward increase in FA within the fronto-

parietotemporal ROIs is consistent with this interpretation. Although high FA/RD ratios have been used to identify increases in myelination (Li, Legault, & Litcofsky, 2014), this study found no significant changes in RD. This is likely because we were limited to measuring FA and RD within predominantly gray matter ROIs and not in the white matter connections between the ROIs where the majority of myelination increases might occur.

Leftward dominance has also been found in the human frontoparietotemporal mirror system. Patients with lesions show more imitative deficits when the damage is on the left side (Goldenberg, 1996). Specifically, damage to the left IPL impairs patient's ability to conceptualize the action to be imitated (Halsband et al., 2001; Goldenberg, 1999). In a pivotal study, bilateral activation was seen following finger movement imitation in controls but only left activation was seen in split-brain patients, indicating that bilateral neural involvement in imitation may be driven by callosal connections from left to right hemispheres (Fecteau, Lassonde, & Théoret, 2005). Thus, the current study's findings implicating left dominance within a frontoparietotemporal imitation system in chimpanzees further supports the notion of homologous neural underpinnings of imitation in human and nonhuman apes.

There are three primary limitations of this study. First, by using ROIs we excluded large portions of neural architecture, which might have experienced DAID training-related changes, from our analyses. However, more inclusive techniques (e.g., Tract-Based Spatial Statistics) require much greater sample sizes and were therefore not feasible under the current methodology. Second, ideally the baseline initial scans would have occurred immediately before training; however, to limit the stress placed on the animals, we opted to use previously

collected DTIs. This choice necessitated the inclusion of a control group matched for the time between pre- and postscans, such that natural changes with time would be similar across conditions. Thus, bilateral positive and negative changes could be reasonably expected in both IM and CO subjects. We suggest that the almost entirely positive, unilateral changes within the left mirror system of IM subjects is even more striking, given the bidirectional changes that likely occurred before training. Note, all lateralized trained actions (imitative and control) were presented equally for left and right sides. Second, we chose body part presentation as the control training procedure because, like imitation training, it involves full body, bilateral movements and a high degree of experimenter–subject interaction. Notably, some of the cues for body parts are similar to the actions themselves (ex. present hand cue is EXP’s hand, palm down), making this control extremely conservative, as some of the control behavior cues and responses border on imitative. Although we did not test CO subjects’ body part presentation abilities following training, subjectively they appeared to improve. Of course, we are not advocating that frontoparietotemporal regions are exclusively involved in imitative behaviors; thus, it is plausible that some of CO subjects’ changes in these regions were a function of their own training.

The observed left-biased mirror system related to imitation in chimpanzees has some potential implications for the evolution of language. The neural underpinnings of speech are typically left-lateralized and involve Broca’s area, a region morphologically and cytoarchitectonically homologous to the chimpanzee IFG (Keller, Roberts, & Hopkins, 2009; Schenker et al., 2008; Sherwood, Broadfield, Holloway, Gannon, & Hof, 2003). Furthermore, in chimpanzees, the left IFG is involved in gestural and vocal intentional communication (Tagliabue, Russell, Schaeffer, & Hopkins, 2008). When we consider the extent to which imitation plays a role in the development of language and other social skills, it follows that similar neural regions might underlie these abilities. Indeed, we have previously found that chimpanzees that perform better on an imitation recognition task also perform significantly better on measures of social cognition and sociocommunicative competencies (Pope et al., 2015). Thus, the current study indicates that a left-dominant imitation system might have predated the *Pan–Homo* divergence, thereby providing indirect support for theories suggesting that language might have been built upon or in conjunction with the emergence of increasingly sophisticated imitation recognition and learning skills.

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