

3-1-2018

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

Sarah M. Pope
Georgia State University

Jared P. Tagliatela
Kennesaw State University

Sara A. Skiba
Kennesaw State University

William D. Hopkins
Georgia State University

Follow this and additional works at: <https://digitalcommons.kennesaw.edu/facpubs>



Part of the [Ecology and Evolutionary Biology Commons](#)

Recommended Citation

Pope, Sarah M.; Tagliatela, Jared P.; Skiba, Sara A.; and Hopkins, William D., "Changes in Frontoparietotemporal Connectivity following Do-As-I-Do Imitation Training in Chimpanzees (*Pan troglodytes*)" (2018). *Faculty Publications*. 4135.
<https://digitalcommons.kennesaw.edu/facpubs/4135>

This Article is brought to you for free and open access by DigitalCommons@Kennesaw State University. It has been accepted for inclusion in Faculty Publications by an authorized administrator of DigitalCommons@Kennesaw State University. For more information, please contact digitalcommons@kennesaw.edu.

1 Changes in fronto-parieto-temporal connectivity following Do-As-I-Do imitation training
2 in chimpanzees (*Pan troglodytes*)

3
4

5 Sarah M. Pope^{1,2}, J. P. Tagliatela^{3,4}, S. A. Skiba³, and W. D. Hopkins^{1,4}

6
7

Accepted for publication in the Journal of Cognitive Neuroscience: November 11th, 2017

8

9 ¹ Neuroscience Institute and Language Research Center, Georgia State University,
10 Atlanta, Georgia, USA; ² Laboratory of Cognitive Psychology, CNRS and Aix-Marseille
11 University, Marseille, France; ³ Department of Ecology, Evolution and Organismal
12 Biology, Kennesaw State University, Kennesaw, GA, USA, ⁴ Ape Cognition and
13 Conservation Initiative, Des Moines, IA, USA

14
15

16 Dr William D. Hopkins,
17 Neuroscience Institute
18 Georgia State University
19 100 Piedmont Ave SE
20 Atlanta, GA 30303 USA

21

22 E-mail: whopkins4@gsu.edu

23

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

Abstract

Human imitation is supported by an underlying ‘mirror system’ principally composed of inferior frontal (IF), inferior parietal (IP), and superior temporal (ST) cortical regions. Across primate species, differences in fronto-parieto-temporal connectivity have been hypothesized to explain phylogenetic variation in imitative abilities. However, if and to what extent these regions are involved in imitation in non-human primates is unknown. We hypothesized that ‘Do As I Do’ (DAID) imitation training would enhance white matter integrity within and between fronto-parieto-temporal regions. To this end, four captive chimpanzees (*Pan troglodytes*) were trained to reproduce 23 demonstrated actions, while 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 minutes of training over an average of 112 days. Bilateral and asymmetrical changes in fronto-parieto-temporal 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 fronto-parieto-temporal connectivity, particularly in the left hemisphere, may have facilitated the emergence of increasingly complex imitation learning abilities.

1

2

Introduction

3

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.

6

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

10

suite of human socio-cognitive processes such as empathy (Carr, Iacoboni, Dubeau,

11

Mazziotta, & Lenzi, 2003; Iacoboni, 2009; Pfeifer, Iacoboni, Mazziotta, & Dapretto,

12

2008; Schulte-Ruther, Markowitsch, Fink, & Piefke, 2007; Williams, Nicolson, Clephan,

13

de Grauw, & Perrett, 2013), joint-attention (Carpenter & Tomasello, 1995; Charman et

14

al., 1997), mirror self-recognition (Asendorpf, Warkentin, & Baudonnière, 1996; Nielsen

15

& Dissanayake, 2004) and action/intention understanding (Rizzolatti & Fogassi, 2014).

16

Further, imitation's role in human social learning likely underlies cultural transmission of

17

specific behavior patterns (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009)

18

including language (Corballis, 2010; Iacoboni, 2009; Iacoboni & Wilson, 2006; Nadel,

19

2002; Rizzolatti & Craighero, 2004). These collective findings have led some to assert

20

that imitation is what distinguishes humans from other species (Meltzoff, 1988).

21

22

To what extent imitative abilities are uniquely human is a matter of considerable

23

debate (Buttelmann, Carpenter, Call, & Tomasello, 2013; Tennie, Call, & Tomasello,

24

2012; Visalberghi & Fragaszy, 2002; see also Galef, 2012 for a review of social learning

1 across animal taxa). Some have suggested that truly imitative behaviors are nonexistent
2 in nonhuman primates (Tennie, Call, & Tomasello, 2009; Tomasello, 1996; Tomasello,
3 Kruger, & Ratner, 1993); however, a large body of evidence indicates considerable
4 similarities between apes' and humans' imitative capacities (see Whiten, 2017 for a
5 review). Like human infants, there is evidence that newborn chimpanzees can imitate
6 some facial expressions (Bard, 2007; M. Myowa-Yamakoshi, Tomonaga, M., Tanaka, M.,
7 & Matsuzawa, T., 2004) and similar findings have been reported in some macaque
8 species (Paukner, Pedersen, & Simpson, 2017; Paukner, Simpson, Ferrari, Mrozek, &
9 Suomi, 2014). There is also evidence of species differences in imitation recognition and
10 production abilities. For instance, the ability to recognize when one is being imitated is
11 present in all great apes that have been tested to date (Asendorpf et al., 1996; Haun &
12 Call, 2008; Nielsen & Dissanayake, 2004; Pope, Russell, & Hopkins, 2015) but is
13 equivocal in Old and New World monkeys (Paukner, Anderson, Borelli, Visalberghi, &
14 Ferrari, 2005; Paukner, Suomi, Visalberghi, & Ferrari, 2009). This imitation recognition
15 likely relies, at least in part, on neural networks that also serve imitation production.

16 Humans tend to copy the specific actions used during a demonstration, even
17 irrelevant ones (Horner & Whiten, 2005) whereas chimpanzees tend to reproduce the
18 end-state of demonstrations, ignoring the details of the actions (Buttelmann, Carpenter,
19 Call, & Tomasello, 2007; Call, Carpenter, & Tomasello, 2005; Carpenter & Call, 2009;
20 M. Myowa-Yamakoshi & Matsuzawa, 2000; Tennie, Call, & Tomasello, 2006); yet
21 importantly they are capable of invoking more specific action-copying (Horner & Whiten,
22 2005). Indeed, evidence has shown that apes can learn to play a "Do As I Do" (DAID)
23 imitation game, in which they reproduce demonstrated actions during a training period

1 and then continue to imitate when tested with a battery of novel actions (Call, 2001;
2 Custance, Whiten, & Bard, 1995; Hayes & Hayes, 1952). In contrast, attempts to teach
3 monkeys this same imitation game have been largely unsuccessful and seem to suggest
4 that they may favor end-state copying, by mimicking the environmental effect of
5 demonstrations, rather than copying others' specific actions (Fragaszy, Deputte, Cooper,
6 Colbert-White, & Hemery, 2011; Mitchell & Anderson, 1993; Visalberghi & Frigaszy,
7 2002). In fact, when action-copying is irrelevant, monkeys' ability to learn an abstract
8 response sequence is facilitated by observing a conspecific; a process termed cognitive
9 imitation (Subiaul, Cantlon, Holloway, & Terrace, 2004). Thus, the extent to which
10 action- vs goal-copying behaviors are utilized varies considerably within the primate
11 lineage.

12
13 In the current study, we sought to examine the neural basis of imitation in
14 chimpanzees. If and to what extent the human imitative phenotype relies on the same
15 neural substrates as other primates' action-copying behaviors is controversial (Hickok,
16 2009). The discovery of mirror neurons, which fire both when an action is produced and
17 when the same action (produced by another individual) is observed, within the macaque
18 premotor area F5, has been hypothesized to be a critical neuronal mechanism involved in
19 action copying (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese,
20 Fogassie, & Rizzolatti, 1996). Additional mirror neurons were later found within
21 monkey parietal regions, which innervate the premotor cortex (Gallese, Fadiga, Fogassi,
22 & Rizzolatti, 2002). With the incorporation of superior temporal regions, which are
23 involved in recognizing biological motion (Perrett et al., 1990) *and* are reciprocally

1 connected to parietal regions, a putative macaque imitation system has emerged (Gallese
2 et al., 1996; Rizzolatti, Fogassi, & Gallese, 2002). However, one significant limitation of
3 the mirror neuron system model of imitation in macaque monkeys is the simple fact that
4 the available data indicate that the imitative abilities of species within this genus are
5 notably limited (Visalberghi & Fragaszy, 2002).

6

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

20

21 To explain the spectrum of primate imitative phenotypes, Hecht et al. (2013)
22 compared fronto-parieto-temporal white matter connectivity among macaques,
23 chimpanzees, and humans. These authors found prominent ventral STS to IPL

1 connections in macaques, pronounced dorsal IPL to IFG connections in humans, and
2 more equivalently proportioned dorsal/ventral connections in chimpanzees. According to
3 Hecht et al. (2013) ventral connections, hypothesized to facilitate the understanding of
4 actions' goals, underlie macaques' goal-copying. Whereas dorsal connections,
5 hypothesized to facilitate the understanding of action kinematic details, underlie humans'
6 action-copying abilities. Thus, chimpanzees' intermediate expression of both dorsal and
7 ventral connections is consistent with their intermediate usage of both goal- and action-
8 copying. Although there appears to be homology between the macaque and human
9 fronto-parieto-temporal systems, its functional involvement in chimpanzee imitation is
10 entirely speculative. Indeed, there are no data regarding the functional correlates of
11 imitation in chimpanzees or other great apes; thus, the hypothesis that the same fronto-
12 parieto-temporal regions are involved in ape imitation remains untested.

13

14 As a means of examining the potential neural basis of imitation in chimpanzees,
15 the current study utilized diffusion tensor imaging (DTI) before and after DAID imitation
16 training to assess changes in fronto-parieto-temporal connectivity. DTI has been used in
17 humans to document training-induced cortical changes for numerous motor and cognitive
18 tasks, such as juggling (Scholz, Klein, Behrens, & Johansen-Berg, 2009), second
19 language acquisition (Schlegel, Rudelson, & Peter, 2012), and playing an instrument
20 (Hyde et al., 2009; Zatorre, Fields, & Johansen-Berg, 2012). Additionally, chimpanzees
21 are capable of being taught the DAID imitation game and subsequently apply the 'copy
22 this' rule in order to successfully imitate novel actions (Custance et al., 1995; Hayes &
23 Hayes, 1952). Here, we combined DAID imitation training with DTI scanning to

1 quantify changes in cortical connectivity, specifically within the fronto-parieto-temporal
2 mirror system. After learning the imitation game, we measured chimpanzees' imitative
3 abilities on a list of novel actions (i.e. *not* part of their training). We hypothesized that if
4 IFG, IPL, and STS regions are involved in imitation in chimpanzees, then connectivity
5 between these putative mirror regions would increase following successful DAID
6 imitation game acquisition and participation.

7

8 **Methods**

9

10 Subjects:

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

15

16 Training Procedure:

17 One member from each matched pair was randomly selected to be taught the
18 DAID imitation game (IM) and the other served as a control (CO). Each IM/CO pair was
19 trained concurrently (i.e. on the same days and during the same times of day) via positive
20 reinforcement training. IM subjects learned to reproduce an experimenter (EXP)'s action
21 from a list of 23 DAID behaviors while CO subjects were rewarded for producing basic
22 husbandry behaviors in response to manual cues. Basic husbandry behaviors included
23 presenting body parts, such as arms, legs, hands, feet, back, etc. All DAID actions are

1 listed in Table 1. For lateralized DAID behaviors, IM subjects were trained to use the
2 corresponding ipsilateral body part as the EXP (i.e. EXP's left = ape's right), as if they
3 were looking in a mirror (Bekkering, Wohlschläger, & Gattis, 2000). IM and CO
4 subjects each received 600 minutes of training (apart from one IM/CO pair which
5 received 602 and 589 minutes respectively, due to experimenter error) and the number of
6 days spent training ranged from 73 to 134 ($M = 112.14$, $SD = 19.24$). The number of
7 days of training varied between subjects because of differences in training motivation
8 from day to day but there was no significant difference in the number of training days
9 between the IM and CO groups ($t(6) = -.15$; $p = .884$). The number of training sessions
10 ranged from 36 to 43 ($M = 39$; $SD = 2.19$) and average session length ranged from 13.95
11 to 16.67 minutes ($M = 15.39$; $SD = 0.88$).

12 Two different lists of 23 DAID behaviors were generated (Table 1). IM subjects
13 were trained on one list of 23 actions and then tested for generalization in imitation
14 performance on the remaining *novel*, 23 actions. Lists were comprised of similar but
15 distinct actions in an attempt to minimize differences in difficulty between lists. Training
16 and test lists were counterbalanced such that one male and one female were trained on
17 List 1 and tested on List 2 and vice versa for the remaining two individuals.

18

19 Testing Procedure

20 Following training, all subjects were tested on their generalization in imitative
21 abilities. During each test session, both trained and novel DAID actions were modeled
22 for the subjects; each action was presented on 3 separate occasions for a total of 138 trials.
23 To start a test session, subjects were engaged by prompting familiar, previously trained

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

11

12 Test sessions were video recorded (Canon HD Vixia HFS21) and later scored
13 based on the following criteria: 3 = Subject used the corresponding ipsilateral body part
14 to produce the demonstrated action. For example, EXP cage banged with right hand and
15 the subject responded by cage banging with their left hand at least once within the 10 sec
16 trial. 2 = Subject used a different or the corresponding contralateral body part to produce
17 the demonstrated action or subject used the corresponding ipsilateral body part to produce
18 a similar action. Using the above example (EXP cage bangs with their right hand),
19 subjects would score a 2 if they a) cage banged with their right hand, or b) waved their
20 left hand (or any other action similar to cage bang). 1 = Subject used the corresponding
21 ipsilateral body part to produce any action. Thus, if EXP cage banged with right hand,
22 the subject could produce any action with their left hand and receive a score of 1. 0 =
23 Subject did not use the corresponding body part and did not produce the demonstrated

1 action. When subjects produced multiple actions within the 10s, the behavior with the
2 highest score was recorded. To ensure that experimenter bias did not factor into scoring,
3 132 (12% of the total) test behaviors were re-coded by a second observer who was blind
4 to both the subjects' training condition and the hypothesis. A Spearman rank order
5 correlation between the two observers revealed the scoring of the chimpanzees' actions to
6 be reliable ($\rho = .75, p < .05$).

7
8 To compute each subject's overall performance, a cumulative imitation score was
9 calculated. For IM subjects, 69 of the 138 behaviors presented during test sessions were
10 from the familiar list that they were trained on and the remaining 69 were novel.
11 However, for CO subjects, none of the 138 behaviors were familiar. Thus, IM subjects'
12 imitation scores were calculated from only novel behaviors and because training occurred
13 in CO/IM pairs, CO subjects' imitation scores were calculated based on the list that was
14 novel to their IM counterpart, to control for list difficulty. The three imitation scores for
15 each of the 23 behaviors were summed (69 total scores) to derive a cumulative imitation
16 score for each subject. Performance could vary from 0 to 207 (3 trials * 23 actions * a
17 score of 3). Due to EXP error, one CO subject only received two tests for one of the
18 behaviors (68 total scores); thus, their highest score for that behavior was used again, as a
19 conservative third score.

20

21 Scanning Protocol

22 *In vivo* MRI and DTI scans were obtained at the same time that the chimpanzees
23 were participating in their annual physical examinations, which was coordinated with the

1 end of their training. Subjects were first immobilized by ketamine (10 mg/kg) or telazol
2 (3-5mg/kg) and subsequently anaesthetized with propofol (40–60 mg/(kg/h)) following
3 standard procedures at the YNPRC. Subjects were then transported to the YNPRC MRI
4 facility and were placed in the scanner chamber in a supine position with their head fitted
5 inside the human-head coil. The subjects remained anaesthetized for the duration of the
6 scans as well as the time needed to transport them between their home cage and the
7 imaging facility (total time ~ 1.5 h). After scanning was completed, the apes were
8 returned to their home cage and allowed to fully recover from the anesthesia before being
9 reunited with their group members. Within pairs of subjects, the time between pre- and
10 post-DTI scans ranged from 0.02 to 0.50 years ($M = 0.22$, $SD = 0.23$). Time between
11 final training day and post DTI scan ranged from 6 to 18 days ($M = 11.57$; $SD = 4.49$);
12 however, there was no difference between IM and CO apes ($t(6) = -2.93$; $p = .06$).

13

14 Subjects were imaged using a 3.0 T Siemens Trio scanner (Siemens Medical
15 Solutions USA, Inc., Malvern, Pennsylvania, USA). T1-weighted images were collected
16 using a three-dimensional gradient echo sequence (pulse repetition= 2300 ms, echo time=
17 4.4 ms, number of signals averaged= 3, matrix size = 320 X 320). Scanning parameters
18 were slightly different for the first two DTIs (one CO & one IM) than for the remaining
19 fourteen. For all scans, two whole brain diffusion-weighted data sets, with a single shot
20 EPI sequence and a b value of 1000 s/mm² with 64 (scans 1-2 = 60) diffusion directions,
21 along with an additional image without diffusion weighting (b value = 0 s/mm²) were
22 acquired. Acquisition occurred transaxially: for scans 1-2 FOV = 230 and resolution =
23 1.8x1.8x1.8 mm for 60 slices; for scans 3-16 FOV = 243 and resolution = 1.9x1.9x1.9

1 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 non-brain tissue using the Brain Extraction Tool (BET), 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 maps. Radial diffusivity maps were then calculated from the DTIFIT output by summing the L2 and L3 volumes and dividing by 2. In order 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.

13

14 Regions of Interest:

15

16 To assess changes within and between fronto-parieto-temporal regions, bilateral regions of interest (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.

20

21 Inferior Frontal Gyrus (IFG): In the axial plane, the ROI was defined as the area between the fronto-orbital (FO) and inferior precentral sulci (PCI) with the medial boundary being a straight line between the medial edges of the two sulci. Following axial

1 tracing, the image was returned to the sagittal plane and the first lateral slice where the
2 insula was no longer visible was located. The ROI was extended from the bottom-left
3 corner of this slice either along PCI if it was still apparent or straight down if it was not.
4 This was repeated for all remaining slices, moving laterally.

5 Inferior Parietal Lobe (IPL): First, the image was placed in the sagittal plane,
6 where the most medial slice in which the insula was not visible was identified. A line
7 was then drawn from the most anterior extension of the postcentral sulcus (PoC) straight
8 down to the lateral sulcus (Lt). This served as the anterior boundary. Next, the dorsal
9 boundary was marked as the point that the PoC was no longer parallel to the Lt. Finally, a
10 diagonal line was drawn from this dorsal boundary to the Lt, which served as the
11 posterior boundary. The image was then rotated into the axial plane and the area between
12 the PoC and Lt, within the predefined bounds, was captured.

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

20

21 Fractional Anisotropy and Radial Diffusivity Methods:

22 Within the putative mirror system, changes in fractional anisotropy (FA), which
23 indicates how uniformly directional diffusivity is within a given voxel as a proxy for tract

1 integrity, and radial diffusivity (RD), which indicates myelination by measuring the rate
2 of diffusivity in the perpendicular direction, were compared between training conditions.
3 Processed FA and RD maps for both pre and post scans were linearly registered to
4 subjects' previously collected, T1-weighted MRI scans. Following this registration,
5 subject specific fronto-parieto-temporal ROIs and pre/post FA and RD maps were in the
6 same stereotaxic space. Next, ROIs for each hemisphere were placed on the registered
7 FA and RD volume and the average value within the ROI was calculated. Variation in
8 signal-to-noise ratios between scans was adjusted for by dividing the mean FA and mean
9 RD within each ROI by the mean FA and RD (respectively) within that hemisphere or by
10 the mean whole brain FA and RD (respectively) for bilateral analyses, for each scan.
11 Finally, the pre FA and RD values were subtracted from post FA and RD values to reflect
12 measures of change in white matter integrity within each ROI within the fronto-parieto-
13 temporal regions for each subject.

14

15 Probabilistic Tractography Methods:

16 To assess potential changes in mirror system white matter connectivity, we used
17 FSL's software package for probabilistic tractography, PROBTRACKx (Behrens et al.
18 2007). First, registration matrices were created and used to place diffusion gradient
19 information for each scan (generated from BEDPOSTx) into the same stereotaxic space
20 as subjects' T1-weighted MRI scan. Probabilistic tractography was then used to assess
21 the connectivity distributions between ROIs. To increase the likelihood that streamlines
22 were generated within ROIs and not underlying white matter tracts passing through the
23 ROI, seed ROIs were masked to only include gray matter. We chose to use networks

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

19 We chose not to apply thresholding to connectivity maps for two reasons. First,
20 thresholding is typically used to exclude erroneous streamlines from analysis; however,
21 our inclusion of the control group already addresses this issue (i.e., error should be
22 equally distributed across IM and CO subjects). Second, thresholding would limit
23 analyses to only the most established tracts, which may be less likely to change –

1 due to ceiling effects – following training. In other words, training-induced increases in
2 connectivity may occur less readily in voxels already containing a large proportion of the
3 streamlines.

4

5 Data Analysis

6

7 We analyzed the data two ways. First, we identified mean FA, mean RD, tract
8 strength, and tract volume when summed across the two hemispheres for each ROI/tract
9 to identify bilateral fronto-parieto-temporal changes. Second, we tested for changes in
10 lateralization of mean FA, mean RD, tract strength, and tract volume to gain an
11 understanding of any asymmetrical fronto-parieto-temporal changes. To assess the
12 magnitude and direction of lateralized changes following imitation training, asymmetry
13 quotients (AQ) were calculated following the formula $[AQ = (R - L) / ((R + L) * .5)]$
14 where R and L represented the normalized mean FA and RD and mean strength and
15 volume within each tract for the right and left hemispheres. Negative values indicated
16 leftward asymmetries while positive values indicated rightward biases. Next, changes in
17 AQ scores (ΔAQ) were calculated by subtracting each subject's pre scan AQ score from
18 the post scan AQ score, of which the absolute value indicated the magnitude of the
19 change but not the direction. We then differentiated between leftward and rightward
20 changes by setting these magnitude values to negative and positive, respectively. This
21 was done for IFG, IPL, and STS ROIs and IFG-IPL, IFG-STS, and IPL-STS tracts.

22

23

Results

1

2 Behavioral Analysis

3

4 To determine if DAID imitation training generalized to imitation of novel
5 behaviors, DAID scores were compared between training conditions. IM subjects had
6 significantly higher mean novel imitation scores ($M = 100.5$, $SD = 21.49$) as compared to
7 CO subjects ($M = 52.50$, $SD = 9.75$), $t(6) = 4.069$, $p=0.007$. The results were consistent
8 across all 4 IM/CO pairs with the IM subjects performing significantly better than their
9 CO match (see Table 2).

10

11 FA and RD

12 As a measure of overall change in fronto-parieto-temporal white matter integrity,
13 bilateral changes in mean FA and mean RD were calculated. Left and right hemisphere
14 values were summed and pre scan values were subtracted from post scan values, for each
15 ROI. Mixed model repeated measures ANOVAs revealed no significant effects of
16 training condition for overall fronto-parieto-temporal FA or RD values.

17 Next, lateralized effects of training condition on fronto-parieto-temporal white
18 matter integrity were assessed. A mixed model repeated measures analysis of variance,
19 with ΔAQ as the repeated measure and training condition as the between subjects
20 revealed a significant between subjects effect of training condition on mean FA [$F(1,$
21 $6)=6.12$, $p = 0.048$] (Figure 3). IM subjects showed leftward increases in FA for all
22 fronto-parieto-temporal ROIs. There were no significant changes in ΔAQ for mean RD.
23 Means and standard deviations for all FA and RD measures are presented in Table 3.

1

2

3 Tractography

4 To assess overall changes in white matter connectivity between fronto-parieto-
5 temporal ROIs, bilateral tract strength and volume measures were calculated. Values
6 from left and right hemispheres were summed and pre scan values were subtracted from
7 post scan values, for each tract. Mixed model repeated measures ANOVAs revealed no
8 significant changes in overall fronto-parieto-temporal connectivity.

9 Next, lateralized effects of training condition on white matter connectivity were
10 determined. Changes in AQ for mean tract strength and volume were assessed using
11 mixed model repeated measures analyses of variance, with Δ AQ as the repeated measure
12 and training condition as the between group factor. A significant between subjects effect
13 of training condition was found for mean tract strength [$F(1, 6)=6.910, p = 0.039$] (Figure
14 4). Similar to FA within ROIs, IM subjects showed leftward increases in mean tract
15 strength between all fronto-parieto-temporal ROIs. No significant changes were found
16 for tract volume Δ AQ. Means and standard deviations for all tract strength and volume
17 measures are presented in Table 4.

18

19

Discussion

20

21 The current study reports two main findings. First, adult chimpanzees that were
22 DAID trained were better able to copy novel behaviors than non-imitation trained
23 controls. This generalization from trained imitative behaviors to the imitation of novel

1 actions has been previously reported in juvenile chimpanzees (Custance et al., 1995).
2 However, this is the first instance in which such transfer occurred in adults, illustrating
3 continued behavioral plasticity for DAID imitation learning past the period of juvenile
4 development in chimpanzees. Secondly, this study is the first to show imitation related
5 neural plasticity in non-human apes. Specifically, following DAID imitation training,
6 significant leftward increases were found in the white matter integrity of fronto-parieto-
7 temporal regions that make up the putative chimpanzee mirror system.

8 Our findings provide further evidence that chimpanzees are capable of imitative
9 behaviors (see Whiten, 2017 for review), which may be honed through DAID training.
10 We suggest that DAID practice strengthened IM subjects' existing fronto-parieto-
11 temporal imitation system, the presence of which has been indicated by other recent
12 findings showing that juvenile chimpanzees exhibit seemingly automatic motor mimicry
13 while learning nut-cracking behavior (Fuhrmann, Ravignani, Marshall-Pescini, & Whiten,
14 2014). To clarify, control subjects' decreased propensity towards imitative behaviors
15 during testing should not be taken as evidence that they did not know how to imitate or
16 that imitation itself was trained in IM subjects. DAID training simply provided IM
17 subjects with an environment in which imitation was rewarded and subsequently
18 practiced. Thus, during testing, CO subjects were playing a game for which they did not
19 know the rules.

20 DAID training and participation induced left lateralized increases in fronto-
21 parieto-temporal white matter integrity in chimpanzees. These changes were found in
22 mean FA (a measure of tract integrity) within fronto-parieto-temporal ROIs and in mean
23 tract strength (the number of identified streamlines passing through any given voxel)

1 connecting those ROIs. It is likely that this reflects increased myelination of existing
2 pathways such that they became strong enough for inclusion by the probabilistic
3 tractography algorithm. Further, the significant leftward increase in FA within the
4 fronto-parieto-temporal ROIs is consistent with this interpretation. While high FA:RD
5 ratios have been used to identify increases in myelination (Li, Legault, & Litcofsky,
6 2014), the present study found no significant changes in RD. This is likely because we
7 were limited to measuring FA and RD *within* predominantly gray matter ROIs and not in
8 the white matter connections *between* the ROIs where the majority of myelination
9 increases might occur.

10 Leftward dominance has also been found in the human fronto-parieto-temporal
11 mirror system. Patients with lesions show more imitative deficits when the damage is on
12 the left side (Goldenberg, 1996). Specifically, damage to the left IPL impairs patient's
13 ability to conceptualize the action to be imitated (Goldenberg, 1999; Halsband et al.,
14 2001). In a pivotal study, bilateral activation was seen following finger-movement
15 imitation in controls but only left activation was seen in split-brain patients, indicating
16 that bilateral neural involvement in imitation may be driven by callosal connections from
17 left to right hemispheres (Fecteau, Lassonde, & Theoret, 2005). Thus, the current study's
18 findings implicating left dominance within a fronto-parieto-temporal imitation system in
19 chimpanzees further supports the notion of homologous neural underpinnings of imitation
20 in human and non-human apes.

21 There are three primary limitations of this study. First, by using ROIs we
22 excluded large portions of neural architecture, which might have experienced DAID
23 training-related changes, from our analyses. However, more inclusive techniques (e.g.

1 Tract Based Spatial Statistics) require much greater sample sizes and were therefore not
2 feasible under the current methodology. Second, ideally the baseline initial scans would
3 have occurred immediately prior to training; however, to limit the stress placed on the
4 animals, we opted to use previously collected DTIs. This choice necessitated the
5 inclusion of a control group matched for the time between pre- and post- scans, such that
6 natural changes with time would be similar across conditions. Thus, bilateral positive
7 and negative changes could be reasonably expected in both IM and CO subjects. We
8 suggest that the almost entirely positive, unilateral changes within the left mirror system
9 of IM subjects is even more striking given the bidirectional changes that likely occurred
10 prior to training. Note, all lateralized trained actions (imitative and control) were
11 presented equally for left and right sides. Second, we chose body part presentation as the
12 control training procedure because, like imitation training, it involves full body, bilateral
13 movements and a high degree of experimenter-subject interaction. Notably, some of the
14 cues for body parts are similar to the actions themselves (ex. present hand cue is EXP's
15 hand, palm down), making this control extremely conservative, as some of the control
16 behavior cues and responses border on imitative. Although we did not test CO subjects'
17 body part presentation abilities following training, subjectively they appeared to improve.
18 Of course, we are not advocating that fronto-parieto-temporal regions are exclusively
19 involved in imitative behaviors; thus, it is plausible that some of CO subjects' changes in
20 these regions were a function of their own training.

21

22 The observed left-biased mirror system related to imitation in chimpanzees has
23 some potential implications for the evolution of language. The neural underpinnings of

1 speech are typically left-lateralized and involve Broca's area, a region morphologically
2 and cytoarchitectonically homologous to the chimpanzee IFG (Keller, Roberts, &
3 Hopkins, 2009; Schenker et al., 2008; Sherwood, Broadfield, Holloway, Gannon, & Hof,
4 2003). Further, in chimpanzees, the left IFG is involved in gestural and vocal intentional
5 communication (Tagliabata, Russell, Schaeffer, & Hopkins, 2008) . When we consider
6 the extent to which imitation plays a role in the development of language and other social
7 skills, it follows that similar neural regions might underlie these abilities. Indeed, we have
8 previously found that chimpanzees who perform better on an imitation recognition task
9 also perform significantly better on measures of social cognition and socio-
10 communicative competencies (Pope et al., 2015). Thus, the current study indicates that a
11 left-dominant imitation system might have pre-dated the *Pan-Homo* divergence; thereby
12 providing indirect support for theories suggesting that language might have been built
13 upon or in conjunction with the emergence of increasingly sophisticated imitation
14 recognition and learning skills.

15

16 Acknowledgements

17 This research was supported by NIH grants NS-42867, NS-73134, HD-60563 to
18 WDH, and DC-011005 to JPT. Additionally, SMP is funded by Georgia State
19 University's Second Century Initiative Primate Social Cognition, Evolution, and
20 Behavior fellowship and the Kenneth W. and Georganne F. Honeycutt Fellowship. We
21 would also like to thank Kendall Davidek for her time and efforts in verifying inter-rater
22 reliability. American Psychological Association and Institute of Medicine guidelines for
23 the treatment of animals were followed during all aspects of this study. Inquiries

1 regarding this paper may be sent to: William D. Hopkins, Neuroscience Institute and
2 Language Research Center, Georgia State University, P.O. Box 5030, Atlanta, Georgia
3 30302-5030. Email: whopkins4@gsu.edu or whopkin@emory.edu

4

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33

Table 1. DAID behaviors comprising List 1 & 2

List 1	List 2
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

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

Table 2. Novel DAID behavior test scores for each IM/CO subject pair.

IM	Sum	CO	Sum
Carl	84	Fritz	59
Jacqueline	100	Cissie	48
Faye	87	Evelyne	41
Gelb	131	David	62
Average	100.5		52.5
s.e.	10.74		4.87

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

Table 3. Means and standard deviations (in parentheses) for the differences in FA and RD between pre and post scans.

	IFG		IPL		STS	
	CO	IM	CO	IM	CO	IM
FA total	.001 (.163)	-.061 (.071)	-.064 (.062)	-.012 (.157)	-.026 (.245)	.068 (.214)
RD total	-.041 (.065)	.027 (.082)	.042 (.057)	-.003 (.089)	-.004 (.164)	-.040 (.132)
FA AQ	.004 (.038)	-.036 (.066)	.072 (.048)	-.052 (.096)	.005 (.074)	-.079 (.168)
RD AQ	.009 (.030)	-.001 (.020)	-.015 (.022)	.011 (.044)	.006 (.015)	.018 (.070)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

Table 4. Means and standard deviations (in parentheses) for the differences in tract strength and volume between pre and post scans.

	IFG-IPL		IFG-STG		IPL-STG	
	CO	IM	CO	IM	CO	IM
Strength total	.242 (.307)	.096 (.277)	.197 (.264)	.016 (.198)	.036 (.297)	.140 (.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	.366 (.329)	-.990 (.575)	.258 (.623)	-1.00 (1.14)	.565 (.882)	-.844 (.946)
Volume AQ	-.371 (.425)	.022 (.533)	-.474 (.390)	.052 (.764)	-.212 (.137)	.127 (.418)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44

References

- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends in Cognitive Sciences*, 4(7), 267-278.
- Asendorpf, J. B., Warkentin, V., & Baudonnière, P. M. (1996). Self-awareness and other-awareness II: Mirror self-recognition, social contingency awareness, and synchronic imitation. *Developmental Psychology*, 32(2), 313-321.
- Autrey, M. M., Reamer, L. A., Mareno, M. C., Sherwood, C. C., Herndon, J. G., Preuss, T., . . . Hopkins, W. D. (2014). Age-related effects in the neocortical organization of chimpanzees: gray and white matter volume, cortical thickness, and gyrification. *Neuroimage*, 101, 59-67. doi:10.1016/j.neuroimage.2014.06.053
- Bard, K. A. (2007). Neonatal imitation in chimpanzees (Pan troglodytes) tested with two paradigms. *Anim Cogn*, 10(2), 233-242. doi:10.1007/s10071-006-0062-3
- Bekkering, H., Wohlschläger, A., & Gattis, M. (2000). Imitation of gestures in children is goal-direction. *The Quarterly Journal of Experimental Psychology*, 53A(1), 153-164.
- Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Dev Sci*, 10(4), F31-38. doi:10.1111/j.1467-7687.2007.00630.x
- Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2013). Chimpanzees, Pan troglodytes, recognize successful actions, but fail to imitate them. *Animal Behaviour*, 86(4), 755-761. doi:10.1016/j.anbehav.2013.07.015
- Call, J. (2001). Body imitation in an enculturated orangutan (*Pongo pygmaeus*). *Cybernetics and Systems: An International Journal*, 32, 97-119.
- Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: chimpanzees (Pan troglodytes) and human children (Homo sapiens). *Anim Cogn*, 8(3), 151-163. doi:10.1007/s10071-004-0237-8
- Carpenter, M., & Call, J. (2009). Comparing the imitative skills of children and nonhuman apes. *Revue de primatologie*, 1.
- Carpenter, M., & Tomasello, M. (1995). Joint-attention and imitative learning in children, chimpanzees, and enculturated chimpanzees. *Social Development*, 4(3), 217-237.
- Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc Natl Acad Sci U S A*, 100(9), 5497-5502. doi:10.1073/pnas.0935845100
- Charman, T., Baron-Cohen, S., Swettenham, J., Cox, A., Baird, G., & Drew, A. (1997). Infants with autism: an investigation of empathy, pretend play, joint attention, and imitation. *Developmental Psychology*, 33(5), 781-789.
- Corballis, M. C. (2010). Mirror neurons and the evolution of language. *Brain Lang*, 112(1), 25-35. doi:10.1016/j.bandl.2009.02.002

- 1 Custance, D. M., Whiten, A., & Bard, K. A. (1995). Can young chimpanzees (*Pan*
2 *troglydotes*) imitate arbitrary actions? Hayes and Hayes (1952) revisited.
3 *Behaviour*, 11(12), 837-859.
- 4 di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992).
5 Understanding motor events: a neurophysiological study. *Exp Brain Res*, 91,
6 176-180.
- 7 Fabbri-Destro, M., & Rizzolatti, G. (2008). Mirror neurons and mirror systems in
8 monkeys and humans. *Physiology (Bethesda)*, 23, 171-179.
9 doi:10.1152/physiol.00004.2008
- 10 Fecteau, S., Lassonde, M., & Theoret, H. (2005). Modulation of motor cortex
11 excitability during action observation in disconnected hemispheres. *Cognitive*
12 *Neuroscience and Neuropsychology*, 16(14), 1591-1594.
- 13 Frigaszy, D. M., Deputte, B., Cooper, E. J., Colbert-White, E. N., & Hemery, C. (2011).
14 When and how well can human-socialized capuchins match actions
15 demonstrated by a familiar human? *Am J Primatol*, 73(7), 643-654.
16 doi:10.1002/ajp.20941
- 17 Galef, B. G. (2012). Social learning and traditions in animals: evidence, definitions,
18 and relationship to human culture. *Wiley Interdiscip Rev Cogn Sci*, 3(6), 581-
19 592. doi:10.1002/wcs.1196
- 20 Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (2002). Action representation and
21 the inferior parietal lobule. In W. P. B. Hommel (Ed.), *Attention and*
22 *performance* (pp. 247-266). Oxford: Oxford University Press.
- 23 Gallese, V., Fogassie, L., & Rizzolatti, G. (1996). Action recognition in the premotor
24 cortex. *Brain*, 119(2), 593-609.
- 25 Goldenberg, G. (1996). Defective imitation of gestures in patients with damage in the
26 left or right hemispheres. *Journal of Neurology, Neurosurgery, and Psychiatry*,
27 61, 176-180.
- 28 Goldenberg, G. (1999). Matching and imitation of hand and finger postures in
29 patients with damage in the left or right hemispheres. *Neuropsychologia*,
30 37(5), 559-566.
- 31 Halsband, U., Schmitt, J., Weyers, M., Binkofski, F., Grützner, G., & Freund, H. J. (2001).
32 Recognition and imitation of pantomimed motor acts after unilateral parietal
33 and premotor lesions: A perspective on apraxia. *Neuropsychologia*, 39(2),
34 200-216.
- 35 Haun, D. B., & Call, J. (2008). Imitation recognition in great apes. *Curr Biol*, 18(7),
36 R288-290. doi:10.1016/j.cub.2008.02.031
- 37 Hayes, K. J., & Hayes, C. (1952). Imitation in a home-raised chimpanzee. *Journal of*
38 *comparative and physiological psychology*. *Journal of comparative and*
39 *physiological psychology*, 45(5), 450.
- 40 Hecht, E. E., Gutman, D. A., Preuss, T. M., Sanchez, M. M., Parr, L. A., & Rilling, J. K.
41 (2013). Process versus product in social learning: comparative diffusion
42 tensor imaging of neural systems for action execution-observation matching
43 in macaques, chimpanzees, and humans. *Cereb Cortex*, 23(5), 1014-1024.
44 doi:10.1093/cercor/bhs097
- 45 Heyes, C. M. (1993). Imitation, culture and cognition. *Anim Behav*, 46, 999-1010.

- 1 Hickok, G. (2009). Eight problems for the mirror neuron theory of action
2 understanding in monkeys and humans. *J Cogn Neurosci*, 21(7), 1229-1243.
3 doi:10.1162/jocn.2009.21189
- 4 Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation
5 switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*).
6 *Anim Cogn*, 8(3), 164-181. doi:10.1007/s10071-004-0239-6
- 7 Hyde, K. L., Lerch, J., Norton, A., Forgeard, M., Winner, E., Evans, A. C., & Schlaug, G.
8 (2009). Musical training shapes structural brain development. *J Neurosci*,
9 29(10), 3019-3025. doi:10.1523/JNEUROSCI.5118-08.2009
- 10 Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annu Rev Psychol*, 60,
11 653-670. doi:10.1146/annurev.psych.60.110707.163604
- 12 Iacoboni, M., & Wilson, S. M. (2006). Beyond a Single Area: Motor Control and
13 Language Within a Neural Architecture Encompassing Broca's Area. *Cortex*,
14 42(4), 503-506. doi:10.1016/s0010-9452(08)70387-3
- 15 Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G.
16 (1999). Cortical mechanisms of human imitation. *Science*, 286(5449), 2526-
17 2528.
- 18 Keller, S. S., Roberts, N., & Hopkins, W. (2009). A comparative magnetic resonance
19 imaging study of the anatomy, variability, and asymmetry of Broca's area in
20 the human and chimpanzee brain. *J Neurosci*, 29(46), 14607-14616.
21 doi:10.1523/JNEUROSCI.2892-09.2009
- 22 Koski, L., Wohlschläger, A., Bekkering, H., Woods, R. P., Dubeau, M. C., Mazziotta, J. C.,
23 & Iacoboni, M. (2002). Modulation of motor and premotor activity during
24 imitation of target-directed actions. *Cerebral Cortex*, 12, 847-855.
- 25 Li, P., Legault, J., & Litcofsky, K. A. (2014). Neuroplasticity as a function of second
26 language learning: anatomical changes in the human brain. *Cortex*, 58, 301-
27 324. doi:10.1016/j.cortex.2014.05.001
- 28 Meltzoff, A. N. (1988). *The human infant as Homo*
29 *imitans*. (T. R. G. Zentall, B.G. Ed.). Hillsdale, NJ: Erlbaum.
- 30 Meltzoff, A. N. (1990). Foundations for developing a concept of self: The role of
31 imitation in relating self to other and the value of social mirroring, social
32 modeling, and self practice in infancy.
- 33 Meltzoff, A. N., & Moore, M. K. (1977). Imitation of Facial and Manual Gestures by
34 Human Neonates. *Science*, 198(4312), 75-78.
- 35 Mitchell, R. W., & Anderson, J. R. (1993). Discrimination Learning of Scratching, but
36 Failure to Obtain Imitation and Self-recognition in a Long-tailed Macaque.
37 *Primates*, 34(3), 301-309.
- 38 Myowa-Yamakoshi, M., & Matsuzawa, T. (2000). Imitation in intentional
39 manipulatory actions in chimpanzees (*Pan troglodytes*). *Journal of*
40 *Comparative Psychology*, 114(4), 381-391.
- 41 Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2004). Imitation
42 in neonatal chimpanzees (*Pan troglodytes*). *Developmental Science*, 7(4), 437-
43 442.
- 44 Nadel, J. (2002). Imitation and imitation recognition: Functional use in preverbal
45 infants and nonverbal children with autism. *The Imitative Mind: Development,*
46 *Evolution, and Brain Bases*.

- 1 Nielsen, M., & Dissanayake, C. (2004). Pretend play, mirror self-recognition and
2 imitation: a longitudinal investigation through the second year. *Infant*
3 *Behavior and Development*, 27(3), 342-365. doi:10.1016/j.infbeh.2003.12.006
- 4 Paukner, A., Anderson, J. R., Borelli, E., Visalberghi, E., & Ferrari, P. F. (2005).
5 Macaques (*Macaca nemestrina*) recognize when they are being imitated. *Biol*
6 *Lett*, 1(2), 219-222. doi:10.1098/rsbl.2004.0291
- 7 Paukner, A., Pedersen, E. J., & Simpson, E. A. (2017). Testing the arousal hypothesis
8 of neonatal imitation in infant rhesus macaques. *PLoS One*, 12(6), e0178864.
9 doi:10.1371/journal.pone.0178864
- 10 Paukner, A., Simpson, E. A., Ferrari, P. F., Mrozek, T., & Suomi, S. J. (2014). Neonatal
11 imitation predicts how infants engage with faces. *Dev Sci*, 17(6), 833-840.
12 doi:10.1111/desc.12207
- 13 Paukner, A., Suomi, S. J., Visalberghi, E., & Ferrari, P. F. (2009). Capuchin monkeys
14 display affiliation toward humans who imitate them. *Science*, 325(5942),
15 880-883. doi:10.1126/science.1176269
- 16 Perrett, D., Harris, M. H., Mistlin, A. J., Hietanen, J. K., Benson, P. J., Bevan, R., . . .
17 Brierly, K. (1990). Social Signals Analyzed at the Single Cell Level: Someone is
18 Looking at Me, Something Moved! *International Journal of Comparative*
19 *Psychology*, 4(1).
- 20 Pfeifer, J. H., Iacoboni, M., Mazziotta, J. C., & Dapretto, M. (2008). Mirroring others'
21 emotions relates to empathy and interpersonal competence in children.
22 *Neuroimage*, 39(4), 2076-2085. doi:10.1016/j.neuroimage.2007.10.032
- 23 Pope, S. M., Russell, J. L., & Hopkins, W. D. (2015). The association between imitation
24 recognition and socio-communicative competencies in chimpanzees (*Pan*
25 *troglodytes*). *Front Psychol*, 6, 188. doi:10.3389/fpsyg.2015.00188
- 26 Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annu Rev Neurosci*,
27 27, 169-192. doi:10.1146/annurev.neuro.27.070203.144230
- 28 Rizzolatti, G., & Fogassi, L. (2014). The mirror mechanism: recent findings and
29 perspectives. *Philos Trans R Soc Lond B Biol Sci*, 369(1644), 20130420.
30 doi:10.1098/rstb.2013.0420
- 31 Rizzolatti, G., Fogassi, L., & Gallese, V. (2002). Motor and cognitive functions of the
32 ventral premotor cortex. *Current Opinion in Neurobiology*, 12, 149-154.
- 33 Schenker, N. M., Buxhoeveden, D. P., Blackmon, W. L., Amunts, K., Zilles, K., &
34 Semendeferi, K. (2008). A comparative quantitative analysis of
35 cytoarchitecture and minicolumnar organization in Broca's area in humans
36 and great apes. *The Journal of Comparative Neurology*, 510(1), 117-128.
37 doi:10.1002/cne.21792
- 38 Schlegel, A. A., Rudelson, J. J., & Peter, U. T. (2012). White matter structure changes
39 as adults learn a second language. *Journal of Cognitive Neuroscience*, 24(8),
40 1664-1670.
- 41 Scholz, J., Klein, M. C., Behrens, T. E., & Johansen-Berg, H. (2009). Training induces
42 changes in white-matter architecture. *Nat Neurosci*, 12(11), 1370-1371.
43 doi:10.1038/nn.2412
- 44 Schulte-Ruther, M., Markowitsch, H. J., Fink, G. R., & Piefke, M. (2007). Mirror Neuron
45 and Theory of Mind Mechanisms Involved in Face-to-Face Interactions: A

- 1 Functional Magnetic Resonance Imaging Approach to Empathy. *Journal of*
2 *Cognitive Neuroscience*, 19(8), 1354-1372.
- 3 Sherwood, C. C., Broadfield, D. C., Holloway, R. L., Gannon, P. J., & Hof, P. R. (2003).
4 Variability of Broca's area homologue in African great apes: Implications for
5 language evolution. *The Anatomical Record*, 271A(2), 276-285.
6 doi:10.1002/ar.a.10046
- 7 Subiaul, F., Cantlon, J. F., Holloway, R. L., & Terrace, H. S. (2004). Cognitive imitation
8 in rhesus macaques. *Science*, 305(5682), 407-410.
9 doi:10.1126/science.1099136
- 10 Tagliatalata, J. P., Russell, J. L., Schaeffer, J. A., & Hopkins, W. D. (2008).
11 Communicative signaling activates 'Broca's' homolog in chimpanzees. *Curr*
12 *Biol*, 18(5), 343-348. doi:10.1016/j.cub.2008.01.049
- 13 Tennie, C., Call, J., & Tomasello, M. (2006). Push or Pull: Imitation vs. Emulation in
14 Great Apes and Human Children. *Ethology*, 112(12), 1159-1169.
15 doi:10.1111/j.1439-0310.2006.01269.x
- 16 Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the
17 evolution of cumulative culture. *Philos Trans R Soc Lond B Biol Sci*, 364(1528),
18 2405-2415. doi:10.1098/rstb.2009.0052
- 19 Tennie, C., Call, J., & Tomasello, M. (2012). Untrained chimpanzees (*Pan troglodytes*
20 *schweinfurthii*) fail to imitate novel actions. *PLoS One*, 7(8), e41548.
21 doi:10.1371/journal.pone.0041548
- 22 Thorndike, E. L. (1898). Animal Intelligence: an experimental study of the
23 associative processes in animals. . *The Psychological Review: Monograph*
24 *Supplements*, 2(4), i.
- 25 Tomasello, M. (1996). Do apes ape? In C. M. Heyes & B. G. Galef (Eds.), *Social*
26 *Learning in Animals: The Roots of Culture* (Vol. 319-346). London: Academic
27 Press.
- 28 Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and*
29 *Brain Sciences*, 16, 495-552.
- 30 Visalberghi, E., & Frigaszy, D. (2002). "Do Monkeys Ape?" - Ten Years After. In K.
31 Daughernhahn & C. L. Nehavniv (Eds.), *Imitation in Animals and Artifacts*.
32 (pp. 471-499). Cambridge (MA): MIT Press.
- 33 Whiten, A. (2017). Social Learning and Culture in Child and Chimpanzee. *Annual*
34 *Review of Psychology*, 68, 129-154.
- 35 Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation,
36 imitation, over-imitation and the scope of culture for child and chimpanzee.
37 *Philos Trans R Soc Lond B Biol Sci*, 364(1528), 2417-2428.
38 doi:10.1098/rstb.2009.0069
- 39 Williams, J. H., Nicolson, A. T., Clephan, K. J., de Grauw, H., & Perrett, D. I. (2013). A
40 novel method testing the ability to imitate composite emotional expressions
41 reveals an association with empathy. *PLoS One*, 8(4), e61941.
42 doi:10.1371/journal.pone.0061941
- 43 Zatorre, R. J., Fields, R. D., & Johansen-Berg, H. (2012). Plasticity in gray and white:
44 neuroimaging changes in brain structure during learning. . *Nature*
45 *neuroscience*, 15(4), 528-536.
- 46