



Effects of primatological training on anthropomorphic valuations of emotions



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ABSTRACT

Anthropomorphism implies the attribution of human like emotions and cognition to non-human animals. This tendency may be conditioned by similar morphologies between mammals and is particularly important in primatology. Some neurocognitive findings suggest that prefrontal brain activity associated to conceptual learning influences anthropomorphic judgments, nevertheless, individual differences are also presented indicating that training on primate behavior may influence anthropomorphism. We identified and interpreted brain activity registered by functional magnetic resonance imaging while seven trained primatologists (39.42 ± 10.86 yr.) inferred emotions in human primates, non-human primates and non-primate animals; comparisons were made with seven matched scholars with no primatological training (38.71 ± 9.34 yr.). Primatologists manifested cerebellar, occipital and frontal activity related to sensory and motor processes when valuating humans and non-human primates, but not for other animals. So, primatological training and experience may elicit brain plasticity processes allowing inner motor and sensory models through frontal and cerebellar interactions.

1. Introduction

Anthropomorphism implies the attribution of human like emotions and cognition to other animals. This tendency discussed since Darwin's animal's emotions proposal involves complex human cognitive properties permitting the inference of other's psychological states (Kiley-Worthington, 2017). Contemporary neurocognitive approaches to study anthropomorphism has been developed over the years; a more anthropomorphic thinking is correlated to a larger gray matter volume in the left temporo-parietal brain region involved in mentalizing (Cullen et al., 2014). Also, the recognition of humans, non-human primates, and dogs' emotions involves the activation of the prefrontal brain region cognitively associated to causal explanations, but the degree of this activation varies according to the individuals' beliefs about the non-human animals' mental abilities (Spunt et al., 2017).

Anthropomorphic attributions have been suggested as a consequence of similarities between human and non-human animals' morphologies, which may influence the accuracy to interpret complex behaviors and cognition in non-human primates and involves methodological discussions in ethology, anthropology, evolutionary psychology, conservation, or philosophy of mind (Chan, 2012; Kiley-

Worthington, 2017; Spunt et al., 2017). Emotions are particularly important in the anthropomorphic discussion since they are used as social cues to be interpreted (Spunt et al., 2016) based on occipital, parietal, frontal and cerebellar brain functions allowing inner models throughout sensory and motor processes to interpret own and others' expressions (Fusar-Poli et al., 2009).

In this study we aimed to identify and interpret the neurofunctional correlates while trained primatologists infer emotions in human primates, non-human primates and non-primate animals, and to compare these functions with non-trained individuals. We expected frontal, occipital and cerebellar brain activity related to visual, motor and conceptual inferences when primatologists infer non-human primates' emotions.

2. Method

2.1. Participants and task

Seven academic specialists on primate behavior trained during at least eight years (3 women, mean age = 39.42 ± 10.86 yr.) and seven biomedical researchers with no primate behavior training (4 women,

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Table 1
Empathic dimensions evaluated in the Interpersonal Reactivity Index.

Empathic dimensions	Primatologist		Control	
	M ± S.D.	Median	M ± S.D.	Median
Perspective Taking	16.85 ± 5.52	16	15.14 ± 4.09	16
Fantasy	16.14 ± 7.84	14	10.71 ± 3.63	10
Empathic Concern	21.14 ± 5.61	22	19.28 ± 4.53	20
Personal Distress	8.85 ± 2.03	8	13.14 ± 4.59	14

Note: No statistical differences between groups were observed when the Kruskal-Wallis test was applied.

Table 2
Non-human primate species represented in the pictures used for the experimental design.

	Common name	Species
New world primates	Black-handed spider monkey	<i>Ateles geoffroyi</i>
	Black-headed spider monkey	<i>Ateles fusciceps</i>
	Mantled howler monkey	<i>Alouatta palliata</i>
	Black howler monkey	<i>Alouatta caraya</i>
	White-headed capuchin	<i>Cebus capucinus</i>
	Kaapori capuchin	<i>Cebus kaapori</i>
	Red uacari	<i>Cacajao calvus</i>
	Old world primates	Rhesus macaque
Arunachal macaque		<i>Macaca munzala</i>
Tonkin snub-nosed monkey		<i>Rhinopithecus avunculus</i>
Vervet monkey		<i>Chlorocebus pygerythrus</i>
African green monkey		<i>Chlorocebus aethiops</i>
Putty-nosed monkey		<i>Cercopithecus nictitans</i>
Mandrill		<i>Mandrillus sphinx</i>
Hamadryas baboon		<i>Papio hamadryas</i>
Lar gibbon		<i>Hyllobates lar</i>
Chimpanzee		<i>Pan troglodytes</i>
Bonobo		<i>Pan paniscus</i>
Bornean orangutan		<i>Pongo pygmaeus</i>
Sumatran orangutan		<i>Pongo abelii</i>
Western lowland gorilla		<i>Gorilla gorilla gorilla</i>

mean age = 38.71 ± 9.34 yr.) were recruited. Participants were right-handed and had a good mental health as verified by a neuropsychiatric interview. Since empathy may influence the brain function related to inferring others' emotions (Banissy et al., 2012), the Interpersonal Reactivity Index (Pérez-Albéniz et al., 2003) was applied to verify similar empathic attitudes in both groups (see Table 1). All the participants were pet owners (dogs and/or cats) and all of them signed an informed consent. The protocol was conducted in accordance with the Declaration of Helsinki and was approved by the Bioethics Committee of the Neurobiology Institute, Universidad Nacional Autónoma de México.

The functional MRI session consisted of three series alternating pictures in a block designed task implemented in the E-prime 2.0 software (e-Prime Psychology software tools, inc. Pittsburgh, Pa). Series 1 alternated four blocks of human faces and four blocks of non-human primate faces; Series 2 alternated four blocks of non-human primate faces and four blocks of non-primate animal faces; Series 3 alternated four blocks of non-primate animals faces and four blocks of human faces. Also, each series alternated four blocks of scattered faces to avoid the influence of non-face elements.

Only to control attention and induce others' emotions inferences, participants were instructed to watch each picture and to press a button using a ResponseGrip (Nordic Neurolab Bergen, Norway) when they considered the picture represented happiness.

Each block comprised 10 pictures representing the same kind of stimuli (humans, non-human primates, non-primate animals, or scattered faces) and each picture was projected during 2 s allowing a total of 40 same-kind stimuli per block. A fixation cross with 1 s duration was projected after each picture to permit the motor response indicating the inference about the projected face's emotion made by the participant.

Table 3
Non-primate animal species represented in the pictures used for the experimental design.

	Common name	Species
Mammals	Porcupine	<i>Coendou prehensilis</i>
	Polar bear	<i>Ursus maritimus</i>
	Grizzly bear	<i>Ursus arctos horribilis</i>
	Giant panda	<i>Ailuropoda melanoleuca</i>
	Red panda	<i>Ailurus fulgens</i>
	Koala	<i>Phascolarctos cinereus</i>
	Wild pig	<i>Sus scrofa</i>
	White rhinoceros	<i>Ceratotherium simum</i>
	African elephant	<i>Loxodonta africana</i>
	Indian elephant	<i>Elephas maximus indicus</i>
	Camel	<i>Camelus dromedarius</i>
	Cow	<i>Bos primigenius taurus</i>
	Donkey	<i>Equus africanus asinus</i>
	Horse	<i>Equus ferus caballus</i>
	Sheep	<i>Ovis aries</i>
	Elk	<i>Alces alces</i>
	Chipmunk	<i>Sciurus vulgaris</i>
	Rabbit	<i>Oryctolagus cuniculus cuniculus</i>
	Weasel	<i>Mustela nivalis nivalis</i>
	Cat	<i>Felis silvestris catus</i>
	Leopard	<i>Panthera pardus pardus</i>
	Bengal tiger	<i>Panthera tigris tigris</i>
	Wolf	<i>Canis lupus lupus</i>
	Dog	<i>Canis lupus familiaris</i>
	Dolphin	<i>Delphinus delphis</i>
	Seal	<i>Hydrurga leptonyx</i>
	Sea cow	<i>Trichechus manatus</i>
Birds	Royal owl	<i>Bubo bubo</i>
	Red-lored parrot	<i>Amazona autumnalis</i>
	Red macaw	<i>Ara macao</i>
	Rooster	<i>Gallus gallus domesticus</i>
	Domestic duck	<i>Anas platyrhynchos domesticus</i>
	Upland goose	<i>Chloephaga picta</i>
	Mallard	<i>Anas platyrhynchos</i>
Reptiles	Iguana	<i>Iguana delicatissima</i>
	Galapagos tortoise	<i>Chelonoidis donfaustoi</i>
	Crocodile	<i>Cocodylus moreletii</i>

This experimental design permitted series with a 360 s of total duration comprising four blocks with 30 s duration each one which is regularly used to detect BOLD signals and to perform reliably statistical contrasts between cognitive conditions. Also, we consider 2 s as enough time to watch each picture considering previous designs to evaluate emotions reported by our group (p.e. Mercadillo et al., 2011) as well as by reports focused on anthropomorphic valuations (e.g. Chaminade et al., 2007; Spunt et al., 2016).

To neutralize the effect of the finger movements over motor brain functions, we counterbalanced the experimental design so, four participants in each group (primatologist and control group) used their right index finger while the rest used the left one to indicate their emotional inferences. As well, to avoid the effect of mere visual stimulation over the primary occipital cortex, the scrambled pictures were edited with the same intensity and gray color than the pictures representing faces.

Human pictures represented 20 female and 20 male faces; non-human primate pictures represented seven new world primates and 14 old world primates species (see Table 2); non-primate animals represented 27 terrestrial or marine mammals, seven birds, and three reptiles species (see Table 3).

2.2. Brain images acquisition and analysis

Brain images were acquired in a 3 T Discovery MR750 GE MRI scanner (General Electric Company USA), with a 32-channel head coil, at the Resonance Magnetic Unit, Institute of Neurobiology, Universidad Nacional Autónoma de México. Anatomical high-resolution images were acquired using a 3D SPGR (spoiled gradient sequence) protocol:

Table 4

Activated brain regions when contrasting the primatologists vs. the control group, and the control group vs. the primatologists, while watching faces of human primates, non-human primates and non-primate animals.

Brain region	Location	Lat.	B.A.	Z value	Cluster size	Coordinates		
						x	y	z
Watching humans primates vs. others								
<i>Control > Primatologists</i>								
Null								
<i>Primatologists > Control</i>								
Postcentral Gyrus	Parietal Lobe	R	3	5.10	14337	23	-28	53
Precentral Gyrus	Frontal Lobe	R	6	4.77		45	-16	63
Cerebellar Tonsil	Posterior Lob.	L	*	5.16	13585	-2	-53	-45
Culmen	Anterior Lob.	L	*	5.23	9939	-2	-56	4
Precuneus	Occipital Lobe	R	31	4.42		19	-58	29
Watching non-humans primates vs. others								
<i>Control > Primatologists</i>								
Null								
<i>Primatologists > Control</i>								
Pyramis	Posterior Lob.	R	*	8.02	8683	41	-81	-34
Inf. Semi-Lunar Lob.	Posterior Lob.	R	*	6.66		44	-81	-35
Inf. Semi-Lunar Lob.	Posterior Lob.	L	*	5.75	6844	-29	-81	-37
Inferior Occipital Gyrus	Occipital Lobe	L	18	5.27		-27	-88	-7
Middle Frontal Gyrus	Frontal Lobe	L	6	5.06	6794	-37	7	60
Superior Frontal Gyrus	Frontal Lobe	L	8	4.92		-19	36	48
Watching non-primate animals vs. others								
<i>Control > Primatologists</i>								
Inferior Frontal Gyrus	Frontal Lobe	R	45	4.01	6498	57	23	2
Precentral Gyrus	Frontal Lobe	R	44	3.75		53	13	4
Lingual Gyrus	Occipital Lobe	R	18	4.63	6102	4	-79	0
Cuneus	Occipital Lobe	R	23	4.36		12	-72	8
Lingual Gyrus	Occipital Lobe	L	18	4.3		-10	-77	-1
<i>Primatologists > Control</i>								
Null								

Notes: Results at $p < 0.05$ with the multiple comparison correction performed. L= left, R= right. Cluster size= number of voxels comprising the extended located brain region. Null= any activated brain region was identified for the contrast, suggesting that a similar function was presented for both groups.

272 slices, TR = 8.2 ms, TE = 3.2 ms, flip angle = 12°, matrix = 256 × 256 mm, with 1 × 1 × 1 mm³ resolution voxels. Functional images were acquired using a BOLD EPI-GRE (blood-oxygen level dependent echo planar imaging gradient-echo) protocol: 30–35 slices, 4-mm thick slices with zero separation, TR = 3000 ms, TE = 40 ms, flip angle = 90°, FOV = 25 cm, matrix = 64 × 64 mm, vol = 120.

Image analyses were performed with FSL (FMRIB Software Library) (Smith et al., 2004). Voxels belonging to the neck and other non-brain tissues were eliminated for each participant's series of images by using the BET software. Functional images were analyzed using the FEAT tool (FMRI Expert Analysis Tool) implemented in FSL with statistical execution based on the General Linear Model. Data pre-processing included slice-timing and motion correction, spatial smoothing with a gaussian kernel (FWHM = 6 mm) and brain extraction. For each participant, functional datasets were co-registered with their high-resolution images and these to the MNI-152 brain template (Montreal Neurological Institute anatomical brain template).

Since the two contrasted groups included seven subjects, and may not be considered to have statistical power, we acquired three independent runs per subject combined with a mixed effects subject average to strengthen the statistical results. In addition, all our fMRI data analysis included corrections for multiple comparisons. Activation maps contrasting the kind of stimuli were estimated with FSL's FILM (FMRIB's Improved Linear Model), and contrasts between groups (primatologists vs. controls) and between conditions in the primatologists group (human vs. non-human primate vs. non-primate animals faces) were estimated using FLAME (FMRIB's Local Analyses of Mixed Effects) correcting for multiple comparisons. Since each run series alternated two kind of stimuli (human or non-human primates, or non-primate animals faces) presented in other run series too, the statistical contrast

to obtain the brain functional maps associated to each kind of stimuli considered the same stimuli presented in two run series so, the statistical contrast was formally made considering 14 subjects for each contrasted group.

3. Results

Contrasted brain activity between primatologists and control subjects while watching humans, non-human primates and non-primate animals is presented in Table 4 and Fig. 1.

Brain activity identified for the primatologist group and contrasted while watching human, non-human primates and non-primate animals is presented in Table 5 and Fig. 1.

4. Discussion

Cerebellar activity was present in primatologists when their activation map was contrasted with the control group while watching both, human and non-human primates. Although the cerebellum is classically related to motor functions, some neurological proposals indicate its role in emotional regulation and other higher cognitive functions (Schmahmann, 1991) which is supported by cerebellar lesions provoking lack of affective recognition (Richter et al., 2005). Our results agree with a cerebellar role in anthropomorphic perception since its activity is reported by fMRI when performing anthropomorphic valuations of computerized-animations (Chaminade et al., 2007). Particularly, it may be necessary for emotional valuations performed by primatologists for both human and non-human primate species, since fMRI studies report cerebellar activity when evaluating the valence of human faces expressing a variety of basic emotions such as, fear,



Fig. 1. Coronal and sagittal views illustrating the activated brain regions. Superior red representing the *primatologists > control group* contrast while watching: 1. *Human faces*: A. right postcentral gyrus, B. left cerebellar tonsil, C. right cerebellar culmen and precuneus; 2. *Non-human primate faces*: A. right cerebellar pyramis, B. left posterior cerebellum and occipital cortex, C. left middle and superior frontal cortex. Superior blue representing the *control group > primatologists* contrast while watching: 3. *Non-primate animals*: A. right inferior frontal gyrus, B. right and left lingual gyrus and cuneus. Inferior figure representing the brain activation for *primatologists only* while contrasting watching *human > non-human primates* faces (yellow): right medial frontal gyrus; watching *non-human primates > human* faces (blue): left lingual gyrus and right middle occipital cortex; watching *non-human primates > non-primates animals* faces (green): left cuneus, right cerebellar uvula, and bilateral lingual gyrus.

happiness, anger, neutral expressions (Fusar-Poli et al., 2009), empathy (Nomi et al., 2008) or even social emotions (Mercadillo et al., 2011).

Activity in the precuneus was observed in primatologists when contrasted with the control group while watching human faces. The function of this brain region is related to self-references of own body representations, and its joint activation with the cerebellum suggests attentional processes to bodily experiences related to sensory representations may be restricted for human valuations (Soon et al., 2008). Conversely, primatologists presented frontal activation in pre-motor and supplementary motor related regions (BA 6 and 8) associated with integrative functions required for complex and coordinated movements. Since motor activations provoked by the finger movement was neutralized in the experimental design, this cortical activity may

imply imaginary processes involving attention to sensory and motor experiences, as previously reported while incited attention and imagery body members (Bauer et al., 2014).

Different than primatologists, the control group manifested activity in the frontal cortex, lingual gyrus and cuneus when watching non-primate animals. This activity agrees with previous reports indicating anthropomorphic judgments and visual analysis when people with no training in animal behavior watch animated movements (Chaminade et al., 2007) or non-human animals (Cullen et al., 2014).

So, primatologists may implement fine motor and sensory processes through a network comprising cerebellar, sensory and motor cortical functions to carefully infer only primate (human and non-humans) emotional expressions, but a biological bias indicated by the precuneus

Table 5

Activated brain regions for only the primatologists group identified when contrasting the three conditions: human primates, non-human primates and non-primate animals faces.

Brain region	Location	Lat.	B.A.	Z value	Cluster size	Coordinates		
						x	y	z
<i>Human primates > Non-human primates</i>								
Medial Frontal Gyrus	Frontal Lobe	R	6	3.79	16390	9	-22	48
<i>Non-human primates > Human primates</i>								
Middle Occipital Gyrus	Occipital Lobe	R	18	8.99	60149	32	-82	4
Lingual Gyrus	Occipital Lobe	L	17	7.49		-15	-93	-1
<i>Human primates > Non-primate animals</i>								
Null								
<i>Non-primate animals > Human primates</i>								
Null								
<i>Non-human primates > Non-primate animals</i>								
Cuneus	Occipital Lobe	L	17	5.02	11779	-14	-95	-1
Lingual Gyrus	Occipital Lobe	R	18	4.80		3	-85	-13
Lingual Gyrus	Occipital Lobe	L	17	4.77		-15	-93	-1
Uvula	Posterior Lobe	R	*	4.74		27	-74	-26
<i>Non-primate animals > Non-human primates</i>								
Null								

Notes: Results at $p < 0.05$ with the multiple comparison correction performed. L= left, R= right. Cluster size= number of voxels comprising the extended located brain region. Null= any activated brain region was identified for the contrast, suggesting that a similar brain function is presented for both conditions.

may be presented when watching humans (Chaminade et al., 2007).

Analysis performed for only the primatologist group identified activity in motor cortical regions related to interpret own and others' actions (Brodmann area 6) (Chaminade et al., 2007) when contrasting humans vs. non-human primates, but not when contrasting humans vs. non-primate animals. Also, when contrasting non-human vs. human primates, activation was observed in the lingual gyrus and the occipital association cortex suggesting a more accurate visual analysis of emotions (Fusar-Poli et al., 2009; Mercadillo et al., 2011). These results may suggest that the influence of training over primatologists is presented for primate species but not for other non-primate animals.

In addition, no activation was identified when contrasting non-primate animals vs. humans and non-human primates, implying that the brain function required to process non-primate animals is also used to process primates (humans and non-human). In this sense, it is interesting that we did not identify contrasting activation of the amygdala, typically related to emotional inferences, this may be due to the fact that our results show contrasts of the same task between groups, i.e. infer emotion while watching human, non-human primates and non-primate animals. A similar rationale can be applied to the temporoparietal brain junction related to mentalizing and theory of mind required to infer others' emotional states (Saxe and Wexler, 2005) because these processes may be required for any kind of animal stimuli.

5. Conclusions

Results supported our hypothesis about that primatologists perform sensory and motor processes based on frontal, occipital and cerebellar functions to infer emotions in non-human primates. The differences with the control group may suggest that training and experience influences the anthropomorphic attributions of primatologists, possibly allowing more accurate interpretations of emotional expressions of primates, but not of other animals. Also, agree with proposals indicating that emotional attributions are not only made by conceptual learning but by sensory and motor learning and practices (Spunt et al., 2016). So, the influence of training and experience may be considered as a brain plasticity process which allows the generation of inner motor and sensory models through frontal and cerebellar interactions (Di Pino et al., 2014) which require imagined movements guided by learned information (Bennett and Hacker, 2005).

Future designs with larger samples are necessary to elucidate the influence of similar morphologies between species (Kiley-Worthington, 2017) to identify networks of brain activity to infer emotions to be useful for the elaboration of more accurate ethological methodologies and discussions about animal mind. Also, the category of the species such as, domestic, in danger or popular, could be considered since this cultural issue may influence anthropomorphic judgments used for biological conservation (Chan, 2012).

Declarations of interest

None.

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