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Brain Functional Asymmetry of Chimpanzees (Pan troglodytes): the Example of Auditory Laterality

Abstract*: The aim of this study was to verify whether chimpanzees (*Pan troglodytes*) demonstrate an auditory laterality during the orientation reaction, and which hemisphere is responsible for processing the emotional stimuli and which for the species-specific vocalizations.*
The study involved nine chimpanzees from the Warsaw Municipal Zoological Garden. They were tested individually in their bedrooms. Chimpanzees approached a tube filled with food, located in the centre of the cage. Randomly selected sounds were played from the speakers when the subject was focused on getting food. Individual reactions were observed and outcomes reported. The four types of sound used: thunderstorm, dog barking, chimpanzee vocalization and a zoo-keeper's voice.
To test whether chimpanzees demonstrate auditory laterality we used a single sample X^2 test. The existence of auditory laterality has been confirmed. The sound of the storm caused the orientation reaction to the left, while chimpanzee vocalization – to the right. On this basis we can conclude that among chimpanzees, arousing stimuli are being processed by the right hemisphere, and species-specific vocalizations by the left. However, the set of stimuli was limited so the study did not unequivocally resolve this issue.

Key words*: auditory laterality, chimpanzee behaviour, functional asymmetry, lateralization, orientation reaction*

Introduction

Functional cerebral asymmetry (also called lateralization) is a division of functions between two hemispheres. It has been known for years that various forms of lateralization are characteristic of a wide range of representatives from the animal kingdom, and that it developed very early in evolution (Vallortigara et al., 2011; Rogers et al., 2013).

However, many years have passed between the discovery of this phenomenon in humans (control of speech) and the first attempts to examine the functional asymmetry in animals. It was associated with the belief that functional cerebral lateralization is a feature represented only by mankind (Rogers, 1989). Currently, studies of functional asymmetry are conducted on a number of animal species, from invertebrates (Byrne et al., 2006a, 2006b) to non-human primates (Chapelin & Blois-Heulin, 2009).

Lateralization is a very useful phenomenon for any organism. One of the most popular concepts, explaining the reasons for lateralization's development, says that thanks to it, the organism avoids the increased load of neural circuits performing the same function (Levy, 1977), and also prevents interference associated with the overlapping of different functions. In the case of fish, whose eyes are placed laterally, the dominance of one cerebral hemisphere prevents simultaneous initiation of contradictory reactions in the organism (Vallortigara, 2000).

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There are a few different types of lateralization based on its function and the sense it represents. In our paper, we propose classification which includes motor, visual, chemical (olfactory) and – the subject of this publication – auditory laterality. We have chosen to examine auditory laterality as, until now, it has been one of the least studied types of functional asymmetry of the brain. Moreover, the results obtained in previous studies of auditory laterality are not consistent, which means that this phenomenon requires a much more intensive analysis.

Broca's and Wernicke's conclusions, that the left hemisphere specializes in the perception and production of speech, have been confirmed by numerous psychophysiological studies and neuroimaging. Research has also found neuroanatomical equivalents of Broca's and Wernicke's areas in primates' brains (Cantalupo & Hopkins, 2001). Vocal production control seems to be the task of the left hemisphere in primates, birds and anurans. Among a large amount of animal species, left brain dominance is also responsible for the reception of sounds related to communication (Boye et al., 2005).

In one experiment on auditory laterality, auditory stimuli were randomly played to the left or right ear of Japanese macaques (*Macaca fuscata*) and other related species (vervets, pig-tailed macaques and Indian macaques). The monkeys showed auditory laterality in response to vocalizations of their own species (left hempishere processing), however, they did not demonstrate lateralization in response to vocalizations of other (closely related) species (Beecher et al., 1979).

The auditory laterality is most often examined with an orientation reaction occurring after the sound. Hence, it is necessary to observe which way the animal's head turns. This direction is considered to be dominant to a particular class of stimuli, which is processed by the opposite hemisphere.

Our study was designed to test chimpanzees' auditory laterality in the research paradigm described above. In addition, assuming the existence of lateralization in chimpanzees, we wanted to determine which hemisphere is responsible for the processing of emotional stimuli, and which for the processing of species-specific vocalizations. Emotional stimuli have high relevance for the survival and well-being of the animal. Some of them could signal threats, for example the approach of a predator and others the opportunity to mate or obtain food. These stimuli require rapid responses – for example approaching the positive stimulus. The choice of emotional stimuli was made on the basis of previous studies undertaken by both ourselves and other researchers. We assumed that the sound of a storm and a dog barking would be appropriate emotional stimuli. The two others stimuli were semantic (chimpanzee's vocalization and human speech).

Method

Animals

The study was conducted on nine chimpanzees from the Warsaw Municipal Zoological Garden – six females and three males, aged 10–49 years (Hannah – 20, Judy – 49, Kimberly – 24, Liza – 12, Lucy – 10, Mandy – 19, Patrick – 16, Simon – 28, Zamo – 16). Chimpanzees live in groups with a varying composition of individuals created by zoo staff. They have at their disposal the use of an external enclosure (400 m^2), fenced by a moat, internal enclosure and rooms that serve as bedrooms (220 m^2 in total). There are high wooden structures with shelves, fire-hoses and ropes to climb in enclosures. Chimpanzees receive a food enrichment (termitary, fine-grained food, or food closed in containers), and the enrichment of a different nature, for example: blankets, toys, building blocks, shovels, etc.

Research on chimpanzees, that live in Warsaw Municipal Garden – need no approval from the ethical committee in our country (Poland) – the study was conducted only by zoo-keepers, who know the animals and their habits. Thus, this study was not evaluated by an ethical committee at any point. Chimpanzees took part in experiments only as volunteers. What is more – we think that it was a nice experience for them, because it broke routine in some way, and they got some reward for the participation. During the experiment, chimpanzees were exposed to light of 158 lux.

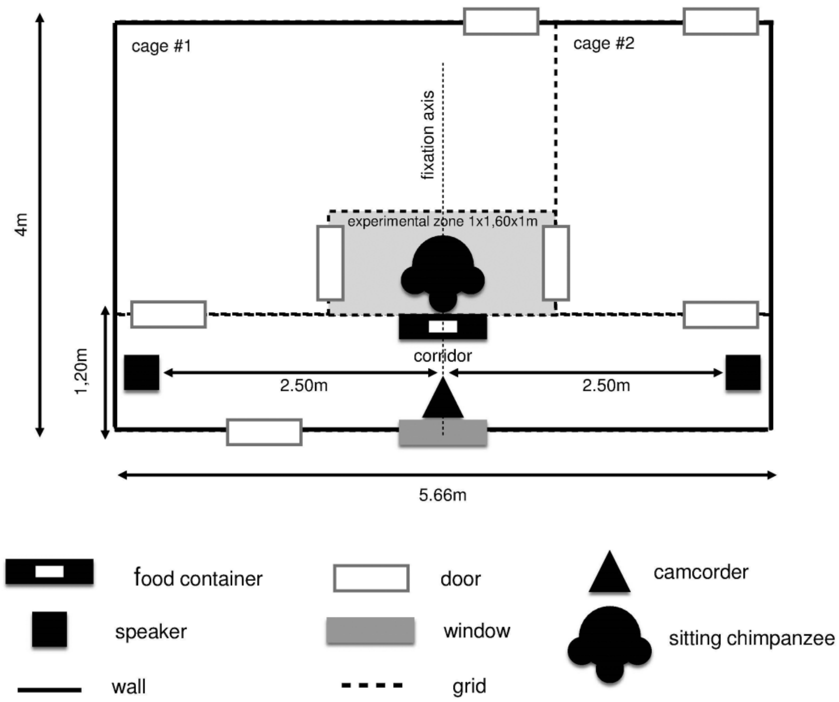
Apparatus and stimuli

The study took place in the chimpanzees' bedrooms (5 m × 4 m × 4 m). The research area (1 m × 2 m × 1 m) was located in the central part of the bedroom where there was a tube filled with food. On both sides of the chimpanzee, at an equal distance (2.5 m) two loudspeakers were located. The study was recorded on a camcorder, placed in front of the examined subject (fig. 1). Chimpanzees in our experiment heard four types of sounds: thunderstorm, dog barking, chimpanzee vocalization and a zoo-keeper's voice (saying a word that they had often heard – "target"). Dog barking from our experiment had been recorded in a situation when a dog heard a knock at the door. Thus, taking into account subtypes based on context, it belongs to the "disturbance" group (Yin & McCowan, 2004). Chimpanzee vocalization came from the zoo's database for educational purposes – it was a greeting vocalization. All sound were of the same intensity – up to 60 dB (measured at the chimp's position). They were original records, not filtered or edited. We used only 4 elements – it was impossible to implement more auditory stimuli because of the rapid habituation to these sounds. All chimpanzees listened to the same records.

Procedure

The subjects were examined individually. Randomly selected sounds were played from the speakers when the subject approached the tube and was focused on getting food from it. Fixation on difficult to access food allowed us to control the animal position. The experimenter waited to start playbacks until sounds were played to the subject's ears at the same angle. After each sound we waited for the individual's reaction and reported the outcome – the study was also video recorded. The study of a single chimpanzee lasted from 1 minute to 5 minutes. The subject was examined until habituation, i.e. when the orientation reaction to a sound stimulus did not occur anymore. The maximum score was 10 attempts.

Figure 1



Results

To test whether chimpanzees demonstrate auditory laterality we used the VCODE program and the SPSS statistical package (version 22). Because the dependent variable – the direction of head turn – is dichotomous, we used a single sample X^2 test. We excluded one individual from the analysis (Hannah), because she did not make enough attempts to be statistically significant (she habituated too rapidly). The test results indicate that chimpanzees reacted to the sound of the storm, X^2 (1, N = 9) = 10.24; p = 0.001, and chimpanzee vocalizations, X^2 (1, N = 9) = 12.55; p = 0.001, they react to the dog barking at a random level, X^2 (1, N = 9) = 1.25; p = 0.265, and definitely ignore the zoo-keeper's voice, X^2 (1, N = 9) = 7.33; p = 0.007. We also present table with data about lateralization at the individual level (tab. 1, tab. 2). Table one shows results for the thunder sound and table two shows results for the chimpanzee vocalization. In both tables we present only statistically significant results.

Table 1. Lateralization at the individual level – for the thunder sound (only statistically significant results are presented)

Individual	X^2 (1)	p
Judy	14.29	0.01
Kimberly	19.03	0.01
Patrick	21.20	0.01
Zarno	9.88	0.01

Table 2. Lateralization at the individual level – for the chimpanzee vocalization (only statistically significant results are presented)

Individual	X^2 (1)	p
Lucy	18.93	0.01
Mandy	20.43	0.01
Patrick	10.80	0.01
Shimmy	21.20	0.01

The analysis of the direction of reaction was tested using a single sample X^2 statistic – it showed that chimpanzees turn their head significantly more often to the left side in response to the sound of the storm, X^2 (1, N = 9) = 4.26; p = 0.039, and to the right in response to the chimpanzee vocalizations, X^2 (1, N = 9) = 5.33; p = 0.021. X^2 statistics for direction of head rotation in response to dog barking and zoo-keeper voice were not statistically significant.

The charts show the percentage of orientation reaction to the left and to the right at the group (fig. 2) and individual level (fig. 3, fig. 4, fig. 5, fig. 6).

General discussion

The present study was designed to test whether chimpanzees demonstrate auditory laterality during their orientation reaction, and verify which cerebral hemisphere are responsible for the processing of emotional stimuli and species-specific vocalizations.

Figure 2

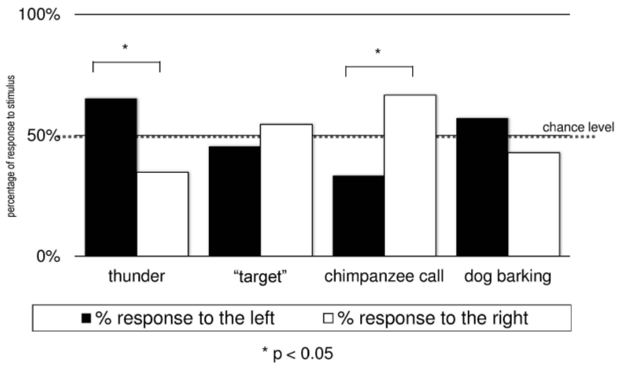


Figure 4

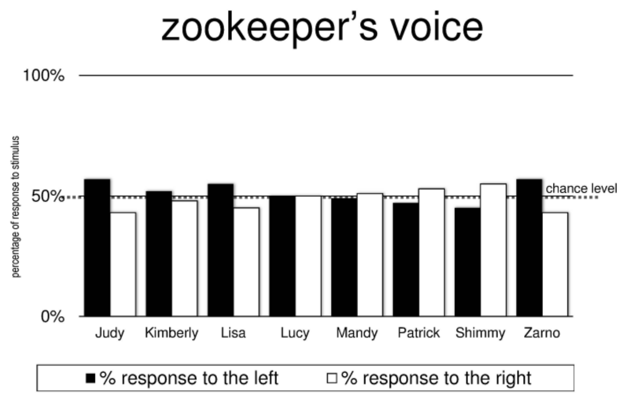


Figure 3

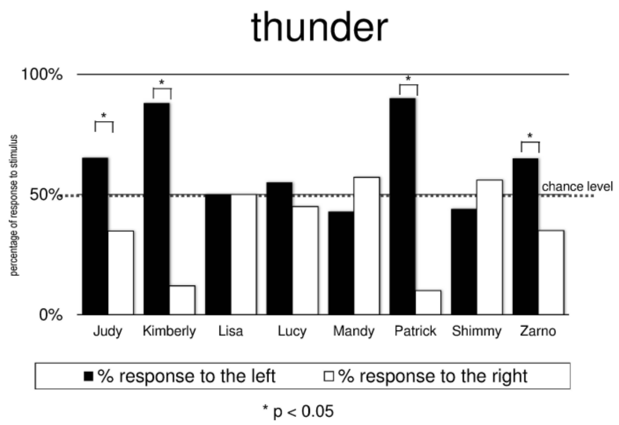


Figure 5

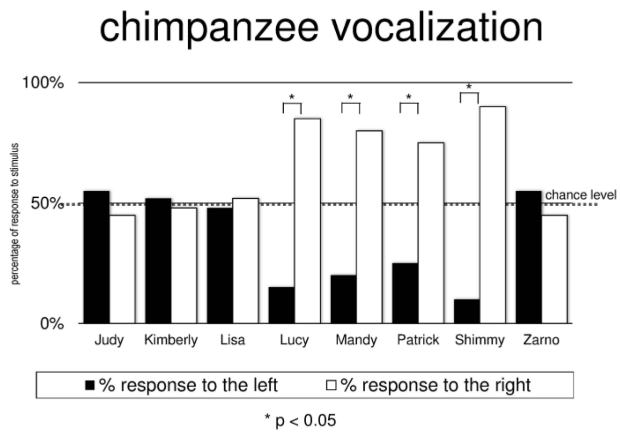
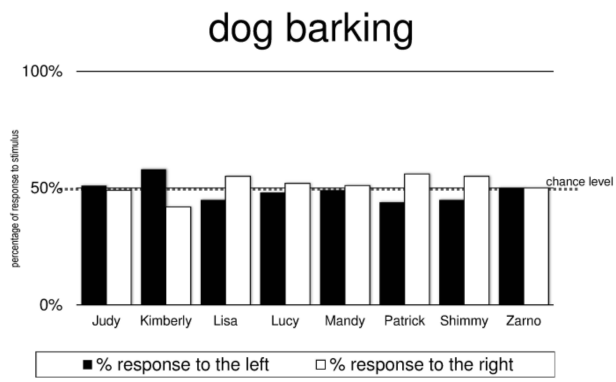


Figure 6



The experiment was based on the paradigm using the orientation reaction occurring immediately after a sound. Scheumann and Zimmermann (2008) emphasize that "a sound is played back to the subject at exactly the same angle to both ears. An unconditioned behavioural response to the sound, the head turn, and its direction is taken as an indicator for an ear and hemispheric advantage in sound perception. As the connection of one ear to the contralateral hemisphere is dominant over the ipsilateral connection, a right head turn is taken as a behavioural indicator for the dominance of the left hemisphere and vice versa".

The results of the present study may indicate that in chimpanzees arousing stimuli are being processed by the right hemisphere, and species-specific vocalizations by the left hemisphere. The examined individuals turned their head significantly more often to the left side in response to the sound of the storm, and to the right in response to chimpanzee vocalizations.

In addition, the chimpanzees ignored a dog barking and a zoo-keeper's voice. The fact that individuals were ignoring a dog barking, can be explained by the fact that it was a completely unknown stimulus for them (they could not hear a dog barking, even when they were outdoors) and the zoo-keeper's voice was taken out of context. The word "target" is used in the presence of zoo-keepers, who use it to make chimpanzees move to the target. In the experimental situation, chimps heard the word "target", but there was neither a target nor a zoo-keeper – so perhaps that is the reason why the command was ignored.

However, due to the fact that the set of stimuli was limited (only 4 sounds), the study did not unequivocally provide proof of our thesis. It was impossible to implement more auditory stimuli in this study because of the rapid habituation to these sounds. We think that further studies with different set of stimuli may resolve this issue.

The auditory laterality and processing of the sounds produced by conspecifics were the subject of many studies, often giving conflicting results. Depending on the species, the animals in these studies demonstrated the dominance of the left or right hemisphere. Thus, Japanese macaques (*Macaca fuscata*) (Petersen et al., 1978), California sea lions (*Zalophus californianus*) (Boye et al., 2005), and dogs (Siniscalchi et al., 2008), processed the stimuli associated with vocalization by the left hemisphere, while starlings (*Sturnus vulgaris*) and chimpanzees – by the right hemisphere (Basile et al., 2009).

Furthermore, there is also a study that reported no signs of auditory laterality in processing vocalizations of conspecifics (Teufel et al., 2007). The examined Barbary macaques (*Macaca Sylvanus*) did not show any side preference while listening to conspecifics' vocalizations, as well as other species' vocalizations.

Thus, if there is a consensus that emotional stimuli are being processed by the right hemisphere, we still have conflicting results in research about auditory laterality in terms of analysis and processing the species-specific vocalizations.

There might be several reasons for such discrepancies. The first possible explanation is the fact that sometimes animals in response to vocalizations turn their head to the left (and therefore they process stimuli by the right hemisphere) because the sounds elicit strong emotions (especially fear). It should be emphasized that it is extremely difficult to decide which emotions can be triggered by a sound, because first – it is necessary to know the exact meaning of the sound, and second – one should empathize with the recipient of this message.

Another reason may be the character of ethological research – they differ not only in terms of methodology, but also the number of examined individuals and conditions in which they live. However, the most important, is the fact that the methods of studying the phenomenon of laterality have not yet been standardized and depend on the experimenters' concepts. The aforementioned studies differed in the way they were conducted – in most experiments where animals processed the stimuli by the left hemisphere, indicators of lateralization were behavioral (direction the animal turns its head), while in the two studies where the results indicated the dominance of the right hemisphere, experimenters used advanced neuroimaging techniques. Moreover, in these studies the stimuli were repeated many times. Therefore there was no element of surprise, and so the reactions could be learned.

There are only a few studies that include behavioral lateralization indicators in their procedure, and indicate that species-specific vocalizations are being processed by the right hemisphere. One of them was performed on dogs and it was based on the orientation reaction paradigm. Dogs heard four types of auditory stimuli – three of them had meaning for dogs (cat meowing, dog barking, and the command "sit") and one was neutral (the word "wir" – meaning, "whirl" in Polish). As expected, the orientation reaction occurred in response to the significant stimuli. Dogs were turning their heads more often to the left when they heard the sounds of cats and other dogs, which shows the dominance of the right hemisphere when processing these stimuli (Reinholz-Trojan et al., 2012).

Here, however, one could argue that the dog barking in this experiment was a more emotional, rather than semantic stimulus. The meaning of the stimulus is not known. Additionally, vervets (*Cercopithecus aethiops*) in the experiment conducted by Gilda-Costa and Hauser (2006) turned their head to the left when they heard species-specific vocalizations (known and unknown individuals). They did not demonstrate lateralization in response to vocalizations of other primates, as well as other types of sounds. The authors of the study suggest that the functional cerebral asymmetry in terms of conspecifics vocalization processing is a common feature among primates, but its direction is very flexible.

Research on auditory laterality leave the field clear for ethologists and comparative psychologists, because apart from sex differences and influence of age on lateralization, one can examine many other aspects of functional asymmetry. One way may be by using various modifications of the species-specific vocalizations. In one study, conducted on dogs, the results suggest that temporal features are determinant auditory cues for call sound recognition (Siniscalchi et al., 2012). Recorded material might consist of known and unknown individuals' vocalization, those who have a different status in the group, with different gender and age.

In addition, vocalizations could be isolated from many different situations and have a different emotional sense. While examining the qualitative changes of audio material, it could be observed whether or not individuals demonstrate a lateralization of the same strength. One can also manipulate the emotional stimuli. In our study, chimpanzees animatedly react to the sound of the storm. It would be worth checking if they will react in the same way to the sound of a firearm (does the sound of a storm elicit such emotions because of its character, or simply because it is a loud and unexpected sound). Furthermore, chimpanzees did not react to a dog barking (which was the intended emotional stimulus) – we wonder if animals living in the zoo would react in response to vocalizations of a leopard, which is very dangerous for them in the wild.

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