

Short report

**A preliminary test on conceptual matching between silhouettes and photographs in chimpanzees (*Pan troglodytes*).**

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### **Abstract**

Chimpanzees were tested to assess whether they recognize the silhouette of their own species as representing a chimpanzee using a matching-to-sample task. Five chimpanzees were tested with four stimulus categories: chimpanzee, dog, human, and chair. Initially, they were trained on identity matching tasks (where the sample and comparison stimuli were the same) and categorical matching tasks (where the sample and comparison stimuli were different but belonged to the same category) using photographs and silhouettes. Subsequently, they received test trials in which the sample stimulus was a photograph and the comparison stimulus was a silhouette, or vice versa. The results showed that the chimpanzees performed well not only in identity matching but also in categorical matching. However, in the test trials using photographs and silhouettes, performance significantly exceeded chance levels only in the chimpanzee–chair and dog–chair pairs. Overall, they showed strong biases toward the chair stimuli for both photographs and silhouettes in the test trials. These findings did not provide strong evidence that chimpanzees recognize silhouettes of each stimulus category based on conceptual properties beyond perceptual similarity.

**Keywords:** Conceptual matching, Body perception, Silhouette, Chimpanzees, Comparative cognition

## Introduction

The body, like the face, provides crucial information for social interactions (Peelen & Downing, 2007). Research on humans has reported an inversion effect in body perception, akin to that observed for face recognition (Farah et al., 1995; Reed et al., 2003, 2006; Valentine, 1988; Yin, 1969). Furthermore, brain regions specialized for processing body-related information have also been identified (Peelen & Downing, 2007). Similarly, just as faces are important for non-human primates and are processed in a manner similar to humans (citation), studies on chimpanzees and tufted capuchin monkeys have demonstrated a body inversion effect parallel to the face inversion effect (Gao et al., 2020; Gao & Tomonaga, 2018, 2020a, b; Matsuno & Fujita, 2018).

In visual search tasks, both humans and chimpanzees have been shown to efficiently search for face stimuli among distractors (Hershler & Hochstein, 2005; Tomonaga & Imura, 2015). Tomonaga and Imura (2024) conducted visual search tasks using silhouette stimuli with chimpanzees and found that they efficiently searched for silhouettes of their own species' body compared to silhouettes from other categories, such as chairs. Furthermore, the study suggested that the spatial configuration of body parts played a critical role in this process. However, no definitive evidence of an inversion effect, an indicator of configural processing, was observed, as the inversion effect was found across all stimulus categories. Additionally, in the generalization test, the chimpanzees performed comparatively poorly with familiar human silhouettes, while they were more efficient at detecting unfamiliar quadruped silhouettes, such as those of elephants and horses. These findings suggest that, rather than recognizing the silhouettes of chimpanzees as representing their own species, chimpanzees may rely on perceptual patterns characteristic of quadrupeds.

Several methods can be considered to examine whether chimpanzees actually recognize silhouettes of their own species as representing chimpanzees. One such method is the use of matching-to-sample tests. The matching-to-sample task involves selecting a stimulus based on the correspondence between a sample stimulus presented first and a choice stimulus presented subsequently. In the context of the present study, a conceptual matching test could be designed by using stimuli from the same category that are perceptually distinct as the sample and choice stimuli. Here, 'conceptual matching' refers to matching between stimuli that are not perceptually similar but belong to the same conceptual class (Thompson & Oden, 2000; Vonk & Povinelli, 2006); for example, matching the voice of a dog to a photograph of the dog (e.g., Adachi et al., 2006, 2007). In this experiment, specifically, a body silhouette was used as the sample stimulus, while the choice stimuli consisted of a face from the same species and a face from a different species, to examine whether the chimpanzees could select the corresponding species' face.

This short report presents the results of a conceptual matching test conducted on the chimpanzees that demonstrated efficient search for silhouettes of their own species in the visual search tasks. Using silhouette stimuli, the study aimed to investigate whether the chimpanzees could conceptually match stimuli from the same category, providing further insight into their cognitive processing of body-related information.

## Methods

## Participants

Five chimpanzees (*Pan troglodytes*) participated in the present study: Ai (female, 31 years old at the onset of the study, Great Ape Information Network (GAIN; <https://shigen.nig.ac.jp/gain/>), ID#0434), Chloe (female, 26 years old, #0441), Cleo (female, 7 years old, #0609; see Figure 2), Pan (female, 23 years old, #0440), and Pendesa (female, 30 years old, #0095). In the preceding visual search tasks, seven chimpanzees, including the five in the current study, participated (Tomonaga & Imura, 2025). However, due to scheduling constraints with other ongoing studies, two chimpanzees did not take part in the present experiment. The chimpanzees had previously participated in various computer-controlled perceptual and cognitive experiments, including visual search and matching-to-sample tasks (Matsuzawa et al., 2006; Tomonaga, 2001, 2010; Tomonaga et al., 2003; cf. Kawaguchi et al., 2020; Ueda & Tomonaga, 2024; Wilson & Tomonaga, 2018). All chimpanzees were housed as part of a social group consisting of 14 individuals in indoor and outdoor enclosures (770 m<sup>2</sup>) at the Primate Research Institute, Kyoto University (Matsuzawa, 2006). No food or water deprivation was imposed during the study.

## Ethics statements

The care and use of the chimpanzees followed the 2nd edition of *the Guide for the Care and Use of Laboratory Primates* provided by the institute. The experimental protocols for the chimpanzee study were approved by the institute's Animal Welfare and Animal Care Committee (2010-031). All procedures also complied with *the Guidelines for Animal Experimentation* of the Japanese Society of Animal Psychology, *the Guidelines for the Care and Experimental Use of Captive Primates* by the Primate Society of Japan, *the Code of Ethics and Conduct* of the Japanese Psychological Association, and the Japanese *Act on Welfare and Management of Animals*.

## Experimental setting

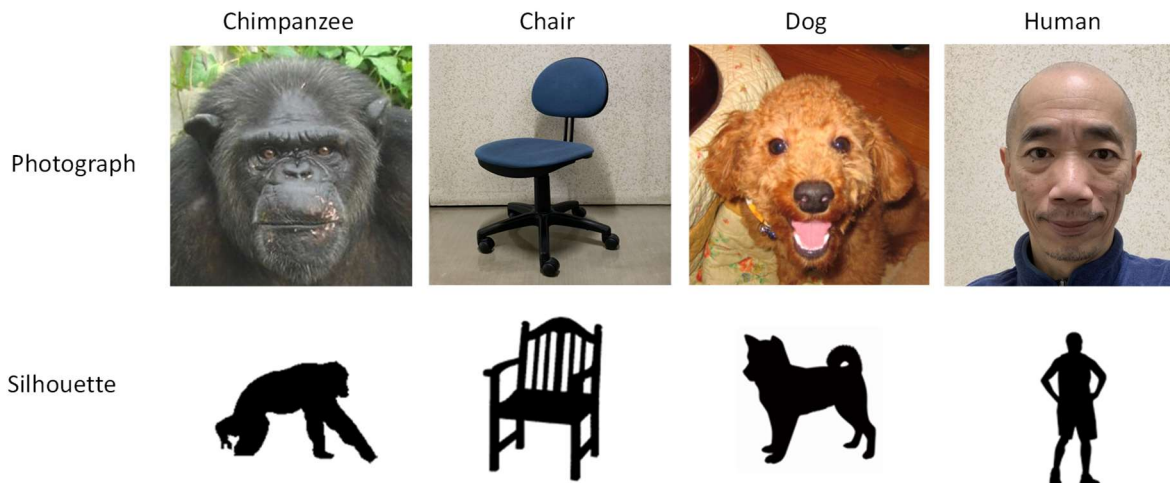
All experimental sessions were conducted in a booth measuring 1.8 m (W) × 2.15 m (L) × 1.75 m (H), located within a laboratory adjacent to the chimpanzee housing facility. The chimpanzees accessed the booth via an overhead passageway connecting the housing area to the experimental booth. Two 17-inch LCD monitors (I-O Data LCD-AD172F2-T, resolution: 1280 × 1024 pixels; pixel size: 0.264 mm × 0.264 mm) equipped with touch panels were mounted on the booth wall. The monitors were positioned at a viewing distance of approximately 40 cm. Food rewards (small apple pieces) were dispensed by a universal feeder (Biomedica BUF-310) situated outside the booth. All equipment and experimental procedures were controlled by a computer system.

## Stimuli

In the present study, two types of stimuli were used: black silhouette stimuli on a white background and color photographs (Figure 1). Four stimulus categories were prepared for each stimulus type: chimpanzee, dog, chair, and human. Among these, the categories of chimpanzee and chair were those previously used in visual search experiments, the human category was used in a generalization test, and the dog category was

Figure 1. Examples of stimulus categories in this study.

Note that the human face photograph shown in Figures 1 and 2 is of the author, and the author has agreed to its use.



included in the quadruped category. Each stimulus measured  $150 \times 150$  pixels in size. For each category and stimulus type, 20 unique stimuli were prepared. The silhouette stimuli depicted the overall shape of each category, while the photographic stimuli differed by category: for the chimpanzee, human, and dog categories, close-up photographs of faces were used, whereas for the chair category, photographs of the entire chair were employed. Consequently, the silhouette and photographic stimuli for chairs were perceptually similar to each other compared to those in the other categories.

The present study incorporated four types of baseline trials that combined silhouette and photographic stimuli. Figure 2 shows some examples of these trial types. These included: (1) PP-ID trials, where both the sample stimulus and the correct choice stimulus were identical photographs; (2) SS-ID trials, where both the sample stimulus and the correct choice stimulus were identical silhouettes; (3) PP-cat trials, where the sample stimulus and the correct choice stimulus were both photographs from the same perceptual category but depicted different images; and (4) SS-cat trials, where the sample stimulus and the correct choice stimulus were silhouettes with the same perceptual categorical relationship. In addition to these baseline trials, two types of test trials were prepared: (1) PS trials, where the sample stimulus was a photograph and the choice stimuli were silhouettes, and (2) SP trials, where the sample stimulus was a silhouette and the choice stimuli were photographs (Figure 2).

Additionally, six category pairs were prepared from the four stimulus categories.

## Procedure

**Matching-to-sample task.** Figure 3 illustrates the typical procedure of a matching-to-sample trial. Following a 2-second intertrial interval, a blue square (100 x 100 pixels) serving as a warning signal (WS) appeared at a random position near the bottom of the screen. When the chimpanzees touched the WS twice, a sample stimulus

Figure 2. Examples of baseline and test trial types for Chimpanzee–Human pair.

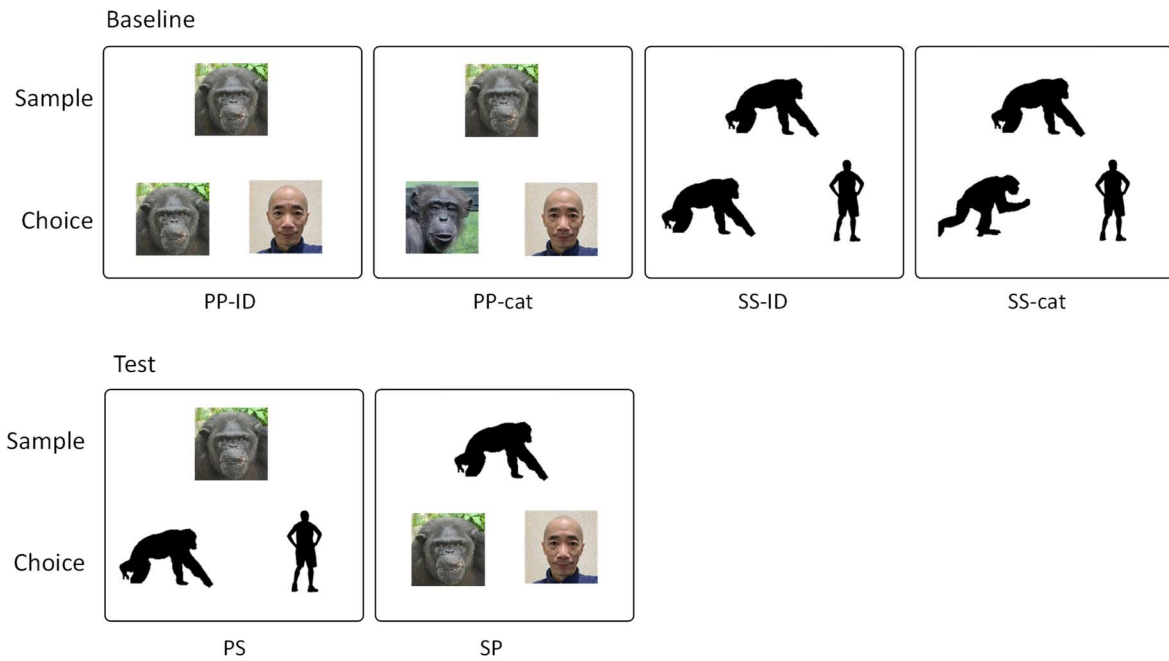
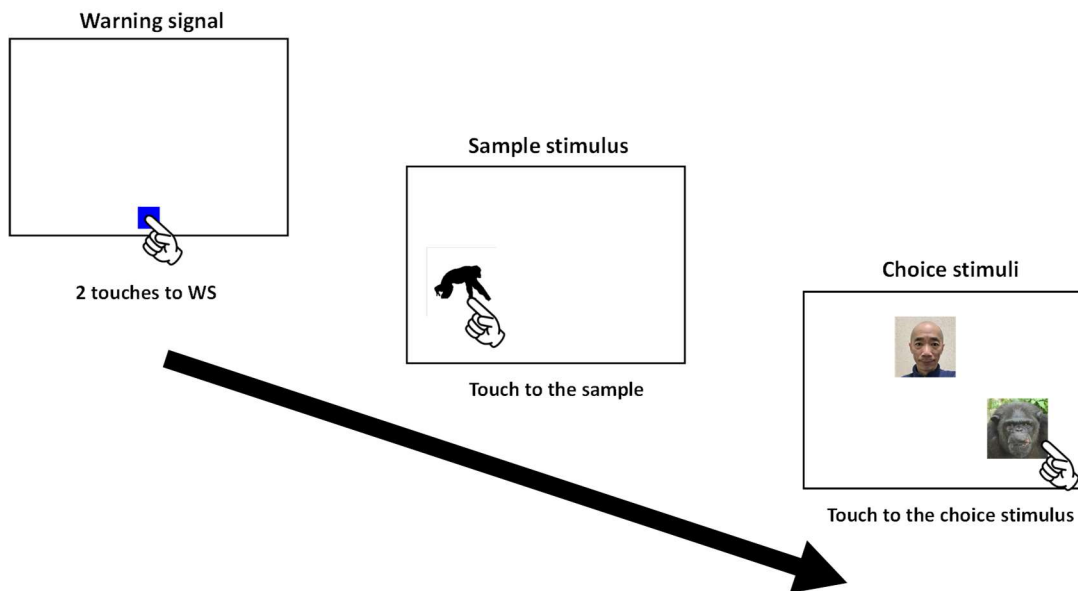


Figure 3. Typical example of a matching-to-sample trial (Chimpanzee–Human SP trial).



was displayed in one of six positions arranged in a 3 x 2 grid. Upon touching the sample stimulus, it disappeared, and two choice stimuli were presented in the remaining two positions. All stimuli were removed from the screen once the chimpanzees selected one of the choice stimuli. A correct response was followed by a food reward accompanied by a chime, whereas an incorrect response resulted in the presentation of a buzzer sound without

any reward. In cases of incorrect responses, a correction trial was conducted, during which only the correct choice stimulus was displayed following the sample stimulus. In the test trials, a food reward and the chime were delivered regardless of the chimpanzees' choice.

**Preliminary training.** The chimpanzees were already familiar with the matching-to-sample procedure, so no specific acquisition training was required. Before the test sessions, preliminary training was conducted on the four types of baseline trials. Each session consisted of 48 trials, with 12 trials for each trial type. Additionally, the six category pairs were presented twice for each baseline trial type. This training was conducted over 12 sessions. The baseline trial types, category pairs, and stimulus positions were randomized in every trial.

**Test sessions.** After completing the preliminary training, the chimpanzees proceeded to the test sessions. Each test session consisted of 48 baseline trials, with 12 additional test trials. Within each session, either PS or SP test trials were exclusively presented. PS and SP test sessions alternated, with six sessions of each type provided to the chimpanzees.

### Data analysis

The accuracies of the test sessions were analyzed using a generalized linear mixed modeling (GLMM) with a binomial distribution, separating baseline trials and test trials. Fixed effects included trial type, category pair, and their interaction, while random effects consisted of chimpanzee and session (nested within chimpanzee). These analyses were performed using *lmerTest* package in R version 4.2.0.

## Results

The chimpanzees demonstrated consistently high accuracy from the first session of preliminary training ( $M = 90.4\%$ ,  $SE = 1.3$ ) and maintained this high level of performance through the final session ( $M = 90.0\%$ ,  $SE = 1.1$ ). Table 1 summarizes the accuracy for each trial type and category pair in the final session of the preliminary training.

Figure 4 presents the results of baseline trials during the test sessions. Tables 2 and 3 summarize the results of the GLMM analyses. Similar to the preliminary training phase, chimpanzees' performances were better in identity matching trials (PP-ID and SS-ID) compared to perceptual-category matching trials (PP-cat and SS-cat; Table 2). Moreover, the chimpanzees exhibited accuracy significantly above chance level across all trial types and category pairs (Table 3).

Figure 5 illustrates the results of the test trials, depicting the accuracy by sample stimulus category for each trial type and category pair. Dashed lines indicate the mean percentage of correct trials for each category pair. Accuracies significantly above chance level were observed only for Chimpanzee–Chair pairs in PS and SP trials and Chair–Dog pair in PS trials, all of which included the Chair category (Table 4). Furthermore, strong stimulus biases toward one of the categories were observed in many pairs. The strongest bias was toward the Chair category, followed by the Chimpanzee category.

Table 1. Mean percentages of correct trials in the final session of preliminary training.

Note. SE: standard error across individuals. Chimp: chimpanzee

		Mean	SE
Trial type	PP-ID	98.3	1.5
	SS-ID	93.3	3.7
	PP-cat	83.3	2.4
	SS-cat	85.0	1.5
Category pair	Chimp-Chair	95.0	4.5
	Chimp-Dog	90.0	4.2
	Chimp-Human	87.5	6.1
	Chair-Dog	90.0	4.2
	Chair-Human	92.5	2.7
	Dog-Human	85.0	6.5

Figure 4. Mean percentages of correct baseline trials in the test sessions.

Error bars represent the standard error across chimpanzees.

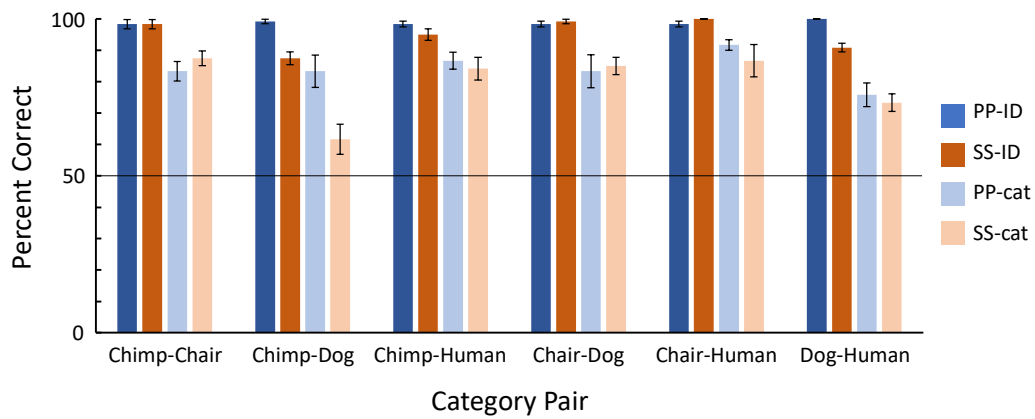




Table 2. Summary of GLMM for the baseline trials in the test sessions: Comparison among trial types.

Note. Estimate: parameter estimate for comparison, SE: standard error, CI: confidence interval, na: Not available for analysis because one of the trial types used for comparison achieved a 100% accuracy.

Category Pair	Comparison	Estimate	SE	p	95%CI	
Chimpanzee-Chair	PP-ID vs. PP-cat	-2.477	0.758	0.001	-3.962	-0.991
	PP-ID vs. SS-ID	0.005	1.015	0.996	-1.984	1.995
	PP-ID vs. SS-cat	-2.137	0.769	0.005	-3.643	-0.630
	PP-cat vs. SS-ID	2.481	0.751	0.001	1.010	3.952
	PP-cat vs. SS-cat	0.340	0.370	0.358	-0.385	1.065
	SS-ID vs. SS-cat	-2.136	0.769	0.005	-3.643	-0.629
Chimpanzee-Dog	PP-ID vs. PP-cat	-3.176	1.029	0.002	-5.192	-1.160
	PP-ID vs. SS-ID	-2.836	1.036	0.006	-4.866	-0.806
	PP-ID vs. SS-cat	-4.332	1.017	0.000	-6.324	-2.339
	PP-cat vs. SS-ID	0.340	0.371	0.359	-0.387	1.068
	PP-cat vs. SS-cat	-1.155	0.310	0.000	-1.764	-0.547
	SS-ID vs. SS-cat	-1.496	0.336	0.000	-2.154	-0.838
Chimpanzee-Human	PP-ID vs. PP-cat	-2.211	0.766	0.004	-3.712	-0.709
	PP-ID vs. SS-ID	-1.132	0.832	0.173	-2.762	0.498
	PP-ID vs. SS-cat	-2.415	0.760	0.001	-3.904	-0.925
	PP-cat vs. SS-ID	1.081	0.497	0.030	0.106	2.056
	PP-cat vs. SS-cat	-0.203	0.368	0.582	-0.924	0.519
	SS-ID vs. SS-cat	-1.284	0.487	0.008	-2.239	-0.329
Chair-Dog	PP-ID vs. PP-cat	-2.479	0.747	0.001	-3.943	-1.015
	PP-ID vs. SS-ID	0.704	1.220	0.564	-1.687	3.094
	PP-ID vs. SS-cat	-2.352	0.750	0.002	-3.823	-0.881
	PP-cat vs. SS-ID	3.184	1.031	0.002	1.164	5.204
	PP-cat vs. SS-cat	0.127	0.355	0.721	-0.570	0.823
	SS-ID vs. SS-cat	-3.051	1.041	0.003	-5.093	-1.010
Chair-Human	PP-ID vs. PP-cat	-1.683	0.792	0.034	-3.234	-0.131
	PP-ID vs. SS-ID	na	na	na	na	na
	PP-ID vs. SS-cat	-2.215	0.767	0.004	-3.719	-0.711
	PP-cat vs. SS-ID	na	na	na	na	na
	PP-cat vs. SS-cat	-0.530	0.429	0.216	-1.370	0.310
	SS-ID vs. SS-cat	na	na	na	na	na
Dog-Human	PP-ID vs. PP-cat	na	na	na	na	na
	PP-ID vs. SS-ID	na	na	na	na	na
	PP-ID vs. SS-cat	na	na	na	na	na
	PP-cat vs. SS-ID	1.165	0.382	0.002	0.415	1.914
	PP-cat vs. SS-cat	-0.134	0.299	0.653	-0.720	0.451
	SS-ID vs. SS-cat	-1.298	0.380	0.001	-2.043	-0.553

Table 3. Summary of GLMM for the baseline trials in the test sessions: Intercept for each category pair.

Note. Estimate: parameter estimate for intercept, SE: standard error, CI: confidence interval, na: Not available for analysis because the trial type achieved a 100% accuracy.

Category Pair	Trial Type	Estimate	SE	p	95%CI	
Chimpanzee-Chair	PP-ID	4.119	0.720	<0.001	2.707	5.531
	PP-cat	1.642	0.256	<0.001	1.140	2.145
	SS-ID	4.119	0.720	<0.001	2.707	5.531
	SS-cat	1.981	0.286	<0.001	1.421	2.542
Chimpanzee-Dog	PP-ID	4.818	1.001	<0.001	2.856	6.781
	PP-cat	1.642	0.257	<0.001	1.139	2.145
	SS-ID	1.982	0.286	<0.001	1.421	2.543
	SS-cat	0.486	0.202	0.016	0.091	0.881
Chimpanzee-Human	PP-ID	4.119	0.721	<0.001	2.707	5.531
	PP-cat	1.907	0.279	<0.001	1.360	2.454
	SS-ID	2.988	0.424	<0.001	2.156	3.820
	SS-cat	1.703	0.261	<0.001	1.191	2.216
Chair-Dog	PP-ID	4.121	0.709	<0.001	2.730	5.511
	PP-cat	1.642	0.257	<0.001	1.139	2.145
	SS-ID	4.820	1.012	<0.001	2.837	6.803
	SS-cat	1.768	0.267	<0.001	1.245	2.291
Chair-Human	PP-ID	4.123	0.722	<0.001	2.708	5.537
	PP-cat	2.438	0.340	<0.001	1.771	3.104
	SS-ID	na	na	na	na	na
	SS-cat	1.908	0.279	<0.001	1.360	2.455
Dog-Human	PP-ID	na	na	na	na	na
	PP-cat	1.168	0.226	<0.001	0.725	1.612
	SS-ID	2.332	0.326	<0.001	1.693	2.972
	SS-cat	1.034	0.220	<0.001	0.603	1.465

Figure 5. Mean percentages of correct test trials in the test sessions.

Each bar represents the mean percentage for each sample category. Dashed line shows the mean percentage for each category pair. Error bars represent the standard error across chimpanzees.

\*\* :  $p < 0.01$ , \* :  $p < 0.05$

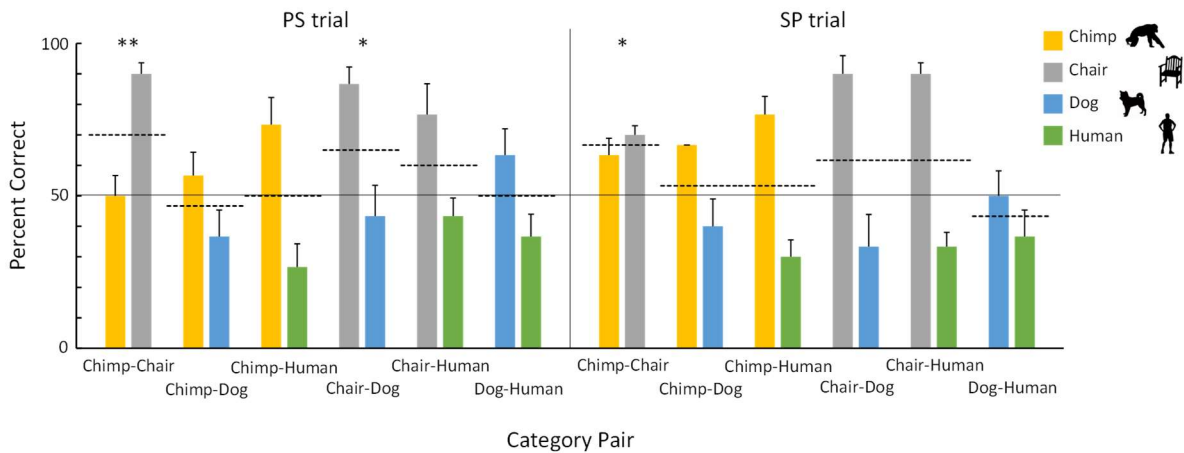


Table 4. Summary of GLMM for the test trials in the test sessions.

Note. Estimate: parameter estimate for intercept, SE: standard error, CI: confidence interval

Trial Type	Category Pair	Estimate	SE	p	95%CI	
PS	Chimpanzee-Chair	0.848	0.283	0.003	0.293	1.403
	Chimpanzee-Dog	-0.134	0.260	0.608	-0.644	0.377
	Chimpanzee-Human	0.000	0.260	1.000	-0.509	0.509
	Chair-Dog	0.620	0.272	0.023	0.086	1.153
	Chair-Human	0.406	0.265	0.126	-0.114	0.926
	Dog-Human	0.000	0.260	1.000	-0.509	0.509
SP	Chimpanzee-Chair	0.694	0.275	0.012	0.154	1.234
	Chimpanzee-Dog	0.134	0.260	0.608	-0.377	0.644
	Chimpanzee-Human	0.134	0.260	0.608	-0.377	0.644
	Chair-Dog	0.476	0.267	0.075	-0.048	0.999
	Chair-Human	0.476	0.267	0.075	-0.048	0.999
	Dog-Human	-0.268	0.262	0.306	-0.782	0.245

## Discussion

This preliminary study investigated whether chimpanzees are capable of conceptual matching independent of perceptual similarity, using silhouette and photographic stimuli. The results showed that, in the test trials involving silhouette and photographic stimuli, they did not perform significantly above chance level for most category pairs. The only exceptions were a few pairs that included the Chair category, demonstrating

higher accuracy than chance level.

The higher accuracy for the test pairs involving the Chair category compared to other pairs was likely due to the high perceptual similarity between the photographs and silhouettes of chairs (Figure 1). In contrast, for other stimulus categories involving photographs, performance remained close to chance. Notably, the chimpanzees participating in the present experiment had little exposure to real dogs in their daily lives. While they may have recognized dog faces as faces (Tomonaga, 2007), they were unlikely to perceive them as "dog faces." Accordingly, the Chimpanzee–Human pair appeared to be the most appropriate category pair for testing conceptual matching in this experiment. The chimpanzees were familiar with human faces, as they frequently encountered them in their environment and in many experiments where human faces were used as stimuli (). However, the mean percentage of correct test trials for this pair was 51.7% (SE = 2.5), which was approximately at chance level. Based on these results, it can be concluded that the chimpanzees are unlikely to conceptually recognize silhouettes in the present experiment.

However, several limitations in this preliminary test need to be addressed. One issue is that the use of the Chair category, which preserves perceptual similarity between photographs and silhouettes, may have strengthened a bias toward this stimulus category. Additionally, it should also be noted that, among the remaining three categories, the face–body correspondence for dogs was unfamiliar to the chimpanzees. Japanese macaques and rhesus macaques, familiar to the chimpanzees, lived adjacent to their living area. Using these macaques as a category instead of dogs might have yielded different results.

Furthermore, the limited number of test trials in this experiment must also be pointed out. The number of trials for each category pair was only 12 per test type. While this may be effective in preventing the development of inappropriate responses during the test sessions, such as positional or stimulus biases, it reduces the statistical power of the analysis. This aspect requires careful consideration in future studies.

In the test trials, a nondifferential reinforcement method was employed, where reinforcement was provided regardless of the chimpanzees' choices. Alternatively, differential reinforcement could be introduced to promote discrimination learning. Under this approach, a reversal-training condition, in which the correspondence between the categories in photographs and silhouettes is reversed (e.g., selecting a human silhouette for a chimpanzee face sample), could be implemented to directly compare learning speeds with the original condition. This comparison between the original and reversal conditions could be conducted under a between-participant design, although the small number of chimpanzees may present a challenge.

In conclusion, the present preliminary test did not provide evidence that the chimpanzees conceptually recognized their own body silhouettes beyond a perceptual level while performing the visual search task in the previous study (Tomonaga & Imura, 2025). Further refinement of the testing methods and additional investigations will be necessary to draw definitive conclusions in future research.

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## **Conflict of Interest**

The authors declare that they have no conflicts of interest.

## **Author's contribution**

Conceptualization: MT, Methodology: MT, Software: MT, Validation: MT, Formal analysis: MT, Investigation, NS & MT, Resources: NS & MT, Data Curation: MT, Writing- Original Draft, Review, & Editing: MT, Visualization: MT, Supervision: MT, Project administration: MT, Funding acquisition: MT

## **Data availability**

The dataset used in this study is provided in the Supplementary Material.

## References

- Adachi, I., Kuwahata, H., & Fujita, K. (2007). Dogs recall their owner's face upon hearing the owner's voice. *Animal Cognition*, 10(1), 17–21. <https://doi.org/10.1007/s10071-006-0025-8>
- Adachi, I., Kuwahata, H., Fujita, K., Tomonaga, M., & Matsuzawa, T. (2006). Japanese macaques form a cross-modal representation of their own species in their first year of life. *Primates*, 47, 350–354. <https://doi.org/10.1007/s10329-006-0182-z>
- Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception and Performance*, 21(3), 628–634. <https://doi.org/10.1037/0096-1523.21.3.628>
- Gao, J., Kawakami, F., & Tomonaga, M. (2020). Body perception in chimpanzees and humans: The expert effect. *Scientific Reports*, 10, 7148. <https://doi.org/10.1038/s41598-020-63876-x>
- Gao, J., & Tomonaga, M. (2018). The body inversion effect in chimpanzees (*Pan troglodytes*). *PLoS ONE*, 13(10): e0204131. DOI: 10.1371/journal.pone.0204131.
- Gao, J., & Tomonaga, M. (2020a). Body perception in chimpanzees (*Pan troglodytes*): The effect of body structure changes. *Journal of Comparative Psychology*, 134, 222–231. DOI: 10.1037/com0000214
- Gao, J., & Tomonaga, M. (2020b). How chimpanzees and children perceive other species' bodies: Comparing the expert effect. *Developmental Science*, 23, e12975. <https://doi.org/10.1111/desc.12975>.
- Hershler, O., & Hochstein, S. (2005). At first sight: A high-level pop out effect for faces. *Vision Research*, 45(13), 1707–1724. <https://doi.org/10.1016/j.visres.2005.01.006>
- Kawaguchi, Y., Nakamura, K., & Tomonaga, M. (2020). Colour matters more than shape for chimpanzees' recognition of developmental face changes. *Scientific Reports*, 10, 18201. <https://doi.org/10.1038/s41598-020-75284-2>
- Matsuno, T., & Fujita, K. (2018). Body inversion effect in monkeys. *PLoS One*, 13(10), Article e0204353. <https://doi.org/10.1371/journal.pone.0204353>
- Matsuzawa, T. (2006). Sociocognitive development in chimpanzees: A synthesis of laboratory work and fieldwork. In: T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 3–33). Springer, Tokyo.
- Matsuzawa, T., Tomonaga, M., & Tanaka, M. (Eds.). (2006). *Cognitive development in chimpanzees*. Springer-Verlag. <https://doi.org/10.1007/4-431-30248-4>
- Peelen, M. V., & Downing, P. E. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience*, 8(8), 636–648. <https://doi.org/10.1038/nrn2195>
- Reed, C. L., Stone, V. E., Bozova, S., & Tanaka, J. (2003). The body-inversion effect. *Psychological Science*, 14(4), 302–308. <https://doi.org/10.1111/1467-9280.14431>
- Reed, C. L., Stone, V. E., Grubb, J. D., & McGoldrick, J. E. (2006). Turning configural processing upside down: Part and whole body postures. *Journal of Experimental Psychology: Human Perception and Performance*, 32(1), 73–87. <https://doi.org/10.1037/0096-1523.32.1.73>
- Thompson, R. K. R., & Oden, D. L. (2000). Categorical perception and conceptual judgments by nonhuman primates: The paleological monkey and the analogical ape. *Cognitive Science*, 24(3), 363–396. [https://doi.org/10.1016/S0364-0213\(00\)00029-X](https://doi.org/10.1016/S0364-0213(00)00029-X)

- Tomonaga, M. (2001). Investigating visual perception and cognition in chimpanzees (*Pan troglodytes*) through visual search and related tasks: From basic to complex processes. In T. Matsuzawa (Ed.), *Primate origin of human cognition and behavior* (pp. 55-86). Tokyo, Japan: Springer.
- Tomonaga, M. (2007). Visual search for orientation of faces by a chimpanzee (*Pan troglodytes*): Face-specific upright superiority and the role of facial configural properties. *Primates*, 48(1), 1–12.  
<https://doi.org/10.1007/s10329-006-0011-4>
- Tomonaga, M. (2010). Do the chimpanzee eyes have it? In: E. V. Lonsdorf, S. R. Ross, & T. Matsuzawa T (Eds.) *The mind of the chimpanzee: Ecological and empirical perspectives* (pp 42–59). University of Chicago Press, Chicago.
- Tomonaga, M., & Imura, T. (2015). Efficient search for a face by chimpanzees (*Pan troglodytes*). *Scientific Reports*, 5(1), 11437. <https://doi.org/10.1038/srep11437>
- Tomonaga, M., & Imura, T. (2024). Chimpanzee's in black: Efficient search for the conspecific body silhouette by chimpanzees (*Pan troglodytes*). Manuscript in preparation.
- Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2003). *Cognitive and behavioral development in chimpanzees: A comparative approach*. Kyoto University Press. (Japanese text only)
- Ueda, S., & Tomonaga, M. (2024). Examining the long-term retention of associative stimulus relations in chimpanzees (*Pan troglodytes*). *International Journal of Primatology*, <https://doi.org/10.1007/s10764-024-00456-0>
- Valentine, T. (1988). Upside-down faces: A review of the effect of inversion upon face recognition. *British Journal of Psychology*, 79(4), 471–491. <https://doi.org/10.1111/j.2044-8295.1988.tb02745.x>
- Vonk, J., & Povinelli, D. J. (2006). Similarity and difference in the conceptual systems of primates: The unobservability hypothesis. In E. A. Wasserman & T. R. Zentall (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 363–387). Oxford University Press.
- Wilson, D. A., & Tomonaga, M. (2018). Visual discrimination of primate species based on faces in chimpanzees. *Primates*, 59, 243-251. <https://doi.org/10.1007/s10329-018-0649-8>
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, 81(1), 141–145.  
<https://doi.org/10.1037/h0027474>