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# Gap Effect for Manual Responses in Chimpanzees (*Pan troglodytes*): Temporal Aspects of Attentional Disengagement, Cognitive aging, and the Test for Attentional Bias Toward Infant Faces

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**Abstract** – This study examined factors influencing the gap effect, a phenomenon where the saccadic latency is faster when the fixation point disappears than when it overlaps with the target. The gap effect has been used in basic attentional research, as well as in developmental, neurophysiological, and comparative research. This effect is found not only in oculomotor tasks but also in manual response tasks in humans. In this study, we conducted a gap-overlap task using manual spatially orienting responses in chimpanzees and examined several factors that influence this effect. The results confirmed the gap effect for manual orienting responses in chimpanzees. Response times for gap trials showed a floor effect at around the gap with 200 ms and more. The duration of the fixation point did not affect the gap effect, although it did affect the chimpanzees' response times. The presence or absence of auditory stimuli at the fixation point offset did not affect the gap effect. We also analyzed the data from two geriatric individuals (51 years old) who participated in this study and confirmed the usefulness of this effect for studying comparative cognitive-aging studies. In a second task we examined attentional bias for infant faces, an effect which has been reported in humans. However, while a gap effect was observed overall, there was no significant difference in the gap effect among stimulus types.

**Keywords** – Chimpanzees, Gap effect, Attention, Cognitive aging, Infant face

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There is a wide variety of information in our environment and attention plays an important role in selecting and processing the necessary information. Attention has been defined in various ways (Atkinson & Braddick, 2012; Colombo, 2001; Posner & Cohen, 1984), but here we use the definition of attention as “the ability to deploy the [cognitive] resources... so as to optimize performance towards behavioral goals” (Atkinson & Braddick, 2012, p. 589). Attention is shifted to a particular space or object in a top-down or bottom-up manner to facilitate processing those objects and inhibit other processing and then is disengaged (or released) from them to shift to the next objects.

Various tasks have been developed to investigate the properties of these components of attention, especially visual attention. For example, the dot-probe task (MacLeod et al., 1986) and the pre-cueing task (Posner, 1980) have been used to study attentional capture and shift, while the gap-overlap task (Saslow,

1967) has been used to study disengagement of attention in various situations. In particular, gap-overlap tasks have been used in basic research on the properties of human attention, including developmental research (Cousijn et al., 2017; Sacrey et al., 2014) and neurophysiological research (Dorris et al., 1997; Munoz et al., 1998), but have not been used extensively in comparative cognition research. One reason may be that this task was developed primarily as an oculomotor response task and was suitable for neurophysiological studies requiring strict eye movement control.

In a typical gap-overlap task, two types of trials are presented: *gap* and *overlap* trials. In gap trials, a fixation point (FP) is first presented on the screen. After a certain period, the FP disappears, followed by a target at one of the left and right positions to the FP after another period (“gap”). Observers are required to saccade (look) to the target as quickly as possible. On the other hand, in overlap trials, the FP remains on the screen until the observer’s saccade to the target. The difference in saccadic latencies between these two types of trials is defined as the “gap effect” and is used as a measure of attentional disengagement (e.g., Saslow, 1967). In contrast, previous studies examined the gap effect using manual responses, instead of oculomotor responses, the effect was not observed (Reuter-Lorenz et al., 1991; Tam & Ono, 1994). Recently, however, several researchers have reported the gap effect even in manual tasks that do not involve a keypress response but require a spatially manual orienting response to the target, as in the oculomotor tasks (Bekkering et al., 1996; Pratt et al., 1999). These results suggest that the gap effect in orientation tasks may be produced by a common function of the superior colliculus (Pratt et al., 1999).

Until recently, research on the gap effect in nonhuman primates had been conducted only from the neurophysiological perspective (Dorris & Munoz, 1995; Dorris et al., 1997; Paré & Munoz, 1996), but not the comparative perspective. Kano and colleagues (Kano et al., 2011; Kano & Tomonaga, 2011) examined the gap effect by the oculomotor task in chimpanzees using an eye tracker. However, no gap effect was observed in the chimpanzees studied, but was in humans and other great apes (Kano et al., 2011; Kano & Tomonaga, 2011). The authors suggested that one of the reasons for this may be that chimpanzees have a faster saccade latency than humans. In the present study, we examined the gap effect in chimpanzees using a gap-overlap task, which requires spatially orienting responses to a target stimulus using a touchscreen. If the gap effect is observed, we will provide feedback to the oculomotor task by exploring under what conditions the effect is stably observed.

For this purpose, we manipulated several factors affecting response times and the gap effect. First, we investigated temporal aspects. In a previous study, the manual response times for the gap trials show a floor effect at a gap duration of around 200 ms in humans (Pratt et al., 1999). Therefore, we manipulated the gap duration to examine its effect on response times and the gap effect. Moreover, the duration of the FP presentation was examined. Although the present study was not an oculomotor but a manual response task, the FP was presented until the presentation of the gap. It has long been known that the duration of the FP (i.e., foreperiod) affects response time (Johanson, 1922; Keller & van der Schoot, 1978; Niemi & Näätänen, 1981) and the gap effect in the oculomotor gap-overlap tasks (Pare & Munoz, 1996; Saslow, 1967). Therefore, we further manipulated the FP duration to examine the effects on the response times and the gap effect.

Kingstone and Klein (1993) and Pratt et al. (1999) proposed two components contributing to the gap effect. One is the fixation offset effect, in which the disappearance of the fixation point affects the *oculomotor* response, and the other is the general warning effect, in which the disappearance of the FP warns the target’s appearance. In Pratt et al.’s experiments, a short auditory stimulus was presented as a warning signal immediately before (or at the same time as) the gap presentation in both gap and overlap trials to control the warning effect of the fixation offset. In the present study, we also presented an auditory stimulus (a clicking sound) to control warning by the FP offset. We also gave the chimpanzees an additional condition in which the clicking sound was not presented to examine the effect of the general warning.

More recent work has shown that the type of FP is also known as a factor that can affect the gap effect. These studies use the gap-overlap tasks to study the relationship between stimulus properties and attention by presenting a variety of stimuli as the FP. For example, using faces (Kikuchi et al., 2011) or emotional stimuli (Kissler & Keil, 2008; Nishiguchi et al., 2015; West et al., 2011) as the FP elicits a larger

gap effect. Moreover, certain types of faces, such as attractive faces (Valuch et al., 2015), and faces with direct gaze (Senju & Hasegawa, 2005; Ueda et al., 2014), have stronger effects.

Therefore, in a second experiment, we compared the robustness of the gap effect for different fixation stimuli, namely infant faces versus adult faces in chimpanzees. Since infant care is critical for survival, infants require getting attention from adults. In humans, the attentional bias for infant faces has been reported using manual tasks such as go/no-go or dot-probe tasks (e.g., Brosch et al., 2007, 2008; Hodsoll et al., 2010; Pearson et al., 2010). Previous comparative cognitive studies reported that nonhuman primates show longer looking times at infants than adults in free viewing tasks (e.g., chimpanzees, Kawaguchi et al., 2019; Japanese macaques and Campbell's monkeys, Sato et al., 2012; Barbary macaques, Almeling et al., 2016). On the contrary, Koda et al. (2013) examined attentional bias for infant faces in Japanese macaques using a manual task (dot-probe task) but found no such evidence (see also for bonobos, Kawaguchi et al., 2019). Given the mixed results, it is possible that infant stimuli play a role in certain aspects of attention (e.g., disengagement) but not others (e.g., engagement) in nonhuman primates. Therefore, we aimed to test whether chimpanzees show more difficulty disengaging their attention from infant faces than adult ones by using a gap-overlap task.

Lastly, the gap-overlap task has been used to study the development of attentional functions in humans. In particular, this task is often used to study cognitive aging processes, and it has been reported that the gap effect decreases with age (Munoz et al., 1998; but see Crawford et al., 2013). As two of the chimpanzees participating in the present study were 51 years old at the time of this study (categorized as “super-old”; cf. Ouchi et al., 2017), we were able to conduct preliminary investigations of age effects. To explore the applicability of the manual gap-overlap task in comparative cognitive-aging research, we analyzed the results of these two older individuals separately from the other chimpanzees.

## Experiment 1

### Ethics Statement

The care and use of the chimpanzees adhered to the 3rd edition of the *Guide for the Care and Use of Laboratory Primates* of the Primate Research Institute, Kyoto University. The experimental design in the present study was approved by the institute's Animal Welfare and Animal Care Committee (#2016-064, 2017-106). All procedures also adhered to the *Guideline of the Animal Experimentation* of the Japanese Society of Animal Psychology, *Guideline for the Care and Experimental Use of Captive Primates* of the Primate Society of Japan, *Code of Ethics and Conduct* of the Japanese Psychological Association, and the *Japanese Act on Welfare and Management of Animals*.

Experiments with humans adhered to the *Code of Ethics and Conduct* of the Japanese Psychological Association. Informed consent was obtained from each human participant.

### Methods

#### *Participants*

Eight chimpanzees (*Pan troglodytes*) participated in the present study (Table 1). No specific preliminary training was required since they had prior experience participating in various computer-controlled perceptual and cognitive experiments (e.g., Matsuzawa et al., 2006; Tomonaga, 2001; Tomonaga et al., 2003). All chimpanzees lived in a group of 13 individuals in indoor and outdoor compounds (770 m<sup>2</sup>) at the Primate Research Institute, Kyoto University (Matsuzawa, 2006). During the present study, they were never deprived of food or water.

**Table 1***Chimpanzees that Participated in the Present Study*

Name	Age <sup>1</sup>	Sex	Experiment 1	Experiment 2	GAIN ID <sup>2</sup>
<i>Puchi</i> <sup>3</sup>	51	<i>Female</i>	✓		#0436
<i>Gon</i>	51	<i>Male</i>	✓	✓	#0437
Ai	40	Female	✓	✓	#0434
<i>Mari</i>	40	<i>Female</i>		✓	#0274
Pendesa	39	Female	✓	✓	#0095
Chloe	36	Female	✓	✓	#0608
<i>Popo</i>	35	<i>Female</i>	✓	✓	#0438
Ayumu	16	Male		✓	#0608
Cleo	16	Female	✓	✓	#0609
Pal	16	Female	✓	✓	#0611

*Note. Italics:* excluded from the main analyses. See text for more details.

<sup>1</sup>Age at the onset of the first participation.

<sup>2</sup>ID number assigned by the Great Ape Information Network (<https://shigen.nig.ac.jp/gain/>).

<sup>3</sup>Died during Experiment 1.

In addition to the chimpanzees, ten human adults (eight females) also voluntarily participated in the experiment. Three were the authors themselves, and the others were postdoctoral fellows, undergraduate students, and graduate students. Participants other than the authors were not familiar with the gap-overlap task and/or the gap effect. All participants had normal or corrected-to-normal vision.

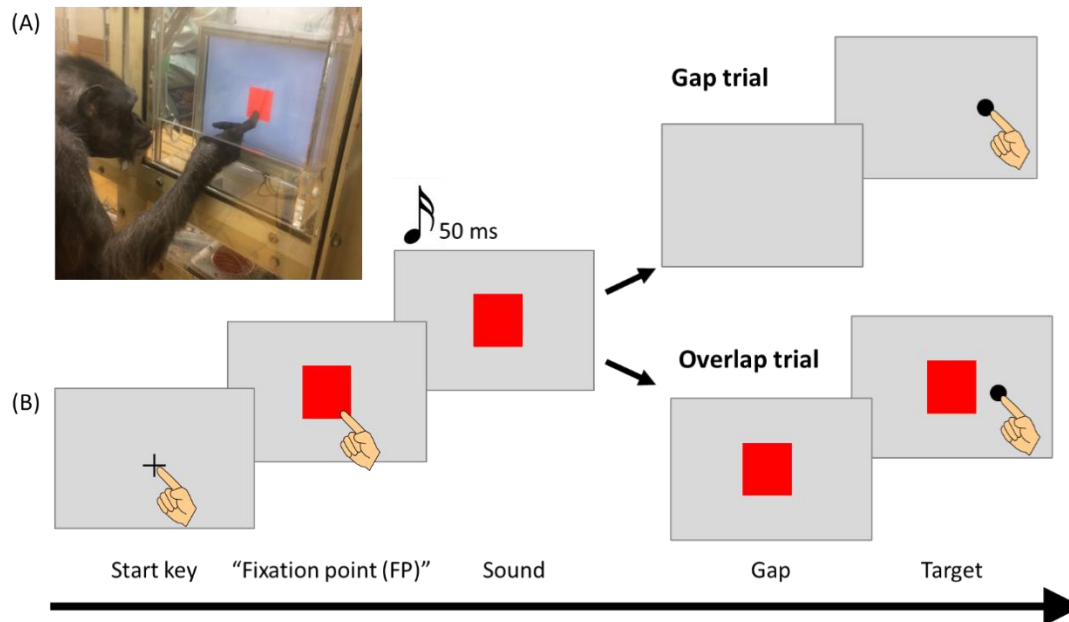
### ***Apparatus and Experimental Setting***

Experiments with the chimpanzees were conducted in a testing booth (1.8 X 2.15 X 1.75 m) in the experimental room adjacent to the chimpanzee facility. Each chimpanzee voluntarily came to the room and entered the booth via an overhead walkway directly connecting the facility and booth. Three sets of 17-inch LCD monitors (I-O Data LCD-AD172F2-T, 1280 X 1024 pixels, pixel size: 0.264 mm X 0.264 mm) with a touchscreen were installed on the wall of the booth; the two were placed approximately 30 cm from the floor, and the remaining one was placed approximately 15 cm from the ceiling. The viewing distance was approximately 40 cm. Food dispensers outside the booth delivered a food reward (a piece of apple or pellet (Bio-Serv® F0035)). The computers controlled all equipment and experimental events.

### ***Procedure***

**Gap-Overlap Task.** The gap-overlap task with manual responses was used in this experiment. Figure 1B shows a schematic diagram of the task. After the 2 s intertrial interval, a start key (cross-shaped, 50 X 50 pixels) was presented slightly below the center of the screen. After two touches, the start key disappeared, and a red rectangle (250 X 300 pixels) was presented in the center of the screen. This stimulus corresponded to the FP in the oculomotor task. In the present task, we did not require the chimpanzees to fixate on the FP but instead required them to touch this FP (Figure 1A). When the chimpanzees touched it twice (i.e., fixed-ratio schedule), a click sound was presented (approximately 50 ms). In the case of gap trials, the FP disappeared immediately after the click sound, and after a predetermined gap duration, a black circle target was presented on one of the two sides of the screen (70 pixels in diameter, 325 pixels from the center of the screen to the center of the target). In the overlap trials, the FP remained on the screen until the manual orienting response to the target. If the chimpanzees touched the target, all stimuli disappeared, and a food reward was given simultaneously with the chime. If there was no response within 8 s, all stimuli disappeared, and the intertrial interval began.

Figure 1

*The Experimental Setup*

Note. (A) Chimpanzee Pendesa performing the gap-overlap task. (B) Typical trial flow of the gap-overlap task.

**Baseline Test.** As a baseline test, we initially tested the chimpanzees under a constant gap duration of 200 ms. A session consisted of 48 trials, with eight sessions per individual, except for Gon, who received nine sessions<sup>1</sup>. Target positions (left or right) and trial types (gap or overlap) appeared randomly for each trial. In this test, the FP duration varied depending on the time required for each individual's fixed-ratio responses. The mean duration of the FP was 721 ms (standard error:  $\pm 33$  ms).

**Effect of the Gap Duration.** Following the baseline test, we examined each of the factors that might affect the manual response times and the gap effect. First, we investigated the effect of the gap duration. In this test, we did not require responses to the FP (although the chimpanzees continued to touch during this test). After the 650 ms fixed duration, the click sound and the target were presented. The gap duration randomly varied between 0, 200, and 500 ms. The FP continued to be presented during these gap durations in the overlap trials. Each individual received eight sessions consisting of 48 trials.

**Effects of Auditory Stimulus.** We then examined the effect of the auditory stimulus (the click sound) presented immediately before the appearance of the gap. In this test, the click sound was not presented for half of the trials in one session. The FP duration was fixed at 650 ms, and the gap duration was fixed at 200 ms. Each chimpanzee completed eight sessions consisting of 48 trials.

**Effect of the FP Duration.** In the final test, the gap duration was fixed at 200 ms, and the FP duration preceding it was randomly varied between 200, 650, and 900 ms. A session consisted of 48 trials, with eight sessions conducted per individual.

<sup>1</sup> Gon's first session had longer response times than the following sessions. Therefore, we conducted one more session than the other chimpanzees. It was possible to exclude the first session from the data analysis, but we decided to continue the analysis with nine sessions because the exclusion criterion would be arbitrary.

**Human Experiment.** We also conducted a positive control experiment to confirm that the setting and task used in this study sufficiently caused a gap effect in humans. The experiment was conducted in the same experimental testing booth as the chimpanzees, after being thoroughly cleaned and sanitized. The procedure was the same as for the chimpanzees, except that the intertrial interval was reduced to one second, and a food reward was not delivered for each correct response. They received only the baseline test. Each participant was verbally instructed to detect and touch a target as fast as possible and received one session of 96 trials.

## Data Analysis

The two geriatric chimpanzees, Gon and Puchi, were analyzed independently from the other five individuals. Both were estimated to be 51 years old at the time of the experiment (Great Ape Information Network, 2022). The average lifespan of captive chimpanzees in Japan who survived to adulthood is estimated to be about 40 years (Havercamp et al., 2019), and the estimated survival rate to age 51 is 17% for females and 20% for males. Thus, they were classed as “super-old” (following Ouchi et al., 2017). These rates correspond to that for 97-year-old women and 92-year-old men (defined as “super-old”) in Japan (Ouchi et al., 2017; Ministry of Health, Labour and Welfare, 2022). Before completing the sessions for the effect of the auditory stimulus, Puchi died of subarachnoid hemorrhage due to a ruptured cerebral artery (Hayashi et al., 2017). Thus, the test of the FP duration could not be conducted with her.

Besides Gon and Puchi, Popo was excluded from the main data analyses. Popo was the only individual who performed the task using a test set-up close to the ceiling in the testing booth (she refused to go down to the floor). While performing the task, she was in an unstable posture, sitting on a swing-like rope suspended from the ceiling grid (Figure S1), causing her response time to be longer than for the five chimpanzees used in the main data analysis. (658 ms for Popo and an average of 385 ms for the other five chimpanzees). We, therefore, separately analyzed Popo’s data, resulting in the data from five individuals for the main analysis.

We applied Generalized Linear Mixed Model (GLMM) for our analyses. The objective variable was response times. We excluded response times shorter than 150 ms and longer than and equal to 5000 ms from the analyses (2.1% of the total trials for the five chimpanzees, 1.0% for Gon and Puchi, and 0.1% for humans). In each test, manipulated factors and their interactions, including trial type, gap duration, and the presence or absence of auditory stimulus, were incorporated as fixed effects. We prepared all possible random-intercept models for each test, in which participants and sessions nested within participants were set as random effects. Among these models, we selected a model with the smallest AIC. In the present study, the differences in AIC between the best (i.e., selected) and second-best models were all greater than 2. Lognormal distributions were applied to response time data. Since we applied the “model-selection” approach, we did not show any test statistics, confidence intervals, and *p*-values in the text. However, we show these values in Tables S1-5 for reference. These analyses were performed using *lmerTest* (Kuznetsova et al., 2017) and *MuMIn* (Bartoń, 2022) packages in R version 4.2.0 (R Core Team, 2022).

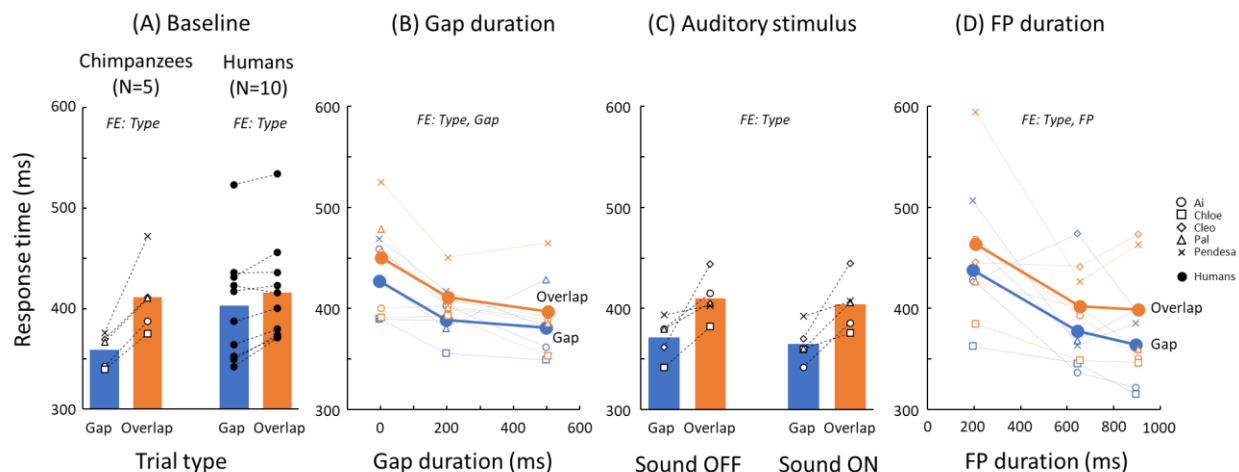
Data from Gon, Puchi, and Popo were also each subjected to separate GLMM analyses with random effects of session.

## Results

Figure 2 shows the results of each test, and Table S1 shows the summaries of GLMM analyses. Popo’s results are shown in Figure S1 and Table S2. Although her response times were longer than the other individuals, the gap effect was observed.

Figure 2

Results of Experiment 1



Note. (A) Baseline test, (B) effect of gap duration, (C) effect of auditory stimulus, and (D) effect of fixation point (FP) duration. Blue: gap trials, orange: overlap trials. Each symbol designates the data for each participant. Each panel also shows the fixed effect(s) (FE) in the selected model.

### Baseline Test

Response times on gap trials were faster than on overlap trials in all chimpanzees (Figure 2A). The selected model included trial type as a fixed effect ( $\beta = 0.128$ , standard error of mean (SEM) = 0.009), indicating a gap effect. Nine out of the ten human participants had faster response times on the gap trials than on the overlap trials (Figure 2A). The selected model included trial type as a fixed effect ( $\beta = 0.037$ , SEM = 0.011), confirming that the present manual gap-overlap task was sufficient for detecting the gap effect also in humans.

### Factors Affecting the Gap Effect

Although response times decreased with increasing gap duration, there was no interaction between the trial types and gap duration. Figure 2B shows the results of the test examining the effect of gap duration. As in the baseline test, the chimpanzees showed faster response times in the gap trials than in the overlap trials. The selected model included trial type and gap duration as fixed effects but not their interaction (trial type:  $\beta = 0.052$ , SEM = 0.011; gap:  $\beta = 1.97e-04$ , SEM < 0.001).

The presence or absence of the auditory stimulus (click sound) immediately before the gap did not affect response times or the gap effect. Figure 2C shows the results of the test for auditory stimulus presentation. The selected model included trial type as a fixed effect ( $\beta = 0.105$ , SEM = 0.013).

As the FP duration increased, response times became faster, but the FP duration did not affect the gap effect. Response times in the gap trials were faster than in the overlap trials. Figure 2D shows the results of the test for the FP duration. The selected model included trial type and FP duration as fixed effects but not their interaction (trial type:  $\beta = 0.078$ , SEM = 0.013; FP:  $\beta < 0.001$ , SEM < 0.001).

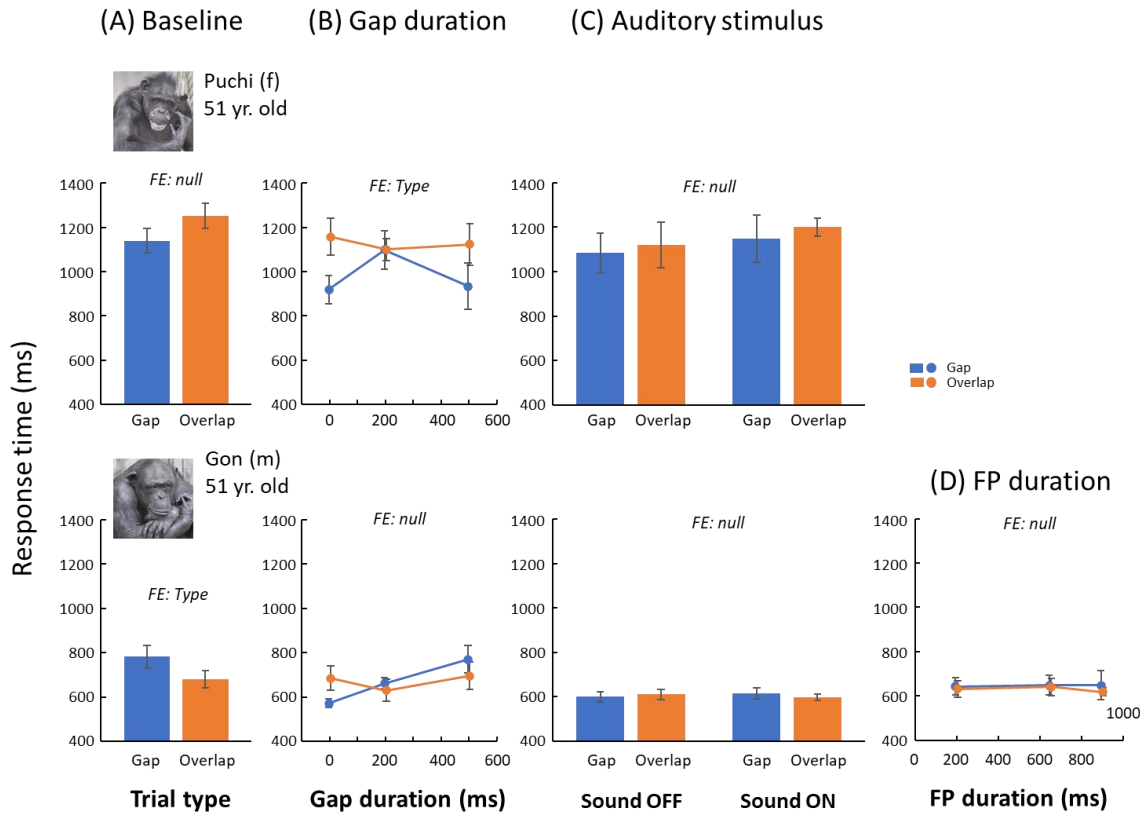
### Super-Old Chimpanzees

Figure 3 shows the results for the two super-old geriatric chimpanzees. Table S3 shows the summaries of GLMM analyses. The results of the baseline test show that they exhibited longer response times than the other five chimpanzees (super-old individuals: average = 964 ms, other individuals: average

= 385 ms). Puchi exhibited faster response times in the gap trials than in the overlap trials during the gap duration test. The selected model included trial type as a fixed effect ( $\beta = 0.133$ , SEM = 0.042). In contrast, Gon showed an opposite result in the baseline test, with faster response times for the overlapping trials. The selected model included trial type as a fixed effect ( $\beta = -0.117$ , SEM = 0.036). No other chimpanzees (including Popo) showed such a trend in Experiment 1. However, the Null models were selected for the other tests (i.e., gap duration test, auditory stimulus presentation test, FP duration test) in both chimpanzees.

**Figure 3**

*Results of the Two Geriatric (“Super-Old”) Chimpanzees*



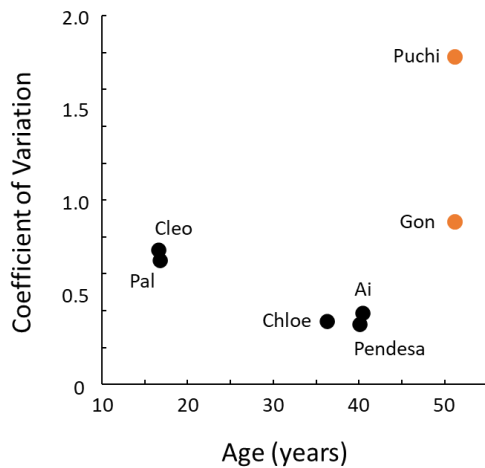
*Note.* (A) Baseline test, (B) effect of gap duration, (C) effect of fixation point (FP) duration, (D) effect of auditory stimulus. *null* indicates that the selected model was the null model. Error bar indicates the standard error of mean across sessions.

In addition, we observed individual differences in the variability of response times across sessions. To assess this variability, we calculated the coefficients of variation of response times for seven chimpanzees, including the two super-old individuals in the baseline test. Brown-Forsythe test for homogeneity of variance showed that variability of the response time within individuals is different among individuals ( $F(6,50) = 3.08$ ,  $p = .012$ ). More specifically, the coefficients of variation showed U-shaped changes with age, with younger and super-old chimpanzees exhibiting relatively higher coefficients of variation than middle-aged individuals (Figure 4).



**Figure 4**

*Coefficients of Variation for Each Chimpanzee as a Function of Age*



*Note.* Orange symbols indicate the two super-old chimpanzees.

## Discussion

The present study examined the gap effect in a manual-response gap-overlap task in chimpanzees. Although no gap effect had been observed in a previous study using an oculomotor task (Kano & Tomonaga, 2011), the gap effect was observed in the present task that required spatially orienting manual responses. The same effect was also observed in human participants who performed the same task, indicating that the present task was sufficient to detect a gap effect for manual responses across species.

Previous studies on humans have reported that the gap effect increased (i.e., response times in gap trials decreased) up to a gap duration of around 200 ms and became stable at longer gap durations (Pratt et al., 1999; Reulen, 1984; Saslow, 1967). In contrast, the gap effect did not change in the present experiment as the gap duration increased. It should be noted, however, that the definitions of the gap effect in the previous and present studies differ slightly. For example, in the overlap trials included in the study by Pratt et al. (1999), the time between the presentation of the auditory stimulus and the target onset (corresponding to the “gap” in the gap trials) was fixed at 200 ms. By contrast, the time corresponding to the “gap” in the overlap trials also varied in our study (i.e., matched control to “gap” trials). We defined the gap effect as the difference between the response times of the gap and overlap trials with the same “gap” durations. Instead, when focusing on the response times for the gap trials, they decreased as the gap duration increased to 200 ms. Therefore, the time course of the gap effect can be considered similar to that in previous studies.

Response times for the overlap trials in the gap-duration test also decreased as the “gap” duration increased. This fact may reflect the preparatory effect of the FP (Keller & van der Shoot, 1978; Niemi & Näätänen, 1981). Because in the overlap trials, the longer gap duration (the FP actually remained on the screen) meant a longer FP duration. The results of the subsequent FP-duration test that the response times decreased with increasing FP duration might support this possibility. On the other hand, the presence or absence of auditory stimulus before the gap did not affect the gap effect. Since oculomotor responses were not required in this task, the fixation offset effect, which facilitated preparations of oculomotor responses (Kopecz, 1995), cannot explain the present results (Pratt et al., 1999). Therefore, the FP offset might have a warning effect and affected response times in the gap trials in chimpanzees.

The two super-old geriatric chimpanzees showed longer response times than the other chimpanzees but initially showed different trends concerning the gap effect from each other. One individual, Puchi, showed a similar gap effect as the other chimpanzees, but the second chimpanzee, Gon, showed faster response times on the overlap trials. The reason for his opposite pattern of results is unclear; however, the

effect of trial type disappeared in subsequent tests for both individuals. Human studies reported that the gap effect weakens with cognitive aging (Munoz et al., 1998). There are still controversies about the reasons why, but our results may suggest similar cognitive aging in attentional disengagement in these two chimpanzees (but see also Crawford et al., 2013).

We also found U-shaped changes in the inter-session variability of the gap effect with age. This variability might suggest that sustained attention in the younger and super-old chimpanzees fluctuated from session to session. In humans, sustained attention and variability in reaction times also show U-shaped changes with age (Fortenbaugh et al., 2015; cf. Filley & Cullum, 1994; Vallesi et al., 2021). The relatively higher inter-session variability observed in the present study may be related to decreased sustained attention in the two super-old chimpanzees (and also in the younger chimpanzees).

The results of the present experiment demonstrated the gap effect in the manual orienting task in chimpanzees, while no gap effect had been observed in the previous oculomotor task (Kano & Tomonaga, 2011). A procedural issue may explain the lack of a gap effect in the oculomotor task. In the eye-tracking task, the chimpanzees were not forced to fixate on the stimulus presented in the center of the screen (i.e., the FP), although trials in which saccade responses occurred before the target presentation were excluded from their analysis. The average fixation duration under free viewing conditions in chimpanzees has been reported to be approximately 230 ms (Kano & Tomonaga, 2011). In contrast, in the task conducted by Kano and Tomonaga (2011), the FP was presented for 300 ms, and the gap duration was 260 ms (the FP continued to be presented for the same duration in the overlap trials), which was longer than the average fixation duration. A gap effect might have been observed even in the oculomotor task if they had set a shorter FP and gap.

The other explanation would be, of course, species differences. Kano et al. (2011) performed the same oculomotor gap-overlap tasks with the other great apes, that is, gorillas (*Gorilla gorilla*), orangutans (*Pongo abelii*), and bonobos (*Pan paniscus*), and found the gap effects in these species. Furthermore, they found no species differences in saccadic latency on the gap trials, indicating the species differences in latency on the overlap trials. These results suggest that the specific strategy in looking behaviors in chimpanzees, that is, quicker saccadic latency and longer fixation duration (Kano et al., 2011; Kano & Tomonaga, 2011), affected the gap effect. In contrast, since species differences might not restrict the manual responses, similar gap effects might have been observed during the manual-response gap-overlap tasks between chimpanzees and humans.

The present study indicates that the manual-response gap-overlap task can be an important tool for investigating attentional disengagement in chimpanzees, allowing for intra- and inter-species comparisons. As an example of its application, we observed the lack of the gap effect in super-old chimpanzees. In humans, gap-overlap tasks have been used not only to study the life-long development of attention but also to study the relationship between stimulus properties and attention by presenting a variety of stimuli as the FP. Previous studies demonstrated delayed attentional disengagement from some stimulus types, such as faces (Kikuchi et al., 2011; Valuch et al., 2015), gaze (Senju & Hasegawa, 2005, Ueda et al., 2014), and emotional stimuli (Kissler & Keil, 2008, Nishiguchi et al., 2015, West et al., 2011). Nonhuman primates may also show more difficulty in disengaging attention from one type of stimuli than the other in the manual gap-overlap task.

Attentional engagement (instead of attentional disengagement) is often tested in nonhuman primates and humans using a dot-probe task. For example, chimpanzees showed attentional bias toward conspecific and human faces compared with other objects (Tomonaga & Imura, 2009). Similarly, the attentional bias for conspecific emotional stimuli is reported in bonobos (Kret et al., 2016) but not in chimpanzees (Willson & Tomonaga, 2018) using a dot-probe task. These results suggest that certain stimuli capture attention more strongly than other stimuli in nonhuman primates (see also Leinwand et al., 2022). In Experiment 2, we aimed to test if the gap-overlap task can be used to test attention *disengagement* from different types of stimuli in nonhuman primates.

## Experiment 2

We presented pictures of chimpanzee faces and nonfaces as the FP in a manual-response gap-overlap task and examined how stimulus types affected the gap effect. We used face (conspecific adult or infant) and nonface (phase-scrambled adult/infant face or gray square) images as stimuli and compared the gap effect among stimulus types. Our first prediction was that the gap effect would be larger for face stimuli than nonface stimuli, as has been reported in humans (Kikuchi et al., 2011). If there is an attentional bias toward faces, the robustness of the bias may also be affected by the different types of faces. For example, humans show an attentional bias for infant faces, as measured using dot-probe tasks (Brosch et al., 2007, 2008, Hodsoll et al., 2010, for review, see Lucion et al., 2017). Such attentional bias toward infant faces is thought to promote infants' survival by inducing parental care. Therefore, it is reasonable to expect that attentional bias toward infant faces may also exist in nonhuman primates since providing infant care is also crucial for them. Indeed, a free-viewing eye-tracking study also reported a longer looking time to infant faces than adult ones in chimpanzees (Kawaguchi et al., 2019). However, a previous study with a dot-probe task in rhesus macaques failed to find an attentional bias toward infant stimuli (Koda et al., 2013). Nevertheless, we may still find attentional bias for infants in nonhuman primates with a gap-overlap task (attentional disengagement) instead of a dot-probe task (attentional engagement). Therefore, the second prediction is that the gap effect would be larger for infant stimuli than for adult stimuli.

### Methods

#### *Ethics Statement*

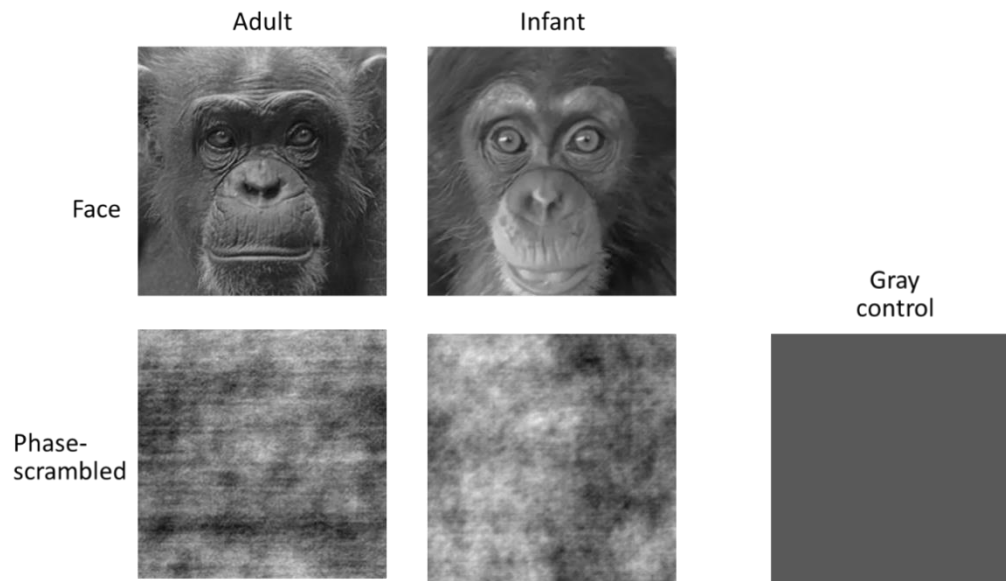
This study was reviewed and approved as per Experiment 1.

#### *Participants and Experimental Setting*

In addition to the chimpanzees who participated in Experiment 1 (except Puchi), Ayumu (male, 16-years old) and Mari (female, 40-years old) also participated in Experiment 2 (see Table 1). Two of them were males (Ayumu and Gon). However, as in Experiment 1, Popo and Gon were excluded from the analysis. Furthermore, Mari had difficulty manipulating her fingers precisely due to previous injuries, resulting in longer response times. Therefore, her data were also excluded from the analysis, resulting in the data from six individuals. The average response times of these excluded three individuals were 638, 757, and 735 ms, respectively, longer than those of the remaining six individuals (540 ms on average). The results for these three chimpanzees are shown in Figure S2 and Table S5 but were not analyzed in more detail. The experimental setting was the same as in Experiment 1.

#### *Stimuli and Procedure*

In this experiment, five different stimulus types were used as the FP: faces of adult chimpanzees, faces of infant chimpanzees, phase-scrambled images of adult faces, phase-scrambled images of infant faces, and a gray rectangle. Figure 5 shows examples of stimuli used in Experiment 2. Phase-scrambled stimuli are often used as control stimuli for complex visual stimuli because shape properties of the original stimulus were lost but low-level features such as brightness, contrast, and spectral energy, are retained in these stimuli (e.g., Wilson & Tomonaga, 2018). Each stimulus was 250 X 250 pixels in size. Twelve photographs of chimpanzee faces with neutral expressions were prepared for each category (adult and infant), and they were all unfamiliar to the participants. At the time of collection, however, many of these stimuli already lacked sex information. These pictures were presented as grayscale images, and the brightness was controlled among stimuli. Phase-scrambled images were created using *imscramble* script (Hebart, 2022) in MATLAB®.

**Figure 5***Examples of Stimuli Used for Fixation Point in Experiment 2*

The procedure was identical to Experiment 1, except that the blue rectangle (100 x 100 pixels) was presented as an additional start key at the bottom of the screen before the cross-shaped start key, and the auditory stimulus presented was changed to a 100-ms beep sound (see Video S1). We prepared two FP durations (150 and 500 ms) and two gap durations (50 and 200 ms). In this experiment, 150-ms FP and 50-ms gap, and 500-ms FP and 200-ms gap were always paired. One session consisted of 60 trials, and the five different FP stimulus types were presented randomly within a session. The trial type and target position also changed randomly in each trial. The chimpanzees initially received 12 “long-duration” sessions with 500 ms FP and 200 ms gap, followed by 12 “short-duration” sessions with 150 ms FP and 50 ms gap. Ayumu participated in only four sessions in the short-duration condition due to time-sharing with other studies.

### Data Analysis

As noted above, the data from the three chimpanzees, Popo, Mari, and Gon, were excluded from the main data analyses (see their results in supplementary materials). We excluded response times shorter than 150 ms and longer than and equal to 5000 ms from the analyses (0.5% of the total trials).

As in Experiment 1, we applied the GLMM analyses for the remaining six chimpanzees’ data. The objective variable was the response time. The following factors were included as fixed effects: FP types (adult, infant, scrambled adult, scrambled infant, square), trial types (gap or overlap), FP/Gap duration pairs (short- / long-duration), and their interactions. Although previous studies have reported that the sex of observers and stimuli influences the observer’s attention (Lewis et al., 2021; Lonsdorf et al., 2019), due to the sex imbalance of the participants and the lack of stimulus sex information, these effects were not included in the analyses in this study.

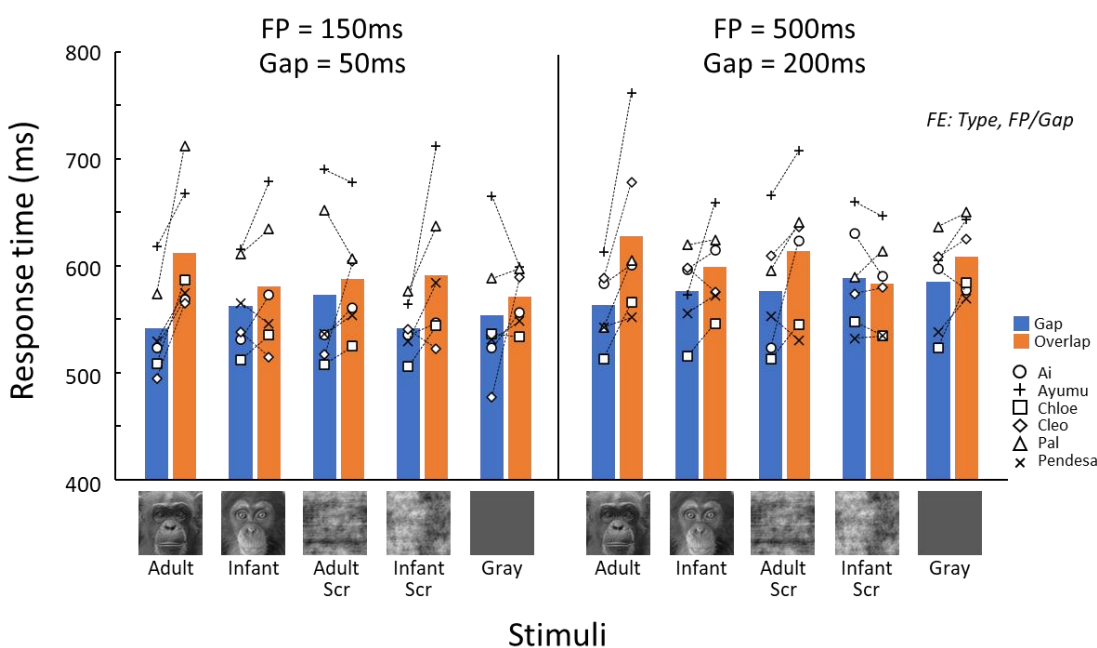
We prepared all possible random-intercept models, including stimuli, participants, and sessions nested within participants. Among these models, we selected a model with the smallest AIC. Lognormal distributions were applied to response time data.

## Results

The results for the six chimpanzees are shown in Figure 6. The summary of the statistical analysis is shown in Table S4. The results for Gon, Mari, and Popo are shown in Figure S2 and Table S5. The model selected by the GLMM analysis included the fixed effects of trial type ( $\beta = 0.054$ ,  $SEM = 0.006$ ) and FP/gap durations ( $\beta = 0.035$ ,  $SEM = 0.006$ ), indicating that the response time was longer in overlap trials than in gap trials, and longer in long-duration trials than in short-duration trials. However, the selected model did not include the type of FP and the interactions. In other words, although the gap effect was found, the types of the FP and FP/gap durations did not affect the gap effect. The FP/gap durations affected the response times, but unlike in Experiment 1, as the FP/gap durations increased, so did response times.

**Figure 6**

Results of Experiment 2



## Discussion

In Experiment 2, we used the gap-overlap task to examine the differential effects of types of visual stimuli on attentional disengagement. Although an overall gap effect was observed, no differences were found in the gap effect among the types of stimuli, such as adult vs. infant face or *face versus* nonface. These results are similar to the previous results with Japanese macaques, which reported no attentional bias toward conspecific infant faces compared with adult ones in a dot-probe task (Koda et al., 2013) and also partially correspond to those by Wilson and Tomonaga (2018), who reported no differential attentional capture effect between different types of faces (i.e., emotional vs. neutral face) under the dot-probe task in chimpanzees.

Several reasons can be considered for the lack of differences in the gap effect among stimulus types in this experiment. The first possibility is that there may not be distinct differences in attentional disengagement among stimulus types in chimpanzees. However, another study found that the same chimpanzees looked longer at infant faces than at adult faces in a free-viewing task (Kawaguchi et al., 2019). Moreover, the attentional bias for faces compared with nonface objects is also reported in chimpanzees by various tasks (Kano & Tomonaga, 2009; Tomonaga & Imura, 2015; Wilson & Tomonaga, 2018). Together, these attentional biases for infant faces or conspecific faces may be related to certain

aspects of attention but not attentional disengagement in chimpanzees, which may have resulted in no effect of stimulus types in our study.

The more plausible possibility, however, is that the gap-overlap task may simply not be sensitive enough to detect chimpanzees' biases among different types of stimuli rather than there being no bias among them. Particularly, several procedural issues may have affected the results. First, we used grayscale face images with controlled brightness to minimize potential artifacts. However, this processing may have made face images less clear, especially for recognition at a glance. Using naturalistic stimuli and controlled stimuli always needs to be compromised. In our previous free-viewing study, however, chimpanzees showed preferential looking toward infant faces over adult faces only when presented in color but not in grayscale with brightness controlled (Kawaguchi et al., 2019). Thus, the visual properties of faces which are critical to retain chimpanzees' attention in faces may have been missing in our stimuli.

Second, temporal variables may not have been ideal. FP durations were set as either 150 or 500 ms in Experiment 2. Although FP duration did not affect the size of the gap effect in both Experiments 1 and 2, 500 ms may not have been enough for chimpanzees to fully recognize the content in the stimulus. In Experiment 1, the results showed that the response times of gap trials became shorter as FP and gap durations increased. Conversely, in Experiment 2, response times increased with increasing FP and gap durations. It may be simply due to order effects because the longer-trial condition was conducted first in Experiment 2. Alternatively, however, the complexity of the stimuli we used may cause the results; we used a red square in Experiment 1, while we used intact and phase-scrambled face stimuli besides a gray square in Experiment 2. Free-viewing eye-tracking study reported that the looking time for face stimuli is generally longer than 500 ms in chimpanzees (Kano & Tomonaga, 2009, 2010; Kawaguchi et al., 2019). Thus, it is possible that 500 ms FP and gap durations may not be long enough for those stimuli used in Experiment 2. Further examination of these temporal variables would reveal a time course that could detect differential gap effects among stimulus types. Such an attempt would also provide important insights into species-specificity in the behavioral properties of attention in chimpanzees compared to the other primate species (*cf.* Kano et al., 2011; Kano & Tomonaga, 2011).

## General Discussion

In this study, we investigated whether the gap-overlap task, commonly used to study attentional disengagement in humans, can also be applied in studies on comparative cognition in chimpanzees. Instead of using the standard oculomotor task, we tested the chimpanzees on a manual-response spatial orienting task, recently shown to cause a clear gap effect in humans. The chimpanzees exhibited a gap effect, which differed from the findings of a previous study that did not observe a gap effect in the oculomotor task (Kano et al., 2011; Kano & Tomonaga, 2011). These results suggest that the chimpanzee-specific eye-gaze behavior, that is, quicker saccade latency and longer fixation duration than humans, may have influenced the gap effect observed in the oculomotor task.

We further demonstrated two examples of applying the manual gap-overlap task to comparative cognition research. In Experiment 1, we could show the potential for using the gap effect as an indicator of cognitive aging in comparative studies based on the results from the two super-old chimpanzees. We did not find a consistent gap effect among the oldest individuals in our sample. However, we did observe a U-shaped pattern of variability in the gap effect within individuals that changed as a function of age, similar to the lifelong development of attentional function in humans.

In Experiment 2, we attempted to detect attentional bias toward social stimuli by examining the difference in gap effects between stimulus types. However, while a gap effect was observed overall, there was no significant difference in the gap effect among stimulus types. Specifically, the difference in gap effect was not found between infant and adult faces or even between face and nonface stimuli. On the contrary, differences in the gap effect between the various stimulus categories have been reported in humans (Kikuchi et al., 2011; Kissler & Keil, 2008; Senju & Hasegawa, 2005). The first possibility of this discrepancy is that there may not be differences among stimulus types in attentional disengagement in chimpanzees. The previously reported attentional prioritization for faces (of infants/conspecific in general)

in chimpanzees may be related to other aspects of attention but not attentional disengagement in chimpanzees, which may have resulted in no effect of stimulus types in our study. Alternatively, due to some procedural issues (i.e., temporal variables or stimuli may not have been ideal), our gap-overlap task may not be sensitive enough to detect attentional bias in chimpanzees.

The gap-overlap task was designed primarily to detect the disengagement aspect of attention (Saslow, 1967). In contrast, it may also be possible to examine bias in attentional capture using tasks such as the dot-probe and visual search tasks. However, concerns about the effectiveness of the dot-probe task (especially using emotional stimuli) have been discussed in humans (Schmukle, 2005; Thigpen et al., 2018; Waechter et al., 2014). It will be necessary to examine the effectiveness of each task from the perspective of comparative cognition in the future (*cf.* Kret et al., 2016; Wilson & Tomonaga, 2018). For this purpose, since some great ape species other than chimpanzees have shown gap effects in oculomotor tasks (Kano et al., 2011), it may initially be important to examine gap effects in the manual gap-overlap task for these species.

From our results, however, it would be premature to draw definitive conclusions regarding the lifespan development of attention and the differential disengagement effects between stimuli in chimpanzees, given the small sample size in this study. Further investigation with larger sample sizes is necessary. In recent years, experiments with nonhuman primates using touch screens have been actively introduced in zoos (Allritz et al., 2016; Altschul et al., 2017; Brady et al., 2021; Déaux et al., 2021; Martin et al., 2022; Shumaker, 2018; Tanaka, 2016; Vonk et al., 2022). Since the gap-overlap task is relatively simple and does not require discrimination learning between stimuli, it can be readily introduced. In the future, large-scale research based on multi-facility collaborations may become possible (ManyPrimates et al., 2019a, b; 2022).

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**Conflict of Interest:** The authors declare that they have no conflicts of interest.

**Data Accessibility:** The datasets used for the data analyses in the present study: <https://doi.org/10.6084/m9.figshare.c.6870511>

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Supplementary Materials

Video S1

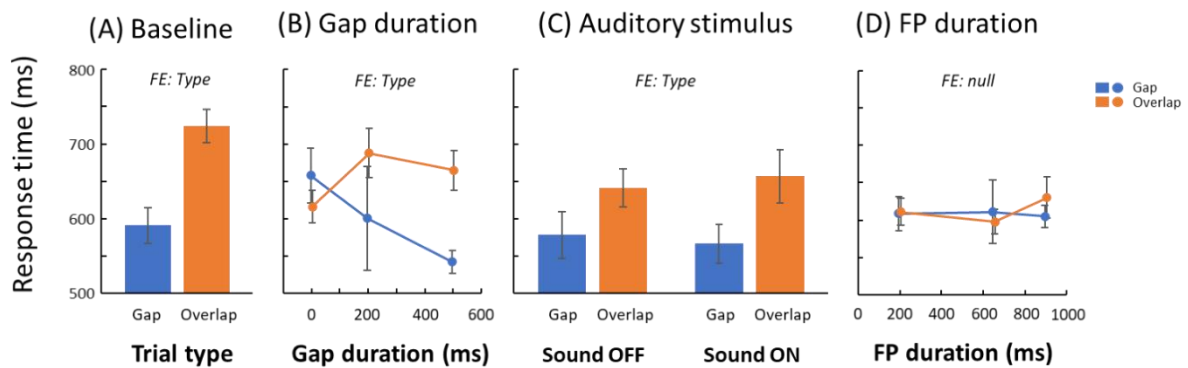
Chimpanzee Cleo performing the gap-overlap task in Experiment 2

<https://doi.org/10.6084/m9.figshare.c.6870511>

Figure S1

Results of Popo in Experiment 1

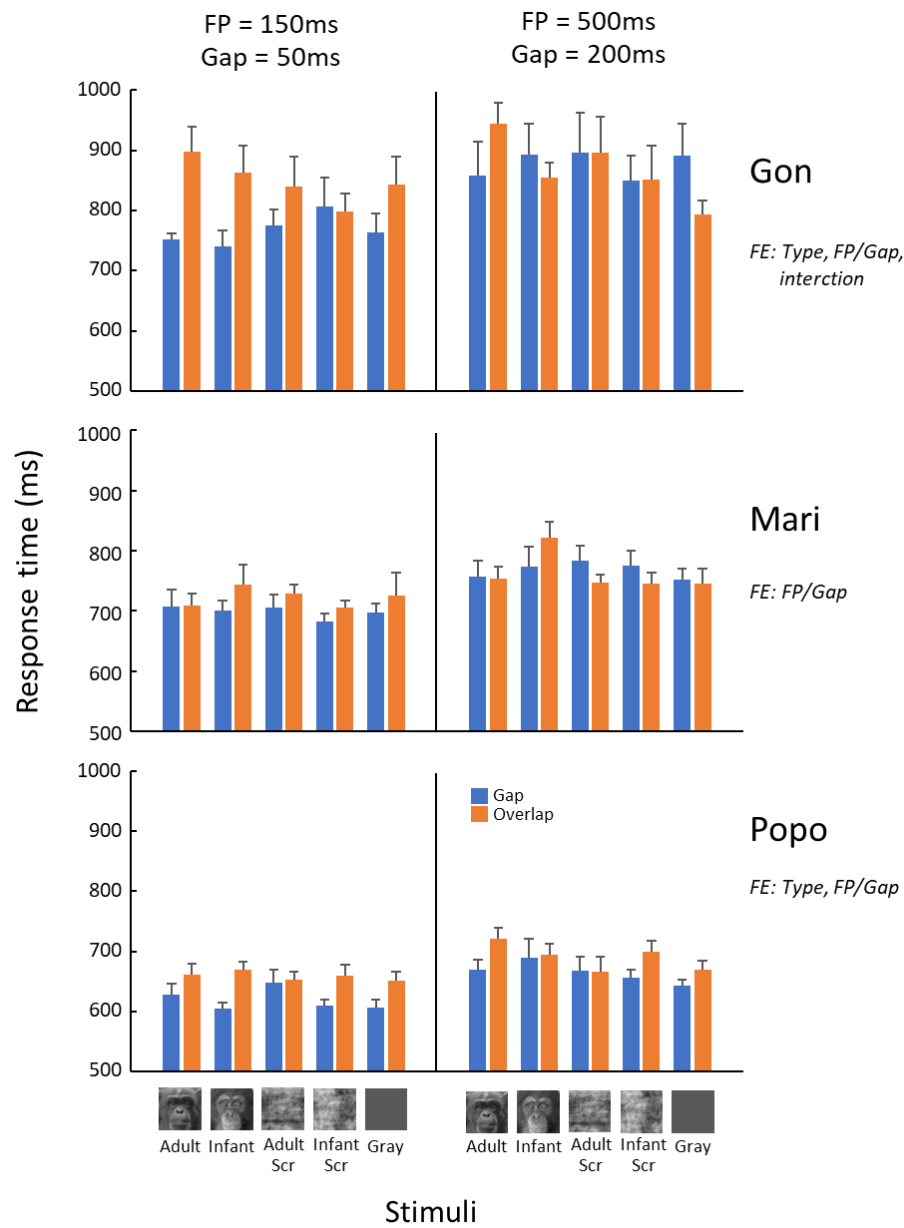
Popo



Note. Error bar indicates the standard error of mean across sessions.

Figure S2

Results of Gon, Mari and Popo in Experiment 2



Note. Error bar indicates the standard error of mean across sessions.

**Table S1***Summary of the GLMM Analyses in Experiment 1*

Test	Species	Log likelihood	AIC	Fixed effects	Estimate	SEM	95%CI	df	t	p	Random effect	SD
Baseline test	Chimpanzees	295.05	-580.1	(intercept)	5.86	0.03	5.81 5.91	4.2	215.15	9.80E-10	Session:Chimpanzee	0.03
				Trial Type	0.13	0.01	0.11 0.15	1873.0	13.72	<2.0E-16	Chimpanzee	0.06
	Humans	287.31	-566.6	(intercept)	5.97	0.04	5.89 6.05	9.4	148.01	<2.0E-16	Participant	0.13
				Trial Type	0.04	0.01	0.02 0.06	954.0	3.31	0.001		
Gap duration	Chimpanzees	-4.12	20.2	(intercept)	5.99	0.03	5.93 6.05	4.6	194.41	3.06E-10	Session:Chimpanzee	0.04
				Trial Type	0.05	0.01	0.03 0.07	1859.0	4.76	2.06E-06	Chimpanzee	0.06
				Gap	-1.97E-04	2.66E-05	-2.49E-04 0.00	1859.0	-7.40	2.09E-13		
Auditory stimulus	Chimpanzees	-234.55	479.1	(intercept)	5.86	0.01	5.84 5.88	8.6	515.40	<2.0E-16	Session:Chimpanzee	0.02
				Trial Type	0.10	0.01	0.08 0.13	1786.0	8.19	5.11E-16	Chimpanzee	0.01
FP duration	Chimpanzees	-350.27	712.5	(intercept)	6.05	0.04	5.97 6.13	5.2	151.41	9.81E-11	Session:Chimpanzee	0.04
				Trial Type	0.08	0.01	0.05 0.10	1940.0	6.10	1.30E-09	Chimpanzee	0.08
				FP	-2.41E-04	2.20E-05	-2.84E-04 0.00	1939.0	-10.96	<2.0E-16		

**Table S2***Summary of the GLMM Analyses in Experiment 1 (Popo)*

Test	Chimpanzee	Log likelihood	AIC	Fixed effects	Estimate	SEM	95%CI	df	t	p	Random effect	SD
Baseline test	Popo	-107.80	223.6	(intercept)	6.31	0.02	6.27 6.36	22.8	259.51	<2.0E-16	Session	0.02
				Trial Type	0.21	0.03	0.14 0.27	373.1	6.36	5.95E-10		
Gap duration	Popo	-81.78	169.6	(intercept)	6.31	0.02	6.27 6.36	382.0	270.19	<2.0E-16	Session	0.00
				Trial Type	0.12	0.03	0.06 0.19	382.0	3.68	2.63E-04		
Auditory stimulus	Popo	-72.74	153.5	(intercept)	6.30	0.03	6.25 6.35	13.9	232.82	<2.0E-16	Session	0.05
				Trial Type	0.11	0.03	0.06 0.17	374.0	3.91	1.10E-04		
FP duration	Popo	-81.78	169.6	(intercept)	6.37	0.02	6.33 6.40	7.0	411.80	<2.0E-16	Session	0.01

**Table S3***Summary of the GLMM Analyses in Experiment 1 (Super-Old Chimpanzees)*

Test	Chimpanzee	Log likelihood	AIC	Fixed effects	Estimate	SEM	95%CI		df	t	p	Random effect	SD
Baseline test	Gon	-195.08	398.2	(intercept)	6.55	0.05	6.47	6.64	11.2	143.91	<2.0E-16	Session	0.11
				Trial Type	-0.12	0.04	-0.19	-0.05	420.0	-3.28	1.15E-03		
	Puchi	-262.57	531.1	(intercept)	6.94	0.03	6.90	6.99	373.0	276.70	<2.0E-16	Session	0.00
Gap duration	Gon	-146.64	299.3	(intercept)	6.43	0.03	6.37	6.48	7.0	242.80	4.72E-15	Session	0.05
				Trial Type	6.80	0.03	6.74	6.85	378.0	231.94	<2.0E-16		
	Puchi	-200.84	409.7	(intercept)	6.80	0.03	6.74	6.85	378.0	231.94	<2.0E-16	Session	0.00
				Trial Type	0.13	0.04	0.05	0.22	378.0	3.20	0.001		
Auditory stimulus	Gon	-18.33	42.7	(intercept)	6.37	0.02	6.33	6.41	7.0	305.10	1.05E-15	Session	0.05
				Trial Type	6.91	0.05	6.82	7.01	3.0	141.10	6.58E-07		
	Puchi	-118.97	243.9	(intercept)	6.91	0.05	6.82	7.01	3.0	141.10	6.58E-07	Session	0.07
FP duration	Gon	-104.62	215.2	(intercept)	6.39	0.02	6.35	6.43	7.0	294.20	1.61E-15	Session	0.04



**Table S4***Summary of the GLMM Analyses in Experiment 2*

Species	Log likelihood	AIC	Fixed effects	Estimate	SEM	95%CI	df	t	p	Random effect	SD
			(intercept)	6.27	0.02	6.22 6.32	5.3	251.09	4.61E-12	Session:Chimpanzee	0.04
Chimpanzees	-1289.88	2593.8	Trial Type	0.05	0.01	0.04 0.07	8041.0	8.57	<2.0E-16	Chimpanzee	0.06
			FP/Gap	0.04	0.01	0.02 0.05	8109.0	5.49	4.26E-08	Stimuli	0.00

**Table S5***Summary of the GLMM Analyses in Experiment 2 (Gon, Mari, Popo)*

Chimpanzee	Log likelihood	AIC	Fixed effects	Estimate	SEM	95%CI	df	t	p	Random effect	SD
Gon	-207.54	429.1	(intercept)	6.61	0.02	6.57 6.65	32.6	320.66	<2.0E-16	Session	0.05
			Trial Type	0.08	0.02	0.04 0.12	1372.7	4.06	5.30E-05	Stimuli	0.03
			FP/Gap	0.11	0.02	0.07 0.16	1382.4	5.48	5.17E-08		
			interaction	-0.08	0.03	-0.14 -0.03	1373.1	-2.87	0.004		
Mari	-76.12	162.2	(intercept)	6.57	0.01	6.55 6.60	19.9	546.64	<2.0E-16	Session	0.03
			FP/Gap	0.10	0.01	0.07 0.12	1570.0	7.64	3.90E-14	Stimuli	0.00
Popo	-45.91	103.8	(intercept)	6.42	0.02	6.39 6.45	25.4	422.31	<2.0E-16	Session	0.04
			Trial Type	0.07	0.01	0.04 0.09	1400.0	5.01	6.19E-07	Stimuli	0.01
			FP/Gap	0.05	0.01	0.03 0.08	1309.0	3.95	8.41E-05		