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4 Stream/Bounce Perception and the Effect of Depth Cues in Chimpanzees (*Pan troglodytes*)

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Abstract

The stream/bounce display represents an ambiguous motion event in which two identical visual objects move toward one another and the objects overlap completely before they pass each another. In our perception, they can be interpreted as either streaming past one another or bouncing off each other. Previous studies have shown that the streaming percept of the display is generic for humans, suggesting the inertial nature of the motion integration process. In this study, chimpanzees took part in behavioral experiments using an object-tracking task to reveal the characteristics of their stream/bounce perception. Chimpanzees did not show a tendency towards a dominant "stream" perception of the stream/bounce stimulus. However, depth cues, such as X-junctions and local motion coherence, promoted the stream percept in chimpanzees. These results suggest both similarities and differences between chimpanzees and humans with respect to motion integration and object individuation processes.

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3 In our dynamically changing visual environment, an important task of the visual  
4 system is to pursue and identify moving objects and to maintain their inner representations  
5 across time and space. Recent studies have focused a great deal of attention on such  
6 perceptual aspects as the identification of moving objects. The investigations of the  
7 perceptual characteristics of stream/bounce displays are prominent examples of such  
8 studies.

9 In a stream/bounce display, two discs approach each other, overlap at the center  
10 of the display, and then separate again. The discs in this ambiguous display can be  
11 interpreted either as streaming past or as bouncing off each other. This stream/bounce  
12 display enables examination of how visual systems interpret events involving object  
13 movements, as well as the type of information selected and integrated to identify and  
14 represent moving objects in time and space. Thus, the visual interpretation of this bistable  
15 stream/bounce display has been tested using variable intramodal (Bertenthal, Banton, &  
16 Bradbury, 1993; Kanizsa, 1979; Metzger, 1934; A. B. Sekuler & Sekuler, 1999) and  
17 intermodal stimulus manipulations (Kawachi & Gyoba, 2006; R. Sekuler, Sekuler, & Lau,  
18 1997; K. Watanabe & Shimojo, 2001b). In general, the human visual system interprets the  
19 solo presentation of the ambiguous stream/bounce display as streaming, but this can be  
20 altered to a bouncing interpretation, depending on intramodal and crossmodal perturbations.  
21 These perceptual tendencies reflect the inertial properties of our visual system (Anstis &  
22 Ramachandran, 1987), which bias the recruitment of local motion signals to a straight  
23 motion path rather than a returning path, and the vulnerability of the maintenance processes  
24 of continuous motion to some perturbations.

1           In addition to the motion integration processes, depth is important feature in the  
2 perception of stream/bounce displays. The ambiguity of the stream/bounce perception is  
3 due to the two-dimensional nature of the display. In the natural world, the two objects  
4 stream past or bounce off each other depending on their three-dimensional spatial  
5 relationship. Therefore, perception of the stream/bounce display might involve visual  
6 interpretation of the depth dimension. Bertenthal, Banton and Bradbury (1993) tested this  
7 by adding depth information defined by binocular disparity to the stream/bounce stimuli,  
8 and demonstrated that depth cues play a crucial role in the resultant percepts.

9           Although the characteristics of object identification in this kind of bistable  
10 motion perception have been well analyzed in humans, few behavioral studies have directly  
11 addressed these issues in other animals. For example, in a field experiment on free-ranging  
12 rhesus macaques (*Macaca mulatta*), Flombaum et al. (2004) demonstrated tunnel effects,  
13 which also concern the individuation process of moving objects. They showed real objects  
14 (a lemon and a kiwifruit) in motion to monkeys in order to attract their attention. When the  
15 first object (a lemon) moved behind an occluder and the second object (a kiwifruit)  
16 appeared from the other side of the occluder at the appropriate time, the monkeys generally  
17 failed to search for the first object as if they had noticed only one continuously moving  
18 object. When continuity of the motion was disrupted, the tunnel effect disappeared, as is  
19 the case in human studies. These results suggest that properties of the motion integration  
20 process that maintain object identity may be shared by humans and monkeys. However,  
21 direct comparisons of the spatiotemporal characteristics of such motion integration  
22 processes between humans and nonhuman primates are lacking, and therefore further  
23 comparative experiments using controlled stimuli are helpful to explore the phylogenetic  
24 background of our visual recognition processes.





1           To assess chimpanzees' perception of ambiguous stream/bounce displays in the  
2 absence of verbal reports of their subjective experience, we adopted an object-tracking task  
3 (e.g. Pylyshyn & Storm, 1988; Figure 1). In the stream/bounce display, two discs appeared,  
4 one each at the right and left side of the display, with one of the discs cued by flickering at  
5 the beginning of each trial. Then, the two discs started to approach each other, completely  
6 overlapped at the center of the display, and separated again. Participants were required to  
7 visually track the initially cued disc through the movement phase and to point to the disc  
8 after the two discs stopped moving. Pointing to the disc at the side where the cued disc was  
9 initially located indicated that the participant perceived the discs as bouncing, whereas  
10 pointing to the disc at the opposite side indicated that the participant perceived streaming.

11           Experiment 1: Stream/bounce perception in chimpanzees and humans.

12           Experiment 1 investigated chimpanzee perception of the stream/bounce stimulus.  
13 In the test sessions, two stimulus conditions were tested by varying the movement speed of  
14 the discs. In the 100% overlap condition (stream/bounce stimuli), the two discs completely  
15 overlapped at the center of the display. In the 50% overlap condition (intermediate partial-  
16 overlap stimuli) used as a control, the two discs stopped overlapping when the edge of one  
17 disc reached the center of the other disc. We expected that the participants would more  
18 frequently perceive the partial-overlap stimuli as bouncing than the completely overlapping  
19 stream/bounce event.

## 20 *Methods*

### 21 *Participants*

22           Six chimpanzees, and 5 adult humans (females) ranging in age from 18 to 25  
23 (mean = 21.2), participated in the experiment. All the human observers had normal or  
24 corrected-to-normal visual acuity.





1 across trials: 720 ms on average). After the delay period, a gray square (38 x 38 mm)  
2 appeared around each disc to signal the start of the response phase. Chimpanzees were  
3 required to indicate the cued disc. A correct response was followed by a chime sound and  
4 delivery of a food reward. An incorrect response was followed by a buzzer sound and a 4-s  
5 timeout. The interval between the end of the trial and the presentation of the warning  
6 stimulus for the next trial was 2-s.

7 A training session under the static condition consisted of 64 trials. The left -  
8 right position of the cued disc was counterbalanced in a session. The training phase was  
9 continued until the participant reached the criterion for learning, which was set as >90%  
10 accuracy in three consecutive sessions.

#### 11 *Second training phase (movement condition)*

12 In the second phase of training, chimpanzees were trained to track the  
13 movement of the target disc with two types of movement path, unambiguous streaming and  
14 unambiguous bouncing. Four kinds of trials, two for the streaming movement and two for  
15 the bouncing movement, were prepared (Figure 2). In the training trials, the vertical  
16 locations of the two discs were initially set to be differentiated at the length of radius of the  
17 disc. Under one condition, the discs moved horizontally to the opposite side of the display  
18 (Figure 2A). The discs partially overlapped at the center of the display, but their identity  
19 was not ambiguous due to the vertical misalignment; human observers perceived  
20 unambiguous streaming of the discs. Under another condition (Figure 2B), the discs moved  
21 horizontally and reversed their direction at the point where they touched an imaginary  
22 vertical center line of the display. Therefore, the discs did not partially overlap, and human  
23 observers perceived unambiguous bouncing. Under these two conditions, the vertical  
24 relationship of the two discs was maintained in each trial, so the chimpanzees could detect

1 a cued disc by attending to the vertical position without tracking the disc. Therefore, in the  
2 other two types of trials, the relative vertical positions were reversed between pre- and  
3 post- oblique movements (Figures 2C and D). Under these conditions, two discs moved  
4 with slight vertical displacements so that their relative vertical positions were reversed at  
5 the center of the display. The two discs moved on (streaming) or returned at the point  
6 where the discs touched the imaginary vertical center line of the display (bouncing). Initial  
7 vertical positions (upper or lower of left or right stimuli) were random across trials.

8           At the movement phase, the discs were horizontally displaced at 144, 287, 431,  
9 or 574 mm ( $18.1^\circ$ ,  $35.4^\circ$ ,  $51.1^\circ$ , or  $65.1^\circ$ , respectively) per second. Each stimulus frame  
10 lasted 13.3 ms, and the displacement at a frame was less than the size of the disc radius  
11 even at the highest speed.

12           Each trial proceeded as in the static condition except that the disc movement  
13 phase described above was inserted just after the cueing flash of one disc ended.  
14 Chimpanzees were required to indicate the position of the target disc when the discs  
15 stopped moving and a gray squares appeared around each disc to signal the start of the  
16 response phase.

17           A training session with disc movement consisted of 128 trials (eight trials for  
18 each movement speed and movement path condition). Each training phase was continued  
19 until the participant reached the criterion for learning, which was set as  $>90\%$  accuracy in  
20 three consecutive sessions.

### 21           *Test phase*

22           In the test phase, we tested how the stream/bounce stimuli and partial-overlap  
23 stimuli were perceived. In test probe trials, two discs were initially horizontally aligned and  
24 then horizontally moved toward one another. In the stream/bounce display (Figure 3A), the

1 discs completely overlapped and moved on to the sides of the display. In the partial-overlap  
2 display (Figure 3B), the discs turn their movement directions when the edge of one disc  
3 reached at the center of the other disc. The discs moved at 144, 287, 431, or 574 mm (18.1°,  
4 35.4°, 51.1°, or 65.1°, respectively) per second.

5           Probe trials were intermixed with baseline trials, which were the same as those  
6 in the training session with moving discs. For chimpanzees a test session consisted eight  
7 probe trials, during which each combination of movement speed and overlap condition was  
8 tested, and 128 baseline trials. The eight probe trials appeared randomly in a session. The  
9 left - right position of the cued disc was counterbalanced in a session. Each chimpanzee  
10 participated in 20 test sessions. Feedback in baseline trials was the same as in the second  
11 training phase. In probe trials, no feedback was given, and the next trial started after 2-s  
12 interval.

### 13           *Test in humans*

14           For humans, a test session consisted of 80 probe trials. Ten trials under each  
15 combination of overlap and speed condition were randomly intermixed in the session. Each  
16 human participated in one test session. Prior to the test session, each human observer  
17 received 16 baseline trials. They were instructed to track an initially cued disc and touch it  
18 after the discs had stopped.

### 19           *Results*

#### 20           Training phase

21           In the first training phase, in which static stimuli were used, chimpanzees  
22 required 32 sessions on average to reach the learning criterion (53, 10, 5, 24, 80, and 21  
23 sessions for Ai, Ayumu, Chloe, Cleo, Pal, and Pendesa). Individual differences did not  
24 reflect age, but probably on their motivation on the new task.

1 Performance in the second training phase with moving stimuli (Figure 2) was  
 2 significantly better than chance level (50%) even in the first session (71.1% correct on  
 3 average,  $t(5) = 4.1, p < .01$ ) both in the streaming condition (73.9%) and the bouncing  
 4 condition (68.3%). Chimpanzees required 23 sessions on average to reach criterion (33, 4,  
 5 8, 18, 59, and 17 sessions for Ai, Ayumu, Chloe, Cleo, Pal, and Pendesa).

6 The generalization of performance from the first training phase (static discs) to  
 7 the second training phase (moving discs) means that chimpanzees spontaneously tracked  
 8 the cued disc when the disc moved position. This also guaranteed that chimpanzees did not  
 9 solve the task by learning one-to-one stimulus-response associations (associations of 2 cue  
 10 positions, 4 movement patterns and left/right responses). This was also supported by  
 11 another study (Matsuno & Tomonaga, in preparation), conducted after this one, in which  
 12 four of the six chimpanzees were tested on tracking of a target disc among 4 discs that  
 13 rotationally moved on a shared path. They successfully tracked the target disc (74.5%  
 14 correct on average) in the first session, irrespective of the novelty of movement patterns.  
 15 These results confirm that results in the following test probe trials reflected object tracking  
 16 abilities rather than the other processes associated with the specific cues in the training  
 17 displays.

18 Test phase

19 -----

20 Insert Figure 4 about here

21 -----

22 The performance of chimpanzees and humans in the probe trials is shown in  
 23 Figure 4. Response tendencies differed between the two groups. Humans predominantly  
 24 perceived the ambiguous stream/bounce event (100% overlap condition) as streaming, even

1 in the partial-overlap condition at high speed. However, chimpanzees predominantly  
2 perceived the two discs as bouncing, irrespective of the conditions.

3 A two-way analysis of variance (ANOVA) of overlap and speed conditions in  
4 humans revealed a significant main effect of the overlap condition,  $F(1, 4) = 63.4, p < .01$ ,  
5 and an interaction,  $F(3, 12) = 10.0, p < .01$ . Post-hoc simple main effect analyses revealed  
6 that performance under the partial-overlap condition varied with movement speed,  $F(3, 12)$   
7  $= 5.08, p < .05$ . The simple main effect of overlap condition was significant at the slowest  
8 speed,  $F(1, 5) = 13.8, p < .05$ , but not at other speeds.

9 In chimpanzees, the main effects of moving speed,  $F(3, 15) = 0.8, p > .10$ , and  
10 degree of overlap,  $F(1, 5) = 6.1, p > .05$ , were not significant but their interaction was,  $F(3,$   
11  $15) = 4.5, p < .05$ . Analysis of the simple main effect revealed that performance varied with  
12 movement speed under the partial-overlap condition,  $F(3, 15) = 4.2, p < .05$ , but not under  
13 the 100% overlap stream/bounce condition,  $F(3, 15) = 1.7, p > .10$ . The simple main effect  
14 of overlap condition was significant only at the slowest speed,  $F(1, 5) = 13.8, p < .05$ .

15 The average streaming responses of chimpanzees in the 100 % overlap  
16 stream/bounce display (29.2%) were significantly below chance,  $t(5) = 3.0, p < .05$ . In  
17 contrast, those of humans (81.0%) were significantly above chance,  $t(4) = 3.9, p < .01$ .

### 18 *Discussion*

19 Humans perceived the stream/bounce stimuli as streaming, consistent with  
20 previous studies (Bertenthal, Banton, & Bradbury, 1993; A. B. Sekuler & Sekuler, 1999).  
21 They also perceived the partial-overlap stimuli as streaming more frequently when the  
22 speed of movement was higher. The effects of speed could be due to the difference in the  
23 size of stimulus displacement per frame. At higher speeds, the frame-by-frame  
24 displacement was larger relative to the size of the stimuli, and the motion correspondence

1 between frames was more ambiguous.

2           In contrast to humans', the performance of the chimpanzees unexpectedly  
3 showed a tendency to perceive both the stream/bounce stimuli and the partial-overlap  
4 stimuli as bouncing. Baseline trial performances were very accurate (92% correct on  
5 average), indicating the idea that the chimpanzees tracked the target correctly, regardless of  
6 the type of movement. In addition, their performance varied depending on the combination  
7 of overlap and speed conditions, similar to humans. Therefore, it is difficult to explain the  
8 results as a simple response bias such as neglecting the tracking task and merely selecting  
9 the disc on the side where the cued disc initially appeared.

10           What do these results indicate about differences in visual interpretation between  
11 chimpanzees and humans? A difference was seen in the overall frequency of percepts of  
12 streaming. On the other hand, the similar speed effects in the partial-overlap condition and  
13 the shared direction of the effect of stimulus overlap suggest common perceptual  
14 mechanisms for resolving the ambiguous motion event. Therefore, the observed species  
15 difference might reflect differences in the degree, but not kind, of perceptual functions  
16 needed to track and identify a moving object.

17           As noted previously, humans sometimes predominantly perceive bouncing  
18 (Bertenthal, Banton, & Bradbury, 1993; A. B. Sekuler & Sekuler, 1999; R. Sekuler, Sekuler,  
19 & Lau, 1997; K. Watanabe & Shimojo, 1998; K. Watanabe & Shimojo, 2001b). The human  
20 visual system has a default tendency to assume the continuous movement of objects to  
21 individuate them and maintain object identity. Thus, streaming percepts are dominant in  
22 solo presentations of a stream/bounce display. However, when an external perturbation  
23 interrupts the continuous motion-integration process, such as the abrupt onset of a click  
24 sound and sudden cessation of movement, the percept transforms to bouncing. Thus, one

1 possible reason for the observed species difference is that the motion integration process to  
2 one direction is more easily perturbed in chimpanzees than in humans. Although we did not  
3 include explicit perturbations to the display, the stimulus configuration of the  
4 stream/bounce display itself may have contained perturbing factors to which chimpanzees  
5 might have been more sensitive. This might also apply to the small number of trials in  
6 which humans perceived the 100% overlap stream/bounce displays as bouncing.  
7 Conceivably, a change in stimulus configuration to be less disruptive to and to facilitate the  
8 individuation of each object at their coincidence would promote dominant stream percepts  
9 in chimpanzees. To investigate this issue further, the stream/bounce perception of  
10 chimpanzees was tested in the following experiments.

11 Experiment 2: Stream/bounce perception in chimpanzees using ring stimuli

12 In the second experiment, we confirmed that the streaming percept is also the  
13 default state in chimpanzees when no external perturbation exists and the two discs are  
14 more readily individuated. Because no distractor stimulus was used in Experiment 1, the  
15 factors that disturb the chimpanzees' motion integration for one direction could have been  
16 the overlap or fusion of the two discs themselves. When the two filled stimuli touched, part  
17 of the stimulus edge started to fuse and disappeared. Consequently, the local directional  
18 signal of the target disc decreased, and the two stimuli became difficult to individuate. This  
19 could impair motion integration. Thus, in this experiment, we used open ring stimuli  
20 (Figure 3C), that provided an explicit depth cue (X-junctions) when two objects crossed.  
21 When open ring stimuli partially overlapped, their edges were still salient and the junctions  
22 of the two stimuli could be an explicit signal for the cross-over of the two objects. In  
23 addition, the local motion signal was more salient with the ring stimuli than with the filled  
24 disc. This might promote continuous motion integration to one direction.

## 1 *Methods*

2 Four chimpanzees participated in the experiment. Stimuli and procedures were  
3 the same as in Experiment 1 except as described here. Displays consisted of the two gray  
4 discs used in Experiment 1 or two gray open ring stimuli that matched the contours of the  
5 discs (Figure 3C). At the movement phase, the objects were horizontally displaced at 144  
6 mm (18.1°) per second.

7 In each test session, the configuration of stimuli (filled disc or open ring) was  
8 fixed, and the two stimulus conditions were presented in alternate sessions. A test session  
9 consisted of 128 baseline trials, which were the same as in Experiment 1 except for the  
10 stimuli (open ring in half of the sessions), and eight probe trials, during which four trials in  
11 each overlap condition (stream/bounce condition with 100% overlap or partial-overlap  
12 stimuli with 50% overlap) were presented. All responses in probe trials were positively  
13 reinforced, as were correct responses in baseline trials. Each chimpanzee participated in 10  
14 sessions (five sessions under each stimulus condition). No additional training sessions were  
15 conducted.

## 16 *Results*

17 -----  
18 Insert Figure 5 about here  
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20 Chimpanzee perception of the ring stimuli stream/bounce display became  
21 predominantly streaming, whereas bouncing was perceived with the uniformly filled gray  
22 discs, as in Experiment 1 (Figure 5).

23 A two-way ANOVA revealed significant main effects of stimulus,  $F(1, 3) =$   
24  $26.7, p < .05$ , and overlap conditions,  $F(1, 3) = 154.7, p < .01$ , and their interaction,  $F(1,3)$



1 = 55.4,  $p < .01$ . Analysis of the simple main effect confirmed that the percentages of  
2 perceived streaming differed significantly between stimulus conditions (filled discs or open  
3 rings) in the stream/bounce condition with 100% overlap of stimuli,  $F(1, 3) = 243.0$ ,  $p$   
4  $< .01$ , but not in the partial-overlap condition,  $F(1, 3) = 0.3$ ,  $p > .10$ . The simple effects of  
5 the overlap condition were significant under both filled disc and open ring conditions,  $F(1,$   
6  $3) = 33.0$  and  $211.0$ ,  $p < .01$ .

7           The average streaming response to the 100 % overlap ring stimuli (78.8%) was  
8 significantly above chance,  $t(3) = 4.0$ ,  $p < .05$ . The chimpanzees performed very accurately  
9 in baseline trials with open rings (93% correct responses on average), similar to their  
10 performance with filled discs (94%),  $F(1, 3) = 1.2$ ,  $p > .10$ .

### 11 *Discussion*

12           Chimpanzees predominantly perceived the 100% overlap stream/bounce display  
13 as streaming when open ring stimuli were used. The filled disc display was less frequently  
14 perceived as streaming, though the percentage increased with increasing overlap, as in  
15 Experiment 1. The alternation of chimpanzees' perception with stimulus manipulation  
16 further confirmed that chimpanzees did not blindly select the disc on the side where the  
17 target initially appeared in probe trials. Furthermore, these results suggest that the  
18 difference between chimpanzee and human perception shown in Experiment 1 reflects  
19 differences in the degree, but not the kind, of the perceptual function needed to track and  
20 identify a moving object.

21           When the two stimuli in stream/bounce displays overlap, the visual system tends  
22 to integrate the local motion signals along the same trajectory and to interpret the event as  
23 continuous smooth motion. Such default streaming percepts by chimpanzees, however,  
24 may be more easily perturbed. The open ring stimuli provided an explicit cue of a crossover

1 of the two objects in the depth dimension (X-junctions of the contours), which made  
2 individuation of the two stimuli easier, and unambiguous local motion signals. This  
3 enhanced saliency may compensate for the vulnerability of the motion integration process  
4 in chimpanzees.

### 5 Experiment 3: Stream/bounce perception in chimpanzees using random dot stimuli

6 In Experiment 3, we examined the effect of another depth cue, motion  
7 transparency, on the perception of stream/bounce displays in chimpanzees. Coherently  
8 moving dots produce the percept of motion transparency in humans (Braddick, Wishart, &  
9 Curran, 2002; Edwards & Greenwood, 2005). Using random dot stimuli that coherently  
10 moved in opposite directions from each other, we expected that the two objects would be  
11 perceived at different depth dimensions and would be easily discriminated when they were  
12 crossing. We tested chimpanzee perception of the stream/bounce display with random dot  
13 stimuli compared to a display with uniformly filled stimuli.

### 14 *Methods*

15 Five chimpanzees participated in the experiment. Stimuli and procedures were  
16 the same as in Experiment 2 except as described here. Displays consisted of the two  
17 identical gray squares or two identical random dot squares of 10% density (Figure 3D).  
18 Each stimulus was subtended about 23 x 23 mm ( $2.9^\circ \times 2.9^\circ$  of visual angle at a viewing  
19 distance of 45 cm). In the movement phase the squares were horizontally displaced at 144  
20 mm ( $18.1^\circ$ ) per second.

21 In each test session, the configuration of stimuli (filled squares or random dot  
22 squares) was fixed, and sessions of each stimulus condition alternated. A test session  
23 consisted of 128 baseline trials, the same as in Experiment 2 except for the stimuli (filled  
24 squares or random dot squares), and eight probe trials, in which four trials of each overlap

1 condition were presented. All responses in the probe trials were positively reinforced, as  
2 were correct responses in baseline trials. Each chimpanzee participated in 10 sessions (five  
3 sessions in each stimulus condition), with no additional training sessions.

#### 4 *Results*

5 -----  
6 Insert Figure 6 about here  
7 -----

8 Chimpanzees tended to perceive the stream/bounce display as streaming when  
9 the stimuli were random dot squares, whereas bouncing was perceived with uniformly  
10 filled gray squares (Figure 6). A two-way ANOVA revealed significant main effects of the  
11 stimulus,  $F(1, 4) = 42.0, p < .01$ , and overlap conditions,  $F(1, 4) = 115.1, p < .01$ , and their  
12 interaction,  $F(1,4) = 15.8, p < .05$ . Analysis of the simple main effect confirmed that in the  
13 stream/bounce condition with 100% overlap of stimuli the percentages of perceived  
14 streaming differed significantly between stimulus conditions,  $F(1, 4) = 42.5, p < .01$ , but  
15 not in the partial-overlap condition,  $F(1, 4) = 1.1, p > .10$ . The simple main effects of  
16 degree of overlaps were significant under both filled square and random dot stimulus  
17 conditions,  $F(1, 4) = 13.4$  and  $76.9, p < .05$ .

18 The average streaming responses of chimpanzees when perceiving the 100 %  
19 overlap random dot stimuli (64%) was above chance, at a marginally significant level with  
20 a two-tailed  $t$ -test,  $t(4) = 2.5, p = .07$ . The performance in baseline trials with random dot  
21 squares (93% correct responses on average) was highly accurate, and not significantly  
22 different from that with filled squares (94%),  $F(1, 4) = 1.1, p > .10$ .

#### 23 *Discussion*

24 Chimpanzees tended to perceive the stream/bounce display as streaming when



1 motion by temporally integrating the proximal dot positions. The performance of the  
2 chimpanzees in the incoherent random dot condition was compared to that in the filled  
3 square condition, which was identical to that in Experiment 3. Other procedures were the  
4 same as in Experiment 3. No additional training sessions were given.

### 5 *Results*

6 -----  
7 Insert Figure 7 about here  
8 -----

9 The perception of the stream/bounce display was not at all biased toward  
10 streaming when the random dots were not coherently updated (Figure 7). Performance in  
11 the random dot condition did not differ much from that in the filled square condition, even  
12 when the stimuli overlapped 100%.

13 A two-way ANOVA revealed a significant main effect of overlap,  $F(1, 4) = 17.0$ ,  
14  $p < .05$ , but neither the main effect of stimuli,  $F(1, 4) = 4.1$ ,  $p > .10$ , nor the interaction,  
15  $F(1,4) = 2.5$ ,  $p > .10$ , was significant. The streaming responses to the 100% overlap  
16 stream/bounce displays with random dot stimuli (37 % on average) was not significantly  
17 different from chance,  $t(4) = 2.0$ ,  $p > .10$ . Performances in baseline trials with both random  
18 dot squares (93% correct responses) and filled squares (91% correct responses) were  
19 similarly accurate,  $F(1, 4) = 1.8$ ,  $p > .10$ .

20 Direct comparison between performance in the coherently moving random dot  
21 condition in Experiment 3 and that in the incoherently moving random dot condition in this  
22 experiment revealed that streaming was perceived significantly more frequently in the  
23 former condition. A two-way ANOVA revealed a significant main effect of overlap  
24 condition,  $F(1, 4) = 63.7$ ,  $p < .01$ , and the interaction between overlap and coherency.

1 Analysis of the simple main effect confirmed that the percentages of perceived streaming  
2 differed significantly between the experiments in the 100% overlap condition,  $F(1, 4) =$   
3  $15.7, p < .05$ , but not in the partial-overlap condition,  $F(1, 4) = 0.0, p > .10$ .

#### 4 *Discussion*

5           Although the stimuli used were almost the same as in Experiment 3, except for  
6 the temporal coherence of each dot, they strongly influenced the chimpanzees' perception.  
7 In this experiment, chimpanzees tended to perceive the stream/bounce display as bouncing,  
8 irrespective of stimulus type. The streaming responses diminished significantly with  
9 incoherently moving random dot stimuli compared to coherently moving random dot  
10 stimuli. These results suggest that what promoted the perception of streaming in  
11 Experiment 3 was neither the low luminance intensity nor the doubling of the dot density at  
12 the overlap of the stimuli. Instead, coherent local motion and, conceivably, the perceived  
13 motion transparency arising from the coherent motion likely helped the chimpanzees to  
14 maintain their continuous tracking of the target.

15       Experiment 5: Stream/bounce perception in humans using ring and random dot stimuli

16           In Experiment 5, human participants were tested with the filled disc, filled  
17 square, open ring, and coherent and incoherent random dot stimuli used in Experiments 2  
18 to 4, in order to reevaluate the chimpanzees' performances in Experiments 2 to 4 in  
19 comparison with those of humans.

#### 20 *Methods*

21           Six humans (1 male and 5 female) ranging in age from 22 to 29 years (mean =  
22 24.4) were tested. Stimuli were the same as those used in Experiments 2 (filled discs and  
23 open rings), 3 and 4 (filled squares and coherently and incoherently moving random dot  
24 stimuli). In the movement phase the objects were horizontally displaced at 144 mm (18.1°)

1 per second as in Experiments 2 to 4.

2 A test session consisted of 100 probe trials. Ten trials of each combination of 2  
 3 overlap (stream/bounce condition with 100% overlap or intermediate partial-overlap  
 4 stimuli with 50% overlap) and 5 stimulus configuration conditions (filled discs, open rings,  
 5 filled squares, and coherently or coherently moving random dots) were randomly  
 6 intermixed in the session. Each participant received a single test session, preceded by 20  
 7 baseline trials as used in the tests with chimpanzees. They were instructed to track an  
 8 initially cued disc and touch the disc after the discs had stopped.

### 9 *Results*

10 -----

11 Insert Figure 8 about here

12 -----

13 The results of Experiment 5 are shown in Figure 8. The data for circular (filled  
 14 disc and open ring) and rectangular stimuli (filled square and coherent and incoherent  
 15 random dot) were analyzed separately, as each corresponds to the analysis in Experiment 2  
 16 or Experiments 3-4.

17 With circular stimuli, humans predominantly perceived streaming of the  
 18 stream/bounce stimuli, irrespective of the stimulus configuration. In addition, with open  
 19 ring stimuli streaming was perceived more frequently than with filled discs.

20 A two-way ANOVA of overlap and stimulus configuration conditions revealed  
 21 significant main effects of overlap,  $F(1,5) = 136.0, p < .01$ , and stimulus configuration,  $F(1,$   
 22  $5) = 15.1, p < .05$ . The interaction was not significant,  $F(1, 5) = 1.6, p > .10$ . The streaming  
 23 responses to 100% overlap with open ring stimuli (98.3 % on average) was significantly  
 24 above chance,  $t(5) = 29.0, p < .01$ .

1           The participants also predominantly perceived filled square and coherently and  
2 incoherently moving random dot stimuli to be streaming when the two stimuli completely  
3 overlapped. Partial-overlap events were perceived as streaming less frequently than  
4 stream/bounce events, and the frequency varied among the conditions of stimulus  
5 configuration. Participants perceived partial-overlap of two random dot conditions as  
6 streaming more frequently than partial-overlap of filled squares.

7           A two-way ANOVA revealed significant main effects of overlap condition,  
8  $F(1,5) = 53.9, p < .01$ , and stimulus configuration,  $F(2, 10) = 7.6, p < .01$ , and a significant  
9 interaction,  $F(2, 10) = 10.9, p < .01$ . Post-hoc simple main effect analyses revealed that  
10 performance under the partial-overlap condition varied with stimulus configuration,  $F(2,$   
11  $10) = 10.8, p < .05$ , but the performance under the stream/bounce condition did not,  $F(2,$   
12  $10) = 0.7, p > .10$ . The multiple comparison (paired  $t$  test with Holm's correction) of  
13 performances with 3 stimulus configurations in the partial-overlap condition revealed that  
14 stream responses to filled disc stimuli were significantly less frequent than to coherent and  
15 incoherent random dot stimuli,  $t(5) = 3.6$  and  $3.4, p < .05$ . The two random dot conditions  
16 were not significantly different from each other,  $t(5) = 2.0, p > .10$ . The streaming  
17 responses to the 100% overlap stream/bounce displays with coherently and incoherently  
18 moving random dot stimuli (98.3 and 96.7 % on average) were significantly above chance,  
19  $t(5) = 29.0$  and  $22.1, p < .01$ .

## 20 *Discussion*

21           Human participants predominantly perceived the 100% overlap stream/bounce  
22 event with open rings and coherently moving random dot stimuli as streaming. In addition,  
23 these stimuli were perceived as streaming more than the filled stimuli. These results recall  
24 those of chimpanzees in Experiments 2 to 4, though the overall frequency of streaming





1           These results reveal both differences and similarities between the perceptual  
2 processes of chimpanzees and humans. Chimpanzees, like humans, perceived ambiguous  
3 stream/bounce events as streaming when the two stimuli were readily discriminable from  
4 each other due to the addition of depth cues, thus indicating that the tendency to keep track  
5 of a unidirectional and continuous movement, and its resultant default streaming percepts,  
6 is shared by chimpanzees and humans. However, this tendency appears to be more readily  
7 perturbed in chimpanzees. Previous studies have identified multiple factors that can  
8 alternate stream/bounce perception (Bertenthal, Banton, & Bradbury, 1993; Grassi & Casco,  
9 2009; Kawabe & Miura, 2006; A. B. Sekuler & Sekuler, 1999; K. Watanabe & Shimojo,  
10 2001a, 2001b), and determining a single mechanism that would fully explain the  
11 vulnerability of the streaming perception in chimpanzees is difficult.

12           One possible explanation is that the spatiotemporal integration process of local  
13 motion signals may differ between the species. Previous studies in humans have proposed  
14 that the dominant streaming perception can be explained by the intrinsic directional bias  
15 involving the temporal integration arising from the cooperative interaction between local  
16 motion detectors (e.g. Bertenthal, Banton, & Bradbury, 1993). In our study, one prominent  
17 difference between stimuli to which chimpanzees did and did not perceive more streaming  
18 (open ring and coherent random dot vs. filled and incoherent random dot stimuli) was  
19 concerned continuity of the local motion at the brief interval when target and nontarget  
20 stimuli crossed over. This implies that the temporal integration window may be smaller in  
21 chimpanzees than in humans and that chimpanzees' perception may rely more on the local  
22 motion mechanism. Although the temporal integration process has not been well studied in  
23 chimpanzees, several comparative studies between chimpanzees and humans revealed  
24 species differences in spatial integration processes (e.g. Fagot & Tomonaga, 1999; Fagot &

1 Tomonaga, 2001). In these studies, chimpanzees were less sensitive to the global  
2 configuration of visual stimuli. The relative local bias in chimpanzees' visual processing  
3 may be common between temporal and spatial domains.

4           Another possible explanation related to the motion integration process is a  
5 difference in the quality of sustained attention between chimpanzees and humans. Visual  
6 attention has a critical role in motion perception, selecting and integrating visual  
7 information across time and space and keeping track of and identifying moving objects (e.g.  
8 Cavanagh, 1992; Choi & Scholl, 2004; Pylyshyn & Storm, 1988). Research on the effects  
9 of the state of visual attention on stream/bounce perception has revealed that poorer  
10 attentional resources directed to the moving object cause more frequent bouncing percepts  
11 (K. Watanabe & Shimojo, 1998), suggesting that sufficient quality of attention is required  
12 for constant motion-integration processing and thus the perception of streaming. Thus, the  
13 more frequent bouncing responses of chimpanzees might indicate that chimpanzees'  
14 attention is more readily disrupted than that of humans.

15           Species differences in the quality of pursuit of moving objects may also explain  
16 the different perception of stream/bounce displays. In our experiments, both chimpanzee  
17 and human participants were allowed to observe the display freely, without fixation. Pursuit  
18 eye movements can modulate perceived object motion (Baker & Graf, 2010; Kerzel, 2000)  
19 and promote streaming percepts in our display. Therefore, the difference in pursuit eye  
20 movements between chimpanzees and humans could influence how each species perceives  
21 stream/bounce displays. However, previous studies have shown that humans perceive  
22 streaming of the stream/bounce stimuli even when the eyes were fixated (e.g. Bertenthal,  
23 Banton, Bradbury, 1993; Sekuler & Sekuler, 1999), and the frequency of streaming  
24 percepts in those study (approximately 80 to 95%) was similar to that in this study.

1 Therefore the higher rate of streaming perception by humans in our study can not be  
2 explained simply by effects of pursuit eye movement. Comparative data on smooth pursuit  
3 of moving objects between chimpanzees and humans are lacking; such data are needed to  
4 examine this issue in more detail.

5           The effect of visual experience during training sessions should also be  
6 considered. Prior to test sessions, our chimpanzees experienced an equal number of  
7 unambiguous streaming and bouncing displays in training trials. However, in the natural  
8 world, a plausible assumption is that an object moving in one direction continues to move  
9 in that direction (Hall-Haro, Johnson, Price, Vance, & Kiorpes, 2008; Spelke, 1994); and  
10 any bouncing event is accidental (K. Watanabe & Shimojo, 2001a). This is consistent with  
11 the tendency of our visual system to interpret bistable ambiguous visual information, such  
12 as a stream/bounce display, as unidirectional movement (Anstis & Ramachandran, 1987;  
13 Bertenthal, Banton, & Bradbury, 1993). Thus, equalized experiences of streaming and  
14 bouncing percepts are unrealistic. This abnormally increased experience of bouncing  
15 percepts may have distorted the prior stochastic expectancy of the event perception by the  
16 chimpanzees, which may have biased their responses to include more bouncing percepts.

17           However, our data do not seem to support this idea. First, the number of training  
18 sessions experienced by each chimpanzee (ranging from 4 to 59 sessions) and percentages  
19 of perceived bouncing were not positively correlated (Pearson's correlation;  $r = -.14$ ;  $p$   
20  $>.10$ ). Second, in additional tests, human participants, who received prolonged experiences  
21 of baseline trials, maintained their predominant streaming percepts (Supplementary  
22 Materials: Experiment S1). The comparative test in humans, however, assessed the effect of  
23 limited number of baseline trials (256 trials) and was not fully equivalent to the tests in  
24 chimpanzees. The effect of longer-term visual experience on the stream/bounce perception

1 should be evaluated in future studies.

2           An alternative interpretation of the results focuses on differences in the  
3 perception of depth when two-dimensional discs are presented on a flat monitor surface.  
4 Our interpretation of a computerized stream/bounce display may relate to structural  
5 constraints and the physical laws of the three-dimensional natural world, in which two solid  
6 objects on the same depth plane collide and those on different planes pass through (Scholl  
7 & Nakayama, 2002; A. B. Sekuler & Sekuler, 1999; K. Watanabe & Shimojo, 2001a).  
8 When humans perceive the stream/bounce stimuli as streaming, the two objects are  
9 perceived to be on different surfaces, not only in the open ring and random dot conditions  
10 but also in the filled disc condition. Chimpanzees may not perceive such depth dimensions  
11 on the planar surface of a CRT monitor when explicit depth cues are not given to the  
12 objects, and their perceptual processing may interpret objects on the same surface as never  
13 passing through, due to physical laws. Although evidence suggests that chimpanzees are  
14 capable of correlating projected movies to the real world (e.g. Hirata, 2007; Leighty,  
15 Menzel, & Frigaszy, 2008; Menzel, Savage-Rumbaugh, & Lawson, 1985) and perceiving  
16 depth from some 2D pictorial cues (Imura & Tomonaga, 2003, 2009; Imura, Tomonaga, &  
17 Yagi, 2008), we cannot be sure that they employed these abilities in viewing our stimulus  
18 displays without such cues. Given that 2D iconic expressions of the 3D world are a human-  
19 specific innovation and that human and chimpanzee participants differed enormously in  
20 previous exposure to such media, species differences in responding to such computerized  
21 graphical images would not be surprising.

22           According to this explanation, streaming perception with open ring and coherent  
23 random dot stimuli may reflect chimpanzees' sensitivity to two kinds of explicit depth cues,  
24 X-junctions and motion transparency. As noted above, the ambiguity of stream/bounce

1 displays derives from a conflict between the perception of two moving objects with depth  
2 deviation (streaming) and without depth deviation (bouncing). The increase in streaming  
3 percepts supports the validity of stimulus manipulations as depth cues for chimpanzees'  
4 perception.

5 X-junction is known to be a strong cue for the detection of transparency or  
6 overlapping of objects in human vision (e.g., Dresch, Durand, & Grossberg, 2002; Kanizsa,  
7 1979; T. Watanabe & Cavanagh, 1993). Several studies in nonhuman primates have also  
8 investigated the role of junctions (T, L, or X) in the perception of object overlap, revealing  
9 that monkeys and apes perceive the occlusion or transparency of two-dimensionally  
10 displayed objects using the clues of the junctions (e.g. Fujita & Giersch, 2005; Nagasaka,  
11 Nakata, & Osada, 2009; Sato, Kanazawa, & Fujita, 1997; Sugita, 1999). Our results, which  
12 demonstrate that the addition of X-junctions promoted the streaming percepts, are  
13 consistent with the results of these studies.

14 Aggregations of coherently moving dots moving in opposite directions also  
15 strongly induce depth percepts of two different planes in humans (Braddick, Wishart, &  
16 Curran, 2002; Edwards & Greenwood, 2005). On the other hand, the perception of motion  
17 transparency has not received much attention in comparative perception studies, partly  
18 because it is difficult to find behavioral indices to assess such subjective percepts in  
19 nonverbal organisms. The method used here to measure the effects of motion transparency  
20 cues on stream/bounce perception may be valuable for assessing such visual sensitivity in  
21 other species.

22 In conclusion, our study is the first to demonstrate the perception of  
23 stream/bounce displays by chimpanzees. The visual interpretation of chimpanzees differed  
24 from that of humans, suggesting species differences in the process of identification of

1 moving objects. Our study also provides evidence of the chimpanzees' sensitivity to two  
2 kinds of depth cues, X-junctions and motion transparency, which could be used to  
3 perceptually resolve the interpretations of ambiguous motion events. Further studies  
4 comparing other animals would be valuable for tracking the evolutionary origins of the  
5 perceptual mechanisms that underlie our representation of the dynamic visual world.

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## References

- 1  
2 Anstis, S., & Ramachandran, V. S. (1987). Visual inertia in apparent motion. *Vision*  
3 *Research*, 27(5), 755-764.
- 4 Baker, D. H., & Graf, E. W. (2010). Extrinsic factors in the perception of bistable motion  
5 stimuli. *Vision Res*, 50(13), 1257-1265.
- 6 Bertenthal, B. I., Banton, T., & Bradbury, A. (1993). Directional bias in the perception of  
7 translating patterns. *Perception*, 22, 193-207.
- 8 Braddick, O. J., Wishart, K. A., & Curran, W. (2002). Directional performance in motion  
9 transparency. *Vision Research*, 42, 1237-1248.
- 10 Cavanagh, P. (1992). Attention-based motion perception. *Science*, 257(5076), 1563-1565.
- 11 Choi, H., & Scholl, B. J. (2004). Effects of grouping and attention on the perception of  
12 causality. *Perception & Psychophysics*, 66, 926-942.
- 13 Dresp, B., Durand, S., & Grossberg, S. (2002). Depth perception from pairs of overlapping  
14 cues in pictorial displays. *Spatial Vision*, 15(3), 255-276.
- 15 Edwards, M., & Greenwood, J. A. (2005). The perception of motion transparency: A signal-  
16 to-noise limit. *Vision Research*, 45, 1877-1884.
- 17 Fagot, J., & Tomonaga, M. (1999). Global and local processing in Humans (*Homo sapiens*)  
18 and chimpanzees (*Pan troglodytes*): use of a visual search task with compound  
19 stimuli. *Journal of Comparative Psychology*, 113, 3-12.



- 1 Fagot, J., & Tomonaga, M. (2001). Effects of element separation on perceptual grouping by  
2 humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*): perception of Kanizsa  
3 illusory figures. *Animal Cognition*, 4, 171-177.
- 4 Flombaum, J. I., Kundey, S. M., Santos, L. R., & Scholl, B. J. (2004). Dynamic object  
5 individuation in rhesus macaques. A study of tunnel effect. *Psychological Science*,  
6 15, 795-800.
- 7 Fujita, K., & Giersch, A. (2005). What perceptual rules do capuchin monkeys (*Cebus*  
8 *apella*) follow in completing partly occluded figures? *Journal of Experimental*  
9 *Psychology-Animal Behavior Processes*, 31(4), 387-398.
- 10 Grassi, M., & Casco, C. (2009). Audiovisual bounce-inducing effect: attention alone does  
11 not explain why the discs are bouncing. *Journal of Experimental Psychology:*  
12 *Human Perception and Performance*, 35(1), 235-243.
- 13 Hall-Haro, C., Johnson, S. P., Price, T. A., Vance, J. A., & Kiorpes, L. (2008). Development  
14 of object concepts in macaque monkeys. *Developmental Psychobiology*, 50(3), 278-  
15 287.
- 16 Hirata, S. (2007). A note on the responses of chimpanzees (*Pan troglodytes*) to live self-  
17 images on television monitors. *Behavioural Processes*, 75(1), 85-90.
- 18 Imura, T., & Tomonaga, M. (2003). Perception of depth from shading in infant  
19 chimpanzees (*Pan troglodytes*). *Animal Cognition*, 6(4), 253-258.

- 1 Imura, T., & Tomonaga, M. (2009). Moving shadows contribute to the corridor illusion in a  
2 chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology*, *123*(3), 280-  
3 286.
- 4 Imura, T., Tomonaga, M., & Yagi, A. (2008). The effects of linear perspective on relative  
5 size discrimination in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*).  
6 *Behavioural Processes*, *77*(3), 306-312.
- 7 Kanizsa, G. (1979). *Organization in vision*. New York: Praeger Publishers.
- 8 Kawabe, T., & Miura, K. (2006). Effects of the orientation of moving objects on the  
9 perception of streaming/bouncing motion displays. *Perception & Psychophysics*,  
10 *68*(5), 750-758.
- 11 Kawachi, Y., & Gyoba, J. (2006). Presentation of a visual nearby moving object alters  
12 stream/bounce event perception. *Perception*, *35*(9), 1289-1294.
- 13 Kerzel, D. (2000). Eye movements and visible persistence explain the mislocalization of  
14 the final position of a moving target. *Vision Res*, *40*(27), 3703-3715.
- 15 Leighty, K. A., Menzel, C. R., & Fragaszy, D. M. (2008). How young children and  
16 chimpanzees (*Pan troglodytes*) perceive objects in a 2D display: putting an  
17 assumption to the test. *Developmental Science*, *11*(5), 778-792.
- 18 Matsuno, T., Kawai, N., & Matsuzawa, T. (2004). Color classification by chimpanzees  
19 (*Pan troglodytes*) in a matching-to-sample task. *Behavioural Brain Research*, *148*,

- 1           157-165.
- 2   Matsuno, T., & Tomonaga, M. (2006). Visual search for moving and stationary items in  
3           chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). *Behavioural Brain*  
4           *Research*, 172, 219-232.
- 5   Matsuno, T., & Tomonaga, M. (2007). An advantage for concavities in shape perception by  
6           chimpanzees (*Pan troglodytes*). *Behavioural Processes*, 75(3), 253-258.
- 7   Matsuno, T., & Tomonaga, M. (2008). Temporal characteristics of visibility in chimpanzees  
8           (*Pan troglodytes*) and humans (*Homo sapiens*) assessed using a visual masking  
9           paradigm. *Perception*, 37, 1258-1268.
- 10   Menzel, E. W., Savage-Rumbaugh, E. S., & Lawson, J. (1985). Chimpanzee (*Pan-*  
11           *Troglodytes*) spatial problem-solving with the use of mirrors and televised  
12           equivalents of mirrors. *Journal of Comparative Psychology*, 99(2), 211-217.
- 13   Metzger, W. (1934). Beobachtungen uber phanomenale Identitat. *Psychologische*  
14           *Forschung*, 19, 1-60.
- 15   Nagasaka, Y., Nakata, R., & Osada, Y. (2009). Perception of neon-color spreading in  
16           squirrel monkeys. *Japanese Psychological Research*, 51(3), 132-145.
- 17   Ochiai, T., & Matsuzawa, T. (1997). *Planting trees in an outdoor compound of*  
18           *chimpanzees for an enriched environment*. Paper presented at the Third  
19           International Conference on Environmental Enrichment, Orlando, Fla.

- 1 Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: Evidence  
2 for a parallel tracking mechanism. *Spatial Vision*, 3, 179-197.
- 3 Sato, A., Kanazawa, S., & Fujita, K. (1997). Perception of object unity in a chimpanzee  
4 (*Pan troglodytes*). *Japanese Psychological Research*, 39, 191-199.
- 5 Scholl, B. J., & Nakayama, K. (2002). Causal capture: Contextual effects on the perception  
6 of collision events. *Psychological Science*, 13, 493-498.
- 7 Sekuler, A. B., & Sekuler, R. (1999). Collisions between moving visual targets: what  
8 controls alternative ways of seeing an ambiguous display. *Perception*, 28, 415-432.
- 9 Sekuler, R., Sekuler, A. B., & Lau, R. (1997). Sound alters visual motion perception.  
10 *Nature*, 385, 308.
- 11 Spelke, E. (1994). Initial knowledge: Six suggestions. *Cognition*, 50(1-3), 431-445.
- 12 Sugita, Y. (1999). Grouping of image fragments in primary visual cortex. *Nature*, 401 269-  
13 272.
- 14 Tomonaga, M. (2001). Investigating visual perception and cognition in chimpanzees (*Pan*  
15 *troglodytes*) through visual search and related tasks: from basic to complex  
16 processes. . In T. Matsuzawa (Ed.), *Primate origins of human cognition and*  
17 *behavior* (pp. 55-86). Tokyo: Springer.
- 18 Watanabe, K., & Shimojo, S. (1998). Attentional modulation in perception of visual motion  
19 events. *Perception*, 27, 1041-1054.

1 Watanabe, K., & Shimojo, S. (2001a). Postcoincidence trajectory duration affects motion

2 event perception. *Perception & Psychophysics*, 63(1), 16-28.

3 Watanabe, K., & Shimojo, S. (2001b). When sound affects vision: effects of auditory

4 grouping on visual motion perception. *Psychological Science*, 12, 109-116.

5 Watanabe, T., & Cavanagh, P. (1993). Transparent Surfaces Defined by Implicit X

6 Junctions. *Vision Research*, 33(16), 2339-2346.

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## Figure captions

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*Figure 1.* Schematic diagram illustrating a trial in the object-tracking task.

*Figure 2.* Depictions of stimulus displays used in the training sessions and the baseline trials. Arrows indicate motion. A: unambiguous streaming display without vertical displacement. B: unambiguous bouncing display without vertical displacement. C: unambiguous streaming display with vertical displacement. D: unambiguous bouncing display with vertical displacement.

*Figure 3.* Depictions of stimulus displays used in the experiments. Arrows indicate motion. A: stream/bounce display with filled disc stimuli. B: partial-overlap display with filled disc stimuli. C: stream/bounce display with open ring stimuli. C: stream/bounce display with random dot stimuli.

*Figure 4.* Collected response data from probe trials in Experiment 1. The vertical axis represents the percentage of stream responses; 0% indicates a bounce response from all subjects in all of the trials, and 100% indicates complete stream responses. The left four bars represent the 100% overlap condition, and the others represent the 50% overlap condition. Each bar indicates a different movement speed condition. Error bars are 1 SE.

*Figure 5.* Percentages of streaming responses in Experiment 2. The left two bars represent the 100% overlap condition, and the others represent the 50% overlap condition. Each bar indicates a different stimulus condition. Error bars are 1 SE.

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*Figure 6.* Percentages of streaming responses in Experiment 3. The left two bars represent the 100% overlap condition, and the others represent the 50% overlap condition. Each bar indicates a different stimulus condition. Error bars are 1 SE.

*Figure 7.* Percentages of streaming responses in Experiment 4. The left two bars represent the 100% overlap condition, and the others represent the 50% overlap condition. Each bar indicates a different stimulus condition. Error bars are 1 SE.

*Figure 8.* Percentages of streaming responses in Experiment 5. The left graph represents the conditions using circular stimuli as in Experiment 2. The right graph represents the conditions using rectangular stimuli as in Experiments 3 and 4.



Figure 1.

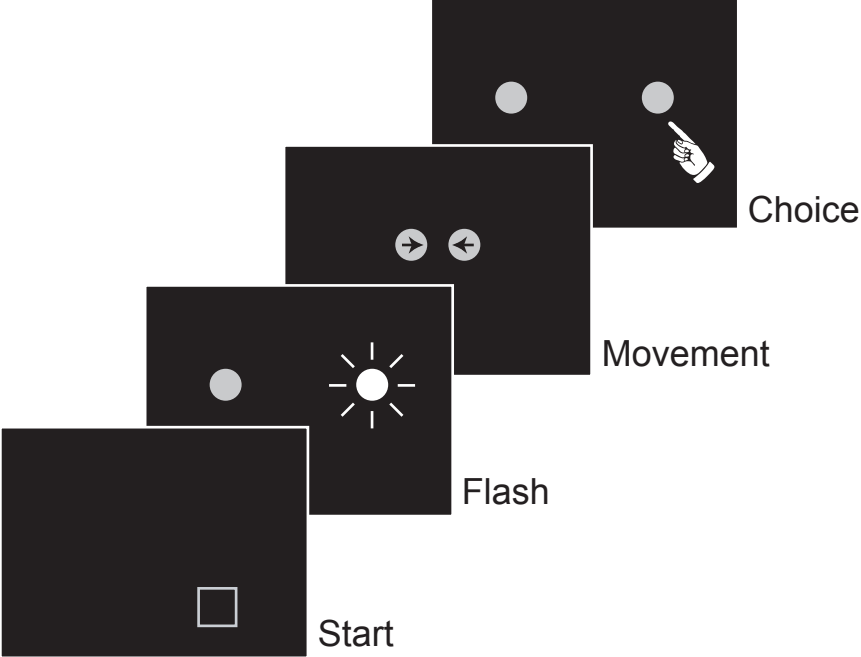


Figure 2.

A. Streaming without vertical displacement

B. Bouncing without vertical displacement

C. Streaming with vertical displacement

D. Bouncing with vertical displacement

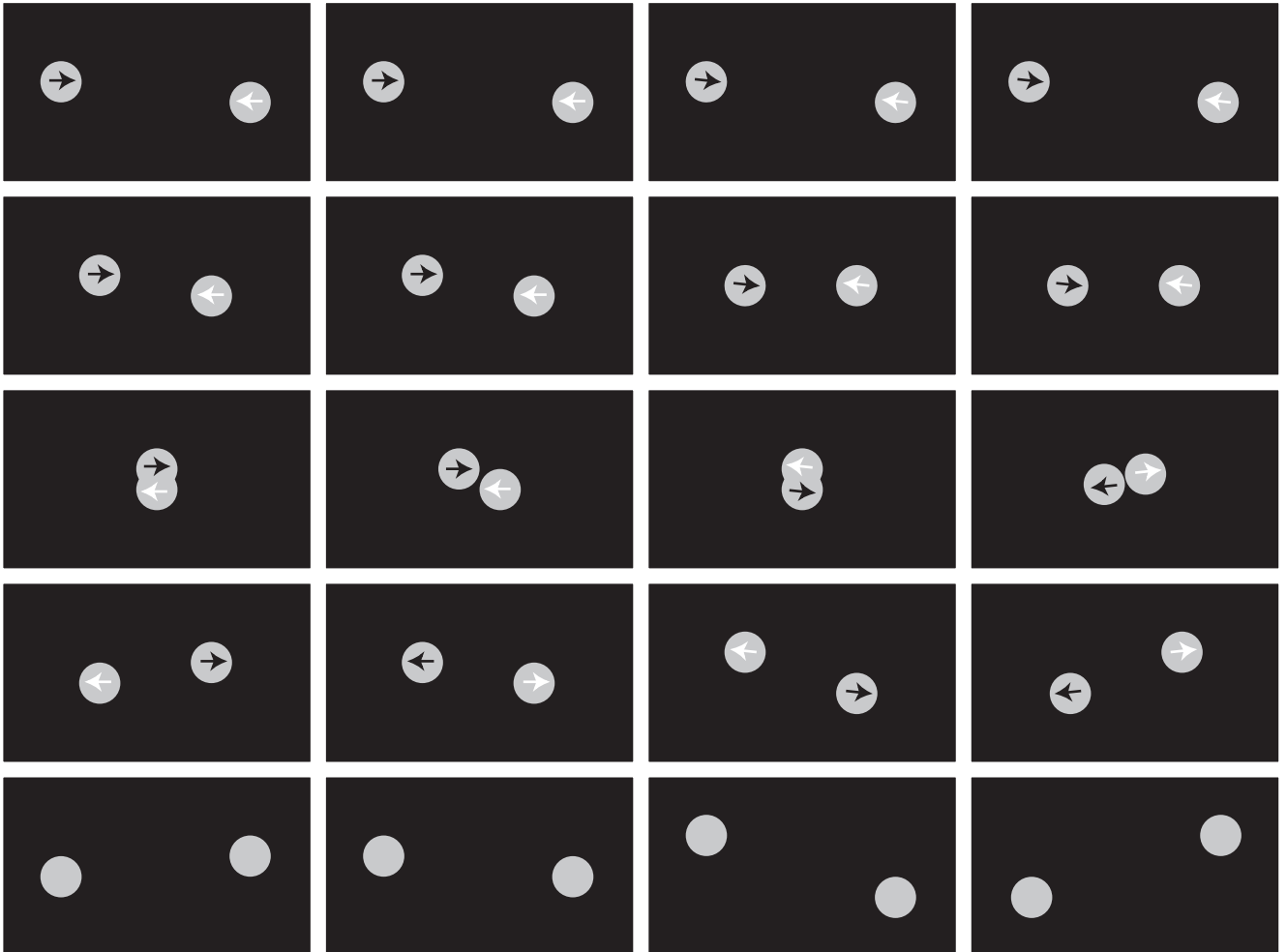


Figure 3

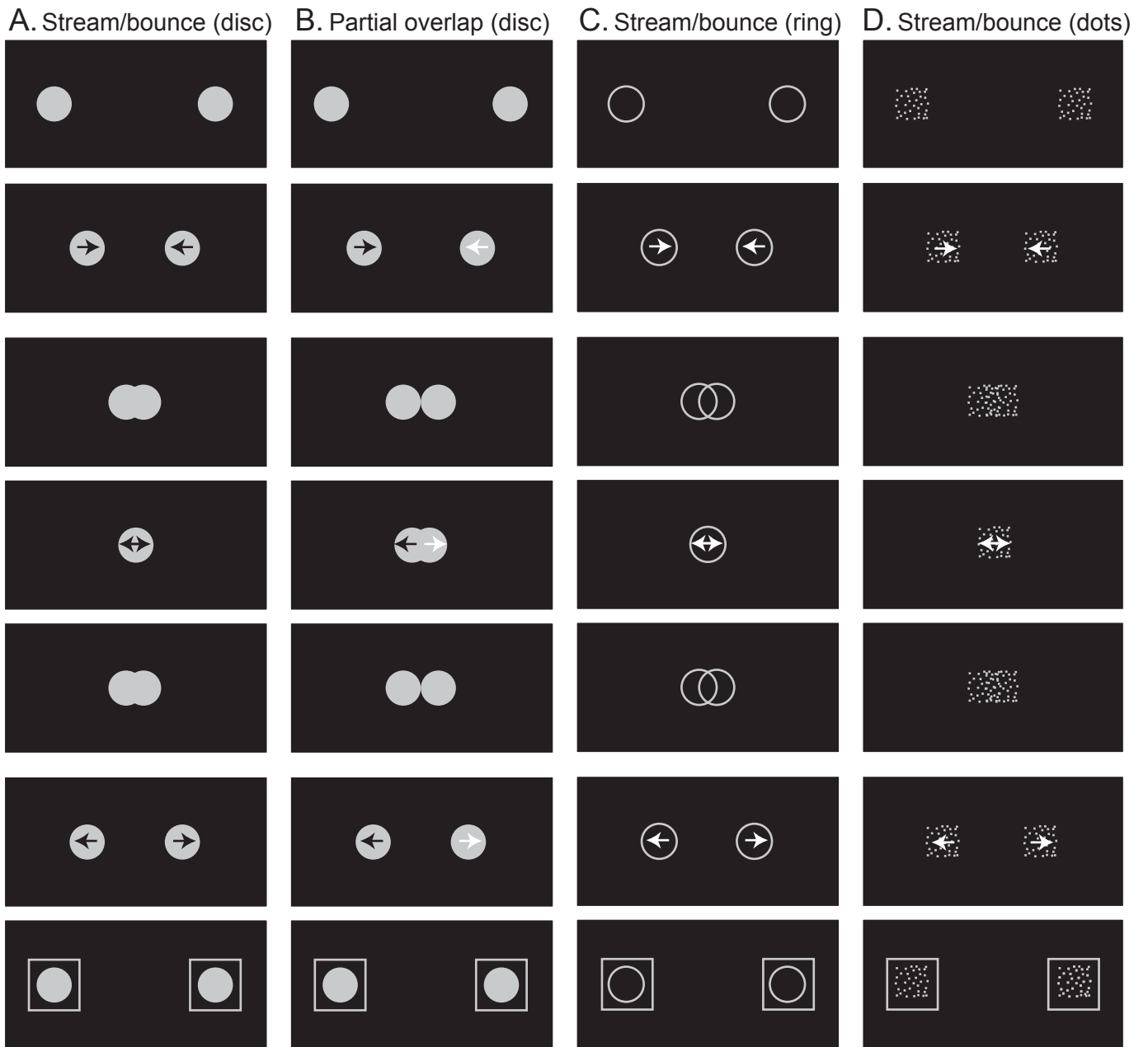


Figure 4.

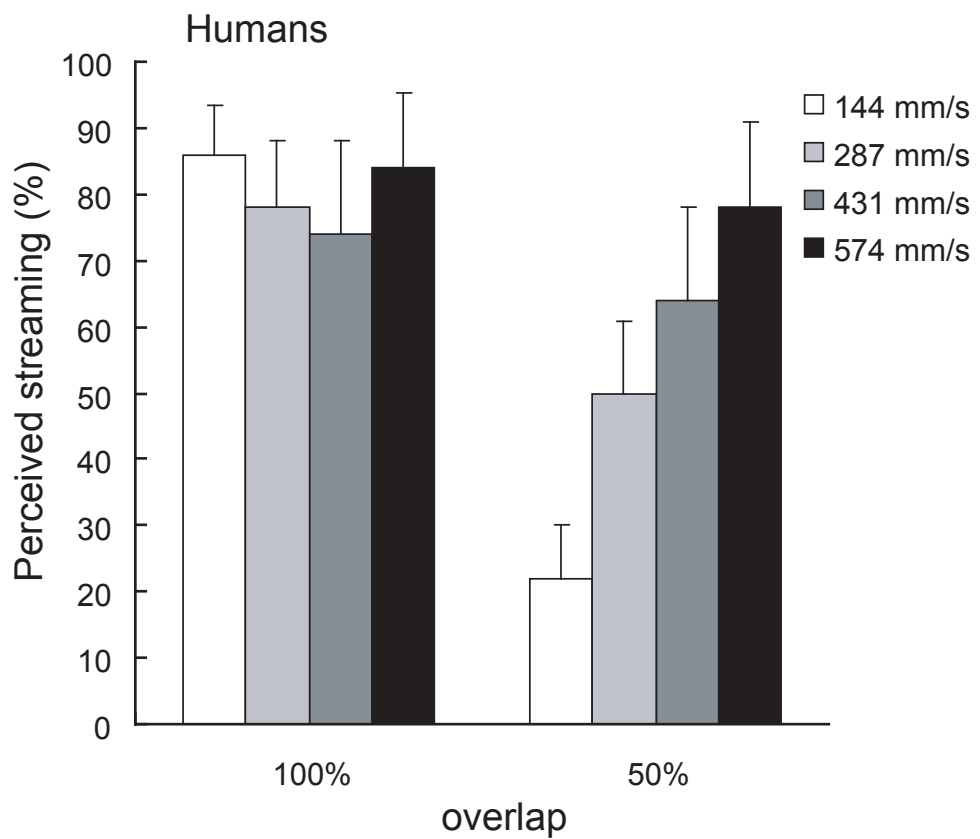
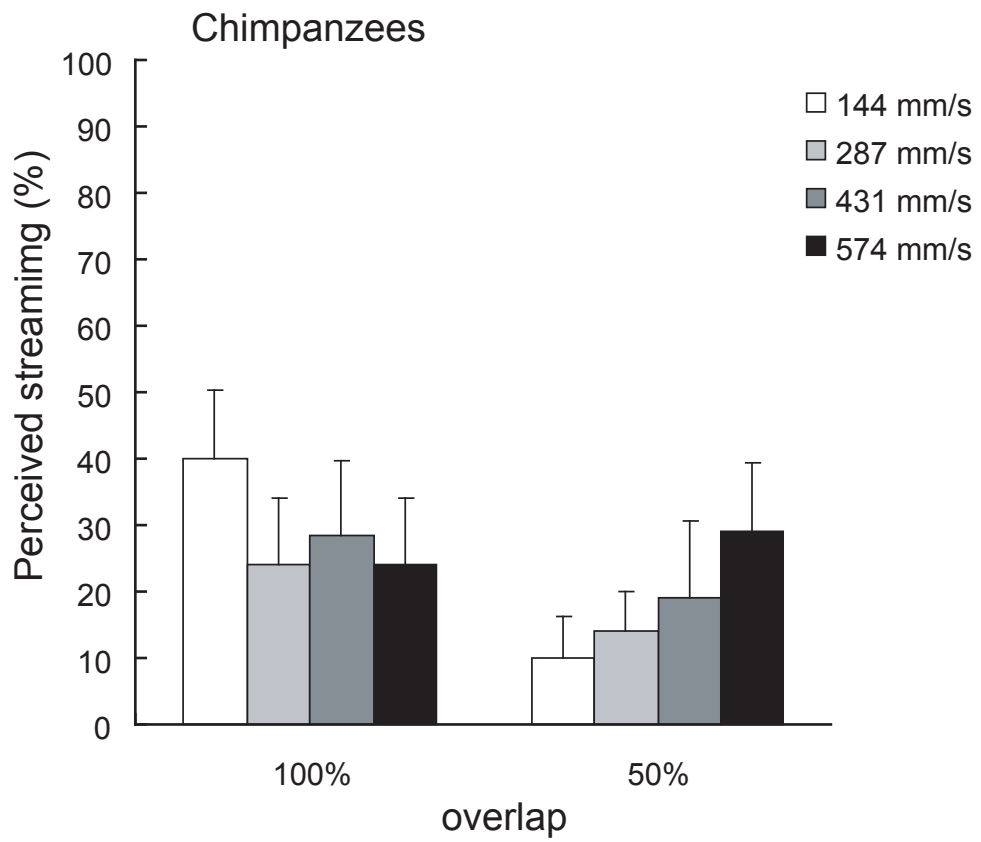


Figure 5

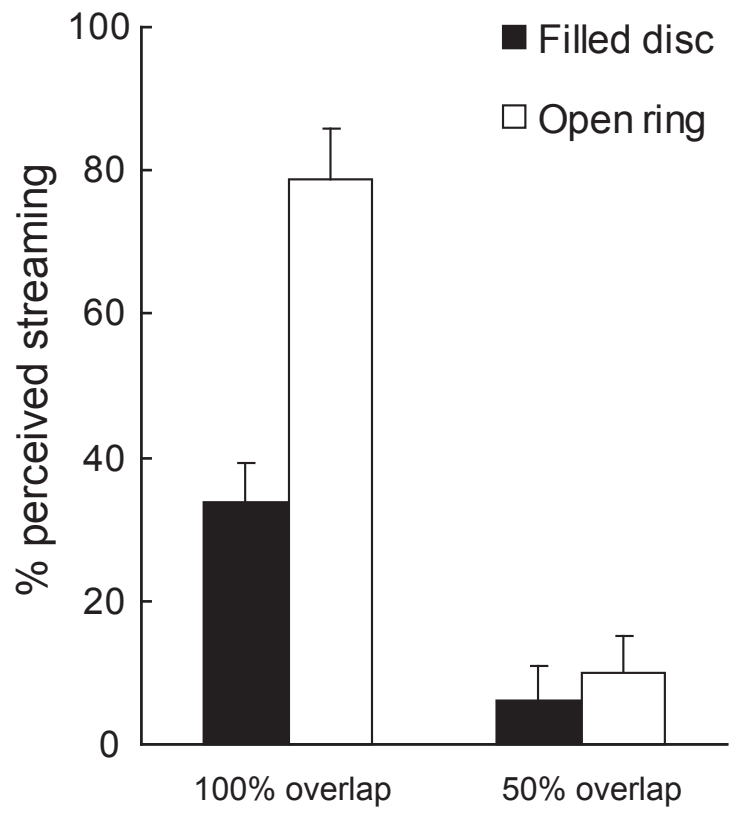


Figure 6

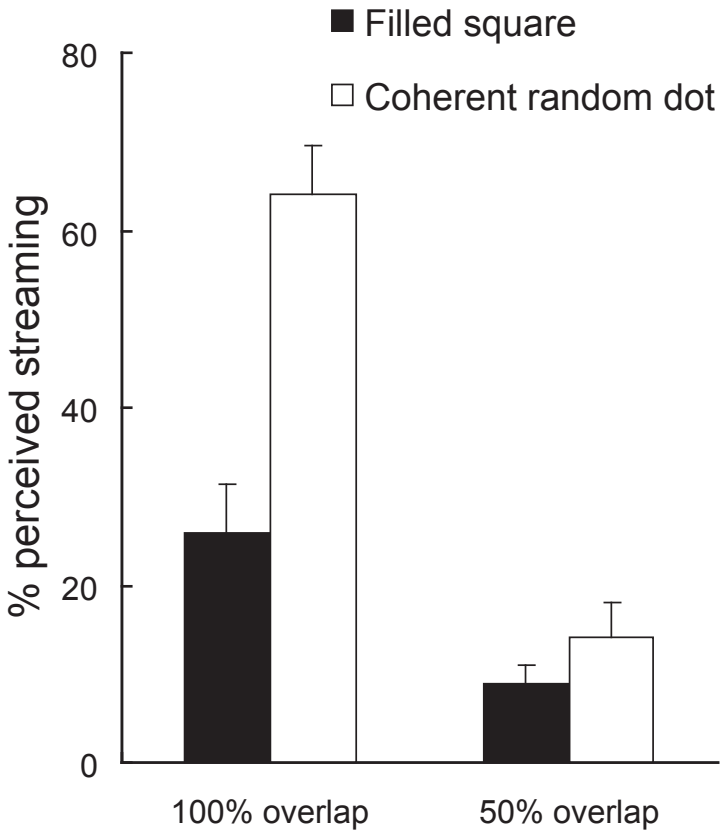


Figure 7

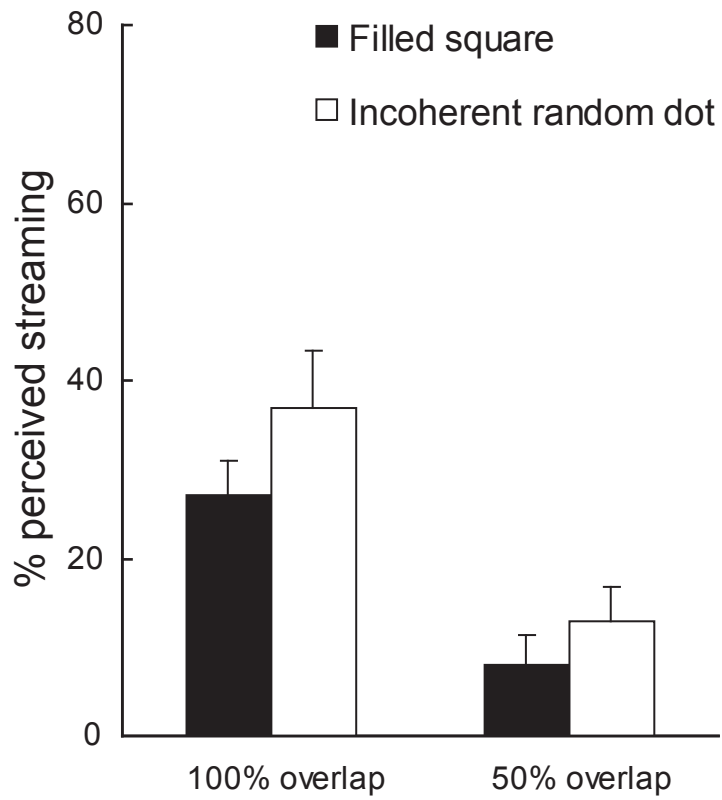


Figure 8

