

Contribution of global and local biological motion information to speed perception and discrimination

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To respond to movements of others and understand the intention of others' actions, it is important to accurately extract motion information from body movements. Here, using original and spatially scrambled point-light biological motions in upright and inverted orientations, we investigated the effect of global and local biological motion information on speed perception and sensitivity. The speed discrimination task revealed that speed sensitivity was higher for the original than for scrambled stimuli (Experiment 1) and higher for upright than for inverted stimuli (Experiment 2). Perceived motion speed was slower for the original than for scrambled stimuli (Experiment 2), but regardless of the orientation of the display (Experiment 1). A subsequent experiment comparing different scrambled stimuli of the same actions showed that the higher speed discrimination sensitivity to upright stimuli was preserved even in the scrambled biological motions (Experiment 3). Taken together, our findings suggest that perception of the speed of biological movements emanates from both global and local biological motion signals.

attached to the major joints (point-light display; Johansson, 1973). Previous studies of biological motion perception have revealed that humans can extract various information from point-light motion, including its action (Dittrich, 1993), gender (Cutting & Kozlowski, 1977; Mather & Murdoch, 1994; Troje, 2002), and familiar individuals (Cutting & Kozlowski, 1977; Hill & Pollick, 2000; Troje, Westhoff, & Lavrov, 2005). These abilities are preserved even under masked or noise-added conditions (Bertenthal & Pinto, 1994; Gilaie-Dotan, Saygin, Lorenzi, Rees, & Behrmann, 2015; Thornton, Pinto, & Shiffrar, 1998). The understanding of various information conveyed by biological motions has made it possible to synthesize biological motions containing specific information (e.g., movement style and gender; Giese & Poggio, 2000; Hill & Pollick, 2000; Pollick, Fidopiastis, & Braden, 2001; Troje, 2002) by model-based control.

Biological motion is thought to be composed of two types of information, which are the global configuration and local motion (e.g., Troje, 2008). The global configuration is a dynamic structure of the point-light biological motion. This information is believed to give us a vivid impression of a human figure as well as its higher order characteristics. If configural processing of biological motion is disrupted by inverting the display, some perceptions, such as locomotion (Dittrich, 1993; Pavlova & Sokolov, 2000), emotion (Dittrich, Troscianko, Lea, & Morgan, 1996), and gender (Barclay, Cutting, & Kozlowski, 1978), are largely impaired (the inversion effect in biological motion). Functional MRI studies also have shown that the neural substrates of

Introduction

The ability to accurately detect and interpret the movements of others is vitally important for humans as social animals. This evolutionary significance of biological motion perception might explain why people can readily recognize a human figure even with minimal information from the motion of several light spots

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biological motion perception are different when configural processing is disrupted by randomly changing the position of the point-light dots (i.e., scrambled biological motion; Grossman et al., 2000; Servos, Osu, Santi, & Kawato, 2002). On the other hand, local motion information is carried solely by the motion of the individual point-light dots (i.e., body parts). Several studies have pointed out the importance of local motion features for biological motion perception (Casile & Giese, 2005; Mather, Radford, & West, 1992; Thornton et al., 1998). Moreover, other studies have shown that humans perform better in motion direction discrimination (Chang & Troje, 2009a; Troje & Westhoff, 2006), animacy detection (Chang & Troje, 2008), and visual search tasks (Wang, Zhang, He, & Jiang, 2010) with an upright scrambled motion display than with an inverted scrambled motion display (the local inversion effect in biological motion). These studies suggest that some biological motion information is preserved in the point-light display even without the global configuration and that local motion information is susceptible to the inversion effect.

Despite the recent advances in our understanding of biological motion perception, little consideration has been given to what effect biological information has on visual motion processing *per se*. In particular, it is not well understood whether visual perception of or sensitivity to the movement of point-light dots representing biological motion is affected by the extent of the biological information available. Although many studies have demonstrated that human observers have high sensitivity to biological motion, several have argued that certain types of sensitivity to biological motion are not different from sensitivity to nonbiological motion (Hiris, 2007; Jastorff, Kourtzi, & Giese, 2006). Indeed, Hiris (2007) revealed that the better performance observed in detecting biological motion compared to unstructured biological motion was not different from that for structured nonbiological motion. It is thus conceivable that the high detection sensitivity to biological motion is not due to the biological information itself but due to some other cues such as visual processes for determining structure from motion (Ullman, 1979).

While the above studies raise questions about our special sensitivity to biological motion, it has also been suggested that a functional linkage between perception and action makes our sensitivity to biological motion different from that to the other motions (Casile & Giese, 2006; Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1997; Thornton et al., 1998). For example, Prinz (1997) found that the performance of an action influences observers' perception of the same action, suggesting that perception and action of the same kind are linked to each other by a shared representation (the common/event coding theory; Hommel et al., 2001).

Supporting this notion, neurophysiological studies have shown that observing an action performed by another individual activates the same neurons involved in the execution of the action (mirror neuron system; e.g., Iacoboni et al., 1999; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Therefore, while its actual function is still controversial, the mirror system may play a role in understanding others' action and observational learning (Rizzolatti & Craighero, 2004). Given the close relationship between perception and action, it is hypothesized that perceptual performance would be better in movements that represent an action of the human body more saliently.

The present study investigated the influence of global and local biological motion information on visual motion perception. To distinguish and elucidate the influence of the global and local biological motion signals, we used original and scrambled point-light displays in upright and inverted orientations. Since local motion vectors remained unchanged in the scrambled display, the difference between original and scrambled motion stimuli may be attributable to the global configuration, while the difference between the upright and inverted orientations of the scrambled motion would suggest the influence of local motion signals. In three experiments, the perceived speed of and speed sensitivity to the point-light motions were measured as a function of global and local biological motion signals. In Experiment 1, the perceived speed was compared between the upright and inverted biological motions, and the speed discrimination sensitivity was compared between the original and scrambled displays. In other words, we examined the influence of orientation (hence, local motion signals) on speed perception (i.e., the inversion effect on perceived speed) and the influence of global motion signals on speed discrimination sensitivity. In contrast, in Experiment 2, the perceived speed was compared between the original and scrambled biological motions, and the speed discrimination sensitivity was compared between the upright and inverted displays. This enabled us to examine the influence of global motion signals on speed perception and the influence of local motion signals on speed discrimination sensitivity. In addition, in Experiment 3, the speed discrimination sensitivity was directly compared between the upright and inverted scrambled biological displays, which enabled us to test if there is the local inversion effect in speed discrimination sensitivity.

Experiment 1

In Experiment 1, upright and inverted biological motion sequences were presented in two successively

viewed intervals on each trial. The relative speed of the two motion sequences was parametrically varied with the method of constant stimuli. Participants indicated which of the two intervals contained the faster point-light motions in a two-interval forced-choice (2IFC) task. In separate blocks, the original or scrambled figures were used. A psychometric function was obtained for each participant and each configuration condition as a function of the speed differences between the upright and inverted displays (see Methods section for details).

The psychometric functions for the original or scrambled stimuli served two purposes. First, the point of subjective equality (PSE, 50% percentile; see Methods for details) provided a measure of the speed difference at which the speeds of the upright and inverted motion sequences were perceived to be equal. That is, a shift in the PSE value from 0 indicates a perceptual bias of the velocity perception between the upright and inverted orientations. In particular, a bias in the original stimuli indicates the general biological motion inversion effect, whereas that in the scrambled stimuli indicates the local biological motion inversion effect. Second, the just noticeable difference (JND, one-half of 75%–25% percentile; see Methods for details) gave a measure of the speed discrimination sensitivity between the upright and inverted displays, where the smaller JND meant the better speed discrimination performance. Therefore, the comparison of the JNDs for the intact and scramble stimuli could determine whether the speed discrimination sensitivity is better for the intact or the scramble stimuli. In other words, Experiment 1 examined (a) the difference in perceived speed between the upright and inverted displays and (b) the difference in speed discrimination sensitivity between the original and scrambled conditions.

Methods

Participants

Sixteen paid volunteers (eight men and eight women, aged 19–44 years; $M = 28.2$, $SD = 9.25$) with normal or corrected-to-normal vision participated in Experiment 1. They all gave written informed consent prior to participation. All experimental protocols were approved by the NTT Communication Science Laboratories Research Ethics Committee and were in accordance with the Declaration of Helsinki.

Experimental setting and apparatus

The experiment was conducted in a dark room. A chinrest was used to stabilize the participant's head. Visual stimuli were generated using MATLAB (MathWorks, Natick, MA) with the Psychophysics Toolbox

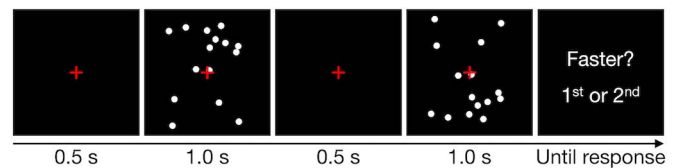


Figure 1. The trial sequence and exemplary stimuli used in Experiment 1. Each motion sequence was presented for 1.0 s after a preceding fixation period of 0.5 s (or an interstimulus interval of 0.5 s). Participants were asked to indicate the observation interval in which they perceived the point-light dots as moving faster.

extensions (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) and were presented on a 21-in. CRT monitor with a refresh rate of 120 Hz.

Stimuli and procedure

Sample frames of the stimuli are depicted in Figure 1. The visual stimuli consisted of a red fixation cross (0.5° in visual angle) and point-light figures composed of 15 white dots (0.2°), which subtended 7.0° in height and 2.6° – 3.6° in width depending on the figure. All the stimuli were presented on a black background.

The point-light sequences of five different human actions (walking, throwing, kicking, and two exercise movements, or, more specifically, jumping jacks and elbow-to-knee motion) recorded at a sampling rate of 120 Hz were adopted from the HDM05 motion capture database (Müller et al., 2007). For each action, the center of the motion sequence was defined as the frame in which the highest speed of the point-light dot motions occurs. For the sake of simplicity, we used 15 point-light dots representing the motion of the head, neck, shoulders, trunk, elbows, wrists, hips, knees, and ankles. The point-light dot(s) of the head, neck, trunk, wrists, and hips were obtained by averaging the motions of multiple markers placed around them—for example, the single point-light dot representing the head motion was obtained by averaging the motions of four markers recorded from the left and right sides of the front and back of the head. The point-light actions of walking, throwing, and kicking were presented in sagittal views, and the jumping jacks and elbow-to-knee were presented in frontal views, where larger point-light motions can be seen. The mean position of the point-light dots in each frame was used as the spatial center of each image frame because the present study focused on the articulation aspect (positional changes in the body parts relative to each other) rather than the translational aspect (changes in the body location in space over time) of human movements (Masselink & Lappe, 2015). Scrambled biological motions were created by randomizing the starting positions of each point while keeping its motion path within the area covered by the

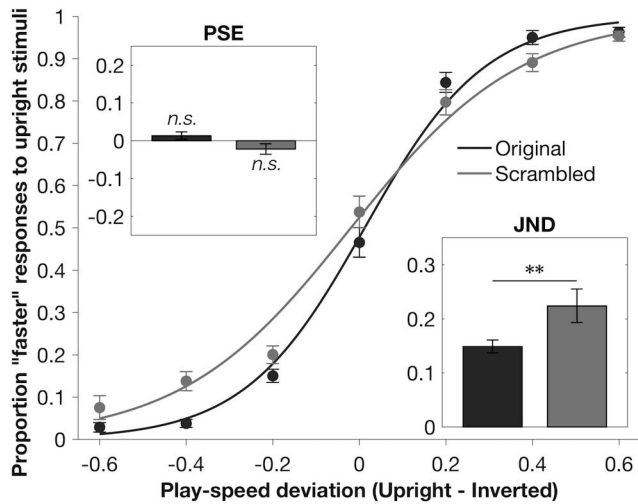


Figure 2. Mean proportion of “faster” response to upright stimuli compared with inverted stimuli and their psychometric curves for original and scrambled stimuli as a function of the play-speed difference between two stimuli (upright – inverted). The embedded bar graphs represent the mean PSEs and JNDs for original (black) and scrambled (gray) stimuli. Error bars denote standard errors of the means ($N = 16$).

original biological motion. With this manipulation, the global configuration of the biological motion signals is collapsed, but the local motion information (e.g., motion velocity and acceleration) remains unchanged. The scrambled biological motions were created for each individual participant. Thus, all the participants used different scrambled biological motions. Inverted stimuli of original and scrambled biological motions were created as their counterpart by flipping the location of point-light dots about the horizontal axis.

In each trial, the point-light displays of the same action but in a different orientation (upright or inverted) were sequentially presented in the center of the display. Each motion sequence was presented for 1.0 s after a preceding fixation period of 0.5 s—that is, each motion sequence was interleaved with an inter-stimulus interval of 0.5 s. In the pair of the sequentially presented stimuli, one of the stimuli was randomly chosen as the standard stimulus and was presented at its original (recorded) speed. The other test stimulus was presented 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, or 1.6 times faster than the standard one. The play speed was controlled by skipping the frames of the original frames for faster speeds or by increasing the duration of each frame for lower speeds—for example, a 1.6 \times stimulus was created by evenly skipping 72 frames of the original 192 frames (120 Hz \times 1.6 s) so that the length of the stimulus would be 1 s. Consequently, there was a total of seven test conditions, in which the difference of the moving speed between the standard and test stimuli was -0.6 , -0.4 , -0.2 , 0.0 , 0.2 , 0.4 , and 0.6 . The presentation order of the two stimuli (standard and

test) and the presentation speed of the test stimulus were randomized within each block. The initial frame of the point-light display was also randomized (± 0.1 s) for each motion sequence. Participants were required to make a 2IFC task indicating which of the two intervals contained the faster point-light patterns regardless of their form and display style. They were also instructed to keep their gaze on the fixation cross during each trial.

The original stimuli (upright vs. inverted) and the scrambled stimuli (upright vs. inverted) were tested in a different block. The order of the blocks was counter-balanced across the participants. In each block, the participants performed 140 trials, consisting of 5 kinds of actions \times 7 test conditions \times 4 repetitions. The intertrial interval was 1.0 s.

Results and discussion

The results of Experiment 1 are shown in Figure 2. The data points represent the mean proportion of trials on which the upright display appeared to move faster than the inverted one for each original and scrambled stimulus. The data were fitted with a logistic regression as a function of the difference in speed between two stimuli (upright – inverted). Note that the curves in Figure 2 are fitted to the data across participants only for illustrative purposes. All statistical analyses were conducted on those fitted to each individual’s data. The PSE and JND were obtained from the fitted curves as an indicator of perceived speed difference and speed discrimination sensitivity, respectively. The PSE was taken from the x value at which the fitted curve had a y value of 0.5, and the JND was calculated from one-half of the difference between the x values at which the fitted curve had a y value of 0.25 and 0.75.

The mean PSEs of the original ($M = 0.01$, $SD = 0.04$) and scrambled ($M = -0.02$, $SD = 0.06$) biological motion condition are shown in the embedded bar graphs in Figure 2. A positive PSE value means that the upright biological motion was perceived slower than the same play speed of the inverted biological motion, whereas a negative PSE means the opposite. One-sample t tests (two-tailed) against the PSE value of 0 (i.e., the perceived speeds of upright and inverted stimuli appeared the same when the playing speeds of those stimuli were actually the same) showed that the PSE of neither the original nor the scrambled biological motion condition was significantly different, $t(15) = 1.35$, $p = 0.20$, $d_z = 0.34$, and $t(15) = 1.58$, $p = 0.13$, $d_z = 0.40$, respectively. That is, the apparent motion speeds of upright and inverted biological motion stimuli were comparable when their physical motion speeds were the same. These results indicate that the inversion of biological motion stimuli has no effect on their

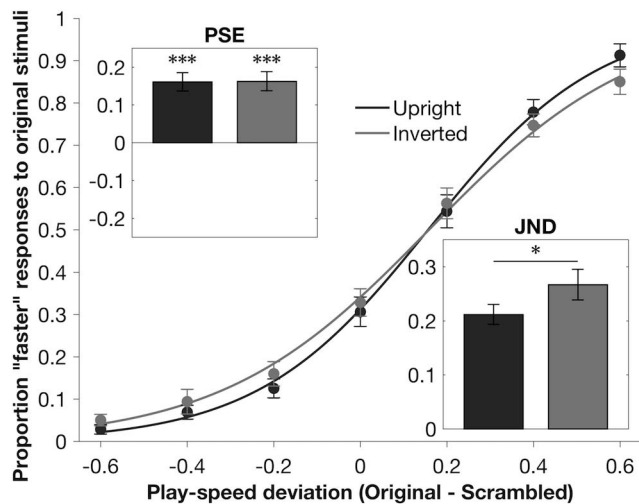


Figure 3. Mean proportion of “faster” response to original stimuli compared with scrambled stimuli and psychometric curves for upright and inverted stimuli as a function of the play-speed difference between two stimuli (original – scrambled). The embedded bar graphs show mean PSEs and JNDs for upright (black) and inverted (gray) stimuli. Error bars are standard errors of the means ($N = 16$).

perceived speed regardless of its global configuration (original or scrambled).

The mean JNDs for the original ($M = 0.15$, $SD = 0.05$) and scrambled ($M = 0.22$, $SD = 0.12$) biological motion conditions are shown in the embedded bar graphs in Figure 2, where the smaller JND value indicates finer speed discrimination. A paired t test (two-tailed) comparison of the mean JNDs showed that the JND for the original stimuli was significantly smaller than that for the scrambled stimuli, $t(15) = 3.17$, $p < 0.01$, $d_z = 0.80$. This means that the observers showed better speed discrimination sensitivity to the original than to the scrambled biological motion stimuli. In other words, the global biological motion signals did affect the speed discrimination performance. In particular, a clear global configuration (i.e., human figure) provided better discrimination sensitivity to the moving speed of the point-light dots.

Experiment 2

In Experiment 2, the original and scrambled biological motion stimuli in the same orientation, either the upright or inverted, were presented in the same 2IFC task as in Experiment 1. The upright and inverted orientation conditions were tested in separate blocks. A shift in the PSE from 0 indicates a perceptual bias of the velocity perception between the original and scrambled stimuli. In contrast, the JNDs indicate the speed discrimination sensitivity for the upright and

inverted displays. Therefore, Experiment 2 examined (a) the difference in perceived speed between the original and scrambled conditions and (b) the difference in speed discrimination sensitivity between the upright and inverted displays.

Methods

Sixteen new paid volunteers (five men and 11 women, aged 19–49 years: $M = 29.7$, $SD = 9.82$) participated in Experiment 2. The stimuli and procedures were the same as in Experiment 1, except for the pair of stimuli presented in each block: the upright stimuli (original vs. scrambled) in one block, and the inverted stimuli (original vs. scrambled) in the other block. The order of the blocks was counterbalanced across the participants.

Results and discussion

Figure 3 shows the mean proportion of trials on which the original biological motion stimulus appeared to move faster than the scrambled one for each stimulus condition (upright and inverted), along with their fitted psychometric curves as a function of the play-speed difference (original – scrambled).

The mean PSEs for each biological motion condition, upright ($M = 0.16$, $SD = 0.10$) and inverted ($M = 0.16$, $SD = 0.10$), are plotted in the embedded bar graphs in Figure 3, where a positive PSE value means that the original biological motion stimuli were perceived to be slower than the scrambled stimuli of the same action. One-sample t tests (two-tailed) showed that the PSE was significantly higher than 0 (i.e., no bias of the speed perception between original and scrambled biological motions) in both the upright, $t(15) = 6.62$, $p < 0.001$, $d_z = 1.66$, and inverted $t(15) = 6.44$, $p < 0.001$, $d_z = 1.61$, display conditions. This means that the speed of the moving point-light dots appeared to be slower for the original stimuli than for the scrambled stimuli in both the upright and inverted displays. A further paired t test (two-tailed) showed that there was no significant difference in the PSEs of the upright and inverted displays, $t(15) = 0.07$, $p < 0.95$, $d_z = 0.02$. Therefore, together with the results of Experiment 1 that the perceived speed was comparable between the upright and inverted displays as long as the global configuration (original or scrambled) was the same, the results of Experiments 2 indicate that the presence of the global configuration reduces the perceived speed of comparable size in the upright and inverted displays.

The mean JNDs for each orientation condition, upright ($M = 0.21$, $SD = 0.07$) and inverted ($M = 0.27$, $SD = 0.11$), are also plotted in Figure 3, where a smaller

JND value indicates better speed discrimination performance. Comparison between the two mean JNDs (upright vs. inverted) showed that the JND of the upright display was significantly smaller than that of the inverted one, $t(15) = 2.23$, $p < 0.05$, $d_z = 0.56$. In other words, the sensitivity of the speed discrimination was better for upright stimuli than for inverted stimuli. This suggests that the inversion effect in biological motion perception is not unique to detection (Bertenthal & Pinto, 1994; Pavlova & Sokolov, 2000) or direction discrimination (Bertenthal & Pinto, 1994; Troje & Westhoff, 2006), but also occurs in speed discrimination.

Experiment 3

The results of Experiment 2 showed that speed discrimination sensitivity was better for pairs of stimuli presented upright than for those presented inverted. However, because the sensitivity was estimated from the comparison between the original and scrambled stimuli, it is not clear whether the inversion effect (i.e., degradation of the speed sensitivity) occurred in the original or scrambled stimuli or both. Previous studies have demonstrated that scrambled biological motion, as well as original biological motion, causes the inversion effect, suggesting that local motion information alone could contribute to biological motion perception (Chang & Troje, 2008, 2009a, 2009b; Troje & Westhoff, 2006; Wang & Jiang, 2012; Wang et al., 2010).

In Experiment 3, to verify whether the inversion effect in speed discrimination sensitivity occurs only with local biological motion signals (i.e., the local inversion effect), we created two different scrambled motions for each action and compared their moving speeds in the same 2IFC task as in Experiments 1 and 2. The upright and inverted conditions were tested in separate blocks. The larger JND for the inverted scrambled stimuli indicates the local inversion effect in speed discrimination sensitivity of biological motion signals.

Methods

Sixteen new paid volunteers (five men and 11 women, aged 20–46 years: $M = 30.7$, $SD = 9.37$) participated in the experiment. Two different scrambled stimuli were created for each action used in Experiments 1 and 2. The stimuli of the same action were paired and presented sequentially in the same orientation. As in Experiments 1 and 2, one of the paired stimuli was randomly chosen as the standard

stimulus and presented at its recorded speed. The other test stimulus was presented 0.4, 0.6, 0.8, 0.9, 1.1, 1.2, 1.4, or 1.6 times faster than the standard speed, which resulted in the test conditions of eight-speed deviations, -0.6 , -0.4 , -0.2 , -0.1 , 0.1 , 0.2 , 0.4 , and 0.6 . Note that the same speed as the standard stimulus was not tested because the test (and hence standard) stimuli in Experiment 3 were determined only by their play speed, and thus, if the play speed of the paired stimuli was the same, we had no way to determine which of two arbitrarily scrambled biological motions would be the test (or standard) stimulus. Trials were blocked by the orientation condition (upright or inverted), and the order of the blocks was counterbalanced across participants. The two scrambled stimuli of each action were created for each participant differently and used for both upright and inverted conditions. The other stimuli and procedures were identical to those in Experiments 1 and 2. The participants were not informed about the biological nature of the scrambled stimulus, and none of them became aware of it during the experiment.

Results and discussion

Because the difference between two scrambled biological motions was completely arbitrary (depending on how the positions of the point-light dots were randomized) and was able to distinguished only by their play speeds (the standard stimuli with the original speed and test stimuli with a different speed), we calculated the proportions of “faster” response to the test stimuli to fit the data with the psychometric curves. The fitted psychometric curves are plotted for each presentation condition (upright and inverted) in Figure 4. We did not analyze PSEs because the PSEs here reflect only the difference in perceived speed between two arbitrarily scrambled stimuli (the standard stimuli with the original speed and test stimuli with a different speed), and which shows no meaningful information.

The mean JNDs for the upright ($M = 0.19$, $SD = 0.07$) and inverted ($M = 0.22$, $SD = 0.09$) conditions obtained from the individual’s fitting curve are plotted in Figure 4. A paired t test (two-tailed) showed that the JND for the upright scrambled biological motion was significantly smaller than for the inverted scrambled biological motion, $t(15) = 2.20$, $p < 0.05$, $d_z = 0.55$. This indicates that even without the configural information of the human body and knowledge of biological nature of the stimuli, the speed discrimination of motion signals is better for the upright stimuli than for the inverted stimuli. Therefore, this result is consistent with the previous finding that the local motion signals, which are preserved even when the global configuration is entirely disrupted by spatially scrambling the

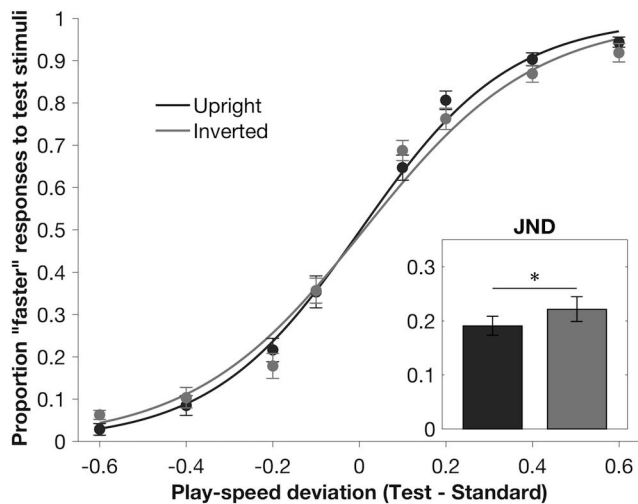


Figure 4. Mean proportion of “faster” response to test scrambled stimuli (eight different speeds) compared with standard scrambled stimuli (veridical speed with a different scrambled form of the test scrambled stimuli). The psychometric curves for upright and inverted stimuli are plotted as a function of the play-speed difference between two stimuli (test – standard). The embedded bar graphs show the mean JNDs for upright (black) and inverted (gray) stimuli. Error bars represent standard errors of the means ($N = 16$).

positions of individual point-light dots, were impaired when display orientation was inverted (Chang & Troje, 2009a; Troje & Westhoff, 2006).

General discussion

The results of this study showed that observers could discriminate the speed of the original biological motions better than they could that of the scrambled biological motions (Experiment 1). Thus, the results are consistent with the previous finding that scrambling the positions of the point-light dots greatly impairs biological motion perception (Grossman et al., 2000; Servos et al., 2002) and with the notion that human observers are highly sensitive to human movement (e.g., Pinto & Shiffrar, 1999). Furthermore, extending the previous findings that human observers can extract various kinds of information contained in biological movements, the present results also demonstrated that human observers can also detect speed differences more accurately in the structured compared to the unstructured biological motion displays.

However, as mentioned in the Introduction, several studies have shown that some of the effects, including motion detection and learning, which had been thought to be specific to biological motion perception, occur even for visual forms grouped by other visual processes (Hiris, 2007; Jastorff et al., 2006). One possible

explanation for the difference in speed discrimination sensitivity to motion with and without global configuration information is a greater intervention of high-level cognitive mechanisms for the global percept. The global percept of biological motion or its retrieval is thought to be mediated by active top-down motion processing that requires allocation of attentional resources (Cavanagh, 1992; Cavanagh, Labianca, & Thornton, 2001; Thornton, Rensink, & Shiffrar, 2002). With the support of attentive processes, the visual system can store and deploy the motion of familiar events or objects as a pattern (or a “sprite”), and this form of information may assist in the efficient tracking and prediction of such familiar motions, including biological ones (Cavanagh et al., 2001). Therefore, according to this hypothesis, it is plausible that high-level cognitive mechanisms for perceptually grouped visual stimuli contribute to the speed sensitivity of biological motions with global form. Further explorations would be required to clarify this point.

Meanwhile, the subsequent experiments also revealed that speed discrimination was better for upright than for inverted orientations of biological motion displays. It has been suggested that inversion of the display impairs the configural processing of the body parts (Atkinson, Tunstall, & Dittrich, 2007; Bertenthal & Pinto, 1994; Reed, Stone, Bozova, & Tanaka, 2003). In this regard, the consequence of the inverted display in Experiment 2 supports the conclusion drawn from Experiment 1 that speed sensitivity to the structured biological motion is superior to that to unstructured biological motion. However, it has also been argued that the inversion effect in biological motion perception is not solely caused by impairment of global form processing, because it occurs even in scrambled biological motion in which global configuration is entirely disrupted (Chang & Troje, 2008, 2009a; Troje & Westhoff, 2006). In those studies, Troje and colleagues indicated that the information susceptible to inversion is local motion, especially the lower limb acceleration of a point-light walker, which was characterized by the interaction between body-specific ballistic motion and gravitational force. Consistent with their argument, the results of Experiment 3 revealed that speed discrimination performance was impaired when scrambled biological motions were shown inverted compared to their upright display. These results indicate that local motion signals also contribute to the speed sensitivity to biological motion.

How does local motion information contribute to visual motion sensitivity? Troje (2008) has suggested that among the several processing levels of biological motion perception, the ballistic movements of the limbs (or local motion signals) are processed at an early level, without previous experience, to provide an invariant cue for life detection. This process is believed to work

well when the movements are presented upright and to help observers trigger a fast behavioral response or guide attention to important events. If this is the case, it is possible that life motion signals induced by local motion in the upright display might direct observers' attention to specific point-light dots resulting in superior speed discrimination performance. In this regard, a recent study has shown that the perception of the movement direction of biological motion is caused by different body parts depending on the type of actions (Davila, Schouten, & Verfaillie, 2014). Thus, together with the previous findings, the results of the present study show that actions other than walking might also be mediated by such innate life detection mechanisms.

Another possible explanation is that observers' previous experience of performing similar movements was involved in the inversion effect in speed discrimination (Casile & Giese, 2006; Jacobs, Pinto, & Shiffrar, 2004; Prinz, 1997). Jacobs et al. (2004) showed that visual sensitivity to walking speed is better for forward walking than for the biomechanically impossible reverse of forward walking (i.e., not backward walking). Intriguingly, they also found that there is no significant difference in speed sensitivity between familiar and unusual walking (from the viewpoint of the relationship between stride amplitude and frequency), indicating that motor experience, but not visual experience, contributes to human sensitivity to biological movements (Casile & Giese, 2006). Based on these findings, it is possible that the difference observed between orientation conditions in the present study also reflects the motor experience of the observers because we have never experienced inverted actions due to the gravitational constraint. In any case, it is interesting to examine whether the perception-action linkage is also observed between the perception of biological motion without the global configuration.

In addition to the effect of global and local biological motion information on speed discrimination sensitivity, we also found that perceived speed was slower for the original stimuli than for the scrambled stimuli (Experiment 2). This indicates that the perceived speed of biological motion is not simply determined by the local motion signals, and the global configuration of the biological motion reduces the perceived speed of point-light dots. In this regard, recent studies by Kohler, Caplovitz, and Tse (2009, 2014) have also shown that perceptual grouping of simple motion signals reduces the perceived speed. They used a bistable motion stimulus consisting of four pairs of rotating dots, which were perceived as either four individually rotating dot pairs (i.e., local percept) or two translating squares (i.e., global percept), and found that the global percept appears to move more slowly than the local one (the global slowdown effect).

However, it is also noteworthy that, unlike other effects observed in biological motion perception, such as enhancement of perceptual performance (e.g., Bertenthal & Pinto, 1994; Chang & Troje, 2008; Pavlova & Sokolov, 2000; Troje & Westhoff, 2006) or lengthening of perceived time duration (Wang & Jiang, 2012), the global slowdown effect of biological motion perception was resistant to the inversion effect; we found a comparable size of the global slowdown effect in the upright and inverted displays (Experiment 2). Furthermore, since the inversion effect was not observed with the scrambled stimuli (Experiment 1), which are considered to contain life-motion signals without global configuration, it is unlikely that information unique to living organisms have an influence on speed perception. Previous studies have also shown that some of the enhancement effects observed in biological motion detection and learning actually occurs independently from life motion signals but with global perception (Hiris, 2007; Jastorff et al., 2006). Therefore, as in the previous studies, the motion slowdown effect observed in biological motion perception may be attributable to the general process of perceptual organization in the visual system and hence not limited to biological motion perception.

In summary, the present study has demonstrated that biological motion information is employed differently for human visual speed perception and discrimination. The global form of biological motion, not local motion, makes the perceived speed slower and this may reflect a general property of perceptual grouping. On the other hand, in addition to the global form, local motion signals, even without the knowledge of the biological nature of the stimuli, could help with speed discrimination. The results of the present study do not clarify whether these phenomena are biologically innate or due to previous experience. However, these results provide insights into the role of biological motion signals in motion perception, which serves to make reliable judgments about others' actions.

Keywords: biological motion, global and local, inversion effect, perceived speed, speed discrimination

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