

The influence of biological motion perception on structure-from-motion interpretations at different speeds

Jaap A. Beintema

Department of Functional Neurobiology and Helmholtz Institute, Utrecht University, Utrecht, Netherlands



Anna Oleksiak

Department of Functional Neurobiology and Helmholtz Institute, Utrecht University, Utrecht, Netherlands



Richard J. A. van Wezel

Department of Functional Neurobiology and Helmholtz Institute, Utrecht University, Utrecht, Netherlands



Nonrigid point-light representations of biological motion are ideal to test higher level influences on structure-from-motion (SFM) perception. Here, we investigated the influence of biological motion perception on 3D SFM interpretations at different speeds. We presented nonrigid biological motion and rigid structures rotating around the vertical axis. The familiarity of the stimuli was changed by presenting three walker types: normal, inverted, and phase scrambled. Subjects had to discriminate rotation in depth and rigidity. We found that at lower-than-natural gait speeds, subjects perceived nonrigid biological motion to be rotating in depth, especially when the walker type was less familiar. In contrast, the percept of rigidity was correct at all speeds. A second experiment, in which a constant fraction of the gait cycle was presented, confirmed the influence of speed and additionally showed that brief displays of a familiar form at a high speed facilitate biological motion interpretations. The more veridical percept of rotation toward higher speeds fits the idea of biological motion channels tuned to higher—more natural walking—speeds that overrule a default assumption to perceive trajectories in depth. We also speculate that the rotation-in-depth percept at lower speeds points toward the existence of low-speed-tuned object motion channels.

Keywords: structure from motion, biological motion perception, speed tuning

Introduction

One recurring issue in vision research is how humans perceive depth from two-dimensional (2D) retinal projections. Visual motion or a sequence of views helps to constrain possible 3D interpretations of objects, living creatures, or the scene in which we move. This is nicely demonstrated by displays of dynamic point-lights that represent biological motion. Whereas a single view of point-lights on the joints of a human body contributes little to the percept of the 3D structure of the underlying figure, observers immediately recognize a walking human figure when the points move (Johansson, 1973). This feat requires higher cognitive information because other percepts easily arise when the same point-light figure is presented upside down, leading to poor recognition (Sumi, 1984) and reports of rotation in depth (Pavlova & Sokolov, 2003).

A minimum of three views of four non-coplanar points on a rigid body is required to unambiguously reconstruct the distance of points and their motion in depth (Ullman, 1984). Ullman proposed a scheme to recover structure from motion (SFM) that assumes minimal object changes between successive frames, known as the “rigidity assumption.” With this assumption, the 3D structure and motion can be recovered based on information that is local

in space and time, allowing depth information at an early stage in the visual pathway. This rigidity assumption holds in many situations, including moving point-light or line displays where motion and form information is sparse. For instance, Wallach and O’Connell (1953) showed that observers prefer an interpretation of a rigid rectangle receding in depth or rotating in depth over a nonrigid rectangle deforming in the fronto-parallel plane, calling this the kinetic depth effect. Furthermore, Jansson and Johansson (1973) found that observers prefer rotation, bending, and stretching, in that order, thus picking out the most rigid interpretation available.

Nevertheless, a more global analysis of the spatiotemporal structure seems to play a role as well. A rigid structure that rotates about an axis in the fronto-parallel plane is perceived as nonrigid when observers associate its 2D projection with a learned 3D form (Sinha & Poggio, 1996; Sparrow & Stine, 1998). This shows the influence of form recognition. Braunstein and Andersen (1984) reported that a rigid 2D line pattern rotating in the fronto-parallel plane is perceived as a distorting 3D shape. They explained this deviation from a rigid interpretation by the presence of contours spiraling out from the center, whose rotation is known to induce motion-in-depth sensations. Apparently, the rigidity assumption may be overruled by activation of expanding motion detectors, thus showing the influence of detectors for complex motion patterns.

Biological motion perception from dynamic point-lights illustrates the necessity of additional rules to interpret 3D structure (Johansson, 1973). In point-light figures, the body is nonrigid, with no more than two points per rigid limb segment. Local SFM solutions are still feasible when assuming pairwise rigidity (Hoffman & Flinchbaugh, 1982; Webb & Aggarwal, 1982), although Proffitt, Bertenthal, and Roberts (1984) pointed out the need for additional assumptions to prevent ambiguities in depth order or reversals of motion direction. However, biological motion perception may involve more specialized rules because the stimulus also carries form and temporal sequence information on movements. Mechanisms that use more elaborate form or motion templates to recognize the pattern of movement (see Aggarwal & Cai, 1999, for review) might therefore also help to perceive the depth structure and connectivity of points.

Several lines of evidence plead for a specialized system for perceiving biological motion. Less than 200 ms of stimulus presentation is sufficient to recognize the type of actions (Johansson, 1973), and the detection of biological motion is robust against background noise (Cutting, Moore, & Morrison, 1988). In contrast, unfamiliar inverted walkers take longer to recognize and are less well detected in the presence of background noise (Bertenthal & Pinto, 1994). Single-cell recordings show selectivity to biological motion patterns in area STPa (Oram & Perret, 1994), and various human imaging studies also suggest that the STS is selective to biological motion (Grossman et al., 2000; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001; see Giese and Poggio, 2003, for an overview).

Only a few studies investigated the influence of biological motion perception on perceived depth structure. After initial investigations by Johansson (1973), the focus of biological motion perception studies shifted to perception of other stimulus aspects, such as the ability to categorize action (Barclay, Cutting, & Kozlowski, 1978; Dittrich, 1993), to discriminate walking movements (Mather, Radford, & West, 1992), or to detect humans in noise (Bertenthal & Pinto, 1994; Cutting et al., 1988; Neri, Morrone, & Burr, 1998). Sinha and Poggio (1996) reported that a rigid 3D human form induced the percept of nonrigid biological motion when rocked back and forth. Bülthoff, Bülthoff, and Sinha (1998) showed that recognition of biological motion overrules stereoscopically defined depth structure. Here, we wish to extend these studies on the role of biological motion perception in SFM perception by varying speed.

Our idea to vary speed was inspired by studies that indicate differences in the processing of fast and slow motion (Edwards, Badcock & Smith, 1998; van de Grind, van Hof, van der Smagt, & Verstraten, 2001; Verstraten, Fredericksen, van Wezel, Boulton, & van de Grind, 1996). Such segregation in slow- and fast-speed channels has been implicated to reflect a separate evolution of slow-speed object motion and high-speed self-motion detection

systems. Indirect support for this was given recently by Anstis (2005), who showed stimuli that are interpreted as rigid rotation at lower speeds and as nonrigid radial motion at higher speeds. In a similar vein, we hypothesized that low-level SFM processes, which assume rigidity, as well as higher level biological motion processes might have a speed-dependent influence on the perceived depth structure.

Speed has been an experimental factor in a number of studies on biological motion perception. Barclay et al. (1978) found that recognition of gender was slightly reduced at gait speeds four times slower than natural. Giese and Lappe (2002) found that subjects are able to indicate what speed appears natural. Jacobs, Pinto, and Shiffrar (2004) recently showed that unnatural low gait speed reduced identity discrimination. These studies suggest that biological motion perception is tuned to speed. However, none of these studies explicitly addressed whether speed influenced the perceived depth structure.

Our initial observations indicated that slow speeds resulted in percepts of structures rotating in depth about the vertical. To quantify this percept, we asked subjects to indicate whether the structure rotated in depth or not. In a separate task, we asked subjects to indicate whether the structure was rigid or not. These tasks can be performed independent of whether biological motion was recognized. As a control on how speed affects perceived depth for structures that truly rotate, in half of the trials, we presented rigid structures that rotated. As a further check on whether the effect of speed is specific to biological motion perception, we compared the performance for normal walkers with performance for less familiar inverted or phase-scrambled versions. Biological motion perception is known to reduce by inverting the display upside down (Pavlova & Sokolov, 2000; Shipley, 2003; Sumi, 1984), as well as by disturbing the phase relations between points (Bertenthal & Pinto, 1994).

First, we investigated the influence of speed for stimuli that were presented for a fixed duration of 2.0 s. Given that one gait cycle at natural speed lasted 1.6 s, the effects of lowering the speed could well be confounded with effects of reduced phase information. Therefore, in a second experiment, speed was varied independently of phase information by presenting a fixed 1/4 cycle.

Methods

Experimental setup and stimuli

Stimuli were computer generated and displayed on a 35.7×27.5 cm monitor (75 Hz refresh rate, $1,024 \times 768$ pixels). Subjects viewed the display monocularly with the right eye from a distance of 123 cm while seated in a dark room. The head was supported by a chin rest.

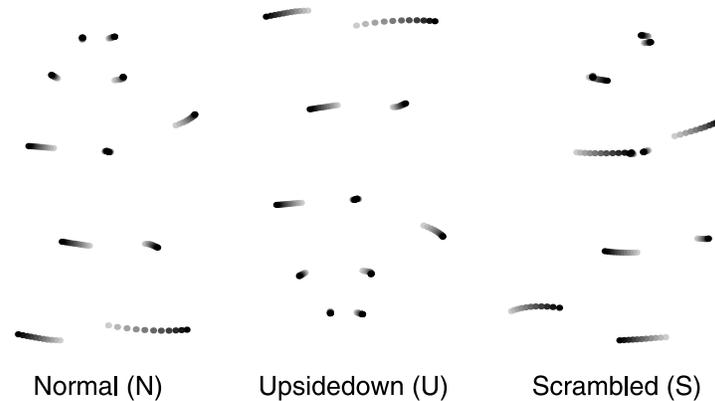


Figure 1. Three versions of the point-light walker used in this study. See online QuickTime [movies 1–3](#) for normal, upsidedown and scrambled versions of biological motion at a speed of 30 deg/s.

The stimulus consisted of 12 bright dots (squares that subtended 0.17 deg in visual angle) positioned in the center of the dark screen. Its height was maximally 3.4 deg. The stimulus was based on the 3D joint positions of a male walking at natural pace, captured at the laboratory of Prof. Lappe (Münster, Germany) using MotionStar Wireless (Ascension Technology Corp., Burlington, USA). The locations of sensors, attached to the ankle, knee, hip, wrist, elbow, and shoulder joints, were registered at 86 frames/s. After smoothing, centering, and clipping, each stimulus was the side view of a single walking cycle, normalized to 0.625 cycles/s. The average hip position was subtracted from the walker’s position as to have the walker remain at the same location, much like walking on a treadmill.

Speed was varied by replaying the motion sequence at 30, 60, 120, 240, and 480 deg/s, with 360 deg representing a full gait cycle or rotation cycle. The natural gait speed corresponded to 240 deg/s.

Three types of point-light walkers were used to test the contribution of biological motion perception on SFM interpretations (see [Figure 1](#)). The normal (N) walker was presented upright and facing rightward. The upside-down walker (U) was an inverted version of the normal walker, thus preserving all spatial and temporal relations between the points. The scrambled walker (S) differed from a normal walker by setting the initial phase of an individual point at random each trial, thus disturbing the temporal relations between the points while preserving the spatial configuration. Both inverting and phase scrambling the point-light walker have been shown to be effective in rendering the stimuli less recognizable. Whereas naive observers recognize normal walkers spontaneously from exposure durations of less than 200 ms (Johansson, 1973), upside-down point-light walkers require much longer time to recognize. Moreover, upside-down and phase-scrambled walkers are harder to detect against a background of dynamic noise than upright walkers (Bertenthal & Pinto, 1994; Cutting et al., 1988). We therefore classify

the inverted and phase-scrambled walkers as being less familiar.

Perception of rotation depth and rigidity was tested for two types of motion: A nonrigid structure of points that move along biological motion trajectories (BM) and a rigid structure of points that simulate rotation in depth about a vertical axis (R; see [Figure 2](#)). See the hyperlinks in the legends of [Figure 2](#) for animations of BM and R stimuli for a normal walker at 240 deg/s.

To measure the possible influence of speed and higher visual processing, we purposely removed depth cues that otherwise might help to distinguish biological motion trajectories from real rotation in depth. First of all, the stimuli were presented monocularly. Secondly, presenting the walker facing sideways minimized perspective information. The simulated walker distance was 10 m, and perspective cues were minimal anyway. Thirdly, the rotating R figures were presented as flat, coplanar structures. From a mathematical point of view, the minimum configuration to recover 3D depth from three views requires five points that are non-coplanar (see Longuet-Higgins & Prazndy, 1980). Informal observations showed that the illusion of rotation indeed disappears if BM stimuli are presented in 3D. To assure matched projections of BM stimuli and rotating R stimuli, we projected the BM stimuli orthographically. Finally, we removed depth order information from point occlusions, as this has been shown to lead to multistable percepts in point-light displays of biological motion (Proffitt et al., 1984). As [Figure 2](#) shows, the point-lights in biological motion follow to large extent the sinusoidal acceleration profile and elliptical trajectories that would result from pure rotation of a rigid planar structure about the vertical axis.

For biological motion stimuli (BM), the starting phase of a walking cycle was randomized per trial because a pilot study showed an effect of starting phase, especially when only part of a step cycle was presented. For R stimuli, the points simulated a “frozen” walker rotating

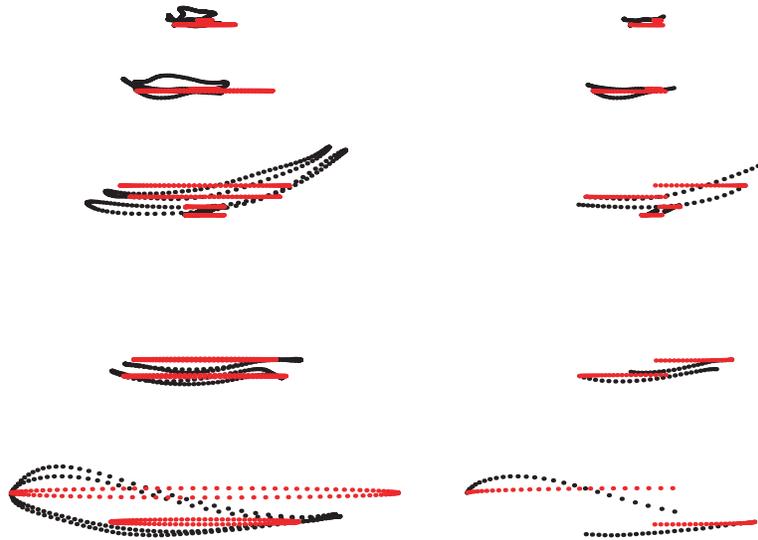


Figure 2. Normal walker motion trajectories for a biological motion (BM) stimulus (black dotted lines) and rotation (R) stimulus (red dotted lines). The left figure depicts a full-cycle trajectory. The right figure depicts 1/4-cycle trajectories (Experiment II), with BM's initial gait phase set to that of a frozen walker. See online QuickTime [movies 4](#) and [5](#) for biological motion (BM) and rotation (R) stimulus.

about a vertical axis through the mean hip position. To assure the same variation in visual width as the biological motion stimuli, we froze the normal and scrambled walker types in the most extended position with the legs fully apart. For the phase-scrambled walker, the frozen walker differed from trial to trial because it was based on a frame of a new random phase-scrambled walker. Because the rotating stimuli (R) were coplanar, they would be seen in profile twice during a cycle. This profile view of vertically aligned points might be an undesired cue for rotation, as it does not occur in the biological motion (BM) stimuli. To minimize attention to such possible cue, the rotating stimulus always started in the fronto-parallel plane with the walkers facing rightward.

Experimental design and procedure

Before starting an experimental session, subjects were verbally instructed and given a few minutes of practice trials without feedback. In the rotation task, subjects were asked to indicate whether they perceived the structure to rotate in depth or not. In the rigidity task, subjects were asked to indicate whether the structure was rigid or not. The task was clarified by showing a continuous animation of N, U or S walkers at normal velocity that moved biologically (BM), or frozen walkers that rotated in depth (R). Next, subjects were told that some stimuli would contain rotation and some would not, or in the rigidity task, some might be rigid and some might not. They were also told that intermediate stimuli of nonrigid rotating structures could be presented and that stimuli could differ in type of walker or velocity. Subjects were asked to perform the two-choice detection tasks by pressing a left or right key as quickly as possible after the

stimulus disappeared. Each trial was preceded by a black 0.5-s interval. In each experiment, the subject performed one session with the rigidity task and another one with the rotation task. The order of sessions was counterbalanced across subjects. Three factors were varied: velocity, walker type (N, U, or S), and motion stimulus (BM or R). This resulted in a $5 \times 3 \times 2$ experimental design. The order of trials was randomized.

The same eight subjects (four females and four males) participated in both experiments. Subjects had normal or corrected-to-normal vision. Two subjects had encountered the point-light displays before (J.P. and L.L.), but they were unaware of the purpose of this study. The other subjects had never been confronted with the point-light displays before.

Data analysis

For each experimental condition and subject, we determined the proportion of correct answers for the two motion conditions: p_{BM} for biological motion stimuli and p_{R} for rotating stimuli. To obtain an unbiased estimate of how well the observer could discriminate the two motion stimuli, we computed the sensitivity measure (d') using signal detection theory. On the assumption of equal variance, the sensitivity (d') was computed from the Z transforms of each fraction correct by $d' = Z(p_{\text{BM}}) + Z(p_{\text{R}})$. The response bias was measured by the log-likelihood ratio $\log(\beta) = 1/2[Z^2(p_{\text{R}}) - Z^2(p_{\text{BM}})]$ (Green & Swets, 1966; MacMillan & Creelman, 2005; Wickens, 2002). To avoid infinite Z values, we clipped p values at $1 - 1/n$ on the assumption of an error in p due to the limited number of observations n . Analyses of variance

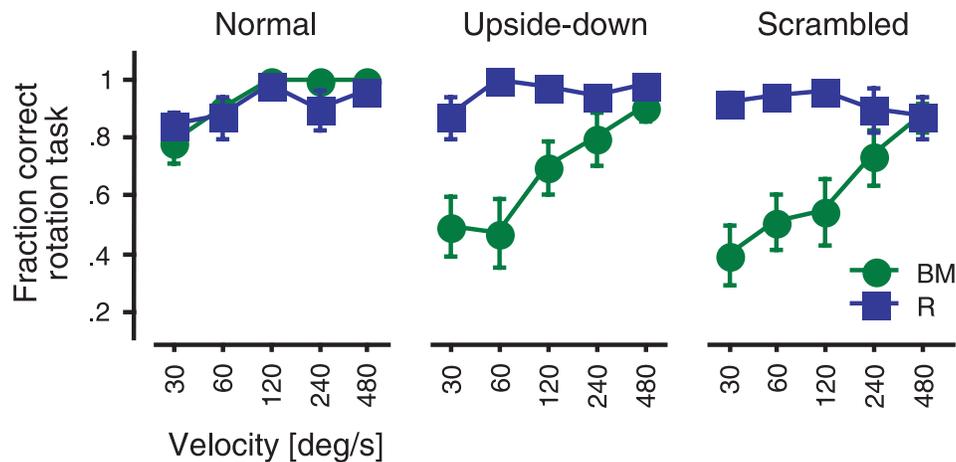


Figure 3. **Experiment 1** (2-s presentation): Fraction correct in the rotation task. Each panel shows the fraction correct for BM and R stimuli (p_{BM} and p_R) as a function of velocity split by walker type (normal, upside down, scrambled). Upside-down and scrambled biological motion stimuli (BM) are perceived to be rotating in depth at lower speeds. Rotating frozen walker stimuli (R) are perceived to be rotating, independent of walker type. Natural gait speed is 240 deg/s, where 360 deg represents a full cycle of gait or rotation. Data and error bars represent the mean \pm SE across eight subjects.

(ANOVAs) were conducted on d' and $\log\beta$ values pooled over eight subjects; t tests were regarded as significant when p values were below 5% chance level. This criterion was Bonferroni corrected in case of multiple comparisons.

Experiment 1: Fixed 2-s duration

The aim of this article is to investigate the role of speed in SFM interpretations of dynamic point-lights that resemble human gait. Pavlova and Sokolov (2003) noted that naive observers describe an inverted point-light walker as a rotating-in-depth “whirlwind” or “funnel.” Given this, we expected the subjects to interpret the biological motion displays either as motion in the fronto-parallel plane or as rotation in depth. By varying speed, we investigated whether specific velocities are associated with one or the other percept. We looked at three walker types to compare a possible velocity influence across familiar and less familiar configurations. In one task, we asked subjects to discriminate rotating from nonrotating displays. In another task, we asked whether stimuli were rigid or nonrigid. Stimuli were counterbalanced over subjects to remove effects of learning. This way, we tested whether nonveridical percepts of stimuli rotating in 3D were accompanied by percepts of rigid structures, as would follow from Ullman’s “rigidity assumption.” Display duration was 2.0 s, independent of the speed. Each condition was repeated 10 times (300 trials in total).

Results

Rotation task: Fixed 2-s duration

Walker type and speed clearly influenced the perceived 3D trajectories in the rotation task, as shown by the group-

average fraction of correct responses (Figure 3). For normal walkers, the fraction correct for biological motion stimuli (BM, green circles) only slightly decreased toward lower speeds, reaching ceiling level ($p = 1.0$) at speeds of 120 deg/s or higher. For upside-down and phase-scrambled walkers, however, the BM conditions showed a strong decrease toward lower speeds, down to fractions as low as 0.5 and 0.4, respectively. See the hyperlinks in the legends of Figure 1 for animations of normal, upside-down, and phase-scrambled BM stimuli at the lowest speed of 30 deg/s. The rotation conditions (R, blue squares) showed a similar decrease toward lower speeds for normal walkers but remained high for the less familiar walkers.

These rotation-in-depth judgments show that BM stimuli were judged correctly as nonrotating only when the figure’s orientation, its speed, and the phase-relations between points were consistent with natural human gait. At lower speeds, the perception of less familiar BM stimuli was clearly biased toward an interpretation of rotation in depth. This might suggest that slow motion is by default interpreted as an object undergoing rotary motion. Did subjects also perceive these structures to be rigid?

Rigidity task: Fixed 2-s duration

In contrast to the rotation judgments, the rigidity judgments (Figure 4) were close to veridical at all speeds with proportions correct near or at ceiling level ($p = 1.0$). Biological motion stimuli (BM, green circles) were correctly judged as “nonrigid,” including nonfamiliar walkers at low speeds, although the fraction correct was still decreased at the lowest speed (30 deg/s). Rotating structures (R, blue squares) were perceived as “rigid,” including the lowest speed for normal walkers, with

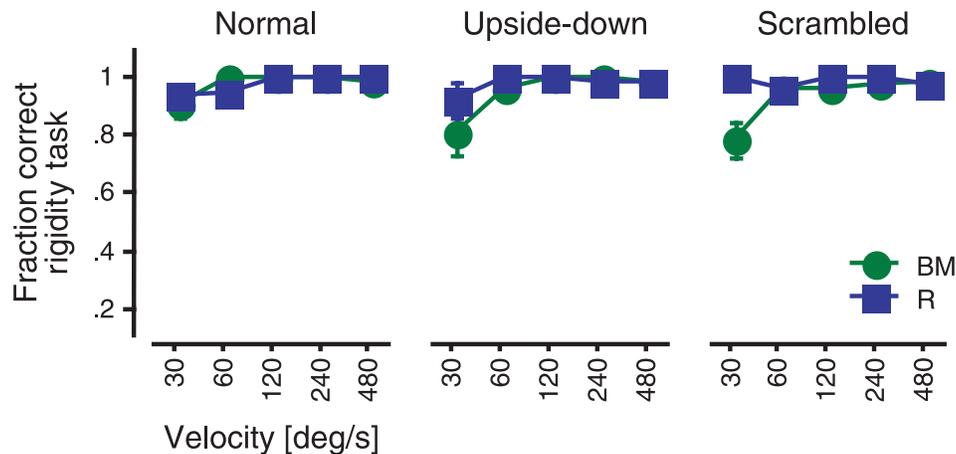


Figure 4. Experiment I (2-s presentation): Fraction correct in the rigidity task. Scores remained high in all conditions. For legend details, see Figure 3.

fractions correct equally high as in the rotation task. These results suggest that rigidity and rotation judgments are not directly coupled for BM stimuli.

Sensitivity and bias: Fixed 2-s duration

In the rotation task, the fraction correct for less familiar walkers was strongly reduced toward lower speeds for BM stimuli but remained high for R stimuli. One interpretation is that the perception of low-speed BM stimuli is biased toward rotation in depth. However, the lowered performance for BM stimuli could also be interpreted as an increased response bias together with a reduced ability to discriminate between BM and R stimuli. For that reason, we also analyzed the data in terms of sensitivity (d') and log-likelihood ratio ($\log\beta$; Figure 5).

Generally, the sensitivity (d' ; Figure 5, upper panels), reduced toward lower speeds, most noticeably for the less familiar walker types in the rotation task (blue circles). A two-way ANOVA on rotation task data shows that velocity and walker type both significantly affected the sensitivity (d'), $p < .001$, $F(4,105) = 12.9$, and $p < .001$, $F(2,105) = 4.45$, respectively, without interaction, $p = .89$, $F(8,105) = 0.44$. The sensitivity was highest for normal walkers, differing significantly from upside-down and scrambled walkers ($p < .001$, $df = 39$ for paired t tests on N vs. U or N vs. S). We found no difference between upside-down and scrambled walkers ($p = .06$, $t = 1.9$ on U vs. S), using $p = .0167$ as criterion (5% level Bonferroni corrected for three comparisons). The sensitivity in the rigidity task (black triangles) was significantly higher than in the rotation task, even for the normal walker condition, $p = .005$, $t(78) = 3.0$ in a paired t test on rigidity versus rotation for the normal walker. The sensitivity (d') was significantly affected by speed but not by walker type, ANOVA with velocity: $p < .001$, $F(4,105) = 9.76$; walker type: $p = .47$, $F(4,105) = 0.76$; Velocity \times Walker Type:

$p = .82$, $F(8,105) = 0.6$. Note that d' values reached ceiling levels at the higher speeds. Therefore, the effect of walker type could not be properly assessed. Also, the distribution of d' values did not meet the normality assumption due to ceiling effects, but the effect of speed was still significant in a ranking test ($p = .01$ in the Kruskal–Wallis test).

The log-likelihood ratio ($\log\beta$; Figure 5, lower panels) revealed a clear bias toward perception of R stimuli for less familiar walkers, especially in the rotation task (blue circles). The bias in the rotation task increased slightly toward lower speeds, but the effect of speed was not significant in the two-way ANOVA, speed: $p = .12$, $F(4,104) = 1.89$; walker type: $p < .001$, $F(2,104) = 11.12$. Judgments in the upside-down and scrambled walker conditions were clearly biased toward rotation percepts. No bias was found for normal walkers (one-group t test on data pooled over five velocities and eight subjects): $p = .6$, $t(39) = -0.52$. In the rigidity task (black squares), a bias is evident only at the lowest 30 deg/s speed ($p = .0067$ for data pooled over walker type). Pooled over five velocities and corrected for three comparisons, the bias was significant only in the scrambled condition, $p = .05$, $t(39) = 0.2$ (upside-down condition) and $p = .003$, $t(39) = 3.2$ (scrambled condition), and again not for the normal walker, $p = .65$, $t(39) = -0.46$. Note that here as well, ceiling effects did not allow us to assess the bias at the higher velocities. Effects of speed did not reach significance in the Kruskal–Wallis test ($p = .63$ and $p = .06$ for the upside-down and scrambled condition, respectively).

Discussion

We found a clear influence of speed on perceived rotation in depth, but not on perceived rigidity. Lowering the speed increased the perceived rotation in depth when the dynamic point-lights simulated human gait (BM

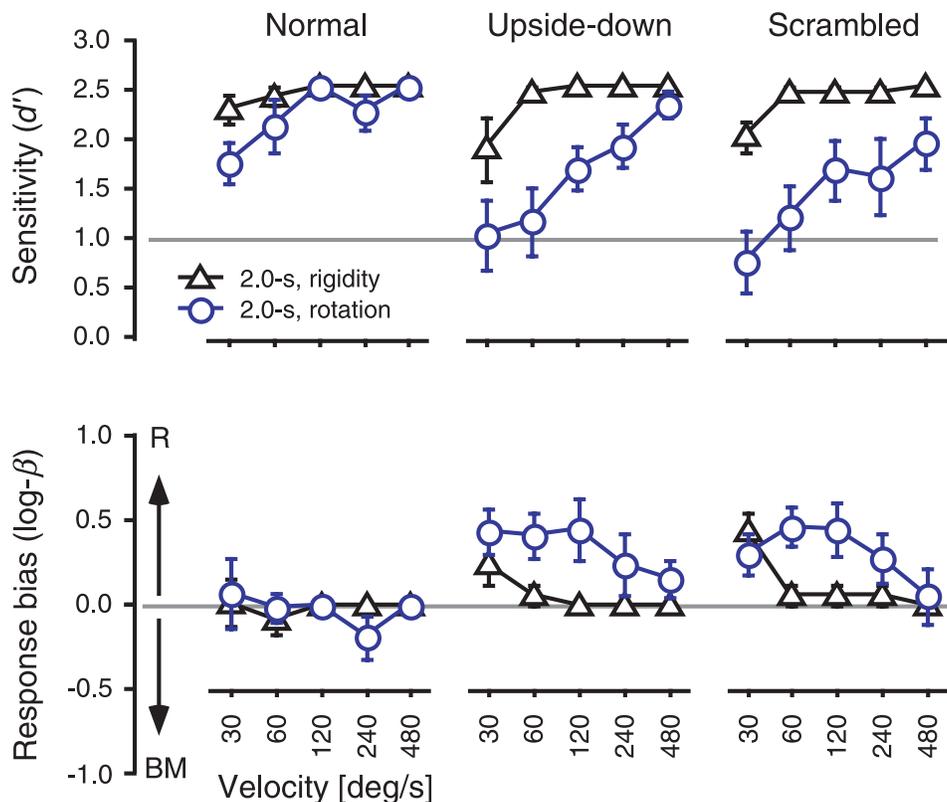


Figure 5. **Experiment I** (2.0-s presentation): Sensitivity (d') and response bias ($\log-\beta$) as a function of velocity for three walker types in the rigidity (triangles) and rotation task (circles). Upper panels: The sensitivity (d') is reduced toward lower speeds but most noticeably for upside-down and phase-scrambled walker types in the rotation task. Lower panels: Log-likelihood ratio $\log-\beta$, where positive values indicate a response-bias toward R stimuli. Perception of upside-down and scrambled walkers was biased toward “rotation in depth” for most speeds and only biased toward “rigidity” at the lowest speed. Data represent the mean \pm SE across eight subjects.

stimuli) but not when the frozen walker truly simulated rotation in depth (R stimuli). Analysis of the combined data from BM and R conditions showed an overall drop in sensitivity (d') toward lower speed that was enlarged for less familiar walker types in the rotation task. The log-likelihood ratio ($\log-\beta$) also showed a bias toward rotation-in-depth percepts for less familiar walker types but not an influence of speed.

The reported effect of walker orientation (normal vs. upside down) on rotation-in-depth judgments confirms an earlier finding that static form recognition influences SFM processing (Sinha & Poggio, 1996). The effect of phase scrambling also shows that the phase relations need to be consistent with biological motion to overcome the bias toward rotation in depth. This result is in line with observations by Bülthoff et al. (1998) that biological motion perception influences SFM processing. Our results are novel because we show that speed mediates the influence of biological motion on SFM processing.

Our experimental design cannot dissociate a perceptual bias from a cognitive shift in the criterion. One could argue that the increased bias for less familiar

walkers is explained by a default response strategy to choose R stimuli if subjects are less certain. The d' values of 1.0 or greater, however, indicate that subjects were not guessing at low speeds. Verbal debriefings after each session confirmed that subjects actually perceived inverted and scrambled walkers to be rotating at low speeds. This strongly suggests that the nonzero $\log-\beta$ values reflect a perceptual bias related to underlying neural processing, rather than cognitive shifts in the criterion.

The effects of speed and walker type were much larger on perceived rotation in depth than on perceived rigidity. Possibly, a trend as a function of velocity or walker type in the rigidity task was cut off at the higher velocities because the performance for both R and BM stimuli reached ceiling levels (i.e., $p_{\text{BM}} = 1.0$ and $p_{\text{R}} = 1.0$). Indeed, at the lowest speed (30 deg/s), less familiar walker types did show an increased bias and lowered sensitivity (d') compared with normal walkers. Anyhow, the overall bias was higher in the rotation task than in the rigidity task. Thus, upside-down or phase-scrambled walkers at low speed were perceived to be rotating and nonrigid at the same time. Such percepts of nonrigidity for less

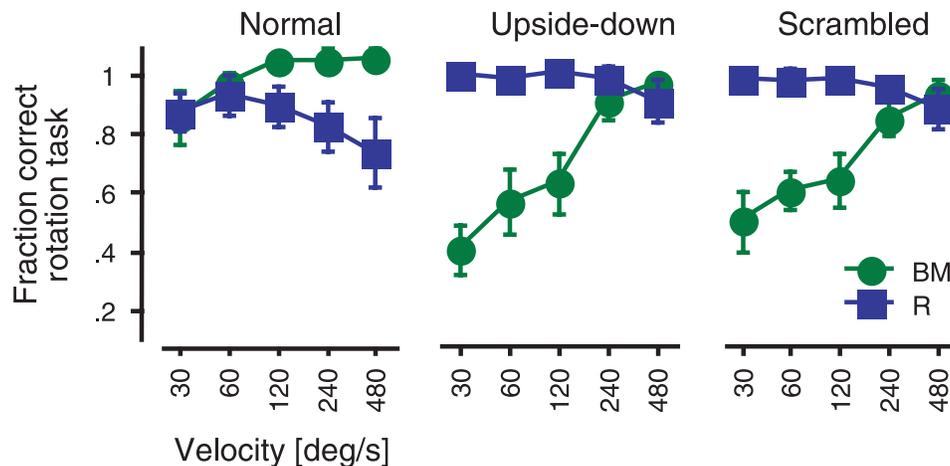


Figure 6. **Experiment II** (1/4-cycle presentation): Fraction correct in the rotation task as a function of velocity for three walker types. The trends for upside-down and scrambled walkers remain the same as in **Experiment I** (compare with [Figure 3](#)). For normal walkers, rotation stimuli (R) are misjudged at higher velocities. Data represent the mean \pm SE over eight subjects.

familiar walker types counteract the idea that the visual system by default assumes a rigid structure (Sinha & Poggio, 1996; Ullman, 1984). Moreover, the larger bias and lower sensitivity in the rotation task suggest that the perception of rotation in depth and rigidity are independently processed.

Because the stimuli were presented for a constant duration of 2.0 s, the sequence information increased toward higher velocities. Therefore, we could not differentiate whether the more veridical judgments of rotation in depth toward higher speeds was caused by speed tuning of motion processes or simply by increased sequence information. Therefore, we repeated the experiment with stimuli that were presented for a fixed fraction of a cycle.

Experiment II: Fixed 1/4 cycle

Earlier research showed that the number of step cycles of a biological motion display limits the temporal summation process (Neri et al., 1998), not the exposure duration per se. In **Experiment I**, the number of step cycles increased with higher velocity because the trial duration was kept constant (2.0 s). That way, the increased performance toward higher velocities may have been caused by additional phase information, rather than speed-dependent processing. We here present all conditions for a quarter of a cycle (90 deg). This resulted in exposure times of 3.0, 1.5, 0.75, 0.375, and 0.1875 s for velocities 30, 60, 120, 240, and 480 deg/s, respectively. The starting phase of a step cycle was randomized from trial to trial. The same eight subjects performed rotation and rigidity discrimination tasks with the previously described set of stimuli (10 repetitions for BM and 20

for R motion conditions; 450 trials in total). R stimuli were presented twice as often as in **Experiment I** to allow a more accurate measurement of the high fractions correct in the rigidity task.

Results

Rotation task: Fixed 1/4 cycle

The fraction of correct responses in the rotation task ([Figure 6](#)) for the BM conditions showed the same trends as in **Experiment I**. BM stimuli were still perceived more correctly toward higher speeds for upside-down and scrambled walkers, whereas normal BM walkers showed only a small trend that reached ceiling level at a speed of 120 deg/s and higher. This similarity in performance rise for unfamiliar walkers is remarkable because the presentation duration was now reduced 16-fold at the highest speed. The less familiar walker types (upside down and scrambled) showed similar high performance as in **Experiment I**, except that the fraction correct was now decreased at the highest velocity. Also different from **Experiment I**, the fraction correct for the perception of rotating figures (R) in the normal condition decreased at 60 deg/s and higher velocities.

Rigidity task: Fixed 1/4 cycle

The rigidity task in **Experiment II** ([Figure 7](#)) showed trends in the fraction correct that were similar to **Experiment I**. As in **Experiment I**, the inverted and scrambled configurations were judged veridically at all velocities: R walkers as rigid structures and BM walkers as nonrigid. However, like in the rotation task, performance started to decrease for normal walkers in the R condition at the highest velocities (240 and 480 deg/s). In these cases, the

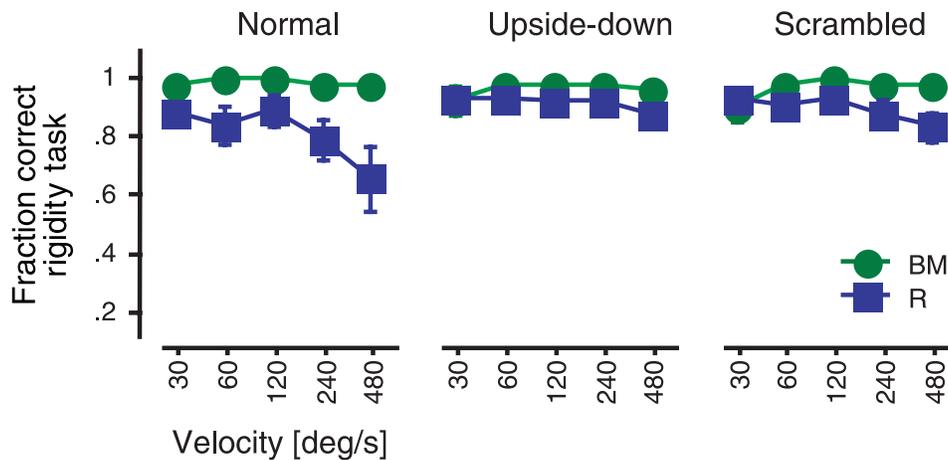


Figure 7. **Experiment II** (1/4-cycle presentation): Fraction correct in rigidity task. The trends for upside-down and scrambled walkers remain the same as in **Experiment I** (compare with [Figure 4](#)). For normal walker types, rigidity is now misjudged at higher velocities for the rotating stimuli (R). Data represent the mean \pm SE over eight subjects.

frozen rotating walkers were perceived to be less rigid toward higher velocity.

Sensitivity and bias: Fixed 1/4 cycle

Similar to **Experiment I**, for perception of unfamiliar walkers, we found a decrease in sensitivity (d') toward lower speeds in the rotation task, whereas sensitivity in the rigidity task remained high ([Figure 8](#), upper panels). For the rotation task, the two-way ANOVA revealed a significant effect of velocity, $p = .008$, $F(4,104) = 2.4$, but without a significant effect of walker type, $p = .06$, $F(2,104) = 2.92$, or an interaction, $p = .2$, $F(8,104) = 1.33$. For the rigidity task, the two-way ANOVA showed no significant effect of velocity, $p = .07$, $F(4,104) = 2.53$, but did show a significant effect of walker type, $p = .04$, $F(2,104) = 3.3$, and no interaction, $p = .9$, $F(8,104) = 0.47$. For normal walkers, in both the rotation and rigidity task, sensitivity (d') decreased at speeds higher than 120 deg/s, although the difference between 120 and 480 deg/s did not reach significance, paired t test: $p = .11$, $t(7) = -1.85$ and $p = .08$, $t(7) = -2.01$, respectively. In the rigidity task, the sensitivity (d') remained high at velocities lower than 120 deg/s.

The trends in $\log\beta$ ([Figure 8](#), lower panels) were also similar to **Experiment I**. For the rotation task, subjects were strongly biased toward rotation for the less familiar walker types (one-group t test on $\log\beta$ values with $df = 39$: $p < .001$ for inverted and scrambled walkers) and not for the normal walker ($p = .8$, $t = -0.24$). Different from **Experiment I**, however, the two-way ANOVA showed a significant effect of speed, speed: $p = .01$, $F(4,104) = 3.29$; walker type: $p < .001$, $F(2,104) = 13.5$; Speed \times Walker Type: $p = .68$, $F(8,104) = 0.71$. In the rigidity task, one-group t tests ($p = .001$, $t = 3.47$ and $p = .03$, $t = 2.22$ for upside down and scrambled, respectively) show that the responses were significantly biased for upside-down

walkers (p values less than .0167, corrected for multiple comparisons), but the effect of speed or walker type was not significant in the two-way ANOVA, speed: $p = .09$, $F(4,104) = 2.09$; walker type: $p = .07$, $F(2,104) = 2.6$.

For comparison, the results for **Experiments I** and **II** have been plotted together in [Figure 9](#). Because the d' and $\log\beta$ values did not always meet the normality assumption at high velocities in **Experiment I**, we tested for differences using a Wilcoxon's Signed Rank Test on data matched for each subject, velocity, and walker type. Overall, the sensitivity (d') in the rotation task (upper panels, open and solid circles) did not differ significantly between experiments ($p = .84$, $z = -0.2$). Unlike **Experiment I**, d' values for normal walkers in **Experiment II** (filled symbols) dropped at velocities of 240 and 480 deg/s, but the difference between experiments did not reach significance at a speed of 480 deg/s ($p = .09$, $z = -1.68$). For the rigidity judgments ([Figure 9](#), open and solid triangles), the overall sensitivity d' ($p = .17$, $z = -1.4$) did not differ significantly between **Experiments I** and **II**. For normal walkers at the highest speed of 480 deg/s, sensitivity (d') was reduced in **Experiment II** but not significantly ($p = .18$, $z = -1.35$). For inverted and scrambled walker types at the lowest speed of 30 deg/s, we did find that the sensitivity (d') was lowered in **Experiment II** ($p = .02$, $z = -2.4$; $p = .04$, $z = 2.0$ for inverted and scrambled walkers, respectively). We also found a clearly higher response bias ($\log\beta$) for the rotation task in **Experiment II** ($p = .008$, $z = -2.65$), as is most evident for the unfamiliar walkers. The response bias for the rigidity task was also somewhat increased in **Experiment II** but not significantly ($p = .15$, $z = -1.4$).

Discussion

We replicated the two main findings of **Experiment I**. First of all, point-light representations of human gait (BM

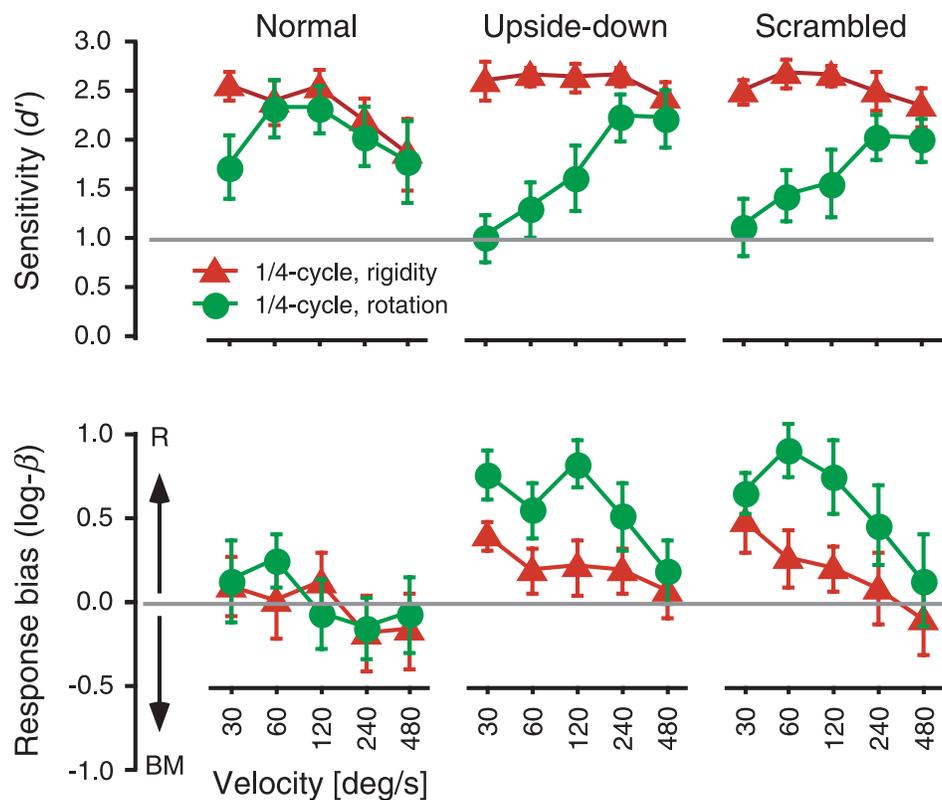


Figure 8. **Experiment II** (1/4-cycle presentation): Sensitivity and bias for rigidity and rotation-in-depth tasks as a function of velocity for three walker types. For details, see the legend in [Figure 5](#).

conditions) were perceived to rotate in depth at lower-than-natural speed, especially if the walkers were less unfamiliar. Secondly, perception of rigidity was more veridical than perception of rotation in depth. In contrast to [Experiment I](#) (2-s presentation duration), the sequence information was kept constant. As a result, the presentation duration decreased reciprocally with higher speed. Despite these changes, rotation-in-depth judgments of BM stimuli were still increasingly more veridical toward higher velocities. This shows that the perception of SFM is speed dependent. The qualitative observations from the fraction correct were supported by statistical analyses on sensitivity and bias. Moreover, for rotation-in-depth judgments, lowering the velocity not only significantly reduced the sensitivity d' , like in [Experiment I](#), but also significantly increased the response bias ($\log-\beta$) for less familiar walkers.

At higher speeds, the rotating frozen walker was judged incorrectly as not rotating ([Figure 6](#)) and to be nonrigid ([Figure 7](#)). This might suggest that these displays were perceived containing less depth (structure deforming in 2D) or possibly as “a walking person.” This would be in line with findings by [Bülthoff et al. \(1998\)](#) and [Sinha and Poggio \(1996\)](#) that the recognition of a familiar configuration of a normal walker influenced the subjects’

expectations with regard to the motion pattern (“a walking human” and not rotating rigid structure).

Comparisons between [Experiments I](#) and [II](#) not only showed great similarity but also revealed some differences that deserve discussion. First of all, for unfamiliar walkers, the bias ($\log-\beta$) in the rotation task was significantly larger in [Experiment II](#). This is not surprising in the light of the unbalanced stimulus repetitions in [Experiment II](#). Because R stimuli were presented twice as often as BM stimuli, this may well have increased the response bias toward R stimuli. Secondly, the rigidity task results in [Experiment II](#) at the lowest speed of 30 deg/s no longer showed a decrease in sensitivity for less familiar walkers. At a speed of 30 deg/s, the presentation duration was about equal (2 s in [Experiment I](#) and 3 s in [Experiment II](#)) and subjects participated in both experiments. Therefore, the larger sensitivity (d') for [Experiment II](#) may have resulted from learning. This effect of learning must be small because we found no significant improvement in the rotation task for unfamiliar walkers at 30 deg/s. Alternatively, the improved sensitivity at 30 deg/s could be related to the somewhat longer presentation duration (3 s) compared to [Experiment I](#) (2 s). If exposure time influenced the sensitivity, however, we would expect d' values to decrease at higher speeds. For unfamiliar walkers,

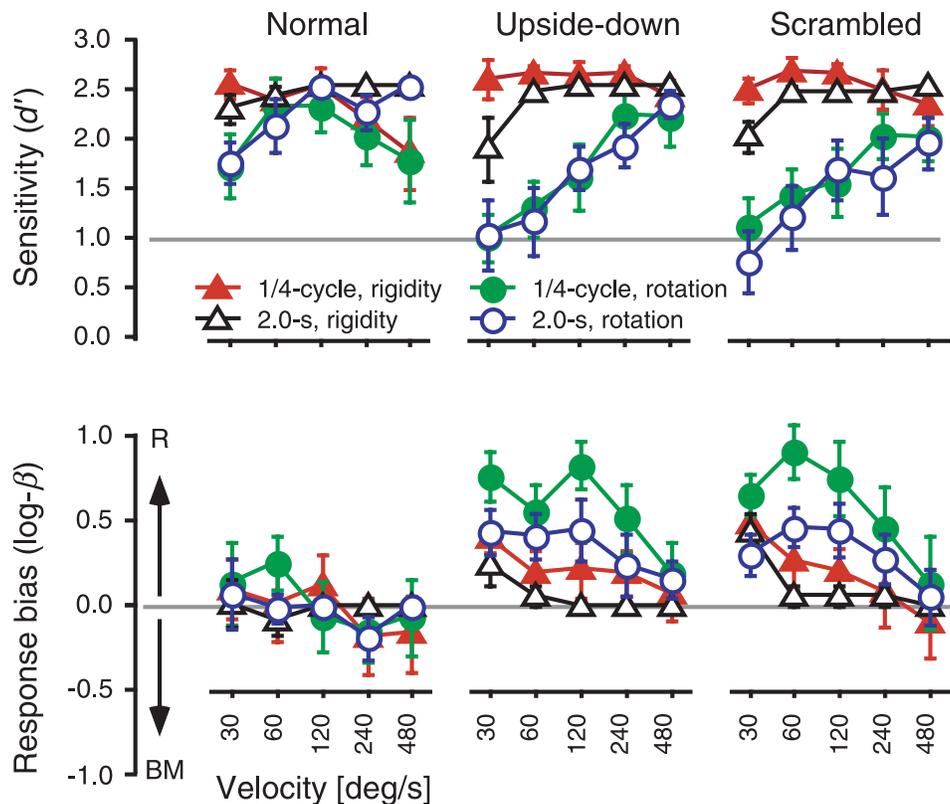


Figure 9. Comparison across [Experiments I](#) and [II](#) of sensitivity and bias as a function of velocity for three walker types. Upper panels: Sensitivity (d'). Lower panels: Bias. Data represent the mean \pm SE over eight subjects.

we could not confirm this trend because d' values were already at clipping levels due to the limited number of repetitions. However, the data for normal walkers do suggest that sensitivity decreased with shorter exposure time.

The decrease in sensitivity in [Experiment II](#) at higher speeds occurred only for normal walkers. The effect did not reach significance but was present for the rigidity and the rotation task. Also, at higher speeds, the bias in both tasks became slightly negative, suggesting a bias toward perception of BM stimuli. These trends may be caused by a decreased exposure duration (at 480 deg/s, it was 0.19 s in [Experiment II](#) vs. 2.0 s in [Experiment I](#)) and would fit with the reversal hierarchy theory (Hochstein & Ahissar, 2002; Jokisch, Daum, Suchan, & Troje, 2005). This theory accounts for the pop-out effect of perceptually familiar stimuli, as in our case—an upright point-light walker. Hochstein and Ahissar (2002) suggested that “vision at a glance” compares a scene with the stored, generalized, categorical interpretations in a feed-forward manner. It is associated with spread-attention that would allow a crude initial percept of a visual scene. When an observer has time and is required to focus attention to the specific units, “vision with scrutiny” comes into play. According to this theory, discrimination depends on reentry of a higher level signal to the low-level receptive fields for

feature binding. In the light of this model, we suggest that when the display was very brief (in the order of 200–400 ms), the subjects only had the global crude percept of the stimulus in the case of familiar configurations, and their decisions were based on the associated expectations.

General discussion

In two experiments (fixed 2.0-s duration and fixed 1/4 cycle), we found that the SFM interpretation of dynamic point-lights that simulate human gait was strongly affected by speed and task. First of all, less-than-natural gait speed reduced the sensitivity to rotation in depth and biased the percept toward rotation interpretations. Secondly, these speed effects were largest for less familiar walker types. Thirdly, rigidity judgments were much less influenced by speed or familiarity. [Experiment II](#) (fixed 1/4 cycle) confirmed the speed dependency and showed that brief presentations of familiar form slightly reduced sensitivity for rotation in depth and slightly biased judgments toward perception of biological motion.

Our finding that familiar orientation reduces the response bias ($\log\beta$) and increases the sensitivity (d') at

low speed could be in line with earlier reports that static cues on 3D shape dominate the perception of rigid rotating stimuli (Sinha & Poggio, 1996) or nonrigid rotating stimuli (Sparrow & Stine, 1998). Our finding that manipulations of the phase relations had a similar effect indicates that motion dynamics also plays an important role. These findings support the view by Bülthoff et al. (1998) that lower level SFM processing is influenced by higher level biological motion perception. For instance, showing biological motion in reverse is under certain conditions perceived as a figure moving forward (Pavlova, Krageloh-Mann, Birbaumer, & Sokolov, 2002). Here, we show that the influence of biological motion recognition is actually speed dependent.

Lowering the speed significantly reduced the sensitivity (d') and significantly enlarged the bias ($\log\beta$) for rotation-in-depth judgments. Speed effects on the bias were primarily found for less familiar walker types (see Experiment II), whereas speed effects on sensitivity were found for all three walker types (see Experiment I). The latter suggests that lower speed degrades information at a common earlier processing stage. We compared human thresholds for motion discrimination (direction or speed) with the maximal motion differences based on a single point-light (see Appendix). These results showed that the poor sensitivity at the two lowest velocities could indeed result from limited speed and motion direction discrimination. In addition, a more global analysis must play a role because at low speed, sensitivity was significantly better for perception of normal walkers as compared with less familiar walkers. Thus, the bias ($\log\beta$) and the sensitivity (d') both point toward a speed-dependent global analysis that influences SFM perception.

It remains intriguing why perception was biased toward rotation interpretations if the stimulus was less recognizable as biological motion. It might indicate that humans have a default assumption to perceive structures (or individual points) to rotate in depth instead of motion in the fronto-parallel plane (Johansson, 1973) as soon as stimuli cannot be recognized. Then, this default is overridden at higher speed because (1) more precise local motion information is available and (2) biological motion detectors are tuned to higher speeds. At the same time, however, the results are consistent with the idea of object motion channels that are tuned to slow speeds (van de Grind et al., 2001) so that unfamiliar BM stimuli may be classified as rigid rotating objects because of their low speed. Our results do not allow us to differentiate between these possibilities.

If recognition of biological motion underlies the speed effects, one might expect a peak in the sensitivity and the bias (toward BM stimuli) at a speed of 240 deg/s that is most natural. In Experiment II, the sensitivity in the rotation task for perception of normal walkers reached a maximum at a speed of 120 deg/s, which is indeed close to the natural gait speed. For perception of normal walkers, a slight bias toward BM stimuli can also be

observed at higher speeds, although this was not significant. However, as discussed in Experiment II, these effects are most likely related to the very brief exposure duration and the presence of familiar form. Then, are our results specific to biological motion? We think so because phase scrambling left much of the form of a walker intact, only influencing the phase-relations between points. The difference in performance as compared to a normal walker must therefore be attributed not only to recognition of form but also to the analysis of motion dynamics as in biological motion perception. In this respect, it is interesting to note that Heptulla-Chatterjee, Freyd, and Shiffrar (1996) found that the perception of the hand trajectory in depth was more biomechanically correct, that is, around the object instead of through the object, with increasing stimulus onset asynchrony (up to 500 ms). Their interpretation was that the use of biomechanical rules required more time. Our finding that very brief exposure duration leads to more biological interpretations suggests that the results of Heptulla-Chatterjee et al. reflect a speed effect, in that the very short SOA (100 ms) leads to nonbiological paths because the speed became unrealistically high.

Rotation and rigidity independently perceived

A comparison between rigidity and rotation judgments could not be very quantitative because various data points for the rigidity task suffered from ceiling effects. Nevertheless, the data show that the influence of familiarity at low speeds differs between the tasks of judging rotation and judging rigidity. The analysis of d' values suggests that speed effects on rotation judgments are largely caused by reduced sensitivity. Interestingly, though, subjects were able to tell BM and R stimuli apart because the rigidity task showed fractions correct well above chance for both R and BM stimuli. Naive subjects were also told that intermediate stimuli or nonrigid rotating could be presented. However, the authors, aware of the experimental design, showed the same effects. This adds to the conclusion that rigidity and rotation are processed differently.

Our finding that rotation and rigidity judgments are largely independent seems at odds with other SFM studies (Sparrow & Stine, 1998; Todd, Akerstrom, Reichel, & Hayes, 1988). Structures that are perceived to be less rigid are perceived to be shallower in depth. Sparrow and Stine (1998), for example, reported a common trend in perceived rigidity and reversal of depth when varying familiarity. Several differences in stimulus size and task can be pointed out. Another possible difference is that the point-lights of biological stimuli carry salient acceleration and trajectory information. This might allow judgment of rotation in depth to be based on a single point, whereas judgment of rigidity requires integration over more points. The rotation-in-depth judgments in our study are based on information from more than one point-light. Because performance differs between phase-scrambled and normal

walkers, the rotation-in-depth judgments may be based on fewer points than rigidity judgments. Indeed, informal observations on the perceived trajectories in depth from only a single point-light on the ankle already suggest remarkable effects of speed and orientation (upright/upside down). The importance of acceleration and trajectory information from single moving point-lights in the perception of biological motion has been stressed before (Beintema, Georg, & Lappe, *in press*; Mather et al., 1992).

Separate mechanisms for rigid and biological motion

One could argue that BM and R stimuli were so distinct that they might be processed by different mechanisms. Indeed, speed, familiarity, and task primarily affected the perception of stimuli that followed biological motion trajectories (BM) and not those that followed rotation-in-depth trajectories (R). As discussed in [Experiment 1](#), however, a possible trend as function of speed could not be assessed for R stimuli because the fraction correct was already at ceiling level at low speeds. Clearly, however, performance at low speeds was much lower for judgments of BM stimuli than for those of R stimuli.

Evidence for different processing of rigid motion and nonrigid biological motion has been investigated before (Neri et al., 1998; Poom & Olsson, 2002). These studies compared spatiotemporal integration characteristics of perception of biological motion, translational motion (Neri et al., 1998), and rotation in depth (Poom & Olsson, 2002). They found that the spatiotemporal summation curves for perception of biological motion, translation, and rigid rotation differ. The claim of different mechanisms for rigid rotation and biological motion perception also has support from fMRI studies in which separate neural substrates were described (Grèzes et al., 2001; Peuskens, Vanrie, Verfaillie, & Orban, 2005). Both motion patterns evoked activation in the occipitotemporal junction, which likely included MT/V5, LOS/KO, and the posterior STS areas. More important, the responses to rigid rotation were consistently found to be localized posterior to those elicited by nonrigid biological motion.

However, as pointed out by Poom and Olsson (2002), a possible flaw in these studies is that differences in performance may reflect differences in low-level description of the stimulus, such as periodicity, spatial distribution, and motion trajectories of points, rather than the existence of different mechanisms. With this in mind, Poom and Olsson introduced two additional stimuli: (1) a rigid point-light human form rotating in depth along its vertical and (2) a rigid nonbiological form (a half prolate spheroid) rotating, which, similar to biological motion, was periodical. They found that temporal integration in the frozen rotating walker condition was speed independent, whereas nonrigid biological motion gave different

constants of summation, depending on the time period of the step cycle (faster summation at higher velocity). Thus, the specificity of temporal integration strategy of biological motion perception was not due to its oscillatory feature.

We extend Poom and Olsson's (2002) comparison between biological motion and rigid structure rotation, controlling the periodicity by always presenting 1/4 of a cycle. We demonstrated that rotation-in-depth perception is not affected by this spatiotemporal manipulation and that observers can correctly perceive rotation at all speeds, confirming and elaborating previous findings (Poom & Olsson, 2002). Surprisingly, we found much less speed effect for normal walker under biological motion conditions. This discrepancy with the studies by Neri et al. (1998) and Poom and Olsson might be due to different tasks and the absence of dynamic noise in our case. However, we did show a speed effect in biological motion conditions with the less familiar walkers (inverted and phase scrambled). In agreement with Neri et al. and Poom and Olsson, the slower displays were more ambiguous and extended exposure times did not significantly improve the performance.

Conclusions

We find that 3D SFM interpretations of point-light displays of biological motion are strongly affected by speed. The perceived motion in depth was more veridical at speeds that are natural to human gait. The contribution of biological motion perception was most noticeable at lower speeds. At low speeds, humans showed a general tendency to perceive less familiar structures to rotate in 3D. The latter not only suggests a default assumption to perceive unfamiliar objects as rotating in depth rather than in the plane but also could indicate the existence of object motion channels tuned to low speeds.

Appendix: Theoretical limits on discriminating biological motion from rotation in depth

Although the velocity effect on judged rotation in depth was strongest for less familiar walker types, sensitivity for the perception of the normal walker also showed a decline toward lower speeds. This suggests that part of the observed velocity effect need not be specific to biological motion analysis but might result from reaching the lower limits of local motion detection. Here, we estimate at what walker velocity the motion of single points in BM and R stimuli would no longer be distinguishable, according to literature on motion thresholds. Motion thresholds typically follow Weber's law for retinal velocities above 1 deg/s, with just-noticeable differences in speed of about

10% and 6 deg in direction (De Bruyn & Orban, 1998; Pasternak & Merigan, 1984), but they rise steeply for velocities less than 1 deg/s. For the range of stimulus velocities in our experiment (30 to 480 deg/s), the highest retinal speed attained by the ankle ranged from 0.3 to 5 deg/s. As Figure 2 (right) illustrates, the motion trajectories of an ankle point for BM and R stimuli differ at most by 0.2 deg visual angle for 1.0 deg trajectories, corresponding to differences of, at most, 12 deg in direction or 20% in speed. Thus, this upper limit for motion difference is at the perceptual threshold for the retinal speeds of 0.6 deg/s or lower (60 and 30 deg/s walker velocities). From this, we conclude that part of the reduction in sensitivity toward lower velocities reflects impaired motion detection at a stage before higher level biological motion perception.

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Corresponding author: Richard van Wezel.

Email: r.j.a.vanwezel@bio.uu.nl.

Address: Padualaan 8, 3584 CH Utrecht, The Netherlands.

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