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Contributions of form, motion and task to biological motion perception

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The ability of human observers to detect ‘biological motion’ of humans and animals has been taken as evidence of specialized perceptual mechanisms. This ability remains unimpaired when the stimulus is reduced to a moving array of dots representing only the joints of the agent: the point light walker (PLW) (G. Johansson, 1973). Such stimuli arguably contain underlying form, and recent debate has centered on the contributions of form and motion to their processing (J. O. Garcia & E. D. Grossman, 2008; E. Hiris, 2007). Human actions contain periodic variations in form; we exploit this by using brief presentations to reveal how these natural variations affect perceptual processing. Comparing performance with static and dynamic presentations reveals the influence of integrative motion signals. Form information appears to play a critical role in biological motion processing and our results show that this information is supported, not replaced, by the integrative motion signals conveyed by the relationships between the dots of the PLW. However, our data also suggest strong task effects on the relevance of the information presented by the PLW. We discuss the relationship between task performance and stimulus in terms of form and motion information, and the implications for conclusions drawn from PLW based studies.

Keywords: biological motion, vision, perception

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Introduction

Humans are impressively sensitive to biological motion, even when the depiction of the agent is reduced to a moving constellation of dots (Johansson, 1973). Such stimuli, commonly referred to as point light walkers (PLWs), are not only robust to noise (Blake, 1993; Cutting, Moore, & Morrison, 1988; Neri, Morrone, & Burr, 1998), but carry information about gender and identity (Cutting & Kozlowski, 1977; Mather & Murdoch, 1994; Pollick, Kay, Heim, & Stringer, 2005). These stimuli usually depict a person walking on the spot and, despite a typical gait cycle lasting 1–2 seconds, the duration required for detection is most commonly cited as around 200 ms (Johansson, 1976). Ideas about what mediates this rapid detection can be split into those which emphasize the role of motion (Casile & Giese, 2005; Thurman & Grossman, 2008), and those which highlight the influence of the form inherent in the configuration of the dots (Beintema & Lappe, 2002; Bertenthal & Pinto, 1994; Hiris, 2007).

Form and motion are inherently linked in the PLW stimulus, and recent work has focused on the interaction between these two sources of information (Garcia &

Grossman, 2008; Hiris, 2007). It was initially suggested that the PLW lacked any form signals and contained only the motion information of the joints (Johansson, 1973). The aptitude demonstrated in biological motion tasks lead to suggestions of specialized mechanisms existing to process biological motion on a perceptual (Troje & Westhoff, 2006) or neural (Giese & Poggio, 2003) level. However Hiris (2007) demonstrated that, when form information is added to non-biological stimuli, performance improves in line with that of the PLW. The PLW was conceived as a stimulus free of “interference from figural perception” (Johansson, 1973, p. 201) but this misrepresents the nature of the information within the PLW. Static form has certainly been degraded by reducing the stimulus to a sparse array of dots, but the coherence in the relationships between these dots make the PLW qualitatively different from displays of nonbiological motion lacking such relationships. Hiris (2007) suggested that the lack of such relationships in comparable non-biological motion may be the reason why perceptual systems appear attuned to biological motion stimuli.

Motion information in point light displays can be characterized as existing at two levels. Each point of light has its own local motion signal but integration of these signals produces relative motion, which constitutes an

independent source of information (Casile & Giese, 2005). Although this information is dynamically presented, it has been argued that its importance is due to it revealing the articulation of the stimulus (Mather, Radford, & West, 1992) and should be considered “motion-mediated structure” (Troje, 2002, p. 372) rather than motion information. While purely dynamic information, such as the local motions of the individual dots, can be presented outside the context of the bodily action, the correct integration of these signals relies on intact spatiotemporal relationships between the dots. This integrative motion signal forms the basis of the “opponent motion” commonly referred to in the biological motion literature (Casile & Giese, 2005; Thurman & Grossman, 2008). It can, however, be more widely seen to underlie the grouping or recognition of any two or more dots through some knowledge of their relative motion characteristics. The effect of the integrative motion signal is therefore to imply both the structure and the hierarchy of connections within the global form of the PLW.

The potency of a signal based on the relative motions of two or more dots may be subject to changes in that relationship (Casile & Giese, 2005). Such changes, along with changes in the form information presented by a PLW, occur in the course of the gait cycle (Mather & Murdoch, 1994; Thurman & Grossman, 2008). The impact of these variations can be studied by comparing detection performance throughout the gait cycle. Thurman & Grossman used short presentations of a PLW embedded in a noise mask created from the constituent dots of the stimulus to measure these changes. Such an approach provides insight into the ability to segregate the stimulus from a noise mask that shares the same characteristics at a local level, but may be limited by potential problems with noise mask tasks: Beintema and Lappe (2002) have previously suggested that processing of the stimulus is not all that is being measured in noise-based biological motion tasks, as segregation from the background could plausibly permit successful detection without an understanding of the stimulus.

Thurman and Grossman’s (2008) results show that the PLW is most detectable in noise when the limbs are crossing the midline of the body. During this phase, the profile of the PLW is a roughly vertical band of dots with little discernable bodily form. At the same point in the gait cycle, Thurman & Grossman argue that the integrative motion signal is at its greatest due to the relative motion signal produced by opposing limbs crossing. This inverse relationship between the strength of form and motion signals led them to interpret their results as evidence for the reliance of biological motion perception on motion information.

On the other hand the importance of form information is emphasized by Hiris (2007) who, also using a noise threshold design, found that noise tolerance for non-biological motion with form was similar to that for biological motion. Both this study and Thurman and

Grossman’s used the trajectories of the stimulus’ constituent dots on a trial-by-trial basis to create the noise mask. The efficiency of a noise mask is dictated by the similarity of the stimulus to the noise masking it and, as previous studies have shown, noise generated by scrambling the PLW is the most effective noise for biological motion tasks (Cutting et al., 1988; Thompson, Hansen, Hess, & Troje, 2007). However, such noise does not contain the spatiotemporal relationships between the dots characteristic to biological motion stimuli and so cannot mask this source of information. Arguably this is evidence for the influence of global processing in such a task, as in this case the noise matches the local information of the stimulus (Thompson et al., 2007). The absence of the motion relationships among the noise dots is possibly more relevant to the present study: variability in these relationships over the gait cycle will be reflected in the effectiveness of the mask over that cycle.

The nature of noise mask tasks and the specific noise used to mask the stimulus may influence the discriminations being measured and could help explain the contradictory ideas that either form or motion information underpins biological motion processing. Careful experimental design and stimulus creation is essential because artifacts in the data, caused by task effects, can dramatically affect the results and their interpretation. The challenge of designing an elegant task with which to gather a clean measure of a specific perceptual ability becomes more difficult as the stimulus needed to elicit the ability becomes more complex. Attempts to separate form and motion information in the PLW are hampered by the intimate relationship between the two in biological motion stimuli (Troje, Westhoff, & Lavrov, 2005). Therefore not only is it important to consider the informational content of both the signal and noise, but also to compare performance across a number of tasks probing the same question. Such an approach will demonstrate if a particular measure or effect is task dependent.

An alternative to noise mask based detection tasks is a discrimination task using a control that has been scrambled in such a manner as to reduce recognition performance. By offsetting the path of each dot of the PLW by a random number of frames, the PLW is phase-scrambled. This control corrupts the temporal relationships between dots but preserves the local motion of the dots. Because the local motion trajectories of the stimulus and control are the same any discrimination must arise from the relationship between the component motions (i.e. motion integration). Such a control is widely employed within the literature (Ahlström, Blake, & Ahlström, 1997; Bertenthal & Pinto, 1994) and prevents the organization of the constituent dots into a walking person by destroying the internal coherence and phase relations of the dots, while maintaining the temporal and spatial characteristics of each individual dot at a local level. This task also allows for much shorter display durations than a noise mask task, allowing the variations in the gait cycle to be

studied in greater detail. The contributions of static form and motion integration to biological motion processing can also be assessed by comparing performance against static presentations of the same discrimination task.

The reported temporal detection limit of 200 ms for a PLW (Johansson, 1976) is considerably shorter than the duration of a full gait cycle. Therefore, to prevent ceiling effects in PLW tasks, presentation times are regularly limited to a fraction of the total cycle. Common practice dictates that the portion of gait cycle displayed in any experimental interval is randomized throughout the experimental task. However recent research suggests that the form inherent in biological motion displays is a crucial source of information for human performance (Hiris, 2007; Lange, Georg, & Lappe, 2006). The periodic changes in form throughout the gait cycle present an opportunity to test the assumption that the strength of form information remains constant throughout the gait cycle. The following experiments were designed to address these issues. Our experiments examined the detection and discrimination of biological motion in briefly presented segments of gait cycle.

Our results may indicate that the perception of biological motion may be driven by form information, and that static form is supported by form expressed through integrative motion signals. However, we find that the choice of task affects this relationship, and therefore conclusions should be drawn cautiously. Different experimental designs and different actions could potentially lead to different interpretations of the relationship between form and motion information in the PLW. Biological motion, as represented by the PLW, is a complex visual stimulus and the types of information within are highly interrelated. Methodological details can dramatically influence the findings; and our results demonstrate the importance of using a number of approaches, and the convergent evidence they produce, to study biological motion.

Experiment 1

The duration threshold for the identification of a PLW was first measured by Johansson (1976), and the figure reported then of between 0.1 and 0.2 sec remains the most commonly cited. Johansson used a videotaped walker, filmed and presented by playing the videotape (at 24 Hz), while tachistoscopically ‘blanking’ the electron beam of the monitor upon which the video was displayed. This methodology gave a minimum resolution of 0.1 sec. Subjects could correctly interpret the dots as representing a person 40% of the time at this lower temporal limit, and performance had reached ceiling at 0.2 sec. In the following experiment, we measured the temporal detection threshold using equipment with a temporal resolution

far greater than that readily available to Johansson. This was done to ascertain an appropriate gait segment duration for the investigation of gait phase on discrimination.

Methods

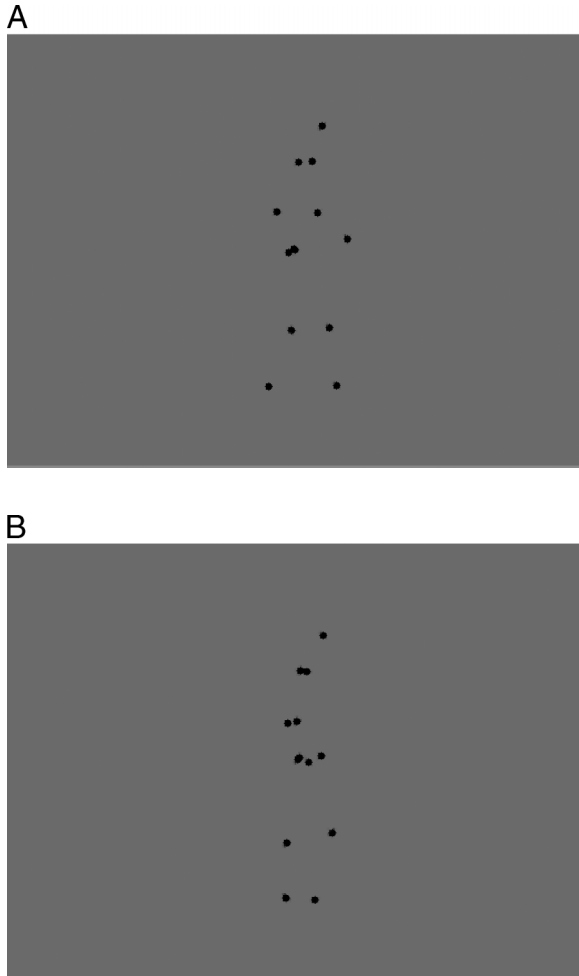
Stimulus creation

Animate motion was captured with a custom built motion capture system (AccessMocap, Bournemouth Media School, Bournemouth University), employing an active optical system equipped with an array of sensors recording the position of 28 infra-red LEDs distributed around the body and limbs of the subject at an effective resolution of ± 1 mm at 30 Hz within a $3 \times 3 \times 3$ meter recording studio. As these LEDs were clustered at points of interest on the body surface, rather than at the center of the joints themselves, the location of the 13 points which traditionally make up a PLW (the joints of the ankles, the knees, the hips, the wrists, the elbows, the shoulders, and the center of the head) were calculated from these 28 markers using linear interpolation. Ten males walked at 1.5 m/sec for a minute, and the resulting data were then split into gait cycles to allow an average gait cycle for each person to be calculated. These averages were then used to create a group-average gait cycle, allowing the creation of a smooth, loopable PLW shown in [Movie 1](#).

Stimulus display

Stimuli were displayed on a 21" monitor (Iiyama Vision Master Pro 513) with a temporal resolution of 200 Hz and a spatial resolution of 640×480 pixels. Participants were placed in front of the screen at a distance of 57 cm so that the PLW subtended approximately 4° degrees of visual angle in height and 2° in width under maximum excursion; each constituent circular dot of the PLW subtended 1.5 arcsec. PLWs were rendered as required during the experiments and interpolated (cubic spline) to the required frame rate. Stimulus presentation was conducted using the Cogent graphics toolbox (developed by John Romaya at the LON at the Wellcome Department of Imaging Neuroscience). All PLWs were presented sagittally, orthogonal to the viewpoint of the participant, and appeared to be walking rightwards on a treadmill.

The PLW was always presented in the center of the screen. 20 clip lengths were employed, ranging from two frames to 40 frames (0.01 sec to 0.2 sec). A random portion of the 248-frame gait cycle was selected to fill the required clip for each trial. Each clip length was presented 20 times during the experiment, producing a total of 400 responses. The stimulus was presented as minimum luminance dots on a uniform gray background with luminance 20.2 cd/m². Each presentation of a clip of the PLW was paired with a phase-scrambled control. This control, matched in duration with the stimulus, was generated for each trial by looping the frames of the full PLW animation and then randomly



Movie 1. Movies of the unscrambled (A) and scrambled (B) PLW stimuli. Portions of the animation were used in Experiments 1–3, as described in the respective method sections.

selecting a starting frame for each dot of the PLW. A portion of the resulting animation sequence of the correct length was then selected and displayed.

Procedure

Sixteen observers (eight females), including the three authors, took part in the experiment. A temporal 2AFC paradigm was used, and participants were instructed to report which interval contained the non-scrambled PLW. Method of constants was used in order to accurately measure both the threshold duration, and also the duration above which performance saturated. The interval containing the non-scrambled PLW was randomly determined for each trial. Feedback was given after each trial, and three breaks were given during the testing session. All testing was completed in a single session.

Results

Psychometric functions were fitted using the `psignifit` toolbox version 2.5.6 for Matlab (see <http://bootstrap-software.org/psignifit/>) which implements the maximum-likelihood method described by Wichmann and Hill (2001a). Using the Weibull function, thresholds were calculated as the 75% correct response point. The average threshold was reported as 46.2 ms (standard deviation = 34.5 ms). This equates to approximately 4% of the gait cycle.

Discussion

The threshold reported here is dramatically reduced from Johansson's original measurement, but this presumably derives from the lower temporal resolution of Johansson's equipment (100 ms) compared to ours (10 ms) and the use here of the 75% correct level for the threshold, as opposed to Johansson's (1976) more conservative measurement of asymptotic performance.

Experiment 2

In light of the reported temporal threshold, the display duration was fixed at the 75% threshold of 50 ms; in order to allow space for an increase or decrease in performance over the gait cycle. The PLW was presented at a frame rate of 100 Hz meaning the gait cycle comprised 124 frames. The gait cycle was split into 24 equal parts of 5 frames, each segment representing 4.2% of the total. Informal testing suggested that experienced observers are able to recognize a PLW from a single static frame. The experiment was therefore also conducted using a 50 ms static presentation of a single frame. This allowed the influence of static form on task performance to be isolated and compared to performance with the PLW in motion.

Methods

A temporal 2AFC design was employed; the task was to discriminate the interval containing the PLW from that containing the phase-scrambled control. Each clip was presented 20 times in a random order producing a total of 480 responses. Feedback was given after each trial, and three breaks were given during the testing session.

Six observers, one author (MT) and five naive, participated in the experiment. Three participants, including one author, completed the task with the moving presentations first and the static presentations second, while the other three completed the experiment in the reverse. All stimulus and display settings were as before,

except that a resolution of 1280×1024 pixels was employed with the refresh rate of 100 Hz, allowing the PLW to be displayed at its native frame rate without resampling. Both the duration of the gait cycle and the visual angle subtended by the walker and the dots on the screen remained as in [Experiment 1](#). For the static presentations, the first frame from each of the previously defined gait segments was used for comparability.

Results

The dots representing the ankles and wrists of the PLW have the most spatially extended trajectories and so a simple description of the changing form is the distance between the ankles; the lateral extension of the PLW. The change in performance tracks this metric across the gait cycle ([Figure 1](#)). As [Figure 1](#) shows, the processing of biological motion stimuli in the absence of a noise mask is better in frames displaying a more extended form. These changes in form, as described by lateral spread, significantly predict the variations in performance through the gait cycle in both static [$r = 0.913$, $p < .001$] and moving [$r = 0.821$, $p < .001$] presentations. The removal of motion cues resulted in a significant reduction in performance

across all participants throughout the gait cycle ($t(22) = -2.858$, $p = 0.09$). Importantly, it is clear from these results that the oft-cited statement that observers are unable to perceive the PLW from a single, static frame ([Johansson, 1973](#)) is misleading.

Previous work has suggested that human performance levels could be explained without recourse to local motion signals ([Lange et al., 2006](#)); however the performance advantage derived from the inclusion of motion cues compared to static presentations of the same gait segments demonstrates the influence of motion information on the processing of biological motion. Because local motion was intact in the control stimulus, it appears that integration of the local motion signals of two or more dots contributes significantly to biological motion processing.

These results show not only the influence of motion integration on the perception of biological motion, but also the extent to which that processing is based upon the form information contained in the PLW. It seems plausible that motion integration aids grouping of the dots into the relevant form. For example, motion may help the grouping of dots into limb segments or the identification of corresponding left and right body parts. At the phases of the gait cycle where the limbs cross and form information is weakest, the addition of motion information

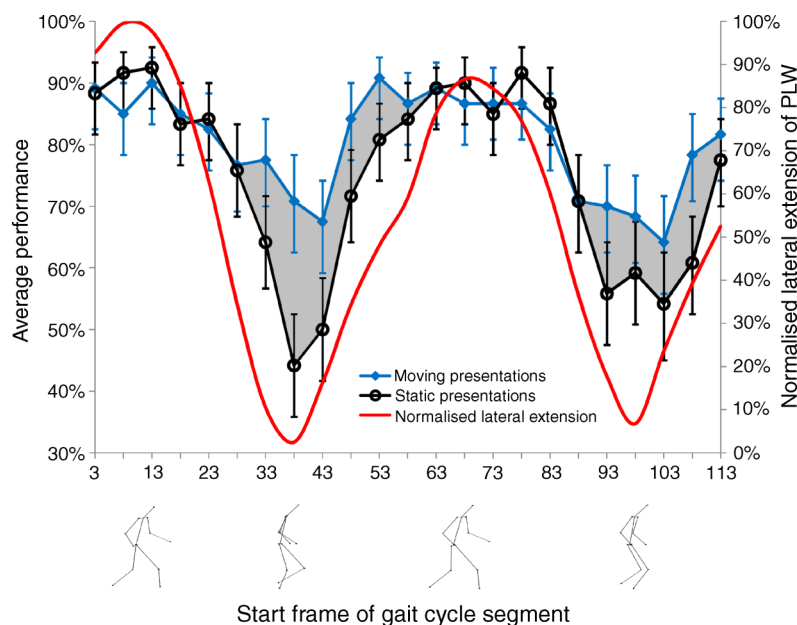


Figure 1. Average detection performance (across five subjects) in both static and moving presentations is plotted across the gait cycle. The lateral extension—the absolute distance between opposite ankles—is plotted to demonstrate the correlation between the phase of the gait cycle and detection performance. Error bars were calculated through bootstrapping the individual subject data and then calculating means from those bootstrapped data at each point. We derive 100,000 bootstrapped means for each data point and then calculate the 95% confidence limits using the percentile method ([Efron & Tibshirani, 1993](#)). Note that where subjects score 100% correct we calculate P as $1 - 1/2N$ (rather than 1); this adjustment is conservative and is common practice in signal detection based analyses ([Macmillan & Creelman, 1991](#)). Single frames of the experimental stimulus representing the variation in form are shown at their corresponding positions in the gait cycle (the lines are included for clarity and were omitted in experimental presentations). The four poses shown illustrate the oscillation between maximal laterally extended and compressed form during the cycle. The shaded areas denote the increase in performance caused by the addition of motion.

has a much more pronounced effect on performance. This phase of the gait cycle is also where the motion of the limbs is ‘strongest’ (Thurman & Grossman, 2008), but it is not possible to conclude from this experiment whether this is due to the potency of motion information or the weakness of form information at these points. What can be concluded is that neither component is wholly responsible for performance, and that in presentations containing more ambiguous form information, motion information assumes greater influence. Equally, in cases of masked form motion information would be expected to have a larger influence, and this may explain an apparent contradiction with the recent finding that crossed rather than extended walkers are more easily recognized in noise masks (Thurman & Grossman, 2008).

An alternative interpretation of the data suggests that participants could have exploited low level differences between the control and the intact walker to perform the current task. Because the limbs swing in antiphase during the gait cycle, phase scrambling the walker has the inevitable result of bringing these extremities closer together. Similar results to those reported would be predicted if such a form-based cue was underpinning performance. It is not possible to rule out the influence of such low level cues on performance, but it should be noted that they cannot explain the improvement in performance gained by the addition of motion information.

Experiment 3

Previous work using a noise mask threshold measurement to investigate the relationship between task performance and the changes within the gait cycles have suggested the reverse relationship to that found in [Experiment 2](#) (Thurman & Grossman, 2008). Given the differences between the two methodologies and results, we sought to replicate their results. Thurman and Grossman (2008) employed both a direction discrimination task, and a detection task, but both their own and subsequent research (Chang & Troje, 2008) has shown that detection and direction discrimination tasks share the same pattern of detection across the gait cycle. Using the segments of interest established in [Experiment 2](#), and a noise mask created from the constituent motions of the PLW as employed by Thurman and Grossman, a detection task was employed in order to establish the noise threshold for the different gait periods.

Methods

The periodic changes in form of the gait cycle become clearer if it is divided into times when the limbs cross and times when the extension is greater. During a single gait

cycle, the limbs cross twice and the form is at its most extended twice, reflecting the two foot falls of a cycle. The segments previously presented from within these four, 200 ms, periods of cycle were collapsed into two segments representing minimal and maximal lateral extension as defined earlier. Segments of 200 ms are also a more realistic duration for a noise mask threshold task than the previous segments of 50 ms, and are comparable to those used by Thurman and Grossman (2008).

The PLW size and frame rate were as in [Experiment 2](#). Using the 200 ms segments of interest, noise masks were created by replicating the constituent dots of the PLW and randomly locating their start locations within a rectangle measuring 7 by 5 degrees of visual angle. A temporal 2AFC design was employed and, in any given trial, one interval contained a display consisting solely of noise dots while the other contained a display where 11 of the noise dots were replaced with those of the PLW. An eleven dot PLW was used here, omitting the far-side shoulder and hip from the previous experiments; these dots have very limited trajectories and were removed in order to attempt to minimize the clustering of dots at such bodily points providing a cue to performance. In each interval, the position of the PLW was jittered by up to 1.5 degrees of visual angle from the center of the noise mask and the direction of walk—left or rightward—was randomly assigned to further prevent low-level cues aiding performance. The task, as previously, was to select the interval containing the walker.

There were three participants, one author (MT) and two naive, all with normal or corrected to normal vision. Trials were blocked into crossed and spread segments. In each session, dual PEST procedures (Findlay, 1978) were used to estimate the number of dots making up the noise mask necessary for 75% performance. The order of the blocks was counterbalanced for each participant.

Results

Data analysis was the same as in [Experiment 1](#), and threshold measures were calculated using the Weibull function. An advantage was found for the segments of the gait cycle which would intuitively seem to present the weakest form information. This result mirrors that found by Thurman and Grossman (2008). [Figure 2](#) shows that performance for all three participants was better when the PLW was in a crossed posture, reflected in the higher density of noise mask required to reduce performance to threshold (75% performance) levels, than in an extended pose.

Comparing these results with those of [Experiment 2](#), and those reported by Thurman and Grossman (2008), it is clear that the demands of the task dictate which period of gait is most informative. Thurman and Grossman (2008) also found that those periods of the gait cycle less readily detected when presented in motion were easier to detect

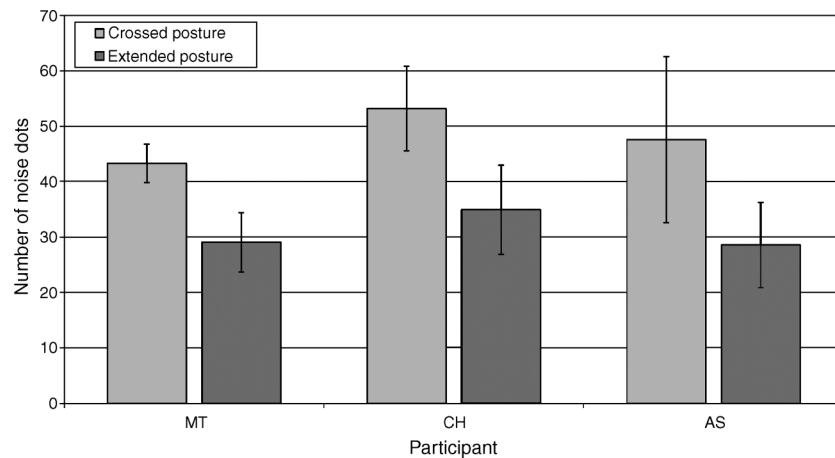


Figure 2. Detection in Noise Mask Thresholds by participant and segment of gait presented. Fewer noise dots were required to mask segments of gaits containing more extended form. This suggests that, in contrast to [Experiment 2](#), more extended form is more difficult to detect. Error bars represent bootstrapped 95% confidence intervals of calculated threshold (Wichmann & Hill, 2001b).

when presented statically. This was not reflected in the static and moving presentations of [Experiment 2](#). In static presentations of a detection from noise task, and in moving and static presentations of a discrimination task, the changing strength of form information explains performance convincingly. It is not possible to ascertain whether the different pattern of performance found solely in moving presentations of a noise mask task, replicated here, is specifically due to biological motion processing or whether the different stimuli and tasks are giving rise to different low-level cues which are guiding performance.

Thurman and Grossman (2008) used an alternative motion stimulus, to assess the contribution of local motion velocity and opponent motion to the detection of the PLW in noise. During the gait cycle the point at which the opponent motion displayed by the ankles is at its peak is also the point at which the local motion of each ankle dot is maximal. By using a jumping jack stimulus these two factors were separated out and performance was found to correlate with opponent motion rather than local motion velocity. However, the point of maximal opponent motion in the jumping jack and in the gait cycle coincides with the peak of local density of the point light display. The spread of the point light display increases and decreases during the action displayed, and these changes are reflected in the density gradient between the noise mask and the stimulus. Local mask density has previously been discussed as an explanation for performance on biological motion in noise task, and even suggested to be the critical factor in explaining the variability in mask effectiveness (Hiris, 2007). The possibility of such a cue driving performance makes it difficult to draw conclusions beyond the relationship between signal and noise mask from noise mask tasks alone. Nonetheless, that the two actions share similar performance patterns in noise is important. Therefore [Experiment 2](#) was repeated using a jumping jack

stimulus in order to ascertain whether the performance similarities between the two actions would persist in a different task.

Experiment 4

A frontal view of a jumping jack point light stimulus has a number of different characteristics to the side view of the gait cycle used previously. The motion of the jumping jack is entirely in the image plane unlike the gait cycle, so there is no depth information to be conveyed and no ambiguity to resolve. Thurman and Grossman (2008) used the jumping jack as it pitted two motion factors against one another through their variations in the movement cycle, here we are using it to compare the influence of motion and form information. During a jumping jack the body posture moves from a neutral pose to an extended pose and back again. The absence of a point at which the dots of the stimulus cross in the animation means that the form information of the stimulus remains much more constant, and arguably stronger than in portions of the gait cycle. Therefore any variations in performance in the discrimination from phase scrambled control task may more easily be attributed to the variations in motion information on display.

Methods

A jumping jack point light display was obtained from an online corpus of point light stimuli (Shipley & Brumberg, 2003). The jumping jack was resized and resampled to closer match the dimensions of the walker

stimulus used in the previous experiments using the same methods previously described (Movie 2).

The display parameters and the procedure was the same as in Experiment 2. Participants were required to indicate which interval contained the unscrambled jumping jack for 23, 50 ms segments—the difference resulting from a slightly shorter animation length (119 frames at 100 Hz). One author and two naive participants performed the task on both static and moving presentations of the stimulus. The order of the blocks was counterbalanced for each participant.

Results

No difference in performance was found for gait segment in either static or moving presentations. Perfor-

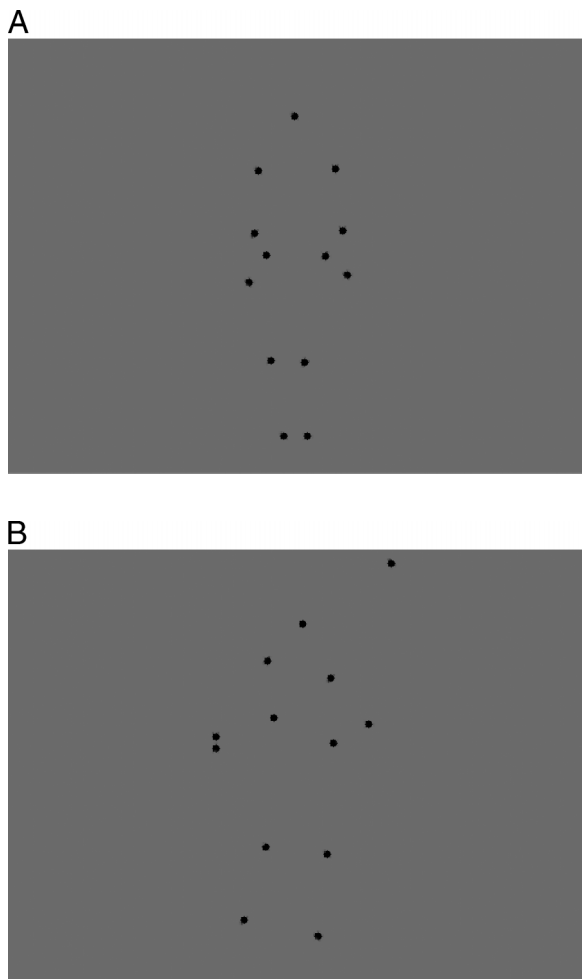
mance remained close to ceiling for all participants for all segments presented as shown in Figure 3.

This contrasts with the significant changes in performance reported throughout the jumping jack display in a noise mask threshold task (Thurman & Grossman, 2008). The lack of effect produced by presenting different segments of the jumping jack could be explained in terms of the form information remaining strong enough for performance to stay at ceiling throughout the action. That performance on the task is high, if not at ceiling, for all segments of the task when presented statically means that there can be no measurable improvement in performance due to motion. This is not to say that motion information, which does vary during the jumping jack, has little or no influence on performance, but rather that this task is trivial without the additional information motion might supply. These results clearly show that measures of biological motion sensitivity are strongly affected by methodology.

Differences in task performance found when using the gait cycle are absent when that action is replaced with the jumping jack. It is possible that the duration of the display suitable for studying the changes in the gait cycle as reported in Experiment 1 is not suitable for other actions. This seems unlikely as static presentations of single frames from the jumping jack produce the same saturated performance as moving presentations of the chosen duration. Informal testing using the procedure of Experiment 1 showed that task performance did not decrease even when presentation duration was reduced to 5 ms. As in previous experiments, it is important to consider the influence of low-level cues to performance. The improved performance found with a jumping jack might be explained by participants exploiting the symmetry within the form of the intact target. Such a cue could feasibly be stronger in the jumping jack stimulus than in the walker and therefore present a reliable signal to the participant throughout the task. The results suggest that measures of biological motion perception are not only task dependent, but that commonly used biological motion tasks are action dependent, and conclusions beyond the specific experimental task should be made cautiously.

General discussion

Our findings demonstrate the intrinsic link between form and motion information in biological motion. Neither type of information can convey biological motion alone, and the contradictory results produced by different tasks or different actions reflects the interrelated nature of the information contained in point light displays. Because of the complex nature of the stimulus, studies of biological motion using the PLW are particularly vulnerable to the presence of artifacts in the method which can skew the results. Careful consideration of possible artifacts is



Movie 2. Example movies of the unscrambled (A) and unscrambled (B) jumping jack stimuli. During Experiment 4, 50 ms segments of these stimuli were presented, as described in the method section.

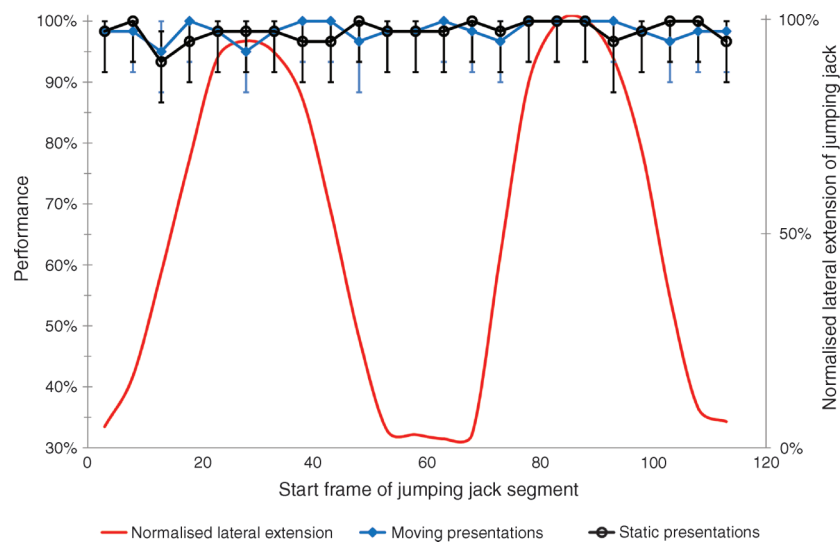


Figure 3. Average detection performance (across three subjects) in both static and moving presentations is plotted for the jumping jack animation. The normalized lateral extension of the point light jumping jack is plotted for ease of comparison with [Experiment 1](#) and [Figure 1](#). Error bars are bootstrapped 95% confidence intervals as in [Figure 1](#). As can clearly be seen, unlike in the gait cycle, the changes in the stimulus caused by the action of the jumping jack have little to no effect on task performance.

essential when interpreting data from biological motion experiments.

The difficulties of noise mask detection tasks have been discussed previously (Beintema & Lappe, 2002; Hiris, 2007; Thompson et al., 2007) and, as mentioned earlier, the phase scrambled control is also open to the influence of low level cues. The current experiments demonstrate the necessity of taking a number of approaches to studying biological motion, as it is clear the results are greatly affected by methodological details. We found that the changes in form information across the gait cycle largely predict performance in the discrimination of PLW animations from phase-scrambled controls, and that the direction of this relationship is reversed in moving presentations of the PLW within a noise mask. When the action presented was changed we no longer found the effect in the discrimination from phase-scrambled control task, despite it persisting in a noise-mask task (Thurman & Grossman, 2008). Both tasks contain low-level cues which predict similar results as those found, but in neither case can that artifact be said to present motion information.

In the case of noise mask threshold tasks, local density of the mask provides a cue to performance, and in the discrimination task the spread of the dots in the PLW compared to those of the phase scrambled control plays a similar role. Both these tasks fail to eliminate form-based cues and as such cannot provide strong evidence for the relative importance of form and motion information within the PLW stimulus to biological motion processing. The changes in the PLW which the gait cycle provides affect the low level cues as much as they affect the information within the PLW itself, and this alone could explain the contradictory pattern of results. From the

results reported it is clear that form cues, present either in the PLW itself or inadvertently provided by the methodology, affect performance in both tasks. On the other hand, the improvement in discrimination performance produced by the addition of motion information is strong evidence of the involvement of integrative motion signals in task performance.

Such integration of motion signals as a route to form has been suggested previously as the basis of biological motion (Beintema & Lappe, 2002). Further, static form has been suggested to be unnecessary to biological motion processing through stimuli where no single frame displays the intact form of the PLW (Beintema, Georg, & Lappe, 2006; Neri et al., 1998), and in displays where the background and stimuli are separable only through motion (Ahlström et al., 1997; Singer & Sheinberg, 2008). We suggest our results show that form is important to biological motion processing and that static form, rather than being discarded when the stimulus is in motion, is supported by form information obtained through motion integration.

Models of biological motion processing which emphasize the influence of form information either suggest that the configuration of the dots of the PLW are sufficient for processing (Beintema & Lappe, 2002), or highlight the absence of form from non-biological, comparison, motions (Hiris, Krebeck, Edmonds, & Stout, 2005). We demonstrate that the form information contained in the PLW is sufficient to perceive the figure of a person. Other investigations into the role of form have shown that distortions which produce biologically plausible, though anatomically incorrect, form do not disrupt the processing of biological motion (Pinto & Shiffrar, 1999) and that detection of non-biological motion can be as acute as that

of biological motion if form is added to the non-biological motion (Hiris, 2007). Form clearly plays a crucial role in biological motion processing.

Despite the apparent potency of form information, it is also clear that processing is aided by motion signals. While some theories of biological motion perception focus on the contribution of the local motion signals of the constituent dots (Giese & Poggio, 2003; Neri et al., 1998), others emphasize the possibility of temporal integration of form (Lange et al., 2006) as a route to the global motion of the PLW. Certainly, the characteristics of biological motion seem to facilitate processing (Beintema, Oleksiak, & van Wezel, 2006) and are differentiated from non-biological motion trajectories displayed outside the context of bodily form (Bidet-Ildei, Orliaguet, Sokolov, & Pavlova, 2006; Viviani & Stucchi, 1992), but it would appear the inherent form has a critical role in the visual processing of humans and animals in motion.

By splitting the gait cycle into threshold duration segments and employing a number of tasks it can be seen that changes in the information presented, both through changes inherent to the gait cycle and stimulus design, affect biological motion processing. The pattern of performance reported suggests that both motion (in the form of integrative motion signals) and form information—influence biological motion perception. We suggest that although purely dynamic cues contribute to processing, possibly by aiding segmentation, form-based mechanisms may ultimately constrain human perception of biological motion in PLWs. More importantly, our results highlight the difficulties in interpreting the results of tasks employing the PLW and demonstrate the highly task and action dependent nature of biological motion processing.

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