

The time to passage of biological and complex motion

Sandra Mouta

Vision and Control of Action Group,
Departamento de Psicologia Básica,
Universitat de Barcelona, Catalonia, Spain, &
INESC Porto, Instituto de Engenharia de Sistemas
e Computadores, Portugal



Jorge A. Santos

Departamento de Psicologia Básica and Centro Algoritmi,
Universidade do Minho, Portugal, &
Centro de Computação Gráfica, Guimarães, Portugal



Joan López-Moliner

Vision and Control of Action Group,
Departamento de Psicologia Básica,
Universitat de Barcelona, Catalonia, Spain, &
IR3C, Institute for Brain, Cognition and Behavior,
Catalonia, Spain



A significant part of human interactions occur with other human beings and not only with inanimate objects. It is important in everyday tasks to estimate the time it takes other people to reach (time to contact) or pass us (time to passage). Surprisingly, little is known about judging time to contact or time to passage of biological or other complex motions. In two experiments, rigid and non-rigid (biological, inverted, scrambled, and complex non-biological) motion conditions were compared in a time-to-passage judgment task. Subjects could judge time to passage of point-light-walker displays. However, due to relative and opponent movements of body parts, all articulated patterns conveyed a noisier looming pattern. Non-rigid stimuli were judged as passing sooner than rigid stimuli but reflected more uncertainty in the judgments as revealed by precision judgments and required longer reaction times. Our findings suggested that perceptual judgments for complex motion, including biological patterns, are built on top of the same processing channels that are involved on rigid motion perception. The complexity of the motion pattern (rigid vs. non-rigid) plays a more determinant role than the “biologicity” of the stimulus (biological vs. non-biological), at least concerning time-to-passage judgments.

Keywords: biological motion, complex motion, time-to-passage judgment, reaction time

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Introduction

On a daily basis, people move in the world and interact with other agents, either with inanimate objects or with other individuals. For instance, in team sports, highly trained performers must respond not only to an inanimate object (e.g., a ball) but also to predict when other players will reach a specific location in the field (e.g., a goalkeeper and a forward) or when a driver must deal with several road events involving other vehicles along with moving pedestrians. During these interactions, it is important to estimate the time it takes an object to reach us, time to contact (TTC). When an object moves toward the observer’s eyes, its image expands isotropically during the trajectory. It has been argued that the estimation of interceptive timing can be done directly from optical variables as visual angle θ , rate of expansion θ' , or its ratio, tau (τ) parameter (Lee, 1976; Regan & Hamstra, 1993; Regan & Vincent, 1995). Other studies showed that observers do not exclusively

use τ in TTC estimations, but other possible combinations of optical variables can be used instead of or in addition to it (López-Moliner & Bonnet, 2002; Smith, Flach, Dittman, & Stanard, 2001; Sun & Frost, 1998; Tresilian, 1999; Wann, 1996). As observers do not always interact with objects that are moving toward the observer’s eyes at a constant speed, in the current work we used time-to-passage (TTP) estimations as might occur in everyday life situations. Truly, the human visual system needs to deal more often with objects that will pass by arbitrary points of interest in space (López-Moliner, Brenner, & Smeets, 2007). TTP is not directly related to the relative rate of expansion as time to contact, but it is specified by different optical measures extracted from angular velocity and binocular vision (Bootsma & Craig, 2002; Gray & Regan, 2000; Lee, Georgopoulos, Clark, Craig, & Port, 2001). Surprisingly, little is known about judging TTC or TTP of biological motion or other complex motion patterns.

Regarding the social functioning of humans, it has been suggested that the visual system has specialized

mechanisms to detect and recognize biological motion patterns. Since the studies of Johansson (1973), this phenomenon has been regarded as a major example of the resourcefulness of the visual system. When a cloud of points corresponding to the head and main joints of the human body—a Point Light Walker (PLW)—is animated with the common translational component removed, observers instantaneously recognize a human motion pattern. The seminal findings of Johansson have been replicated and extended to the recognition of actions such as running, jumping, eating, or dancing (Dittrich, 1993; Norman, Payton, Long, & Hawkes, 2004), gender (Pollick, Kay, Heim, & Stringer, 2005; Troje, 2002), specific identity of walkers (Cutting & Kozlowski, 1977; Troje, Westhoff, & Lavrov, 2005), one's own walking pattern (Beardsworth & Buckner, 1981), emotions (Atkinson, Dittrich, Gemmell, & Young, 2004; Pollick, Paterson, Bruderlin, & Sanford, 2001), and even to the estimation of the weight of lifted objects from only observing the lifting motion (Bingham, 1993). The results obtained from this kind of discrimination tasks have demonstrated that observers might detect subtle variations in gait, gesture, or action from biological motion displays.

Masking experiments have found that recognition or direction discrimination required a longer time window when PLW were presented within a mask, but the observers' performance frequently remained highly accurate (Thirkettle, Benton, & Scott-Samuel, 2009). Although the most efficient masks are the ones composed by dynamic PLW dots randomly distributed in the image, the perception of biological motion was only partially impaired (Cutting, Moore, & Morrison, 1988; Thornton, Pinto, & Shiffrar, 1998). Even when the lifetime of the individual dots of PLW is limited, by randomly jittering the point lights (PLs) on different locations of the body, the recognition of biological motion is maintained almost intact (Beintema & Lappe, 2002; Pinto & Shiffrar, 1999). This fact reveals that the recognition of biological motion is extremely resistant to the interference of noisy patterns, ambiguous or impoverished conditions. In sum, all the studies quoted above suggest that our perceptual visual system might be prepared to quickly and efficiently extract meaningful information from biological motion patterns. Nonetheless, the sensitivity to perceive biological motion increases with the number of point lights presented in the animation and with the duration of the stimulus' presentation (Neri, Morrone, & Burr, 1998; Thornton et al., 1998). Furthermore, the recognition of the pattern as being biological requires coherence on the spatiotemporal relation of the moving dots (Ahlström, Blake, & Ahlström, 1997; Bertenthal & Pinto, 1994; Troje & Westhoff, 2006). Scrambled motion contains no configural information, but local motion is kept intact. Dots are randomly displaced within the area of the stimulus, thereby disrupting the structure of the display. This kind of control stimulus prevents the organization of the PLs into a human walker by disrupting the internal coherence of the patterns, while

maintaining the spatiotemporal components of each dot. A control that has been scrambled can be used in order to reduce recognition performance and animacy perception.

However, PLW recognition is view dependent, optimal only for upright viewing perspective. Recognition rates decrease significantly for inverted biological motion stimuli, even if the structural information and the complexity of these inverted stimuli are similar to the upright biological motion stimuli (Pavlova & Sokolov, 2000; Sumi, 1984). This phenomenon is analogous to what happens in face recognition where the global form is used as a crucial cue (Farah, Drain, & Tanaka, 1995; Tanaka & Farah, 1993). After learning, observers are able to detect inverted PLW, but their performance is equivalent to discrimination of any other cluster or pattern of points (Hiris, Krebeck, Edmonds, & Stout, 2005). Considering the reviewed research, it has been argued that biological motion recognition is optimized but relies on very specific mechanisms and view-dependent cues.

Concerning motion integration, biological motion is more complex than rigid motion. For a rigid object moving along a linear path in a front-parallel or orthogonal plane to the observer, all and each of its surface points have a similar speed vector and only a visual translational component. Therefore, both the integration of local signals and the perception of global patterns should be relatively straightforward. In contrast, biological stimuli are far more complex. Based on current evidence, the authors developed opposing models differing mostly on the role of form and/or motion contributions for the perception of biological motion. For instance, for different PL displays, (gender, orientation, or other) discrimination can be based on structural cues inherent to the configuration of the dots (Beintema & Lappe, 2002; Bertenthal & Pinto, 1994; Hiris, 2007) or on motion cues given by the global pattern, relative body sway, or local motion signals (Casile & Giese, 2005; Mather & Murdoch, 1994; Troje, 2002). Recently, Thurman, Giese, and Grossman (2010) postulated that the way that motion and form are computed and the height of their contributions for biological motion perception depend on the quantity and type of available information and task demands.

Various models following psychophysical or computational approaches were proposed in order to identify critical features for biological motion perception. According to Johansson (1976) and his "vector analysis theory," the visual motion primitive combines rotational and pendulum-like components with translational components. The vectors of body parts are linked along fixed axes resulting in a "structure-from-motion" percept (Hoffman & Flinchbaugh, 1982; Webb & Aggarwal, 1982). Troje (2002) decomposed spatiotemporal features of biological motion using a principal component analysis and identified the dynamic part of the motion as being more crucial for biological motion recognition than motion-mediated structural cues. In turn, Casile and Giese (2005) presented a neurally inspired model that exploited mid-level motion

features that achieved substantial recognition rates, even for degraded point-light stimuli. Most of these critical features relied on the sinusoidal opponent horizontal motion of different body parts. More recently, relative opponent motion of the limbs and acceleration of the feet were identified as facilitating cues for BM perception (Chang & Troje, 2009; Thurman et al., 2010).

In sum, even assuming a special tuning of the human visual system for biological motion recognition, it is reasonable to argue that spatiotemporal integration and, consequently, spatiotemporal estimations are more demanding for biological (as being a more complex pattern) than for rigid motion. However, little research has addressed the perception of translational biological patterns. The specialization of the human visual system on biological motion recognition occurs presumably due to the importance for survival and ecological functioning in a dynamic world. Nevertheless, the computation of spatiotemporal variables of biological motion seems to be more complex or at least more sensitive to different processing constraints. For instance, familiarity, speed, and task do affect the perception of biological motion trajectories and not rigid rotation-in-depth trajectories (Beintema, Oleksiak, & van Wezel, 2006). The claim of different mechanisms for rigid and biological motion perception has some support from psychophysical and fMRI studies (Neri et al., 1998; Peuskens, Vanrie, Verfaillie, & Orban, 2005; Poom & Olsson, 2002). Greater temporal integration was required for the detection and direction discrimination of biological motion and its efficiency was not constant when compared with rigid translational motion (Neri et al., 1998). Responses to rigid rotation seem to be localized posteriorly to those elicited by biological motion. However, those differences may reflect differences in low-level features of the stimuli that were compared rather than the existence of different channels (Peuskens et al., 2005; Poom & Olsson, 2002).

In the present experiments, we intended first to explore if observers were able to conduct accurate judgments of time to passage, of BM, as they do for rigid motion. If they could, our second question was to what extent is the perception of biological motion different from rigid motion, in a time-to-passage estimation. Specifically, our goal was to study if biological motion shows the same levels of accuracy and precision as rigid motion when judging TTP. In order to do so, in [Experiment 1](#), we compared judgments for rigid and biological motion patterns that were approaching the observer. Note that the same structural information was shared by both patterns, but in the first case, opponent limb movement was removed from the presentation, as a looming “frozen” PLW. On the one hand, if only non-specific motion channels are recruited to solve the task, we expect less precision in BM than RM because of the local noise of the former. However, if the noisier expansion of BM is treated as noise but integrated by using BM channels, we do not expect a loss of precision. In [Experiment 2](#), we used a

similar procedure but compared TTP judgments for rigid, biological, and other complex motions in blocked conditions. Therefore, we compared biological motion with a rigid pattern and three non-rigid patterns that varied on recognition, structural information, and/or naturalness stages. If the human visual system is more sensitive to biological motion in TTP judgments, then we should expect to have greater precision when compared with inverted, scrambled, or complex non-biological motion, even if the computational demand is the same.

Experiment 1

Participants

Eight volunteers (4 females, 4 males, 26 ± 3 years old, mean \pm SD, one left-handed) took part in [Experiment 1](#). Three participants had prior experience with biological motion stimuli. All had normal or corrected-to-normal vision, as assessed by Ergovision screening test (Essilor). All participants gave informed consent to take part in the study.

Stimuli display

Stimuli were displayed on a large screen ($2.10 * 2.80$ m) by a 3-Chip DLP projector Christie Mirage S+4K with a spatial resolution of 1400×1050 pixels and a temporal resolution of 96 Hz, in the Laboratory of Visualization and Perception of the University of Minho and Centro de Computação Gráfica. A StereoGraphics EXXR emitter controlled a CristalEyes stereo shutter eyewear system. The experiment was programmed with custom software running on top of OpenGL and VR/Net Juggler.

Simulated PLWs were generated from two models (males) captured with a Vicon motion capture system, recording the position of 39 infrared markers distributed around the body and limbs, at 240 Hz. The position of traditional PLW dots was calculated by interpolation from the location of markers. Each PLW comprised 13 dots signaling the motion of head and left and right ankles, knees, hips, wrists, elbows, and shoulders.

The stimuli conformed to one of two conditions: rigid (one single frame of the step cycle, the first of the corresponding biological motion segment, [Movie 1](#)) and biological (32 frames of a step cycle, interpolated from the motion capture data, [Movie 2](#)). Thus, two looming motion patterns with the same structural information were presented, but one without the biological motion information depicted during the step cycle (e.g., opponent movements of the limbs). Simulated looming velocities of all stimuli were constant. Captured data were split into gait cycles to allow for the computation of average velocities. Therefore, original translational components were removed

for biological motion; an average velocity replaced the particular non-linear velocity profile given by the different point-to-point trajectories during the step cycle. Even so, for each simulated velocity, a different PLW was used with the specific gait pattern (marker location) extracted from corresponding step cycles. We randomly presented combinations of 2 models (real walkers) and 3 different initial phases of the step cycle (32 frames were selected from the starting, middle, and final phases of the step cycle), to avoid both the interference of artifacts and to allow for the later analysis of related effects. Observers might use different spatiotemporal cues depending on the phase of the step cycle that is presented (Thirkettle et al., 2009; Thurman et al., 2010).

The 3D coordinates of each dot were generated and rendered as white spheres ($12 * 10$ pixels when the 3D coordinates of PLW matched the 3D coordinates of the screen plane). The luminance of the dots was 63 cd/m^2 and that of the (dark) background was 2.5 cd/m^2 . Two different inputs were rendered for each eye in order to be viewed binocularly. PLW moved orthogonally to the frontal plane along a line that passed 40 cm (referring to the PLW's midpoint) to the right of the midpoint between the participant's eyes. The physical vertical size (height) of the model was 1.75 m and it subtended an initial angle within the range of 53° – 65° .

Like in López-Moliner, Brenner et al. (2007), seven simulated velocities were combined with seven starting distances, to encourage the use of time to passage and not of other correlated cues. However, the use of potential correlated cues will be checked. The simulated velocity could be 0.76, 0.83, 0.91, 1.0, 1.10, 1.20, or 1.32 m/s. The simulated initial distance could be 0.78, 0.85, 0.93, 1.0, 1.09, 1.18, or 1.29 m. These combinations resulted in 49 levels of TTP: 24 conditions that arrive before 1 s and 24 that arrive after 1 s. The shortest TTP was 0.594 s, and the longest was 1.7 s. The TTP was defined with respect to the front part of the body of the PLW. The stimuli were presented in stereoscopy to allow for almost passage and factual passage situations, i.e., trials with short TTPs. It has been previously reported (Gray & Regan, 1998) that stereo information is only used for very small visual angles, so having stereo presentation did not necessarily mean that subjects did not use monocular cues. There were no conflicting cues and both monocular and binocular information were available.

Procedure

Visual stimuli were presented at the defined velocity and starting distance during a pseudorandom presentation time between 0.5 and 0.7 s. Participants' heads were aligned by the left edge of the image in order to increase the visual field on the right (since PLW were laterally displaced). Participants stood at 1 m from the screen in a dark room. A fixation square ($7 * 7$ pixels) was always

present at the level of the subjects' eyes during visual stimuli display. We used an auditory "beep" to signal the reference time for TTP judgment, which was always presented 1 s after the visual stimulus started to approach (Gray & Regan, 1998; López-Moliner, Brenner et al., 2007). Participants were asked to indicate whether the PLW passed the eye plane (an imaginary vertical plane that passes through the observer's eyes) before or after the auditory beep, pressing one of two mouse buttons. The experiment comprised 12 repetitions (2 repetitions * 2 PLW models * 3 initial phase) of 98 stimuli, 49 for BM and 49 for RM, combined in two blocks. Each participant had a learning period divided in two phases. First, participants performed a two-alternative forced-choice task to adapt to 3D stimulus and to access stereo-acuity. Five repetitions of a static PLW were presented in all initial distances and on the extreme final distances used in the experiment. Participants had to report if the PLW was either in front or behind a reference plane defined by a square (coincident with the fixation point in the experience and placed on the screen plane). The presentation of this task was repeated until participants reached a 75% accuracy level (which was usually reached on the first run). Second, a practice task on TTP judgment was performed, with two repetitions of 25 trials randomly chosen from all the possible stimuli. Experimental and training blocks were completed in about 1-h session.

Analysis

A psychometric function was fitted to each motion condition that provided distributions of the proportion of trials in which visual stimuli were seen as arriving "later than beep." We fitted cumulative Gaussian curves to derive 2 parameters, point of subjective simultaneity (PSS) and standard deviation (*SD*). The goodness of the fit was tested by using the deviance statistic, which follows a Chi-square distribution with degrees of freedom equal to the number of data points minus the number of parameters on the model. Larger *p*-values (>0.05) indicate that the model is a good descriptor of the data. A PSS larger than 1 s (curves shifted to the right) means that the PLW appeared to arrive earlier than what was simulated. *SD* is inversely related to the slope of the function. We derived these two parameters both from single individual data and from pooled data for the eight participants. We plotted data as a function of theoretical initial TTP provided by physical stimuli (directly computed from initial distance and velocity) and two other variables: final rate of expansion (θ') and predicted TTP (TTP_p) at the end of the visual presentation. PLW (for both biological and rigid conditions) were rendered in the same way, as the 13 PLs were inside a virtual area that included all 13 point coordinates, with the same physical size and shape. We computed the final θ' of that global area, which was the same for both motion conditions. TTP_p was

predicted from Equation 1: a combination of object's physical size [height (S)], final vertical rate of expansion (θ' ; Sun & Frost, 1998), and velocity (V), as described in López-Moliner, Field, and Wann (2007):

$$\text{TTP}_p = \frac{1}{\sqrt{\theta'}} \cdot \sqrt{\frac{S}{V}}. \quad (1)$$

We used bootstrap (Efron & Tibshirani, 1993) to obtain 95% confidence intervals of the two parameters (PSS and SD) and used maximum likelihood to fit the model. This procedure was applied to motion type (independent variable). When conclusions could not be drawn by merely looking at the overlap between two confidence intervals, parametric bootstrap and Monte Carlo simulations were used to compare two given psychometric curves by testing the null hypothesis, which assumed that the observed difference between the two PSSs (or the two slopes) was not different from zero.

Although we encouraged subjects to be accurate, we also recorded reaction times (RTs) and plotted them as a function of TTP, θ' , and TTP_p . Analysis relating to RT and accuracy (Pins & Bonnet, 2000) can provide information on the uncertainty level of judgments.

Results and discussion

The overall mean differences of proportion of “later” responses and RT for PLW's model [$t(7) = 1.16$, $p = \text{n.s.}$] and initial step cycle phase [$F(2,7) = 12.18$, n.s.] had no significant effect. It is true that the phase of the step cycle could affect performance in recognition or discrimination, depending on the task and the available amount of information (Thirkettle et al., 2009). However, in our study, the potential effect of the initial frame of the step cycle was reduced due to relative long presentation time of our trials (0.5 to 0.7 s). Thus, at least 16 frames of the step cycle were presented in each trial depicting different form and motion information. For further analyses, data were averaged for all models and initial step cycle phases. Figure 1A shows the proportion of “later” responses as a function of TTP with the best fit for each condition (Deviance = 2.51, $p = 1$ for BM; Deviance = 3.37, $p = 1$ for RM). BM appears to arrive earlier than RM. PSS was greater when the biological motion was presented (1.11 s) as compared to rigid motion (1.04 s). This difference in accuracy was significant ($p < 0.05$). Individual PSS and SD were derived from separate fits. Differences on accuracy were similar for all subjects as can be seen in Figure 1B. A tendency for SD to be higher for the BM condition was verified for all but subjects 6 and 8 (that showed global higher SD). However, after bootstrapping this parameter, the difference was not significant ($p > 0.5$, n.s.). Averaged SD was around 21% and 18% for BM and

RM, respectively. These values are greater than those found in previous rigid motion studies (Gray & Regan, 2000; López-Moliner, Brenner et al., 2007; Regan & Hamstra, 1993).

To further analyze whether subjects were sensitive to time information, we also plotted the proportion of “later” responses as a function of TTP_p and θ' (see Figures 1C and 1E, respectively). Although data distribution was not better explained by θ' alone, the fit was not significantly worse than that obtained with TTP (Deviance = 5.38, $p = 1$ for BM; Deviance = 5.55, $p = 1$ for RM). SD percentage was 22% for both motion conditions. However, when we looked at the distribution as a function of TTP_p , we verified that this variable is a good predictor of time-to-passage estimate (Deviance = 2.27, $p = 1$ for BM; Residual deviance = 3.05, $p = 1$ for RM) but is not significantly better than θ' ($p > 0.05$ for BM; $p > 0.05$ for RM). Regarding accuracy, significant differences were again found between motion conditions. PSS was greater when BM (0.51) was presented as compared to RM (0.45). Individual results were quite consistent along subjects (see Figure 1D). The difference on accuracy of estimation between motion conditions was again significant ($p < 0.05$). An increase of precision when the proportion of “later” responses was plotted as a function of TTP_p was verified (19% for BM and 17% for RM). Even so, the effect of motion condition on SD is still not significant.

Our results also showed that, although differences in accuracy were found, estimation for both conditions might share the same processes. The computation of arriving time was modulated by the same combination of cues. TTP judgments were analyzed from a 2AFC through the computation of psychometric parameters from binary responses. Chronometric analysis would add informative data to understand the processes underlying TTP estimation for BM. On average, observers required about 0.72 and 0.73 s ($SD = 0.30$ s and 0.29 s) for RM and BM, respectively. We conducted a t -test comparison that revealed no significant effects of motion condition in averaged results [$t(7) = 1.1$, $p = 0.29$]. Reaction time tends to decrease with increasing differences between actual TTP and the reference time (Figures 2A, 2B, and 2C, for TTP, TTP_p , and θ' , respectively). The linear fit for RT as a function of the absolute value of logit of accuracy (see Figure 2D) mirrors the relationship between an accuracy index and the readiness to answer (Pins & Bonnet, 2000). The following equations fit the present data for RM and BM, respectively:

$$\text{RT} = 0.783 - 0.030 \logit(p), \quad (2)$$

and

$$\text{RT} = 0.769 - 0.018 \logit(p), \quad (3)$$

where $\logit(p) = \ln(p/(1 - p))$.

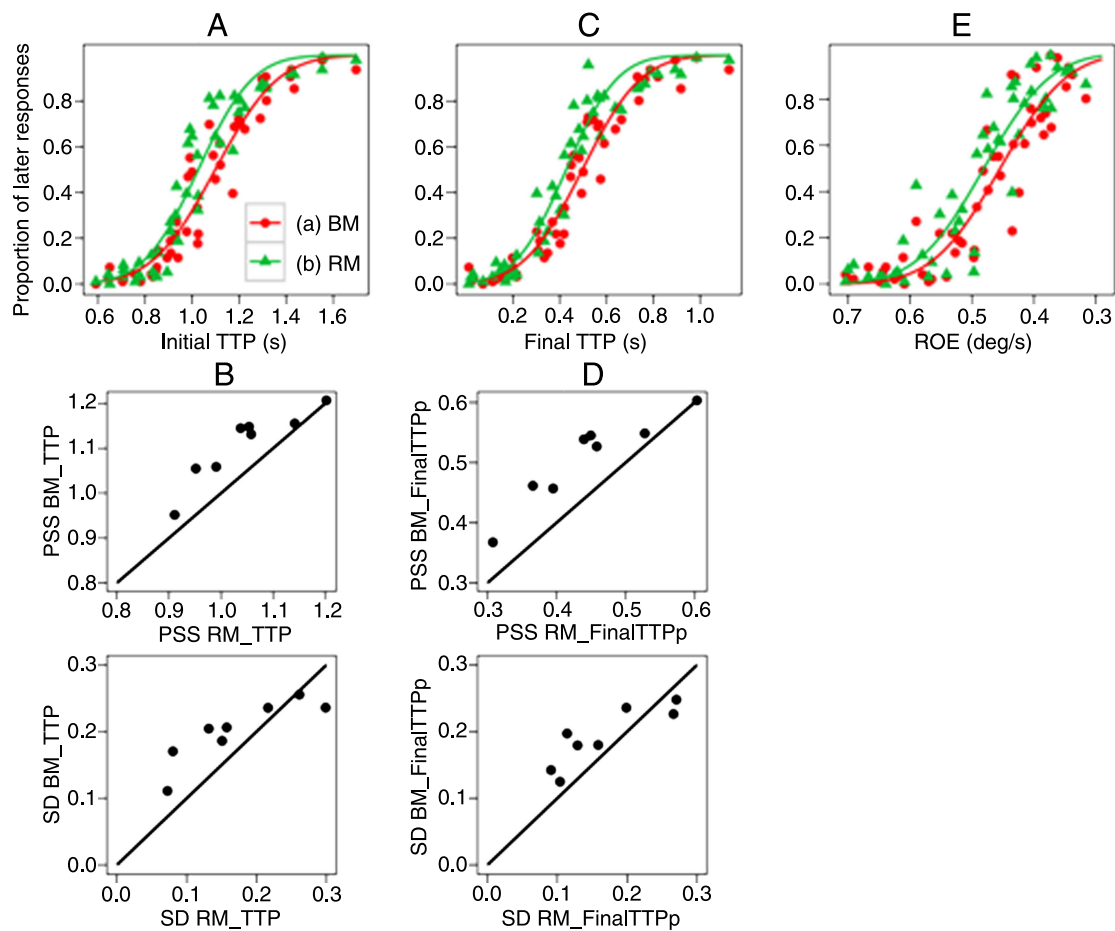


Figure 1. Data points are averages across all 8 subjects. The curves denote the best fit of a cumulative Gaussian function. (A) Proportion of trials in which the object was judged to have passed later than when the tone was sounded, as a function of TTP. (B) Individual values, estimated from separate fits, of PSS and SD for BM were plotted as a function of PSS and SD for RM. Each point corresponds to a participant. Points above the unity line correspond to higher values of PSS and SD for BM and below the unit line to higher values of PSS and SD for RM. (C) Proportion of trials in which the object was judged to have passed later than when the tone was sounded, as a function of TTP_p . (D) Same for (B) but as function of final TTP_p . (E) Proportion of trials in which the object was judged to have passed later than when the tone was sounded, as a function of ROE.

The goodness of the fit is indicated by R^2 for BM (0.91, $p < 0.01$) and RM (0.89, $p < 0.01$). The slope for RM was higher revealing a greater decrease on RT with increasing accuracy (slope = -0.030 for RM and slope = -0.018 for BM). RT was less sensitive to the decrease of uncertainty for the BM condition. This difference in slope, however, did not have significance [$t(7) = -1.4$, n.s].

In summary, subjects seem to be a little more conservative anticipating passage in the presence of BM, since they consistently judged this pattern as passing earlier than RM. However, even anticipating the passage of BM, subjects seem to have the same or greater amount of uncertainty in its judgment as they have for RM. The anticipation on estimates and the well-reported robustness of the human visual system to recognize BM did not promote a greater precision in performance. Reaction time analysis showed no significant differences on averaged values. In general, RT decreased with the decrease of uncertainty of the task, i.e., when the probability to have a

correct answer is higher. We do not have a clear message on precision. Since BM and RM presentations were interleaved, subjects could monitor both channels, which could mask possible differences on variability between both motion patterns.

Experiment 2

In the previous experiment, we compared performance on TTP estimation for two motion stimuli in looming, with the same constant translational velocities. What differed between them was the presence of relative motion between body parts (in this case, in the BM condition). So, we can argue that, from a computational perspective, BM is noisier. BM was perceived as arriving earlier and even so the judgment was less precise when compared to RM.

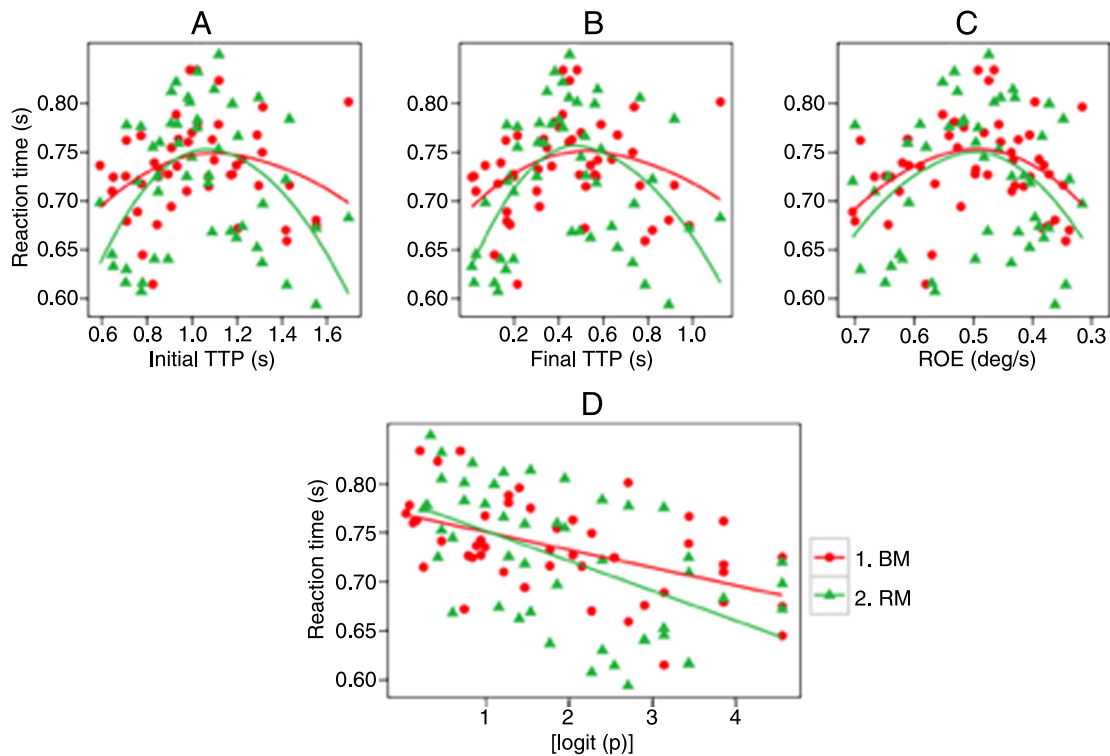


Figure 2. Reaction time as a function of (A) TTP, (B) TTP_p, and (C) θ . Data points are averages across all 8 subjects. A smooth (curve) gives the best fit for each motion condition. (D) Proportion of trials in which the object is judged to have passed later was transformed in logit. Reaction time was plotted as a function of the absolute value of logit. The two linear functions give the best fit for each motion condition.

In order to understand why these patterns occurred, we carried out [Experiment 2](#). We maintained RM and BM conditions and added three more conditions: inverted (IM), scrambled (SM), and complex non-biological motion (COMP-NBM). IM and SM have the same local motion information as BM, but the recognition of the stimulus as being a moving agent is impaired. The recognition of the first is impaired due to the inversion effect (Chang & Troje, 2009; Pavlova & Sokolov, 2000; Sumi, 1984) and of the second due to the disruption of the structural configuration (Ahlström et al., 1997; Troje & Westhoff, 2006). In the COMP-NBM condition, the structural information was also preserved, but a constant velocity function replaced the specific biological profile of the limb's markers, for each phase of the step cycle. In this way, performance can be compared between BM and two non-rigid motions. The first is still non-rigid biological motion but enhances different recognition levels (IM); the second is still non-rigid biological motion but with neither form nor structural information (SM); and the third is a non-rigid non-biological pattern (COMP-NBM). Assuming that BM is processed when estimating TTP by independent and specialized channels, then we should find significant differences between TTP judgments of BM and COMP-NBM. If not, we might assume that performance is based on the same perceptual mechanisms and differences between biological and non-biological conditions can be

due to different levels of uncertainty or computational load of the task. Moreover, the IM and SM conditions will allow for the approaching of the role of familiarity and animacy on the TTP judgment.

Participants

Six (3 females, 3 males, 26 ± 3 years old, mean \pm SD, one left-handed) of the eight volunteer participants recruited in [Experiment 1](#) took part in [Experiment 2](#). All had normal or corrected-to-normal vision, as assessed by Ergovision screening test (Essilor). All participants gave informed consent to take part in the study.

Methods

We used the same apparatus and procedure of [Experiment 1](#) with some modifications. First, in [Experiment 2](#), BM was compared with RM, IM, SM, and COMP-NBM. IM stimuli were the same PLW presented on BM condition but rotated 180° , i.e., “upside-down” PLW. Therefore, we might compare two motion patterns, BM and IM, with the same global and local motion and structural global information but with different recognition stages. SM ([Movie 3](#)) stimuli were generated by

randomizing the initial positions of each marker within the original area for all the displays used in [Experiment 1](#).

Biological motion has a specific velocity profile that is mathematically described by the “minimum-jerk model,” which is a cost function that minimizes jerkiness over a specified trajectory (Cook, Saygin, Swain & Blakemore, 2009; Flash & Hogan, 1985). In the COMP-NBM ([Movie 4](#)) condition, we employed stimuli in which this minimum-jerk (MJ) velocity profile was removed from the limb’s markers through a moving mean of order n , with n being the total number of frames within each phase of the step cycle, used in each trial. Thus, a constant velocity was found for each phase of the step cycle, and not for all the cycle, to keep the contra-phase between them (e.g., left and right elbows and left and right knees). The use of this control as a non-rigid non-biological pattern is supported by the fact that the human visual system is quite sensitive to the differences between biological and non-biological velocity profiles (Bingham, Schmidt, & Rosenblum, 1995; Chang & Troje, 2009). Furthermore, Cook et al. (2009) found that control adults (with no autism spectrum condition) had an increased sensitivity to identify perturbations on biological over non-biological velocity profiles, using minimum jerk as a 100% natural biological motion condition. Finally, it is well documented that the interference caused by movement observation on movement execution occurs only when the observed action is performed by a human and not by a robot, with a non-biological movement profile (Kilner, Paulignan, & Blakemore, 2003). Thus, evidence suggests that removing the minimum jerk from biological motion clearly changes the perceptual and motor performance of observers.

Second, while in [Experiment 1](#) we presented mixed blocks (RM and BM in the same block), in the present experiment we ran independent blocks, one for each motion condition. If the differentiation of channels matters, in so doing we remove the uncertainty inherent to monitoring more than one channel at the same time. All subjects participated in the four blocks; the presentation order was counterbalanced between subjects and they were informed of the motion pattern that would be presented before each block. Experimental and training blocks were completed in about 1-h and 20-min sessions.

Analysis

The analysis procedures of [Experiment 1](#) were used in the current experiment. A psychometric function was fitted to each motion condition providing distributions of the proportion of trials in which visual stimuli were seen as arriving “later than beep.” We fitted cumulative Gaussian curves to derive 2 parameters, point of subjective simultaneity (PSS) and standard deviation (SD), both from single individual data and from pooled data for

the six participants. In the previous experiment, TTP_p (predicted TTP at the end of the visual presentation) generated a better fit for data. Therefore, the results of [Experiment 2](#) will be presented as function of TTP_p . Reaction times were averaged across subjects and plotted as a function of TTP_p .

Results

The overall mean differences of proportion of “later” responses and RT for PLW’s model [$t(5) = 1.7$, $p = n.s.$] and initial step cycle phase [$F(2,5) = 1.12$, $n.s.$] had no significant effect. Therefore, for further analyses, data were averaged over model and initial step cycle phase. The proportion of “later” responses while varying TTP_p is illustrated in [Figure 3A](#). Again, data adjustment was good for TTP_p (Deviance = 2.48, $p = 1$ for BM; Deviance = 2.99, $p = 1$ for RM; Deviance = 3.84, $p = 1$ for SM; Deviance = 4.33, $p = 1$ for IM; Deviance = 3.18, $p = 1$ for COMP-NBM).

BM, IM, SM, and COMP-NBM stimuli were judged to arrive earlier than RM. In the RM condition, PSS (0.42) was lower than in BM (0.49), IM (0.51), SM (0.49), and COMP-NBM (0.48) conditions. With no exception, all subjects judge non-rigid motion patterns to arrive earlier ([Figure 3B](#)). Both parameters extracted from Gaussian fits were compared with bootstrap, revealing a significant effect of motion condition ($p < 0.05$). For PSS, these differences were significant between the RM and the complex motion patterns ($p < 0.01$) and between IM and COMP-NBM ($p < 0.05$).

Additionally, the presentation of blocked conditions caused a decrease on variability on the task of about 4% for BM and 9% for RM when compared to [Experiment 1](#), and now a significant effect of motion condition was found for precision. SD was lower for RM condition (0.14, 0.18, 0.19, 0.19, and 0.17, respectively, for RM, BM, IM, SM, and COM-NBM conditions). Again, differences were significant between the RM and the complex motion patterns ($p < 0.01$), between COMP-NBM and IM ($p < 0.05$), and between COMP-NBM and SM ($p < 0.05$).

Mean RT was plotted as a function of TTP_p ([Figure 4A](#)). On average, observers required about 0.512, 0.682, 0.604, 0.583, and 0.522 s (SD . 0.22, 0.31, 0.28, 0.27, and 0.25) for RM, BM, IM, SM, and COMP-NBM conditions, respectively. We conducted a repeated measures ANOVA that revealed significant effects of motion condition on RT [$F(3,5) = 75.6$, $p < 0.01$]. Tukey’s multiple comparison tests revealed significant differences between all motion conditions but between RM and COMP-NBM.

[Figure 4B](#) shows the linear fit for RT as a function of the logit of accuracy ($R^2 = 0.91$ ($p < 0.01$) for BM, $R^2 = 0.92$ ($p < 0.01$) for RM, $R^2 = 0.89$ ($p < 0.01$) for IM, $R^2 = 0.87$ ($p < 0.01$) for SCR, and $R^2 = 0.90$ ($p < 0.01$) for COMP-NBM). The following equations fit RT data as a

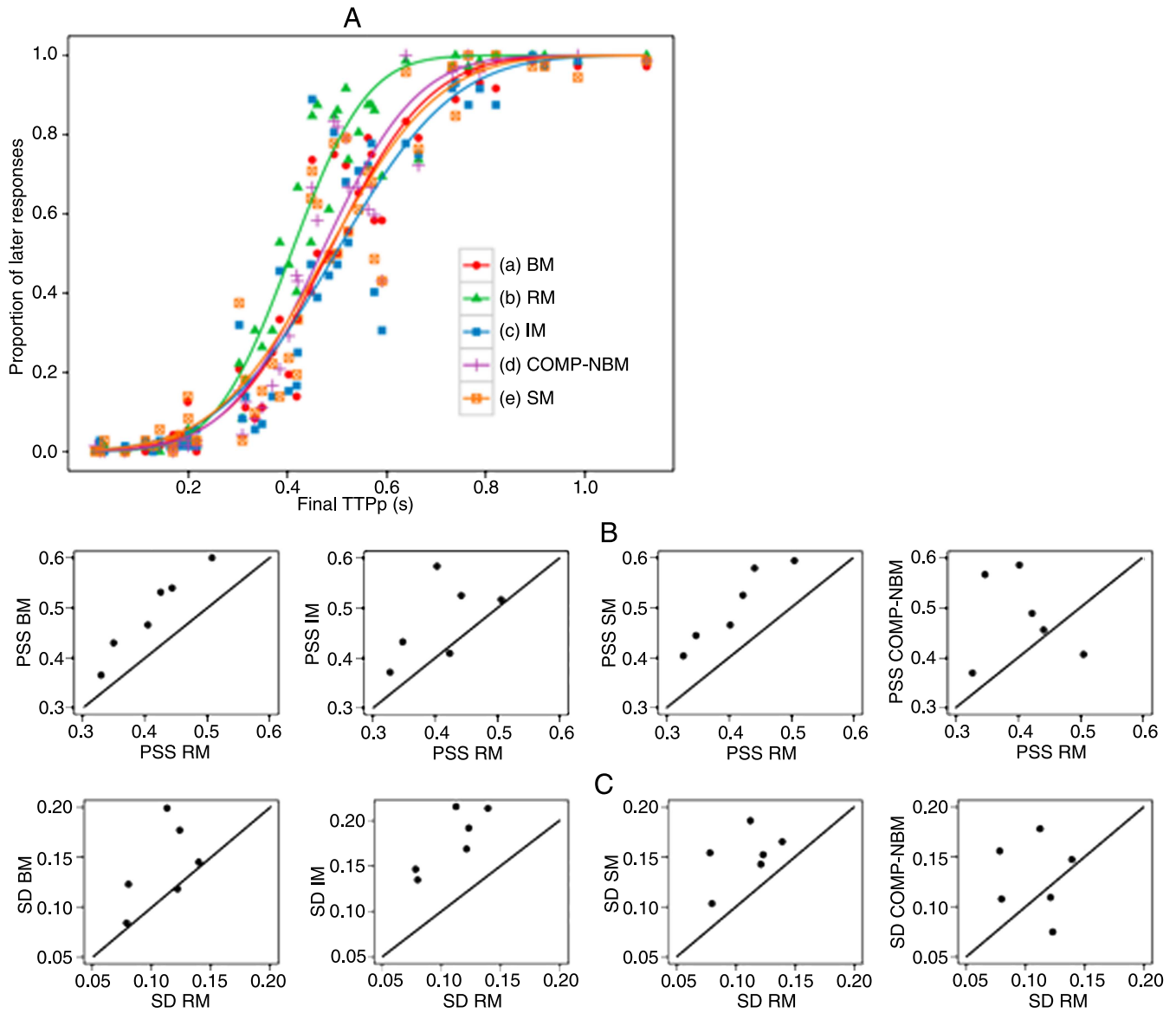


Figure 3. (A) Proportion of trials on which the object is judged to have passed later than when the tone was sounded, as a function of TTP_p . Data points are averages across all 6 subjects. The curve denotes the best fit of a cumulative Gaussian function. (B) Individual values, estimated from separate fits, of PSS for BM, IM, SM, and COMP-NBM were plotted as a function of PSS for RM. Each point corresponds to a subject. (C) The same as (B) for individual values of the estimated variability (SD). Each point corresponds to a subject.

function of $\logit(p)$ for RM, BM, IM, SM, and COMP-NBM, respectively: and

$$RT = 0.590 - 0.029 \logit(p), \tag{4}$$

$$RT = 0.727 - 0.019 \logit(p), \tag{5}$$

$$RT = 0.651 - 0.019 \logit(p), \tag{6}$$

$$RT = 0.631 - 0.019 \logit(p), \tag{7}$$

$$RT = 0.591 - 0.030 \logit(p). \tag{8}$$

Confirming ANOVA results, significant differences on the intercept of these functions were found between three groups of motion conditions: RM/COMP-NBM; IM/SM, and BM. Having a 95% confidence interval, these intervals were found: $[-0.561$ to $-0.620]$ for RM, $[-0.700$ to $0.755]$ for BM, $[-0.626$ to $-0.676]$ for IM, $[-0.606$ to $-0.655]$ for SM, and $[-0.557$ to $-0.624]$ for COMP-NBM. Slopes for non-biological pattern (RM and

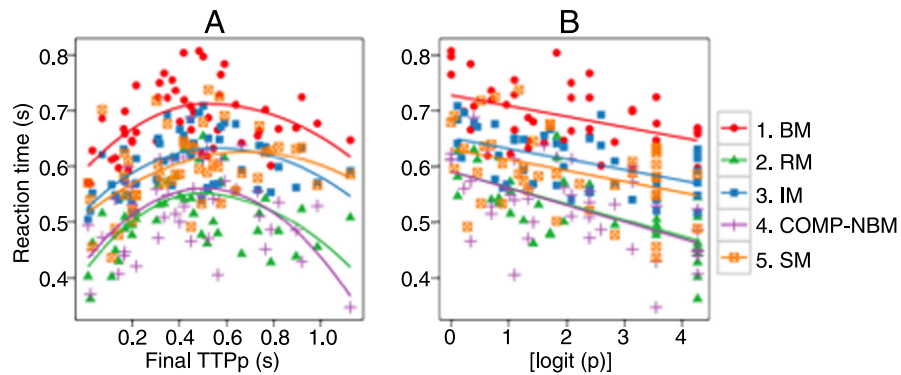


Figure 4. (A) Reaction time as a function of TTP_p . Data points were averaged across all 6 subjects. The four functions give the smooth curves for each motion condition. (B) Proportion of trials on which the object is judged to have passed later was transformed in logit units. Reaction time was plotted as function of logit units. The two linear functions give the best fit for each motion condition.

COMP-NBM) conditions were slightly higher, revealing a greater decrease on RT against accuracy. For BM, IM, and SM, RT decreased less as a function of uncertainty. Even so, the difference on slope was not significant between all motion conditions [$F(4,5) = 0.48$, n.s.]. The lack of significant differences between the slopes of the linear fit suggests that the differences obtained between motion conditions are due to the effect of an additive mechanism in the processing of biological patterns on top of that of RM but not a different channel with different sensitivity. Thus, the differences in precision on the TTP judgment could be due to variability introduced at later steps.

Conclusion

The present work intended to find if observers were able to extract accurately temporal information from biological motion. In [Experiment 1](#), we compared TTP judgments for biological and rigid motion (a single frame of the step cycle). Subjects could easily judge TTP with BM. However, passage of biological motion was anticipated in about 0.110 s. Observers were instructed to use as judgment reference the front part of the PLW. Even so, with the relative motion of the limbs during biological motion presentation, observers could use the foremost part of the body as reference to their judgment (e.g., wrist when moving forward). Thus, different rates of expansion could occur within a single PLW and observers could use different strategies to deal with this fact (e.g., using an averaged θ' , maximum θ'). We calculated the relative displacement between the extremity of the upper limb (wrist) and a more fixed trunk marker (hip) from 3D coordinates of PLW and then we computed the temporal difference between them in terms of TTP. The temporal difference is on average (between velocities, models, and phase of the step cycle) of about 0.06 s. So, even if

observers used different body references to judge TTP, this value cannot account for the whole difference we found on PSS.

We do not have a clear explanation for judging biological motion as arriving earlier than rigid motion. The anticipation bias does not seem to be due to differences on perceived speed. First, each initial TTP was computed through a combination of speeds and initial distances, to prevent the use of these variables alone. Moreover, a previous study showed that biological motion is perceived as being slower than rigid motion in a speed discrimination task (Mouta & Santos, 2011). Thus, if the perceived speed accounted for the results, then the bias should have been reversed (delay on BM passage estimation). Perhaps passage's anticipation might be explained by an adaptive response in the presence of a motion agent identified as being biological or more computationally demanding. In the presence of a noisier likelihood, judgments could be more conservative. Irrespective of this anticipation, precision or promptness on estimates of biological motion was not dramatically impaired. The opposite effect did not occur as well. We suggest that time-to-passage estimates of rigid and biological motion share the same processing channels.

In [Experiment 2](#), three new conditions—an inverted, a scrambled, and a complex non-biological motion—were included in the procedure. The inverted motion did not enhance an automatic and robust recognition as the biological motion does, even if both share the same local motion signals. The scrambled motion had the same local motion of the thirteen PLs, but the structural coherence of the patterns was disrupted by randomizing the initial position of each marker. The complex non-biological motion had the same spatial information of BM and the same contra-phase relative movements between limbs but with a constant velocity profile (minimum jerk removed) for each marker and for each phase of the step cycle. The rationale for using this control, a non-rigid non-biological pattern, is supported by the fact that the human visual

system is quite sensitive to differences between biological and non-biological velocity profiles (Bingham et al., 1995; Chang & Troje, 2009). Therefore, we might argue that a non-rigid non-biological target should be recognized as a clearly different pattern from biological ones, even if all do share a similar level of motion complexity. In [Experiment 2](#), we also presented motion patterns in blocked conditions, thereby decreasing the uncertainty level of the task. In fact, blocked conditions caused a decrease on variability on the task (Ball & Sekuler, 1980). In [Experiment 2](#), passage of biological, inverted, scrambled, and complex non-biological motion was anticipated in about 0.07, 0.09, and 0.06 s while accuracy for rigid motion continued to be very close to veridical values of TTP. These results denote an anticipation of noisier patterns (non-rigid), regardless of the nature of local motion that could be either biological (BM, IM, and SM) or non-biological (COMP-NBM). Nevertheless, when we looked at precision, we found again that this anticipation did not reduce performance's uncertainty. On the contrary, variability was significantly higher for non-rigid patterns (with relative and opponent motion).

Carrozzo, Moscatelli, and Lacquantini (2010) presented different experiments in which subjects were asked to intercept a moving target or to discriminate the duration of a stationary flash while viewing different scenes. These authors found that subjects rushed to intercept a moving target in the presence of an animate context and time estimates were systematically shorter in the sessions involving human characters moving in the scene than in those involving inanimate moving characters. Moreover, these authors showed that the presence of even only animate context had an effect on time estimation (underestimation). Carrozzo et al. suggested that neural time mechanisms involve systems differentially tuned to animate and inanimate motion. In fact, our results showed a clear bias on anticipating passage in the presence of biological motion, which did not happen for rigid motion. However, we also found the anticipatory bias for the inverted, scrambled, and complex non-biological conditions. These results suggest that the anticipation bias in TTP is not due to familiarity, animacy, or biologicity of the stimuli but to the noisier pattern provided by all complex motion patterns. The anticipation of passage seems to be a strategy for observers to deal with the higher uncertainty provided by complex patterns. This fact can be interpreted as an adaptive process in the way that it is equally relevant to estimate passage or collision of animate or inanimate approaching objects.

Since we observed again an anticipation of passage for the complex motion patterns, we calculated the relative displacement between the extremities of the lower limb to allow for the comparison with the displacement of the upper limb. In [Experiment 2](#), this question is pertinent because, in the inverted condition, the lower limbs are closer to the participant's eyes. The spatial difference between a more fixed marker (hip) and the extremities of

the upper and lower limbs (upper—wrist for BM and COMP-NBM; lower—ankle for IM) was calculated, and then we computed the temporal difference between them. The temporal difference of the lower limb (mean = 0.005) is quite disparate from the upper limb (mean = 0.06). The movement of the legs is more symmetric than the movements of the arms. Thus, the displacement of the ankle is made in two ways, and on average, the temporal difference tends to disappear due to the difference of signs. Nonetheless, there were no differences either on accuracy or on precision, between biological motion and inverted motion, which means that effects of motion pattern could not be explained by the highest indeterminacy of the reference provided by articulated motion patterns.

COMP-NBM is a multi-jointed motion pattern but without biological local features. The fact that the anticipation of passage is common between all non-rigid patterns suggests that the higher complexity provided by the articulated patterns is critical on the TTP judgment. The lack of differences between biological and inverted patterns would be very adaptive since observers might need to estimate TTP from a diversity of viewing points (e.g., while lying on the floor, looking up). An informal study explored the role of local cues on TTP estimation for biological and inverted conditions. Since we presented “real” size stimulus, we questioned if local cues could affect judgments. In our experiments, the bottom part of PLW was aligned with the ground plane, which means that biological and inverted conditions had different local information in the upper and lower parts of PLW. To test the role of local cues, three subjects performed the same task of [Experiment 2](#) but with the center of PLW aligned by the height of the observer's eyes. Thus, local information projected nearest to the foveal area was the same between biological and inverted stimuli. The results were consistent with those presented in this work, suggesting that TTP judgments were based on global patterns. Results for scrambled pattern revealed a similar trend. The absence of significant differences on precision between biological and scrambled patterns suggested that passage estimation was based on integrating local motion into a global pattern by similar mechanisms in both situations. Apparently, higher order structural information is not considered in this process and the reduction of noise is equally efficient in the BM and SM conditions.

Reaction time was analyzed as complementary data and it gave some clues about the nature of each motion pattern. Reaction time data as a function of accuracy yielded similar slopes for all motion patterns. Rigid motion is the simpler condition due to the absence of relative motion of body parts and it requires a lower reaction time. Surprisingly, the complex non-biological motion required the same reaction time as the rigid motion. It seems that it is not the articulation but the presence of a biological velocity profile (maybe noisier) that created the need for an extra time to reach a perceptual decision. The difference between this pattern and biological, inverted, and

scrambled patterns reveals that observers were sensitive to the acceleration profile of human motion, in agreement with the work of Chang and Troje (2009). We should also stress that the slope was the same for all RT distributions. In fact, our similar slopes of reaction time as a function of accuracy are consistent with the hypothesis that all motion stimuli are tapping the same sensory channels or, at least, different channels with the same sensitivity (Bonnet, 1996; Pins & Bonnet, 2000). Differences on intercept of RT distribution might be explained by an additive factor due to decisional processes (Pins & Bonnet, 2000). Therefore, we can argue that the biological motion local features functioned as an additive factor. In turn, biological motion required even a longer time than inverted and scrambled motions. Biological motion perception may involve more specialized rules because the stimulus carries form and motion information. The superior temporal sulcus (STS) and the temporal polysensory area (STP) in particular (Oram & Perrett, 1994) have a crucial role in biological motion perception. Several behavioral and brain functional studies suggested that this area integrates motion information from the dorsal system and object information from the ventral system (Vaina, 1994; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990). Our data suggest that the ventral stream information influences the time required for a time-to-passage estimation during recognition/interpretation of biological motion stimuli. Recognition acts as a second additive factor incrementing the required time to react and simultaneously not increasing the precision of the response. Our reaction time results showed that biological motion patterns required a long time to answer but reveal the same sensitivity to changes in uncertainty. This suggests that time-to-passage estimations involve the same sensory processes irrespective of the biological component of the motion pattern.

We can conclude that complexity of the motion pattern (rigid vs. non-rigid) plays a more determinant role than the “biologicity” or animacy of the stimulus (biological vs. non-biological), concerning time-to-passage judgments. We suggest that the same motion integration mechanisms of local signals and noise suppression are engaged for all kinds of non-rigid motion irrespective of the presence of higher order structures relevant for other task such as recognition.

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Corresponding author: Sandra Mouta.

Email: smouta@psi.uminho.pt.

Address: Centro de Computação Gráfica, Universidade do Minho, Campus de Azurém, 4800-058 Guimarães Portugal.

References

- Ahlström, V., Blake, R., & Ahlström, U. (1997). Perception of biological motion. *Perception*, *26*, 1539–1548. [PubMed]
- Atkinson, A. P., Dittrich, W. H., Gemmell, A. J., & Young, A. W. (2004). Emotion perception from dynamic and static body expressions in point-light and full-light displays. *Perception*, *33*, 717–746. [PubMed]
- Ball, K., & Sekuler, R. (1980). Models of stimulus uncertainty in motion perception. *Psychological Review*, *87*, 435–469.
- Beardsworth, T., & Buckner, T. (1981). The ability to recognize oneself from a video recording of one's movements without seeing one's body. *Bulletin of the Psychonomic Society*, *18*, 19–22.
- Beintema, J., & Lappe, M. (2002). Perception of biological motion without local image motion. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 5661–5663. [PubMed] [Article]
- Beintema, J. A., Oleksiak, A., & van Wezel, R. J. (2006). The influence of biological motion perception on structure-from-motion interpretations at different speeds. *Journal of Vision*, *6*(7):4, 712–726, <http://www.journalofvision.org/content/6/7/4>, doi:10.1167/6.7.4. [PubMed] [Article]
- Bertenthal, B. I., & Pinto, J. (1994). Global processing of biological motion. *Psychological Science*, *5*, 221–225.
- Bingham, G. P. (1993). Scaling judgments of lifted weight: Lifter size and the role of the standard. *Ecological Psychology*, *5*, 31–64.
- Bingham, G. P., Rosenblum, L. D., & Schmidt, R. C. (1995). Dynamics and the orientation of kinematic forms in visual event recognition. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 1473–1493.
- Bonnet, C. (1996). Sensory/decisional problem: An expansion of Link's theory. In S. C. Masin (Ed.),

- Fechner Day 96* (pp. 137–142). Padua: International Society for Psychophysics.
- Bootsma, R. J., & Craig, C. M. (2002). Global and local contributions to the optical specification of time to contact: Observer sensitivity to composite tau. *Perception, 31*, 901–924. [PubMed]
- Carrozzo, M., Moscatelli, A., & Lacquaniti, F. (2010). Tempo rubato: Animacy speeds up time in the brain. *PLoS ONE, 5*, 1–12.
- Casile, A., & Giese, M. (2005). Critical features for the recognition of biological motion. *Journal of Vision, 5*(4):6, 348–360, <http://www.journalofvision.org/content/5/4/6>, doi:10.1167/5.4.6. [PubMed] [Article]
- Chang, D. H., & Troje, N. F. (2009). Acceleration carries the local inversion effect in biological motion perception. *Journal of Vision, 9*(1):19, 1–17, <http://www.journalofvision.org/content/9/1/19>, doi:10.1167/9.1.19. [PubMed] [Article]
- Cook, J., Saygin, A. P., Swain, R., & Blakemore, S. J. (2009). Reduced sensitivity to minimum-jerk biological motion in autism spectrum conditions. *Neuropsychologia, 47*, 3275–3278.
- Cutting, J. E., & Kozlowski, L. T. (1977). Recognizing friends by their walk: Gait perception without familiarity cues. *Bulletin of the Psychonomic Society, 9*, 353–356.
- Cutting, J. E., Moore, C., & Morrison, R. (1988). Masking the motions of human gait. *Perception & Psychophysics, 44*, 339–347.
- Dittrich, W. H. (1993). Actions categories and the perception of biological motion. *Perception, 22*, 15–22. [PubMed]
- Efron, B., & Tibshirani, R. J. (1993). *An introduction to the bootstrap*. New York: Chapman & Hall.
- Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception and Performance, 21*, 628–634. [PubMed]
- Flash, T., & Hogan, N. (1985). The coordination of arm movements: An experimentally confirmed mathematical model. *Journal of Neuroscience, 5*, 1688–1703.
- Gray, R., & Regan, D. (1998). Accuracy of estimating time to collision using binocular and monocular information. *Vision Research, 38*, 499–512.
- Gray, R., & Regan, D. (2000). Estimating the time to collision with a rotating nonspherical object. *Vision Research, 40*, 49–63. [PubMed]
- Hiris, E. (2007). Detection of biological and non-biological motion. *Journal of Vision, 7*(12):4, 1–16, <http://www.journalofvision.org/content/7/12/4>, doi:10.1167/7.12.4. [PubMed] [Article]
- Hiris, E., Krebeck, A., Edmonds, J., & Stout, A. (2005). What learning to see arbitrary motion tells us about biological motion perception. *Journal of Experimental Psychology: Human Perception and Performance, 31*, 1096–106. [PubMed]
- Hoffman, D. D., & Flinchbaugh, B. E. (1982). The interpretation of biological motion. *Biological Cybernetics, 42*, 195–204.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics, 14*, 201–211.
- Johansson, G. (1976). Spatio-temporal differentiation and integration in visual motion perception. *Psychological Research, 38*, 379–393.
- Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. *Current Biology, 13*, 522–525.
- Lee, D. N. (1976). A theory of visual control of braking based on information about time-to-collision. *Perception, 5*, 437–459. [PubMed]
- Lee, D. N., Georgopoulos, A. P., Clark, M. J., Craig, C. M., & Port, N. L. (2001). Guiding contact by coupling the taus of gaps. *Experimental Brain Research, 139*, 151–159. [PubMed]
- López-Moliner, J., & Bonnet, C. (2002). Speed of response initiation in a time-to-contact discrimination task reflects the use of η . *Vision Research, 42*, 2419–2430. [PubMed]
- López-Moliner, J., Brenner, E., & Smeets, J. B. J. (2007). Interceptive timing. *Perception & Psychophysics, 69*, 887–894. [PubMed]
- López-Moliner, J., Field, D. T., & Wann, J. P. (2007). Interceptive timing: Prior knowledge matters. *Journal of Vision, 7*(13):11, 1–8, <http://www.journalofvision.org/content/7/13/11>, doi:10.1167/7.13.11. [PubMed] [Article]
- Mather, G., & Murdoch, L. (1994). Gender discrimination in biological motion displays based on dynamic cues. *Proceedings of the Royal Society of London B, 258*, 273–279.
- Mouta, S., & Santos, J. A. (2011). Percepção de velocidade do movimento: Mais resistente ao fenómeno de interferência? *Estudos de Psicologia, 28*, 475–488.
- Neri, P., Morrone, M. C., & Burr, D. C. (1998). Seeing biological motion. *Nature, 395*, 894–896. [PubMed]
- Norman, J. F., Payton, S. M., Long, J. R., & Hawkes, L. M. (2004). Aging and perception of biological motion. *Psychology and Aging, 19*, 219–225. [PubMed]
- Oram, M. W., & Perrett, D. I. (1994). Responses of anterior superior temporal polysensory (STPa) neurons

- to “biological motion” stimuli. *Journal of Cognitive Neuroscience*, *6*, 99–116. [PubMed]
- Pavlova, M., & Sokolov, A. (2000). Orientation specificity in biological motion perception. *Perception & Psychophysics*, *62*, 889–899. [PubMed]
- Peuskens, H., Vanrie, J., Verfaillie, K., & Orban, G. (2005). Specificity of regions processing biological motion. *European Journal of Neuroscience*, *21*, 2864–2875. [PubMed]
- Pins, D., & Bonnet, C. (2000). The Piéron function in the threshold region. *Perception & Psychophysics*, *62*, 127–136. [PubMed]
- Pinto, J., & Shiffrar, M. (1999). Subconfigurations of the human form in the perception of biological motion displays. *Acta Psychologica*, *102*, 293–318. [PubMed]
- Pollick, F. E., Kay, J. W., Heim, K., & Stringer, R. (2005). Gender recognition from point-light walkers. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 1247–1265. [PubMed]
- Pollick, F. E., Paterson, H. M., Bruderlin, A., & Sanford, A. J. (2001). Perceiving affect from arm movement. *Cognition*, *82*, B51–B61. [PubMed]
- Poom, L., & Olsson, H. (2002). Are mechanisms for perception of biological motion different from mechanisms for perception of nonbiological motion? *Perceptual Motor Skills*, *95*, 1301–1310. [PubMed]
- Regan, D., & Hamstra, S. J. (1993). Dissociation of discrimination thresholds for time to contact and for rate of angular expansion. *Vision Research*, *33*, 447–462. [PubMed]
- Regan, D., & Vincent, A. (1995). Visual processing of looming and time to contact throughout the visual field. *Vision Research*, *35*, 1845–1857. [PubMed]
- Smith, M. R., Flach, J. M., Dittman, S. M., & Stanard, T. (2001). Monocular optical constraints on collision control. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 395–410. [PubMed]
- Sumi, S. (1984). Upside-down presentation of the Johansson moving light-spot pattern. *Perception*, *13*, 283–286. [PubMed]
- Sun, H., & Frost, B. J. (1998). Computation of different optical variables of looming objects in pigeon nucleus retundus neurons. *Nature Neuroscience*, *1*, 296–303. [PubMed]
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology*, *46A*, 225–245. [PubMed]
- Thirkettle, M., Benton, C. P., & Scott-Samuel, N. E. (2009). Contributions of form, motion and task to biological motion perception. *Journal of Vision*, *9*(3):28, 1–11, <http://www.journalofvision.org/content/9/3/28>, doi:10.1167/9.3.28. [PubMed] [Article]
- Thornton, I. M., Pinto, J., & Shiffrar, M. (1998). The visual perception of human locomotion. *Cognitive Neuropsychology*, *15*, 535–552. [PubMed]
- Thurman, S. M., Giese, M. A., & Grossman, E. D. (2010). Perceptual and computational analysis of critical features for biological motion. *Journal of Vision*, *10*(12), 1–14, <http://www.journalofvision.org/content/10/12/15>, doi:10.1167/10.12.15. [PubMed] [Article]
- Tresilian, J. R. (1999). Visually timed action: Time-out for tau? *Trends in Cognitive Science*, *3*, 301–309.
- Troje, N. F. (2002). Decomposing biological motion: A framework for analysis and synthesis of human gait patterns. *Journal of Vision*, *2*(5):2, 371–387, <http://www.journalofvision.org/content/2/5/2>, doi:10.1167/2.5.2. [PubMed] [Article]
- Troje, N. F., & Westhoff, C. (2006). The inversion effect in biological motion perception: Evidence for a “life detector”? *Current Biology*, *16*, 821–824. [PubMed] [Article]
- Troje, N. F., Westhoff, C., & Lavrov, M. (2005). Person identification from biological motion: Effects of structural and kinematic cues. *Perception & Psychophysics*, *67*, 667–675. [PubMed]
- Vaina, L. M. (1994). Functional segregation of color and motion processing in the human visual cortex: Clinical evidence. *Cerebral Cortex*, *4*, 555–572. [PubMed]
- Vaina, L. M., Lemay, M., Bienfang, D. C., Choi, A. Y., & Nakayama, K. (1990). Intact “biological motion” and “structure from motion” perception in a patient with impaired motion mechanisms: A case study. *Visual Neuroscience*, *5*, 353–369. [PubMed]
- Wann, J. (1996). Anticipating arrival: Is the tau-margin a specious theory? *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 1031–1048. [PubMed]
- Webb, J. A., & Aggarwal, J. K. (1982). Structure from motion of rigid and jointed objects. *Computer Vision & Image Understanding*, *19*, 107–130.