Vision Research 140 (2017) 13–24

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Flash-lag effects in biological motion interact with body orientation and action familiarity

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ARTICLE INFO

Article history:
Received 7 May 2016
Received in revised form 7 June 2017
Accepted 30 June 2017

Keywords:
Flash-lag effect
Biological motion
Moving objects
Localization
Action familiarity
Action prediction

ABSTRACT

The ability to localize moving joints of a person in action is crucial for interacting with other people in the environment. However, it remains unclear how the visual system encodes the position of joints in a moving body. We used a paradigm based on a well-known phenomenon, the *flash-lag* effect, to investigate the mechanisms underlying joint localization in bodily movements. We first found that observers perceived a strong flash-lag effect in biological motion: when a briefly-flashed dot was presented physically in perfect alignment with a continuously moving limb, the flash dot was perceived to lag behind the position of the moving joint. Importantly, our study revealed that for familiar forward walking actions, the strength of the flash-lag effect for a joint depends on body orientation. Specifically, observing a walker with a natural body orientation (i.e., upright) yielded a significantly stronger flash-lag effect for the critical foot joint than did viewing an inverted walker. In contrast, the hand joint showed a weaker flash-lag effect in the upright walker than the inverted walker. These findings suggest that the impact of body orientation on encoding joint locations depended on body part. Furthermore, we found that action familiarity modulates the impact of body orientation on the flash-lag effect. Body orientation impacted location encoding in familiar forward walking actions, but not in unfamiliar actions (e.g., backward walking, jumping-jack). Simulation results showed that generic motion mechanisms, such as the temporal averaging model, cannot fully account for these empirical findings regarding the flash-lag effect in biological motion. The present study provides compelling evidence that action processing interacts with position processing to localize the moving joints in whole-body actions, and that this influence depends on body orientation and familiarity of actions.

1. Introduction

The ability to localize a person and their body parts in action is crucial for action recognition and interaction with other people in the environment. For example, we avoid collision with an approaching pedestrian by estimating her moving body position in order to plan our own movements accordingly. In order to shake hands with a friend, we need to localize the position of her hand embedded within a moving arm. A couple performing ballet must accurately judge limb and body positions of their partner in order to perform well-coordinated dance movements. Although humans perform these tasks well, localizing the positions of joints nested within a moving body is not a trivial task. Due to intrinsic neural delay of position signal processing for moving objects, by the time the visual input arrives in cortical areas selective to biological motion, the joints and the body have already moved on to different positions. It remains unclear how the visual system encodes the position of joints in a moving body.

In contrast to the dearth of research on joint localization in biological motion, there is a large body of research examining the mechanisms underlying localization of objects moving along simple movement trajectories (e.g., a moving bar in translation, a rotating line, a dot moving along a circle). When a briefly flashed object is presented physically in perfect alignment with a continuously moving object, observers perceive that the flash appears to lag behind the moving object (Mackay, 1958; Nijhawan, 1994). This well-known illusion, the *flash-lag* (FL) effect, provides a compelling demonstration that the visual system has developed mechanisms to cope with neuronal latencies in processing dynamic stimuli.

Two major classes of mechanisms have been proposed to account for the motion-induced position bias that constitutes the flash-lag illusion. The first class relies on generic spatial and temporal processing to either compensate for neuronal latencies, or reduce the delays in processing motion stimuli. For example, a

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http://dx.doi.org/10.1016/j.visres.2017.06.010
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model based on motion extrapolation assumes that the visual system makes spatial compensations by extrapolating the trajectory of a moving stimulus into the future, so that positions of the moving object are perceived to be ahead of the actual positions of the visual stimuli (Nijhawan, 1994). A differential latency model suggests that the visual system processes moving objects more quickly than briefly flashed stationary objects (Baldo & Klein, 1995; Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney, Murakami, & Cavanagh, 2000). This temporal difference yields the flash-lag percept, because the moving object has already shifted to a new position by the time the flashed object is processed.

A second class of mechanisms accounts for the flash-lag effect by assuming various forms of interaction between detection of the flash object and ongoing motion processing. For example, the temporal averaging model (Krekelberg & Lappe, 2000) suggests that the flash triggers temporal processing to integrate position signals of a moving object over a time window of 500 ms. Eagleman and Sejnowski (2000) proposed that the flash resets the window of motion integration processing, signaling the visual system to integrate post-flash position signals of the moving object. Although none of these mechanisms is sufficient to explain all the empirical findings related to the flash-lag effect, it is conceivable that multiple mechanisms could coexist and contribute differentially depending on stimulus complexity, object representation in space and time, and task demands (Whitney, 2002).

It is unclear, however, whether these mechanisms for extracting positions of moving objects with simple translation or rotation movements can account for the localization of components in more complex motion patterns, such as bodily movements in human actions. Furthermore, if these generic mechanisms do apply to human body movements, how do these mechanisms interact with action representations to encode joint positions in a moving body?

Kessler, Gordon, Cessford, and Lages (2010) aimed to address these questions by examining the flash-lag effect with arm movements (e.g., moving an arm to reach out for a cup). These researchers confirmed the existence of the flash-lag effect for arm movements (i.e., a flashed stationary object was perceived as lagging behind the positions of a moving hand even when the two stimuli were spatially aligned). This finding generalized the FL effect to complex motion trajectories of a biological movement. Furthermore, the FL effect obtained when observing the original videos of arm movements was significantly greater than the effect measured in a control condition that showed symbolic moving shapes (i.e., removing human body appearance while maintaining the same motion trajectories). Hence, representing the motion stimulus as biological movement resulting from meaningful human actions enhances the FL effect. In addition, Kessler et al.'s study revealed that two other factors specific to human body movements (first-person perspective and sense of agency) modulate the magnitude of the FL effects when observing arm movements.

The present study aimed to extend previous research to investigate how the visual system encodes positions of moving joints when observing actions involving *whole-body* movements, and to determine how action representation interacts with generic mechanisms for localization of moving features to bias perceived positions of moving joints. To examine the mechanisms involved in encoding joint positions in a moving body, stationary joints were briefly flashed during the viewing of a walking action in a point-light display, and the magnitude of the FL effect was measured to assess the perceived location of moving joints. Given the dynamic nature of biological motion stimuli, we expected that participants would misperceive the relative position between flash joints and moving limbs in the action.

To identify whether the FL effect depends on action processing, we used a critical control condition based on *inverted* actions. Perception of biological motion is known to be sensitive to body orientation and body structure. For example, recognition performance is impaired if a point-light actor is presented upside-down (Lu, 2010; Sumi, 1984; Thurman & Lu, 2013a,b, 2014; van Boxtel & Lu, 2011). Since the motion profiles of joint trajectories are matched between upright and inverted actions, the role of action-specific mechanisms involved in localizing moving joints would be revealed by a difference in FL between the two conditions. In addition, we examined how familiarity of an action impacts the FL effect in biological motion.

In order to disentangle the contributions of action processing versus generic motion mechanisms in localizing joint positions in a moving body, we compared human performance with a baseline model in which the FL effect was elicited solely by generic mechanisms in motion processing. To do so, we applied the temporal averaging model (Krekelberg & Lappe, 2000) to biological motion stimuli used in our studies, allowing us to estimate the component of the FL effect that can be explained by general motion mechanisms, and to compare human performance with predictions derived from generic mechanisms based on the temporal averaging model.

2. Experiment 1: Joint flash-lag effect in walking actions

To investigate the mechanisms involved in localizing positions of moving joints, Experiment 1 used stimuli in which a stationary joint flashed briefly during the viewing of a walking action. We measured the flash-lag effect of two separate joints (hand and foot) in different body orientations of an actor (upright vs. inverted) performing a familiar or unfamiliar action (forward vs. backward walking). We mixed hand and foot joints in the experiment for two reasons. First, the randomized presentation order of flash joints prevented participants from tracking a particular joint movement when viewing the action. Tracking through smooth-pursuit eye movement can significantly influence the magnitude of the FL effect (Nijhawan, 2001). Using randomized flashes of different joints can minimize the strategy of tracking body parts, because participants did not know where the dot would be flashed in a given trial. Second, the inclusion of two joints made it possible to examine whether localization of joints in a moving body depends on the functional importance of a joint to a particular action. Previous research has shown that the movements of foot joints play a more important role in discriminating bipedal actions (e.g., walking vs. running) than do hand joints (van Boxtel & Lu, 2012; van Boxtel & Lu, 2015). If joint localization varies with the functional importance of the joints, we would expect to observe a difference in FL between different joints.

2.1. Participants

The participants were 14 undergraduate students (9 females, M_{age} = 19.4 years) in the Psychology Department at the University of California, Los Angeles (UCLA). Participants reported normal or corrected-to-normal vision, and received two class credits for the 2-h session required for the study. All studies in the present paper were approved by the UCLA IRB board. Consent forms and debriefing documentations were provided in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Stimuli

The walker stimulus was generated from the CMU motion capture database (http:/mocap.cs.cmu.edu), and displayed from a sagittal view using the Biomotion Toolbox (van Boxtel & Lu, 2013b) in conjunction with the PsychToolbox (Brainard, 1997; Pelli, 1997). The moving walker was presented in the format of a skeleton display, consisted of 8 segments, including 4 limbs (i.e., two hands and two feet), 1 neck segment, 1 shoulder segment, 1 hip segment, and 1 torso segment formed by connecting the middle shoulder joint and the middle hip joint (see Fig. 1). The skeleton walker was rendered as grey, except that one lower-arm and one lower-leg on the opposite side of the body were colored red, indicating that they were the limbs relevant to the task. The walker, located at the center of the screen, subtended about 4.39 degrees of visual angle in height and 2.01 degrees of visual angle in width. The walker completed one walking cycle (i.e., 60 frames) in 1 s. The extrinsic movements of the walker were removed to create the appearance of walking on a treadmill. The facing direction (either left or right) was randomly selected for a participant, and remained constant across the entire experiment for each participant. Facing directions were counterbalanced across participants. The walker was displayed with body orientation either upright or inverted, and in walking directions either forward or backward, creating four conditions in the experiment. The backward-walking action was generated by playing the forward-walking video in reverse starting with an intermediate frame, so that the same posture was tested at the same time as in corresponding forward trials.

On each trial, a green dot in the size of 0.12 visual degrees was flashed for 33.3 ms at some point during the movement of the walker. The location of the flash dot was determined by the reference joint (a foot or a hand joint) in frame 53, corresponding to 3/4 of the second step in the walking stimulus. The flash dot always appeared at the same physical location across all the conditions but at different time points. As shown in Fig. 1, when the flash dot appeared several frames prior to, in the same frame as, or several frames after the time when the lower leg (or arm) reached the dot position, these stimuli were respectively labeled *behind*, *aligned*, and *ahead*, based upon the relative temporal relation between the position of the moving limb and the dot at the time of the flash. To minimize participants' confusion regarding which limb served as the reference for the judgment of relative spatial position, only the limb of interest (e.g., lower leg in Fig. 1) was shown within the temporal window of +/− one frame around the time of presenting the flash.

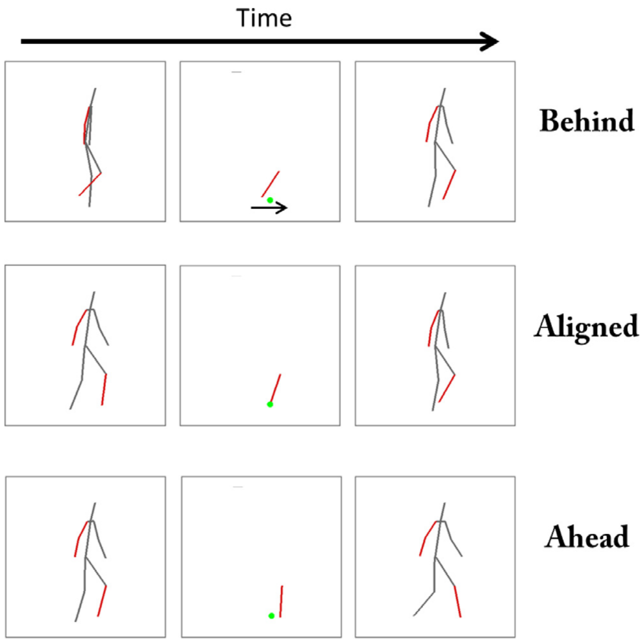

Fig. 1. Stimulus illustration for Experiment 1. The moving limb (lower leg in this example) was physically behind (top panel), aligned with (middle panel) and ahead of (bottom panel) the stationary flashed dot. The location of the flash dot was determined by the reference joint, either a foot or a hand joint. The flash dot always appeared at the same physical location across all the conditions but at different time points. The arrow indicates the general moving direction of the reference limb around the time when the dot was flashed. See Supplemental movies for the illustration, in which flash dot is perfectly aligned with moving body.

The temporal offsets between the flash dot and the moving walker varied in a range of −100 to +100 ms with a step size of 33.3 ms (i.e., 2 frames), resulting in seven levels of temporal offsets. Negative offsets indicate that the moving limb was temporally behind the flash dot, zero indicates perfect alignment between the flash dot and the moving limb, and positive offsets indicate that the moving limb was temporally ahead of the flash.

The experiments were conducted in a dark room. The stimuli were displayed on a calibrated Viewsonic CRT monitor with a refresh rate of 60 Hz and resolution of 1280 × 1024 pixels, and viewed from a constant distance of 45 cm maintained by a chin rest.

2.3. Procedure

The experimental design involved three within-subject factors: reference joint (hand vs. foot), walking direction (forward vs. backward) and body orientation (upright vs. inverted). Observers participated in one session on the first day and a second session after a week, with either upright or inverted walkers being shown in each session. A session consisted of one block with forward walking direction and another block with backward walking direction. The order of walking direction and body orientation were counterbalanced across participants. In each block of 280 trials (2 joints × 7 offset levels × 20 trials per condition), hand/foot reference joints were randomly intermixed.

On each trial, participants were asked to judge whether the flash dot appeared on the left or the right side of the red limb. Due to the brief presentation of the flash dot, participants were also allowed to report that they did not observe the flash. Responses were re-coded into whether the moving limb was perceived ahead of or behind the flash dot according to the motion trajectory of each reference joint around the location of the flash. Participants completed 10 practice trials prior to the experiment without feedback. The presentation of the practice trials was twice as slow as the experimental trials in order to show participants the brief presentation of the flash dot.

2.4. Results

The analysis was based on the mean proportion of trials on which the moving reference limb was reported ahead of the flash dot as a function of spatial offsets between the flash and reference joint location of the walker at the time of flash. To quantify the strength of FL in each condition, we measured the shift of the point of subjective equality (PSE), which reveals the average spatial displacement at which participants would yield 50% "ahead" responses when indicating the perceived alignment between the moving limb and the flash dot. Trials on which participants reported failure to observe a flash dot were removed from data analyses. Overall, the miss rate was very low (mean proportion of 1.3%).

For individual observers in each condition, we fitted the data with a Gaussian cumulative distribution function with two parameters, mean μ and standard deviation σ, as shown in Fig. 2 (top panel). For all observers, this function fitted their data well (R^2 of 0.946 ± 0.075). The estimate of the μ parameter was taken as the PSE estimate, corresponding to the spatial offset yielding 50% "ahead" responses, and provided the measure of the strength of

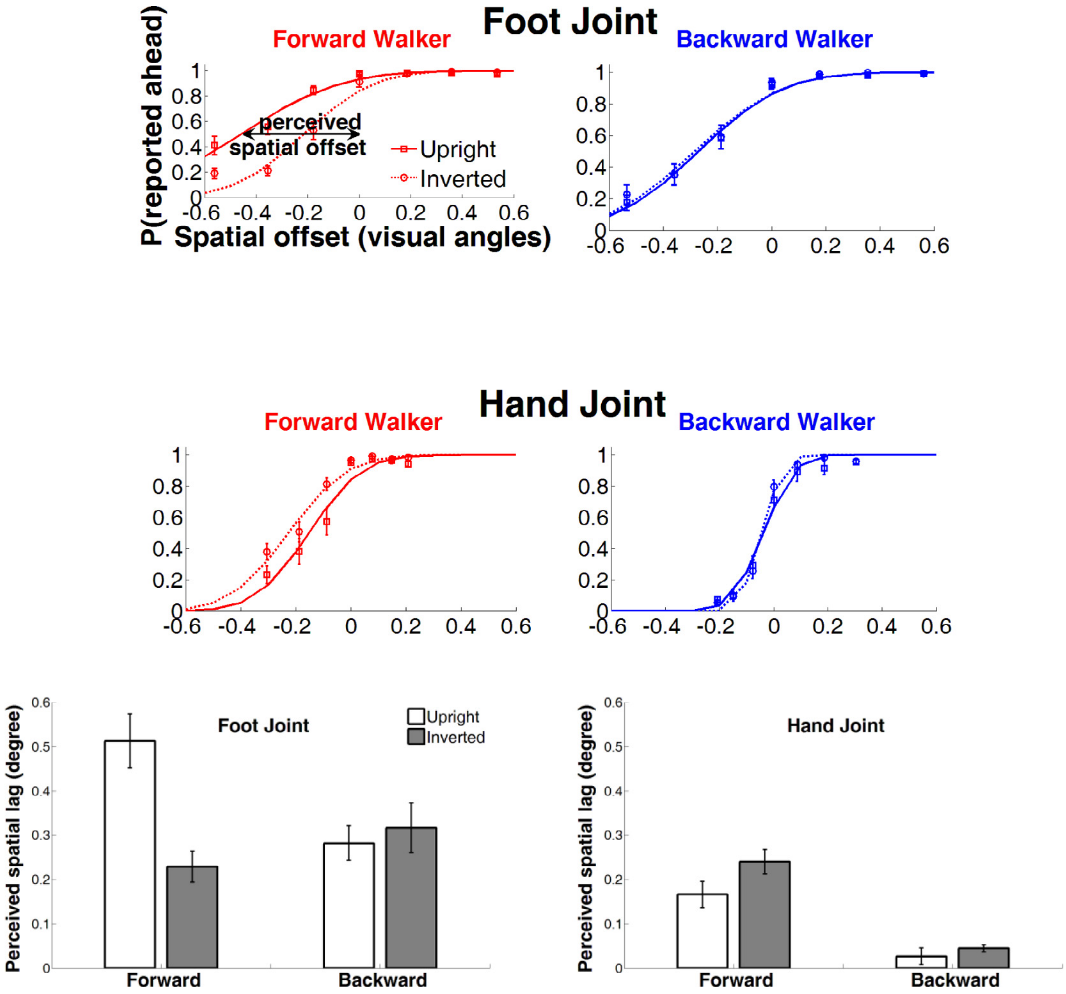

Fig. 2. Results for joint FL effect in Experiment 1. Top panel: the fitted psychometric functions based on the average performance for different joints and walking directions. Bottom panel: the strength of FL in terms of the perceived spatial lag varied depending on body orientation (upright vs. inverted), walking direction (forward vs backward) and reference joints (foot vs. hand). The error bars indicate SEM in all the plots of the paper.

the FL (perceived spatial lag). A PSE of zero indicates absence of a flash-lag effect (i.e., participants yielded 50% "ahead" responses when the flash dot was aligned with the moving reference limb); a negative PSE indicates presence of a flash-lag effect (i.e., a moving limb that spatially lagged behind was perceived to be in alignment with the flash), which is reported as a positive value of perceived spatial lag in the present paper; and a positive PSE indicates presence of a flash-lead effect (i.e., a moving limb spatially ahead of the flash was perceived to be in alignment), reported as a negative value of perceived spatial lag.

As shown in Fig. 2 (bottom panel), flash-lag effects were observed in most conditions, as indicated by the perceived spatial lag. A repeated-measures ANOVA with three within-subject factors (foot vs. hand joint, body orientation, and walking direction) revealed a significant three-way interaction effect ($F(1,13) = 18.97$, $p = 0.001$, $\eta_p^2 = 0.59$), suggesting that the impact of body orientation on localizing joint position in a walking body depends on specific joints and familiarity of the walking action. Specifically, for the familiar action of forward walking, the magnitude of the FL effect showed a difference between upright and inverted body orientation. However, for the unfamiliar action of backward walking, body orientation did not influence FL effects. More detailed analyses are presented below, examining how the three factors interact to influence FL effects.

When the flash dot was located at the foot joint, we found a significant two-way interaction ($F(1,13) = 20.04$, $p = 0.001$, $\eta_p^2 = 0.61$) between body orientation and walking direction. The perceived location lag for the upright forward walker was significantly stronger (mean = 0.51 degrees) than for the inverted forward walker (mean = 0.23 degrees) ($t(1,13) = 4.75$, $p < 0.001$). However, the impact of body orientation on the FL effect of foot joints was not significant for the unfamiliar action of backward walking ($p = 0.526$). These results suggest that, for a familiar action (forward walking), FL appears to depend on two mechanisms: action-specific mechanisms that are sensitive to body orientation, and general motion mechanisms that depend on specific motion trajectory of joints. However, when observing an unfamiliar action such as backward walking, FL may be mainly elicited by generic mechanisms based on motion trajectories of individual joints, which are not sensitive to body orientation in the whole-body action.

When the flash dot was located at the hand joint, significant flash-lag effects were observed in most conditions ($ps < 0.01$ except in the upright backward walker condition), indicating a perceived spatial lag of the hand joint in the moving body. A much stronger FL effect was found for the familiar action of forward-walking than for the unfamiliar backward-walking action ($F(1,13) = 39.63$, $p < 0.001$, $\eta_p^2 = 0.75$), consistent with the hypothesis that action familiarity impacts the perceived mislocalization of moving joints. We also found a main effect of body orientation ($F(1,13) = 10.69$, $p = 0.006$, $\eta_p^2 = 0.45$), indicating stronger FL of hand joints in the inverted walker than in the upright walker. This difference was in contrast to the results found for the foot joint. For a forward walking action, the flash lag effect of hand joint for the inverted walker (mean = 0.24 degrees) was larger than for the upright walker (mean = 0.17 degrees), $t(13) = 2.43$, $p = 0.030$. We speculate that multiple factors may contribute to this discrepancy between results for the foot and the hand joint. First, a spatial attention preference may be applied to the closer-to-ground body parts in bipedal action (such as walking, running), which constitute informative cues for a life-detector mechanism based on foot movements (Troje & Westhoff, 2006). When the body orientation is upside-down, the hand joints are placed in relatively lower positions than foot joints. Second, as shown in Fig. 3, the hand motions of the inverted walker produce vertical velocity and acceleration profiles consistent with the foot motions of an upright walker. A previous study by Chang and Troje (2009) showed clear evidence that the joint movement profile of lifting upward then downward serves as a critical cue to signal biological movements and facilitate detection and recognition of actions. Hence, for an inverted walking action, the hand may provide more informative signals specialized to biological movements, resulting in a stronger FL effect for the hand joint in the inverted condition than in the upright condition.

In summary, Experiment 1 demonstrated the presence of a flash-lag effect in biological motion for localizing the moving joints of walking actions, and the dependency of the FL effect on body orientation, action familiarity and specific joints. An alternative way of comparing the flash-lag effects between conditions is to measure the lag effect in units of time, rather than spatial lag as shown in Fig. 2. We converted the FL effect into time units, and found the mean temporal lags for the foot joint were 94 ms for upright-forward condition, 43 ms for inverted-forward, 52 ms for upright-backward foot, and 59 ms for inverted-backward foot. For the hand joint, we found lags of 57 ms, 82 ms, 14 ms and 19 ms for the four corresponding conditions. Overall, the two units of measurement (temporal and spatial) yielded similar results.

3. Experiment 2: Flash-lag effect in the absence of action perception

In Experiment 1, we demonstrated the existence of a FL effect for joint movements in biological motion, and also the impact of body orientation on the misperception of joint positions for familiar walking actions. If these findings indeed signal the involvement of action processing in the flash-lag effect, then the impact of body orientation on FL should disappear if the action is not perceived (e.g., if the movement of reference limb is shown without the other body parts in the display). Experiment 2 aimed to test this hypothesis by presenting the same reference limbs and flash dot as in the previous experiment, but in the absence of other body parts. Hence, we expect that the pattern of FL effects obtained in Experiment 2 will be well-predicted by the temporal averaging model.

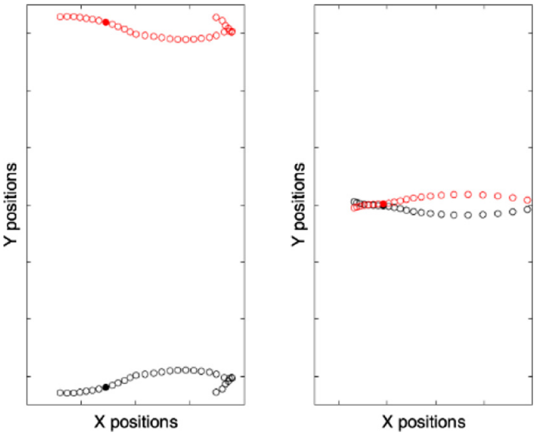

Fig. 3. Illustration of motion trajectories. The two panels depict the movements of foot and hand in the upright (black) and inverted (red) conditions, respectively. The circles indicate positions of each joint when moving from right to left. The solid circles indicate the position of the flash dot in Experiment 1. When the body orientation is inverted, the hand motion shows similar vertical motion profiles (moving upward then downward) as the foot motion in the upright walking condition. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.1. Participants

Twelve undergraduate students (8 females, 4 males, $M_{\text{age}} = 20.9$ years) in the UCLA Psychology Department (who had not participated in Experiment 1) participated in this experiment to receive two class credits. All participants reported normal or corrected-to-normal vision. Data for two participants were removed from the analysis due to poor psychometric curve fitting (i.e., R^2 less than 0.7).

3.2. Stimuli and procedure

The stimuli in Experiment 2 were the same as those in Experiment 1 except that only the two reference limbs were shown in the display without presenting other parts of the body. Specifically, only one lower leg and one lower arm were shown on the screen. Because the other body parts were absent, participants typically perceived the stimuli as two bars moving as pendulums, and were not aware that these movements were derived from human walking actions. Fig. 4 illustrates the stimuli used in the limb-only display. The procedure was identical to that of Experiment 1.

3.3. Results

An FL effect was still observed for the limb-only display, as evidenced by the significant spatial lag perceived by participants in most conditions ($ps < 0.01$ except in upright backward walker

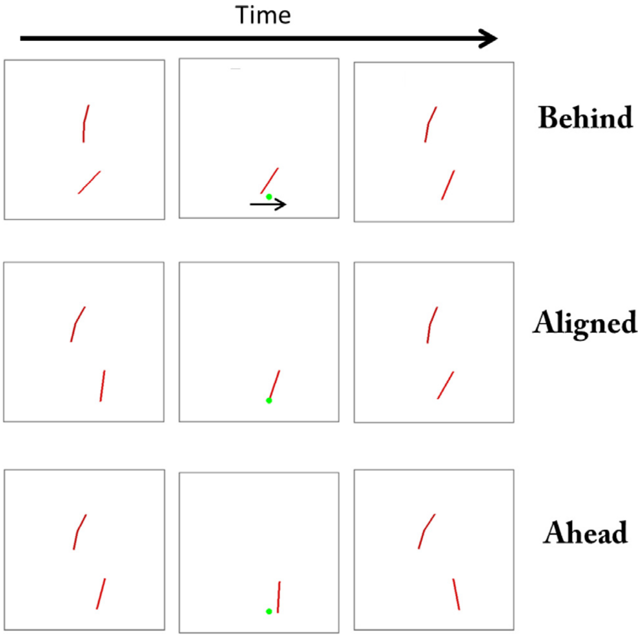

Fig. 4. Illustration of the display used in Experiment 2. The moving reference line was physically behind, aligned with or ahead of the stationary flashed dot. The arrow indicates the general moving direction of the line around the time when the dot was flashed.

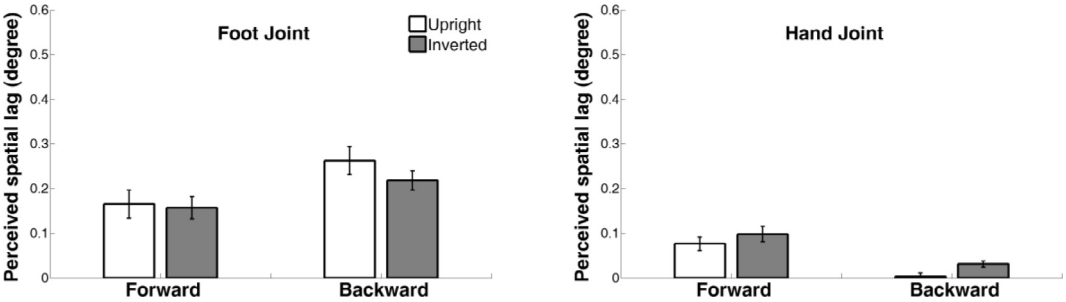

Fig. 5. Results of joint FL effect in Experiment 2. When only relevant limbs were presented, the strength of FL was significantly weakened, and was not influenced by whether the reference limbs were from an upright or inverted walker.

condition) (see Fig. 5). However, there was no significant difference between the upright and inverted body orientations for any action/joint conditions in Experiment 2. Since the limb-only display did not provide sufficient input information to recruit action processes, localization of moving joint were not influenced by the body orientation, as was predicted. A repeated-measures ANOVA revealed a significant main effect of joint ($F(1,9) = 60.45$, $p < 0.001$), showing a greater FL effect for the foot joint than the hand joint. This difference can be explained by the difference of movement speeds between the two joints: foot joints moved such faster than hand joints in the walking action, as predicted by the temporal averaging model (see model section in the later part of the paper).

We did not find a significant three-way interaction between the three factors (i.e., joint, walking direction and body orientation), in contrast to the result observed in Experiment 1. The limb-only display in Experiment 2 showed a significant two-way interaction of joint and walking direction, revealing that the FL strength for foot joint in backward walking was greater than the effect in forward walking, whereas the hand joint showed an opposite pattern ($F(1,9) = 14.75$, $p = 0.004$, $\eta_p^2 = 0.62$). This interaction effect is due to the different motion profile involved in the trajectory for the two conditions, as predicted by the temporal averaging model. In the modeling simulation section, we will provide more detailed discussion of this interaction effect.

We compared the findings of the first two experiments. For the forward walking action, the strength of FL for foot joint in the limb-only display of Experiment 2 (0.17 degrees) was significantly reduced relative to the FL strength when the whole-body action was observed in Experiment 1 (0.28 degrees, $t(22) = 4.49$, $p < 0.01$). When we analyzed the results from Experiments 1 and 2 in a four-way mixed ANOVA using the appearance of body configuration (presence or absence of the body) as a between-subject factor, together with the other three within-subject factors, we found a significant four-way interaction ($F(1,22) = 14.38$, $p = 0.001$, $\eta_p^2 = 0.40$). This result was driven by a significant three-way interaction of body orientation, walking direction and joints in Experiment 1 with the whole-body display, but lack of such an interaction effect in Experiment 2 with the limb-only display. Hence, the limb-only display effectively removed the modulation of body orientation (upright vs. inverted) on localization of a moving joint in action.

4. Experiment 3. Flash-lead effect in walking actions stops at the instant the flash occurs

In the previous two experiments, we found robust flash-lag effects in biological motion, such that a moving joint aligned with a flash was seen as further ahead in the direction of the corresponding limb movement. Although flash-lag effects are commonly observed in many different situations involving moving objects, the effect can be abolished or even reversed in some conditions. For example, if the moving object stops motion at the time of the flash, the flash-lag effect is not observed; instead the flash and moving object are perceived to be aligned (Eagleman & Sejnowski, 2000; Kanai, Sheth, & Shimojo, 2004; Nijhawan, 2001). In some cases, an opposite effect, flash-*lead*, is observed such that perceived position of the moving object at its termination undershoots its physical position (Krekelberg & Lappe, 2000; Maus & Nijhawan, 2009; Patel, Ogmen, Bedell, & Sampath, 2000; Roulston, Self, & Zeki, 2006). Experiment 3 was designed to test the flash-termination conditions to examine whether action representation still interacts with localization processing of moving joints when human actions terminate at the instant the flash occurs.

4.1. Participants

Thirteen undergraduate students (7 females, $M_{age} = 20.9$ years) in the Psychology Department at UCLA participated in this experiment. Participants reported normal or corrected-to-normal vision, and received one class credit for the 1-h session required for the study.

4.2. Stimuli

The stimuli were the same as the forward walking session Experiment 1, except that the walking stimuli disappeared right after the dot flashed on the screen, as shown in Fig. 6. Experiment 3 did not include the backward walking conditions because we did not find evidence that body orientation impacts the FL in the unfamiliar backward walking condition. Note that some flash-termination stimuli in previous studies (e.g. Eagleman & Sejnowski, 2000) differed from the stimulus manipulation in Experiment 3 in which the moving limbs disappeared at the end of its movement, rather than stopping. Participants were asked to judge whether the flash dot was located on the left or right side of the reference limb.

4.3. Results

Fig. 7 shows the negative values for perceived spatial lag. The negative values indicate a flash-lead effect in which the moving joint is perceived to lag behind the stationary flashed dot even when they were physically aligned. This result is consistent with previous findings that participants misperceive the final position of a moving limb prior to its disappearance in the direction opposite to its motion trajectory (Maus & Nijhawan, 2009; Roulston et al., 2006). A repeated-measures ANOVA revealed only one significant effect, the main effect of joint ($F(1,12) = 5.95$, $p = 0.031$, $\eta_p^2 = 0.33$), indicating a larger flash-lead effect for the foot than the hand joint. This difference is likely due to the different movement speeds of the two joints, consistent with the previous finding of a speed dependency for the strength of the flash-lead effect (Roulston et al., 2006).

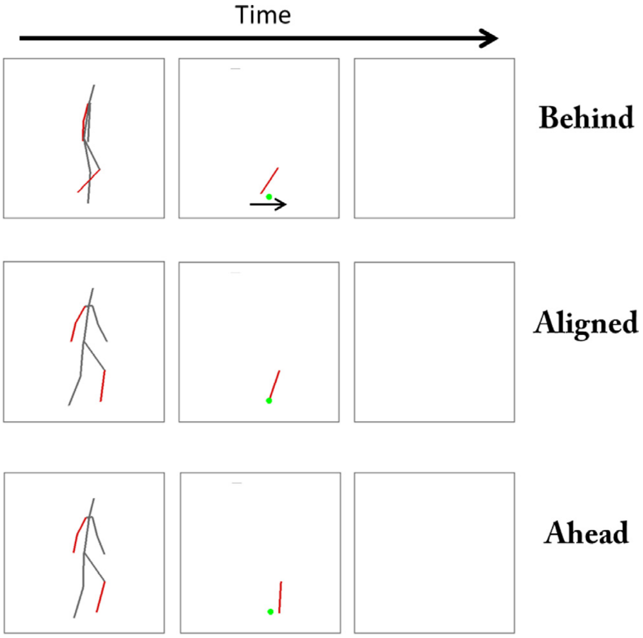

Fig. 6. Illustration of the display used in Experiment 3. The flash dot appeared at the same spatial location but at different time points across all conditions. When the dot flashed, the moving reference limb was either physically behind, aligned with or ahead of the stationary flashed dot in three conditions. The arrow indicates the general moving direction of the line around the time when flashing the dot. The walker disappeared right after the dot flashed.

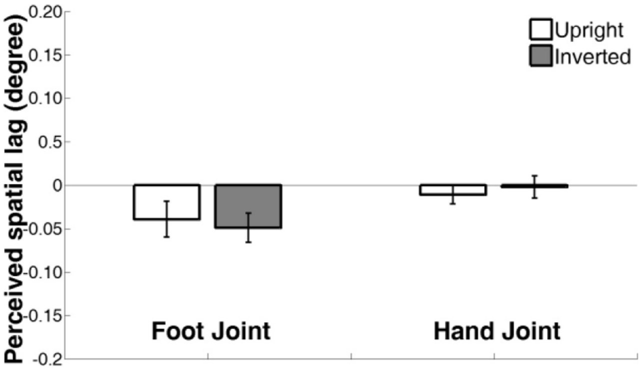

Fig. 7. Results of Experiment 3: perceived spatial offsets in the flash-termination display with forward walking. The negative values of perceived spatial lag indicate that the moving joint was perceived to lag behind the stationary flashed dot even when they were physically aligned.

Importantly, Experiment 3 did not reveal any difference in the flash-lead effect between upright and inverted walkers. This result contrasts with the finding in Experiment 1 where the flash-lag effect depended on body orientation in the forward walking condition. A mixed ANOVA comparing the two experiments for the forward-walking conditions confirmed this difference. This analysis yielded a significant three-way interaction between the two experiments, joints and body orientations ($F(1,25) = 15.81$, $p = 0.001$, $\eta_p^2 = 0.39$). The significant three-way interaction was mainly driven by the lack of any impact of body orientation on localization of moving joints in the flash-termination display of Experiment 3, in contrast to the strong influence of body orientation on the flash-lag effect in Experiment 1 when the moving stimuli continued to be displayed after the flash. The finding implies that the interaction between action representation and location perception of moving joints likely takes place at or after the flash event by integrating the post-flash spatial information with the moving stimuli.

5. Experiment 4. Flash-lag effect in jumping-jack actions

Experiment 4 employed the jumping-jack action to further examine whether the flash-lag effect of moving joints occurs for other biological movements, and whether the impact of body-orientation on the FL is present in other actions less familiar to humans than walking.

5.1. Participants

Twenty-one undergraduate students (15 females, $M_{age} = 20.8$ years) in the Psychology Department at UCLA participated in this experiment for course credit.

5.2. Stimuli and procedure

The stimuli used a jumping-jack action from the CMU motion capture database, as illustrated in Fig. 8. The stimulus parameters were the same as the walker stimulus in Experiment 1, except for the following changes. The jumping jack action lasted for 3.3 s (200 frames), showing jumping up twice in a row. The flash dot was briefly presented for 33.3 ms. The location of the flash dot was determined by the reference joint (a left or right hand joint) in frame 155, in which the lower arm reached a horizontal position. The temporal offsets between the flash dot and the jumper varied in a range of −100 to +100 ms with a step size of 33.3 ms (i.e., 2 frames), resulting in seven levels of temporal offsets. Participants were asked to judge whether the flash dot was located above or below the reference limb. Other aspects of the experimental setup and procedure were the same as in Experiment 1.

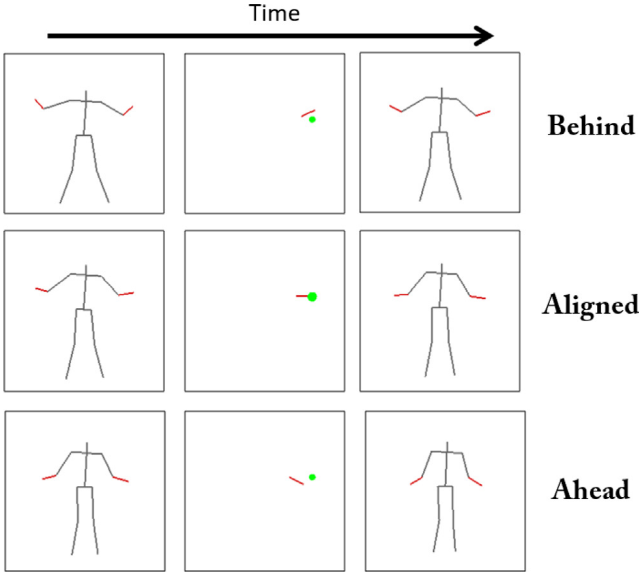

Fig. 8. Stimulus illustration for Experiment 4. The moving limb (left arm in this example) was physically behind, aligned with and ahead of the stationary flashed dot. The location of the flash dot was determined by the reference joint, either the left or the right hand joint. The flash dot always appeared at the same physical location across all the conditions but at different time points.

5.3. Results

An FL effect was observed for the jumping-jack action for both upright and inverted conditions, as evidenced by the significant spatial lag perceived by participants (mean ± standard deviation, upright: -0.074 ± 0.042; inverted: -0.081 ± 0.047, $p < 0.001$). However, there was no significant difference between the upright and inverted body orientations for jumping-jack actions ($p = 0.80$). These findings suggest that the flash-lag effect is found in biological motion for localizing moving joints, but the modulation of body orientation on the effect size depends on the familiarity to the action. Numerous studies have shown enhanced success in action prediction for commonly-performed actions with rich motoric experience (Aglioti, Cesari, Romani, & Urgesi, 2008; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). These findings are consistent with our experimental finding that body orientation in the visual stimuli impacts the localization of moving joints in familiar walking actions, but not in the jumping-jack action, which is rarely performed in daily life and may entail large individual differences in kinematic movements (e.g., some people jump higher and faster than others, and with different rhythms).

6. Model simulation results using the temporal averaging model

Based on the four experiments reported in the present paper, we found that the magnitude of FL effects depended on body orientation of the observed actions (upright vs. inverted actors), familiarity of the actions (forward vs. backward walkers, walking vs. jumping-jack), and joints (foot vs. hand joints). Among these three factors that were manipulated, motion trajectories were well-matched between the upright and inverted conditions, as inversion of body orientation maintains local motion signals (e.g., velocity, acceleration). Hence, the difference between upright and inverted forward walking provides strong evidence supporting the involvement of action representation on the localization of moving joints in the body.

However, for the other two factors (familiarity and joints), each condition revealed its own specific dynamics in motion trajectories. For example, hand and foot joints moved at different speeds, and the movements before and after the flash differed between the forward and backward walking conditions. To quantify how low-level motion signals influence the strength of the FL effect across a range of conditions, we employed the well-established temporal averaging model (Krekelberg & Lappe, 2000) to estimate the misperceived location of moving joints based solely on their individual motion trajectory around the time of the flash. The temporal averaging model (Krekelberg & Lappe, 2000) processes motion input with a slow temporal filter and two spatial filters to compute local motion energy, and predicts the perceived position of a moving target to be the location corresponding to the maximum motion energy. To account for the FL effect, the original temporal-averaging model calculates the temporal average of the position difference between the moving object and the stationary location of the flash over a time window of 500 ms.

We will first show that the temporal averaging model can qualitatively account for the flash-lag effect in some conditions (e.g., inverted condition in Experiment 1 and results in Experiment 2), but fails to predict the impact of body orientation on the FL effect in Experiment 1. We will then examine the influence of the possible duration of the temporal window used for integrating spatial information for moving segments, and compare the present findings to those of previous studies using different stimuli and methodology. Finally, we will modify the temporal averaging model to account for the flash-lead effect observed in Experiment 3.

To adapt the model for the walking stimuli used in the present study, two modifications were made. First, the spatial filters only analyzed horizontal movements from an input stimuli consisting of either hand or foot movements. Since participants' task was to judge whether the moving limb was on the right or left side of the flash dot, only perceived horizontal positions were relevant to the task. Accordingly, an analysis based on 1D horizontal movements would produce the same decision as a model based on 2D spatial-temporal filters. Second, the dot was flashed around 3/4 of the duration of the second step in a walking cycle lasting 1 s. The interval from the flash onset to the end of the motion stimuli was less than 500 ms (the temporal window size used in the original temporal averaging model). Our simulations used a temporal averaging window determined by the time interval between the flash onset and the end of the walking sequence. In our setup, the maximum integration duration was 238 ms (in the condition with temporal offset of −100 ms).

The simulation results from the temporal averaging model for Experiment 1 are depicted in Fig. 9. The model provides estimates of the perceived spatial displacement between the moving joint and the dot flashed at any time point during the walking stimulus. The FL effect was measured as the displacement at which the model decided the flash was in alignment with reference limb. Since the perceived spatial displacement followed a linear relation as a function of the physical spatial distance between the moving joint and the flash (linear fit $R^2 > 0.99$), a linear regression was used to estimate the FL effect. As shown in Fig. 9, the model predicts that the FL effect will not vary in magnitude when body orientation is changed from upright to inverted walking. This prediction implies that the general mechanism underlying the FL effect solely relies

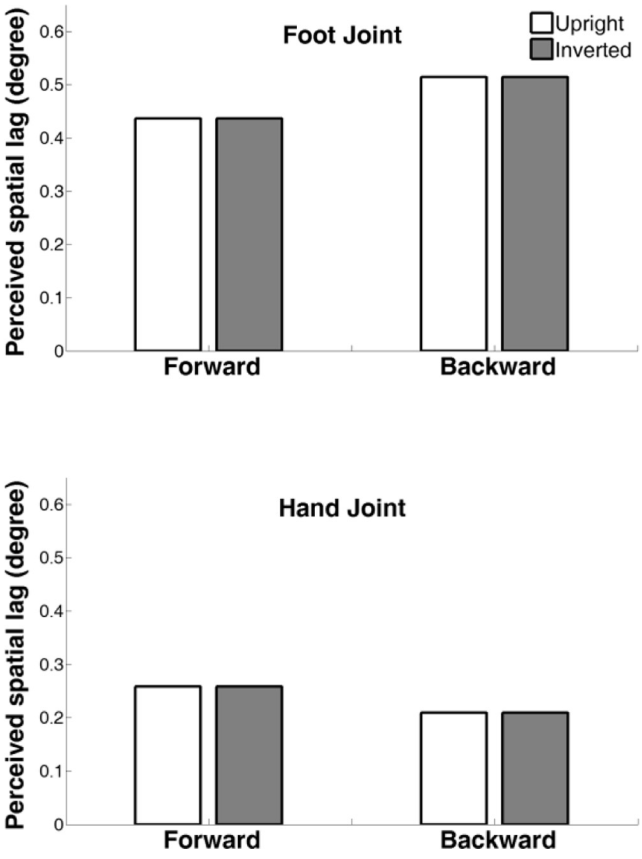

Fig. 9. Temporal averaging model predicts the flash-lag effect for foot and hand joints for Experiment 1. The flash-lag effect is predicted to remain the same when the walking sequence is inverted, but to vary as a function of walking direction (forward vs. backward).

on local joint motion trajectories, and does not interact with action representations.

We also used the model simulation as a means to examine the possible duration of the temporal window used for integrating spatial information in the present study. Since the limb-only display of Experiment 2 did not elicit any involvement of action processing in the localization of joints, the strength of the flash-lag effect measured is informative for estimating the time window for integrating perceived positions after the flash. We considered the integration window as a free parameter in the temporal averaging model of Krekelberg and Lappe (2000), and searched for the best-fitting parameter to account for human performance across all the four upright conditions (foot forward, foot backward, hand forward, hand backward) in Experiment 2. We found that a temporal integration window of 115 ms after the flash yielded the best model predictions (0.16, 0.21, 0.10, 0.07) for the four conditions to fit the average performance of humans, (0.16, 0.24, 0.08, 0.02, respectively). The root mean square deviation (RMSD) between model prediction and human performance was 0.001, and the correlation was 0.99. Overall, human results for Experiment 2 can be well-explained by a generic mechanism model based on temporal averaging. These results further confirm that when whole-body movements were absent in the display, participants fell back on the default of using generic motion mechanisms to perceive the location of a moving segment.

Note that the best-fitted estimate of the temporal window in fitting results of Experiment 2 was much shorter than the temporal integration window of 500 ms proposed in the original study of Krekelberg and Lappe (2000). This difference can be explained by multiple factors. First, movements of joints in human actions involve accelerations and oscillated movements, which may evoke a different temporal integration window than does motion with constant velocity, as used in most previous studies. Second, in our stimulus the time of showing the flash was close to the end of the motion sequence, followed by a rapid disappearance of the stimulus, which may have led to a shortened integration window given the limited input of dynamic information. The best-fitting temporal window (115 ms) in our study is in agreement with the temporal window derived in some previous studies. For example, a study using rotation stimuli derived a temporal range of 80–100 ms underlying the observed flash-lag effect (Eagleman & Sejnowski, 2000). Furthermore, in a recent study using transcranial magnetic stimulation (TMS), the researchers used translation stimuli to show that the maximum effect for TMS pulses in reducing the flash-lag effect occurs 200 ms after the flash (Maus, Ward, Nijhawan, & Whitney, 2013). This estimate is consistent with the value obtained in our simulation results.

Finally, to account for the flash-lead effect revealed in Experiment 3, we introduced a small modification of the temporal averaging model. Perceived location of a movement joint in the flash-termination display can be calculated by disabling the last stage in the temporal averaging model. When the action stimuli suddenly disappear, a strong retinal transient signal could be elicited to possibly suppress the integration stage. In other words, the perceived positions could be directly derived at the time point when the flash occurred with the predicted spatial lag of −0.16, −0.11, −0.03, −0.06, respectively, for the foot-forward, foot-backward, hand-forward and hand-backward conditions. These predictions are qualitatively consistent with human performance.

7. General discussion

The results of the present study provided evidence that people misjudge the locations of joints in a moving body. Action representations interact with generic motion mechanisms underlying position processing of dynamic stimuli to evoke the misperception of joint location in a moving body. First, we found robust flash-lag effects for localizing joints in a walking action and a jumping-jack action, supporting the hypothesis that mislocalization of spatial positions of moving objects in dynamic stimuli results from a primitive operation of the visual system. Based on simulation results from the temporal averaging model obtained by sampling positions in a temporal window, we showed that the model can explain some findings in FL effect in biological motion, such as the presence and absence of a flash-lag effect, as well as changes in the size of the effect across different joints (basically due the faster movements in foot joints than hand joints).

However, this generic motion mechanism of sampling positions in a temporal window cannot account for the key finding in the present study: the magnitude of the FL was influenced substantially by the characteristics of the action in familiar actions. As shown in Experiment 1, observing a walker with a natural body orientation (i.e., upright) yielded a significantly stronger FL effect for the critical foot joint than did viewing an inverted walker. This difference cannot be attributed to general motion extrapolation based on low-level motion cues (e.g., velocity, direction, or acceleration) or temporal averaging mechanisms of perceived position signals, since the characteristics of foot movement trajectories in the upright and inverted conditions were well matched. In addition, foot and hand joints produced different magnitudes of FL. Specifically, observing a walker with a natural body orientation (i.e., upright) yielded a significantly stronger flash-lag effect for the critical joint (i.e., foot in the walking action) than did viewing an inverted walker. In contrast, the hand joint showed a weaker flash-lag effect in the upright walker than the inverted walker. These findings suggest that the precision of the perceived location may vary across different joints in a moving body. The difference in FL effects for upright and inverted walkers disappeared when the actor performed backward walking and jumping-jack actions—unfamiliar actions involving body movements that are unusual in everyday life. Hence, body part such as critical joints and action characteristics such as familiarity modulate the impact of body orientation on the strength of FL to influence the perceived location of joints in body movement.

Experiment 2 showed that the impact of body orientation on the FL results from an interaction between action representation and the processing required to determine the instantaneous position of a continuously moving object. When body parts were absent and only a moving line segment of a reference limb was shown in the display, the flash-lag effect was still observed, but the impact of body orientation on the FL disappeared.

Experiment 3 showed a flash-lead effect, a different type of mislocalization of moving joints, in which the perceived position of the moving joint at its termination undershoots its physical position. However, the flash-lead effect obtained in Experiment 3 with the flash-termination display did not show an impact of body orientation on the misperceived location of moving joints in biological motion. In comparison with the main finding in Experiment 1, the lack of an influence of body orientation on the flash-lead effect in Experiment 3 implies that the interaction between action representation and generic mechanisms for determining the perceived position of a moving joint likely takes place *after* the occurrence of the flash event.

There are apparent functional benefits of perceiving the location of joints in a moving body biased towards the direction of future motion, as revealed by the flash-lag effect in actions reported in the present paper. When a friend walks towards you to shake hands, it is better to overshoot you position estimation so that you put your hand in a future possible location to intersect with his hand movements, rather than underestimating the moving hand position so that you miss his hand altogether. Moreover, our finding that action processing interacts with motion mechanisms for localizing a moving joint are consistent with previous research using relatively simple movement patterns, which suggests an interaction between localization of a moving object and the motion configuration of the object (Kohler, Cavanagh, & Tse, 2015; Whitney & Cavanagh, 2000). For example, Whitney and Cavanagh (2000) showed that the configuration of motion in the visual input impacts the perceived locations of both moving and stationary stimuli, even when the motion patterns are at a substantial distance from the stimuli.

The finding that action representations modulate the localization of moving joints also agrees with findings from a study by Kessler et al. (2010), which showed that first-person perspective and sense of agency can modulate the magnitude of the FL to bias the perceived hand positions in arm movements. Interactions between higher-level processing (i.e., action) and lower-level processing (i.e., localization of a moving element) have also been found between the visual and the sensorimotor system, as active control of the moving stimulus by the participants can impact the magnitude of the flash-lag effect (Ichikawa & Masakura, 2006; Ichikawa & Masakura, 2010; Nijhawan & Kirschfeld, 2003; Scocchia, Grosso, de'Sperati, Stucchi, & Baud-Bovy, 2009). The cross-level interations have also been found in other perceptual effects in biological motion, such as the top-down influence of action representation on depth perception (Lu, Tjan, & Liu, 2006), and multilevel adaptation in biological motion (van Boxtel & Lu, 2013a,b; van Boxtel, Dapretto, & Lu, 2016).

The simulation results reported in the present paper are based on the well-known temporal averaging model developed by Lappe and Krekelberg (1998). This model assumes that the perceived position of a moving target can be derived from motion processing (i.e., the location corresponding to the maximum motion energy). In order to read out the instantaneous position of a moving object at a time point, the perceived position signals are integrated within a temporal window. Such computation to extract position information from motion seems reasonable when we deal with more complex motion stimuli. For human actions involving a dozen moving elements, it would be costly to encode the positions of all the joints at each time frame, since most tasks in action recognition may not involve judgments regarding specific joint positions. However, when a task requires localizing moving joint(s), sampling perceived position information within a temporal window can be performed.

How does action representation interact with the generic mechanisms underlying localization of moving objects? There are several possible ways to extend the computational subcomponents involved in sampling position information within a temporal window. As shown in Fig. 9 (left), one possibility is that the perceived positions that feed into the temporal integration stage are based on *predicted* body movements derived by action simulation processing. Previous research using a priming and representation-momentum paradigm revealed that observers automatically anticipate the future posture of observed actors (Jarraya, Amorim, & Bardy, 2005; Kourtzi & Shiffrar, 1999; Thornton & Hayes, 2004; Verfaillie & Daems, 2002). Recent studies have shown that the visual system is able to predict future postures almost in real-time, supporting the hypothesis that a simulation process operates to enable the prediction of future actions (Graf et al., 2007; Manera, Schouten, Verfaillie, & Becchio, 2013; Sparenberg, Springer, & Prinz, 2012; Springer & Prinz, 2010).

If action prediction takes place for familiar and natural body movements (such as foot movements in an upright action), we would expect that this extension to the future could effectively elicit more spatial extrapolation of the perceived positions in the upright condition (as shown in the red dashed line in Fig. 10, left plot), than in the inverted condition (as shown in the red dotted line in Fig. 10, left plot). Action processing employs prediction-by-simulation mechanisms to extrapolate body movements towards the future in the upright condition, yielding a strong FL effect in Experiment 1. Weaker prediction results in less spatial extrapolation in the inverted condition, leading to a reduced FL effect. Similarly, in Experiment 2, the lack of action prediction in the limb-only condition may have led to the reduced FL effect.

One could argue that the results of our Experiment 3, showing a flash-lead effect in the flash-termination condition, provide evidence against this mechanism. However, the sudden disappearance of action stimuli may send a strong signal to terminate the process of motion extrapolation, as suggested by the results of several previous studies (Maus & Nijhawan, 2008, 2009; Nijhawan, 2008). The visual system may stop the process of prediction-by-simulation because the probability of interacting with this person is very low. Though some lingering extrapolated actions after the

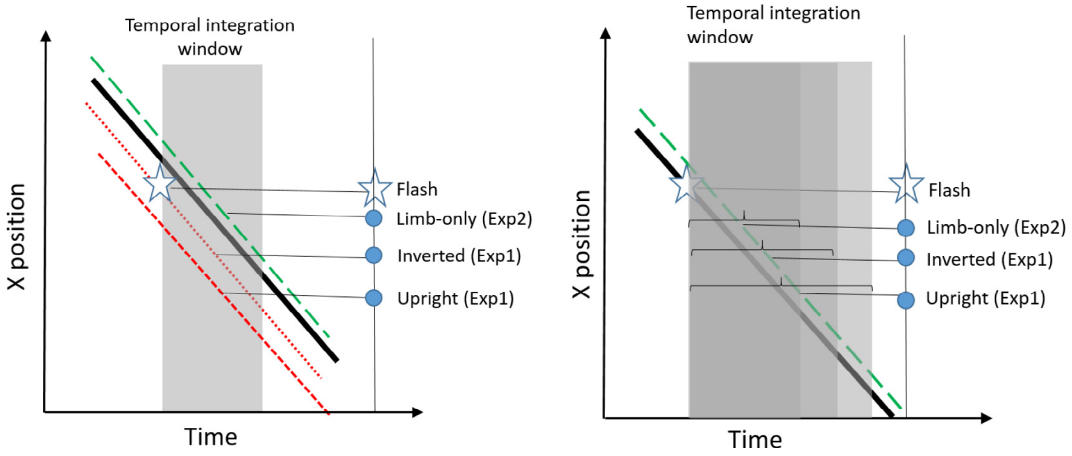

Fig. 10. Illustrations of two possible mechanisms underlying the interaction between action processing and localization of a moving joint. The black line indicated the positions of the moving joint (Y axis) as the function of time (X axis). The star indicates the location and the time for the flash. Left, action processing employs prediction-by-simulation mechanisms to extrapolate body movements towards the future in the upright condition to yield a strong FL effect in Experiment 1 (shown as the red dashed line). Weaker prediction results in less spatial extrapolation in the inverted condition (shown as the red dotted line), reducing the FL effect. Similarly, the lack of action prediction in the limb-only condition in Experiment 2 results in the delayed position encoding of the moving limbs (shown as the green line), which leads to the reduced FL effect in Experiment 2. Right, action processing may vary the subjective time duration for biological movements, which yield a longer integration window for natural and familiar actions (such as the upright condition) than for other conditions in the experiments. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

termination signal may need time to take place, the integrated position signals within the temporal averaging window would likely be more biased towards the past.

An alternative mechanism by which action processing could interact with localization processing might involve varying the temporal integration window in different conditions, as shown in Fig. 10, right plot. If the observed body movements are natural (e.g., with upright rather than inverted body orientation) and familiar, a larger temporal window may be used for temporally averaging perceived location signals, relative to unfamiliar and unnatural actions. As shown in Fig. 10, right plot, the dependency of foot-joint FL effect on body orientation (upright vs. inverted) in Experiment 1 can be explained by a longer temporal integration window imposed for the upright forward walker than for the inverted walker conditions. Why would a larger temporal window be employed for familiar actions with upright body orientation? Wang and Jiang (2012) found that an upright walking sequence was subjectively perceived as longer than an inverted walker, and the same temporal dilation effect was found even when participants viewed movements of only one joint (e.g., foot) without awareness of the walking action. The lengthened temporal duration in the upright walking action may increase the integration window size in subjective time. as proposed in a computational account offered by Rao, Eagleman, and Sejnowski (2001).

The flash-lag effect affords a window to study the interactions between high-level representation of human movements and low-level motion and position processing. More studies are needed to further pin down the interaction between action processing and different mechanisms for perceiving the locations of moving joints and the body. Predicting the location of bodily movements may occur at different time scales, from a fraction of a second for predicting simple movements, to minutes or even hours for understanding dynamic and social events. In the present paper, we examined the mechanisms underlying perception of the location of a moving body in the immediate future (i.e., in the order of a fraction of a second). This type of real-time prediction may be closely connected with the unconscious and automatic tendency to imitate others' behavior (Chartrand & Bargh, 1999; Thurman, van Boxtel, Monti, Chiang, & Lu, 2016; Wilson & Knoblich, 2005), likely by recruiting the mirror neuron system to predict immediate future actions (Dipellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). To predict actions over a longer time scale, action prediction mechanisms may need to connect with the mentalization system (Frantz & Janoff-Bulman, 2000; Malle & Pearce, 2001; Marsh et al., 2010; Su, van Boxtel, & Lu, 2016) to allow inferences based on the goals and intentions of an actor. Future work will be needed to investigate the commonalities and differences among mechanisms involved in predicting actions over a range of time scales and in more complex social environment (e.g., interactions among multiple actors).

Acknowledgments

This research was supported by NSF grant BCS-1353391 to HL. We thank Jiahui He, Yuanyuan Zu, Andy Huang, Tianyi Zhu, Ji Hye Kim, and Brenda Vasquez for help in running participants in the experiment. We also thank anonymous reviewers for constructive and insightful suggestions.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2017.06.010.

References

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience, 11*(9), 1109–1116.

Baldo, M. V. C., & Klein, S. A. (1995). Extrapolation or Attention Shift. *Nature, 378* (6557), 565–566.

Boxtel, J. J. A., & Lu, H. (2015). Joints and their relations as critical features in action discrimination: Evidence from a classification image method. *Journal of Vision, 15*(1), 15.1.20. http://dx.doi.org/10.1167/15.1.20.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*(4), 433–436.

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16*(19), 1905–1910.

Chang, D. H. F., & Troje, N. F. (2009). Acceleration carries the local inversion effect in biological motion perception. *Journal of Vision, 9*(1).

Chartrand, T. L., & Bargh, J. A. (1999). The Chameleon effect: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology, 76*(6), 893–910. http://dx.doi.org/10.1037//0022-3514.76.6.893.

Dipellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding Motor Events – A Neurophysiological Study. *Experimental Brain Research, 91*(1), 176–180.

Eagleman, D. M., & Sejnowski, T. J. (2000). Motion integration and postdiction in visual awareness. *Science, 287*(5460), 2036–2038.

Frantz, C. M., & Janoff-Bulman, R. (2000). Considering both sides: The limits of perspective taking. *Basic and Applied Social Psychology, 22*(1), 31–42. http://dx.doi.org/10.1207/S15324834basp2201_4.

Graf, M., Reitzner, B., Corves, C., Casile, A., Giese, M., & Prinz, W. (2007). Predicting point-light actions in real-time. *Neuroimage, 36*, T22–T32.

Ichikawa, M., & Masakura, Y. (2006). Manual control of the visual stimulus reduces the flash-lag effect. *Vision Research, 46*(14), 2192–2203. http://dx.doi.org/10.1016/j.visres.2005.12.021.

Ichikawa, M., & Masakura, Y. (2010). Reduction of the flash-lag effect in terms of active observation. *Attention, Perception, & Psychophysics, 72*(4), 1032–1044. http://dx.doi.org/10.3758/APP.72.4.1032.

Jarraya, M., Amorim, M. A., & Bardy, B. G. (2005). Optical flow and viewpoint change modulate the perception and memorization of complex motion. *Perception & Psychophysics, 67*(6), 951–961. http://dx.doi.org/10.3758/Bf03193622.

Kanai, R., Sheth, B. R., & Shimojo, S. (2004). Stopping the motion and sleuthing the flash-lag effect: Spatial uncertainty is the key to perceptual mislocalization. *Vision Research, 44*(22), 2605–2619.

Kessler, K., Gordon, L., Cessford, K., & Lages, M. (2010). Characteristics of motor resonance predict the pattern of flash-lag effects for biological motion. *PLoS ONE, 5*(1), e8258. http://dx.doi.org/10.1371/journal.pone.0008258.

Kohler, P. J., Cavanagh, P., & Tse, P. U. (2015). Motion-induced position shifts are influenced by global motion, but dominated by component motion. *Vision Research, 110*, 93–99.

Kourtzi, Z., & Shiffrar, M. (1999). Dynamic representations of human body movement. *Perception, 28*(1), 49–62.

Krekelberg, B., & Lappe, M. (2000). A model of the perceived relative positions of moving objects based upon a slow averaging process. *Vision Research, 40*(2), 201–215.

Lappe, M., & Krekelberg, B. (1998). The position of moving objects. *Perception, 27* (12), 1437–1449.

Lu, H. (2010). Structural processing in biological motion perception. *Journal of Vision, 10*(12), 13. http://dx.doi.org/10.1167/10.12.13.

Lu, H., Tjan, B. S., & Liu, Z. (2006). Shape recognition alters sensitivity in stereoscopic depth discrimination. *Journal of Vision, 6*(1), 7.

Mackay, D. M. (1958). Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature, 181*(4607), 507–508.

Malle, B. F., & Pearce, G. E. (2001). Attention to behavioral events during interaction: Two actor-observer gaps and three attempts to close them. *Journal of Personality and Social Psychology, 81*(2), 278–294. http://dx.doi.org/10.1037//0022-3514.81.2.278.

Manera, V., Schouten, B., Verfaillie, K., & Becchio, C. (2013). Time will show: Real time predictions during interpersonal action perception. *PLoS ONE, 8*(1).

Marsh, A. A., Kozak, M. N., Wegner, D. M., Reid, M. E., Yu, H. H., & Blair, R. J. R. (2010). The neural substrates of action identification. *Social Cognitive and Affective Neuroscience, 5*(4), 392–403. http://dx.doi.org/10.1093/scan/nsq004.

Maus, G. W., & Nijhawan, R. (2008). Motion extrapolation into the blind spot. *Psychological Science, 19*(11), 1087–1091.

Maus, G. W., & Nijhawan, R. (2009). Going, going, gone: Localizing abrupt offsets of moving objects. *Journal of Experimental Psychology: Human Perception and Performance, 35*(3), 611–626. http://dx.doi.org/10.1037/a0012317.

Maus, G. W., Ward, J., Nijhawan, R., & Whitney, D. (2013). The perceived position of moving objects: Transcranial magnetic stimulation of area MT+ reduces the flash-lag effect. *Cerebral Cortex, 23*(1), 241–247. http://dx.doi.org/10.1093/cercor/bhs021.

Nijhawan, R. (1994). Motion extrapolation in catching. *Nature, 370*(6487), 256–257.

Nijhawan, R. (2001). The flash-lag phenomenon: Object motion and eye movements. *Perception, 30*(3), 263–282.

Nijhawan, R. (2008). Visual prediction: Psychophysics and neurophysiology of compensation for time delays. *Behavioral and Brain Sciences, 31*(02), 179–198.

Nijhawan, R., & Kirschfeld, K. (2003). Analogous mechanisms compensate for neural delays in the sensory and the motor pathways: Evidence from motor flash-lag. *Current Biology, 13*(9), 749–753.

Patel, S. S., Ogmen, H., Bedell, H. E., & Sampath, V. (2000). Flash-lag effect: Differential latency, not postdiction. *Science, 290*(5494), 1051.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Purushothaman, G., Patel, S. S., Bedell, H. E., & Ogmen, H. (1998). Moving ahead through differential visual latency. *Nature, 396*(6710), 424.

Rao, R. P., Eagleman, D. M., & Sejnowski, T. J. (2001). Optimal smoothing in visual motion perception. *Neural Computation, 13*(6), 1243–1253.

Roulston, B. W., Self, M. W., & Zeki, S. (2006). Perceptual compression of space through position integration. *Proceedings. Biological Sciences, 273*(1600), 2507–2512. http://dx.doi.org/10.1098/rspb.2006.3616.

Scocchia, L., Grosso, R. A., de'Sperati, C., Stucchi, N., & Baud-Bovy, G. (2009). Observer's control of the moving stimulus increases the flash-lag effect. *Vision Research, 49*(19), 2363–2370. http://dx.doi.org/10.1016/j.visres.2009.06.023.

Sparenberg, P., Springer, A., & Prinz, W. (2012). Predicting others' actions: Evidence for a constant time delay in action simulation. *Psychological Research-Psychologische Forschung, 76*(1), 41–49. http://dx.doi.org/10.1007/s00426-011-0321-z.

Springer, A., & Prinz, W. (2010). Action semantics modulate action prediction. *Quarterly Journal of Experimental Psychology, 63*(11), 2141–2158.

Su, J., van Boxtel, J. J., & Lu, H. (2016). Social interactions receive priority to conscious perception. *PLoS ONE, 11*(8), e0160468. http://dx.doi.org/10.1371/journal.pone.0160468.

Sumi, S. (1984). Upside-down presentation of the Johansson moving light-spot pattern. *Perception, 13*(3), 283–286.

Thornton, I. M., & Hayes, A. E. (2004). Anticipating action in complex scenes. *Visual Cognition, 11*(2–3), 341–370. http://dx.doi.org/10.1080/13506280344000374.

Thurman, S. M., & Lu, H. (2013a). Complex interactions between spatial, orientation, and motion cues for biological motion perception across visual space. *Journal of Vision, 13*(2), 8. http://dx.doi.org/10.1167/13.2.8.

Thurman, S. M., & Lu, H. (2013b). Physical and biological constraints govern perceived animacy of scrambled human forms. *Psychological Science, 24*(7), 1133–1141. http://dx.doi.org/10.1177/0956797612467212.

Thurman, S. M., & Lu, H. (2014). Perception of social interactions for spatially scrambled biological motion. *PLoS ONE, 9*(11), e112539. http://dx.doi.org/10.1371/journal.pone.0112539.

Thurman, S. M., van Boxtel, J. J., Monti, M. M., Chiang, J. N., & Lu, H. (2016). Neural adaptation in pSTS correlates with perceptual aftereffects to biological motion and with autistic traits. *Neuroimage, 136*, 149–161. http://dx.doi.org/10.1016/j.neuroimage.2016.05.015.

Troje, N. F., & Westhoff, C. (2006). The inversion effect in biological motion perception: Evidence for a "life detector"? *Current Biology, 16*(8), 821–824.

van Boxtel, J. J., Dapretto, M., & Lu, H. (2016). Intact recognition, but attenuated adaptation, for biological motion in youth with autism spectrum disorder. *Autism Research*.

van Boxtel, J. J., & Lu, H. (2011). Visual search by action category. *Journal of Vision, 11*(7). http://dx.doi.org/10.1167/11.7.19.

van Boxtel, J. J. A., & Lu, H. (2012). Signature movements lead to efficient search for threatening actions. *PLoS ONE, 7*(5).

van Boxtel, J. J., & Lu, H. (2013a). Impaired global, and compensatory local, biological motion processing in people with high levels of autistic traits. *Frontiers in Psychology, 4*, 209.

van Boxtel, J. J. A., & Lu, H. (2013b). A biological motion toolbox for reading, displaying, and manipulating motion capture data in research settings. *Journal of Vision, 13*(12).

Verfaillie, K., & Daems, A. (2002). Representing and anticipating human actions in vision. *Visual Cognition, 9*(1–2), 217–232. http://dx.doi.org/10.1080/13506280143000403.

Wang, L., & Jiang, Y. (2012). Life motion signals lengthen perceived temporal duration. *Proceedings of the National Academy of Sciences of the United States of America, 109*(11), E673–677. http://dx.doi.org/10.1073/pnas.1115515109.

Whitney, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Sciences, 6*(5), 211–216. http://dx.doi.org/10.1016/S1364-6613(02)01887-9.

Whitney, D., & Cavanagh, P. (2000). Motion distorts visual space: Shifting the perceived position of remote stationary objects. *Nature Neuroscience, 3*(9), 954–959.

Whitney, D., Murakami, I., & Cavanagh, P. (2000). Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli. *Vision Research, 40*(2), 137–149.

Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin, 131*(3), 460–473. http://dx.doi.org/10.1037/0033-2909.131.3.460.