



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



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## 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.

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## 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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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,  $M_{\text{age}} = 19.4$  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

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