

ARTICLE

Life motion signals bias the perception of apparent motion direction

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Funding information

the STI2030-Major Projects, Grant/Award Number: 2021ZD0203800 and 2022ZD0205100; the National Natural Science Foundation of China, Grant/Award Number: 31830037; the Science Foundation of Institute of Psychology, Chinese Academy of Sciences; the Fundamental Research Funds for the Central Universities

Abstract

Walking direction conveyed by biological motion (BM) cues, which humans are highly sensitive to since birth, can elicit involuntary shifts of attention to enhance the detection of static targets. Here, we demonstrated that such intrinsic sensitivity to walking direction could also modulate the direction perception of simultaneously presented dynamic stimuli. We showed that the perceived direction of apparent motion was biased towards the walking direction even though observers had been informed in advance that the walking direction of BM did not predict the apparent motion direction. In particular, rightward BM cues had an advantage over leftward BM cues in altering the perception of motion direction. Intriguingly, this perceptual bias disappeared when BM cues were shown inverted, or when the critical biological characteristics were removed from the cues. Critically, both the perceptual direction bias and the rightward advantage persisted even when only local BM cues were presented without any global configuration. Furthermore, the rightward advantage was found to be specific to social cues (i.e., BM), as it vanished when non-social cues (i.e., arrows) were utilized. Taken together, these findings support the existence of a specific processing mechanism for life motion signals and shed new light on their influences in a dynamic environment.

KEYWORDS

biological motion, motion direction perception, social attention, walking direction

INTRODUCTION

Living creatures, including both humans and non-humans, possess remarkable abilities to effortlessly detect the movements of conspecifics and heterospecifics in a complex environment (Blake & Shiffrar, 2007; Matsushima et al., 2022; Peng et al., 2021; Vallortigara, 2021). This ability remains intact even when biological motion (BM) signals are presented using point-light displays that consist of a few moving point lights attached to the head and major joints (Johansson, 1973). Despite their sparseness and simplicity, these degraded motion cues are sufficient to convey rich meaningful information about social and biological relevance, such as gender (Pollick et al., 2002; Sarangi et al., 2020; Troje, 2003), emotion (Dittrich et al., 1996; Halovic & Kroos, 2018; Roether et al., 2009), identity (Coste et al., 2021; Loula et al., 2005) and intention (Roche et al., 2013). Among them, walking direction is a particularly important attribute of BM signals, as it directly conveys information about the intention and disposition of the biological entity. In fact, humans appear to have an intrinsic sensitivity towards the walking direction of living entities. For instance, the walking direction of BM signals can be discriminated even when they are embedded in dynamic noises or displayed in peripheral vision (Aaen-Stockdale et al., 2008; Thompson et al., 2007; van Boxtel et al., 2017). Such sensitivity emerges early in life and is observed even in infants (Bardi et al., 2015; Kuhlmeier et al., 2010; Lunghi et al., 2020). Furthermore, a broad range of non-human species (e.g., chicks and monkeys) have been found to exhibit susceptibility to the walking direction of BM, even without visual experience (Vallortigara et al., 2005), suggesting an evolutionary basis for the mechanism underlying walking direction processing (Vallortigara & Regolin, 2006; Vangeneugden et al., 2009).

Critically, the intrinsic sensitivity to the walking direction conveyed by BM signals is considered functionally significant and could exert further influences on human behavioural responses. Research has shown that the walking direction of BM but not non-BM cues could reflexively direct observers' spatial attention, suggesting the existence of a specialized attention mechanism for BM signals (Shi et al., 2010). The cueing effect induced by walking direction is typically assessed using a modified central cueing task (Friesen & Kingstone, 1998), which is a variant of the Posner cueing paradigm (Posner, 1980). Specifically, targets (e.g., gratings) are randomly presented to the left or right side of the central BM cues. Although walking direction cannot predict the location of the following targets, informed observers still automatically attend to the direction signalled by the BM cues (Ji et al., 2020; Shi et al., 2010; Yu et al., 2020). Consequently, the average response time is significantly shorter for targets presented congruent with the walking direction than for those presented in the opposite direction. This attentional effect is also observed in preschool children and 6-month-old infants (Bardi et al., 2015; Zhao et al., 2014). Moreover, the BM-induced cueing effect persists even when the global configuration of BM cues is absent and observers are unaware of their biological nature (Hirai et al., 2011; Wang et al., 2014), indicating the pivotal role of local BM signals in the attentional effect (Sun et al., 2022; Troje & Westhoff, 2006; Wang et al., 2018, 2022).

Previous studies concerning the functional role of the sensitivity towards walking direction have primarily focused on the attentional guidance and processing enhancement of the related static information (e.g., gratings and cartoon pictures; Bardi et al., 2015; Ding et al., 2017; Wang et al., 2020; Zhao et al., 2014). However, since the world is dynamic and contains animate and non-animate movements, it is important to explore whether the walking direction conveyed by BM signals can also exert an influence on the perception of dynamic stimuli. To probe this issue, the present study investigated whether the walking direction of BM could modulate observers' perceived direction of apparent motion stimuli. The apparent motion reflects a visual illusion of movement with a subjective explicit or ambiguous moving direction (Laubrock et al., 2008; Miller & Shepard, 1993; Pantle et al., 2000). In the present study, the BM signals were manipulated to walk leftward or rightward as the non-predictive cues and presented at the bottom of the screen, while a grating served as the apparent motion target that moved simultaneously at the top of the screen. Participants were required to report the motion direction of the target. In addition to intact BM cues, feet motion sequences were also used to investigate whether the BM-induced perceptual bias, if observed, could extend to local BM signals without global configuration. Aside from BM cues, the present study also adopted arrows as non-social cues. Given that non-predictive arrow cues can also trigger robust attentional orienting effects (Ristic et al., 2002;

Tipple, 2002; Wang et al., 2020), comparing the perceptual bias induced by BM and arrow cues may provide a better understanding of the distinctiveness of social attention triggered by BM cues.

METHOD

Participants

One hundred and fifty paid participants (80 females and 70 males) aged between 19 and 31 years ($M \pm SD = 22.87 \pm 2.22$) with normal or correct-to-normal vision were recruited for the five experiments. Each experiment included 30 participants, with 17 females in each of Experiments 1 and 2, 12 females in Experiment 3, 16 females in Experiment 4 and 18 females in Experiment 5. All participants were naive to the research purposes, and informed consent was obtained from all participants before the experiment. Prior power analyses were conducted using G*Power 3.1.9.4 (Faul et al., 2007), which indicated that a sample size of at least 24 participants would afford 80% power with alpha set at .05 to detect a medium-high attentional effect (Cohen's d 0.60) induced by BM cues (Shi et al., 2010). The sample size was further increased to 30 participants per experiment to adequately detect potential effects in the present study.

Apparatus and stimuli

The experimental stimuli were programmed and presented via MATLAB (MathWorks) in conjunction with the Psychophysics Toolbox extensions (Brainard, 1997) on a 23.8-inch DELL monitor (1920 × 1080 pixels at 60 Hz refresh rate). Visual stimuli in each trial comprised of a cue (BM, non-BM sequences or arrows) and a target (luminance sinusoidal grating). The BM sequences were adopted from Vanrie and Verfaillie (2004), with 13 point lights attached to the head and the major joints (shoulders, elbows, wrists, hips, knees and ankles), thereby depicting the motion animation of a walking human figure. Each cycle lasted for 1 second and consisted of 30 frames. In the present study, BM stimuli with different walking directions (leftward or rightward) were displayed. In addition, the BM cue presented in the frontal view was used as the neutral cue. Inverted BM sequences were created by mirror-flipping BM stimuli vertically so that the walking direction of the inverted counterpart remained the same as the upright one (see Figure 1a). Non-BM sequences were derived from fragments that were identical to those used in BM stimuli but lacked essential biological characteristics. The motion trajectory of each dot in the non-biological sequences was the same as that of the BM stimuli, whereas the speed was changed to a constant value (the average speed of all the dots) to disrupt the natural velocity profile. Additionally, the initial motion phase of each dot was randomized to interrupt phase relationships of the original BM stimuli. The feet motion sequences that acted as the local BM stimuli were created by retaining only two ankle-motion dots from the original BM sequences. Compared with intact BM cues, local BM cues removed the global configuration information while retaining the local motion signals. The arrow images ($2.62^\circ \times 2.62^\circ$) were created using Adobe Photoshop CS6 software by combining a straight line and an arrowhead attached to the leading end of the line. In the neutral condition, arrow cues were replaced with a line without an arrowhead.

The target stimulus was a luminance sinusoidal grating bar with a contrast of 78% and a spatial frequency of 0.11 cycles per degree. The width of the grating was 47.42° , and the height was 3.14° of visual angle. In each trial, the phase of the grating was initially randomized and then shifted by the degree of 150, 160, 170, 180, 190, 200 or 210, respectively, per 167 ms. The grating was bidirectional when it was at 180° and drifted leftward or rightward when the phase shift was less than or greater than 180° , respectively.

Procedure

In Experiment 1, participants were seated at a distance of 60 cm from the monitor, and their visual field was stabilized using a headrest. Figure 1b depicted the timeline of the stimulus presentation.

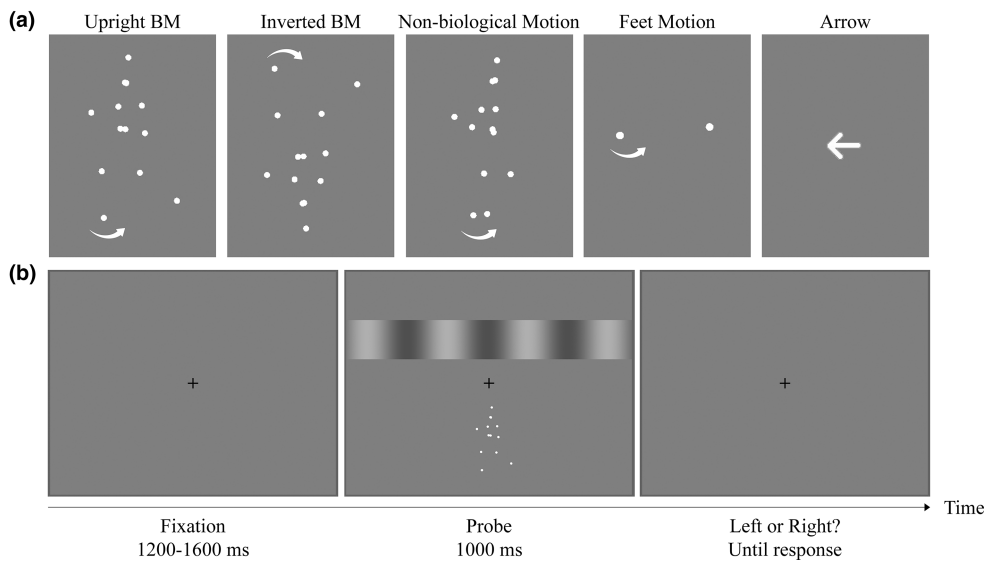


FIGURE 1 Static frames of sample stimuli used in the five experiments and a schematic representation of the experimental procedure. The cues employed in Experiments 1–5 consisted of upright BM cues, inverted BM cues, non-BM cues, feet motion cues and arrow cues, respectively. The direction of cues in the stimuli depicted above is oriented towards the left. Each trial started with a fixation period lasting 1200–1600 ms, followed by the simultaneous presentation of dynamic grating and motion cues for 1000 ms. Afterward, the stimuli vanished, and participants were required to indicate the motion direction of the grating (left or right).

Each trial began with a fixation on a cross ($0.6^\circ \times 0.6^\circ$) displayed in the center of a grey background (RGB: 128, 128, 128). Participants were instructed to maintain their focus on the fixation cross throughout the experiment. A luminance sinusoidal grating bar was then presented on the upper third of the screen and initiated its shift. The grating bar randomly shifted leftward, rightward or bidirectionally with seven shift phase degrees in total (150° , 160° , 170° , 180° , 190° , 200° or 210°). Simultaneously, the BM cue (leftward, rightward or neutral) subtending approximately $3.93^\circ \times 8.69^\circ$ in visual angle (0.26° for each dot) appeared on the lower third of the screen. After 1000 ms, all stimuli disappeared, and participants were instructed to indicate the motion direction of the grating bar (left or right) by pressing the left or right arrow keys, respectively. The inter-trial intervals were jittered between 1200 and 1600 ms. In total, each participant completed 210 trials, with a short break after every 70 trials. Test trials were presented in a new random order for each observer. Prior to the formal experiment, it was emphasized that the motion direction of the upper grating was independent of the movement direction of the point lights below.

The procedures of Experiments 2–5 were analogous to those of Experiment 1 except for the difference in the cues displayed at the bottom of the screen (see Figure 1a). Inverted BM sequences, non-BM sequences, feet motion sequences and arrows were presented in Experiments 2, 3, 4 and 5, respectively. Notably, in Experiment 4, the size of the dots was increased (0.34° for each dot) and participants were informed in advance that the two light dots represented feet.

Data analysis

For each participant under each test condition, the proportions of the rightward responses to a grating motion were calculated and fitted with a Boltzmann sigmoid function: $F(x) = 1/(1 + \exp[(x - x_0)/w])$ (Wang & Jiang, 2012; Zhang et al., 2021). The statistical analyses were conducted based on the point of subjective equality (PSE, the point at which participants perceived the motion direction of the grating

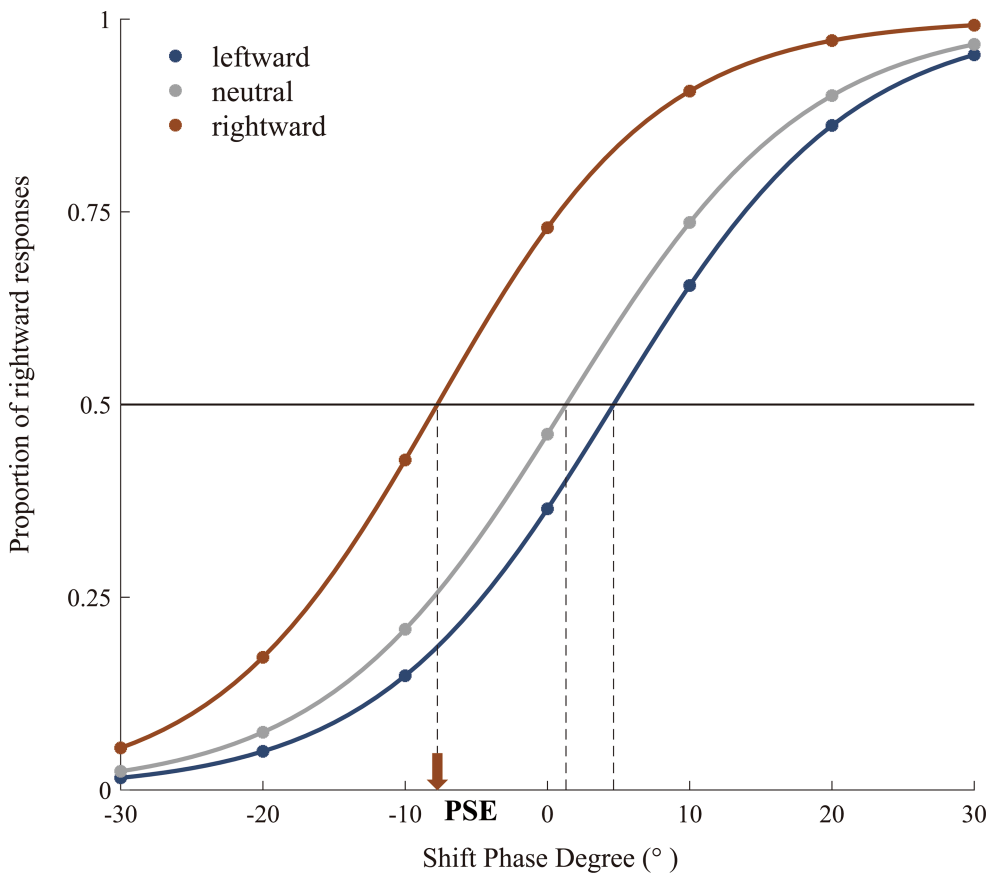


FIGURE 2 Psychometric function of a representative participant in Experiment 1. The data are presented for the leftward (blue curve), neutral (grey curve) and rightward (red curve) conditions. The proportion of rightward responses to the grating motion direction was plotted as a function of the shift phase degree. The point of subjective quality (PSE) is indicated by the red arrow.

as ambiguous), which is estimated by the midpoint of the Boltzmann function. A psychometric curve was drawn for each participant, which depicted the proportion of rightward responses to the grating motion direction as a function of the shift phase degree (see Figure 2). The shift phases (from 150° to 210° in a step of 10°) were transformed into -30°, -20°, -10°, 0°, 10°, 20° and 30° for analyses. As a result, a PSE of 0° indicates consistency between the perceived and physical motion direction of the grating, whereas a negative PSE indicates the grating was more likely to be perceived as shifting rightward, and vice versa. The more negative the PSE value, the stronger the rightward perception bias was exhibited.

RESULTS

In Experiment 1, a one-way analysis of variance (ANOVA) of the PSEs with cue direction (leftward, rightward and neutral) as the within-subjects variable revealed a significant main effect, $F(2, 58) = 4.364$, $p = .017$, $\eta_p^2 = .131$. Follow-up analyses showed a significant negative shift of PSE in the rightward condition relative to that in the leftward condition, -3.549 versus 2.483, $t(29) = -2.536$, $p = .017$, Cohen's $d = 0.463$, 95% CI for the mean difference [-10.897, -1.168], indicating that participants tended to perceive the apparent motion direction as congruent with the walking direction

even when they had been explicitly informed that BM cues were not predictive of the target motion direction (see Figure 3). Additionally, there was a significant negative shift of PSE in the rightward condition compared to that in the neutral condition, -3.549 versus 0.330 , $t(29) = -2.127$, $p = .042$, Cohen's $d = 0.388$, 95% CI for the mean difference $[-7.609, -0.150]$. However, the difference between the PSEs in the leftward condition and the neutral condition was not significant, 2.483 versus 0.330 , $t(29) = 1.095$, $p = .283$, Cohen's $d = 0.200$, 95% CI for the mean difference $[-1.869, 6.175]$. These results indicated that the motion direction perception was more affected by rightward rather than leftward BM cues. Moreover, one-sample t -tests showed a marginally significant negative PSE in the rightward condition, $t(29) = -2.018$, $p = .053$, whereas PSEs in the leftward and neutral conditions did not differ significantly from 0° ($ps > .100$). Taken together, these findings demonstrated that rightward BM cues had an advantage in modulating motion direction perception relative to leftward BM cues, indicating that motion direction processing seemed to be more susceptible to the rightward walking direction. Furthermore, the perceptual bias and the rightward advantage were replicated in an additional experiment that varied the display duration (i.e., 750, 1000 and 1250 ms) of the BM cues (see the Supplemental Material for more details).

In contrast to Experiment 1, the main effect of cue direction was not significant when the BM cues were presented inverted in Experiment 2, $F(2, 58) = 1.632$, $p = .204$, $\eta_p^2 = .053$, which is consistent with the inversion effect reported in previous BM studies (Troje & Westhoff, 2006). Further analyses showed that the PSEs did not differ significantly between the leftward and neutral conditions, 0.466 versus -1.426 , $t(29) = 1.467$, $p = .153$, Cohen's $d = 0.268$, 95% CI for the mean

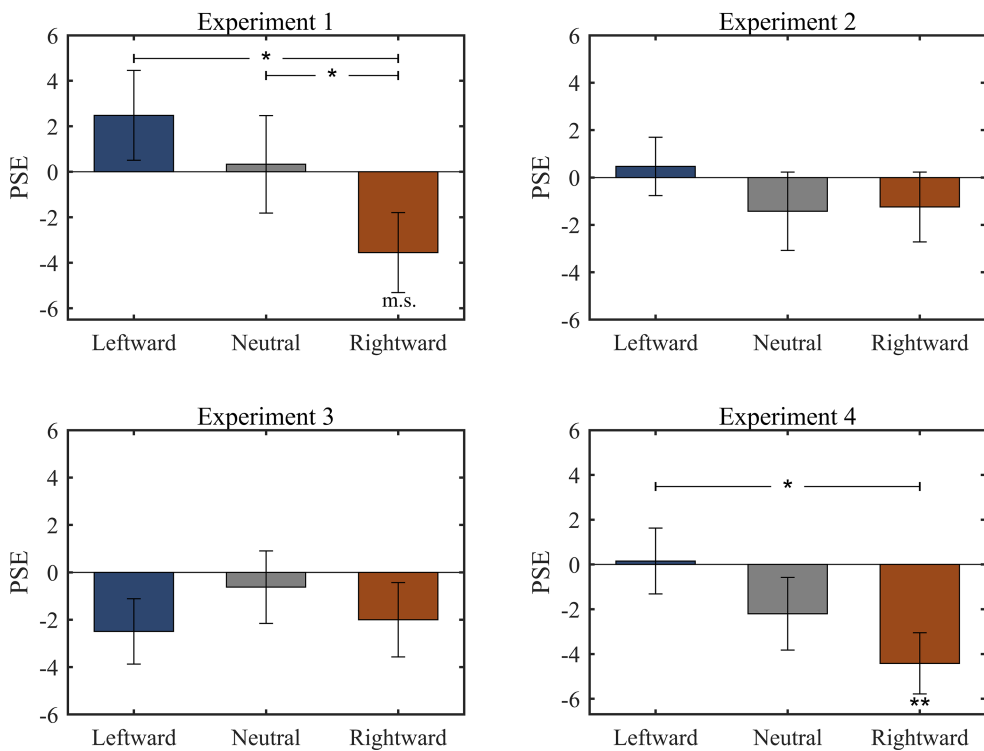


FIGURE 3 Average PSEs were calculated for three cue direction conditions in Experiments 1–4. In Experiment 1, BM cues were found to modulate the perception of the apparent motion direction, with the effect specific to the rightward direction. This effect vanished when BM cues were shown inverted (Experiment 2) or were deprived of critical biological characteristics (Experiment 3). Feet motion cues without intact BM form were also found to alter the motion direction perception in Experiment 4, moreover, a rightward advantage was observed. Error bars show standard errors. $*p < .05$; $**p < .01$; m.s., marginally significant.

difference $[-0.745, 4.529]$, or between the leftward and rightward conditions, 0.466 versus -1.244 , $t(29) = 1.620$, $p = .116$, Cohen's $d = 0.296$, 95% CI for the mean difference $[-0.449, 3.870]$. The difference in PSEs between the neutral condition and the rightward condition was also not significant, -1.426 versus -1.244 , $t(29) = -0.164$, $p = .871$, Cohen's $d = 0.030$, 95% CI for the mean difference $[-2.448, 2.085]$. Furthermore, the PSEs were not significantly different from 0° in all BM direction conditions ($ps > .100$). These results together demonstrated that the observed perceptual bias critically depended on the orientation of BM cues and did not arise from the processing of low-level visual features.

Furthermore, to investigate whether the observed perceptual bias was indeed elicited by the biological characteristics of the BM signals, an additional control experiment (Experiment 3) was conducted in which non-BM sequences were utilized as central cues. As expected, no significant main effect of cue direction was observed, $F(2, 58) = 0.613$, $p = .545$, $\eta_p^2 = .021$. Further analyses showed that there was no significant difference in PSEs between the leftward condition and the rightward condition, -2.495 versus -2.000 , $t(29) = -0.355$, $p = .725$, Cohen's $d = 0.065$, 95% CI for the mean difference $[-3.348, 2.357]$. Similar to Experiment 2, the PSE in the neutral condition was also not significantly different from that in the other two conditions, neutral versus leftward: -0.623 versus -2.495 , $t(29) = 1.015$, $p = .318$, Cohen's $d = 0.185$, 95% CI for the mean difference $[-1.899, 5.642]$; neutral versus rightward: -0.623 versus -2.000 , $t(29) = 0.700$, $p = .489$, Cohen's $d = 0.128$, 95% CI for the mean difference $[-2.645, 5.398]$. Again, the PSEs in the rightward and neutral conditions were not significantly different from 0° ($ps > .100$). The shift of PSE in the leftward condition showed a reverse trend ($p = .081$). In summary, these results indicated that motion cues lacking biological characteristics failed to produce a perceptual bias and a rightward advantage, as observed in BM cues. Moreover, a two-way mixed design ANOVA of PSEs with cue direction (leftward and rightward) as the within-subjects variable and cue type (Experiments 1–3) as the between-subjects variable showed a significant interaction effect, $F(2, 87) = 3.794$, $p = .026$, $\eta_p^2 = .080$, suggesting that the perceptual bias effect found in Experiment 1 differed significantly from those in Experiments 2 and 3.

In Experiment 4, we further investigated whether the global configuration was indispensable to elicit a perceptual bias using two dots that solely conveyed the motion of the feet as cues. Similar to Experiment 1, a significant main effect of cue direction was observed, $F(2, 58) = 3.980$, $p = .024$, $\eta_p^2 = .121$. Subsequent analyses revealed a significant negative shift of PSE in the rightward condition compared to the leftward condition, -4.416 versus 0.156 , $t(29) = -2.525$, $p = .017$, Cohen's $d = 0.461$, 95% CI for the mean difference $[-8.275, -0.868]$, suggesting that local BM cues could also modulate the perception of motion direction. The PSE in the neutral condition was not significantly different from that in the rightward condition, -2.202 versus -4.416 , $t(29) = 1.433$, $p = .162$, Cohen's $d = 0.262$, 95% CI for the mean difference $[-0.945, 5.371]$ or in the leftward condition, -2.202 versus 0.156 , $t(29) = -1.584$, $p = .124$, Cohen's $d = 0.289$, 95% CI for the mean difference $[-5.402, 0.686]$. However, similar to Experiment 1, the PSE in the rightward condition shifted negatively, $t(29) = -3.227$, $p = .003$, while the PSEs in other conditions were not significantly different from 0° ($ps > .100$), suggesting the existence of a rightward advantage even with local BM cues. In summary, these results demonstrated that the walking direction conveyed by local BM signals without global configuration was effective at modulating the perception of motion direction. Additionally, there was no significant interaction between cue direction (leftward and rightward) and cue type (intact and local), $F(1, 58) = 0.239$, $p = .627$, $\eta_p^2 = .004$, indicating that the perceptual bias induced by local BM cues was not different from that induced by intact BM cues in Experiment 1. Finally, combining the results from Experiments 1–4, we found a significant interaction effect between cue direction (leftward and rightward) and cue type, $F(3, 116) = 2.838$, $p = .041$, $\eta_p^2 = .068$.

Lastly, to examine whether the perceptual bias of motion direction identified previously was specific to BM cues, arrows serving as non-social cues were utilized in Experiment 5. Consistent with Experiment 1, a significant main effect of cue direction was observed again using arrow cues, $F(2, 58) = 19.208$, $p < .001$, $\eta_p^2 = .398$. Follow-up analyses revealed a significant negative shift of PSE in the rightward condition compared with that in the leftward condition, -5.564 versus 4.867 , $t(29) = -5.596$, $p < .001$, Cohen's $d = 1.022$,

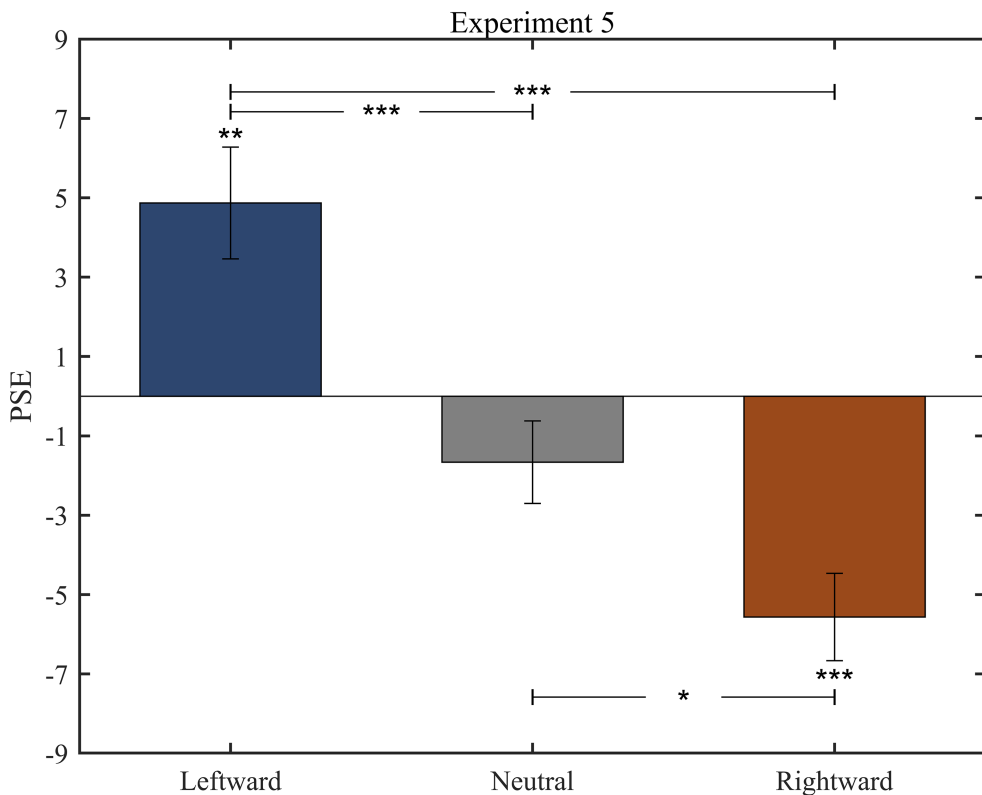


FIGURE 4 Average PSEs under three cue direction conditions in Experiment 5. Non-social arrow cues were found to influence motion direction perception, but no significant rightward advantage was observed for these cues. Error bars show standard errors. * $p < .05$; ** $p < .01$; *** $p < .001$.

95% CI for the mean difference $[-14.244, -6.619]$, indicating that non-social arrow cues could also modulate motion direction perception (see Figure 4). Moreover, the PSE in the rightward condition was significantly different from that in the neutral condition, -5.564 versus -1.663 , $t(29) = -2.437$, $p = .021$, Cohen's $d = 0.445$, 95% CI for the mean difference $[-7.175, -0.626]$. In contrast to Experiments 1 and 4, the PSE in the leftward condition was significantly different from that in the neutral condition, 4.867 versus -1.663 , $t(29) = 4.020$, $p < .001$, Cohen's $d = 0.734$, 95% CI for the mean difference $[3.208, 9.853]$, indicating that there was no evident asymmetric advantage. Different from Experiments 1 and 4, not only did the PSE in the rightward condition shift negatively, $t(29) = -5.053$, $p < .001$, but also the PSE in the leftward condition shifted positively, $t(29) = 3.456$, $p = .002$. Moreover, no significant difference was found between the amplitude of PSEs in the rightward and leftward conditions, $t(29) = 0.734$, $p = .469$. In conclusion, these results suggest that although non-social arrow cues can influence the perception of apparent motion direction congruent with the cue direction, the rightward advantage seems to be specific to BM cues.

DISCUSSION

The focus of the existing literature on the functional role of walking direction processing has traditionally been limited to the enhanced detection of static targets. Our findings extend this line of research by exploring how BM cues modulate the processing of simultaneously presented dynamic stimuli, specifically, the perception of apparent motion direction. Generally, BM cues were found to significantly bias the perceived motion direction to be congruent with the walking direction. Critically, rightward BM cues exerted a greater influence on direction perception than leftward BM cues, reflecting a rightward

advantage. However, when non-social arrow cues were employed, this rightward-based perceptual bias was no longer evident, indicating a disparity in the processing of BM and non-social cues. Furthermore, the perceptual bias disappeared when BM cues were deprived of critical biological characteristics or were displayed upside-down, with the latter consistent with the inversion effect previously reported in research on BM cueing effects (Fitzgerald et al., 2014). More importantly, the BM-induced perceptual bias was not dependent on global configuration since it persisted when local BM cues were utilized. These findings together demonstrated a BM-induced bias in motion direction perception, driven by the biological characteristics embedded in BM cues independent of global configuration.

Perception of simple apparent motion direction has previously been thought to be influenced by low-level physical changes (e.g., contrast, frequency and speed; Davidenko et al., 2022; Watson, 1986; Zhang et al., 2012). Our findings further indicated that high-level visual information (i.e., biological signals) can also influence the perceived direction of apparent motion. Note that some recent studies have also explored how BM signals interact with scene dynamics (e.g., moving grating and optic flow; Fujimoto, 2003; Fujimoto et al., 2009; Fujimoto & Sato, 2006; Fujimoto & Yagi, 2007, 2008; Koerfer & Lappe, 2020; Mayer et al., 2019). For instance, it has been found that BM cues displayed peripherally were processed incidentally and could affect the performance of direction discrimination of the BM walker at the fovea (Thornton & Vuong, 2004). Additionally, when BM walkers were displayed overlapped with counter-phase moving gratings, observers perceived the background grating as shifting in the opposite direction to the walker instead of in the same direction (Fujimoto, 2003; Fujimoto et al., 2009; Fujimoto & Sato, 2006; Fujimoto & Yagi, 2007, 2008). Compared to these studies, our research extends the current knowledge by demonstrating a motion direction bias towards the walking direction of non-overlapping BM cues.

More importantly, a rightward advantage was observed in the present study, whereas no such asymmetry was found in the abovementioned studies (Fujimoto, 2003; Fujimoto et al., 2009; Fujimoto & Sato, 2006; Fujimoto & Yagi, 2007, 2008; Koerfer & Lappe, 2020; Mayer et al., 2019). Such rightward advantage has also been observed with another social cue (i.e., eye gaze). Specifically, rightward gaze shifts were found to be more effective than leftward ones in inducing cueing effects and perceptual biases in motion direction (Stauder et al., 2011; Vlamings et al., 2005; Yamada et al., 2008). Consistent with this finding, neurological evidence has shown that viewing a rightward rather than leftward or straightforward gaze elicited a larger N170, suggesting a rightward processing advantage for gaze cues (Watanabe et al., 2002). Importantly, this rightward advantage was found only with gaze cues rather than arrow cues, suggesting the existence of a specialized 'eye gaze detector' (Stauder et al., 2011; Vlamings et al., 2005). The present study went a further step by demonstrating a rightward advantage in another type of social cue (i.e., walking direction of BM), paralleling previous research showing that individuals seem to be more sensitive towards rightward BM cues (Thornton et al., 2003). Such left-right laterality effects also extend to other fields (e.g., number-space mapping; Bulf et al., 2016; Di Giorgio et al., 2019; Rugani et al., 2010; Rugani, Vallortigara, et al., 2015), which can be explained by cultural factors (e.g., reading and writing directionality) or biological factors (Vallortigara, 2018). Intriguingly, a similar rightward advantage in BM processing has also been reported in visually naïve chicks, which may be modulated by brain asymmetry (Rugani, Rosa Salva, et al., 2015). Taken together, these across-species findings provide evidence for the existence of a unique module devoted to identifying the direction of other creatures' limbs in locomotion (i.e., a 'life motion detector'; Troje & Westhoff, 2006; Wang et al., 2014). Combined with previous evidence obtained from gaze cues, our findings indicated that a shared brain mechanism, tailored for detecting life signals and sensitive to the rightward direction, seems to underlie the perceptual bias of motion direction triggered by social cues. Apart from BM cues, other motion signals that are related to the presence of living organisms (e.g., self-propelled motion and abrupt variations in speed) can also contribute to animacy perception (Rosa-Salva et al., 2016). Future research, utilizing these animate motion cues in the task of motion direction perception, may help to delineate whether there exists a general 'life detector' (Vallortigara, 2021).

Furthermore, our study provides novel insights into the ongoing debate about the distinctiveness of social cues. Previous studies that directly compared social and non-social cues using the cueing task

have produced mixed findings. While some studies have demonstrated that eye gaze can trigger a more strongly reflexive shift of attention than arrows (Friesen et al., 2004; Ristic et al., 2007), others have found indistinguishable attentional effects (Nummenmaa & Hietanen, 2009; Tipples, 2008). Recent research has revealed that unique genetic and neural mechanisms were shared across different social cues, rather than non-social cues (Ji et al., 2020; Liu et al., 2021; Wang et al., 2020). Our findings extend these studies by offering new evidence for the differentiation between social and non-social cues in the context of dynamic stimuli processing. Specifically, our observation of a rightward advantage in the processing of social (i.e., BM) but not non-social (i.e., non-BM, arrow) cues suggests the uniqueness of social cues, and more critically, supports the existence of a specialized 'social attention detector', as implied by previous research (Ji et al., 2020; Wang et al., 2020).

Based on previous studies, attention is supposed to be the possible mechanism underlying the bias of apparent motion direction (Felisberti & Zanker, 2005; Wohlschläger, 2000; Yabe & Taga, 2008). Studies have shown that the perceived direction of apparent motion can be biased in the direction of saccadic movement and attention shift (Shim & Cavanagh, 2006). Therefore, in our study, the BM-induced perceptual bias of motion direction is probably attributed to social attention elicited by the walking direction of BM. Social attention, the ability to share attention with social partners, has previously been proposed as the mechanism underlying the line-motion illusion of static stimuli induced by surrounding social cues (Bavelier et al., 2002). Our findings went a step further by demonstrating that social attention may also affect the directional perception of dynamic stimuli. Notably, we observed a rightward advantage with BM cues but not arrow cues, which is consistent with previous research showing the superiority of rightward cues in guiding social attention rather than non-social attention (Stauder et al., 2011; Vlamings et al., 2005). Furthermore, social attention disappeared when biological characteristics of BM cues were disrupted (Shi et al., 2010), which may explain the absence of perceptual bias under inverted BM and non-BM circumstances.

Notably, this perceptual bias could manifest in local BM cues without any global configuration. Local cues consisting of two point lights depicting feet motion were found to be critical in walking direction perception, despite being devoid of global information (Chang & Troje, 2009; Takahashi et al., 2011; Wang et al., 2010). Given that walking is probably the most common form of motion generated by animals with feet, the visual perception system has evolved to be highly sensitive to the gravitational acceleration pattern contained in the feet motion cues (Chang et al., 2018; Wang et al., 2022). In fact, feet motion cues could still elicit reflexive attention shift even when observers were not explicitly aware of their biological nature (Wang et al., 2014). Overall, the intrinsic sensitivity towards local BM signal, which has also been observed in other non-human species (e.g., new-born chicks; Vallortigara et al., 2005), suggests the existence of a specialized 'life motion detector' that is attuned to limb motion and enables rapid detection of the spatial movement of other articulated terrestrial animals (Johnson, 2006; Troje & Westhoff, 2006). Our findings support this notion and suggest that the automatic processing of local BM cues also occurs in a dynamic context, resulting in a perceptual bias that is congruent with the walking direction. Although the current study found that local motion alone was sufficient to induce the perceptual bias, it remains unclear whether global configuration alone can also alter motion direction perception and how local and global information contributes respectively during such a process. Based on previous research using backward-walking BM cues, which reported that local motion played a dominant role relative to the global configuration in shifting attention (Hirai et al., 2011), we expect that local motion will have an advantage in eliciting the perceptual bias of apparent motion direction over the global configuration. However, this needs to be verified by future investigations directly adopting backward-walking BM cues.

In conclusion, the current study illustrates that the perception of apparent motion direction can be modulated by the walking direction of BM, with a stronger susceptibility towards the rightward walking direction. The perceptual bias that perceived motion direction as congruent with the walking direction is contingent upon the presence of biological characteristics and can be induced by local BM cues without any global configuration. While non-social arrow cues also induced a

perceptual direction bias, the rightward advantage was restricted to BM cues, suggesting differential processing mechanisms for BM and arrow cues. Overall, these findings support the existence of a specialized life motion detector and provide insights into the influences of BM cues on the perception of the dynamic world.

AUTHOR CONTRIBUTIONS

Yiping Ge: Conceptualization; data curation; formal analysis; methodology; writing – original draft. **Yiwen Yu:** Conceptualization; methodology; writing – review and editing. **Suqi Huang:** Methodology; writing – review and editing. **Xinyi Huang:** Data curation; methodology; writing – review and editing. **Li Wang:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing. **Yi Jiang:** Funding acquisition; methodology; supervision; writing – review and editing.

FUNDING INFORMATION

This research was supported by grants from the STI2030-Major Projects (Nos. 2021ZD0203800 and 2022ZD0205100), the National Natural Science Foundation of China (No. 31830037), the Science Foundation of Institute of Psychology, Chinese Academy of Sciences, and the Fundamental Research Funds for the Central Universities.

CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Data are made available at the Knowledge Repository of the Institute of Psychology, Chinese Academy of Sciences (<http://ir.psych.ac.cn/handle/311026/42954>).

ETHICAL STATEMENT

The procedures of the current research were approved by the institutional review board of the Institute of Psychology, Chinese Academy of Sciences.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Ge, Y., Yu, Y., Huang, S., Huang, X., Wang, L., & Jiang, Y. (2023). Life motion signals bias the perception of apparent motion direction. *British Journal of Psychology*, 00, 1–14. <https://doi.org/10.1111/bjop.12680>