



Eye pupil signals life motion perception

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Abstract

The ability to readily detect and recognize biological motion (BM) is fundamental to survival and interpersonal communication. However, perception of BM is strongly disrupted when it is shown upside down. This well-known inversion effect is proposed to be caused by a life motion detection mechanism highly tuned to gravity-compatible motion cues. In the current study, we assessed the inversion effect in BM perception using a no-report pupillometry. We found that the pupil size was significantly enlarged when observers viewed upright BMs (gravity-compatible) compared with the inverted counterparts (gravity-incompatible). Importantly, such an effect critically depended on the dynamic biological characteristics, and could be extended to local feet motion signals. These findings demonstrate that the eye pupil can signal gravity-dependent life motion perception. More importantly, with the convenience, objectivity, and noninvasiveness of pupillometry, the current study paves the way for the potential application of pupillary responses in detecting the deficiency of life motion perception in individuals with socio-cognitive disorders.

Keywords Biological motion · Pupil dilation · Gravity · Life motion detector · Local motion

Introduction

Humans are equipped with extraordinary abilities to process biological motion (BM) signals. For instance, people are adept at rapidly detecting and recognizing the movements of living creatures in the environment, and can readily decipher others' intentions behind their actions to achieve social engagement (Blake & Shiffrar, 2007). Arguably, such an ability is fundamental to survival and interpersonal interaction (Yovel & O'Toole, 2016). Observers can effortlessly extract rich information from BM signals, including direction (Thurman & Grossman, 2008), gender (Fallah et al., 2006), and identity (Loula et al., 2005), even in an

impoverished case in which only a handful of point-lights are attached to the head and the major joints of a human figure (i.e., so-called point-light displays) (Johansson, 1973). However, perception of BM is strongly disrupted when the point-light displays are presented in an upside-down manner, manifesting a classic perceptual inversion effect (Pavlova & Sokolov, 2000; Sumi, 1984).

Early studies have emphasized that this inversion effect mainly originates from the global form (Beintema & Lappe, 2002; Pavlova & Sokolov, 2000; Shipley, 2003). However, there is growing evidence that dynamic motion information plays a critical role in the inversion effect (Hirai & Senju, 2020; Troje & Westhoff, 2006; Wang et al., 2018). In particular, the kinematic trajectory of earth animals consists of constant gravitational acceleration information. That means that the upright BM is composed of pendular or ballistic motion with acceleration profiles consistent with the influence of gravity (Troje & Westhoff, 2006; Vallortigara & Regolin, 2006). It has been shown that when gravitational acceleration information was removed, the inversion effect was destroyed (Chang & Troje, 2009). One recent study with astronauts in spaceflight further demonstrated such an inversion effect is largely shaped by the gravity of earth. They found the BM inversion effect was attenuated after astronauts were

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exposed to microgravity in space (Wang et al., 2022). Furthermore, as earth animals' feet are pushed off the ground and fall down under gravity, the gravity-compatible kinematic clues are more abundant in feet movements (i.e., local motion), which also carries the signals of life (Chang & Troje, 2009; Hirai & Senju, 2020). As evidence, some studies have found that perception of local motion, even stripped of global configural information, is efficacious in grabbing attention and also subject to the inversion effect (Troje & Westhoff, 2006; Wang et al., 2010, 2014). Thus, the inversion effect of BM properly reflects a predisposed gravity bias of the visual system tailored to the locomotion signals (especially the feet motion), and can be used to quantify the gravity-constrained life motion detector (Johnson, 2006; Troje & Westhoff, 2006).

Pupillary responses, primarily controlled by the autonomic nervous system, are considered to reflect mental states (Joshi & Gold, 2020). It has been shown that pupillary responses are tightly intertwined with cognitive processes, especially those involving bio-social information. For example, previous studies have found that pupil size was significantly enlarged when people viewed direct gaze rather than averted gaze (Sepeta et al., 2012), or natural movement rather than mechanical movement (Williams et al., 2019). Furthermore, perception of social interactive agents could also elicit greater pupil size than non-interactive agents (Cheng et al., 2021). However, as detection of life motion signals is assumed as the first step of processing more complex biosocial entities (e.g., goal-directed movement), it is necessary to reveal whether the pupil size captures the life motion perception as well, and if so, whether it depends on global configuration or is tuned to gravity-dependent dynamical cues. In addition, as a convenient, objective, and noninvasive technique, pupillometry can be useful in detecting the deficiency of life motion perception in individuals with socio-cognitive disorders (de Vries et al., 2021; Todorova et al., 2019), especially for preverbal (e.g., infants) or nonverbal participants (e.g., animals, neurological patients).

To this end, the present study investigated whether the inversion effect in BM perception can be reflected in pupil size. We adopted the point-light walkers and first assessed whether the pupils respond more to an upright walker (gravity-compatible) than to its inverted counterpart (gravity-incompatible). To further elucidate the nature of this pupillary change, we conducted two control experiments in which static figures and non-BM stimuli (the gravity-related acceleration information was destroyed) were employed. Finally, we investigated whether such BM-triggered pupillary responses, if observed, could generalize to local motion cues (i.e., the feet motion).

Method

Participants

In total, 72 adults volunteered to participate in the current study. Eighteen subjects took part in each of the experiments (Experiment 1: mean age = 21.17 years, SD = 2.46, five males and 13 females. Experiment 2: mean age = 22.72 years, SD = 2.14, nine males and nine females. Experiment 3: mean age = 23.12 years, SD = 1.92, seven males and 11 females. Experiment 4: mean age = 22.83 years, SD = 2.46, eight males and ten females). The sample size was determined by our previous studies (Cheng et al., 2021) and pilot experiments. All subjects had normal or corrected-to-normal vision and were naïve to the purpose of the experiments. They gave their written informed consent before the experiments, which was approved by the institutional review board of the Institute of Psychology, Chinese Academy of Sciences (H18029). The current study was conducted in accordance with the tenets of the Declaration of Helsinki.

Stimuli

Stimuli were generated with MATLAB (Mathworks, Natick, MA, USA) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Point-light displays were adopted from Biological Motion Database (Vanrie & Verfaillie, 2004), which consist of 13 markers indicating the major joints of the actor (head, shoulders, elbows, wrists, hips, knees, and feet). Each motion cycle was 1 s with 30 frames. In Experiment 1, intact point-light walkers were presented with ten different viewpoints (left 90°, 60°, 50°, 30°, and 10° and right 90°, 60°, 50°, 30°, and 10°). In Experiment 2, the test stimuli were static figures, which were created by capturing the most extended profiles of a gait cycle. In Experiment 3, non-BM sequences were generated by removing the dynamic biological characteristics from the original BM sequences. Specifically, we disrupted the phase relationship of BM by randomizing the initial motion phase of each individual dot. In addition, the natural velocity profile of the BM stimuli was destroyed by manipulating each individual dot with a constant moving speed equal to the average speed of the dot. Such manipulations keep the motion trajectories of individual dots unchanged, but entirely remove the dynamic biological characteristics so that no gravity-dependent acceleration cues were reserved. In Experiment 4, we adopted the feet motion sequences, which were presented with leftward or rightward walking direction. As shown from many previous studies (Chang & Troje, 2009; Troje & Westhoff,

2006), the two point-lights of ankles were selected to specify the motion of the feet. They are composed of two segments: the stance phase where the feet trajectory moved in the opposite direction to the walking direction and the swing phase where the feet trajectory accelerated in both horizontal and vertical directions because of gravitational acceleration and muscle activity. Note that the feet motion sequences serve as local BM cues, because they do not carry any global configurational information. In addition, inverted counterparts (i.e., intact BM, static figure, non-BM, local BM) were created by mirror flipping all the motion sequences vertically (Fig. 1).

Procedure

Stimuli were displayed against a uniform gray background (13.35 cd/m^2) on a 22-in. LCD monitor ($1,920 \times 1,080$ at 60 Hz). Participants were required to put their heads on a chin-rest, and the viewing distance was 60 cm. The experiments were conducted in a dimly lit room. In Experiment 1, each trial began with a central fixation ($0.2^\circ \times 0.2^\circ$) with a variable duration (800–1,200 ms), followed by the point-light BM displays for 3,000 ms in the center of the screen (approximately subtended $4.2^\circ \times 7.2^\circ$). Participants were asked to monitor a sudden luminance change of the point-light displays (31.45 cd/m^2) and maintain their attention on the displays. The luminance change appeared in 20% of trials where their

occurrence time was randomly determined. Participants had to press one of two buttons after the stimulus disappeared to indicate whether they saw the luminance change in the current trial. Participants were required to minimize blinking and maintain their gaze on a fixation at all times except during the inter-trial interval (2,000 ms). Experiments 2 and 3 followed the same procedure as Experiment 1, with the difference being that static frames and non-BM sequences were employed as the stimuli. Experiment 4 was identical in structure to Experiment 1, except that the stimuli were feet motion sequences. Considering that the feet stimuli are comprised of only two dots of the ankles, participants were informed of their biological nature before the formal experiment according to the previous study (Yu et al., 2020). This could prevent participants from arbitrarily guessing these two dots as being something else (e.g., circling dots). In addition, to better hold their attention on the biological nature of the feet stimuli, they were required to judge the walking direction of the feet (toward the left or the right side). However, no feedback was provided, so that participants did not know some of the feet stimuli were upright while others were inverted. There were 40 trials (32 without luminance change) for each condition in Experiments 1–3 and 32 trials for each condition in Experiment 4. In all experiments, the upright and the inverted stimuli were presented equiprobably in random order, and all trials were divided into four blocks.

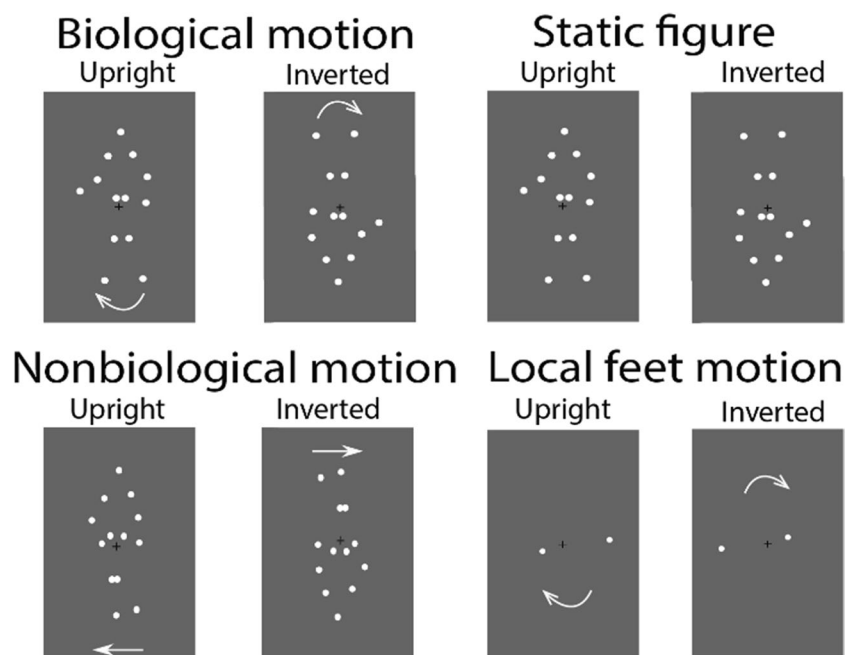


Fig. 1 Static frames of sample stimuli. Intact biological motion (BM) walkers, static figures, non-BM sequences, and local feet motion sequences, including both upright and inverted versions, were used in

the current study. Arrows indicate the motion direction and were not presented in the actual experiments

Pupillometry data analysis

Trials without luminance change of the point-light displays in Experiments 1–3 and all trials in Experiment 4 were used for pupil analysis. Pupil size was collected by an iView X Hi-Speed eye-tracker system (500 Hz; SMI, Berlin, Germany). Through visual inspection, the raw pupillary data were first preprocessed to identify and exclude trials with blinks more than once, saccades outside the visual degree of the BM stimuli, and other artifacts that cannot be further interpolated (1.9% trials excluded on average). For the remaining trials, blinks or blink-like artifacts were further removed by linear interpolation. Finally, the pupil data were down-sampled to 20 Hz and baseline-corrected against the mean pupil size of the 200-ms pre-stimulus period. Consecutive paired-sample t-tests across all time points after the stimulus onset were computed separately for each condition. To avoid the potential problems associated with multiple comparisons, we employed the cluster-based permutation analysis for correction in the Mass Univariate Analysis toolbox (Groppe et al., 2011). Note that all pupil data hereinafter mentioned

were analyzed and reported in arbitrary units (a.u.). In general, a pupil size of ~ 33 a.u. corresponded to a pupil size of 5 mm in the present study.

Results

Experiment 1: Biological motion (BM) signals induce pupil dilation

In Experiment 1, we first explored whether BM signals could induce greater pupil dilation. Participants' behavioral performance was $99.0\% \pm 1.3\%$, suggesting that participants maintained their attention on the displays throughout the experiment. More importantly, we found the pupil size was significantly enlarged in response to the upright point-light walkers than the inverted ones from 1,750 ms to 3,000 ms (see Fig. 2A). The current results provide initial evidence that perception of animacy in BM elicits pupil dilation. To further elucidate the nature of this pupil dilation effect, we conducted Experiments 2 and 3.

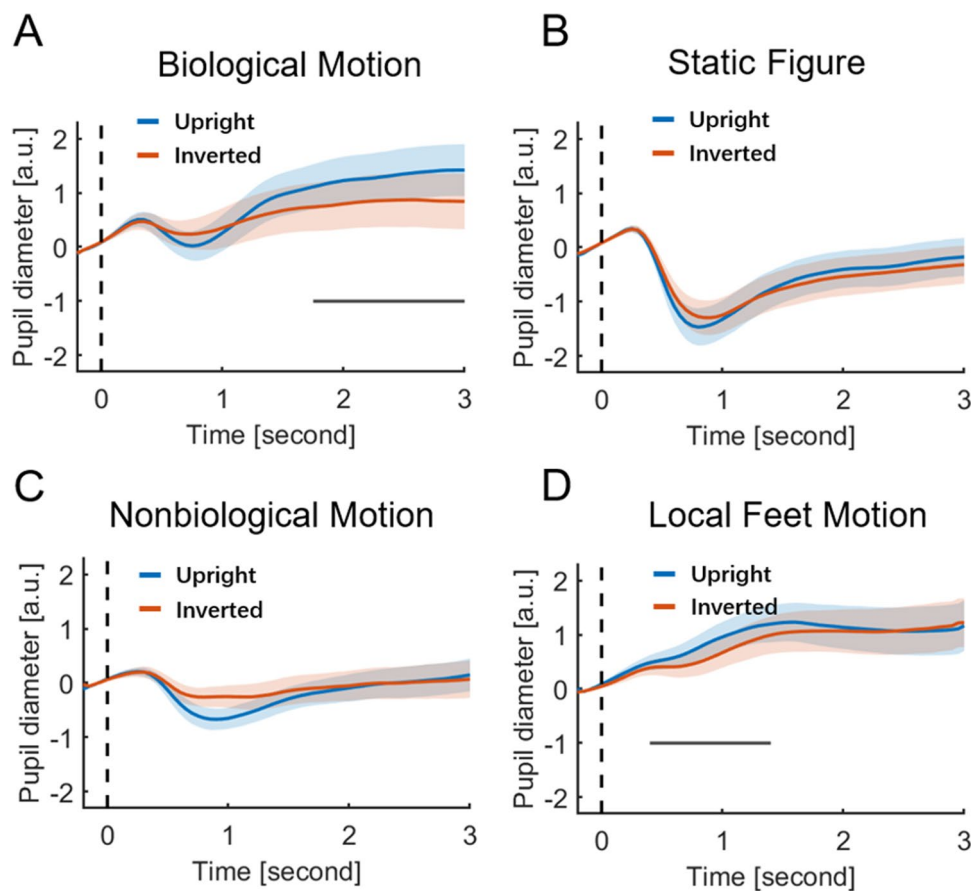


Fig. 2 Results from Experiments 1–4. The solid lines represent mean pupil diameter change as a function of time between different conditions. The shaded areas represent ± 1 standard error within subjects.

The horizontal black lines indicate periods during which there are statistically significant differences between conditions at $p < 0.05$ after correction for the cluster-based permutation

Experiment 2: Static figures fail to induce pupil dilation

We adopted the static point-light figures as test stimuli in Experiment 2 to verify whether the observed pupil dilation effect was merely attributed to the global configuration of human figures. Similarly, participants' mean accuracy in detecting the luminance change was also close to ceiling ($99.2\% \pm 1.1\%$). As shown in Fig. 2B, there was no significant difference in the magnitude of the pupillary response to the upright static figures versus that to the inverted counterparts (see Fig. 2B). This result suggests that the configural information from static figures cannot elicit pupil dilation, thereby ruling out the possibility that such an effect was simply caused by the global form.

Experiment 3: Pupil dilation caused by dynamic biological characteristics in BM

To further confirm that such pupil dilation effect was indeed driven by dynamic biological characteristics (e.g., the gravitational acceleration information) in BM, we examined pupillary responses to a particular type of non-BM stimuli that were created by replacing the natural velocity profile of BM with a constant moving speed. Again, participants responded with high accuracy ($99.1\% \pm 1.1\%$), but their pupils did not differ between the upright and the inverted non-BM stimuli (see Fig. 2C). In other words, the pupil dilation effect disappeared when the natural dynamics of BM were disrupted, demonstrating the indispensable role of dynamic biological characteristics in eliciting the observed pupil dilation effect.

Experiment 4: Local BM signals elicit pupil dilation

We finally investigated whether this pupil dilation effect could be extended to local BM signals. In Experiment 4, feet motion sequences were employed as test stimuli, which did not carry any global configuration information. In line with previous studies (Chang & Troje, 2009; Troje & Westhoff, 2006), behavioral data revealed an obvious inversion effect in perception of the feet motion. Participants' mean accuracy of the direction judgment task was significantly higher in the upright feet motion condition than that in the inverted condition (97.1% vs. 46.9% ; $t(17) = 5.31$; $p < 0.001$; Cohen's $d = 1.25$, $BF_{10} = 460.99$). More importantly, participants' pupil size was significantly enlarged between 400 ms and 1,400 ms in the upright versus the inverted condition (see Fig. 2D). These results suggest that such a pupil dilation effect operated even without global body configuration and could be induced by the local BM signals alone.

Discussion

In addition to the well-known pupillary light reflex, the eye pupil diameter, even under constant luminance, also covaries with a range of cognitive processes, including attention (Mathôt et al., 2013), mental effort (Kahneman & Beatty, 1966), decision making (Urai et al., 2017), etc. In the current study, we adopted minimalist stimuli – point-light displays and contrasted pupillary responses to upright and inverted BM walkers. These stimuli and designs were well-controlled in luminance and motion energy, accordingly ruling out other confounding factors in pupillary responses. We for the first time tested whether gravity-constrained BM perception could be reflected in our pupil size.

Firstly, we found an upright point-light walker (gravity-compatible) elicited larger pupil dilation than the inverted counterpart (gravity-incompatible). Through two control experiments, we further confirmed that such a pupil dilation effect was attributed to the biological nature (i.e., the vertical acceleration pattern due to gravity and muscle activity) rather than the global shape. More interestingly, this effect could be extended to feet motion cues. These findings provide reliable evidence that pupil size is highly sensitive to gravity-dependent life motion signals.

In a natural environment, rapid detection and recognition of the movement trajectory of living organisms is an essential skill for survival and social interaction. Upright BM cues, as the most typical socially salient stimulus, enjoy strong priority in the vision system (Wang et al., 2010). Conversely, the inverted counterparts severely changed gravity-related clues, and thus are short of meaningful biological signatures. For example, 2-day-old infants have been shown to preferentially look at upright BM displays rather than inverted ones in a visual preference task (Klin et al., 2009). This preference is not only observed in humans, but also widely observed in vertebrate animals (Vallortigara & Regolin, 2006; Vallortigara et al., 2005) and even aquatic animals (Ma et al., 2022). Our main findings that the pupil dilates in response to the upright relative to the inverted BM information are consistent with these studies.

Another critical finding that perception of local feet motion cues also elicits enlarged pupillary responses is in line with previous studies that suggest the special role of local feet kinematics in BM perception (Gurnsey et al., 2010; Saunders et al., 2009; Troje & Westhoff, 2006; Wang et al., 2014). A wealth of behavioral and neuroimaging studies has shown that people can process local BM cues independent of the global configuration of the display (Chang & Troje, 2009; Chang et al., 2018; Saunders et al., 2009; Wang et al., 2014). Hence, it is proposed that humans are endowed with the innate ability to detect the limb movements of other vertebrates (Johnson, 2006; Troje & Westhoff, 2006). Along

with this view, local BM processing, which does not rely on postnatal experience, has been demonstrated to be heritable and subserved by a subcortical neural network (Chang et al., 2018; Wang et al., 2018). In the current study, we further demonstrated that pupil size could respond to feet motion cues. It should be noted that we adopted an active task in Experiment 4 to ensure that the participants noticed the biological nature of the feet motion cues, which inevitably made it different from other passive tasks (Experiments 1–3). This active task could potentially explain the earlier differentiation between the upright and the inverted BM signals in pupillary responses relative to that observed in the passive task. The modulation effects of task relevance and task demand on the time course of pupillary responses deserve further exploration.

Considering BMs are both biologically significant and functionally meaningful stimuli, it is plausible that our findings are directly related to the pupil-linked arousal mechanism. It has been shown that the fluctuations in pupil size under constant luminance are positively correlated with the level of the central arousal state (Bradley et al., 2008; Bradshaw, 1967), which is mainly modulated by the locus coeruleus norepinephrine (LC-NE) system (Gilzenrat et al., 2010; Murphy et al., 2014). In line with this, life motion signals, as socially salient stimuli, presumably increase the arousal level through the LC-NE system, which leads to pupil dilation. This explanation is in accord with many previous studies, in which the same pupil dilation effect is initiated by several other bio-social relevant stimuli with high salience, such as emotional face, human body, and social interactive agents (Cheng et al., 2021; Tamietto et al., 2009; Williams et al., 2019).

Of note, besides the significant pupil dilation effect in the study, we also observed a mild pupil constriction effect around 500–1,000 ms across Experiments 1–3 after the upright relative to the inverted BM configuration was shown (although not significant after correction). Such a pupil constriction effect may originate from orienting of attention (Strauch et al., 2022). The global configuration of the upright BM, which still has some biological attributes, probably elicited stronger attention engagement than that of the inverted ones, which in turn leads to the slightly increased pupil constriction (Binda et al., 2013; Mathôt et al., 2013).

Finally, the current findings provide the basis for future investigations of life motion perception or its deficiency using pupillometry, especially on preverbal (e.g., infants) or nonverbal participants (e.g., animals, neurological patients). For example, autism spectrum disorder (ASD) has been associated with substantial deficits in life motion perception, which may be indicated by their pupillary responses (de Vries et al., 2021; Todorova et al., 2019). As opposed to other eye movement indicators (eye fixation, looking

preference, etc.), pupillary responses are regulated by the autonomic nervous system and are largely immune to voluntary control (Laeng et al., 2012). Accordingly, pupillary responses can be applied to some circumstances where other indicators are not applicable, and might gain more insight into the involuntary aspects of socio-cognitive processing. Future investigations are encouraged to evaluate the potential application of the eye pupil in clinical assessment of socio-cognitive disorders including ASD.

In sum, the eye pupil can signal animacy perception and life motion detection, which is independent of the global configuration of BM but critically relies on the local motion cues. Going beyond the biological motion signals, there are other motion signals that also provide cues for animacy perception, such as speed-change stimuli (Rosa-Salva et al., 2016). Whether such a pupil dilation effect is ubiquitous in the perception of animated stimuli remains to be established in future investigations (Buiatti et al., 2019; Salva et al., 2015).

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Data availability All data and code have been made publicly available via the Institutional Knowledge Repository, Institute of Psychology, Chinese Academy of Sciences, and can be accessed at <http://ir.psych.ac.cn/handle/311026/42248>.

Author contributions All authors contributed to the study design. Y.C. collected the data and performed the data analysis under the supervision of X.Y. and Y.J. Y.C. drafted the manuscript, and X.Y. and Y.J. provided critical revisions. All authors approved the final version of the manuscript for submission.

Declarations

Conflict of interest The authors declare no competing financial interest.

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