LETTER TO THE EDITOR

Cortical Contributions to Local and Global Biological Motion Perception: Insights from Transcranial Magnetic Stimulation

**Lianzi Xing[1] · Zhongju Sun[1,2] · Yushu Wang[1,2] ·
Yiru Bao[1,2] · Peng Cai[3] · Rui Wang[1,2] · Yi Jiang[1,2]**

Dear Editor,

The movements of living entities carry rich biological and social information (e.g., direction, action, identity, and emotion), which is fundamental for human survival and social interaction. The human visual system has evolved to efficiently recognize biological motion (BM), even from simplified point-light displays (PLDs) depicting only the person's major joints. Theoretical work suggests that BM perception is mediated by multi-level mechanisms involving the processing of two distinct visual cues: local motion signals from individual joints (local BM cues) and the spatiotemporally integrated body configuration (global BM cues) [1].

Beyond aiding motion-mediated structure recovery, local BM signals contain unique biological properties and can be

Lianzi Xing and Zhongju Sun contributed equally to this work.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12264-026-01604-7.

✉ Peng Cai
caipeng@pku.edu.cn

✉ Rui Wang
wangr@psych.ac.cn

✉ Yi Jiang
yijiang@psych.ac.cn

1 State Key Laboratory of Cognitive Science and Mental Health, Institute of Psychology, Chinese Academy of Sciences, Beijing 100101, China

2 Department of Psychology, University of Chinese Academy of Sciences, Beijing 100049, China

3 School of Psychological and Cognitive Sciences, Beijing Key Laboratory of Behavior and Mental Health, Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing 100871, China

processed independently of global configuration. Specifically, observers can discriminate the moving direction and perceive animacy from scrambled point-light BM sequences [2]. This sensitivity appears innate, as shown by its early emergence in life, strong genetic determination, and resistance to postnatal learning experiences. The preference for local BM over non-BM patterns across species (e.g., chicks) further supports its evolutionary origins [3]. Crucially, local motion processing shows strong orientation dependency, as inverted displays severely impair perception, indicating gravity-constrained motion patterns as a key information source [4, 5]. These findings inspired the "life motion detector" theory, which posits an intrinsic visual mechanism tuned to the characteristic kinematics of animate motion, facilitating rapid and effective detection of biological agents in the environment [6].

How does the brain extract life motion signals from complex visual scenes? A key question is whether BM perception relies on dedicated neural mechanisms for social perception or can be explained by general-purpose motion processing. While behavioral findings support the existence of a specialized life motion detection mechanism, its neural implementation remains unclear. Neuroimaging studies have revealed a broad brain network activated by point-light animations, spanning the dorsal and ventral visual pathways, converging at the posterior superior temporal sulcus (pSTS), and extending to parietal and frontal regions [7]. Within this network, pSTS emerges as a critical node for BM processing, exhibiting robust selectivity for body movements in both humans and non-human primates. Brain stimulation evidence further confirms its causal role in action detection and directional discrimination of BM stimuli [8, 9]. However, these findings are primarily derived from intact PLDs containing both local and global cues, leaving it unclear whether pSTS processes the full spectrum of BM signals,

from local kinematics to global structure. Meanwhile, the human middle temporal complex (hMT+), a key region of the canonical motion system that encodes basic visual motion properties (e.g., direction, speed) [10], also responds to biological kinematic patterns [11]. Beyond cortical areas, recent evidence indicates that evolutionarily conserved subcortical structures contribute to the detection of BM cues [11, 12]. Collectively, while multiple motion-sensitive areas along the subcortical-cortical pathways are found responsive to local biological kinematics, their specific functional roles remain to be fully elucidated.

This study aimed to investigate the causal roles of cortical regions in processing local and global BM signals using transcranial magnetic stimulation (TMS). We focused on pSTS and hMT+, examining whether these two areas, previously implicated in BM and canonical motion processing, respectively, are necessary for the perception of life motion signals. Given the right hemisphere advantage for pSTS in BM processing, we administered off-line continuous theta burst stimulation (cTBS) to the right pSTS and hMT+, with both regions precisely localized in each participant using functional magnetic resonance imaging (fMRI). Participants performed motion direction discrimination tasks with three types of stimuli: intact BM (upright point-light walkers containing both local and global cues), scrambled BM (spatially scrambled point-light walkers isolating local cues), and coherent motion (random-dot kinematograms as a non-BM control) (Fig. 1A). This design allowed us to dissociate the cortical mechanisms underlying local and global BM processing and assess these neural substrates' specificity in distinguishing BM from non-BM.

Twenty-six participants underwent cTBS to the right pSTS and hMT+ in separate sessions (Fig. 1B), and their motion direction discrimination abilities for intact BM, scrambled BM, and coherent motion were measured before and after TMS. Figure 2 illustrates the group and individual accuracies for direction discrimination across all three tasks, comparing pre- and post-TMS performance at both

stimulation sites. A repeated-measures ANOVA with test phase (pre vs. post), stimulation site (pSTS vs. hMT+), and task type (intact BM, scrambled BM, coherent motion) as factors revealed a marginally significant three-way interaction ($F (2, 50) = 2.731$, $P = 0.077$, $\eta_p^2 = 0.098$), suggesting differential TMS effects across tasks and stimulation sites. We then conducted planned paired-samples t tests to evaluate specific effects on each task type. For intact BM, direction discrimination accuracy significantly decreased following pSTS stimulation (pre: 0.74 vs. post: 0.71, $t (25) = 2.815$, $P = 0.009$, Cohen's $d = 0.552$, 95% CI = [0.010, 0.064], $BF_{10} = 4.983$), but showed no significant change after hMT+ stimulation (pre: 0.75 vs. post: 0.74, $t (25) = 0.265$, $P = 0.794$, Cohen's $d = 0.052$, 95% CI = [−0.021, 0.027], $BF_{10} = 0.214$). In contrast, coherent motion discrimination accuracy decreased significantly following hMT+ stimulation (pre: 0.79 vs. post: 0.76, $t (25) = 2.698$, $P = 0.012$, Cohen's $d = 0.529$, 95% CI = [0.007, 0.053], $BF_{10} = 3.963$), but remained unaffected after pSTS stimulation (pre: 0.77 vs. post: 0.77, $t (25) = −0.174$, $P = 0.863$, Cohen's $d = −0.034$, 95% CI = [−0.033, 0.028], $BF_{10} = 0.210$). Notably, TMS delivered to either pSTS or hMT+ had no significant impact on direction discrimination of scrambled BM (pSTS, pre: 0.79 vs. post: 0.78, $t (25) = 0.682$, $P = 0.501$, Cohen's $d = 0.134$, 95% CI = [−0.018, 0.035], $BF_{10} = 0.256$; hMT+, pre: 0.79 vs. post: 0.78, $t (25) = 0.900$, $P = 0.377$, Cohen's $d = 0.176$, 95% CI = [−0.015, 0.040], $BF_{10} = 0.299$).

The TMS effects observed in our experiment were modest (approximately 3% decrease in accuracy for intact BM after pSTS stimulation and coherent motion after hMT+ stimulation), yet comparable to previous findings [9, 13]. Nevertheless, these results demonstrated dissociable roles of pSTS and hMT+ in processing intact BM and simple non-BM information, respectively. However, an important question remained: whether the absence of TMS effects on local BM perception genuinely reflected the functional independence of these regions or was merely a consequence of weak stimulation efficacy. To validate our primary observation that
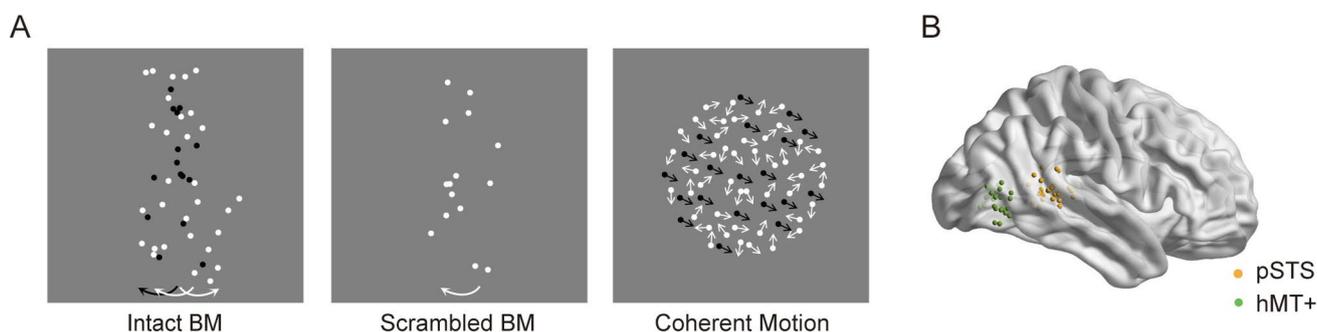

Fig. 1 Schematic of stimuli and TMS sites. **A** Intact point-light BM embedded in noise, scrambled BM, and coherent motion. Signal dots are rendered in black for illustration purposes, but in actual experiments, all the dots were displayed in white. **B** TMS sites of the right pSTS (yellow) and hMT+ (green) identified in each participant.

A

Right pSTS

Right hMT+

B

Fig. 2 Effects of TMS on motion direction discrimination tasks. **A** Group and individual accuracies for the three direction discrimination tasks before and after TMS at right pSTS and hMT+ ($n = 26$). Blue bars represent intact BM, red bars represent scrambled BM, and green bars represent coherent motion. Small open circles indicate individual data, with gray lines showing within-subject changes in accuracy. Error bars represent SEM. **B** TMS-induced changes in accuracy across different tasks and stimulation sites. Box plots display the median and interquartile range (25th–75th percentiles), with whiskers extending to the 5th and 95th percentiles. Smoothed density plots illustrate the distribution of individual data. Asterisks denote significant TMS effects (*$P < 0.05$; **$P < 0.01$).

neither pSTS nor hMT+ stimulation significantly disrupted performance in the scrambled BM condition, we conducted complementary analyses focusing on participants who exhibited effective TMS modulation of these two regions (Fig. S1). Specifically, we identified two subgroups of participants showing clear inhibitory TMS effects (decreased post-TMS accuracy): one for the intact BM task following pSTS stimulation ($n = 18$, pre: 0.76 vs. post: 0.69), and the other for the coherent motion task following hMT+ stimulation ($n = 17$, pre: 0.81 vs. post: 0.74). Crucially, despite these clear TMS effects, local BM performance remained unchanged in both subgroups (pSTS, pre: 0.77 vs. post: 0.77, $t(17) = 0.268$, $P = 0.792$, Cohen's $d = 0.063$, 95% CI = $[-0.030, 0.039]$, $BF_{10} = 0.251$; hMT+, pre: 0.80 vs. post: 0.80, $t(16) = 0.388$, $P = 0.703$, Cohen's $d = 0.094$, 95% CI

= $[-0.030, 0.043]$, $BF_{10} = 0.256$), further suggesting that pSTS and hMT+ are not critically required for the perception of local BM signals in this context.

The present study examined the causal roles of cortical regions in different aspects of BM processing. Combining TMS with motion direction discrimination tasks, we demonstrated a clear double dissociation: interference of the right pSTS selectively impaired intact BM perception without affecting local BM or coherent motion processing, whereas inhibition of hMT+ specifically disrupted coherent motion perception with no significant effects on either intact or local BM processing. These results advance our understanding of neural architecture underlying BM perception by highlighting that: (1) pSTS and hMT+ play distinct functional roles in processing different motion signals; and (2) the absence

of TMS effects on the scrambled BM direction discrimination task at either site suggests a distinct mechanism for processing local biological kinematics, in which pSTS and hMT+ may not constitute critical bottlenecks for local BM perception. These causal findings complement prior fMRI correlational evidence, providing direct mechanistic insights into BM processing.

The observed double dissociation corroborates and extends previous TMS evidence that right pSTS stimulation reduces sensitivity to intact BM [8, 9], whereas hMT+ stimulation disrupts coherent motion discrimination but not BM perception [10, 14]. Importantly, the selective disruption of intact BM perception by pSTS inhibition, while preserving local BM processing, suggests that pSTS is more essential for synthesizing comprehensive BM signals (e.g., integration of global form and motion information), rather than functioning as a general-purpose BM processor. This functional specialization aligns with its anatomical position, receiving convergent inputs from ventral form-processing and dorsal motion-sensitive pathways [7]. Furthermore, as a social brain network hub, pSTS processes diverse dynamic social cues, encompassing not only body movements but also facial expressions and eye gaze, thereby playing a vital role in social perception [15]. In contrast, hMT+ demonstrates specificity for coherent motion processing but not for BM perception-neither local joint movements nor integrated whole-body actions. Although neuroimaging work shows hMT+ activation during BM viewing [11], brain stimulation research indicates that this region does not constitute a necessary bottleneck for BM direction discrimination [10]. Therefore, while recruited for BM perception, the function of hMT+ seems more related to generic motion computations rather than BM-specific processing.

Despite containing motion signals, local BM processing was unaffected by TMS over pSTS and hMT+, suggesting that it may rely on neural mechanisms that are less dependent on these sites compared to general motion processing. This dissociation likely reflects the distinct computational demands of the tasks. Intact BM and coherent motion processing require the spatiotemporal integration of distributed elements, a computation critically dependent on the targeted cortical sites (pSTS and hMT+) [7, 11, 14]. In contrast, local BM perception relies more on the extraction of local kinematic cues from individual elements, probably obviating the need for such integration. The functional specialization for local BM is plausibly grounded in the distinctive kinematics of articulated animal locomotion, particularly ballistic or pendular motion with acceleration profiles shaped by gravitational effects [6]. Crucially, local BM perception shows strong orientation dependency, as inverted displays disrupt perception by violating expected gravitational constraints [6]. This gravity-dependent sensitivity, likely evolved through long-term ecological interactions, enables the visual system to use vertical acceleration as a key cue for rapidly detecting biological agents. Converging evidence from developmental and comparative studies supports the innate nature of this specialized processing mechanism. For instance, two-day-old infants manifest a spontaneous preference for local BM animations [16], and genetic factors play a significant role in shaping individual differences in local BM perception [17]. Similarly, newly hatched chicks exhibit an innate predisposition towards the BM of a predator even when the global configuration is disrupted [3]. These early-emerging capabilities manifest when cortical structures are still immature. Researchers speculate that this cross-species mechanism for life motion detection originates in primitive, homologous subcortical brain regions. In support of this hypothesis, recent neuroimaging studies have demonstrated that subcortical areas, including the ventral lateral nucleus [11] and the superior colliculus (SC) [12], selectively respond to local biological kinematics. Functional connectivity analysis reveals a feedforward subcortical-cortical pathway transmitting local BM signals from the SC to the STS *via* the hMT+. Collectively, these results establish the involvement of subcortical networks in local BM processing and underscore specialized neural mechanisms distinct from general motion processing. However, fundamental questions about how local kinematic signals are routed and integrated for comprehensive BM analysis remain to be further explored.

Based on evidence from behavioral and neurophysiological studies, the two-process theory of BM perception provides a robust framework for understanding the hierarchical nature of BM processing [5]. This model proposes two distinct stages: an initial "step detector" stage that rapidly extracts local biological kinematics through the subcortical network, and a subsequent "bodily action evaluator" stage that processes the fine global structure-from-motion information *via* cortical pathways. In line with this framework, our findings suggest that local BM processing may operate at an earlier stage of visual processing, whereas global BM perception recruits distributed cortical networks. The organization of local and global BM processing parallels the dual-process face perception model [18], which delineates two mechanisms: CONSPEC, an innate subcortical system for rapid face detection and basic feature extraction, and CONLERN, an experience-dependent cortical system for more sophisticated face processing. Analogously, just as CONSPEC enables rapid face detection prior to detailed analysis by CONLERN, a subcortical "step detector" may facilitate quick detection of biological kinematics before more fine-grained action analysis by cortical networks. The presence of such parallel processing architectures in both face and BM perception suggests an evolutionarily conserved neural strategy for processing essential bio-social information,

optimized to efficiently detect diverse social signals crucial for survival across species.

In summary, this TMS study provides causal evidence for distinct neural mechanisms underlying BM processing. By temporarily disrupting cortical function, we demonstrated that pSTS and hMT+ are causally necessary for global BM and coherent motion processing, respectively, while sparing local biological kinematics perception. This functional dissociation, together with previous findings, suggests that local BM processing likely engages alternative neural mechanisms, potentially including subcortical pathways. These results not only advance our understanding of the hierarchical organization of BM processing but also highlight the flexibility of the human visual system in extracting socially relevant information through multi-level mechanisms. However, given the inter-individual variability in pSTS responsiveness and our reliance on functional localization for TMS targeting, these conclusions most directly generalize to individuals exhibiting robust pSTS activation in the fMRI localizer. Importantly, the null TMS effects on local BM processing warrant careful interpretation. Several methodological factors, such as stimulation intensity, cortical depth, targeting precision, and task sensitivity, may have influenced stimulation efficacy, raising the possibility that subtle TMS effects at the tested cortical sites remained undetected. Specifically, the direction discrimination task used in this study may not be sensitive enough to capture subtle impairments in fine-grained kinematic perception, or it may fail to adequately activate other attributes (e.g., animacy) relevant to broader local BM information processing. Consequently, it is plausible that TMS-induced disruption reduced perceptual fidelity or perturbed the processing of higher-order dimensions, without necessarily lowering accuracy on a simple directional judgment. In addition, beyond these methodological considerations, the extraction of local motion signals might be supported by a highly distributed and redundant neural network that is resilient to focal disruption. Given the limited spatial coverage of our stimulation protocol, we cannot rule out contributions from other cortical regions or compensatory interactions within a broader network sustaining local BM processing. Future investigations could employ advanced neuromodulation approaches (e.g., transcranial ultrasound stimulation to maximize focal precision and engage deeper brain regions), combined with high-resolution neuroimaging and carefully designed behavioral tasks, to better delineate the neural mechanisms and functional networks underlying BM processing, with particular attention to cortico-subcortical interactions and their temporal dynamics across visual processing stages.

References

1. Troje NF, Chang DHF. Shape-independent processing of biological motion. In: People watching: Social, perceptual, and neurophysiological studies of body perception. New York: Oxford University Press, 2013: 82–100. https://doi.org/10.1093/acprof:oso/9780195393705.003.0006.
2. Chang DHF, Troje NF. Perception of animacy and direction from local biological motion signals. J Vis 2008, 8(5): 3.1–10.
3. Vallortigara G, Regolin L, Marconato F. Visually inexperienced chicks exhibit spontaneous preference for biological motion patterns. PLoS Biol 2005, 3: e208.
4. Shen L, Yang X, Jiang Y, Wang Y. Understanding biological motion through the lens of animate motion processing. Front Psychol 2025, 16: 1630742.
5. Hirai M, Senju A. The two-process theory of biological motion processing. Neurosci Biobehav Rev 2020, 111: 114–124.
6. Troje NF, Westhoff C. The inversion effect in biological motion perception: Evidence for a "life detector"? Curr Biol 2006, 16: 821–824.
7. Giese MA, Poggio T. Neural mechanisms for the recognition of biological movements. Nat Rev Neurosci 2003, 4: 179–192.
8. Grossman ED, Battelli L, Pascual-Leone A. Repetitive TMS over posterior STS disrupts perception of biological motion. Vision Res 2005, 45: 2847–2853.
9. Vangeneugden J, Peelen MV, Tadin D, Battelli L. Distinct neural mechanisms for body form and body motion discriminations. J Neurosci 2014, 34: 574–585.
10. Mather G, Battaglini L, Campana G. TMS reveals flexible use of form and motion cues in biological motion perception. Neuropsychologia 2016, 84: 193–197.
11. Chang DHF, Ban H, Ikegaya Y, Fujita I, Troje NF. Cortical and subcortical responses to biological motion. Neuroimage 2018, 174: 87–96.
12. Lu X, Hu Z, Xin Y, Yang T, Wang Y, Zhang P. Detecting biological motion signals in human and monkey superior *Colliculus*: A subcortical-cortical pathway for biological motion perception. Nat Commun 2024, 15: 9606.
13. Basil RA, Westwater ML, Wiener M, Thompson JC. A causal role of the right superior temporal sulcus in emotion recognition from biological motion. Open Mind 2017, 2: 26–36.
14. Cai P, Chen N, Zhou T, Thompson B, Fang F. Global versus local: Double dissociation between MT+ and V3A in motion processing revealed using continuous *Theta* burst transcranial magnetic stimulation. Exp Brain Res 2014, 232: 4035–4041.
15. Pitcher D, Ungerleider LG. Evidence for a third visual pathway specialized for social perception. Trends Cogn Sci 2021, 25: 100–110.

16. Bardi L, Regolin L, Simion F. Biological motion preference in humans at birth: Role of dynamic and configural properties. Dev Sci 2011, 14: 353–359.

17. Wang Y, Wang L, Xu Q, Liu D, Chen L, Troje NF, *et al*. Heritable aspects of biological motion perception and its covariation with autistic traits. Proc Natl Acad Sci U S A 2018, 115: 1937–1942.

18. Morton J, Johnson MH. CONSPEC and CONLERN: A two-process theory of infant face recognition. Psychol Rev 1991, 98: 164–181.