Heritable aspects of biological motion perception and its covariation with autistic traits

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The ability to detect biological motion (BM) and decipher the meaning therein is essential to human survival and social interaction. However, at the individual level, we are not equally equipped with this ability. In particular, impaired BM perception and abnormal neural responses to BM have been observed in autism spectrum disorder (ASD), a highly heritable neurodevelopmental disorder characterized by devastating social deficits. Here, we examined the underlying sources of individual differences in two abilities fundamental to BM perception (i.e., the abilities to process local kinematic and global configurational information of BM) and explored whether BM perception shares a common genetic origin with autistic traits. Using the classical twin method, we found reliable genetic influences on BM perception and revealed a clear dissociation between its two components—whereas genes account for about 50% of the individual variation in local BM processing, global BM processing is largely shaped by environment. Critically, participants' sensitivity to local BM cues was negatively correlated with their autistic traits through the dimension of social communication, with the covariation largely mediated by shared genetic effects. These findings demonstrate that the ability to process BM, especially with regard to its inherent kinetics, is heritable. They also advance our understanding of the sources of the linkage between autistic symptoms and BM perception deficits, opening up the possibility of treating the ability to process local BM information as a distinct hallmark of social cognition.

biological motion | behavioral genetics | twins | autistic traits | social cognition

The movements of living creatures, termed as biological motion (BM), provide rich and meaningful information that facilitates social interaction (1, 2). Intrinsically social, humans have an extraordinary ability to readily detect and recognize BM signals, even when the visual cues were comprised solely of a few point lights attached to the head and the major joints of the body (3–6). This ability is considered a hallmark of social cognition, inasmuch as impaired visual processing of BM is inextricably linked to compromised social cognitive abilities in neurodevelopmental disorders (7). A prominent finding is that autism spectrum disorder (ASD), a highly prevalent and heritable disorder (8), is usually accompanied with abnormal perceptual and neural responses to BM cues; however, the mechanisms underlying such association remain elusive as the effect is complicated, varying with factors such as age and task demands (9–20). What are the sources of individual differences in biological motion perception? Do genetic factors contribute to its association with the impaired social cognitive skills related to autistic symptomatology?

The present study investigated these issues using behavioral genetic methodology. We specifically aimed to examine two fundamental abilities underlying BM perception (Fig. 1): namely, the ability to process local motion cues that trace the movements of critical joints (i.e., local BM processing) (21–25) and the ability to process global configuration cues representing the skeletal structure (i.e., global BM processing) (22, 26–28). [Note that the terms "global" and "local" have been used in many different ways in visual processing (29–31). Here, we use these terms in a very particular context to dissociate the utilizations of different cues in BM perception.] It has been shown that local BM cues, extracted by spatially scrambling intact BM stimuli, can convey animacy and walking direction information, all without participants' explicit attention or recognition, and the processing of such cues is less affected by the learning effects or when they are presented in masking noise or in the visual periphery (21–23, 25, 32–36). By contrast, the processing of global BM configurations, in the case where local BM cues were rendered ineffective, requires attention, is susceptible to the learning effects, and is heavily hindered by masking noise or by peripheral presentation (22, 37, 38). Moreover, inversion of BM stimuli not only disrupts the global BM processing but also the local BM processing (23), suggesting that the global and local mechanisms might play independent roles in BM perception. The great distinction between the visual processing of local and global BM cues may be partially explained by the anatomical and functional dissociations of the motion and form pathways engaged in BM perception (39–41) whereas the exact mechanisms responsible for the dissociation remain to be delineated. In the current study, we set out to examine to what extent the individual differences in the abilities to process local and global BM cues and the distinction between them are mediated by genetic factors.

To assess the genetic contribution to the perception of BM information, particularly the abilities to process local and global BM cues, we adopted intact and scrambled BM sequences combined with different behavioral measures (Fig. 2). These measures have been successfully applied to examine the local and global components of BM perception (22, 23, 27). We administered these measures to both monozygotic (MZ) and dizygotic (DZ)

Significance

Impaired visual processing of biological motion (BM) is inextricably linked to compromised social cognitive abilities in autism spectrum disorder (ASD). Using behavioral genetic methodology, we demonstrate that genes contribute to interindividual variation in BM perception abilities and autistic traits. More importantly, the ability to process the local motion rather than the global configuration of BM is heritable, and the former is negatively correlated with autistic traits, with the covariance mainly attributable to shared genetic factors. These findings provide evidence that the ability to process BM and its close connection with social cognitive skills have a genetic basis and highlight the potential for treating the ability to process local BM information as a distinct hallmark of social cognition.

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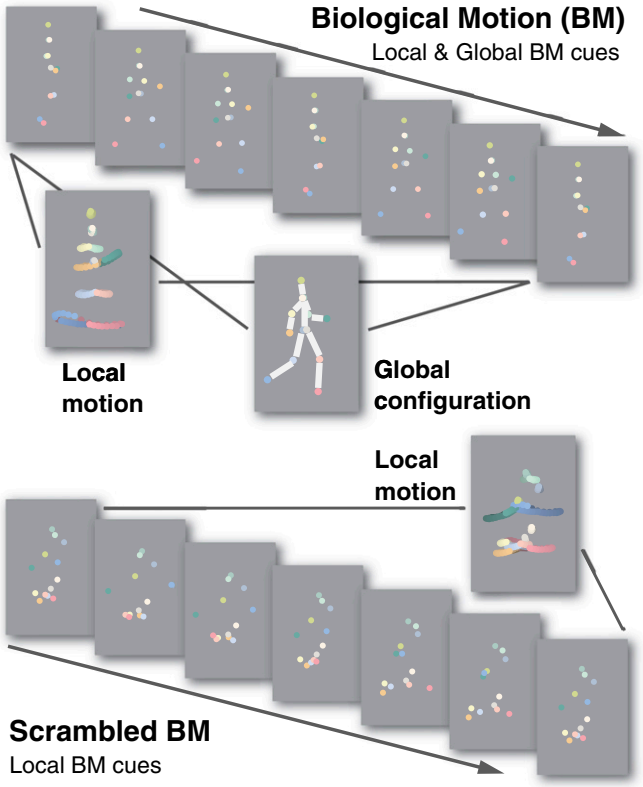

Fig. 1. Illustrations of the intact and spatially scrambled BM sequences, as well as the global and local BM cues conveyed by these stimuli. The intact BM sequence comprises two types of BM cues: i.e., the local motion cue defined by the movements of individual joints (indicated by chromatic trajectories), and the global configuration cue defined by the skeletal structure (indicated by white lines). In the scrambled BM sequence, the global configuration is entirely disrupted by randomly displacing the dots within the restricted display area. However, the local motion signal conveyed by each dot remains the same as that in the intact BM sequence.

twin pairs. With this twin design, we were able to employ individual differences to estimate the genetic and environmental influences on the observed phenotypes, based on the principle that MZ twins and DZ twins share the environmental influence to the same degree, whereas MZ twins share more genes than DZ twins and thus should be more similar in heritable traits (42).

Results

Genetic Contributions to Local BM Processing. To assess participants' ability to process local BM cues, we adopted a motion direction discrimination task on spatially scrambled point-light walkers (experiment 1; Fig. 2, BM-Loc). These scrambled stimuli, devoid of any global structure of the animate agents, still convey information about walking direction and have been successfully applied to probe local BM processing (21–25). Despite that all of the twin participants were naive to the point-light BM displays and were not informed of the nature of the scrambled walkers, their overall discrimination performance was above chance level (Table S1), manifesting an inherent sensitivity to local BM information. To examine to what extent the variance of this ability across individuals was genetically determined, we estimated the familial similarity for MZ and DZ twin pairs, respectively, by calculating the intraclass correlations (ICCs) between the twin pairs. The intraclass correlation of MZ twin pairs was more than twice the DZ correlation (0.52 vs. −0.01) (Fig. 3*A*), suggesting that genes make a substantial contribution to the individual differences in the perception of local BM cues. We further partitioned the phenotypic variation into components due to additive genetic (A), common environmental (C), and nonshared environmental (E) effects (Table 1 and Fig. 3*B*), according to univariate genetic analyses (*SI Materials and Methods*). The heritability, i.e., the proportion of variance that can be accounted for by genetic factors, was estimated to be 48% [95% confidence interval (CI): 26 to 64%, goodness of fit of the AE model: $\chi^2(4) = 4.02$, $P = 0.4$, Akaike information criterion (AIC) = −3.98], suggesting a prominent role of genetic factors in mediating local BM perception.

Common Environment Shapes Global BM Processing. Experiment 1 demonstrates that the ability to process local BM information is significantly influenced by genetic factors. Do genetic factors also contribute to the visual processing of the global configuration of BM? To answer this question, we asked participants to detect intact point-light walkers embedded in dynamic noise. The noise was composed of spatially scrambled walkers which retained pure local motion cues so as to mask the local motion information in the target (experiment 2; Fig. 2, BM-Glb). In this case, the local motion cues provided by the display were uninformative, and the observers had to extract the global configuration of the intact walker for successful target detection. Therefore, the detection accuracy reflects the observer's ability to process global BM information (22, 27). In contrast to the local BM perception experiment, in this global BM task, MZ twin pairs did not show a difference from DZ twin pairs in ICC (0.41 vs. 0.39) (Fig. 3*A*), indicating the absence of genetic influences. Instead, common environmental factors explain 43% (95% CI: 27 to 56%) of the phenotypic variation [goodness of fit of the CE model: $\chi^2(4) = 5.50$, $P = 0.24$, AIC = −2.50; Table 1 and Fig. 3*B*], suggesting that environmental factors rather than an innate mechanism shape global BM processing.

Genetic and Environmental Influences on BM Perception. The first two experiments demonstrate genetic and environmental influences on local and global BM processing, respectively. In experiments 3 and 4, we further examined the relative roles of genes and environment in BM perception without isolating the local or the global component (22, 43), which provides a baseline condition for BM perception in general. Participants were required to judge the walking direction (left or right, as in the BM-Loc experiment) of an intact point-light walker embedded in a scrambled mask (as in the BM-Glb experiment). The mask was set to convey local BM cues in the same direction as the target walker (experiment 3; Fig. 2, BM_1), or to consist of direction-balanced local BM cues to eliminate its potential influence on target walking direction discrimination (experiment 4; Fig. 2, BM_2). In either case, participants could rely on both the global and local BM cues to complete the task, and their performance was better than that in the first two experiments in which only the local, or the global, BM cues were informative according to specific experimental designs (Table S1). Moreover, participants' performance in the general BM perception experiment (experiment 3 had the same twin participants as experiments 1 and 2 did) was significantly correlated with their performance in both the local ($r = 0.41$, $P < 0.001$) and the global ($r = 0.20$, $P = 0.002$) BM perception experiments while their abilities to process local and global BM information were independent of each other ($r = 0.07$, $P = 0.27$).

Despite the difference in experimental settings, the two general BM perception experiments produced quite consistent patterns of the ICC results and the ACE modeling results. In support of the heritability of general BM processing, both experiments demonstrated higher ICCs for MZ twin pairs than for DZ twin pairs (BM_1: 0.33 vs. 0.22; BM_2: 0.42 vs. 0.23) (Fig. 3*A*). Further genetic modeling analysis based on the full ACE model revealed combined effects of genetic and common environmental factors (Table 1 and Fig. 3*B*). The heritability was estimated to be 37% [95% CI: 16 to 55%; goodness of fit of the AE model: $\chi^2(4) = 2.50$, $P = 0.65$, AIC = −5.50] and 44% [95% CI: 13 to 66%; goodness of fit of the AE model: $\chi^2(4) = 1.72$, $P = 0.79$, AIC = −6.28] for the two general BM perception experiments (BM_1 and BM_2), respectively.

These results, together with the findings from the local and global BM perception experiments, consistently suggest that

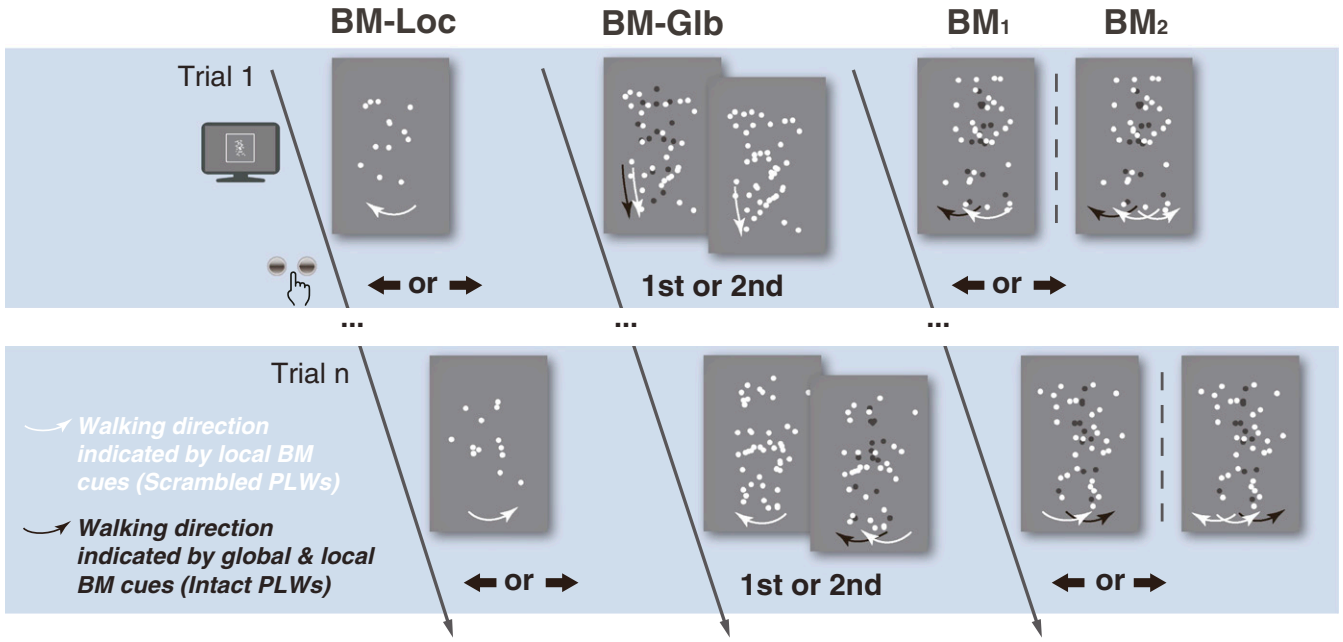

Fig. 2. Experimental paradigms for assessing the participants' abilities to process local, global, and general BM information, respectively. In the local BM perception (BM-Loc) experiment, participants judged the intended locomotion direction (left or right) of a scrambled point-light walker based on local BM cues. In the global BM perception (BM-Glb) experiment, participants judged which of two successively presented intervals contained an intact target walker (with 10 possible walking directions) embedded in a mask comprised of spatially scrambled walkers. Since the two intervals conveyed identical local motion cues, successful detection required the extraction of the global configuration of the target walker. In the general BM perception experiments (BM_1 and BM_2), participants judged the walking direction (left or right) of an intact target walker embedded in a mask consisted of scrambled walkers with the same direction as the target walker or with balanced left and right walking directions. In both cases, participants could rely on global and local BM cues conveyed by the target (along with local BM cues provided by the mask in BM_1) to discriminate the walking direction of the target walker. The point-light walkers embedded in the masks were rendered in black for illustration only. All dots were rendered in white in the experiments.

both genetic and environmental factors influence the ability of BM perception, with the local component substantially accounted for by genetic disposition and the global component largely shaped by common environment.

A Common Genetic Basis for Local BM Processing Ability and Autistic Traits. Motivated by the strong association between compromised visual BM processing ability and ASD (9, 10, 12–18), and the current finding that the specific ability to process local BM information is heritable, we further explored whether local BM processing ability shares a common genetic basis with one's autistic traits. We first measured the autistic traits of the participants using an adapted version of the Autism-Spectrum Quotient (AQ) (44) (*SI Materials and Methods* and Table S2). Univariate genetic analysis revealed a substantial genetic contribution to autistic traits: MZ twins had a higher intraclass correlation than DZ twins (0.58 vs. 0.36) (Table S1), with the heritability estimated at 60% [95% CI: 43 to 73%; goodness of fit of the AE model: $\chi^2(4) = 0.51$, $P = 0.97$, AIC = −7.49] (Table 1). These results are consistent with previous findings of moderate to high heritability for autistic traits in the general population (8, 45). Moreover, the estimated heritability is comparable with that obtained when autistic traits are assessed using the complete AQ questionnaire (46). Furthermore, we found that participants with higher levels of autistic traits performed worse in perceiving local BM information: i.e., their ability to process local BM cues negatively correlated with their autistic traits ($r = -0.15$, $P = 0.02$), particularly on the subdimension of communication ($r = -0.19$, $P = 0.004$) (see Table S2 for complete information about the subdimensions of the AQ questionnaire). Bivariate genetic analysis further revealed that shared genetic effects can account for 75% of the covariance between local BM processing ability and autistic traits and 83% of the covariance between local BM processing ability and communication scores (*SI Materials and Methods*), suggesting a common genetic basis for these phenotypes. Note that, although the ability to process global configuration also correlated with autistic traits ($r = -0.14$, $P = 0.03$) and communication scores ($r = -0.19$, $P = 0.003$), such covariance may be largely explained by environmental factors due to the lack of heritability of global BM processing. Collectively, these results indicate that local BM processing ability and autistic traits share common genetic influences, highlighting the existence of genetic pleiotropy between these phenotypes.

Discussion

The current study investigated the heritability of two fundamental abilities underlying BM perception. We found that the ability to process the local kinematics of BM is substantially influenced by genetic disposition whereas the ability to process the global configuration of BM is largely shaped by environmental factors. Moreover, when both local and global BM cues were informative for perception, we observed a combined effect of genes and shared environment, with the heritability estimated in between that for local BM processing and that for global BM processing. These findings provide direct empirical evidence for the prevailing assumption that the ability to perceive BM, conserved across a wide range of species (47–50), is an intrinsic capacity of the visual system developed through the long history of evolution (5). More importantly, by disentangling the genetic roots of the two major components underpinning BM perception, the current study provides a differentiated solution to the "nature-or-nurture" problem of BM perception, thereby extending the theoretical account that BM perception should be regarded as a multilevel phenomenon (35, 51, 52) from a genetic perspective.

Previous studies have shown that human neonates with less than 24 h of visual experience, as well as newly hatched domestic chicks with no visual experience at all, manifest a spontaneous preference for biological over nonbiological motion stimuli (50, 53).

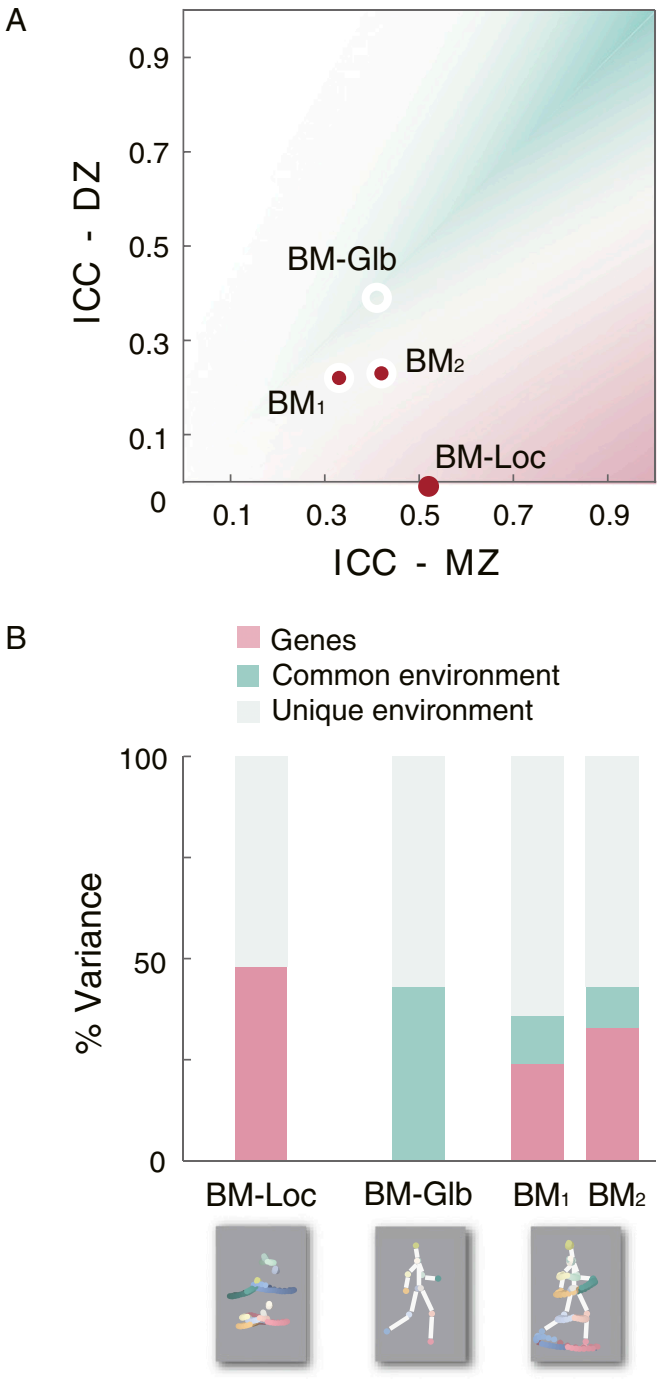

Fig. 3. Results of the BM-Loc, BM-Glb, and general BM perception (BM_1 and BM_2) experiments. (*A*) Intraclass correlation coefficients for MZ and DZ twins (see Table S1 for 95% confidence intervals). The contrast between the local and the global components, i.e., $ICC_{MZ} > 2 \times ICC_{DZ}$ for BM-Loc vs. $ICC_{MZ} \approx ICC_{DZ}$ for BM-Glb, reveals the dominance of genetic and environmental influences, respectively. (*B*) Proportions of the observed phenotypic variance attributable to additive genetic, common environmental, and unique environmental factors based on the full ACE model. Note that heritability was estimated based on the best-fitting submodels reported in Table 1.

Based on our findings, we postulate that, to the newborn's visual system, the cue crucial in triggering preference toward BM might lie in the local motion rather than the global configuration (35), despite that configurational information may latter gain more importance in BM perception at adult age. This view is consistent with the findings from several cross-species infant studies. For instance, human newborns preferred to look at point-light biological motion even if it depicted another species' shape (i.e., a walking hen) (53), and visually inexperienced chicks exhibited a spontaneous preference toward the BM of a predator (cat) or even when the global configuration was entirely disrupted through spatial scrambling (50). Moreover, there was equal inborn preference when intact BM and its spatially scrambled counterpart were directly compared (50, 54). These studies demonstrate that the sensitivity to local rather than global BM cues emerges early in life, implying the existence of an inbuilt mechanism specifically tuned to local BM signals. The current study provides direct evidence for this assumption and suggests that the distinction between the developmental courses of local and global BM processing may stem from the dissociation with regard to their genetic bases. In particular, our findings point to two dissociable mechanisms respectively underlying local motion processing and global configuration processing, with the former to a great extent acquired phylogenetically and the latter mainly obtained through ontogenesis.

In a broader sense, the dissociation of heritability of local and global BM processing can be understood in terms of their functions analogous to that of the innate and the acquired mechanisms in face perception (55). According to Morton and Johnson's model (55), an innate system termed CONSPEC serves to guide one's attention toward faces since birth, which ensures that the developing visual system receives ample exposure to this essential stimulus class. In addition, a second ontogenetically acquired system termed CONLERN is responsible for learning more about the specific forms of the stimulus class (e.g., identity). The local and global mechanisms for BM perception might function in a manner similar to that of CONSPEC and CONLERN, with the former serving as a detection mechanism that automatically directs attention to animate agents in the environment (22, 25, 33, 53, 56) and the latter aiding in more specific identification of the agents based on fine analyses of their articulated shape. Compatible with this view, during the first few months of life, the human infant's neural system manifests advantageous and generalized responses to animate signals in the environment, and it may take several years for such a life detection system to eventually develop into a functionally sophisticated social brain network in which the processing of face, BM, and other important social cues becomes highly specialized (57).

Along with the studies on face perception, results of the current study provide insights into both the origin and the functional development of the human social brain. On the one hand, the heritability of local BM processing and the previous observations that the abilities specifically related to face perception is also heritable (58, 59) offer corroborating evidence for the existence of inherent neural mechanisms tuned to biological signals at the core of the social brain. On the other hand, the innate mechanism for local BM processing and the acquired mechanism for global BM processing substantiate and generalize the CONSPEC and CONLERN systems originally proposed for face perception, providing strong evidence that genetic and environmental factors work in tandem to shape the functional maturation of the social brain.

The current findings also have far-reaching implications for our comprehensive understanding of individual differences in BM perception, especially its relationship with ASD. While typically developing children show endogenous preference and tremendous sensitivity to BM, such abilities are usually compromised in children with ASD (9, 10, 14, 15). Interestingly, however, the impaired sensitivity to BM is not always observed with autistic adolescents and adults (11, 12, 19, 20), yet neuroimaging studies otherwise demonstrate that these individuals show abnormal activities in the neural circuit dedicated to BM processing (12, 17, 18). Despite the complexity in these observations, the current study offers evidence for the linkage between BM processing and autistic traits by demonstrating that the ability to process local BM cues correlates with individual autistic traits on a common genetic basis. The ability to process global configuration also correlates with autistic

Table 1. Results of univariate genetic analyses for the full models and the best-fitting submodels (based on AIC values)

		Parameter estimates			Fit statistics			
Phenotype	Model*	a^2 (95% CI)	c^2/d^2 (95% CI)	e^2 (95% CI)	χ^2	df	*P*	AIC
BM-Loc	ACE	0.48 (0.18, 0.64)	0 (0, 0.21)	0.52 (0.36, 0.74)	4.02	3	0.26	−1.98
	AE	0.48 (0.26, 0.64)	—	0.52 (0.36, 0.74)	4.02	4	0.40	−3.98
	ADE	0 (0, 0.57)	0.52 (0, 0.67)	0.48 (0.33, 0.68)	1.20	3	0.75	−4.80
BM-Glb	ACE	0 (0, 0.53)	0.43 (0, 0.56)	0.57 (0.41, 0.73)	5.50	3	0.14	−0.50
	CE	—	0.43 (0.27, 0.56)	0.57 (0.44, 0.73)	5.50	4	0.24	−2.50
BM_1	ACE	0.24 (0, 0.54)	0.12 (0, 0.44)	0.64 (0.46, 0.87)	2.31	3	0.51	−3.69
	AE	0.37 (0.16, 0.55)	—	0.63 (0.45, 0.84)	2.50	4	0.65	−5.50
BM_2	ACE	0.33 (0, 0.66)	0.10 (0, 0.57)	0.57 (0.34, 0.89)	1.67	3	0.64	−4.33
	AE	0.44 (0.13, 0.66)	—	0.56 (0.34, 0.87)	1.72	4	0.79	−6.28
Autistic traits	ACE	0.51 (0, 072)	0.08 (0, 0.48)	0.41 (0.28, 0.60)	0.40	3	0.94	−5.60
	AE	0.60 (0.43, 0.73)	—	0.40 (0.27, 0.57)	0.51	4	0.97	−7.49

*The ACE/ADE full model includes additive genetic (A), common environmental (C)/dominance genetic (D), and unique environmental (E) factors. The submodels include only two or one of the factors. Results from the best-fitting ACE submodels are reported here.

traits, but such correlation is not genetically determined since the global BM processing ability, which might also involve more general cognitive skills, is largely shaped by environmental factors. The evident dissociation indicates that autistic traits may covary with the abilities of local and global BM processing through fundamentally different mechanisms, which may explain the controversial results regarding the compromised BM perception in ASD. It is likely that children with ASD are genetically predisposed to a deficit in local BM processing, and consequently attend less to BM information during critical developmental periods, compared with their typically developing peers. As a result, these children would not get sufficient exposure to learn to effectively process global aspects of BM, which may account for the observed impairment of general BM perception at the early stage of development. On the other hand, learning strategies related to global BM processing, even beyond the critical periods, may partially compensate for the early deficits in general BM processing and potentially explain the relatively normal behavioral performance observed in adolescents and adults with ASD. While future work is required to verify these conjectures, the heritability of local BM processing ability and the genetic pleiotropy between it and autistic traits open up the possibility to treat the deficits in local BM processing as an endophenotype of ASD.

It is also worth noting that, despite the close relationship between autistic traits and local BM processing observed in the current study, individuals with ASD usually conserve the ability to process local translational motion cues (60). Such difference can be largely accounted for by the distinct brain and genetic mechanisms underlying biological and nonbiological motion perception (61–63), further suggesting that the pleiotropic effect is specific to local BM processing. Moreover, as there are still controversies regarding the etiologic consistency of autistic traits across severity levels (45, 64) and the potential influences of experimental manipulations on BM perception performance (7), it would be of great value to examine autistic traits along the full spectrum from normal to extreme range, ideally with tasks that can assess different aspects of BM processing while controlling for task demands. As an important first step, the current study suggests that the ability to process local BM information may be regarded as a distinct hallmark of social cognition and provides a theoretical account of how the abilities related to BM perception covary with autistic traits on a genetic basis.

Materials and Methods

Participants. One hundred and seventeen same-gender twin pairs (59 MZ and 58 DZ, a total of 234 participants, 148 female, aged between 15 and 27 y with a mean of 18.4 y) took part in the local, global, and general BM perception experiments (experiments 1 to 3) in a fixed order. Such arrangement ensured that we measured the participants' inherent sensitivity to local BM cues when they were naive to the nature of the point-light displays. Fifty-one twin pairs (28 MZ and 23 DZ, a total of 102 participants, 50 female, aged between 15 and 26 y with a mean of 21.3 y) participated in another general BM perception experiment (experiment 4). The twin pairs were recruited from a twin database (65) maintained by the Institute of Psychology, Chinese Academy of Sciences (IPCAS). All participants had normal or corrected-to-normal vision and provided written, informed consent before the experiments. The protocols of the research were approved by the institutional review board of the IPCAS.

Stimuli and Tasks. The stimuli were point-light BM sequences derived from motion-captured data, depicting the motion of a handful of dots representing the head and critical joints of a human figure walking on a treadmill (i.e., without overall translation) (66, 67). The stimuli were presented as white dots against a gray background, lasting 1 s in each walking cycle. The intact walker subtended about 6° of visual angle vertically. For each trial, both the initial frame of the BM sequence and the position of the stimulus relative to the center of the screen (with a horizontal offset of 0° to 0.3°) were randomized. Stimulus presentation and experimental manipulation were realized using MATLAB together with the PsychToolbox extensions (68, 69). The experiments were conducted in rooms with dim light. The viewing distance to the computer monitor was 80 cm.

In experiment 1 (BM-Loc), the dots constituting the point-light walker were randomly relocated within the region occupied by the original walker. By this means, the global configuration of the BM stimulus was entirely disrupted while the local motion signals were preserved. Participants were asked to make forced choices on the intended locomotion direction (either toward left or right) of the undefinable creatures: i.e., the scrambled point-light walkers, by pressing one of two keys after the stimulus disappeared. There were 20 trials for each walking direction condition (left or right), resulting in a total of 40 trials.

In experiment 2 (BM-Glb), participants were required to judge which of two successively presented intervals contained an intact walker (target). Both intervals contained a scrambled mask composed of two spatially scrambled versions of the target walker, which was distributed within an area about 1.44 times the area occupied by the target walker (1.2 times in height and in width). The intact walker was randomly presented in one of the two intervals, and a scrambled version of the target walker was presented in the other interval. The global BM component could be isolated through such manipulation because the local motion cues were the same for the stimuli presented in the two intervals and were hence completely uninformative. In addition, to avoid participants' potential expectations about the shape of the walker, facing directions of the walkers were randomized among 10 equally spaced directions between the left and right profile views across a total of 40 trials.

In experiments 3 and 4 (BM_1 and BM_2), participants were required to judge the locomotion direction of an intact point-light walker embedded in a scrambled mask based on both the global and local BM cues. The procedure and design of experiment 3 were the same as that of the BM-Loc experiment while the stimulus display was the same as the target display used in the BM-Glb experiment, but with only the left or right facing target. The procedures of experiment 4 were exactly the same as those of experiment 3, except that the algorithm to generate the masks had been

modified. In this experiment, half of the dots in the mask were composed of scrambled walkers with the same direction of the target, and the other half of the dots were scrambled walkers with the opposite direction. Consequently, the mask itself did not indicate the walking direction of the target, and the observers could rely solely on the global and the local BM cues conveyed by the intact BM target to accomplish the task. We also varied the density of the mask, setting dot numbers to be either two or six times as many as that of the target walker.

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