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Individual differences in the perception of biological motion: Links to social cognition and motor imagery

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ABSTRACT

Biological motion perception is often claimed to support social cognition, and to rely upon embodied representations and motor imagery. Are people with higher levels of social traits or more vivid motor imagery better at biological motion perception? We administered four experiments measuring sensitivity in using (global) form and (local) motion cues in biological motion, plus well-established measures of social cognition (e.g., empathy) and motor imagery (e.g., kinesthetic motor imagery). This first systematic investigation of individual variability in biological motion processing demonstrated significant relationships between these domains, along with a dissociation. Sensitivity for using form cues in biological motion processing was correlated with social (and not the imagery) measures; sensitivity for using motion cues was correlated with motor imagery (and not the social) measures. These results could not be explained by performance on non-biological control stimuli. We thus show that although both social cognition and motor imagery predict sensitivity to biological motion, these skills likely tap into different aspects of perception.

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1. Introduction

Detecting and interpreting the movements of others is an important problem that the brain must solve to ensure the survival and wellbeing of an organism. The visual system can extract biological motion information even in situations where other visual cues are impoverished. Point-light biological motion stimuli are animations composed solely of points of light attached to the joints of a moving agent (Johansson, 1973). When in motion, such stimuli evoke a vivid percept of a human body in action. Point-light stimuli have allowed researchers to thoroughly investigate the perceptual mechanisms underlying biological motion perception for several decades (Blake & Shiffrar, 2007).

There is significant intersubject variability in the sensitivity to biological motion, the sources of which have been explored in only a few studies. In stroke patients, deficits in biological motion processing correlate with deficits in face processing, but not with motion coherence thresholds (Saygin, 2007). Individual differences in biological motion detection in noise do not correlate with performance on other visual tasks involving grouping and segmentation (Jung, Zabood, Lee, & Blake, 2012). However, this ability is correlated with gray matter volume in the posterior superior temporal sulcus and ventral premotor cortex (Gilaie-Dotan, Kanai, Bahrami, Rees, & Saygin, 2013), brain regions critical for the perception of biological motion (Grossman & Blake, 2002; Pelphrey & Carter, 2008; Saygin, 2007; Saygin, Wilson, Hagler, Bates, & Sereno, 2004; van Kemenade, Muggleton, Walsh, & Saygin, 2012). The correlates of individual variability in biological motion tasks can also extend into more general perceptual and cognitive domains. For example, performance in biological motion tasks correlated with some (e.g., Stroop interference) but not all (e.g., orienting, visual search efficiency) tests of

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attention and executive function (Chandrasekaran, Turner, Bulthoff, & Thornton, 2010).

Here, we used direction discrimination tasks with point-light walkers and with non-biological control stimuli to explore individual differences in sensitivity to biological motion in relation to two different domains: social perceptual and cognitive abilities, and motor imagery.

The first potential source of variability we considered was individual differences in social cognition. Although papers on biological motion perception commonly motivate the research by mentioning how important this ability is for social functions, the link between these domains has not been sufficiently explored. There is also active discussion regarding the relationship between social abilities and biological motion processing in clinical populations such as Autism Spectrum Conditions (ASC, see Section 4); here we aimed to explore this relationship in the non-clinical population.

Another potential correlate of variability in biological motion perception is motor imagery, the ability to imagine the performance of an action from first or third person, either visually or kinesthetically (Lotze & Halsband, 2006). According to simulation theory (often linked with the mirror neuron system; Iacoboni & Dapretto, 2006), both biological motion perception and motor imagery involve a (partial) internal simulation of the seen or imagined action in the viewer's own motor representations (Jeannerod, 2001). Here we explored motor imagery with the rationale that shared resources with biological motion perception may be evidenced by a correlation between the two abilities.

In the visual system, form and motion are processed in partially segregated streams, which are dynamically integrated at multiple levels (Kourtzi, Krekelberg, & van Wezel, 2008). There is active discussion about the relative role of (local) motion information vs. (global) form information in biological motion processing, and the underlying neural systems (Beintema & Lappe, 2002; Garcia & Grossman, 2008; Jastorff & Orban, 2009; Lu, 2010; Thompson, Clarke, Stewart, & Puce, 2005; Thurman, Giese, & Grossman, 2010). Results on the direction discrimination task are especially mixed regarding the involvement of form and motion mechanisms. Some researchers have argued that the individual local motions of the point-light walker's limbs play an important role in direction discrimination (e.g. Troje & Westhoff, 2006). Other data highlight the role of form, since the direction discrimination task can also be solved in the absence of local motion cues (Lange & Lappe, 2007). Thus, the direction discrimination task can be solved by using either form or motion cues. Furthermore, biological motion processing has been found normal in both patients who cannot perceive motion (McLeod, Dittrich, Driver, Perrett, & Zihl, 1996), as well as in patients with visual agnosia who have trouble utilizing form information (Gilaie-Dotan, Bentin, Harel, Rees, & Saygin, 2011).

To distinguish the relative use of form and motion cues, we used "moonwalkers", i.e. walkers whose direction of walking is opposite to the direction they are facing (Lange & Lappe, 2007). In separate experiments, we asked participants to determine either the facing direction of a point-light walker, or the walking (motion) direction of a point-light walker. In the presence of moonwalkers, the facing direction task requires participants to rely heavily on form information since motion is not informative as to the direction of facing. Although it is possible to complete the direction discrimination task with local motion, when half the trials are moonwalkers, motion cues are no longer informative regarding facing direction. Likewise, the walking direction task requires participants to rely heavily upon local motion cues (the movements of the individual dots, or possibly subgroups of dots) since the facing direction is not informative as to the direction of walking when half the trials contain moonwalkers. Although it is conceivable that this task involves some form processing, or integration of form and motion (e.g., if we consider a version of the template-matching model that is sensitive to motion through the temporal sequence of form-based snapshots), the brain would still need to override the straightforward use of form cues, and it is unlikely for this task to be performed without strong reliance on motion cues.

To explore the specificity of effects to biological motion, analogous tasks were also administered with a non-biological control stimuli (a point-light shape, see Section 2).

2. Methods

We administered four experiments of motion processing as well as a number of experimental and questionnaire-based measures of social cognition and imagery [Empathy Quotient, Autism-Spectrum Quotient, Reading the Mind in the Eyes Test, Cambridge Face Memory Test, Vividness of Movement Imagery Questionnaire, which consists of internal, external and kinesthetic imagery]. All participants reported normal or corrected-to-normal vision and no history of mental illness, neurological or cognitive impairments. Although we tried to have all participants complete all tests, some attrition inevitably occurred due to the multiple sessions required to administer all experiments. The experiments were approved by the UCSD IRB and all participants gave informed consent.

2.1. Experiment 1: Biological motion facing direction (Bio-Facing)

2.1.1. Participants

Sixty-seven adults (15 males) between 18 and 31 years of age (mean: 20.8, SD: 1.73) participated in a biological motion task. Subsets of these participants also completed the social cognition and mental imagery measures: Empathy Quotient ($N = 65$), Autism Quotient ($N = 65$), Reading the Mind in the Eyes Test ($N = 59$), Cambridge Face Memory Test ($N = 63$), Vividness of Motor Imagery Questionnaire ($N = 64$).

2.1.2. Stimuli

Stimuli were point-light walkers (Fig. 1) composed of 12 white point-lights, some of which could be briefly occluded during the motion, presented on a black background. The point-light walker was created by videotaping a walker and encoding the joint positions in the digitized video (Ahlstrom, Blake, & Ahlstrom, 1997). The point-light

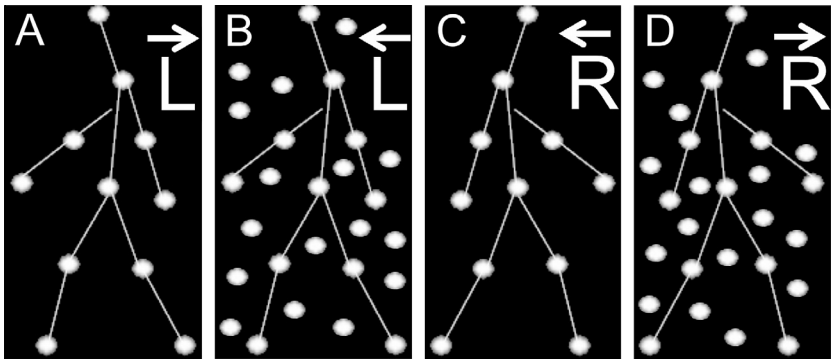

Fig. 1. Examples of single frames from point-light walker stimuli from the experiments. The connecting white lines are used here as a visual aid and were not presented in the studies. The upper case letter indicates the facing direction (L,R). The arrow above the letter indicates the moving direction. Examples depict (A) Point-light walker facing left and moving right (i.e. 'moonwalking'), (B) Point-light walker facing left and moving left, embedded in noise, (C) Point-light walker facing right and moving left (i.e. 'moonwalking'), (D) Point-light walker facing right and moving right, embedded in noise. In Experiment 1 (Bio-Facing), the task was to indicate facing direction (A, B: Left and C, D: Right), in Experiment 2 (Bio-Moving) to indicate moving (walking) direction (B, C: Left and A, D: Right).

walkerfaced either left or right, and either walked forwards or backwards ("moonwalked"). Moonwalking point-light walkers were created by playing the point-light walker in reverse. The point-light walker did not translate across the screen, but walked as if on a treadmill. In each trial, the location of the point-light walker was jittered by a maximum 0.5 degrees of visual angle from the center. The height of the figure subtended approximately 7.3 degrees of visual angle when viewed at a distance of 50 cm. The stimulus was displayed for a full gait cycle, lasting approximately 700 ms.

2.1.3. Noise masking and adaptive thresholding

To obtain a performance threshold, we used the well-established method of adding noise dots to our perceptual stimuli (Gilaie-Dotan et al., 2011; Pinto & Shiffrar, 1999; Saygin, 2007; van Kemenade et al., 2012). Noise dots had identical size, color and motion trajectories as the dots in the point-light walker. As more noise is added, the task difficulty increases. The number of noise dots on each trial was determined adaptively using Bayesian estimation based on the participant's performance on previous trials. We estimated 82% accuracy thresholds using the QUEST algorithm (Watson & Pelli, 1983). Thus the dependent variable of the experiment was the number of noise dots needed to maintain an accuracy of 82%.

2.1.4. Experimental procedures and task

Participants were instructed to determine the facing direction of the point-light walker. The walking and facing direction were congruous for half of the trials (e.g. facing and walking right). On the other half of the trials the walking and facing direction were incongruous, with the appearance of "moonwalking" (e.g. facing left and walking right).

Stimuli were displayed using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for Matlab (Natick, MA). Participants sat in a dimly lit room approximately 50 cm from a CRT Monitor (Sun Microsystems; 1152×870 at 85 Hz). At the beginning of the experiment, a practice block of 20 trials with varying levels of difficulty (noise dots) was administered to familiarize participants with the stimuli and task. After the practice, each participant completed two blocks of 80 trials each. Each trial began with a fixation cross which was displayed for 500 ms, followed by the point-light walker along with the noise dots. 100 ms after the offset of the point-light stimuli, the fixation cross again appeared indicating that participants should make their response by pressing one of two buttons on the keyboard ('Z' for left and 'M' for right). The fixation cross was displayed for a maximum of 2000 ms, and was terminated once a response was made. Participants were given a 10-s break following the 40th trial, and an untimed short break between each block. Participants received feedback on whether they responded correctly during the practice block, but not during the experimental blocks.

2.2. Experiment 2: Biological motion moving direction (Bio-Moving)

2.2.1. Participants

Fifty-seven adults (16 males) between 18 and 31 years of age (mean: 20.9, SD: 1.87) participated. 53 had also participated in Experiment 1. The order in which the participants completed each experiment was counterbalanced. Each experimental session was separated by a maximum of 2 weeks. All 57 participants completed the social cognition and mental imagery tasks.

2.2.2. Stimuli

Identical to Experiment 1.

2.2.3. Noise masking and adaptive thresholding

Identical to Experiment 1.

2.2.4. Experimental procedures and task

Procedures were identical to Experiment 1 with the exception of the task. Participants were instructed to indicate whether the point-light walker moved leftward or

rightward. For example, a point-light walker facing to the left but moonwalking would be moving to the right.

2.3. Experiment 3: Non-biological motion facing direction (NonBio-Facing)

2.3.1. Participants

Participants were the same as those in Experiment 1.

2.3.2. Stimuli

Experiments 3 and 4 aimed to provide a control for general task demands but with a non-biological stimulus. It is challenging to find control stimuli for biological motion. Few non-biologically moving objects have articulated parts; none have the dynamics of animate motion. If low-level visual characteristics are matched, stimuli are difficult to also equate for meaning and novelty/familiarity (Pyles, Garcia, Hoffman, & Grossman, 2007). For some research questions, moving point-light stimuli composed of dots, but depicting non-biological objects such as polygons and letters have been useful (e.g. deWit, Lefevre, Kentridge, Rees, & Saygin, 2011; Gilaie-Dotan et al., 2011; Hiris, 2007; van Kemenade et al., 2012). Here, we chose a translating point-light "E" for three reasons. First, we needed a direction of (non-biological) object movement task, and translating point light shapes can be used in this manner (Hiris, 2007; Saygin, Cook, & Blakemore, 2010). Second, we needed a stimulus that had, like a point-light walker, an obvious "facing direction", which was a more serious constraint. Third, like Experiments 1 and 2, we wanted to keep the same stimuli for both control experiments, changing only the task instructions. The only way we saw of doing this while satisfying the two preceding criteria was to use a translating shape that had a canonical facing direction (i.e., an E).

Stimuli consisted of a point-light shape composed of 12 white point-lights in the shape of a capital E, presented on a black background (Supplementary Fig. 1). The point-light shape "faced" left or right, and translated left or right across the screen. The height of the figure subtended approximately 5.2 degrees of visual angle when viewed at a distance of 50 cm. Each figure translated across the screen for approximately 700 ms at a rate of 1.7 degrees/s.

2.3.3. Noise masking and adaptive thresholding

The noise masking procedure was identical to the previous two experiments with the exception of the motion trajectories of the noise dots. Here, like the point-light shape, the noise dots also translated left or right. Noise dots were assigned a random location as well as movement direction, except 12 noise dots always translated in the opposite direction to the point-light shape so that the overall number of dots moving left or right in the display were balanced and the task could not be performed with a simple summation of all the dots' direction of motion.

2.3.4. Experimental procedures and task

The experimental procedure and task were identical to Experiment 1 with the exception of a small variation in the task instructions: At the start of the experiment, we clarified to the participants that the E's facing direction corresponded to the direction of the letter's three prongs.

2.4. Experiment 4: Non-biological motion moving direction (NonBio-Moving)

2.4.1. Participants

Participants were the same as those in Experiment 2.

2.4.2. Stimuli

Identical to Experiment 3.

2.4.3. Noise masking and adaptive thresholding

Identical to Experiment 3.

2.4.4. Experimental procedures and task

The experimental procedure and task were identical to Experiment 2 with the exception of a small variation in the task instructions: At the start of the experiment, we clarified to the participants that the movement direction of the point-light shape corresponded to the direction in which it translated.

2.5. Social and imagery measures

The Empathy Quotient (Baron-Cohen & Wheelwright, 2004) and Autism-Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) are well-established self-report measures of empathy and autism spectrum trait levels respectively, and have been demonstrated to be valid measures of each construct (Hoekstra, Bartels, Cath, & Boomsma, 2008; Lawrence, Shaw, Baker, Baron-Cohen, & David, 2004). Complex emotion recognition was measured using the revised version of the Reading the Mind in the Eyes Test (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001). We also obtained a measure of face processing (another important socially relevant skill that showed a relationship to biological motion deficits in stroke patients, Saygin, 2007) with the Cambridge Face Memory Test (Duchaine & Nakayama, 2006).

We also administered a revised version of the Vividness of Movement Imagery Questionnaire (Roberts, Callow, Hardy, Markland, & Bringer, 2008), a reliable measure of motor imagery (Eton, Gilner, & Munz, 1998). The Vividness of Movement Imagery Questionnaire measures three components of motor imagery; visual imagery from a third (external imagery) and first-person (internal imagery) perspective, as well as kinesthetic imagery,

The Empathy Quotient, Autism Quotient and Vividness of Movement Imagery Questionnaire are questionnaires, and were adapted to be administered on the computer. The Reading the Mind in the Eyes Test and Cambridge Face Memory Test were also administered online at http://www.testmybrain.org. The order in which subjects completed the motion tasks (Exp. 1–4) and the nine measures was randomized for every subject with the exception of the Reading the Mind in the Eyes Test, which always preceded the Cambridge Face Memory Test due to constraints imposed by the online testing website.

Table 1
Range of scores in all experiments.

	Range	Mean	SD
Bio-Facing	5–48	21.7	8.5
Bio-Moving	2–18	8.2	4.2
NonBio-Facing	11–111	63.3	24.9
NonBio-Moving	11–126	71.5	21.7
EQ	17–66	46.7	10.2
AQ	5–28	16.0	5.1
CFMT	41–72	60.9	33.6
RMET	18–36	28.4	3.5
VMIQ-E	12–48	27.6	9.3
VMIQ-I	12–46	23.7	8.7
VMIQ-K	12–53	26.4	9.4

Bio-Facing = Experiment 1; Bio-Moving = Experiment 2; NonBio-Facing = Experiment 3; NonBio-Moving = Experiment 4; EQ = Empathy Quotient; AQ = Autism Quotient; CFMT = Cambridge Face Memory Test; RMET = Reading the Mind in the Eyes Test; VMIQ-E = Vividness of Movement Imagery Questionnaire Extneral; VMIQ-I = Vividness of Movement Imagery Questionnaire Internal; VMIQ-K = Vividness of Movement Imagery Questionnaire Kinesthetic.

Table 2
Correlations among the social and imagery measures.

Correlated tasks	Pearson's *r*
EQ and AQ	−0.42*
EQ and VMIQ-I	−0.28*
EQ and CFMT	0.22^
AQ and RMET	−0.31*
VMIQ-E and CFMT	0.23^
VMIQ-E and VMIQ-I	0.56*
VMIQ-I and VMIQ-K	0.58*
VMIQ-K and VMIQ-E	0.37*

EQ = Empathy Quotient; AQ = Autism Quotient; CFMT = Cambridge Face Memory Test; RMET = Reading the Mind in the Eyes Test; VMIQ-E = Vividness of Movement Imagery Questionnaire Extneral; VMIQ-I = Vividness of Movement Imagery Questionnaire Internal; VMIQ-K = Vividness of Movement Imagery Questionnaire Kinesthetic.
* Denotes $p < 0.05$.
^ Denotes $0.05 < p < 0.1$.

2.6. Data analysis

As the present study is concerned with investigating individual differences in biological motion perception we performed correlation analyses comparing thresholds from our four experiments with the social and imagery measures, as well as multiple regressions. To account for multiple statistical comparisons, we used bootstrapping to adjust our *p*-values (Westfall & Young, 1993). 10,000 bootstrapping simulations were performed on each correlation and multiple-comparisons-corrected two-tailed *p*-values are reported in all results.

3. Results

We first assessed the relationship between each of our four perceptual tasks. Significant variability was observed in thresholds obtained in all experiments (Table 1; Bio-Facing mean: 21.7, SD: 8.5; Bio-Moving mean: 8.2, SD: 4.2; NonBio-Facing mean: 63.3, SD: 24.9; NonBio-Moving mean: 71.5, SD: 21.7). We found a correlation between thresholds for facing and walking direction tasks with the non-biological shape (NonBio-Facing and NonBio-Moving; $r(51) = 0.53$, $p < 0.0001$) and between thresholds for facing direction of the biological and non-biological stimulus conditions (Bio-Facing and NonBio-Facing; $r(65) = 0.34$, $p < 0.005$). No other correlations were significant, including the facing and movement direction tasks with biological motion (Bio-Facing and Bio-Moving; $r(51) = 0.05$, $p > 0.7$).

The range of scores on each of our social and imagery measures was similar to those previously reported in the literature (Table 1). Correlations between them were also consistent with previous literature (Table 2).

Our main goal was to test the relationship between thresholds from the four perceptual experiments and the social and motor imagery scores. In Fig. 2A, these data are provided in a color-coded "heat map"; with the correlation coefficients additionally listed in Table 3. Because the scoring direction across measures is inconsistent (e.g. a higher Vividness of Movement Imagery Questionnaire score means less vivid imagery, whereas a higher Empathy

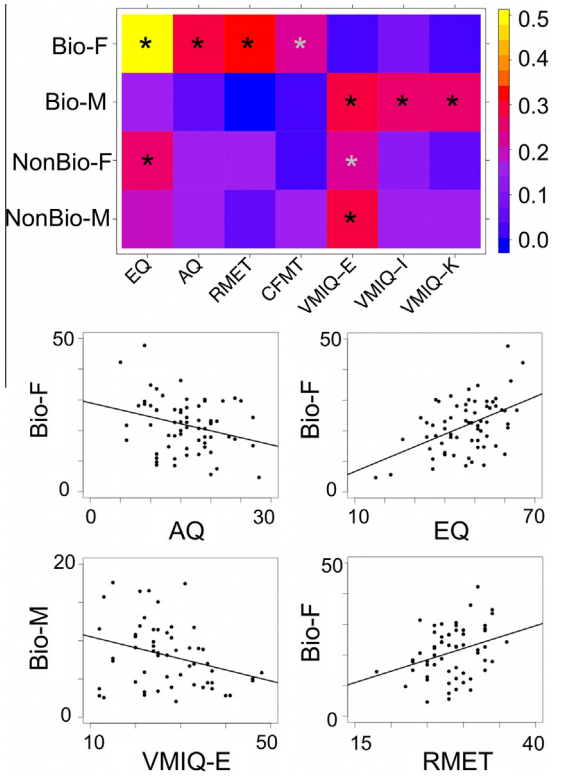

Fig. 2. Experimental correlations. (A) Color-coded "heat map" of the correlations between the point-light tasks and social/imagery measures (see also Table 3). Correlations with $p < 0.05$ are denoted with a black asterisk (*), those with $0.05 < p < 0.1$ are denoted with a grey asterisk. Bio-F, Bio-M, NonBio-F, NonBio-M refer to thresholds obtained in Experiments 1–4; AQ: Autism Quotient; EQ: Empathy Quotient; CFMT: Cambridge Face Memory Test; RMET: Reading the Mind in the Eyes Test; VMIQ-E: Vividness of Movement Imagery Questionnaire-External; VMIQ-I: Vividness of Movement Imagery Questionnaire-Internal; VMIQ-K: Vividness of Movement Imagery Questionnaire-Kinesthetic. (B) Individual plots of select correlations. The *x*-axis of each plot corresponds to the score for the measure. The *y*-axis corresponds to the sensitivity in the point-light tasks (estimated number of noise dots for 82% task accuracy, see Section 2).

Table 3
Correlations between the point-light tasks and social/imagery measures.

	EQ	AQ	CFMT	RMET	VMIQ-E	VMIQ-I	VMIQ-K
Bio-Facing	0.48*	−0.28*	0.22^	0.32*	−0.04	−0.1	−0.03
Bio-Moving	0.16	0.07	0.006	−0.004	−0.31*	−0.27*	−0.25*
NonBio-Facing	0.24*	−0.15	0.03	0.16	−0.22^	−0.13	−0.04
NonBio-Moving	0.19	−0.17	0.16	0.07	−0.30*	−0.14	−0.15

Bio-Facing = Experiment 1; Bio-Moving = Experiment 2; NonBio-Facing = Experiment 3; NonBio-Moving = Experiment 4; EQ = Empathy Quotient; AQ = Autism Quotient; CFMT = Cambridge Face Memory Test; RMET = Reading the Mind in the Eyes Test; VMIQ-E = Vividness of Movement Imagery Questionnaire Extneral; VMIQ-I = Vividness of Movement Imagery Questionnaire Internal; VMIQ-K = Vividness of Movement Imagery Questionnaire Kinesthetic.
* Denotes $p < 0.05$.
^ Denotes $0.05 < p < 0.1$.

Quotient score means more empathic traits), we used the absolute value of the correlation for the heat map.

Bio-Facing noise thresholds (Experiment 1) correlated significantly with the social measures Autism Quotient, Empathy Quotient and Reading the Mind in the Eyes Test (Fig. 2B; Empathy Quotient: $r(63) = 0.48$, $p < 0.0001$; Autism Quotient: $r(63) = -0.28$, $p = 0.02$; Reading the Mind in the Eyes Test: $r(57) = 0.32$, $p = 0.01$). There was a trending significant correlation with the Cambridge Face Memory Test ($r(61) = 0.22$, $p = 0.08$), which became significant when variance shared with the Reading the Mind in the Eyes Test was accounted for ($p = 0.02$). Correlations were positive for all but the Autism Quotient: lower Autism Quotient scores correspond to *fewer* autistic traits, which correlated with increased sensitivity to biological motion. No significant correlations were found between Bio-Facing noise thresholds and any component of the Vividness of Movement Imagery Questionnaire (all p's > 0.4).

Bio-Moving noise thresholds (Experiment 2) correlated with all components of the Vividness of Movement Imagery Questionnaire (Fig. 2B; External: $r(54) = -0.31$, $p < 0.05$; Internal: $r(54 = -0.27$, $p < 0.05$; Kinesthetic: $r(54) = -0.25$, $p < 0.05$). Due to the scoring of the Vividness of Movement Imagery Questionnaire, the negative correlations in fact mean increased vividness of imagery is associated with increased Bio-Moving noise thresholds. No significant correlations were found with any of the other measures (all p's > 0.2).

NonBio-Facing noise thresholds (Experiment 3) correlated with the Empathy Quotient ($r(65) = 0.24$, $p = 0.051$). This correlation was not significant when accounting for shared variance with Bio-Facing ($p = 0.5$). NonBio-Moving noise thresholds (Experiment 4) correlated significantly with External Imagery ($r(54) = -0.3$, $p < 0.05$). This correlation was not significant when accounting for shared variance with Bio-Moving ($p = 0.6$).

We also performed multiple regressions using scores for our measures, age and gender as predictors. A multiple regression with five predictors explained 54.9% of the variance in Bio-Facing thresholds ($R^2 = 0.549$, $F(5,51) = 12.43$, $p < 0.0001$). Scores on the Empathy Quotient ($\beta = 0.40$, $t(56) = 3.88$, $p = 0.005$), the Cambridge Face Memory Test ($\beta = 0.29$, $t(56) = 2.96$, $p < 0.005$), the Reading the Mind in the Eyes Test ($\beta = 0.21$, $t(56) = 2.3$, $p < 0.05$), NonBio-Facing thresholds ($\beta = 0.29$, $t(56) = 3.06$, $p < 0.005$), and the participant's age ($\beta = -0.26$, $t(56) = -2.95$, $p < 0.005$) significantly predicted Bio-Facing performance. No significant multiple regressions were found for the Bio-Moving task, nor for the control tasks.

4. Discussion

In a series of experiments, we explored correlates of individual variability in the ability to use form and motion cues in biological motion tasks. The results demonstrated a dissociation between the individual differences in the ability to complete tasks that rely more heavily on the use of form cues (Bio-Facing) and those that rely preferentially on the use of motion cues (Bio-Moving). Not only did performance in these two experiments not correlate with each other, but they correlated with a non-overlapping set of social and motor imagery measures. Whereas individual ability in using form cues in biological motion processing correlated with all of our measures of social perception, the use of motion cues did not. Instead, individual differences in the use of motion cues in biological motion processing correlated with all types of motor imagery. These correlations were weaker or absent in the control experiments with non-biological stimuli (NonBio-Facing and NonBio-Moving), indicating the results are at least to some degree specific for biological motion and not just due to general task demands.

4.1. Social cognition and biological motion

The processing of others' movements is of paramount importance for communication and adaptive social behavior (see, Pavlova, 2012 for a review). Even sparse point-light stimuli are a rich source of information from which socially relevant features such as gender, identity, and emotion can be extracted (e.g. Atkinson, Dittrich, Gemmell, & Young, 2004; Pollick, Paterson, Bruderlin, & Sanford, 2001). Although it has frequently been postulated that biological motion perception supports social cognition, to our knowledge the present study is the first to systematically investigate this relationship, as well as whether it is dependent upon the cues (form vs. motion) used in processing the biological motion.

In our data, individual ability to use form cues in processing biological motion correlated with measures of social perception. A potential explanation for these findings is that the relationship between social cognition and biological motion is a special case of a relationship with a

general visual form processing mechanism. Arguably, processing the visual form of objects (e.g. food) is also often important in social situations (e.g. dinner parties). However, this explanation is unlikely to account for our data on its own. Any correlation between social cognition and our control experiment with non-biological objects disappeared when accounting for shared variance with the biological motion tasks. The reverse however was not true: Bio-Facing correlations with social cognition held when NonBio-Facing performance was accounted for (all p's < 0.05).

Another explanation is that the visual analysis of the form of a walker has the most relevance to social information above and beyond general form processing. For example, the form (i.e., posture) of a biological agent such as a person can contain important cues regarding where a person is looking, which can then be utilized to gain information about the world, including social information.

A link between social cognition and biological motion perception has been discussed in relation to Autism Spectrum Conditions (ASCs). One hypothesis about the source of the social deficits in ASC is disrupted processing in a network of brain regions implicated in the perception of actions, which includes the posterior superior temporal sulcus and the mirror neuron system (Iacoboni & Dapretto, 2006). Since biological motion perception is supported by this network (Grossman & Blake, 2002; Pelphrey & Carter, 2008; Saygin, 2007; van Kemenade et al., 2012), if this hypothesis is correct, one might expect to find reduced sensitivity to biological motion in ASC. Studies have indeed shown evidence for compromised processing of biological motion in individuals with ASC (Blake, Turner, Smoski, Pozdol, & Stone, 2003; Cook, Saygin, Swain, & Blakemore, 2009; Freitag et al., 2008; Kaiser, Delmolino, Tanaka, & Shiffrar, 2010; see, Kaiser & Shiffrar, 2009 for a review). Some aspects of emotional biological motion processing also appear to be linked to autistic traits (as measured by the Autism Quotient) in the healthy population (Kaiser & Shiffrar, 2012). On the other hand, the role of the mirror neuron system in ASC is not clear cut (Hamilton, Brindley, & Frith, 2007). In particular, some studies have failed to find evidence for deficient processing of biological motion in ASC, including at least three groups using the direction discrimination task (Jones et al., 2011; Murphy, Brady, Fitzgerald, & Troje, 2009; Saygin et al., 2010) demonstrating that perceptual deficits in ASC are limited, and do not indicate a general inability to process biological motion.

Here, we found a significant relationship between the severity of autistic traits in non-clinical participants (as measured by the Autism Quotient, which is highly correlated with the Empathy Quotient) and the sensitivity to the form, but not the motion cues of a point-light walker. Although new studies are needed to establish whether these findings apply to individuals diagnosed with ASC, our data suggest biological motion deficits in these conditions may not be primarily due to compromised motion perception, but instead, to a deficit in processing (biological) form cues. Participants with ASC may be able to use local motion cues to compensate for any losses in the use of form cues, allowing them to discriminate direction (Jones et al., 2011; Murphy et al., 2009; Saygin et al., 2010). The opposite compensatory mechanism may underlie normal biological motion perception for patients with visual agnosia (Gilaie-Dotan et al., 2011). This highlights the importance of the task used to probe biological motion processing in clinical populations.

Empathy and theory of mind, cognitive traits that underlie the ability to understand the mental and emotional states of others, are at the cornerstone of human social interaction (Singer & Lamm, 2009). Self-reported levels of empathy have been shown to correlate with the ability to extract emotional states from a point-light walker (Sevdalis & Keller, 2011), as well as neural activity in the mirror neuron system during the perception of social interactions (Hooker, Verosky, Germine, Knight, & D'Esposito, 2010). We found that self-reported levels of empathy correlated with the sensitivity to the form cues of a point-light walker. Unlike the studies mentioned previously, our finding demonstrates a relationship between empathy and low-level (non-social) visual analysis of a person. Similarly, processing the form but not the motion of a point-light walker correlated with complex emotion recognition as measured by the Reading the Mind in the Eyes Test.

A link between face and biological motion perception had previously been reported for stroke (Saygin, 2007) and congenital prosopagnosia (Lange et al., 2009) patients. Our Cambridge Face Memory Test data demonstrate this relationship in the non-clinical population, and specify that it holds specifically for tasks that rely preferentially on processing the global form of the walkers, and not local motion. Future work on the link between social cognition and configural processing of faces and bodies can be fruitful.

Our multiple regression analyses additionally suggest that empathizing, emotion recognition, and face processing abilities might contribute uniquely to biological form processing (whereas Autism Quotient and Empathy Quotient, being highly correlated, share variance).

In sum, we found that individual differences in biological motion perception correlated with the social measures in our study, but that this relationship was linked to the use of form cues, rather than biological *motion* processing, per se.

4.2. Motor imagery and biological motion

Simulation theory, including work on the aforementioned mirror neuron system, predicts that both biological motion perception and motor imagery are grounded in the body and the motor system (Jeannerod, 2001). Behaviorally, as with perception of apparent biological motion (Shiffrar & Freyd, 1990), motor imagery is constrained by anatomically plausible paths of limb motion (Petit, Pegna, Mayer, & Hauert, 2003). Neuroimaging studies have also demonstrated a link between action perception and motor imagery. In particular, both perceiving and imagining biological motion activate regions of the motor system (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Iseki, Hanakawa, Shinozaki, Nankaku, & Fukuyama, 2008) as well as the posterior superior temporal sulcus (Grossman & Blake, 2001). The perceptual correlates of individual differences in motor imagery has been less explored.

We found a significant correlation between vividness of motor imagery and the ability to discriminate the movement direction of a point-light walker. In the presence of moonwalkers, this task is achieved primarily by focusing on motion cues. This correlation was not only found for external motor imagery, but also for both internal and kinesthetic motor imagery, consistent with embodiment (Jeannerod, 2001). Sensitivity to the movement direction of the non-biological shape was also correlated with external motor imagery, most likely due to similar resources in an early visual motion processing area such as MT+. However, only sensitivity to the movement direction of a point-light walker was correlated with internal and kinesthetic motor imagery scores. Perhaps, cognitive resources that support biological motion are shared between visualizing one's own movements as well as how they feel kinesthetically; whereas a kinesthetic relationship is not found for non-biological motion.

A previous study using fMRI demonstrated that imagination and perception of a point-light walker led to activity in overlapping regions of the posterior superior temporal sulcus (Grossman & Blake, 2001) suggesting a link between the two at a neural level. Our results support this relationship behaviorally, and extend them by specifying that motor imagery shares resources with mechanisms for processing the motion signals in biological motion stimuli. Although we cannot conclusively speak to the specific neural correlates with the present data, premotor cortex is a likely candidate for supporting both abilities, given its known role in motor imagery as well as for point-light biological motion perception (as indicated by fMRI, TMS, and patient studies: Saygin, 2007; Saygin et al., 2004; van Kemenade et al., 2012). Indeed we recently found grey matter intensity in premotor cortex correlated with individual differences in biological motion detection ability (Gilaie-Dotan et al., 2013).

5. Conclusion

Using an individual differences approach, our study demonstrates that biological motion perception is linked to both social cognition and motor imagery. Behavioral performance on biological motion processing tasks were predicted by both social and imagery measurements. However, we found a clear dissociation between the correlates of a task that relies heavily on form cues (Bio-Facing) and one that relies heavily on motion cues (Bio-Moving). This dissociation is unlikely to be due to a lack of power to detect a correlation, as the non-significant correlations were very low or non-existent (Table 1). Furthermore, in addition to not correlating with each other, the two tasks correlated with a non-overlapping set of external measures. The facing discrimination task, which is primarily dependent on the use of form cues, correlated with social measures; the movement discrimination task, which is primarily reliant upon the use of motion cues, correlated with motor imagery measures. Performance on the same tasks with non-biological stimuli could not account for these results. This dissociation between sensitivity for form and motion cues demonstrates that these mechanisms, while both important for biological motion perception, might tap into different aspects of perception and cognition.

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Appendix A. Supplementary materiel

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2013.03.013.

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