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ORIGINAL PAPER

Functional but Inefficient Kinesthetic Motor Imagery in Adolescents with Autism Spectrum Disorder

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Abstract Whether action representation in individuals with autism spectrum disorder (ASD) is deficient remains controversial, as previous studies of action observation or imitation report conflicting results. Here we investigated the characteristics of action representation in adolescents with ASD through motor imagery (MI) using a hand rotation and an object rotation task. Comparable with the typically-developing group, the individuals with ASD were able to spontaneously use kinesthetic MI to perform the hand rotation task, as manifested by the significant biomechanical effects. However, the ASD group performed significantly slower only in the hand rotation task, but not in the object rotation task. The findings suggest that the adolescents with ASD showed inefficient but functional kinesthetic MI, implicating that their action representation might be preserved.

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Keywords Autism spectrum disorder · Motor imagery · Action representation · Motor cognition

Abbreviations

ASD	Autism spectrum disorder
MI	Motor imagery
TD	Typically-developing
RTs	Reaction times
kMI	Kinesthetic motor imagery
vMI	Visual motor imagery
ADOS	Autism Diagnosis Observation Schedule
ANOVA	Analysis of variance

Introduction

Autism spectrum disorder (ASD) is a neurodevelopmental disorder mainly characterized by deficits in social communication and repetitive stereotyped behaviors. In addition to these diagnostic criteria, deficiencies in action imitation (Cossu et al. 2012; Williams et al. 2001), action planning (Fabbri-Destro et al. 2009; Rinehart et al. 2006), praxis (Mostofsky et al. 2006) and the ability to understand others' action intention (Boria et al. 2009) have received substantial attention. Notably, behavioral and neuroimaging evidence reveals that these functions require the engagement of action representation, which is a fundamental component of conceptualizing one's own and others' actions (Jeannerod 1994, 2001, 2006; Sommerville and Decety 2006).

Most previous studies investigated the characteristics of action representation in individuals with ASD through action observation or action imitation tasks. However, the findings remain controversial (Bernier et al. 2007; Hamilton et al. 2007; Oberman et al. 2005; Ruysschaert et al. 2014). The divergent results may be partly explained by the distinction between impaired representations of intransitive actions and intact representations of transitive actions in individuals with ASD (Hamilton 2008; Wild et al. 2012). A hypothesized model suggested that individuals with ASD may have spared capability in emulation tasks that are object-oriented and possess a clear action goal (i.e., transitive condition), but show dysfunction in mimicry tasks that involves spontaneously copying gestures without object-manipulation (i.e., intransitive condition) (reviewed in Hamilton 2008). Nonetheless, due to the lack of active manipulation of action representation in passive action observation tasks, as well as the contamination by the overt motor replication in imitation tasks (Macuga and Frey 2012), it is possible that neither task is optimal to study the characteristics of action representation. In contrast, motor imagery (MI), the mental simulation of a body movement without actual motor output, appears to be an appropriate alternative to study the internal embodiment of action representation (Gabbard 2009). MI shares similar neural mechanism (Decety 1996) and temporal dynamics (i.e. Fitt's law) with motor execution (Decety and Jeannerod 1995), and generally induces higher activations in motor related areas than passive action observation (Macuga and Frey 2012).

MI can be typically classified into visual MI (vMI) and kinesthetic MI (kMI) (Kosslyn et al. 2010). vMI involves visuospatial transformation of an action, while kMI involves a simulation process that implicitly uses information of kinesthetic sensation (Grangeon et al. 2011; Rodrigues et al. 2010). Neuroimaging studies have shown that kMI elicits robust activation in several motor-related brain regions, including the inferior and superior parietal lobules and ventral premotor cortex, while vMI reliably recruits occipital regions. Therefore, kMI appears to share a higher degree of similarity with motor execution than vMI (Guillot et al. 2009; Stinear et al. 2006).

MI has been commonly studied with the well-developed hand rotation paradigm, wherein participants are required to discriminate the laterality of a hand rotated by different angles along one or more axes (Sekiyama 1987). Typically, the *angle effect* of the reaction times (RTs), the phenomenon that the RTs increase as the rotation angles of hand stimuli increase (i.e., away from the neutral position), is considered an evidence that participants perform the task by mentally simulating the rotation of their own hands to match the orientation of the displayed stimulus (Parsons 1994). Furthermore, the presence of the *biomechanical effect*, slower RTs for awkward hand orientations (e.g., lateral rotation: rotation away from mid-sagittal plane of the body) than more natural hand orientation (e.g., medial rotation: rotation toward mid-sagittal plane of the body), represents an indicator that one uses kMI instead of vMI to perform the hand rotation task (Parsons 1994).

Few studies had investigated the capability of MI in ASD with the hand rotation task, and the results were inconclusive. In one study, those ASD subjects with enhanced visuospatial capability performed more accurately and marginally faster than typically-developing group in the mental rotation tasks of 2-D line-drawing hands, and the authors implied that the capability of MI in ASD might be relatively intact (Soulieres et al. 2011). However, due to the lack of evaluating the biomechanical effect, it is difficult to differentiate whether ASD participants were using vMI or kMI to perform the task. Another recent study showed the overall RTs and error rates did not differ between individuals with ASD and typically-developing (TD) controls in the mental rotation task of 2-D line-drawing hands. However, the absence of the biomechanical effect seems to suggest dysfunctional kMI in ASD (Conson et al. 2013). Considering these divergent findings, we speculated that ASD might have deficient kMI, thus adopting vMI as an alternative strategy for mental simulation of action. Importantly, there is convergent evidence (Falter et al. 2008; Soulieres et al. 2011) that individuals with ASD might have enhanced visuospatial transformation that leads to better performance than TD controls in mental rotation tasks with non-corporeal stimuli. Such a visual advantage appears to agree with the 'systemizing hypothesis' of ASD (Baron-Cohen 2008; Brosnan et al. 2010; Falter et al. 2008), delineating a tendency toward processing details in a system. Hence, when performing the hand rotation task with corporeal stimuli, participants with significant autistic traits might adopt vMI, which is more similar to visuospatial transformation used in the mental rotation task with non-corporeal stimuli (e.g., blocks, characters, etc.) (Conson et al. 2013). Additionally, the line-drawing hand stimuli in the aforementioned studies only rotated on a single axis, which might result in insufficient task difficulty (ter Horst et al. 2010), thus decreasing the engagement of kMI in ASD participants. A recent study indeed demonstrated that, when both the back view and the palm view stimuli were included in the hand rotation task (i.e., presenting the stimuli rotated along more than one single axis), the ASD group showed comparable biomechanical effect with the TD group (Conson et al. 2016).

In the current study, we aimed at further clarifying the characteristics of action representation in adolescents with ASD through MI. Specifically, to promote effortful engagements of kMI, we used hand rotation tasks with pictures of 3D-rotated hand-models rotating around multiple axes (ter Horst et al. 2010). In addition, to compare action representations of intransitive and transitive action between adolescents with ASD and TD controls, the hand stimuli were presented in two conditions: a bare-hand and a hand-with-spoon condition. We also included a non-corporeal control condition using the 3D-rotated desk-model stimuli. If the adolescents with ASD can spontaneously use kMI, their performance for the hand rotation task would likely be affected by biomechanical constraints, reflecting their spared ability to activate action representation and to use motor knowledge in action repertoires. In contrast, if individuals with ASD cannot use kMI automatically, they may adopt visuospatial transformation strategies to perform the hand rotation task, resulting in no biomechanical effect, just as when processing the non-corporeal stimuli. Specifically, if adolescents with ASD only have specific impairment in representing non-object-oriented actions, but not in representing object-directed actions, the biomechanical effect might only present in the transitive condition which further elicit kMI through observation of tools that automatically afford the intention of actions (Creem-Regehr and Lee 2005; Gibson 1977), in comparison with the absent biomechanical effect in the intransitive condition.

Methods

Apparatus

A Windows XP PC and a 21″ CRT monitor with a refresh rate of up to 100 Hz were used to present experimental stimuli and collect behavioral data. All stimuli (7° width) were displayed at a constant distance of 70 cm from the participants' eyes. All experimental scripts were coded with the Matlab-based Psychophysics Toolbox (Pelli 1997).

Participants

Twenty-two adolescents with ASD and 22 typically-developing (TD) subjects were recruited to participate in the experiment; Table 1 summarizes their corresponding demographic data. Participants within the age range of 11–15 were specifically recruited, because the emergence of kMI capability evidenced by the existence of biomechanical effect seems to occur during this age range (Butson et al. 2014; Gabbard 2009; Toussaint et al. 2013). The diagnosis of the ASD group was confirmed by multidisciplinary assessments conducted by board-certified child psychiatrists and clinical psychologists based on the DSM-IV (4th ed.; DSM-IV; American Psychiatric Association 1994). The diagnosis was also validated using the Autism Spectrum Quotient (AQ) (Auyeung et al. 2008; Baron-Cohen et al. 2006), and the Autism Diagnosis Observation Schedule (ADOS) (Lord et al. 2000) conducted by qualified psychiatrist. The mean AQ scores in the ASD group reached the criteria for diagnosis. The mean ADOS total score (Module 3) was 13.17 (SD 5.40), which met the criteria of autism. Participants with comorbid psychological and neurological conditions (such as a history of brain injury or epilepsy) were excluded. Only one ASD participant took psychoactive medication, and was requested not to take it on the day of the experiment. The TD group was recruited from the local community and screened for major psychiatric and neurological conditions by conducting structured interviews. The two groups did not differ significantly in age, gender, and intelligence quotient (the Wechsler Intelligence Scale for Children, WISC-IV) (Table 1). All procedures in the current study were approved by the Institutional Review Board of National Taiwan University Hospital (201308032RINB), and all participants signed informed consent before participation.

Table 1 Demographic data of participants of the ASD and TD group

	TD group	ASD group	t Value
N (gender)	22 (20 M, 2 F)	22(20 M, 2 F)	–
Chronological age	13.47 ± 1.24	12.95 ± 1.04	0.144
	(11–15)	(11–15)	
Full IQ	109.64 ± 9.42	108.48 ± 17.70	0.792
	(92–130)	(81–141)	
Verbal comprehension	106.09 ± 7.78	103.38 ± 15.17	0.470
	(93–125)	(78–129)	
Perceptual reasoning	112.59 ± 10.89	109.14 ± 16.37	0.852
	(91–134)	(85–151)	
Working memory	105.95 ± 13.35	100.10 ± 23.91	0.595
	(84–135)	(78–158)	
Processing speed	104.27 ± 13.27	108.48 ± 19.29	0.411
	(75–136)	(65–140)	
AQ (The Autism Spectrum Quotient)	19.05 (≧ 12y, n = 19) 67(< 12y, n = 1)	30.76 (≧ 12y, n = 17) 86.25 (< 12y, n = 4)	
ADOS	–	13.17 ± 5.40	–

Task and Procedures

The Hand Rotation Task

Test stimuli of the hand rotation task consisted of 144 different images of 3D-rotated hand models (ter Horst et al. 2010). There were two basic templates: a bare-hand and a hand-with-spoon. Each hand stimulus rotated with a predefined angle combination within three anatomical planes, including the frontal plane, sagittal plane and transverse plane. There were two angles on the transverse plane (back view and palm view), six angles on the frontal plane (0°, 60°, 120°, 180°, 240° and 300°), and three angles on the sagittal plane (0°, 60° and −60°), which yielded 36 different angle combinations for a hand template of a given laterality (Fig. 1a).

Participants performed four blocks of the hand rotation task. In each block, every possible combination of angles was presented once with a randomized order, resulting in a total of 576 trials [36 (angle combinations) × 2 conditions (a bare-hand or a hand-with-spoon) × 2 (left or right) × 4 blocks]. For each trial, a hand of a certain combination of rotation angles was presented for a duration lasting until the participant's response. Participants were asked whether the stimulus displayed was a right or left hand by pressing the right key or the left key with their right/left index finger, as quickly and accurately as possible (Fig. 1b).

The Object Rotation Task

Test stimuli of the object rotation task consisted of 72 different images of 3D-rotated desk models rotated along similar angle combinations as in the hand rotation task (Fig. 1a). The stimulus could be a desk with a left-sided or right-sided drawer, as defined from the perspective of facing the desk's front, mimicking a decision condition as in the hand rotation task (left hand vs. right hand). Participants performed two blocks of the object rotation task. In each block, every possible rotation angle combination was repeated twice in random order, resulting in 288 trials [2 (front view or back view) × 6 (frontal plane: 0°, 60°, 120°, 180°, 240° and 300°) × 3 (sagittal plane: 0°, 60° and 300°) × 2 (the drawer is on the left or on the right) × 2 repetition × 2 blocks]. Participants were required to judge whether the drawer was on the right or on the left by pressing the right/left key with their right/left index finger as quickly and accurately as possible (Fig. 1b).

The sequence of the two tasks was counterbalanced across participants. Prior to each task, participants performed a practice session to ensure that they had fully understood instructions. During the experiment, the hands of the subjects were covered by a black plastic board above the keyboard to avoid visual cues from hand-viewing.

Data Analysis

The RTs were only calculated for correct trials. Due to the right-skewed tendency of the RT distribution in the current data, we extracted median RTs (instead of mean RTs) of each participant for statistical analysis. The α level was set at 0.05 for all analyses, and the Bonferroni correction for multiple comparisons was used where appropriate.

First, to investigate the general performance in the two groups, we subjected measures of accuracies and RTs (the average of the median RT for each subject) to a two-way mixed-design Analysis of variance (ANOVAs) with the between-subject factor of GROUP (TD vs. ASD) and the within-subject factor of CONDITION (bare-hand, hand-with-spoon and desk).

Second, to probe whether the participants performed mental rotation for all tasks, we investigated the influence of increasing rotational angles on RTs by conducting a three-way mixed-design ANOVA with the between-subject factor of GROUP (TD vs. ASD) and the within-subject factors of CONDITION (bare-hand, hand-with-spoon and desk) and ANGLE (0°, 60°, 120° and 180°). For this analysis, the 60°condition referred to the average of both the 60° and 300° frontal plane rotation stimuli, and the 120° condition referred to the average of both the 120° and 240° frontal plane rotation stimuli. Consequently, each participant performed 48 trials [2 (transverse plane) × 1 (frontal plane) × 3 (sagittal plane) × 2 (left or right)] for each of the 0° and 180° conditions, and 96 trials [2 (transverse plane) × 2 (frontal plane) × 3 (sagittal plane) × 2 (left or right)] for each of the 60° and 120° conditions. A significant angle main effect would indicate that participants indeed mentally rotate these stimuli for laterality judgment. In addition, to investigate whether adolescents with ASD were slower in performing MI (i.e. processing related to mental rotation of the hand stimuli), RTs were linearly regressed against rotational angles (0°, 60°, 120° and 180°) for each participant to extract a slope that represents the processing speed of mental rotation, and an intercept that represents the general processing speed unrelated to mental rotation (e.g., visual encoding, decision making for laterality, etc.) (Just and Carpenter 1985). Two-way ANOVAs were conducted on the slopes and intercepts separately, with the within-subject factor of CONDITION (bare-hand, hand-with-spoon and desk) and the between-subject factor of GROUP (TD vs. ASD).

Third, to dissociate whether participants were performing kMI or vMI for the hand rotation task, we analyzed the significance of the biomechanical effect. We conducted a three-way mixed-design ANOVA with the between-subject factor of GROUP and the within-subject factors of CONDITION (bare-hand, hand-with-spoon and desk) and ORIENTATION (lateral rotation and medial rotation). The Lateral rotation condition includes stimuli with 240° and 300°

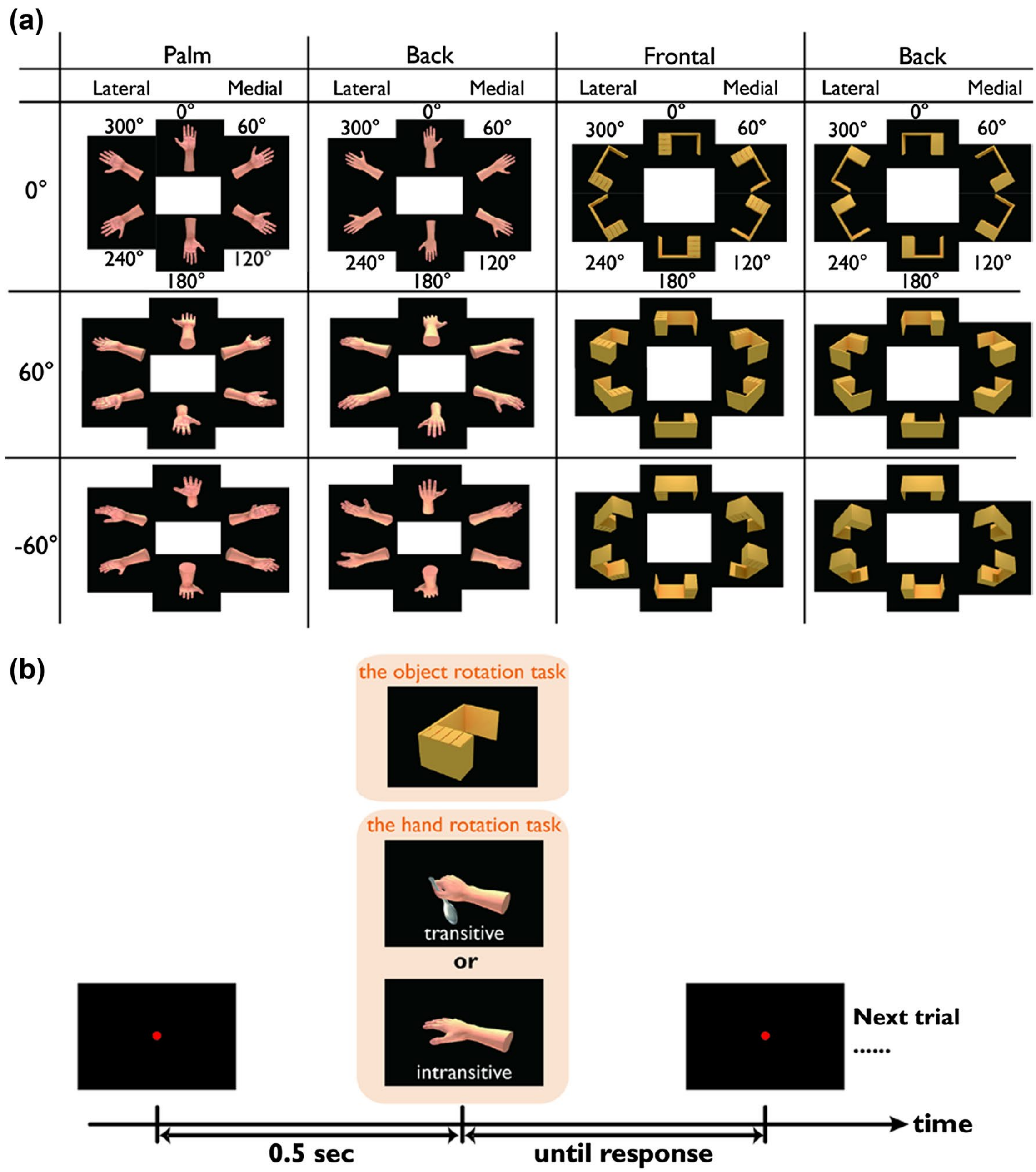

Fig. 1 The hand rotation task and the object rotation task. **a** Stimulus examples: here we show stimulus examples for the left bare-hand templates used in the hand rotation task and the left-drawer desk templates used in the object rotation task. **b** A typical trial sequence: each trial started with a fixation dot (500 ms duration) followed by a test stimulus, which remained on screen until the participants made a response. For the hand rotation task, the stimulus could either be a bare-hand or a hand-with-spoon of a random orientation; for the object rotation task, the stimulus was a desk of a random orientation

frontal plane rotation of right hand and right-drawer desk, and stimuli with 60° and 120° frontal plane rotation of a left hand and a left-drawer desk. The Medial rotation condition includes stimuli with 60° and 120° frontal plane rotation of a left hand and a left-drawer desk, and stimuli with 240° and 300° frontal plane rotation of a right hand and a right-drawer desk. Consequently, each participant performed 96 trials [2 (transverse plane) × 2 (frontal plane) × 3 (sagittal plane) × 2 (left or right)] for each of the lateral rotation and medial rotation conditions. A significant biomechanical effect for the hand rotation task would suggest that the participants were engaging in kMI instead of vMI, and thus influenced by biomechanical constraints. On the other hand, we expected no significant biomechanical effect for the object rotation task, in that a desk presumably does not have a "biomechanical" characteristic that might lead to natural vs. awkward positions.

Fourth, to quantitatively evaluate and compare the size of biomechanical effects between the TD group and the ASD group, we introduced the task-specific Biomechanical Index in each condition for each individual, which is defined as the following formula:

$$\text{Biomechanical index} = \frac{RT_{\text{lateral rotation}} - RT_{\text{medial rotation}}}{RT_{\text{all angles}}} \times 100\%$$

The index therefore represents the percentage of additional processing effort for the lateral rotation compared to the medial rotation condition, and controls for the potential confounding influence of individual differences in overall processing speed. We conducted a two-way mixed-design ANOVA with the within-subject factor of CONDITION (bare-hand and hand-with-spoon) and the between-subject factor of GROUP (TD vs. ASD).

Results

Overall Behavioral Performance

Accuracy

Table 2 summarizes the results for both the accuracies and RTs. The two-way mixed ANOVA on accuracy revealed a significant CONDITION main effect ($F_{2,\ 84} = 13.47$, $p < .001$, $\eta^2 = 0.24$), but no significant GROUP main effect ($F_{1,\ 42} = 3.60$, $p = .07$, $\eta^2 = 0.08$, power = 0.46). No significant interaction between CONDITION and GROUP was found ($F_{2,\ 84} = 2.64$, $p = .09$, $\eta^2 = 0.06$, power = 0.43). Post-hoc comparisons on the CONDITION main effect showed that the accuracy for the desk condition was significantly higher than that for the bare-hand ($p < .05$) and the hand-with-spoon condition ($p < .001$), and the accuracy for the bare-hand condition was higher than that of the hand-with-spoon condition ($p < .005$) for both groups.

Table 2 Accuracies and reaction times (mean ± SD) in overall performance of all stimuli in the two groups

	Typically-developing group	ASD group
Accuracy rate (percentage)		
Bare hand	96.1 ± 3.8%	92.1 ± 9.9%
Spoon	94.6 ± 5.1%	89.2 ± 11.7%
Desk	97.0 ± 3.9%	95.2 ± 4.8%
RTs (ms)		
Bare hand	1325.76 ± 210.39	1688.43 ± 530.43
Spoon	1464.98 ± 305.42	1867.07 ± 717.07
Desk	1100.71 ± 175.33	1271.65 ± 390.04

Reaction Times (RTs)

The two-way mixed ANOVA on RTs showed significant main effects of GROUP ($F_{1,\ 84} = 7.08$, $p = .011$, $\eta^2 = 0.14$) and CONDITION ($F_{2,\ 84} = 50.42$, $p < .001$, $\eta^2 = 0.55$) and a significant CONDITION by GROUP interaction ($F_{2,\ 84} = 3.23$, $p = .045$, $\eta^2 = 0.07$) (see Fig. 2).

Further analysis on the two-way interaction revealed significant simple GROUP effects only in the hand rotation task (bare-hand: $F_{1,\ 126} = 7.11$, $p < .001$, $\eta^2 = 0.12$; hand-with-spoon: $F_{1,\ 126} = 8.74$, $p < .001$, $\eta^2 = 0.14$) with the ASD group performed significantly slower than the TD group (Table 2), but not in the object rotation task ($F_{1,\ 126} = 1.58$, $p = .21$, $\eta^2 = 0.03$). There were also significant simple CONDITION effects in both the TD group ($F_{2,\ 84} = 23.71$, $p < .001$, $\eta^2 = 0.25$) and the ASD group ($F_{2,\ 84} = 55.40$, $p < .001$, $\eta^2 = 0.48$). Post-hoc comparisons revealed that for both groups (Table 2), the RTs of the desk condition were significantly faster than the RTs of the bare-hand and the hand-with-spoon conditions (bare-hand vs. desk in TD: $p < .005$, in ASD: $p < .001$; hand-with-spoon vs. desk in TD: $p < .001$, in ASD $p < .001$), and the RTs of the bare-hand condition were faster than the RTs of the hand-with-spoon condition (bare-hand vs. hand-with-spoon in TD: $p < .001$, in ASD $p < .05$). Results from both the accuracies and RTs indicated that, for both groups, the hand rotation task was more difficult than the object rotation task, and the simulation of

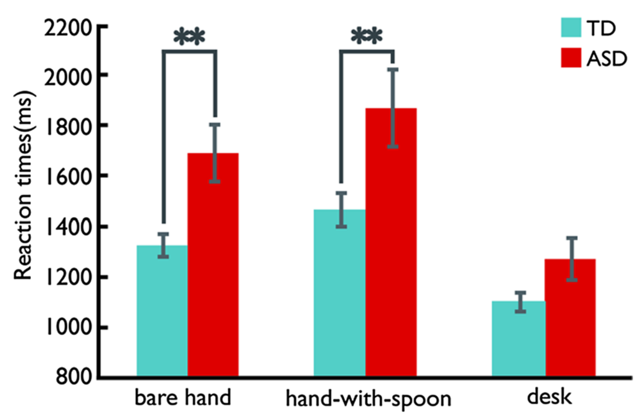

Fig. 2 The mean RTs of the bare-hand, the hand-with-spoon and the desk condition. Blue bars represent the TD group and red bars represent the ASD group. The RTs significantly differed between the TD and ASD group in both conditions of the hand rotation task but did not differ in the object rotation task, indicating comparable capability of visuospatial transformation for non-corporeal stimuli in the individuals with ASD (*p < .05, **p < .01, ***p < .001). (Color figure online)

transitive action was more difficult than that of intransitive action.

The Influence of Increasing Rotational Angles on the RTs

The three-way mixed ANOVA revealed significant main effects of GROUP ($F_{1, 42}=7.38$, p = .009, $\eta^2=0.15$), CONDITION ($F_{2, 84}=48.99$, p < .001, $\eta^2=0.54$), and ANGLE ($F_{3, 126}=102.47$, p < .001, $\eta^2=0.71$). No significant three-way interaction among GROUP, CONDITION and ANGLE ($F_{6, 252}=1.05$, p = .38, $\eta^2=0.02$) was found. A significant two-way interaction was only found between CONDITION and ANGLE ($F_{6, 252}=3.87$, p = .008, $\eta^2=0.08$) (See Fig. 3).

Further analyses on the significant two-way interaction between CONDITION and ANGLE revealed that the average RT of the hand-with-spoon condition was significantly slower than that of the bare-hand and the desk conditions in the two groups for all angles (at 0°: $F_{2, 336}=24.58$, p < .001, $\eta^2=0.13$; at 60°: $F_{2, 336}=23.65$, p < .001, $\eta^2=0.15$; at 120°: $F_{2, 336}=35.95$, p < .001, $\eta^2=0.20$; at 180°: $F_{2, 336}=41.42$, p < .001, $\eta^2=0.24$). We did not present the post-hoc pairwise comparison between conditions here due to its irrelevance to the current paper. In terms of the simple ANGLE effect, there was no significant difference between 0° and 60° (bare-hand: p = .80, hand-with-spoon: p = .49, desk: p = .10), but there were significant differences between the rest of angle pairs for all conditions (p < .001 for all comparisons). These results therefore suggest that participants were indeed performing mental rotation in all three conditions.

Results of estimated slopes and intercepts are summarized in Table 3. The two-way mixed ANOVA on *slopes* revealed significant main effects of GROUP ($F_{1, 42}=4.47$, p = .041, $\eta^2=0.10$, ASD > TD) and CONDITION ($F_{2, 84}=5.04$, p < .01, $\eta^2=0.11$). No significant interaction of slope between CONDITION and GROUP was found ($F_{2, 84}=1.45$, p = .25, $\eta^2=0.03$). Post-hoc analysis for the CONDITION main effects revealed that the desk condition resulted in the lowest slope among the three conditions across groups (bare-hand vs. hand-with-spoon: p = .48, bare-hand vs. desk, p = .20, hand-with-spoon vs. desk: p < .05).

The two-way mixed ANOVA on *intercepts* revealed significant main effects of GROUP ($F_{1, 42}=5.80$, p = .021, $\eta^2=0.12$, ASD > TD) and CONDITION ($F_{2, 84}=35.96$, p < .001, $\eta^2=0.46$), but no significant interaction between CONDITION and GROUP ($F_{2, 84}=1.11$, p = .32, $\eta^2=0.03$). Post-hoc analysis for the CONDITION main effect showed that the desk condition had the smallest intercept among the three conditions across groups

Table 3 Slopes and intercepts (mean ± SD) extracted from regression analyses of RTs against angles

	Typically-developing group	ASD group
Slope (ms/degree)		
Bare hand	2.03 ± 1.51	3.23 ± 2.08
Spoon	2.51 ± 2.22	3.85 ± 2.94
Desk	1.93 ± 1.26	2.16 ± 1.39
Intercept (ms)		
Bare hand	1198.06 ± 212.14	1438.43 ± 442.65
Spoon	1270.40 ± 236.86	1555.95 ± 583.30
Desk	951.63 ± 134.59	1097.94 ± 341.48

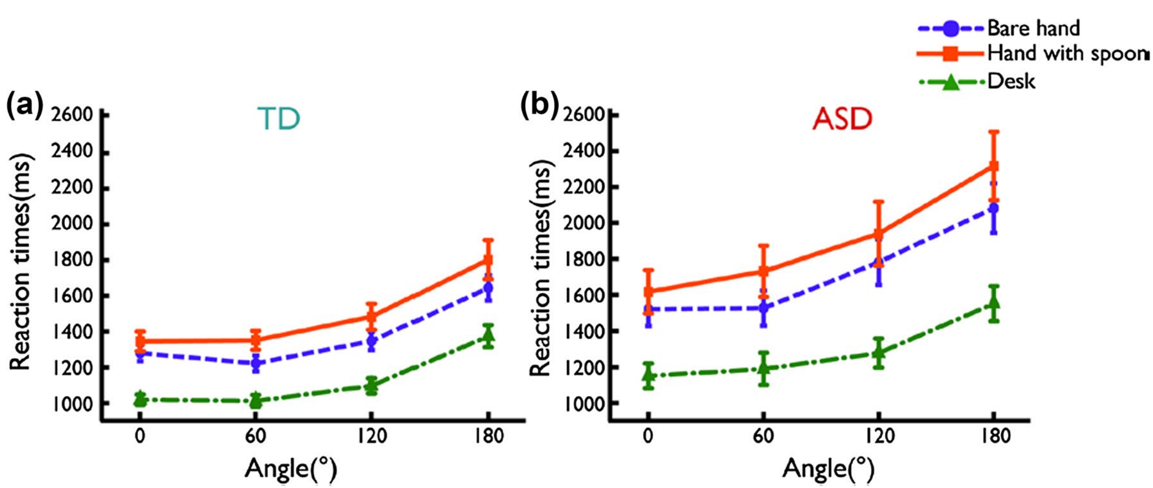

Fig. 3 Significant angle effects in the hand rotation task and the object rotation task in **a** the TD group and **b** the ASD group. For both groups, RTs increased with increasing angles rotated away from the upright position in all three types of stimuli, suggesting both groups used a mental rotation strategy. Purple lines represent the bare-hand condition, orange lines represent the hand-with-spoon condition, and green lines represent the desk condition. (Color figure online)

(bare-hand vs. hand-with-spoon: $p<.05$, bare-hand vs. desk, $p<.001$, hand-with-spoon vs. desk: $p<.001$).

The larger intercept and steeper slope of the angle effect in the ASD group, as compared to the TD group, therefore suggested that the individuals with ASD were slower both in the rotational and non-rotational aspects of mental rotation, regardless of the stimulus types. The steeper slopes in the ASD group suggested that their generally slower performance in the hand rotation task partly resulted from the extra effort they need to exert when performing MI (i.e. the processing of rotational part), and that they required more effort for imagery processes with additional rotation angles than the TD group.

The Influence of the Biomechanical Constraints on the RTs

To test whether individuals with ASD have difficulty in motor simulation, we directly examined the biomechanical effect in the two groups. The three-way mixed ANOVA resulted in significant main effects of GROUP ($F_{1,42}=7.39$, $p=.009$, $\eta^2=0.15$), CONDITION ($F_{2,84}=55.20$, $p<.001$, $\eta^2=0.57$) and ORIENTATION ($F_{1,42}=43.28$, $p<.001$, $\eta^2=0.51$). There was no significant three-way interaction among GROUP, CONDITION and ORIENTATION ($F_{2,84}=1.98$, $p=.15$, $\eta^2=0.05$). There were significant two-way interactions between GROUP and CONDITION ($F_{2,84}=3.75$, $p=.043$, $\eta^2=0.08$), between ORIENTATION and GROUP ($F_{1,42}=5.85$, $p=.020$, $\eta^2=0.12$), and between CONDITION and ORIENTATION ($F_{2,84}=19.96$, $p<.001$, $\eta^2=0.32$) (see Fig. 4a).

Further analyses on the significant two-way interaction between CONDITION and ORIENTATION revealed that there was significant simple ORIENTATION effects (i.e., biomechanical effects) only for the hand rotation task (bare-hand: $F_{1,126}=22.34$, $p<.001$, $\eta^2=0.18$; hand-with-spoon: $F_{1,126}=56.35$, $p<.001$, $\eta^2=0.36$), but not for the object rotation task (desk condition: $F_{1,126}=0.82$, $p=.37$, $\eta^2=0.01$). In terms of the significant two-way interaction between GROUP and CONDITION, further analyses revealed significant simple GROUP effects in both the bare-hand ($F_{1,126}=10.08$, $p<.005$, $\eta^2=0.09$) and the hand-with-spoon ($F_{1,126}=13.74$, $p<.001$, $\eta^2=0.12$) conditions, but not in the desk condition ($F_{1,126}=2.39$, $p=.13$, $\eta^2=0.02$). There were also significant simple CONDITION effects both in the TD group ($F_{2,84}=8.52$, $p<.001$, $\eta^2=0.15$) and the ASD group ($F_{2,84}=21.65$, $p<.001$, $\eta^2=0.34$). Since the desk condition clearly revealed no biomechanical effect, it

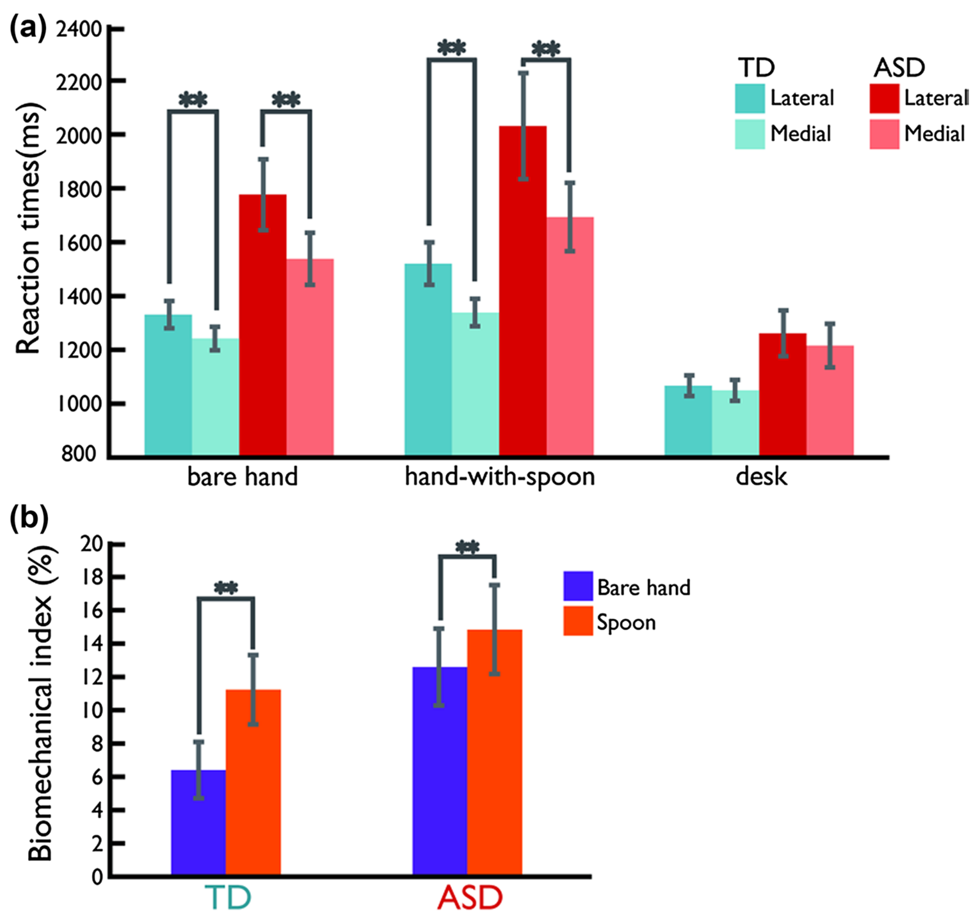

Fig. 4 Effects of biomechanical constraints on RTs. **a** The biomechanical effect. Similar to the TD group, the ASD group showed significant biomechanical effects for both the intransitive and transitive conditions in the hand rotation task. Light and dark blue bars represent the medial rotation and the lateral rotation, respectively in the TD group; light and dark red bars represent the medial rotation and the lateral rotation, respectively in the ASD group. **b** The biomechanical index. The significant task effects of the biomechanical index in both groups indicated that the transitive condition might be more affected by biomechanical constraints than the intransitive condition. Purple bars represent the bare-hand condition, and orange bars represent the hand-with-spoon condition. (Color figure online)

is therefore meaningless to perform further analyses on the two-way interaction between GROUP and ORIENTATION. Instead, we performed the biomechanical index analyses that focused on the hand rotation task in the following section.

Biomechanical Index

In the hand rotation task, two possible scenarios can potentially account for the observed larger RT difference between lateral and medial rotation in the ASD group relative to the TD group: One, it might reflect processes of MI in individuals with ASD that were more sensitive to the modulation by postural changes between an awkward posture and a more natural posture. Two, such an effect could be confounded by the generally slower RTs of the ASD group in the hand rotation task compared to the TD group. To distinguish between these two possibilities, we analyzed the biomechanical index, normalized by each individual's RT, for the hand rotation task. The two-way mixed ANOVA on the biomechanical index with CONDITION (intransitive vs. transitive) as a within-subject factor and GROUP (ASD vs. TD) as a between-subject factor revealed a significant CONDITION main effect ($F_{1, 42} = 4.66$, p = .037, $\eta^2 = 0.10$), but no significant GROUP main effect ($F_{1, 42} = 3.16$, p = .08, $\eta^2 = 0.07$, power = 0.41). No significant two-way interaction between CONDITION and GROUP ($F_{1, 42} = 0.62$, p = .44, $\eta^2 = 0.01$) was found. The absent GROUP main effect confirmed that the larger RT differences in the ASD group resulted from the slower overall RTs, instead of larger interference of the biomechanical constraints. Detailed results are shown in Fig. 4b. The significant larger biomechanical index for the transitive condition than for the intransitive condition in both groups implies that the goal-directed actions elicited more engagements of kMI in both populations.

Discussion

The results in the current study suggest that the adolescents with ASD are capable of using kMI to perform the hand rotation task, as reflected by the similar significant biomechanical effects in their performance as the TD controls. However, the overall slower processing speed for the corporeal stimuli (i.e., bare-hand and hand-with-spoon), but not for the non-corporeal stimuli (i.e., desks), in the ASD group indicates that they are less efficient in implementing kMI than the TD group.

The current findings of less efficient but preserved capability of kMI appear to contradict with some other findings showing that individuals with ASD failed to simulate hand movements using sensorimotor strategies (e.g., Conson et al. 2013). The discrepancy may primarily come from the different levels of perceptual challenge of rotating hands used in the hand rotation task. Using images of 2-D hands that rotate along a single axis greatly reduced the perceptual challenge of rotating hands (ter Horst et al. 2010), and might not able to promote the use of kinesthetic information in the ASD participants. In contrast, by using hand stimuli that rotate in a 3D space and around multiple axes, we showed that the ASD participants can indeed initiate kMI spontaneously. Similarly, a latest research reported comparable biomechanical effects between the TD and ASD group (Conson et al. 2016). The study further found that the ASD participants showed less effective action simulation than the TD controls in that they were more easily disturbed by the mismatching between actual body posture and the corresponding covert motor simulation.

The observed inefficient performance of the ASD group in the hand rotation task may reflect their reduced capacity for MI specifically involving body parts. Such inefficiency cannot be attributed to a general deficit in mental rotation ability due to the lack of a significant group difference in the RT performance for the object rotation task. These results also indicate that individuals with ASD may retain intact visuospatial transformation capability for non-corporeal objects, which is in line with the previous literature reporting that individuals with ASD exhibited normal mental rotation ability for 3D geometric blocks or letters (Falter et al. 2008; Soulieres et al. 2011). Furthermore, in contrast to previous findings that reported intact action representation in the transitive condition but deficient action representation in the intransitive condition (Hamilton 2008; Wild et al. 2012), our results showed that individuals with ASD can perform kMI both in the transitive and intransitive conditions, which is similar to those studies of action imitation on behavioral and neurophysiological level (Carmo et al. 2013; Ruysschaert et al. 2014). Specifically, similar to the TD group, the ASD participants showed larger biomechanical index in the transitive condition than in the intransitive condition, suggesting that the goal-directed action induced higher degree of engagement in kMI for both groups.

There seems to be inconsistency between the present findings and other studies that support the broken mirror hypothesis (Iacoboni and Dapretto 2006; Oberman and Ramachandran 2007), which posits a dysfunctional mirror neuron system (MNS) in individuals with ASD. The MNS mainly encompasses regions in the inferior frontal gyrus and the inferior parietal lobule, and is activated both in performing real actions (i.e., overt execution) and action observation (i.e., covert simulation) (Rizzolatti and Craighero 2004). Previous research has suggested that the MNS is recruited when action representation is activated, including not only during action observation and execution, but during kMI as well (Guillot et al. 2009). Specifically, the MNS appeared to be activated to a higher degree when intense kinesthetic feedback is available (Koski et al.

2002). Some research further demonstrated that, compared to intransitive actions, transitive actions (e.g., tool-using gestures) elicited higher activation of the MNS (Kumar et al. 2013; Li et al. 2015) and induced more salient action representation (Muthukumaraswamy et al. 2004). 'The direct matching hypothesis' further assumed that mapping the visual representation of the observed action onto the corresponding action representation enables us to understand other's action intentions (Iacoboni et al. 2005; Rizzolatti and Fabbri-Destro 2008; Rizzolatti et al. 2001). Based on these assumptions, the 'broken mirror hypothesis' postulated that deficient development of the MNS in individuals with ASD might contribute to their imitation deficit and by extension their difficulty in social cognition (Iacoboni and Dapretto 2006; Oberman and Ramachandran 2007). Various studies have provided empirical support for this account (Bernier et al. 2007; Dapretto et al. 2006). However, recent evidence has cast doubt on this hypothesis by demonstrating that individuals with ASD show relatively intact performance in several behavioral action representation tasks including action observation, action imitation, and gesture recognition (Carmo et al. 2013; Hamilton et al. 2007). These tasks have been shown to recruit activation of the MNS in functional neuroimaging studies in normal adults (Iacoboni et al. 1999; Koski et al. 2002). In addition, the MNS allows individuals to simulate observed actions through automatic and implicit matching between visual perception and motor outputs (Rizzolatti et al. 2001). Given the hand rotation task is thought to elicit "implicit" MI (Osuagwu and Vuckovic 2014) with no explicit instructions, our results concurred and extended the existing literature by suggesting preserved action representation in individuals with ASD, as they were able to spontaneously simulate action through kMI. Although the current study lacks direct neurophysiological evidence, previous research has demonstrated close links between motor simulation in the hand rotation task and suppression in mu rhythms (ter Horst et al. 2013), which has been recognized as an index for activation of the MNS in electroencephalography (EEG) recording (Pineda 2005). Further studies comparing the quality and quantity of MI-induced brain activities (e.g., mu rhythm desynchronization in EEG studies or blood-oxygen-level dependent (BOLD) signals in fMRI research) between the ASD and TD group would be needed to provide the direct neuronal mechanism.

In conclusion, our primary findings suggest functional but inefficient kMI in individuals with ASD. Even though they are generally characterized by and prone to use their enhanced visual perception, our data showed that they can still spontaneously adopt kMI rather than vMI as an alternative strategy. The current results also suggest the possibility of applying kMI rehabilitation as an intervention approach for motor deficits in ASD.

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Authors Contribution YTC conceived of the study, participated in its design, collected all the data, performed data analyses, participated in data interpretation, wrote the paper; KST made diagnosis and organized the recruitment of ASD participants; HLC participated in its design, data analyses and data interpretation, wrote the paper; CCW performed ADOS evaluation; YTF participated in its design, helped edit the paper; CTW conceived of the study, participated in its design, data analyses and data interpretation, applied and secured the funding, supervise and coordinate the project, wrote the paper. All authors read and approved the final manuscript.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical Approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the [institutional and/or national research committee] and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed Consent Informed consent was obtained from all individual participants included in the study.

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