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Body Constraints on Motor Simulation in Autism Spectrum Disorders

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Abstract Developmental data suggested that mental simulation skills become progressively dissociated from overt motor activity across development. Thus, efficient simulation is rather independent from current sensorimotor information. Here, we tested the impact of bodily (sensorimotor) information on simulation skills of adolescents with Autism Spectrum Disorders (ASD). Typically-developing (TD) and ASD participants judged laterality of hand images while keeping one arm flexed on chest or while holding both arms extended. Both groups were able to mentally simulate actions, but this ability was constrained by body posture more in ASD than in TD adolescents. The strong impact of actual body information on motor simulation implies that simulative skills are not fully effective in ASD individuals.

Keywords ASD · Motor simulation · Motor imagery · Proprioception · Mental transformation · Development

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Introduction

Mental transformation refers to humans' ability to imagine and transform the shapes of objects in their mind. Previous research has mainly focused on a specific kind of spatial transformation known as mental rotation, which refers to imagining a rotational movement of a two-dimensional shape or a three-dimensional object in space. Individuals with Autism Spectrum Disorders (ASD) have spared or even enhanced abilities in tasks requiring mental rotation of concrete or abstract objects (Hamilton et al. 2009; Falter et al. 2008; Muth et al. 2014; Pearson et al. 2015; Silk et al. 2006; Soulières et al. 2011). Studies on mental rotation of body or body parts highlight qualitative differences in performance between typical and autistic individuals (Conson et al. 2013a, 2015b; Pearson et al. 2014).

Tasks requiring mental transformation of body and body parts draw on specific cognitive and neural mechanisms not required for object rotation (Dalecki et al. 2012; Keehner et al. 2006; Kosslyn et al. 1998). These include the use of one's own body as a reference for performing spatial transformations (Conson et al. 2012; Pearson et al. 2013), and a motor simulation mechanism (Hétu et al. 2013).

Motor simulation implies that sensorimotor information related to movement execution is also recruited by other motor-related skills such as imitation, action understanding or imaging one's own movements (Decety and Grèzes 2006; Gallese and Sinigaglia 2011). Several studies suggested that motor simulation mechanisms could differ in ASD (for a review see Eigsti 2013). For instance, behavioural findings showed that individuals with ASD are not engaged in motor simulation when required to mentally transform hand images (Conson et al. 2013) or self-body position in space (Conson et al. 2015b; Pearson et al. 2014; 2015). Recently, it has been demonstrated that the severity

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of ASD symptomatology is associated with reduced ability to simulate one's own sensorimotor experience (Eigsti et al. 2015), supporting the view that dysfunctional simulation processes may be related to the social and communicative deficits in ASD (Oberman and Ramachandran 2007). Thus, clarifying functioning of simulation mechanisms could allow to better defining the profile of strengths and weaknesses in ASD (Eigsti 2013; Klin et al. 2003).

Motor processes play a functional role in the acquisition of mental transformation skills in children and adolescents, but mental transformation becomes progressively more independent from overt motor activity during typical development (Piaget 1954, 1971; Funk et al. 2005). In other words, adult individuals are still affected by sensorimotor information during mental transformation of body and body parts (e.g., Conson et al. 2015a; Kessler and Thomson 2010), but are less constrained by sensorimotor feedback with respect to young individuals, likely due to an increased ability to perform covert motor simulations (for a review see Frick et al. 2014).

On this basis, it is possible to hypothesize that atypical motor simulation processes remain strongly constrained by current bodily information, unlike fully effective motor simulation processes. In the present study, we tested this hypothesis by investigating the impact of current sensorimotor information on motor simulation skills of ASD individuals. We manipulated participants' arm position during a classical behavioural task assessing mental transformation of hand images (the hand laterality task; Parsons 1987, 1994), and tested the influence of participants' actual body posture on hand laterality performance.

The hand laterality task requires participants to decide whether a visual stimulus presented in different angular orientations portrays a left or a right hand (Parsons 1987, 1994). Two main indices of the relationship between motor simulation and sensorimotor information can be obtained by analysing hand laterality performance. First, the biomechanical effect which quantifies the ability to mentally activate sensorimotor information during action simulation (Parsons 1987, 1994; Sekiyama 1982). Second, the posture effect which quantifies the subjects' tendency to incorporate the current state of their body during mental simulation of actions (Funk et al. 2005; van Nuenen et al. 2012).

The *biomechanical effect* is the advantage for judging hand images showing physically comfortable versus awkward positions (Parsons 1987, 1994; Sekiyama 1982). More precisely, participants are faster (and more accurate) in judging a 90° oriented left hand (fingers pointing to the right; medial orientation with respect to the body sagittal plane) than a 90° oriented right hand (lateral orientation with respect to the body sagittal plane); analogously, participants show an advantage when judging a 270° oriented right hand (fingers pointing to the left; medial orientation) than a 270° oriented left hand (lateral orientation) (see Fig. 1).

The *posture effect* is the advantage for judging hand positions that match the participants' body posture during the task with respect to hand positions showing non-matching postures (Conson et al. 2015a; de Lange et al. 2006; Funk et al. 2005; Ionta and Blanke 2009; Ní Choisdealbha et al. 2011). For instance, de Lange et al. (2006) asked subjects to judge hand laterality while keeping one arm (left or right) flexed with the hand on their chest. Results showed that when subjects had their left (or right) arm flexed on chest (with fingers oriented towards the contralateral side), identification of the left (or right) hand in opposite orientation was hampered.

Here, participants performed the hand laterality task in different body postures. In the "extended arms posture", subjects kept both arms extended on the desk, while in "flexed arm postures", participants kept left or right arm flexed with their hand placed on a wooden smooth surface in correspondence with their chest. Our main prediction was that if motor simulation was not fully effective in ASD, we would find that current body posture constrained motor simulation more strongly in participants with ASD than in typically developing (TD) participants.

Methods

Participants

Thirty-six right-handed adolescents were recruited for the study; 18 individuals with ASD (1 female; mean age = 14.6, SD = 4.2; age range = 10–20) and 18 TD adolescents (2 females; mean age = 14.8, SD = 3.5; age range 10–20). Diagnosis of ASD was reached after a multidisciplinary assessment by a neuropsychiatrist and a clinical psychologist trained in evaluation of individuals with neurobehavioural disorders according to DSM-V criteria. Clinical diagnosis was validated by means of the Autism Diagnostic Interview-Revised (ADI-R) and the Autism Diagnostic Observation Schedule (ADOS) Module 3. General intelligence was measured by means of the Wechsler Intelligence Scales (WISC-III or WAIS-R depending on participants' age) in ASD individuals. Individuals with a history of epilepsy, neurological abnormalities, genetic syndromes, general learning disability, significant head injury, or psychosis were excluded from the study. TD adolescents, without history of neurological or psychiatric diagnosis and matched for age and gender with the ASD group, were recruited from secondary schools in Naples. Cognitive level of the control group was measured by the Raven's Progressive Matrices (RPM;

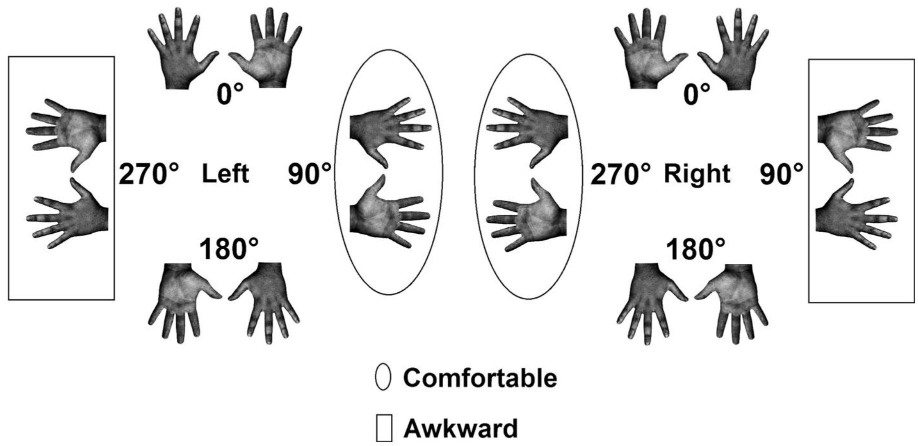

Fig. 1 Stimuli used in the experiment were natural colour pictures of hand images. Hands taken into account to compute the biomechanical effect (the advantage for judging hand images showing physically comfortable versus physically awkward positions) are highlighted with *squares* (awkward orientations) and *circles* (comfortable orientations)

Gugliotta et al. 2009; Raven 1954). Since RPM score is well correlated with Wechsler Full Scale intelligence quotient (IQ) in typical participants (e.g., O'Leary et al. 1991), RPM scores from the TD group were matched with Wechsler Intelligence Scales Full Scale IQ from the ASD group. Independent samples t tests demonstrated that estimated IQ (mean = 104.4, SD = 7.5) of TD adolescents did not differ from the mean Wechsler Full Scale IQ of the ASD adolescents (110.3, SD = 14.7; $t(25.3) = 1.493$, $p = .148$).

All the participants completed the experimental tasks that had been previously approved by the local ethical committee ("Comitato Etico del Dipartimento di Psicologia della Seconda Università di Napoli") and were conducted according to the Helsinki Declaration. Written informed consent was obtained from the parents of each participant involved in the study.

Stimuli and Procedure

The experimental stimuli consisted of full-colour pictures of right and left hands portrayed from back and palm (Fig. 1). The hand images were large approximately 9.5 cm along the widest axis (10.7° of visual angle at a viewing distance of 50 cm). Hands were presented one at a time at the centre of a computer screen in four different orientations (0°, 90°, 180° and 270° clockwise from the upright). Participants were required to decide whether each stimulus consisted of a left or a right hand; they were instructed to respond as fast and accurately as possible by pressing left or right keys on a foot pedal (a left foot press was required in response to a left hand and a right foot press in response to a right hand).

All the subjects sat in front of the computer screen adopting a left or a right flexed arm posture and an extended arms posture. In flexed arm conditions, participants' flexed arm/hand (*left* or *right*) was placed on a wooden smooth surface in correspondence with their chest and the non-flexed arm/hand on their thigh. In the extended arms posture, subjects kept both arms extended on the desk (Fig. 2). In all conditions, both arms were covered with a black cloth and were not visible to the subjects.

The experiment comprised three blocks: left arm flexed, right arm flexed, both arms extended (repeated twice to obtain the same number of trials as in flexed arm conditions); order of blocks was counterbalanced across subjects. Each block comprised 96 trials: six trials were presented for each combination of hand view (palm and back), hand laterality (left or right) and hand orientation (0°, 90°, 180° or 270°). The total number of trials was 384. Before each task, eight practice trials were given and discarded from statistical analysis. Subjects were explicitly required to refrain from moving their head, hands or fingers, and the experimenter (seated behind participants) checked that subjects complied with this instruction for the whole task.

Statistical Analysis

Mean Reaction Times (RTs) and error rates were calculated and then submitted to Analysis of Variance (ANOVA). First, to test whether the biomechanical effect was more constrained by body posture in ASD than in TD participants, we performed an ANOVA with biomechanical complexity (comfortable and awkward), hand view (palm and back) and body posture (extended, left arm flexed and right arm flexed) as within-subjects factors, and with group (ASD and TD participants) as a between-subjects factor.

Second, to test whether the body posture effect was significantly stronger in ASD than in TD participants, we first defined matching and non-matching postures (Fig. 3). A non-matching posture consisted of a left (right) hand palm oriented differently from the subject's left (right)

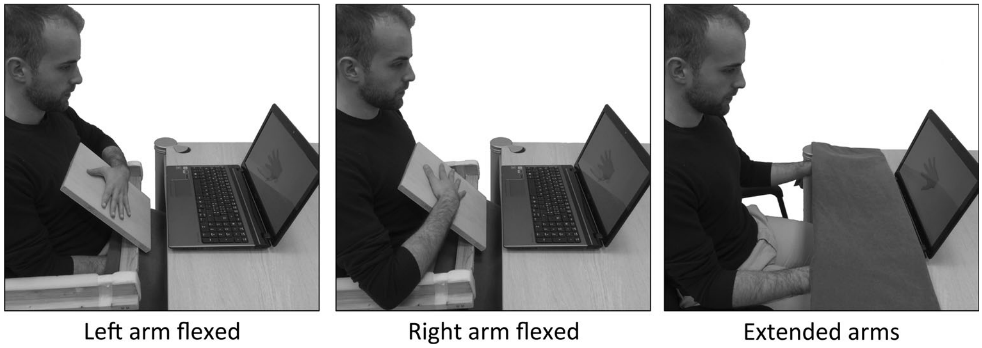

Fig. 2 The experimental task required participants' to judge laterality of hand images while keeping different body postures. In flexed arm conditions, participants' flexed arm/hand (left or right) was placed on a wooden smooth surface in correspondence of their chest and the non-flexed arm/hand on their thigh. In the extended arms posture, subjects kept both arms extended on the desk. In all conditions, both arms were covered with a black cloth and were not visible to the subjects (the cloth is not shown in the flexed arm posture to depict participant's hand position clearly)

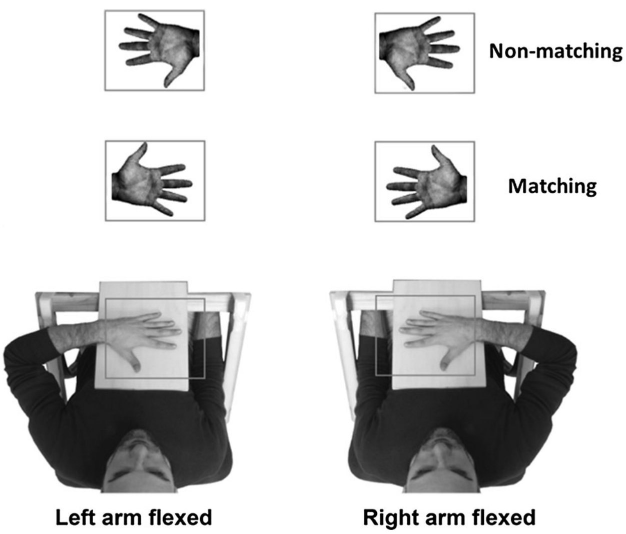

Fig. 3 Description of the stimuli and of body postures used to define non-matching and matching conditions and to calculate the posture effect (the advantage for judging hand images showing positions that match the participants' actual body posture with respect to non-matching postures). A non-matching posture was obtained when the left flexed arm posture combined with a left palm at 270° orientation and the right flexed arm posture combined with a right palm at 90° orientation. A matching posture was obtained when the left flexed arm posture combined with a left palm at 90° orientation and the right flexed arm posture combined with a right palm at 270° orientation

hand, i.e. the left flexed arm posture combined with a left palm at 270° orientation and the right flexed arm posture combined with a right palm at 90° orientation. A matching posture consisted of a left (right) hand palm oriented in the same direction as the subject's left (right) hand, i.e. the left flexed arm posture combined with a left palm at 90° orientation and the right flexed arm posture combined with a right palm at 270° orientation. We performed an ANOVA with body posture (left arm flexed and right arm flexed) and hand/arm matching (matching and non-matching) as within-subjects factors, and with group (ASD and TD participants) as a between-subjects factor.

Statistical analyses were performed using the Statistical Package for Social Sciences (SPSS Inc, version 15.0). Greenhouse-Geisser correction was used whenever the assumption of sphericity was violated, but uncorrected degrees of freedom were reported for transparency. Post-hoc analyses were performed using *t* tests and Bonferroni correction for multiple comparisons was applied when necessary.

Results

Biomechanical Effect and Posture Manipulation

Reaction Times

We first performed an ANOVA with biomechanical complexity (comfortable and awkward), hand view (palm and back) and body posture (extended, left arm flexed and right arm flexed) as within-subjects factors, and with group (ASD and TD participants) as a between-subjects factor. Results showed significant main effects of view [$F(1,34) = 13.424$, $p = .001$, $\eta_p^2 = .283$], with slower RTs to palms (mean = 2523, SEM = 136.5) than backs (mean = 2238, SEM = 116.8), of biomechanical complexity [$F(1,34) = 21.979$, $p = .0001$, $\eta_p^2 = .393$], with slower responses to awkward (mean = 2576, SEM = 148.3) than to comfortable orientations (mean = 2186, SEM = 103.5), and of group [$F(1,34) = 32.258$, $p = .0001$, $\eta_p^2 = .487$], with slower RTs of individuals with ASD (mean = 3068, SEM = 171.1) than TD subjects (mean = 1694, SEM = 170.2).

We also found significant first-order interactions between posture and group [$F(2,68) = 5.062$, $p = .012$,

$\eta^2_p = .130$], view and group [F(1,34) = 4.586, $p = .039$, $\eta^2_p = .119$], and between view and biomechanical complexity [F(1,34) = 20.945, $p = .0001$, $\eta^2_p = .381$]. Moreover, results showed a significant second-order interaction among posture, view and biomechanical complexity [F(2,68) = 4.211, $p = .025$, $\eta^2_p = .110$], and, most relevantly, a significant third-order interaction among posture, view, biomechanical complexity and group [F(2,68) = 4.717, $p = .017$, $\eta^2_p = .122$].

To explore this last interaction, RTs data were submitted to two further ANOVAs, separated by group (ASD and TD participants). In both cases, biomechanical complexity (comfortable and awkward), hand view (palm and back) and body posture (extended, left arm flexed and right arm flexed) were within-subjects factors. For the ASD group, there were significant main effects of view [F(1,17) = 9.264, $p = .007$, $\eta^2_p = .353$], with slower RTs to palms (mean = 3293, SEM = 233.2) than backs (mean = 2842, SEM = 201.5), and of biomechanical complexity [F(1,17) = 13.219, $p = .002$, $\eta^2_p = .437$], with slower responses to awkward (mean = 2576, SEM = 148.3) than to comfortable orientations (mean = 2186, SEM = 103.5). Moreover, we found a significant first-order interaction between view and biomechanical complexity [F(1,17) = 13.216, $p = .002$, $\eta^2_p = .436$], since the biomechanical effect was significant when ASD participants judged palms ($p = .001$) but not backs ($p > .05$). Most relevantly, results showed a significant second-order interaction among posture, view and biomechanical complexity [F(2,34) = 4.974, $p = .018$, $\eta^2_p = .226$], because the biomechanical effect was significant when ASD individuals judged hands in palm view in all the three posture conditions (extended arms: $p = .011$; right flexed arm = .018; left flexed arm: $p = .001$), and hands in back view in the right flexed arm posture ($p = .037$) but not in the other two postures ($p > .05$; Fig. 4, first row). However, the biomechanical effect was larger when judging palms in the left arm flexed condition than in all the other conditions, as the significance survived after Bonferroni correction ($p < .004$).

For the TD group, there were significant main effects of view [F(1,17) = 6.400, $p = .022$, $\eta^2_p = .274$], with slower RTs to palms (mean = 1753, SEM = 142.1) than backs (mean = 1635, SEM = 118.3), and of biomechanical complexity [F(1,17) = 9.378, $p = .007$, $\eta^2_p = .356$], with slower responses to awkward (mean = 1823, SEM = 165.4) than to comfortable orientations (mean = 1564, SEM = 96.5). Moreover we found a significant first-order interaction between view and biomechanical complexity [F(1,17) = 9.020, $p = .008$, $\eta^2_p = .347$], because the biomechanical effect was significant when TD participants judged palms ($p = .002$) but not backs ($p > .05$). Relevantly, the significant second-order interaction among posture, view and biomechanical complexity was not significant ($p > .05$; Fig. 4, second row).

Error Rates

The same ANOVA design as above showed significant main effects of view [F(1,34) = 10.105, $p = .003$, $\eta^2_p = .229$], with more errors to palms (mean = .13, SEM = .02) than backs (mean = .09, SEM = .01), and of biomechanical complexity [F(1,34) = 34.701, $p = .0001$, $\eta^2_p = .505$], with more errors to awkward (mean = .17, SEM = .02) than to comfortable orientations (mean = .06, SEM = .01). Moreover, we found a significant first-order interaction between view and biomechanical complexity [F(1,34) = 8.360, $p = .007$, $\eta^2_p = .197$], since the biomechanical effect was significant when participants judged both palms ($p = .0001$) and backs ($p = .002$), albeit stronger with palms. We also found a significant first-order interaction between biomechanical complexity and group [F(1,34) = 5.029, $p = .032$, $\eta^2_p = .129$], because the biomechanical effect was significant in both ASD ($p = .0001$) and TD ($p = .014$) groups, albeit larger in ASD. No other main effect or interaction was significant ($p > .05$), but it is worth noting that the second-order interaction among posture, biomechanical complexity and group showed a trend towards significance [F(2,68) = 2.730, $p = .097$, $\eta^2_p = .051$], consistent with RTs data (Fig. 5).

Summary of Results

In synthesis, the main results of the analysis on RTs demonstrated a significant biomechanical effect (the advantage for judging hands showing comfortable versus awkward positions) both in ASD and TD participants, but importantly posture manipulation significantly influenced the biomechanical effect in ASD individuals only. Results of analysis on error rates fitted the pattern of RTs revealing a different influence of body posture on the biomechanical effect in the two groups.

Posture Effect

Reaction Times

We performed an ANOVA with body posture (left arm flexed and right arm flexed) and hand/arm matching (matching and non-matching) as within-subjects factors, and with group (ASD and TD participants) as a between-subjects factor. Results showed significant main effects of posture [F(1,34) = 7.514, $p = .010$, $\eta^2_p = .181$], with slower RTs in the left (mean = 2588, SEM = 178.7) than in the right arm flexed posture (mean = 2163,

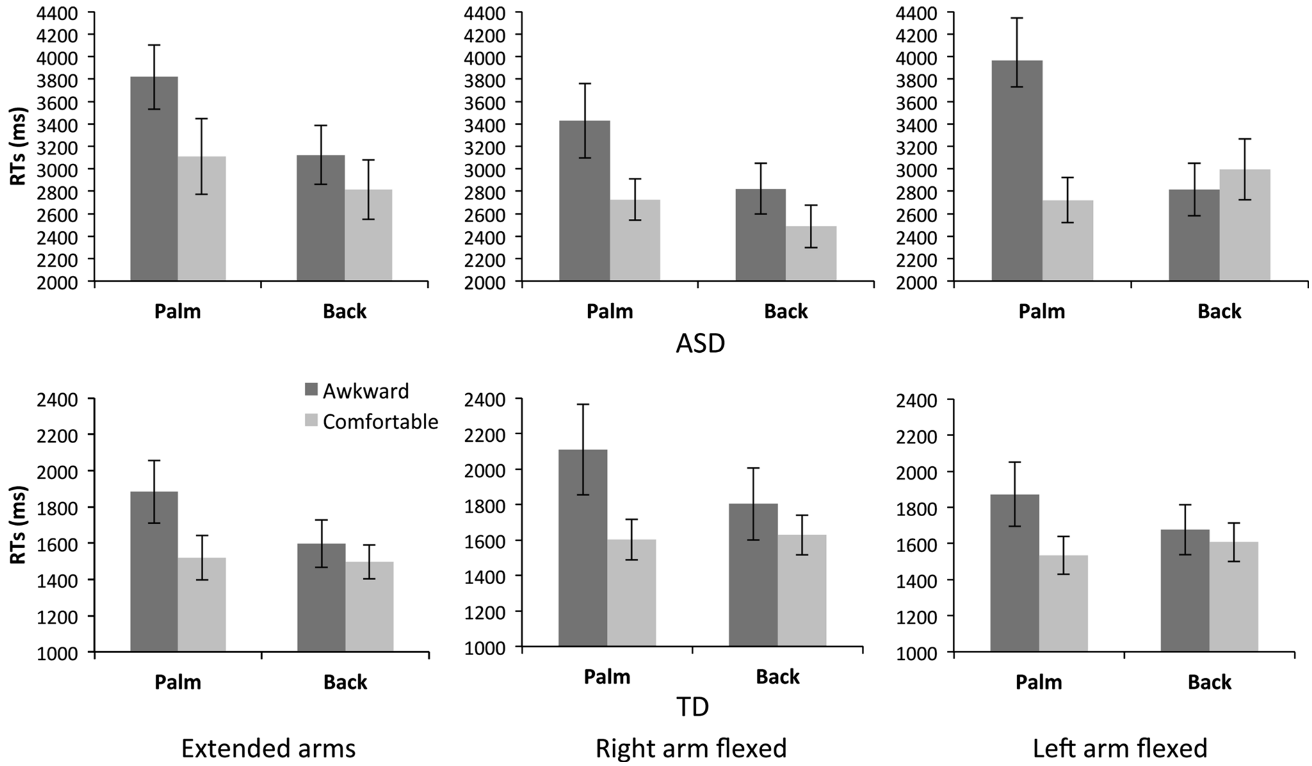

Fig. 4 RTs (*bars* are SEM) to palm and back stimuli in awkward and comfortable orientations, separately for the three body postures in ASD (*upper row*) and TD (*lower row*) adolescents

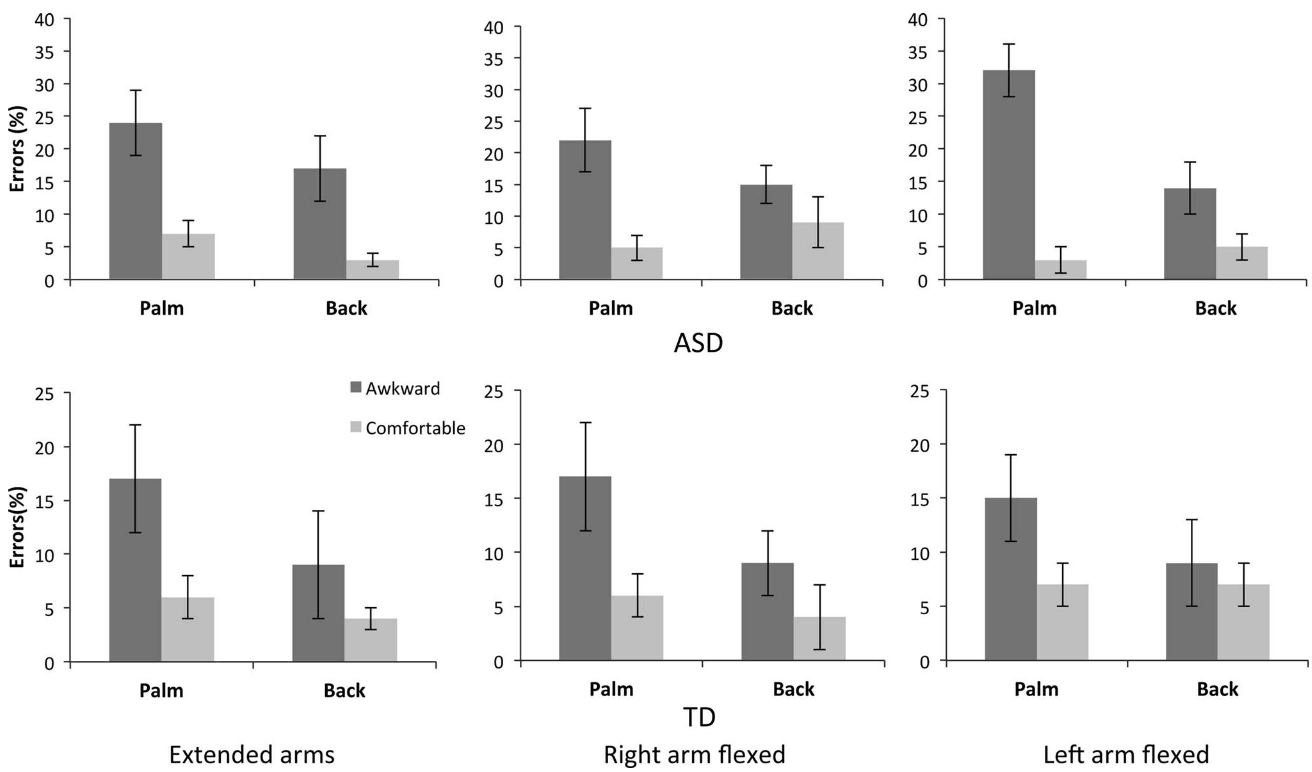

Fig. 5 *Errors* (*bars* are SEM) to palm and back stimuli in awkward and comfortable orientations, separately for the three body postures in ASD (*upper row*) and TD (*lower row*) adolescents

SEM = 108.5), of hand/arm matching [F(1,34) = 22.751, $p = .0001$, $\eta_p^2 = .401$], with slower RTs in the non-matching (mean = 2679, SEM = 172.2) than in matching (mean = 2072, SEM = 100.5) condition, and of group [F(1,34) = 34.888, $p = .0001$, $\eta_p^2 = .506$], with slower RTs of individuals with ASD (mean = 3118, SEM = 177.9) than TD participants (mean = 1633, SEM = 176.8). Moreover, we found significant first-order interactions between posture and group [F(1,34) = 5.497, $p = .025$, $\eta_p^2 = .139$], hand/arm matching and group [F(1,34) = 11.420, $p = .002$, $\eta_p^2 = .251$], and between posture and hand/arm matching [F(1,34) = 8.672, $p = .006$, $\eta_p^2 = .203$]. Crucially, results showed a significant second-order interaction among posture, hand/arm matching and group [F(1,34) = 9.572, $p = .004$, $\eta_p^2 = .220$], because in ASD individuals the posture effect (matching vs. non-matching) was significant when they judged hand stimuli while keeping their left arm ($p = .001$) but not their right arm flexed ($p > .05$); in TD participants instead the posture effect was never significant ($p > .05$; Fig. 6).

Error Rates

The same ANOVA design as above showed a significant main effect of hand/arm matching [F(1,34) = 17.176, $p = .0001$, $\eta_p^2 = .336$], with more errors in the non-matching (mean = .21, SEM = .04) than in matching (mean = .06, SEM = .02) condition. Moreover, we found a significant first-order interaction between hand/arm matching and group [F(1,34) = 4.211, $p = .050$, $\eta_p^2 = .109$], due to a significant posture effect (matching vs. non-matching) in the ASD ($p = .0001$) but not in the TD group ($p > .05$).

We also found a significant second-order interaction among posture, hand/arm matching and group [F(1,34) = 9.572, $p = .004$, $\eta_p^2 = .220$], because in ASD individuals the posture effect was significant in both left arm ($p = .0001$) and right arm flexed posture ($p = .018$), but the effect was stronger in the left than in right arm flexed posture; in TD participants instead the posture effect was never significant in neither left arm flexed or in right arm flexed posture (Fig. 6).

Summary of Results

In synthesis, the main results of the analysis on RTs showed that in ASD participants the posture effect (the advantage for judging hand positions matching the participants' posture with respect to non-matching postures) was significant when they performed the task in the left arm flexed condition, whereas in TD participants the posture effect was never significant. Consistent with RTs data, analysis on errors showed that posture manipulation

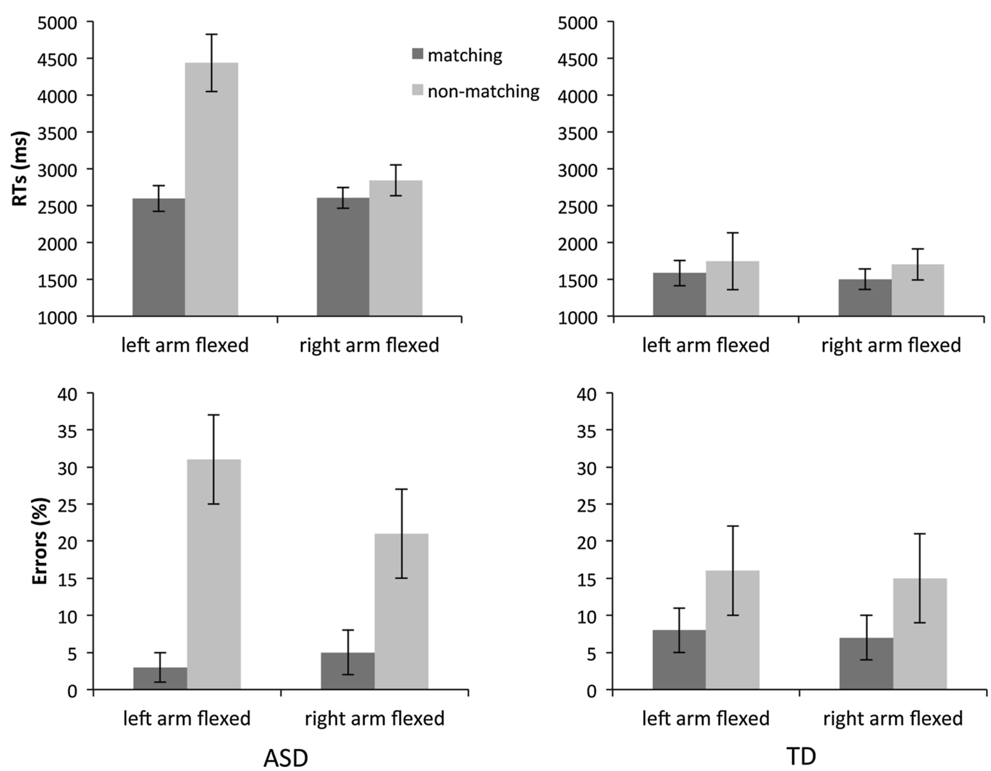

Fig. 6 RTs and *Errors* (*bars* are SEM) in matching and non-matching conditions, separately for the two flexed arm postures in ASD (*left panel*) and TD (*right panel*) adolescents

significantly affected hand laterality judgment in ASD but not in TD adolescents.

Discussion

The present study aimed to assess the impact of current sensorimotor information on mental simulation skills of ASD adolescents, by manipulating body posture (arm position) during the hand laterality task. Results showed the biomechanical effect in both groups, but the effect was significantly influenced by posture manipulation in ASD participants only. Fittingly, the posture effect was significantly present in ASD but not in TD individuals. Taken together, we demonstrated that current sensorimotor information impacts on motor simulative abilities of ASD adolescents, thus supporting the idea that simulation processes are not fully effective in ASD.

Studies on motor imagery of TD children demonstrated that the contribution of motor processes to mental transformation of body parts becomes less relevant during development (Frick et al. 2009; Funk et al. 2005; Krüger and Krist 2009). For instance, in a behavioural study employing an experimental paradigm analogous to that employed here, Funk et al. (2005) required 5- to 6-year-old children and young adults to mentally rotate hands while keeping their own hands in different postures and found that hand position influenced children more than adults. Consistently, Frick et al. (2009) asked 5-, 8-, and 11-year-old children and adults to perform a mental rotation task while executing a circular movement with their own dominant hand. The authors reported a stronger motor influence in 5- and 8-year-old children than in 11-year-old children and adults. Starting from this evidence, Frick et al. (2014) suggested that developmental changes in mental transformation ability imply a continuous refinement of simulative skills allowing implementation of "covert motor simulations" that become progressively more independent from "overt motor activity". The present results fit these developmental findings, but it should be underlined here that the above studies were conducted on children, whereas we assessed motor simulation in adolescents. Studies directly testing the contribution of motor information to mental simulation of adolescents are scarce, but available data demonstrated that the ability to re-enact sensorimotor information during action simulation steadily increases across adolescence (Caeyenberghs et al. 2009; Choudhury et al. 2007a, b; Conson et al. 2013b). In the present study, we find a significant biomechanical effect in TD participants, consistent with the above literature, and this effect was also present in ASD group. Critically, however, the effect was significantly modulated by posture in the ASD but not in the TD group. We also found a significant posture effect in ASD but not in TD participants. The posture effect, measuring the impact of current body constraints on simulative processes (Funk et al. 2005; van Nuenen et al. 2012), is stronger when motor simulation mechanisms are not completely developed (Frick et al. 2014; Funk et al. 2005).

Recently, Conson et al. (2013a) required ASD adolescents to perform a classical hand laterality task and did not show a significant biomechanical effect. Since the biomechanical effect is a hallmark of the ability to mentally activate sensorimotor information during action simulation, the authors suggested that the lack of this effect proved an alteration of simulative skills in ASD. The difference between our previous and the present findings (lack vs. presence of the biomechanical effect, respectively) could be accounted for by two main methodological factors influencing performance on the hand laterality task. First, Conson et al. (2013a) study did not include posture manipulation and, second, the authors used a response modality—hand response—different from that employed in the present study—foot response (see for instance Cocksworth and Punt's 2013 study on the effects of response mode on mental rotation of hands). Notwithstanding the differences between our previous and the present results, both studies concur in suggesting that ASD individuals can simulate actions, but their motor simulation mechanisms are not fully functioning. This would render ASD individuals more liable to influence from current sensorimotor information with respect to TD individuals.

Recently, Eigsti et al. (2013) investigated relationships between motor simulation and affective evaluation of visual stimuli in ASD and TD individuals (age range 11–29 years). The authors found in TD but not in ASD participants that keeping an approach posture while encoding a novel stimulus favoured the association between the stimulus and a positive affective image. Both Eigsti et al.'s (2013) and the present study reported an alteration of simulation processes in ASD, but Eigsti et al. suggested that simulation processes were lacking in ASD while we suggested that they are not completely functioning. The exact nature of the alteration of motor simulation processes in autism warrants further investigation.

A final relevant issue is whether the strong impact of posture on motor simulation in ASD individuals is related to a specific deficit of simulation processes or to a more basic alteration in processing of proprioceptive information interfering with simulation. The present data do not allow us to disentangle these two alternatives, but it is worth noting that recent studies demonstrated abnormal patterns of motor learning in children with ASD due to increased sensitivity to proprioceptive information (Haswell et al. 2009; Izawa et al. 2012; Marko et al. 2015). Such data might suggest that an atypical proprioceptive processing may underlie anomalies of motor simulation in ASD.

A limitation of the present study was the lack of formal assessment of participants' handedness, which was ascertained in an informal interview. Degree of left-hand dominance is higher in ASD than in normal populations (e.g., Soper et al. 1986) and this lateralization can affect individuals' cognitive performance (Fein et al. 1985). The lack of quantitative information about handedness means that we cannot assess whether differences in efficiency for left versus right pedal pressing might have affected the current results. However, we found a stronger influence of posture when the participants' left hand position was manipulated. This finding is consistent with current theories on handedness according to which the non-preferred, left arm/right hemisphere system is advantaged over the preferred, right arm/left hemisphere system in using position-related proprioceptive information (Goble and Brown 2008; Goble et al. 2006; Han et al. 2013; Schmidt et al. 2013).

Conclusions

The present study demonstrated a strong impact of current body information on motor simulation in ASD adolescents. These results can be interpreted in light of both classical (Piaget 1954, 1971) and recent (Funk et al. 2005; Frick et al. 2014) developmental evidence showing that although sensorimotor processes are centrally involved in the first steps of acquisition of mental simulation skills in children, the successive refinement of these abilities implies a progressive disengagement from body information. On this basis, we might suggest that anomalous simulation processes in ASD could be described as not fully effective rather than lacking.

Under the framework of motor simulation, ASD can be related to an alteration of cognitive processes grounded on own one's body (Conson et al. 2013a, 2015a; Dapretto et al. 2006; Gallese et al. 2013; Hobson and Hobson 2007; Oberman and Ramachandran 2007), also consistent with the view of an atypical self-referential processing (Lombardo and Baron-Cohen 2011; Mundy et al. 2010; Pearson et al. 2014). The atypical processing of bodily information (Haswell et al. 2009; Izawa et al. 2012; Marko et al. 2015) could account for the peculiar way in which people with ASD mentally simulate actions.

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