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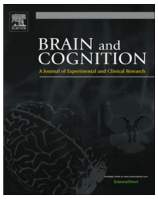

Facilitation of action planning in children with autism: The contribution of the maternal body odor

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ABSTRACT

Imitation is a key socio-cognitive skill impaired in individuals with Autism Spectrum Conditions (ASC). It is known that the familiarity with an actor facilitates the appearance of imitative abilities. Here, we explore whether a highly familiar and socially relevant stimulus presented in the olfactory modality is able to improve spontaneous imitation as early as at the level of action planning. A group of 20 children with ASC and 20 controls observed their own mother or the mother of another child performing a reach-to-grasp action towards an object, under the exposure to their maternal odor, the odor of the mother of another child or no odor. Subsequently, children acted upon the same object with no specific instruction to imitate. Child's movement initiation time (MIT) served as an indicator of motor planning facilitation induced by action observation. Results suggest that for children with ASC (but not controls) MIT was significantly lower when exposed to the maternal odor both when interacting with a familiar or an unfamiliar model. In the former case, the performance is comparable to controls. The familiar model in the absence of any olfactory cue is able to induce a facilitation effect, but the maximal facilitation on MIT is evident when maternal odor and familiar model are paired. We hypothesize that for children with ASC the maternal odor provides relevant social motivation for taking advantage of others' actions when planning movements in an imitative context.

1. Introduction

Imitation is a crucial socio-cognitive skill that favors the establishment and maintenance of appropriate social interactions. As in a virtuous circle, imitation is intensified in the presence of positive social cues, even when subliminal (Cook & Bird, 2011; Lakin & Chartrand, 2003; Leighton, Bird, Orsini, & Heyes, 2010) and the appearance of pro-social behaviors is increased by being imitated (affiliation, altruism and trust; (Bailenson & Yee, 2005; Chartrand & Bargh, 1999; Van baaren, Holland, Kawakami, & Knippenberg, 2004).

It has been proposed that in healthy individuals, the connectedness between an imitator and an imitee is accomplished by the spontaneous activation of the same (neural and representational) structures during action observation and action execution (Bernier, Dawson, Webb, & Murias, 2007; Meltzoff & Decety, 2003). This is true also when no voluntary effort in copying the observed action is engaged (Heyes, 2011). The disruption of this automatic ability to match other's actions onto the self has been hypothesized as the most parsimonious argument for the problematic imitation skills reported by individuals with Autism Spectrum Conditions (ASC; Williams, Whiten, & Singh, 2004). A series of experimental studies supports this view, indicating a dysfunctional mirror neuron system (MNS) as the neural underpinnings of abnormal imitative behavior in ASC (Avikainen, Wohlschläger, Liuhanen, Hänninen, & Hari, 2003; Dapretto et al., 2005; McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006; Oberman et al., 2005; Rogers, Hepburn, Stackhouse, & Wehner, 2003). Some other evidence contrasts this perspective by negating a generalized imitative impairment in ASC and promoting the idea of a dynamic deficit in imitation which emerges according to a specific social context (Bird, Catmur, Silani, Frith, & Frith, 2006; de Hamilton et al., 2007; Dinstein et al., 2010; Gowen, Stanley, & Miall, 2008; Leighton, Bird, Charman, & Heyes, 2008; Press, Richardson, & Bird, 2010; Spengler, Bird, & Brass, 2010). Although highlighting the tight dual relationship linking imitation and social interaction, these controversial findings do stress the need for a more accurate analysis of the variables subliminally influencing imitative skills in ASC.

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A bulk of evidence indicates that the social modulation of the motoric aspects of imitation occurs without a person being aware of such influence. The study of visuomotor priming effects during movement execution and observation revealed that in neurotypical participants observing a person performing a movement facilitates the motor performance of a similar action by the observer (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Brass, Zysset, & von Cramon, 2001). This effect is revealed not only for intransitive actions (such as finger tapping) but it also translates to goal-directed actions (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; Edwards, Humphreys, & Castiello, 2003). When neurotypical participants observed a model grasping an object (or simply gazing at it; Pierno, Mari, Glover, Georgiou, & Castiello, 2006), they were faster and more accurate in subsequently grasping an object of the same dimension. In contrast, children with ASC do not show any motor facilitation (e.g., faster action initiation) from the observation of someone else's action or directed gaze (Pierno et al., 2006), revealing that different social visual stimuli fail to automatically modulate motor execution.

Given the immunity that individuals with ASC show towards visual social contextual information, we searched the literature to identify other forms of contextual information able to successfully trigger social relevance and modulate imitation skills in this population. Experimental findings (Bernier et al., 2007; Dapretto et al., 2005; Kilner, Marchant, & Frith, 2006; Nishitani, Avikainen, & Hari, 2004; Oberman et al., 2005; Theoret et al., 2005; Villalobos, Mizuno, Dahl, Kemmotsu, & Müller, 2005) as well as clinical observations (Bernard-Opitz, 1982; Kasari, Sigman, & Yirmiya, 1993; Knott et al., 1995) suggested to Oberman, Ramachandran, and Pineda (2008) that the familiarity with an actor performing a known movement could result in greater *mu* rhythm suppression, an indication of the degree to which the observer identifies herself with the observed, that is considered an expression of the MNS involvement. Individuals with ASC, both children (Oberman et al., 2008) and adults (Oberman & Ramachandran, 2007) showed greater *mu* rhythm suppression when interacting with a familiar as compared to an unfamiliar model.

Capitalizing on the ability of familiar cues to impact on the MNS functionality and therefore on imitation skills in individuals with ASC, we explored cues expressed in modalities other than the visual. For its intimate relation with the limbic system (Zald & Pardo, 1997), its velocity in joining the central brain areas from the periphery – due to a limited number of synapses required (Zald & Pardo, 1997) and its full development in utero (Schaal, Marlier, & Soussignan, 2000), olfactory stimuli caught our attention. In particular the maternal body odor, which channels both high familiarity and high social relevance. On the one hand, considering the pre–post natal continuity of olfactory perception, the maternal odor is the odor a child has been exposed to the longest (Schaal et al., 2000). On the other hand, the maternal odor is sufficient to prime a series of biologically relevant social experiences promoting social interactions and affiliation, such as the efficient monitoring of mother's proximity (even during sleep time; Porter, 1999), the recognition of the presence of familiar members (Porter, 1999), the appearance of critical sensorimotor behaviors precursors of eating behavior and communication skills (Sullivan & Toubas, 1998).

Recently, we successfully demonstrated that the maternal odor is able to selectively promote the matching between the observation of a reach-to-grasp movement and its execution during an automatic (non-voluntary) imitation task in prepuberal children with ASC (Parma, Bulgheroni, Tirindelli, & Castiello, 2013). Specifically, participants with ASC were faster in completing a reach-to-grasp movement towards a target object, following the observation of the same action performed by others under the exposure of the odor of their mother. Smelling the odor of the mother of another child or no odor at all produced no reduction of the movement duration.

Nevertheless, insights on whether the facilitation mediated by the maternal odor could be already evident as early as in the planning phase of movements are still missing. Motor planning skills, intended as the capacity to translate an abstract goal into a sequence of specific and detailed motor commands, are somewhat compromised in individuals in the spectrum (for a review Gowen & Hamilton, 2012). Participants with ASC require longer time as compared to matched controls to implement a motor plan to perform, for example, a reaching action (Glazebrook, Elliott, & Lyons, 2006; Glazebrook, Elliott, & Szatmari, 2007; Glazebrook, Gonzalez, Hansen, & Elliott, 2009; Mari, Castiello, Marks, Marraffa, & Prior, 2003; Nazarali, Glazebrook, & Elliott, 2009; Rinehart, Bradshaw, Brereton, & Tonge, 2001; Rinehart et al., 2006). Notably, a recent review using a computational approach revealed that one of the domains in which individuals with ASC do show consistent impairment is the poor integration of information for efficient motor planning (Gowen & Hamilton, 2012).

Defining whether children with ASC can use the maternal odor to facilitate motor planning is an intriguing and relevant issue for several reasons. First, motor abilities have shown better predictive value for the outcomes in ASC than severity of autism symptomatology (Sutera et al., 2007). Second, improved imitation skills can have far reaching positive consequences on development (Leary & Hill, 1996), improving social skills and consequently promoting a better adjustment and quality of life (Ingersoll, Lewis, & Kroman, 2006; Jasmin et al., 2008).

Here, we tested whether the maternal odor acts as a facilitator of motor planning abilities in the context of an automatic imitation task. We asked a group of children diagnosed with ASC and a group of gender- and age-matched typically developing (TD) controls to perform a reach-to-grasp action towards an object, after having observed (or not) a model demonstrating the same action, following the exposure to different types of socio-chemosignals, and in the presence of a familiar or unfamiliar model. To exclude that the influence of the maternal odor is a generalized socio-chemosignal consequence, we tested its effect against the odor of the mother of another child and a no odor condition. To verify whether olfactory cues are advantaged in triggering familiarity over visual stimuli, we included as models both the mother of the child (familiar model) and the mother of another child (unfamiliar model). In line with previous research (Edwards et al., 2003; Pierno et al., 2006), we foresee that TD children will solely rely on the relevant visual information provided by the observation of a model's action before executing their own reach-to-grasp. If this is true, we expect that the movement initiation time (MIT), a simple but accurate measure of motor planning facilitation (Edwards et al., 2003; Gowen & Hamilton, 2012; Pierno et al., 2006), will be reduced following action observation for TD children when compared to the no action observation condition. No effect of the model with whom participants are interacting and the odor they are exposed to before the planning of the action started is foreseen. On the contrary, we predict that children with ASC will not speed up the initiation of their movement following action observation when interacting with the unfamiliar model and preliminary presented with no odor or the odor of the mother of another child. Furthermore, we expect a reduction in the MIT following the observation of the action performed by their mother as a model. We hypothesize a reduction in MIT when participants with ASC smell the maternal odor and observe the action performed by any model. No odor and the odor of the mother of another child are not expected to produce the same MIT facilitation (i.e., faster initiation time).

2. Materials and methods

2.1. Participants

The participants included here belong to the same sample described in Parma et al. (2013). Twenty children diagnosed with autism were age, gender, full-scale IQ (Wechsler, 1991), socioeconomic status (Hollingshead, 1975) paired to 20 children in the TD group (Table 1). All the children were right handed, reported normal or corrected-to-normal vision, had no hearing impairments, had no motor impairment to the upper limbs affecting the execution of reach-to-grasp movements nor were currently under medications. State of the art guidelines (American Psychiatric Association, 2000) and standardized instruments – such as the Autistic Diagnostic Observation Schedule (Lord et al., 2000), the Autistic Diagnostic Interview revised (ADI-R, Lord, Rutter, & Le Couteur, 1994) and the Childhood Autism Rating Scale (CARS, Schopler, Reichler, DeVellis, & Daly, 1980) – were used to diagnose ASC and to assess the odor identification functionality (University of Pennsylvania Smell Identification Test, UPSIT; Doty, Shaman, & Dann, 1984). Children meet all diagnostic criteria for ASC, and did not present any neurological or genetic disorders known-to-be-linked to ASC or smell dysfunctions. Reduced olfactory identification ability was revealed in the group of children diagnosed with ASC (23.55 ± 5.75 UPSIT score). The TD children reported no history of ASC themselves and within their first or second-degree relatives; they scored normally to the UPSIT (33.67 ± 4.31 UPSIT score). Participants were recruited from the greater Padova area and the local Institutional Review Board approved the experimental procedures, which were in accordance with the Declaration of Helsinki. All of the mothers signed a written informed consent indicating that they could withdraw from the study at any time without providing any specific motivation.

2.2. Stimuli

The odors were obtained from the models, namely the mothers of the children included in the study. Stimuli classified as 'maternal odors' were collected from each participant's mother; the mother of another child provided the unfamiliar chemosignal. In order to reduce the presence of potential confounding factors in the body odor samples, many precautions were taken: (i) all the mothers were trained to bathe themselves and to launder their clothes with a provided scent-free body and laundry detergents (Lundström, Boyle, Zatorre, & Jones-Gotman, 2009); (ii) all the mothers were instructed to refrain from engaging in activities producing excessive sweating (e.g., situations triggering anxiety reactions, physical exercise) during the body odor collection time (Mujica-Parodi et al., 2009); (iii) the same female experimenter evaluated all the participants, to prevent contextual influences and followed herself the abovementioned washing procedure (Jacob, Hayreh, & McClintock, 2001); (iv) the day of the testing session, both the mothers and the experimenter wore freshly laundered clothes – previously sealed in a plastic bag – within the testing room right before the testing session commenced. The day before the testing session, the mothers wore a cotton pad under both armpits so as to permeate them with their body odor. At the end of the collection time, they removed and froze the pads to prevent the degeneration of the sample (Lundström et al., 2009). On the day of testing, each pad was defrosted and cut into four quadrants, each of which was secured with a tubular net on one glass, right before the testing session begun.

Table 1
Characteristics of the children diagnosed with Autism Spectrum Conditions (ASC) and the typically developing (TD) controls. Means and standard deviations (in parentheses) are shown as well as corresponding F or χ^2 values.

	ASC *M* (SD)	TD *M* (SD)	F or χ^2	*p*
N	20	20	–	–
Age	13.2 (1.82)	13.4 (1.76)	.05	.58
Full scale IQ	103.5 (10.38)	109 (8.52)	1.13	.22
Socioeconomic status	51.23 (6.18)	52.18 (6.55)	.22	.35
Handedness (R:L)	20:0	20:0	.26	.31
Gender (M:F)	10:10	10:10	.22	.37
CARS	36.7 (3.78)	–	–	–

Note: ASC: autistic spectrum disorder; TD: typically developing children; CARS: Childhood Autism Rating Scale.

2.3. Procedure

The child and the model sat at a table facing each other and the object (i.e., a glass) was located in the center aligned with both body midlines. The child and the model rested their right hand on a starting pad, located at a 20-cm distance from the object, gently opposing the index finger and the thumb (Starting position, Fig. 1). Before each trial started, both the child and the model smelled the pad on the object, sensing the maternal odor, the odor of another mother or no odor. At the sound of the first auditory cue, the model could either naturally reach and grasp the object, allowing the child to observe the action or remain still, preventing the child from the observation of a reach-to-grasp movement (Observation of model's movement, Fig. 1). For half the trials, the first auditory cue was followed by the model's performance of a reach-to-grasp action towards the object located at the center of the working area (i.e., a glass; Action, Fig. 1). For the remaining half of trials, following the first auditory cue the model stayed stationary (No Action, Fig. 1). The model was visually prompted by the experimenter – who was positioned behind the child, out of his/her field of view – on which action to perform. In both conditions, the child observed the unfolding of the action remaining still, without being able to predict the model's action ahead of time. After 3 s, the same auditory cue was delivered again as to prompt the child to act upon the object. At the sound of the second signal, the child performed his/her reach-to-grasp movement. It is worth noting that all participants were confident in stating that they could clearly hear the auditory cues, were not annoyed by the pitch of the sounds and were preparing for action at the sound of the second auditory cue. A training session was performed to ensure that each participant understood and complied with the rules of the task in the different conditions. Once the experimenter recorded a correct performance on 8 out of 10 trials, the participant could start the experimental phase. No participant needed more than 10 trials to be admitted to the experimental phase, which was constituted of a total of 120 trials presented in randomized order within four blocks.

2.4. Data analysis

The reaction time or movement initiation time was used as a dependent variable (MIT, (Edwards et al., 2003; Gowen & Hamilton, 2012; Pierno et al., 2006). MIT was chosen to specifically assess whether the experimental manipulations (the interaction with the familiar or the unfamiliar model and the exposure to the maternal odor, the odor of the mother of another child or no odor) can selectively influence how children plan their actions. MIT was calculated via digitization techniques applied post hoc to the videos (Zoia et al., 2006), showing the reach-to-grasp actions of each model and child as recorded during the testing session. MIT was operationalized as the time elapsing from the second auditory cue and the child's actual action onset, defined as the displacement of the digital marker located on the dorsodistal aspect of the styloid process of the wrist reaching towards the object for two

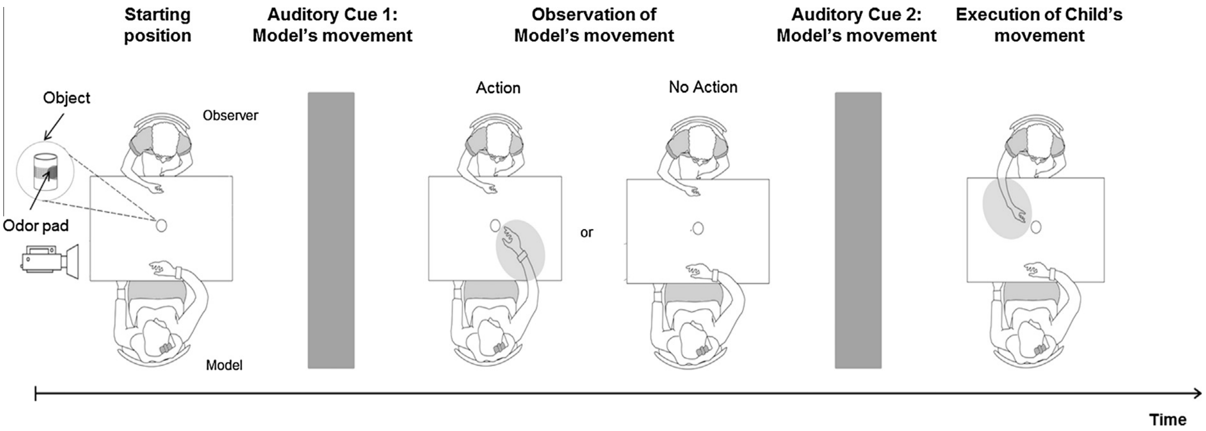

Fig. 1. One child (ASC or TD) and one model (familiar or unfamiliar) were seated at a table facing one another. A glass covered by a pad's quadrant imbued with the maternal odor, the mother of another child odor or no odor was placed in the middle of the table about 20 cm away from both hand starting positions. At the sound of the first auditory cue, the model either reached and grasped the object while the child observed the action (Action) or remained stationary (No Action). Three seconds later a different auditory cue invited the child to act upon the object.

consecutive frames (elapsing time 80 ms, being the video recorded at 25 Hz).

The trials subjected to the final analyses did not include: (1) the trials in which the participants of both groups required a verbal instruction from the experimenter as to assume the correct starting position and comply with the procedures (cumulatively, less than 10% equally distributed between groups); (2) the false alarm trials, i.e. trials in which automatic imitation was not successfully performed. False alarm trials were uniformly distributed among conditions in the group of children with ASC (27.5–29.5% of trials per condition). Automatic imitation was always successfully performed by typically developing children.

Exploratory data analysis preceded inferential statistics as to verify that all assumptions for the statistical test chosen were verified. A full factorial mixed ANOVA with Group the children belong to (ASC vs. TD) as between-subjects factor, and the Model they interacted with (own vs. mother of another child), the type of Observed behavior (action vs. no action) and the Odor they smelled before each trial started (maternal odor vs. odor of the mother of another child vs. no odor) as within-subjects factors was performed to explore the effects of interest. As to minimize the risk of incurring in a type I error, the Bonferroni's correction (alpha level: $p < 0.05$) was applied when appropriate. Independent Student's *t*-tests were used to explore the presence of Group differences.

3. Results

The full factorial mixed ANOVA revealed a number of significant main effects, two-way, three-way interactions, which are reported in Table 2. Overall, the two groups showed a significantly different performance in 11 out of the 12 experimental conditions (Table 3). Participants of the TD group were faster in initiating the movement towards the target as compared to the children with ASC. Only when interacting with the still familiar model (no observed action preceding the participant's action execution) and under the exposure of the maternal odor participants with ASC were as fast as TD children in initiating the reach-to-grasp action (Table 3). Considering the statistical significance of the higher order interaction (Group × Odor × Model × Observed Action: $F[2,76] = 29.41$; $p < 0.0001$; $\eta_p^2 = 0.44$), we explored the effect of the within-subjects factors through post hoc contrasts (Table 4). Fig. 2 graphically represents the MIT in each experimental condition for both groups. TD children were faster in initiating their reach-to-grasp following action observation as compared to when the model remained still, independently of the odor they smelled at the beginning of the trial and the model they were interacting with (Table 5). For children with ASC the preventive observation of action fails to automatically reduce the MIT when interacting with the mother of another child (Table 5). However, MIT is significantly decreased following action observation when children with ASC interacted with their own mother (Table 5). Nonetheless, a significant decrease in MIT became selectively evident in children with ASC when the maternal odor was smelled before the interaction with the mother of another child (Table 5). Exposure to the maternal odor also brought to a significant decrease in the absolute MIT when children with ASC interacted with their own mother as compared to when they were presented with no odor, both when action observation occurred or not (Table 5). As evident in Fig. 2, no absolute reduction of MIT was retrieved when children with ASC smelled the odor of the mother of another child preceding action observation or in the no action condition. Smelling the maternal odor and interacting with the familiar model also induced a significantly greater speeding up of the action following observation as compared to the no odor condition (Table 4).

Table 2
Results of the full factorial mixed ANOVA considering Group as a between-subjects factor and Odor, Model and Observed Action as within-subjects factors.

Effect	*F*	*p*-Value	η_p^2
Model	$F_{1,38} = 42.619$	.000	.529
Odor	$F_{2,76} = 59.518$	.000	.763
Observed behavior	$F_{1,38} = 264.352$	.000	.874
Model * Odor	$F_{2,76} = 13.725$	.000	.426
Model * Observed behavior	$F_{1,38} = 4.860$	.034	.113
Odor * Observed behavior	$F_{2,76} = 17.818$	.000	.491
Model * GROUP	$F_{1,38} = 34.678$	.000	.477
Odor * GROUP	$F_{2,76} = 80.025$	.000	.812
Observed behavior * GROUP	$F_{1,38} = 100.823$	.000	.726
Model * Odor * Observed behavior	$F_{2,76} = 24.164$	.000	.566
Model * Odor * GROUP	$F_{2,76} = 29.308$	.000	.613
Model * Observed behavior * GROUP	$F_{1,38} = 0.857$	.360	.022
Odor * Observed behavior * GROUP	$F_{2,76} = 23.802$	.000	.563
Model * Odor * Observed behavior * GROUP	$F_{2,76} = 34.356$	.000	.650

4. Discussion

In order to assess whether the human maternal odor has the ability to facilitate social interactions for children with ASC as early as at the level of motor planning, we assessed the effect of the

Table 3
Student's *t*-tests exploring the difference between Groups for each experimental condition. Significant results are reported in bold.

	t	df	Sig. (2-tailed)	95% C.I. difference lower	95% C.I. difference upper
Familiar model					
Maternal odor					
Action	5.290	38	**<0.001**[**]	49.474	110.816
No action	1.236	38	.224	−10.729	44.379
Stranger's odor					
Action	10.836	38	**<0.001**[**]	127.827	186.563
No action	8.071	38	**<0.001**[**]	72.519	121.081
No odor					
Action	8.985	38	**<0.001**[**]	122.165	193.225
No action	6.484	38	**<0.001**[**]	85.738	163.572
Unfamiliar model					
Maternal odor					
Action	5.817	38	**<0.001**[**]	55.404	114.556
No action	8.815	38	**<0.001**[**]	86.771	138.509
Stranger's odor					
Action	9.788	38	**<0.001**[**]	144.807	220.323
No action	8.077	38	**<0.001**[**]	76.953	128.427
No odor					
Action	11.360	38	**<0.001**[**]	143.277	205.413
No action	7.021	38	**<0.001**[**]	66.280	119.990

[*] Significant contrast at the level of $p < 0.05$.
[**] Significant contrast at the level of $p < 0.01$.

exposure to different socio-chemosignals in the context of an automatic imitation task. Furthermore, to evaluate whether the maternal odor can outperform the previously shown facilitation effect of model's familiarity (Oberman et al., 2005), we included the action observation of the mother of each participant as well as the mother of another participant as models.

Results indicate that overall visually presenting an action triggers the planning of a similar movement in the observer only in TD children, who are in all conditions faster in initiating the reach-to-grasp action towards the object following action observation. This confirms previous data revealing that the observation of the action performed by whomever model and under whatever olfactory condition is relevant to TD children to achieve their goal, namely reaching and grasping the object on the table (Pierno, Mari, Lusher, & Castiello, 2008; Pierno et al., 2006).

Conversely, facilitation following action observation did not emerge for children with ASC who are refractory to this type of visuomotor priming in the absence of any olfactory stimulation and in the presence of an unfamiliar model (Pierno et al., 2006, 2008). However, the pattern radically changes when children with ASC smell the maternal odor and interact with the familiar model. When interacting with the familiar model, the maternal odor speeds up MIT both following the observation of the mother's action and when no action was executed. No significant difference between these conditions was evident, stressing the ignorance of the visuomotor information by the children with ASC. Notably, children with ASC were as fast in starting the action as TD children under the exposure of the maternal odor and when the familiar model did not perform any action. This reveals that the maternal odor in association with the familiar model allows children with ASC to show normative motor planning skills. Considering the difficulties in this motor domain (Glazebrook et al., 2006, 2009, 2007; Gowen & Hamilton, 2012; Mari et al., 2003; Rinehart et al., 2001; Rinehart et al., 2006), it is noteworthy that a combination of these two stimuli can affect the early stage of action programming and resonates on the subsequent unfolding of the whole reach-to-grasp action (Parma et al., 2013).

Furthermore, the odor of the mother of another child was not effective in allowing the appearance of the automatic imitation effect even in interaction with the familiar model, and the MIT resulted significantly slower than in the TD group. When no odor was smelled, children with ASC did show a faster MIT when interacting with their mother and observing her action as compared to when no action was performed by her. But the absolute time at which movement initiation occurred was significantly higher as compared to when the action was initiated following the exposure to the maternal odor. Taken altogether these findings strengthen the role of the maternal odor in the presence of a familiar model to provide a critical contribution to the planning of automatically imitated actions in prepuberal children with ASC.

When interacting with the unfamiliar model, consequently removing the contribution of model's familiarity, the exposure to the maternal odor significantly reduced the MIT following action observation, but not in the no action condition. This is an important finding because it allows us to exclude that the benefit shown in the familiar model condition is merely driven by a congruency effect. The odor of the mother of another child is also a stimulus congruent with the model's identity (unfamiliar model), but action planning is not facilitated by this chemosignal. One might argue that the different chemical composition of the maternal body odor and the odor of the mother of another child might explain the pattern of results in children with ASC. However, this is not likely because each individual presents a unique olfactory signature, therefore all body odors were different from each other and, nevertheless, the maternal odor was able to produce a facilitation effect on the motor performance of children with ASC. It might also be argued that the hyposmia shown by children with ASC at the standardized test (UPSIT, Doty et al., 1984) is a critical confounding variable. It is worth noting, that the hyposmia revealed by the UPSIT refers to the reduced ability of this group of children with ASC to identify common odors, namely to provide a correct verbal label for the odor source of the odorant presented. The available literature does not yet provide many options to investigate the olfactory perception of individuals with ASC, as well as all other populations of patients who show verbal impairment. Therefore, we chose the state of the art technique, well aware of its limits. Nevertheless, recent evidence has showed how common odors and body odors rely on different neural networks (Lundström,

Table 4
Post hoc contrasts of the four-way interaction Group × Odor × Model × Observed behavior.

	ASC					TD				
	t	df	Sig. (2-tailed)	95% C.I. difference lower	95% C.I. difference upper	*t*	df	Sig. (2-tailed)	95% C.I. difference lower	95% C.I. difference upper
Action–no action										
Familiar model										
Maternal odor	0.391	19	0.700	−8.099	11.819	−10.995	19	**<0.001****	−73.160	−49.760
Stranger's odor	0.194	19	0.849	−13.299	16.009	−10.376	19	**<0.001****	−70.949	−47.131
No odor	−2.661	19	**0.015***	−50.768	−6.062	−15.132	19	**<0.001****	−69.956	−52.954
Unfamiliar model										
Maternal odor	−10.710	19	**<0.001****	−105.126	−70.754	−10.098	19	**<0.001****	−72.774	−47.786
Stranger's odor	1.389	19	0.181	−5.868	29.008	−10.383	19	**<0.001****	−82.074	−54.536
No odor	1.919	19	0.070	−1.063	24.513	−10.445	19	**<0.001****	−83.409	−55.561
Familiar–unfamiliar model										
Action										
Maternal odor	−0.323	19	0.750	−12.602	9.232	0.620	19	0.543	−7.483	13.783
Stranger's odor	−11.119	19	**<0.001****	−108.706	−74.264	1.627	19	0.120	−1.240	9.900
No odor	−1.728	19	0.100	−43.765	4.185	2.126	19	**0.047***	0.088	11.072
No action										
Maternal odor	−1.477	19	0.156	−23.140	3.990	−2.625	19	**0.017***	−6.624	−0.746
Stranger's odor	−1.879	19	0.076	−43.339	2.339	−1.008	19	0.326	−11.842	4.142
No odor	1.841	19	0.081	−2.691	41.971	−1.647	19	0.116	−26.981	3.221
Maternal–stranger's odor										
Action										
Familiar model	−8.311	19	**<0.001****	−90.288	−53.962	1.097	19	0.286	−4.472	14.322
Unfamiliar model	−8.190	19	<0.001**	−113.288	−67.172	1.345	19	0.195	−4.094	18.804
No action										
Familiar model	−5.071	19	**<0.001****	−95.891	−39.859	14.275	19	**<0.001****	62.293	83.697
Unfamiliar model	2.301	19	**0.033***	0.840	17.720	−0.337	19	0.740	−4.835	3.495
Maternal–no odor										
Action										
Familiar model	−4.923	19	**<0.001****	−94.082	−37.948	2.567	19	**0.019***	2.130	20.940
Unfamiliar model	−9.571	19	**<0.001****	−103.381	−66.279	1.013	19	0.324	−4.832	13.902
No action										
Familiar model	−7.310	19	**<0.001****	−123.861	−68.719	2.101	19	0.049	0.043	23.037
Unfamiliar model	2.474	19	**0.023***	2.283	27.387	−1.639	19	0.118	−10.635	1.295
Stranger's–no odor										
Action										
Familiar model	0.486	19	0.633	−20.209	32.429	1.915	19	0.071	−0.613	13.833
Unfamiliar model	0.600	19	0.556	−13.447	24.247	−1.031	19	0.316	−8.546	2.906
No action										
Familiar model	−1.984	19	0.062	−48.619	1.299	0.667	19	0.513	−8.972	17.362
Unfamiliar model	1.503	19	0.149	−2.182	13.292	−2.089	19	0.050	−8.007	0.007

* Significant contrast at the level of $p < 0.05$.
** Significant contrast at the level of $p < 0.01$.

Boyle, Zatorre, & Jones-Gotman, 2008; Lundström et al., 2009; Pause, 2012), opening to a different perceptual experience of the two chemosignals. Our belief is that the participants were able to smell the odors (both the common and the body odors), as they reported when asked, but they were not able to successfully indicate the correct verbal label corresponding to the odorant smelled. This vision seems to be confirmed by a recent publication (subsequent to the present study) revealing how an UPSIT-derived test using visual images rather than verbal labels does not show a difference in olfactory identification abilities between participants with ASC and typically development children of an age similar to those tested here (Cameron & Doty, 2013). Furthermore, in the no odor condition participants with ASC were not facilitated in initiating the action, suggesting that the unresponsiveness to the odor of the mother of another child cannot represent a neophobic reaction motivated by a novel stimulus. Comprehensively, these findings point to the idea that a combination of the maternal odor and model's familiarity is responsible for the facilitation of the automatic imitation performance in children with ASC, with the maternal odor driving the effect.

The peculiarity of the maternal odor seems to be confirmed also by studies performed in animals. In fact, its calming and soothing power in stressful situations is evident for offspring across species (Okabe, Nagasawa, Mogi, & Kikusui, 2012). In rat pups, its "anxiolytic" effect was demonstrated to be mediated via the suppression of glucocorticoids (i.e., corticosterone) levels, promoted by mother presence and inhibited by mother absence (Moriceau et al., 2006). Alone, it seems to be a stimulus capable of reducing the hypothalamic–pituitary–adrenal (HPA) axis reactivity (Fujita, Ueki, Miyoshi, & Watanabe, 2010). The need for this kind of meaningful stimulus is even more emphasized by the mechanism through which even a common odor (e.g., peppermint or citral) if applied to the mother and experienced by pups during mother–infant interactions, can acquire the facilitating properties of the actual maternal odor (Sullivan, Wilson, Wong, Correa, & Leon, 1990). It is such a biologically relevant and imperative signal that it paradoxically protects – during a specific developmental period – from the formation of fearful associations (Moriceau & Sullivan, 2006). With respect to motor performance, both in animals (Marlier, Schaal, & Soussignan, 1998) as well as in human newborns and

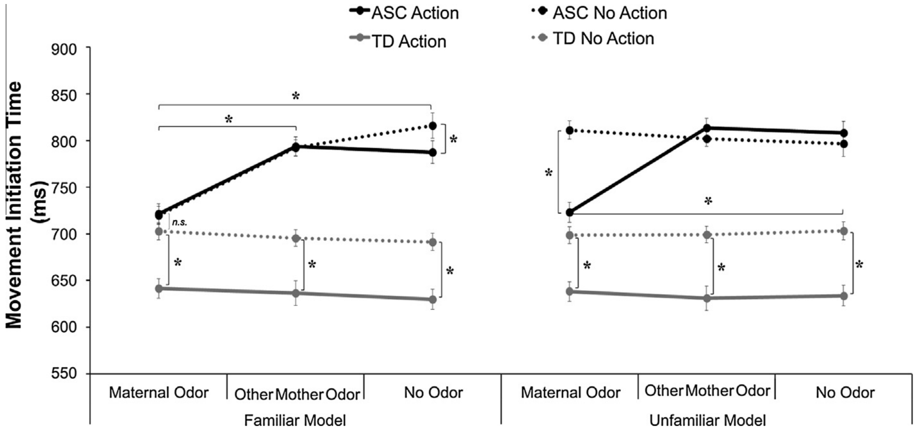

Fig. 2. The lines represent the means of movement initiation time (MIT) in ms recorded under the exposure of the maternal odor, the odor of the mother of another child and no odor when interacting with either the familiar or the unfamiliar model. Gray lines represent the typically developing (TD) group performance. Black lines represent children with ASC performance. Solid lines refer to action observation conditions and dotted lines indicate no action conditions. $^{*}p < 0.05$. n.s.: Non-significant.

Table 5
Mean and SD for the movement initiation time (MIT) expressed in ms for each condition in both the Autism Spectrum Conditions (ASC) and the Typically Developing Children (TD) groups.

	ASC		TD	
	Mean	SD	Mean	SD
Familiar model				
Maternal odor				
Action	721.570	48.358	641.425	47.458
No action	719.710	41.939	702.885	44.116
Stranger's odor				
Action	793.695	35.341	636.500	54.408
No action	792.340	35.925	695.540	39.832
No odor				
Action	787.585	61.825	629.890	48.357
No action	816.000	69.221	691.345	50.989
Unfamiliar model				
Maternal odor				
Action	723.255	39.187	638.275	52.281
No action	811.195	40.949	698.555	39.864
Stranger's odor				
Action	813.485	61.509	630.920	56.341
No action	801.915	42.777	699.225	37.454
No odor				
Action	808.085	42.350	633.740	54.010
No action	796.360	45.766	703.225	37.750

infants, it stimulates the appearance of motor behaviors (e.g., sucking, mouthing; Sullivan & Toubas, 1998).

The fact that the maternal odor does not induce the same facilitation in TD children might constitute an argument against the criticality of the maternal odor in automatic imitation. If the maternal odor is a socially relevant odor why does it not ease the planning of automatically imitated actions in TD children, too? A reason may subsist in the multisensory and social nature of our environment (Aglioti & Pazzaglia, 2011). To increase effective communication of socially relevant information, redundant signals are presented in different modalities (Partan & Marler, 2005). In virtue of its overload, each individual signal can be replaced or removed without necessarily undermine the social message (Partan & Marler, 2005). Therefore, it is not surprising that the sense leading our perception within a multisensory environment is the one tuned on the most relevant information (Lakatos et al., 2009), being relevant a stimulus preferentially processed as to facilitate the achievement of a goal in a specific point in time (Frijda, 2009; Reisenzein, 2012). For TD children, observing a model performing a reach-to-grasp action is relevant to the execution of their own action; therefore this is the information that leads their motor planning and both the olfactory cues and the model's familiarity are deemed irrelevant for the achievement of this goal. The fact that children with ASC do not take advantage of previously observed actions to spontaneously imitate seems to suggest that the canonical visuomotor cues are not "relevant enough" for the planning of their actions. Here, we confirmed that familiarity with the actor is a way to increase stimulus relevance in the context of imitative behavior for individuals with ASC (Oberman et al., 2008), possibly by means of a switch in perspective that increases the social value of the interaction and consequently, the relevance of the goal-related task (Oberman et al., 2005).

Also, for the first time we demonstrate that the maternal odor is able to trigger the same switch in perspective and it amplifies the relevance of the social interaction for children with ASC. This is compatible with previous evidence that recognize the peculiarity of the sensory world experienced by individuals with ASC (Baranek, David, & Poe, 2006), suggesting that the chemical senses are the modalities that best discriminate among phenotypes and predict social impairment in ASC (Hilton, Harper, Kueker, & Lang, 2010; Lane, Young, Baker, & Angley, 2010), and point to the impaired visual information processing in ASC, especially if it is linked to social information (Blake, Turner, Smoski, Pozdol, & Stone, 2003; Happé & Frith, 2006).

The facilitation induced by the maternal odor reveals that for children with ASC the socially relevant information is preferentially embedded within peculiar olfactory rather than visual stimuli. By its very nature, the maternal odor can transfer information regarding kinship and the degree of familiarity of the smelled (Porter, 1999) and, because of the pre–post natal continuity of the olfactory experience, it is the social odor children have most extensively familiarized with (Schaal et al., 2000).

The dissociation evident in the reported findings suggests that olfaction is a sense of little momentum for TD children. In contrast, it might have a more central position in the sensory experience of children with ASC, by allowing specific olfactory stimuli to give access to a more emotional and socially relevant world. Thus, it is tempting to speculate that the development of olfactory perception follows different trajectories in typical and atypical development. Ontogenetically, olfaction is the earliest sensory modality to mature, consequently having the longest time to specialize and perfect (Marlier et al., 1998). In contrast, audition and vision have more prolonged developmental axes (Berardi, Pizzorusso, & Maffei, 2000). An option would be that children with ASC, whose symptoms appear early in life, acquire a strong preference for the most mature sensory modality. Another option would be that the appearance of symptomatology during early development impairs the later maturing of audio–visual systems, causing a misrepresentation and interpretation of that type of information. Along the same lines, it is likely that two different neural networks underpin visuomotor facilitation in TD children and children with ASC. The central reliance of TD children on the preceding action observation suggests that the superior temporal sulcus (STS), an area providing the visual input to the MNS (Harries & Perrett, 2007; Seltzer & Pandya, 1994), plays a central role. STS anatomical and functional abnormalities do have paramount implications on the ASC symptomatology, with particular reference to the impairment of socially relevant information processing (Adolphs, 2003). How can the maternal odor bypass this area and allow for a more efficient functionality of the MNS? As an affiliative stimulus, it may be able to prime a hormonal cascade compatible with an oxytocin (OT) involvement. A putative OT facilitation of automatic imitation in ASC is consistent with evidence from several studies using different approaches. First, genetic and biochemical investigations revealed that OT receptors, which are dispersed in brain areas such as the amygdala – involved in social olfactory processing (Zald & Pardo, 1997) and in emotional and social relevance processing (Vrtička, Sander, & Vuilleumier, 2012), have been linked with ASC social inadequate behavior (Yamasue, 2013). Even more recently, a neuroimaging study recently revealed that OT enhances the connectivity between amygdala and medial frontal cortex (Sridapa et al., 2014) – an area related to the MNS (Molenberghs, Cunnington, & Mattingley, 2009), which has been previously indicated as the neural basis grounding action observation abnormal functionality in ASC (Iacoboni & Dapretto, 2006). The activation of the MNS, which can be triggered by odors (Rossi et al., 2008; Tubaldi et al., 2011), seems particularly effective in facilitating action planning when children with ASC smell their own maternal odor and observe their mother performing the action. Here, the maternal odor, rather than action observation, critically speeds up action initiation. This is witnessed by the absence of significance difference between the MIT in the action and no action conditions. It might well be that the maternal odor allows children with ASC to identify with the model or the object in some personal way – through an olfactory strategy possibly appropriate to their sensorimotor peculiarity (Donnellan, Hill, & Leary, 2013) – and therefore show a more effective MNS functionality (Oberman et al., 2008). The fact that olfactory stimuli uniquely avoid an early synapse at the level of the thalamus would allow the avoidance of the impaired thalamocortical pathway shown in ASC (Nair, Treiber, Shukla, Shih, & Muller, 2013).

Although the present study for the first time reveals that motor planning deficits in ASC can be counteracted by the exposure to salient olfactory information, a number of limitations do warrant consideration. First, the present findings are limited to one specific component of imitation, namely automatic imitation. Whether the same effect could be evident in voluntary imitative tasks has yet to be characterized. Second, to incontrovertibly determine that the motor reaction times are only impacted by the olfactory information and not confounded by other sensory cues, an auditory threshold test would be suggested to verify that the prompt signal for the start of each trial would be equally detectable by participants belonging to both groups. Third, in the light of the small-to-medium (partial eta squared) effect size of the four-way interaction, the importance of future replication is acknowledged. Fourth, results are limited by the inclusion of high-functioning children with ASC. Future research in the field would benefit from the inclusion of participants with more severe deficits to verify whether, with paradigms that can accurately test their performance, they can benefit from the facilitation effect here demonstrated for the maternal body odor.

In conclusion it seems that the maternal odor, by possibly stimulating conserved biochemical pathways, provides children with ASC with the appropriate support for the appearance of normal visuomotor facilitation. In other words, the maternal odor assists prepuberal children with ASC to temporarily get around difficulties in organizing and regulating their multisensory and motor experience and coordinating it with peripheral physiology according to specific behavioral social motivations (Donnellan et al., 2013). These data, which only constitute a first, but encouraging, step towards the shaping of innovative treatment strategies, highlight the need for a more thorough and creative study of sensory processing in ASC with the final goal of impacting domains that have been showed to be chiefly impaired in ASC.

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References

Adolphs, R. (2003). Cognitive neuroscience of human social behaviour. *Nature Reviews Neuroscience, 4*(3), 165–178.

Aglioti, S. M., & Pazzaglia, M. (2011). Sounds and scents in (social) action. *Trends in Cognitive Sciences, 15*(2), 47–55.

American Psychiatric Association (2000). *Diagnostic and statistical manual of mental disorders* (4th ed. text rev.). Washington, DC: American Psychiatric Publishing.

Avikainen, S., Wohlschläger, A., Liuhanen, S., Hänninen, R., & Hari, R. (2003). Impaired mirror-image imitation in Asperger and high-functioning autistic subjects. *Current Biology, 13*(4), 339–341.

Bailenson, J. N., & Yee, N. (2005). Digital chameleons automatic assimilation of nonverbal gestures in immersive virtual environments. *Psychological Science, 16*(10), 814–819.

Baranek, G. T., David, F. J., & Poe, M. D. (2006). Sensory Experiences Questionnaire: Discriminating sensory features in young children with autism, developmental delays, and typical development. *Journal of Child Psychology and Psychiatry, 47*(6), 591–601.

Berardi, N., Pizzorusso, T., & Maffei, L. (2000). Critical periods during sensory development. *Current Opinion in Neurobiology, 10*(1), 138–145.

Bernard-Opitz, V. (1982). Pragmatic analysis of the communicative behavior of an autistic child. *Journal of Speech and Hearing Disorders, 47*(1), 99–109.

Bernier, R., Dawson, G., Webb, S., & Murias, M. (2007). EEG mu rhythm and imitation impairments in individuals with autism spectrum disorder. *Brain and Cognition, 64*(3), 228–237.

Bird, G., Catmur, C., Silani, G., Frith, C., & Frith, U. (2006). Attention does not modulate neural responses to social stimuli in autism spectrum disorders. *NeuroImage, 31*(4), 1614–1624.

Blake, R., Turner, L. M., Smoski, M. J., Pozdol, S. L., & Stone, W. L. (2003). Visual recognition of biological motion is impaired in children with autism. *Psychological Science, 14*(2), 151–157.

Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial, and imitative cues. *Brain and Cognition, 44*(2), 124–143.

Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *NeuroImage, 14*(6), 1416–1423.

Cameron, E. L., & Doty, R. L. (2013). Odor identification testing in children and young adults using the smell wheel. *International Journal of Pediatric Otorhinolaryngology, 77*(3), 346–350.

Castiello, U., Lusher, D., Mari, M., Edwards, M., & Humphreys, G. W. (2002). Observing a human or a robotic hand grasping an object: Differential motor priming effects. In *Common mechanisms in perception and action. Series: Attention and performance XIX* (pp. 315–333). Oxford: Oxford University Press.

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology, 76*(6), 893–910.

Cook, J. L., & Bird, G. (2011). Atypical social modulation of imitation in autism spectrum conditions. *Journal of Autism and Developmental Disorders, 42*(6), 1045–1051.

Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y., et al. (2005). Understanding emotions in others: Mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience, 9*(1), 28–30.

Dinstein, I., Thomas, C., Humphreys, K., Minshew, N., Behrmann, M., & Heeger, D. J. (2010). Normal movement selectivity in autism. *Neuron, 66*(3), 461–469.

Donnellan, A. M., Hill, D. A., & Leary, M. R. (2013). Rethinking autism: Implications of sensory and movement differences for understanding and support. *Frontiers in Integrative Neuroscience, 6*, 1–10.

Doty, R. L., Shaman, P., & Dann, M. (1984). Development of the University of Pennsylvania Smell Identification Test: A standardized microencapsulated test of olfactory function. *Physiology & Behavior, 32*(3), 489–502.

Edwards, M. G., Humphreys, G. W., & Castiello, U. (2003). Motor facilitation following action observation: A behavioural study in prehensile action. *Brain and Cognition, 53*(3), 495–502.

Frijda, N. H. (2009). Emotions, individual differences and time course: Reflections. *Cognition & Emotion, 23*(7), 1444–1461.

Fujita, S., Ueki, S., Miyoshi, M., & Watanabe, T. (2010). "Green odor" inhalation by stressed rat dams reduces behavioral and neuroendocrine signs of prenatal stress in the offspring. *Hormones and Behavior, 58*(2), 264–272.

Glazebrook, C. M., Elliott, D., & Lyons, J. (2006). A kinematic analysis of how young adults with and without autism plan and control goal-directed movements. *Motor Control, 10*(3), 244–264.

Glazebrook, C. M., Elliott, D., & Szatmari, P. (2007). How do individuals with autism plan their movements? *Journal of Autism and Developmental Disorders, 38*(1), 114–126.

Glazebrook, C., Gonzalez, D., Hansen, S., & Elliott, D. (2009). The role of vision for online control of manual aiming movements in persons with autism spectrum disorders. *Autism, 13*(4), 411–433.

Gowen, E., & Hamilton, A. (2012). Motor abilities in autism: A review using a computational context. *Journal of Autism and Developmental Disorders, 43*(2), 323–344.

Gowen, E., Stanley, J., & Miall, R. C. (2008). Movement interference in autism-spectrum disorder. *Neuropsychologia, 46*(4), 1060–1068.

Hamilton, A. F. de C., Brindley, R. M., & Frith, U. (2007). Imitation and action understanding in autistic spectrum disorders: How valid is the hypothesis of a deficit in the mirror neuron system? *Neuropsychologia, 45*(8), 1859–1868.

Happé, F., & Frith, U. (2006). The weak coherence account: Detail-focused cognitive style in autism spectrum disorders. *Journal of Autism and Developmental Disorders, 36*(1), 5–25.

Harries, M. H., & Perrett, D. I. (2007). Visual processing of faces in temporal cortex: Physiological evidence for a modular organization and possible anatomical correlates. *Journal of Cognitive Neuroscience, 3*(1), 9–24.

Heyes, C. (2011). Automatic imitation. *Psychological Bulletin, 137*(3), 463–483.

Hilton, C. L., Harper, J. D., Kueker, R. H., & Lang, A. R. (2010). Sensory responsiveness as a predictor of social severity in children with high functioning autism spectrum disorders. *Journal of Autism and Developmental Disorders, 40*(8), 937–945.

Hollingshead, A. B. (1975). *Four factor index of social status*. Unpublished working paper. New Haven, CT: Yale University, Department of Sociology. <http://www.yale.edu/sociology/faculty/>.

Iacoboni, M., & Dapretto, M. (2006). The mirror neuron system and the consequences of its dysfunction. *Nature Reviews Neuroscience, 7*(12), 942–951.

Ingersoll, B., Lewis, E., & Kroman, E. (2006). Teaching the imitation and spontaneous use of descriptive gestures in young children with autism using a naturalistic behavioral intervention. *Journal of Autism and Developmental Disorders, 37*(8), 1446–1456.

Jacob, S., Hayreh, D. J. S., & McClintock, M. K. (2001). Context-dependent effects of steroid chemosignals on human physiology and mood. *Physiology & Behavior, 74*(1–2), 15–27.

Jasmin, E., Couture, M., McKinley, P., Reid, G., Fombonne, E., & Gisel, E. (2008). Sensori-motor and daily living skills of preschool children with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 39*(2), 231–241.

Kasari, C., Sigman, M., & Yirmiya, N. (1993). Focused and social attention of autistic children in interactions with familiar and unfamiliar adults: A comparison of autistic, mentally retarded, and normal children. *Development and Psychopathology, 5*(3), 403–414.

Kilner, J. M., Marchant, J. L., & Frith, C. D. (2006). Modulation of the mirror system by social relevance. *Social Cognitive and Affective Neuroscience, 1*(2), 143–148.

Knott, F., Lewis, C., & Williams, T. (1995). Sibling interaction of children with learning disabilities: A comparison of autism and Down's syndrome. *Journal of child psychology and psychiatry, 36*(6), 965–976.

Lakatos, P., Connell, M. N. O., Barczak, A., Mills, A., Javitt, D. C., & Schroeder, C. E. (2009). The leading sense: Supramodal control of neurophysiological context by attention. *Neuron, 64*(3), 419–430.

Lakin, J. L., & Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychological Science, 14*(4), 334–339.

Lane, A. E., Young, R. L., Baker, A., & Angley, M. T. (2010). Sensory processing subtypes in autism: Association with adaptive behavior. *Journal of Autism and Developmental Disorders, 40*, 112–122.

Leary, M. R., & Hill, D. A. (1996). Moving on: Autism and movement disturbance. *Mental Retardation, 34*, 39–53.

Leighton, J., Bird, G., Charman, T., & Heyes, C. (2008). Weak imitative performance is not due to a functional "mirroring" deficit in adults with autism spectrum disorders. *Neuropsychologia, 46*(4), 1041–1049.

Leighton, J., Bird, G., Orsini, C., & Heyes, C. (2010). Social attitudes modulate automatic imitation. *Journal of Experimental Social Psychology, 46*(6), 905–910.

Lord, C., Risi, S., Lambrecht, L., Cook, E. H. J., Leventhal, B. L., DiLavore, P. C., et al. (2000). The Autism Diagnostic Observation Schedule—Generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders, 30*(3), 205–223.

Lord, C., Rutter, M., & Le Couteur, A. (1994). Autism Diagnostic Interview-Revised: A revised version of a diagnostic interview for caregivers of individuals with possible pervasive developmental disorders. *Journal of Autism and Developmental Disorders, 24*(5), 659–685.

Lundström, J. N., Boyle, J. A., Zatorre, R. J., & Jones-Gotman, M. (2008). Functional neuronal processing of body odors differs from that of similar common odors. *Cerebral Cortex, 18*(6), 1466–1474.

Lundström, J. N., Boyle, J. A., Zatorre, R. J., & Jones-Gotman, M. (2009). The neuronal substrates of human olfactory based kin recognition. *Human Brain Mapping, 30*(8), 2571–2580.

Mari, M., Castiello, U., Marks, D., Marraffa, C., & Prior, M. (2003). The reach-to-grasp movement in children with autism spectrum disorder. *Philosophical Transactions of the Royal Society B: Biological Sciences, 358*(1430), 393–403.

Marlier, L., Schaal, B., & Soussignan, R. (1998). Neonatal responsiveness to the odor of amniotic and lacteal fluids: A test of perinatal chemosensory continuity. *Child Development, 69*(3), 611–623.

McIntosh, D. N., Reichmann-Decker, A., Winkielman, P., & Wilbarger, J. L. (2006). When the social mirror breaks: Deficits in automatic, but not voluntary, mimicry of emotional facial expressions in autism. *Developmental Science, 9*(3), 295–302.

Meltzoff, A. N., & Decety, J. (2003). What imitation tells us about social cognition: A rapprochement between developmental psychology and cognitive neuroscience. *Philosophical Transactions of the Royal Society B: Biological Sciences, 358*(1431), 491–500.

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2009). Is the mirror neuron system involved in imitation? A short review and meta-analysis. *Neuroscience & Biobehavioral Reviews, 33*(7), 975–980.

Moriceau, S., & Sullivan, R. M. (2006). Maternal presence serves as a switch between learning fear and attraction in infancy. *Nature Neuroscience, 9*(8), 1004–1006.

Moriceau, S., Wilson, D. A., Levine, S., & Sullivan, R. M. (2006). Dual circuitry for odor–shock conditioning during infancy: Corticosterone switches between fear and attraction via amygdala. *The Journal of neuroscience, 26*(25), 6737–6748.

Mujica-Parodi, L. R., Strey, H. H., Frederick, B., Savoy, R., Cox, D., Botanov, Y., et al. (2009). Chemosensory cues to conspecific emotional stress activate amygdala in humans. *PLoS One, 4*(7), e6415.

Nair, A., Treiber, J. M., Shukla, D. K., Shih, P., & Muller, R. A. (2013). Impaired thalamocortical connectivity in autism spectrum disorder: A study of functional and anatomical connectivity. *Brain, 136*(6), 1942–1955.

Nazarali, N., Glazebrook, C. M., & Elliott, D. (2009). Movement planning and reprogramming in individuals with autism. *Journal of Autism and Developmental Disorders, 39*(10), 1401–1411.

Nishitani, N., Avikainen, S., & Hari, R. (2004). Abnormal imitation-related cortical activation sequences in Asperger's syndrome. *Annals of Neurology, 55*(4), 558–562.

Oberman, L. M., Hubbard, E. M., McCleery, J. P., Altschuler, E. L., Ramachandran, V. S., & Pineda, J. A. (2005). EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Cognitive Brain Research, 24*(2), 190–198.

Oberman, L. M., & Ramachandran, V. S. (2007). The simulating social mind: The role of the mirror neuron system and simulation in the social and communicative deficits of autism spectrum disorders. *Psychological Bulletin, 133*(2), 310–327.

Oberman, L. M., Ramachandran, V. S., & Pineda, J. A. (2008). Modulation of mu suppression in children with autism spectrum disorders in response to familiar or unfamiliar stimuli: The mirror neuron hypothesis. *Neuropsychologia, 46*(5), 1558–1565.

Okabe, S., Nagasawa, M., Mogi, K., & Kikusui, T. (2012). The importance of mother–infant communication for social bond formation in mammals. *Animal Science Journal, 83*(6), 446–452.

Parma, V., Bulgheroni, M., Tirindelli, R., & Castiello, U. (2013). Body odors promote automatic imitation in autism. *Biological Psychiatry, 74*(3), 220–226.

Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *The American Naturalist, 166*(2), 231–245.

Pause, B. M. (2012). Processing of body odor signals by the human brain. *Chemosensory Perception, 5*(1), 55–63.

Pierno, A. C., Mari, M., Glover, S., Georgiou, I., & Castiello, U. (2006). Failure to read motor intentions from gaze in children with autism. *Neuropsychologia, 44*(8), 1483–1488.

Pierno, A. C., Mari, M., Lusher, D., & Castiello, U. (2008). Robotic movement elicits visuomotor priming in children with autism. *Neuropsychologia, 46*(2), 448–454.

Porter, R. H. (1999). Olfaction and human kin recognition. *Genetica, 104*, 259–263.

Press, C., Richardson, D., & Bird, G. (2010). Intact imitation of emotional facial actions in autism spectrum conditions. *Neuropsychologia, 48*(11), 3291–3297.

Reisenzein, R. (2012). What is an emotion in the belief-desire theory of emotion? In F. Paglieri, L. Tummolini, R. Falcone, & M. Miceli (Eds.), *The goals of cognition: Essays in honor of Cristiano Castelfranchi*. London: College Publications.

Rinehart, N. J., Bellgrove, M. A., Tonge, B. J., Brereton, A. V., Howells-Rankin, D., & Bradshaw, J. L. (2006). An examination of movement kinematics in young people with high-functioning autism and Asperger's Disorder: Further evidence for a motor planning deficit. *Journal of Autism and Developmental Disorders, 36*(6), 757–767.

Rinehart, N. J., Bradshaw, J. L., Brereton, A. V., & Tonge, B. J. (2001). Movement preparation in high-functioning autism and Asperger disorder: A serial choice reaction time task involving motor reprogramming. *Journal of Autism Developmental Disorders, 31*(1), 79–88.

Rogers, S. J., Hepburn, S. L., Stackhouse, T., & Wehner, E. (2003). Imitation performance in toddlers with autism and those with other developmental disorders. *Journal of Child Psychology and Psychiatry, 44*(5), 763–781.

Rossi, S., De Capua, A., Pasqualetti, P., Ulivelli, M., Fadiga, L., Falzarano, V., et al. (2008). Distinct olfactory cross-modal effects on the human motor system. *PLoS One, 3*(2), e1702.

Schaal, B., Marlier, L., & Soussignan, R. (2000). Human foetuses learn odours from their pregnant mother's Diet. *Chemical Senses, 25*(6), 729–737.

Schopler, E., Reichler, R. J., DeVellis, R. F., & Daly, K. (1980). Toward objective classification of childhood autism: Childhood Autism Rating Scale (CARS). *Journal of Autism and Developmental Disorders, 10*(1), 91–103.

Seltzer, B., & Pandya, D. N. (1994). Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey. *Journal of Comparative Neurology, 343*(3), 445–463.

Spengler, S., Bird, G., & Brass, M. (2010). Hyperimitation of actions is related to reduced understanding of others' minds in autism spectrum conditions. *Biological Psychiatry, 68*(12), 1148–1155.

Sridapa, C. S., Phan, K. L., Labuschagne, I., Welsh, R., Nathan, P. J., & Wood, A. G. (2014). Oxytocin enhances resting-state connectivity between amygdala and medial frontal cortex. *International Journal of Pharmacology, 16*(2), 255–260.

Sullivan, R. M., & Toubas, P. (1998). Clinical usefulness of maternal odor in newborns: Soothing and feeding preparatory responses. *Biology of the Neonate, 74*(6), 402–408.

Sullivan, R. M., Wilson, D. A., Wong, R., Correa, A., & Leon, M. (1990). Modified behavioral and olfactory bulb responses to maternal odors in preweanling rats. *Developmental Brain Research, 53*(2), 243–247.

Sutera, S., Pandey, J., Esser, E. L., Rosenthal, M. A., Wilson, L. B., Barton, M., et al. (2007). Predictors of optimal outcome in toddlers diagnosed with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 37*(1), 98–107.

Theoret, H., Halligan, E., Kobayashi, M., Fregni, F., Tager-Flusberg, H., & Pascual-Leone, A. (2005). Impaired motor facilitation during action observation in individuals with autism spectrum disorder. *Current Biology: CB, 15*(3), R84–5.

Tubaldi, F., Turella, L., Pierno, A. C., Grodd, W., Tirindelli, R., & Castiello, U. (2011). Smelling odors, understanding actions. *Social Neuroscience, 6*(1), 31–47.

Van baaren, R. B., Holland, R. W., Kawakami, K., & Knippenberg, A. V. (2004). Mimicry and prosocial behavior. *Psychological Science, 15*(1), 71–74.

Villalobos, M. E., Mizuno, A., Dahl, B. C., Kemmotsu, N., & Müller, R.-A. (2005). Reduced functional connectivity between V1 and inferior frontal cortex associated with visuomotor performance in autism. *NeuroImage, 25*(3), 916–925.

Vrtička, P., Sander, D., & Vuilleumier, P. (2012). Lateralized interactive social content and valence processing within the human amygdala. *Frontiers in Human Neuroscience, 6*, 1–12.

Wechsler, D. (1991). *WISC-III: Wechsler intelligence scale for children* (3rd ed.). San Antonio, TX: The Psychological Corporation.

Williams, J. H., Whiten, A., & Singh, T. (2004). A systematic review of action imitation in autistic spectrum disorder. *Journal of Autism and Developmental Disorders, 34*(3), 285–299.

Yamasue, H. (2013). Function and structure in social brain regions can link oxytocin-receptor genes with autistic social behavior. *Brain and Development, 35*(2), 111–118.

Zald, D. H., & Pardo, J. V. (1997). Emotion, olfaction, and the human amygdala: Amygdala activation during aversive olfactory stimulation. *Proceedings of the National Academy of Sciences of the United States of America, 94*(8), 4119–4124.

Zoia, S., Blason, L., D'Ottavio, G., Bulgheroni, M., Pezzetta, E., Scabar, A., et al. (2006). Evidence of early development of action planning in the human foetus: A kinematic study. *Experimental Brain Research, 176*(2), 217–226.