


Both the Mirror and the Affordance Systems Might be Impaired in Adults with High Autistic Traits. Evidence from EEG Mu and Beta Rhythms

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The association of autism spectrum disorder (ASD) with an altered mirror neuron system is still controversial. At the same time, the processing of object affordances by persons with ASD is a neglected issue. In this electroencephalographic study, adults differing in their autism quotient (AQ) scores were selected. We found anomalous modulation of mu and beta rhythms in high-AQ, compared to low-AQ persons, while they watched a set of goal-directed manual actions. This confirms that observing actions involving implicit intentions most clearly reveals the impairment of the mirror neurons system (MNS). The high-AQ group also showed anomalous mu and beta modulation when they looked at pictures of manipulable objects, indicating a deficit in processing motor affordances. We conclude that high-AQ adults have neural impairment of both the MNS and the affordance systems, which could underlie their relational problems with both people and objects. *Autism Res* 2019, 00: 1–11. © 2019 International Society for Autism Research, Wiley Periodicals, Inc.

Lay Summary: Adults with autistic traits (high-autism quotient [AQ] scores) and matched controls (low-AQ) observed intentional hand actions, and pictures of manipulable and non-manipulable objects. The high-AQ group compared to the control group, showed anomalous modulation of the electroencephalographic motoric rhythms (mu and beta) while observing familiar goal-directed actions, confirming an impairment of their mirror neuron system. Also, their brain rhythms were anomalous when they watched manipulable objects, which suggest a dysfunction in their relation with objects (affordance system).

Keywords: mirror neuron system; electroencephalography (EEG); affordances; mu rhythms

Introduction

Initially discovered in single-neuron studies with macaques, mirror neurons were found to fire when the animal performed an action, but also when they observed another's actions [Rizzolatti & Craighero, 2004]. Further research indicated that a mirror neurons system (MNS) also exists in humans, as revealed by behavioral [Cardellicchio, Sinigaglia, & Costantini, 2011], neuroimaging [Iacoboni et al., 2005; Keysers & Gazzola, 2010], electrophysiological [Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010; Pfurtscheller, Brunner, Schlögl, & Da Silva, 2006; Pineda, 2005] and noninvasive brain stimulation studies [Fadiga, Craighero, & Olivier, 2005]. A central tenet of the theory is that the MNS is a basic mechanism of social cognition, responsible for understanding others' actions and intentions [Iacoboni et al., 2005; Rizzolatti & Sinigaglia, 2007], understanding facial expressions [Feroni, 2015] or feeling empathy [Singer, 2006]. According to the MNS hypothesis,

mirror neurons discharge both during action production and during action observation and they constitute a possible mechanism to understand the actions of others by directly matching the visual representation of observed actions with our own motor representation of those same actions. A consequence of this motor mirror activity is that it allows us immediately to attribute an intentional meaning to the others' movements [Rizzolatti & Sinigaglia, 2007]. The broken mirror theory posits that autism spectrum disorder (ASD) is associated with a dysfunction in the MNS [Gallese, 2006; Hamilton, 2013; Iacoboni & Dapretto, 2006; Oberman & Ramachandran, 2007; Williams et al., 2006; Williams, Whiten, Suddendorf, & Perrett, 2001]. This would explain why people with ASD have difficulties imitating, empathizing with or understanding others' actions and intentions. But, do the deficits in the MNS explain the impairment of high-order social skills in autism? In a recent integrative review of the functional and neural deficits in ASD, Khalil, Tindle, Boraud, Moustafa, and Karim

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[2018] postulate a multilayer neural network model, including the MNS on a first layer and transforming this information to a higher layer network responsible for the theory of mind skills, comprising the prefrontal cortex, the anterior cingulate cortex, and the temporoparietal junction. Further research will be necessary to verify whether the structural and functional connectivity among MNS and theory of mind networks supports this model.

Some brain rhythms observed in the electroencephalogram (EEG) have been considered signatures of motor processes. In particular, mu (8–14 Hz) and beta (14–24 Hz) rhythms, recorded over central electrodes (C3, Cz, and C4), provide rich information about the underlying neural motor activity. These rhythms are highly synchronized when at rest and become desynchronized when participants move, especially if these movements are manual [Cochin, Barthelemy, Lejeune, Roux, & Martineau, 1998; McFarland, Miner, Vaughan, & Wolpaw, 2000; Pfurtscheller et al., 2006; Pineda, 2005]. Moreover, mu (and to lesser extent beta) rhythms are also desynchronized when people observe others' hand movements [Cochin, Barthelemy, Roux, & Martineau, 1999; Fox et al., 2016; Moreno, De Vega, & León, 2013; Muthukumaraswamy & Johnson, 2004], indexing the activity of the MNS.

ASD and the MNS

The hypothesis that ASD persons have a deficit in the MNS is supported by some studies showing that ASD persons, unlike neurotypical participants, do not exhibit mu rhythm suppression when they observe manual actions [Bernier, Dawson, Webb, & Murias, 2007; Cole, Barraclough, & Enticott, 2018; Dumas, Sousignan, Hugueville, Martinerie, & Nadel, 2014; Oberman & Ramachandran, 2007]. However, other studies failed to show any difference between ASD and control participants in mu suppression during action observation tasks [Fan, Decety, Yang, Liu, & Cheng, 2010; Raymaekers, Wiersema, & Roeyers, 2009], or they only found reduced mu suppression in ASD when the observed action is produced by a familiar person rather than by a stranger [Oberman, Ramachandran, & Pineda, 2008]. The above discrepancy of results has been attributed to the heterogeneity of ASD participants [Raymaekers et al., 2009], the familiarity of the agent performing the action [Oberman et al., 2008], or the particular range of mu frequencies selected for the analysis [Cole et al., 2018; Dumas et al., 2014]. A more radical conclusion is that the current data provide little evidence that ASD persons have a global dysfunction in the MNS [Fan et al., 2010; Hamilton, 2013]. But before definitely rejecting the MNS deficit hypothesis of ASD we must consider some methodological and conceptual issues in the experiments, such as the choice of action-observation stimuli and the task demands, which could be crucial to obtain clearer results. Dealing

with these issues appropriately could improve the quality of the mu rhythms data, helping to establish more robust differences between ASD and neurotypical participants.

Some potential problems concerning the measure of mu rhythms modulation have been raised [Fox et al., 2016; Hobson & Bishop, 2016, 2017]. First, some experiments employed block design to improve the signal-to-noise ratio between the EEG conditions, but this may also involve drawbacks. For instance, Hobson and Bishop [2016], using neurotypical participants, reported that typical block designs with a single long baseline (e.g., a resting 80-sec “block”) do not provide an optimal contrasting condition to measure mu suppression. Instead, they found better results employing within-trial baselines, namely, contrasting the rhythms modulation in each stimulus with its preceding resting time. Second, some experiments just tested mu suppression in central sites (C3, Cz, and C4) and did not report the occipital alpha activity, with the same frequency range, which is highly sensitive to visual attentional processes and could be confounded with motoric mu [Hobson & Bishop, 2017]. In conclusion, employing an event-related rather than a block design, using appropriate baseline and avoiding confounds with other brain rhythms may contribute to more reliable data collection.

Most important, the type of observational stimuli and the task demands chosen in the EEG experiments can be critical to obtain differential effects between ASD and neurotypical individuals in mu suppression. Actions can be described at several hierarchical levels, from intentions and goals to kinematics and muscle movements [Hamilton & Grafton, 2007; Kilner, Friston, & Frith, 2007]. Moreover, the MNS theory postulates that mirror neurons not only react to the observation of others' muscle movements, but also to the goals and intentions [Iacoboni et al., 2005; Rizzolatti & Sinigaglia, 2007]. However, frequently the studies examining the MNS in ASD persons have focused on low-level processes (kinematics and muscle levels) rather than high-order processes (goals and intentions). For instance, some studies used video clips of a simple hand movement (e.g., opening and closing a hand), compared to some baseline condition. But, if persons with ASD have special difficulties to understand others' goals and intentions [Boria et al., 2009; Cattaneo et al., 2007], then using goal-directed actions rather than purposeless low-level actions as stimuli could be more efficient to detect their deficits in MNS. Several studies support this claim. Adults with ASD, compared with neurotypical persons, showed reduction of low mu suppression when they were explicitly asked to judge the intentionality of observed actions [Cole et al., 2018]. Moreover, single pulse TMS applied over M1 in neurotypical participants revealed increased corticospinal excitability when they observed goal-directed hand actions (Avenanti & Urgesi, 2011; Enticott, Kennedy, Bradshaw, Rinehart, & Fitzgerald, 2010;

see Avenanti, Candidi, & Urgesi, 2013, for a review), whereas in ASD persons the corticospinal modulation was generally reduced for these actions [Cole & Barraclough, 2018; Cole et al., 2018; Enticott et al., 2012]. Finally, in a neuroimaging study, high-functioning ASD persons and neurotypical controls were asked to judge the intentionality of ordinary or anomalous actions [Liberio et al., 2014]. Both groups activated the MNS, including the inferior parietal lobule, but the ASD group also increased activation of the left inferior frontal gyrus suggesting that processing intentions demands additional neural resources in this group. In sum, observing intentional goal-directed actions more likely recruits the MNS and could facilitate better discrimination between ASD and control groups.

ASD and Affordances

There is evidence that not only observing actions, but also seeing manipulable objects elicit activations in the motor system. This may happen because we directly perceive the object affordances, namely how objects relate to their uses [Gibson, 2000]. Affordances are relational properties, which depend on the physical features of the object, the body's capabilities and the momentary intentions of the individual. Thus, a door handle affords opening for an adult who wants to go into a room but does not afford anything for a baby. The affordances theory has been tested with behavioral methods, which demonstrated that both manipulable objects and pictures of manipulable objects placed in the peripersonal space automatically trigger their motor affordances [Buccino, Sato, Cattaneo, Rodà, & Riggio, 2009; Costantini, Ambrosini, Scorolli, & Borghi, 2011]. Also, neuroimaging data have provided information on the neural mechanisms of affordances, reporting that watching manipulable objects consistently activates the anterior intraparietal sulcus and the dorsal premotor cortex [Grèzes, Tucker, Armony, Ellis, & Passingham, 2003; Proverbio, Adorni, & D'Aniello, 2011; Thill, Caligiore, Borghi, Ziemke, & Baldassarre, 2013; Valyear, Cavina-Pratesi, Stiglick, & Culham, 2007]. Although the mirror neurons activated during action observation are not exactly the same ones as those involved in processing affordances [Thill et al., 2013], their electrophysiological signatures are quite similar. Thus, mu and beta desynchronization has been reported during the observation of tools, compared to non-tools, indexing the processing of motor affordances in the former [e.g., Kumar, Riddoch, & Humphreys, 2013; Proverbio, 2012].

Do ASD persons have impaired perception of object affordances? When Kanner [1943] established the diagnostic criteria for early infant autism, he emphasized these children's lack of interest in people in contrast with their relatively appropriate interaction with objects. However, Kanner also observed that young children with ASD,

compared with their typically developing controls, show deficits in their interaction with objects, such as the absence of symbolic play, stereotypical and repetitive manipulations, preoccupation with isolated parts of objects, etc. More recently, developmental studies have shown that preverbal children and toddlers with suspected ASD, unlike typically developing children, exhibit anomalous exploratory activity with objects [Kaur, Srinivasan, & Bhat, 2015] and do not monitor adults' activities [Shic, Bradshaw, Klin, Scassellati, & Chawarska, 2011]. These developmental disorders in early autism may develop into anomalous relations with objects in ASD adults, and more critically into impaired affordance processing, given the fact that object affordances are acquired in a socially interactive and observational context [Deák, Krasno, Triesch, Lewis, & Sepeta, 2014; Fagard, Rat-Fischer, Esseily, Somogyi, & O'Regan, 2016; Loveland & Tunali, 1991; Williams, Costall, & Reddy, 1999]. For these reasons, it is surprising to note the absence of studies on affordances processing in individuals with ASD. This article aims to fill this research gap by exploring the perception of object affordances in persons with ASD.

The Present Study

This study tested whether adults with high scores in autism quotient (AQ) (herein high-AQ), compared to neurotypical participants (herein low-AQ), show impairment both in the MNS and in the affordance system. To this end, their EEG rhythms were collected while they observed three kinds of materials: manual actions, pictures of manipulable objects, and pictures of non-manipulable objects. The action stimuli consisted of video clips of goal-directed actions, typically involving the manipulation of two objects, such as "sharpen a pencil" or "turning the cap of a bottle" (Fig. 1, left). The participants were not explicitly requested to make any inference, but the actions were so familiar that we hypothesize that neurotypical individual should be able to immediately predict their implicit goals (e.g., to open the bottle) and intentions (e.g., to drink water), by means of the MNS [Iacoboni et al., 2005; Kilner et al., 2007; Rizzolatti & Sinigaglia, 2007]. As a main signature of MNS activity, the central mu rhythms were analyzed. The motoric beta rhythms were also analyzed since they could also show anomalous modulations in high-AQ persons during actions observation [Cooper, Simson, Till, Simmons, & Puzzo, 2013; Dumas et al., 2014; Honaga et al., 2010]. We expected to obtain reduction of mu rhythm desynchronization in high-AQ persons, compared to low-AQ participants, in action observation, indicating less engagement of motor processes (mirror neurons). We also predict a reduction in mu and beta rhythm desynchronization in high-AQ persons while they observe manipulable objects, whereas we do not expect any

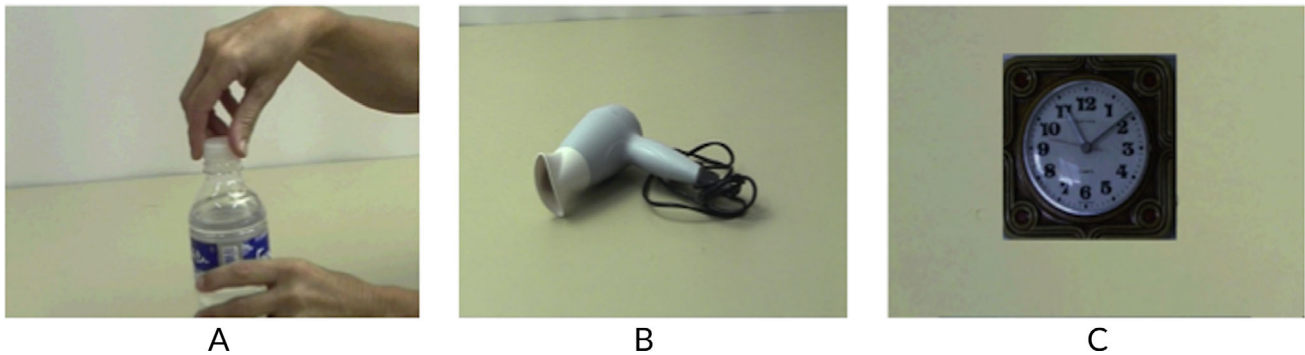


Figure 1. Snapshots of an action clip (A), a manipulable object (B), and a non-manipulable object (C).

modulation in these rhythms during observation of non-manipulable objects, which serve as a control condition. If the latter predictions were confirmed, it would be the first neurobiological evidence, to our knowledge, that high-AQ traits are associated with impairment in the affordance system.

Method

Participants

A group of 16 high-AQ right-handed participants and another group of 16 low-AQ right-handed participants matched in several features were initially selected for the study. One high-AQ and another low-AQ participants were discarded because of excessive ocular artifacts in the EEG recording. The Research Ethics Committee of the University of La Laguna approved this study, and the experiment was conducted according to the principles expressed in the Declaration of Helsinki. The high-AQ participants were selected in two stages. First, we administered the self-report autism-spectrum quotient (AQ, Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) to a sample of about 1500 university students by means of an Internet application programmed in html, JavaScript, and php. Second, 25 of these students who obtained scores of 30 or higher in the AQ were asked to come to the laboratory to perform additional tests. Specifically, they filled out the empathy quotient (EQ, Baron-Cohen & Wheelwright, 2004) and performed a general intelligence test, the Raven Progressive Matrices [Raven, 1975]. The final sample of 15 high-AQ participants was selected according to their low scores in EQ and average scores in intelligence. In parallel, we selected 15 control participants matched in age, educational level, and intelligence but with low and medium scores in the AQ < 20. Table 1 shows descriptors and scores of the selected high-AQ and low-AQ groups. *T*-test comparisons showed significant between-group difference in AQ ($t(28) = 12.36$, $P < 0.0001$; Cohen's $d = 4.64$) and EQ ($t(28) = 4.07$, $P < 0.0001$; Cohen's $d = 1.52$), confirming that the two

groups strongly differ in the two standard questionnaires. By contrast, they did not differ in age ($P = 0.19$) or Raven scores ($P = 0.14$). All participants were paid 10 euros for their participation in the experiment.

Materials

We selected 90 visual stimuli from a previous neuroimaging study [de Vega et al., 2014]. They belonged to three categories: 30 clips depicting manual actions (AC), 30 pictures of manipulable objects (MO), and 30 pictures of non-manipulable objects (NMO). The ACs depicted a human agent's hands performing goal-directed familiar actions using one or two objects (e.g., opening a bottle or sharpening a pencil), with most of them involving the coordination of the two hands (24 out of 30). The MOs were familiar tools (e.g., a hair dryer or a toothbrush) depicted with the right orientation to be used by a right-handed person, and the NMOs were familiar objects that are usually observed, rather than manipulated, in ordinary situations (e.g., a wall clock or a ceiling lamp). Examples of stimuli are shown in Figure 1.

Design and Procedure

Participants were seated in a comfortable chair with instructions to remain relaxed and to minimize blinking during the experiment. They received the whole set of 90 stimulus trials, divided in three blocks of 30 trials. Each block included 10 ACs, 10 MOs, and 10 NMOs,

Table 1. Descriptors and scores of the high- and low-AQ groups

	High-AQ ($N = 15$) M (SD)	Low-AQ ($N = 15$) M (SD)
Age	22 (4.67)	20 (2.30)
Females/males	10/5	8/7
AQ**	33.53 (4.37)	17.13 (2.69)
EQ**	31.66 (12.70)	47.73 (8.47)
RPM	101.73 (8.17)	97.47 (7.21)

Abbreviations: AQ, autism-spectrum quotient; EQ, empathy quotient; RPM, Raven Progressive Matrices.

**Significant difference between groups ($P < 0.0001$).

presented in random order on the computer screen. Each trial followed this sequence: 500-ms fixation point, 2500-ms blank, visual stimulus (clip or picture) during 2500 ms, and, finally, 5000-ms blank aiming to restore the rhythm baseline between trials. To encourage participants to pay full attention to the stimuli they were informed that they would receive a subsequent recognition test. At the end of each block, participants were given the recognition test, in which three frames, either “old” or “new”, were presented. Each frame was presented until the participant responded or for a maximum of 3 sec. Thus, a total of nine recognition probes were performed (five old and four new): three ACs, three MOs, and three NMOs. After each recognition test, a self-administered period of inactivity followed, aiming to restore baseline after the motor responses.

EEG Data Acquisition and Analyses

EEG and EOG signals were recorded using Ag/AgCl electrodes mounted in elastic Quick-caps (Compumedics). EOG signal was measured from two bipolar channels: one from two electrodes placed at the outer canthus of each eye and the other from two electrodes above and below the left eye. EEG signal was recorded from 60 electrodes arranged according to the standard 10–20 system, with additional electrodes placed at cb1/cb2 and also on the left and right mastoids (M1/M2). All EEG electrodes were referenced online to an electrode at vertex and re-referenced offline to an average reference. EEG and EOG signals were amplified at 500 Hz sampling rate using Syn-amp2 amplifier (Neuroscan; Compumedics), with high- and low-pass filters set at 0.05 and 100 Hz, respectively. EEG electrode impedance was kept at <5 k Ω . EEG data preprocessing and analysis were conducted using Fieldtrip Toolbox [Oostenveld, Fries, Maris, & Schoffelen, 2011]. Trials with drifting or large movement artifacts were removed by visual inspection before analysis. Independent component analysis was applied to the data to remove the effects of blinks and eye movements. Remaining trials with EEG voltages exceeding 70 μ V measured from peak to peak at any channel were also removed.

Data were segmented into epochs of 2.5 sec, each starting at the onset of a video clip or picture. Epochs with blinks and eye movements identified by abrupt changes in the EOG waves were submitted to an artifact reduction algorithm, which subtracted the eye movement from the ongoing EEG, improving it before averaging. Data from two participants were excluded from the analysis due to the excessive number of blinks and motor artifacts (facial muscle activity) identified during the session. After the automatic correction of blinks, the remaining data were carefully inspected and trials with artifacts other than movements were rejected. The total rejection rates per stimulus condition in the low-AQ group were: ACs: $M = 28\%$,

$SD = 8$; MOs: $M = 22\%$, $SD = 16$; and NMOs: $M = 30\%$, $SD = 14$. The rejection rates per condition in the high-AQ group were: ACs: $M = 37\%$, $SD = 15$; MOs: $M = 32\%$, $SD = 18$; and NMOs: $M = 32\%$, $SD = 18$. These rejections were unbiased by condition ($F(2, 48) = 1.26$, $P = 0.29$, $\eta^2 = 0.043$), by group ($F(1, 28) = 2.85$, $P = 0.10$, $\eta^2 = 0.092$) or by condition \times group ($F(2, 48) = 0.85$, $P = 0.43$, $\eta^2 = 0.030$).

Our main interest was on mu and beta rhythms defined as oscillatory measures over the sensorimotor cortex, represented by the C3, Cz, and C4 electrodes on the scalp [Cochin et al., 1998; Muthukumaraswamy & Johnson, 2004; Oberman et al., 2005]. Given the fact that the frequency in the mu band overlaps with the frequency in the alpha band in posterior sites, it is possible that recordings from the critical central region might be contaminated by the posterior alpha activity associated with expectancy [e.g., Hobson & Bishop, 2016, 2017]. To test this possibility, alpha rhythms were analyzed in parieto-occipital electrodes (O1, Pz, O2) and, complementarily, in the frontal electrodes (F3, Fz, F4). Finally, beta rhythms were analyzed because, according to the literature, they could also be modulated at central sites during action performance and observation [e.g., McFarland et al., 2000; Pfurtscheller et al., 2006; Pineda, 2005], and anomalous beta modulations have been reported recently in ASD persons [Cooper et al., 2013; Honaga et al., 2010]. For each 2.5-sec epoch, the integrated power in the 8–13 Hz range (mu band) and in the 15–20 Hz range (low beta band) were computed using fast Fourier transforms (FFT) on the cleaned and epoched data (based on 1024 points per segment, using Hanning window). A spectral power analysis, performed on the FFT coefficients, was carried out on the EEG to identify changes in spectral amplitude of the mu and beta frequency bands. The average of EEG of the 500 ms preceding each trial was used as baseline. Following Oberman et al. [2005], logratio values were calculated between each experimental condition and the baseline in the mu and beta frequency bands. Values smaller than zero correspond to power reduction and values larger than zero imply increased power of the mu rhythm. To explore the scalp topography of mu (8–13 Hz) and beta (15–20 Hz) rhythms, data were first grand averaged across trials for each stimulus condition and for each electrode in the whole scalp and were subtracted from the baseline. Thereafter, the plots corresponding to the most relevant pairs of conditions were subtracted (AC–MNO and MO–NMO) to obtain the differential topography of mu and beta.

Results

Behavioral Results

The percent of correct recognition was very high in the two groups (mean low-AQ = 92.6%; $SD = 9.9$; mean high-AQ = 94%, $SD = 7.11$; $t(28) = 0.46$, $P = 0.64$).

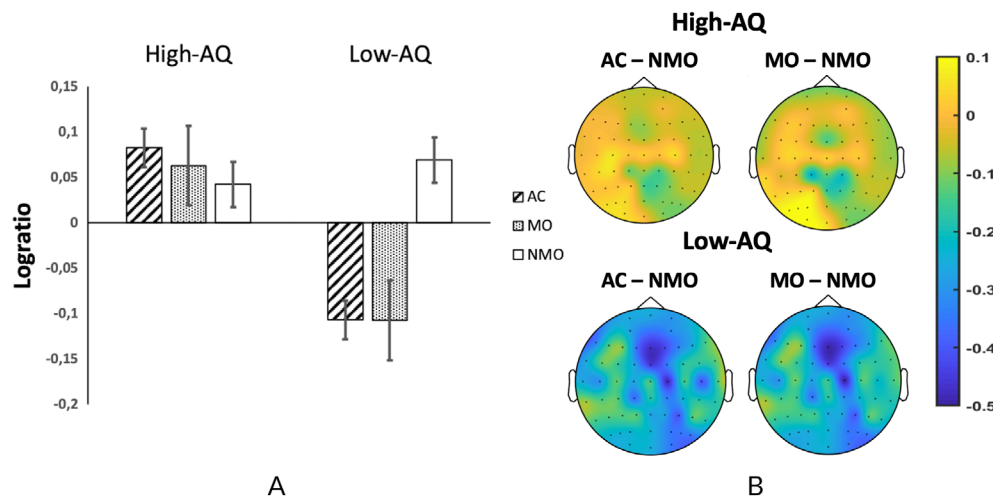


Figure 2. (A) Logratio of mu rhythm power (8–13 Hz) averaged for the central electrodes (C3, Cz, C4), for both the high-AQ and the low-AQ groups. The vertical lines over the bars represent the typical errors. (B) Scalp distribution of mu rhythm power (8–13 Hz), calculated by subtracting the EEG logratio between pairs of conditions for the high-AQ and the low-AQ groups. AC, action clips; MO, manipulable objects; NMO, non-manipulable objects.

Mu Rhythms (8–13 Hz) in Central Electrodes

An analysis of variance (ANOVA) including group (high-AQ vs. low-AQ) \times stimulus (AC, MO, NMO) \times electrode (C3, Cz, C4) was performed on mu rhythm power changes (logratio). The Greenhouse correction was applied for sphericity violations. There was a main effect of stimulus ($F(1, 28) = 3.78, P < 0.048; \eta^2 = 0.12$) and group ($F(1, 28) = 16.60, P < 0.0001; \eta^2 = 0.37$), which were qualified by the important stimulus \times group interaction ($F(1, 28) = 7.53, P < 0.005; \eta^2 = 0.212$). To explore this interaction, new ANOVAs were performed for each group separately, obtaining significant effect of stimulus for the low-AQ group ($F(1, 14) = 6.76, P < 0.015; \eta^2 = 0.326$), but not for the high-AQ group ($F(1, 14) = 1.08, P = 0.352; \eta^2 = 0.072$). Given the fact that electrode did not yield any significant effect, the mu power for the three central electrodes was averaged and submitted to pairwise comparisons among stimuli just for the low-AQ group. There were significant differences between AC and NMO ($t(14) = 5.63, P < 0.0001$; Cohen's $d = 2.25$) and between MO and NMO ($t(14) = 2.42, P < 0.03$; Cohen's $d = 1.061$), but not between AC and MO ($t(14) < 1$). The mu rhythms for stimulus conditions and the scalp distribution of between-pairs differences are shown in Figure 2.

Beta Rhythms (15–25 Hz) in Central Electrodes

An ANOVA including group (low-AQ vs. high-AQ) \times stimulus (AC, MO, NMO) \times electrode (C3, Cz, C4) was performed on beta rhythm power changes (logratio). The only significant effect obtained was the stimulus \times group interaction ($F(1, 28) = 5.32, P < 0.011; \eta^2 = 0.16$). Separate ANOVAs for groups yielded a significant main effect of stimulus for the low-AQ group ($F(1, 14) = 5.78, P < 0.009$;

$\eta^2 = 0.29$), but not for the high-AQ group ($F(1, 14) = 1.23, P = 0.30; \eta^2 = 0.08$). Beta power for the three electrodes was averaged and submitted to pairwise comparisons for the low-AQ group. There were significant differences between AC and NMO ($t(14) = 3.22, P < 0.006$; Cohen's $d = 1.15$), and between MO and NMO ($t(14) = 2.37, P < 0.033$; Cohen's $d = 0.83$), but not between AC and MO ($t(14) < 1$). The beta rhythms for each stimulus condition are shown in Figure 3.

EEG Rhythms in Posterior and Anterior Regions

Complementary analyses were performed in frontal (F3, Fz, F4) and parieto-occipital (O1, Pz, O2) electrodes. The group \times stimulus ANOVAs done in these regions separately

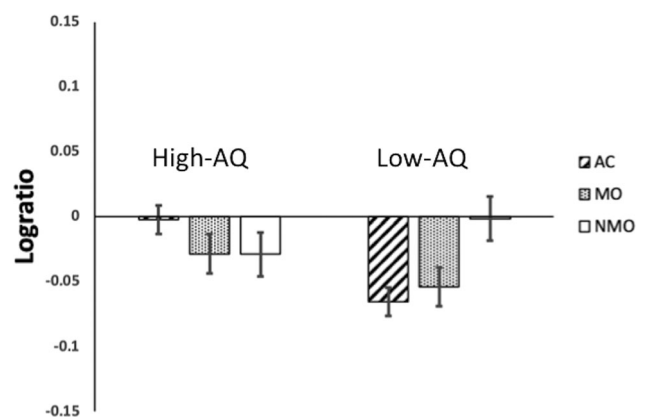


Figure 3. Logratio of beta rhythms (15–25 Hz) averaged for the central electrodes (C3, Cz, C4), for both the high-AQ and the low-AQ groups. The vertical lines over the bars represent the typical errors. AC, action clips; MO, manipulable objects; NMO, non-manipulable objects.

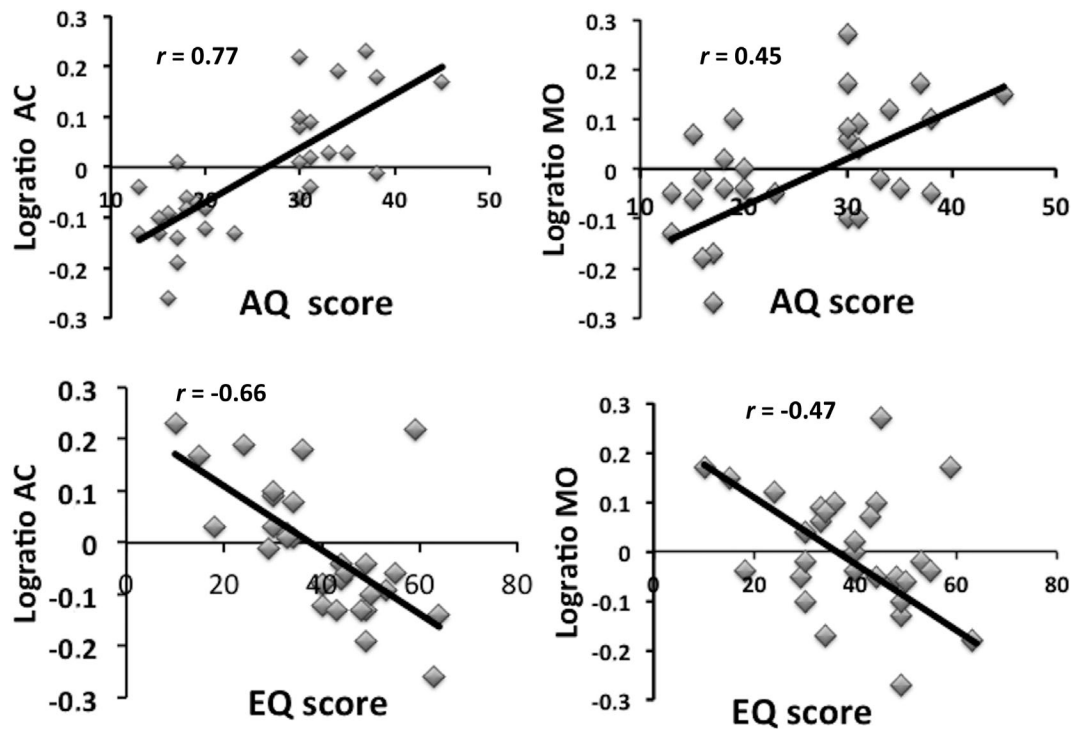


Figure 4. Correlations between AQ and EQ scores and mu rhythm modulations. AC, action clips; MO, manipulable objects.

did not produce any significant effect on either alpha or beta rhythms ($F < 1$, for each variable and interaction). The absence of alpha modulation in parieto-occipital electrodes is particularly relevant, because it allows us to conclude that the obtained mu rhythm modulations were not contaminated by attentional alpha in this study.

Correlational Analysis

To explore whether the modulation of brain rhythms predicts the individual scores obtained in the questionnaires, we computed the correlations between AQ and EQ scores and the modulation of the mu rhythm band in our observation tasks including the whole sample of 30 participants. Only correlations with action clips and manipulable objects were significant; namely: AQ-AC ($r = 0.77$, $P < 0.0001$); AQ-MO ($r = 0.45$, $P < 0.012$); EQ-AC ($r = -0.66$, $P < 0.0001$); and EQ-MO ($r = -0.47$, $P < 0.009$), as Figure 4 illustrates. The only significant correlation obtained in the beta rhythm band was between AQ and AC ($r = 0.56$, $P < 0.001$). Beyond these correlations, there was also an interesting correlation between AC and MO stimuli in the mu band ($r = 0.51$, $P < 0.004$).

Discussion

This research analyzed EEG rhythms in adults with high scores in an autism spectrum scale (AQ), compared to matched controls with low scores in the AQ scale, while

they watched clips of manual actions, manipulable objects, and non-manipulable objects. Several results were remarkable. First, in contrast with low-AQ, high-AQ participants did not show any mu suppression when they observed manual actions, supporting the hypothesis that autism spectrum traits are associated with a functional deficit of the mirror system. Second, unlike the low-AQ group, the high-AQ group did not show mu suppression while observing manipulable objects, indicating also impairment in their affordance system. Third, the low- and high-AQ groups also differed in their beta rhythm response to actions and manipulable objects, confirming, with another neural signature, that high-AQ persons suffer impairment in mirror and affordance systems [Cooper et al., 2013; Dumas et al., 2014; Honaga et al., 2010]. As expected, the two groups did not differ in their neural response to non-manipulable objects (the control stimuli). Finally, there were robust positive correlations between AQ scores and mu modulations by actions and manipulable objects, and negative correlations between EQ scores and mu modulations in such stimuli, suggesting strong associations between our neurobiological measures and self-report measures.

The absence of mu suppression in the high-AQ participants while observing manual actions fits well with previous results obtained in adults with clinical ASD [Bernier et al., 2007; Oberman & Ramachandran, 2007], but conflicts with other studies in the literature that fail to obtain any differential modulation in EEG rhythms between ASD and controls [Fan et al., 2010; Raymaekers et al.,

2009]. Some features of the current study provide a possible explanation for this discrepancy. Rather than using a single repetitive purposeless action (e.g., opening and closing hand) as the action stimulus, in this study participants observed 30 different clips depicting goal-directed manipulation of objects (including tools). Understanding these stimuli involves tracking two-hand coordinated actions (e.g., turning the cap of a bottle) as well as predicting the agent's goals and intentions [Kilner et al., 2007], presumably demanding more mirror neuron resources than simple clips of purposeless hand muscle movements. Some recent experiments confirm that using goal-directed actions as stimuli and asking participants to infer the agent's intentions more likely reduce mu suppression in persons with ASD [Cole et al., 2018]. In our study, we did not ask participants to make intentional inferences or using any other active strategy. However, the use of stereotyped goal-directed actions as observational stimuli was also optimal to reveal the high-AQ person's impairment of mirror neurons.

Although deficits in social interaction have been extensively studied in people with ASD, exploring their relations with objects is a rather neglected issue. Only a few researchers have paid attention to the ASD person's relational deficits with objects [Williams et al., 1999; Loveland & Tunali, 1991]. However, to the best of our knowledge, the perception of object affordances has not been previously explored in persons with autistic traits using EEG measures. Here, we demonstrated for the first time that high-AQ persons show abnormal neural response to objects' manipulability, indicating impairment of their affordance system. This impairment is remarkable, taking into account that our participants were high-functioning individuals, relatively well adapted to the demands of life at university. Also, note that the manipulable objects employed here were ordinary tools (e.g., hair dryer, key, comb, etc.) with strong standard affordances, which in neurotypical participants immediately triggered a motor neural response as indexed by mu and beta desynchronization.

The deficit in the affordance system could have developmental origins. Typically developing children acquire affordances by manipulating objects in a rich interactive social context [Loveland & Tunali, 1991; Williams et al., 1999]. For instance, toddlers learn tool use by observing how adults manipulate them and sharing interactive plays with objects [Deák et al., 2014; Fagard et al., 2016]. But, as stated before, early autism is associated with anomalous exploratory activity with objects [Kaur et al., 2015] and poor monitoring of adults' activities, which in turn could be derived from mirror neuron deficits [Klin, Lin, Gorrindo, Ramsay, & Jones, 2009; Shic et al., 2011; Yang, Rosenblau, Keifer, & Pelphrey, 2015]. It is likely that this early disturbance in social interaction with adults and objects impedes the normal

acquisition of affordances, which persists even in high-functioning adults with nonclinical autistic traits.

The correlational data show that the degree of integrity of the mirror and affordance systems, indexed by mu modulations, predicts AQ and EQ scores. Moreover, the inspection of individual mu data shows that although 14 of the 15 low-AQ participants suppressed mu rhythms while watching actions, only 2 of the 15 high-AQ participants suppressed these rhythms while watching actions. These data allow us to consider that mu modulations by the observation of manual actions and manipulable objects constitute a robust neurobiological marker of high-functioning persons with autism spectrum traits, with potential diagnostic value in clinical contexts. This study does not provide direct evidence of any functional or anatomical relationship between mirror and affordance systems. However, it is remarkable that both systems are indexed by the same kind of modulation of motoric mu and beta rhythms. Also, persons with high-AQ show the same anomalous modulation of these rhythms when they watch both action clips and pictures of manipulable objects, and there was a significant correlation between these stimuli in the mu frequency band.

This study has some limitations that must be overcome in further research. First, we must be cautious about the generalizability of our results. Our participants were high-functioning adults with self-reported autistic traits instead of people diagnosed with clinical ASD. In addition, our sample was biased by gender (10 females and 5 males), contrary to the usual gender ratio of ASD reported elsewhere (at least twice males for each female). Consequently, the neural dynamics associated with the observation of actions and objects reported here do not necessarily correspond to the neural dynamics that could be obtained in clinical populations with ASD. Second, we did not match high- and low-AQ participants in verbal skills, and we cannot rule out that the groups differed in language abilities that could influence their use of verbal encoding strategies during the task (e.g., generating cover verbal descriptions). However, this possibility was minimized by the fact that the task was basically nonverbal, consisting of passively observing videos and pictures for later recognition. Third, some intrinsic characteristic of our stimuli prevent strict matching of their visual features; for instance, our action clips involved motions whereas manipulative and non-manipulative objects were static pictures. Also action clips were more complex, because they included an agent's hands and one or two objects, whereas the other stimuli depicted a single object. These features of stimuli were the price of choosing naturalistic familiar actions and objects, but they could not explain the differential effects between the high- and low-AQ groups. Finally, the possible deficits in the MNS and in the affordance system described here for high-AQ persons, does not rule out that other neural

dysfunctions, such as an impaired theory of mind, may be also responsible of their low social skills.

In sum, we have shown that EEG mu and beta rhythms are signatures of mirror and affordance system activity, because they are suppressed in low-AQ (neurotypical) persons when they observe actions as well as manipulable objects. Most importantly, high-AQ persons do not suppress these motor rhythms in any case (in fact, they enhance their synchronization), clearly indicating difficulties in understanding others' intentions, but also in perceiving objects' functional features. This latter fact demonstrated for the first time that high-AQ persons have abnormal perception of affordances, which extends their relational deficits from the domain of persons to the domain of objects. Further research will be needed to extend and generalize the current findings, by testing brain rhythm modulations in persons diagnosed with ASD when they observe familiar goal-directed actions and objects. It will also be necessary to perform additional studies to know in detail how the affordance system is impaired in ASD. These studies could involve not only EEG measures but also neuroimaging and noninvasive brain stimulation.

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