Children with Autism Spectrum Disorders Have “The Working Raw Material” for Time Perception

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Abstract

The aim of the present study was to investigate whether children with Autism Spectrum Disorders (ASD) have a deficit in time perception. Twelve ASD children of normal intelligence and twelve typically developing children (TD) - matched on sex, chronological age, and mental age – performed four temporal bisection tasks that were adapted to the population. Two short (0.5 to 1 s and 1.25 to 2.5 s) and two long duration ranges (3.12 to 6.25 s and 7.81 to 16.62 s) were thus examined. The findings suggested that the perception of time in bisection is not impaired in ASD.

Introduction

Autism spectrum disorders (ASD) are a group of neurodevelopmental disorders whose etiology is as yet poorly understood [1], [2]. Nevertheless, ASD have a huge impact on three domains of competence that constitute the triad criteria used for the diagnosis of autism (DSM-IV-TR; American Psychiatric Association 2000; ICD 10; World Health Organization 1992). First, individuals with ASD show a marked impairment in social interaction, leading to a restricted and impaired ability to share common experiences with others. Second, their modes of communication, both verbal and non-verbal, are impaired. Language development is retarded and/or language is used inappropriately in pragmatic contexts [3]. The decoding of important communicative signals such as emotional facial expressions or prosody is also disrupted [4–6]. Third, individuals with ASD present stereotyped and repetitive behaviors, and restricted centers of interest.

Clinical reports suggest that subjects with autism have another major deficit - a timing deficit [7–9]. Therefore, the ability to time events and actions is crucial for the adaptation of behavior to the physical and social environment [10–13]. Indeed, the ability to process time correctly ensures that social interaction with others progresses harmoniously and permits, for example, intersubjectivity at an early stage of development [14], [15]. It allows children to understand and learn the dynamic of language (i.e. turn-taking) and non-verbal social cues [16]. It also makes it possible to predict the timing of events. In this domain, some researchers have suggested that autistic children often produce repetitive behaviors to compensate for their difficulties in predicting incoming events [17]. Taken together, the diagnostic criteria and the clinical reports have therefore prompted speculation that difficulties in processing time might be an important factor in autistic disorders and might explain a part or even all of the primary symptoms [17].

Over the last decade, a relative small number of studies has examined the ability to process time information in ASD individuals with classical timing tasks, for a review see [18]. However, the results of these studies are inconsistent and in some cases contradictory. Using a temporal reproduction paradigm, Szelag et al. [25] showed that children with autism were totally unable to reproduce visual and auditory durations, and concluded that such children have a major deficit in duration judgment. Although neither Martin et al. [23] nor Gowen and Miall [21] found that ASD children had major difficulties in processing time, they did observe that these children were less accurate than control subjects in a time reproduction task and a temporal discrimination task (i.e. temporal generalization task) respectively. In the same way, Maister and Plaisted-Grand [22] found children with ASD less accurate than controls in duration reproduction. Using a generalization task, Falter et al. [20] also found a reduced interval timing sensitivity in ASD participants. In a temporal bisection task, in which the participants had to categorize durations as more similar to a short or a long anchor duration, Allman et al. [19] showed that individuals with ASD tended to overestimate durations although no specific impairment of their time sensitivity was observed. In contrast, Wallace and Happé [26] obtained similar performance in individuals both with and without autistic disorders in three different temporal tasks: verbal time estimation, time production and time reproduction. These authors therefore concluded that time perception in children and adolescents with autism is intact. Similarly, Mostofsky et al. [24] showed that people with autism were as accurate as control subjects in their explicit judgments of temporal intervals. Therefore, faced with this lack of consistency in the results of studies of time perception in autistic individuals, the aim of our study was to add results in this research area by using a bisection task that has not been often used up until now except by Allman and collaborators [19], and by...
examining a wide range of durations from a few hundreds of milliseconds to several seconds.

According to the most popular model of time processing, elaborated by Gibbon, Church and Meck [27] in the framework of the Scalar Expectancy Theory (SET) [28], the efficient processing of time results from the interaction between three mechanisms which are involved at different levels of the information processing: a clock, memory processes and decision processes. The clock is thought to consist of a pacemaker that emits pulses which pass into an accumulator via a switch which closes when a duration has to be timed. The functioning of the pacemaker is known to be principally arousal-based [29–33], and that of the switch attention-based [34]. The internal clock system is thus considered to be the primary level at which the representation of time is formed, before higher-level cognitive processes – memory and decision – intervene. However, a growing body of literature suggests the processing of durations shorter than 1–2 s does not involve the same mechanisms as that of longer durations. Short durations are thought to require automatic processes, whereas long durations involve controlled processes [35–38]. Because the processing of time requires the ability to maintain attention throughout the entire duration to be timed [39], the processing of long durations (>2 s) are more demanding both in terms of working memory and attention than the processing of shorter ones. It’s interesting to note that previous studies in people with ASD have tested a wide range of durations, below or near a second [20], [21], [24], less than eight seconds for others [19], [22], [23], [25] and until forty-five seconds for another [26]. However, findings were discrepant whatever the durations used. In addition, the SET model of temporal processing involves what is called the scalar property, i.e., the fact that the variability of time estimates increases proportionally to the mean duration value to be timed. In others words, time performance variability constitutes a constant across a relative scale of durations [40], [41]. Only two studies have examined this mathematical propriety of time in ASD populations, but each leads to a different conclusion, although the two studies used, respectively, long and short durations. Using long durations (i.e. 2 to 8 s) Allman et al. [19] found that the scalar property was not fully respected in a bisection task performance by the group of ASD people, whereas Falter et al. [20] found it preserved in a generalization task performance using shorter durations (i.e. 0.5 to 1.5 s).

Numerous studies have shown a correlation between the ability to process time and intellectual efficiency [42], [43], the individuals with low IQ having low sensitivity to time. In particular, ASD is often associated with mental retardation (DSM-IV-TR). Consequently, the difference in timing performance between ASD and control groups might be mainly due to differences in general cognitive functioning rather than to a deficit in temporal processing mechanisms per se [19], [24]. In support of this, Allman and collaborators [19] indicate in ASD children a significant correlation between an index of time sensitivity and subjects’ scores in tasks reflecting language and working memory capacities. Consequently, if the mental age of the children with autism is the same that their age control group children, we might suppose that differences in temporal performance would be reduced. In addition, the poor performance found in children with autism might be always obtained if they are insufficiently motivated to do a particular activity. Indeed, it is well known that ASD children have restricted fields of interest and are not motivated when the task that they are required to do lies outside of their field of interest [44]. Therefore, in our study we used high functioning children with autism, characterized by no mental retardation, compared with mental age-matched typically developing children. Moreover, in an attempt to maintain ASD children’s interest in the task and promote a high level of performance, we choose to use reinforcements, i.e. a gift, that play a critical role in motivation [44], [45].

The purpose of the present study was thus to test children with ASD using the temporal bisection task which has frequently been administered to children [46–49], and that is considered to be a “pure” perceptual task [49], that minimizes the intervention of higher cognitive processes, i.e. memory [46], [50], [51]. In the temporal bisection task, participants are initially presented with a short and a long anchor duration. They then perform a number of trials and have to judge whether the probe durations (equal to the anchor durations or representing intermediate values) are more similar to the short or the long anchor duration. Each participant performed two sets of bisection tasks: (1) a first set of two bisection tasks examined short duration ranges, i.e. 0.5/1 s and 1.25/2.5 s, (2) another set of bisection tasks examined long durations ranges, i.e. 3.13/6.25 s and 7.81/16.63 s. As previously mentioned, we used these four duration ranges in order to investigate the scalar properties of time with short and the long durations in the ADS children compared to control children, but also to compare their performance with duration ranges that differ in the demands placed upon attention and working memory [52], [38]. Moreover, we slightly modified the bisection task to increase and maintain the children’s interest throughout the task [44], [45]. First, in order to increase motivation, each child was told that they would receive a gift at the end of the experiment. A photo of this gift was presented and gradually revealed during the bisection task, with the gift being given at the end of the session. This gift was chosen for each child as a function of their specific interests as reported by their parents. Second, tasks presented to children with autism have to be well structured in order to improve their understanding of what is expected of them and encourage their self-control [53], [54]. Consequently, in order to show the children how many trials they had completed in the temporal bisection task and how many remained, we presented a set of visual markers (empty circles) representing the trials and these were filled in one-by-one as the child completed the individual trials.

**Methods**

**Participants**

Seventeen ASD children were first recruited from various associations. Children and parents gave written informed consent to participation as required by the Clermont-Ferrand Sud-Est VI Statutory Ethics Committee (CPP), which approved the present study. Criteria for exclusion were mental retardation, absence of language, the subject attrition during all bisection tasks, and inability to perform the training phase of the proposed procedure correctly. The final group of children with autism spectrum disorder (ASD) comprised twelve normal intelligence male children, aged from 9 to 17 years. Nine were diagnosed with Asperger’s Syndrome (AS) and three as exhibiting High-functioning autism or non-specified Pervasive Developmental Disorder (PDD). All ASD subjects had a formal diagnosis made by experienced independent clinicians before the study and based on DSM-IV criteria. Twelve volunteer typically developing children (TD), aged from 8 to 16 years, were recruited for the control group and the group means were matched on sex, chronological age (CA), and mental age (Table 1). Table 1, for each group of participants, shows the different composite scores from the Wechsler Intelligence Scale for Children (WISC-IV): Verbal Comprehension index (VCI), Perceptual Reasoning Index (PRI), Working Memory Index (WMI), Processing Speed Index
Table 1. For each group of children (ASD: Autism Spectrum Disorders; TD: Typically Developing), means and standard deviations for each composite score from the Wechsler Intelligence Scale for Children (WISC-IV): Verbal Comprehension index (VCI), Perceptual Reasoning Index (PRI), Working Memory Index (WMI), Processing Speed Index (PSI), Full Scale IQ (FSIQ).

|          | ASD            | TD             |
|----------|----------------|----------------|
| CA       | 13.00          | 13.21          |
| VCI      | 109.25         | 101.63         |
| PRI      | 100.87         | 102.27         |
| WMI      | 91.37          | 100.81         |
| PSI      | 83.25          | 101.45         |
| FSIQ     | 94.37          | 101.45         |

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(PSI), Full Scale IQ (FSIQ). There were no significant difference between the groups on either chronological age (CA) (Mann-Whitney, $U(65) = -404; p = .71$), nor any composite score, all $p > .1$.

Material

The children were individually tested at home in a quiet room. Visual paper-based material was used to explain the various stages involved in the bisection task procedure. Consequently, screenshots were printed indicating twenty-one circles representing the different trials in a block. These were originally empty and were filled one-by-one as the trials progressed throughout the block. When a block of twenty-one circles had been filled (twenty-one trials completed), the document revealed a picture of a part of the personal gift that each child was to receive at the end of the session. For the bisection task, a PC was used to control the experimental events using E-Prime software (1.2, Psychology Software Tools, Pittsburg, PA). The temporal stimulus was a blue 7 x 3 cm rectangle presented in the center of the computer screen. The picture presenting the twenty-one circles appeared on the computer screen between each trial. In addition, in the training phase of the bisection task, pictures of red and green lights were used as feedback, with the former indicating incorrect and the latter correct discrimination of the probe durations.

Procedure

Each child completed four bisection sessions, for each duration range respectively, with the session order being counterbalanced across subjects who performed two sessions a day to avoid fatigue. Two bisection tasks corresponded to short duration ranges (< 2 s). Range 1: the short and the long anchor durations were 0.50 and 1.0 s and the probe durations 0.50, 0.58, 0.67, 0.75, 0.83, 0.92 and 1.0 s; Range 2: the anchor durations were 1.25 and 2.5 s and the probe durations 1.25, 1.46, 1.67, 1.87, 2.083, 2.29 and 2.5 s. Two other bisection tasks corresponded to long duration ranges (> 2 s). Range 3: anchor durations of 3.13 and 6.25 s and probe durations of 3.13, 3.65, 4.17, 4.69, 5.21, 5.73 and 6.25 s; Range 4 used 7.81 and 16.63 s as anchor durations, and 7.81, 9.12, 10.42, 11.73, 13.03, 14.33 and 16.63 s as probe durations. In each bisection session, the child had to estimate whether the presentation time of the stimulus was more similar to the previously presented short or long anchor stimulus duration. Responses (i.e. short or long) were given verbally, with the experimenter then pressing the corresponding response key, in order to reduce motor skills’ impact on performance. Each bisection task consisted of three phases. In the first phase, the short and the long anchor durations were presented three times each. Then, in a second phase, the participants were trained to respond “Short” or “Long” on eight trials, four for each anchor duration. In this training phase, feedback was given in the form of the green or red light depending on whether the provided response was correct or not. When the participants responded correctly on 75% of the trials, the training terminated and the third (test) phase started. This consisted of three blocks of twenty-one trials each (i.e. sixty-three trials in total), with the seven probe stimulus durations being presented three times in each block. At the beginning of each block, the anchor durations were again presented three times each. Between each trial, the picture of the twenty-one circles with one more filled appeared on screen. In addition, between each block, a picture of a part of the present was revealed to the child using the visual printed material.

Results

As mentioned in introduction, because shorter and longer duration ranges involve different kind of processes [35–39], and in order to clarify this section, results are presented first for the two short duration ranges, and second for the two long ones.

Short Duration Ranges (Range 1: 0.50/1.0 s – Range 2: 1.25/2.5 s)

An overall ANOVA, with two within-subjects factors (2 durations ranges and 7 stimulus durations per range), and group (ASD vs. TD) as a between-subjects factor, was run on the proportion of long responses (see Figure 1). This analysis yielded neither a significant main effect of group, $F(1, 22) = .11, p = .74$, nor any interaction involving this factor, all $p > .1$. There was only a significant main effect of stimulus duration, $F(2, 57, 56.59) = 160.45, p < .001$, and a significant main effect of duration range, $F(1, 22) = 5.87, p = .02$. This finding indicates that the proportion of long responses increased with stimulus duration irrespective of group (with or without autism). This suggests that children with ASD seem to be able to discriminate probe durations in the same way as other children.

To evaluate temporal discrimination in ASD children in greater detail, we calculated three supplementary indexes: BP, DL and WR (Table 2). These three indices were derived from the intercept and the slope of the logarithmic regression that significantly fitted the individual bisection functions for each subject. The Bisection Point (BP) corresponds to the duration value at which short and long responses occur with equal frequency ($p (\text{long}) = .50$). Mann-Whitney two by two comparisons showed that the BP values did not differ between groups for either ranges (Range 1: $U(51) = -92, p = .38$; Range 2: $U(54) = -74, p = .49$). The Difference Limen (DL) is equal to half the difference between the stimulus duration giving rise to 75% of “long” responses and the duration giving rise to 25% of such responses. The DL is thus an index of absolute time sensitivity and indicates the shortest discriminable difference between the employed stimulus durations. We found no difference in DL values between the groups of subjects for either of the two ranges examined (Range 1: $U(47) = -1.17, p = .26$; Range 2: $U(51) = -92, p = .38$). In sum, the minimum observable temporal difference was similar in the children with and without autism.

The Weber Ratio (WR) corresponds to the DL divided by the BP. The WR is also a parameter of time sensitivity. A lower Weber Ratio value indicates a better sensitivity to time [48]. However, compared to the DL, it provides an index not of absolute but of
relative sensitivity to time. Moreover, it allows us to test the scalar property of variance, which is a sort of Weber’s Law [28].

According to this property, the variability in perceived time increases proportionally to the mean duration value to be timed. Consequently, the WR, which is considered to be a type of coefficient of variation (DL/BP), should remain constant across duration ranges if the scalar property holds [40], [55]. An ANOVA was therefore run on Weber Ratio values with duration range as a within-subjects factor, and group as a between-subjects factor. This statistical analysis revealed no main effect of duration range, $F(1, 20) = .44, p = .51$, nor of group, $F(1, 20) = .1, p = .76$, and no interaction involving these two factors, $F(1, 20) = .000$, 

Figure 1. Mean proportion of “long” responses plotted against stimulus durations, for both ASD and TD participants, and for duration range 1 (upper panel), and duration range 2 (lower panel).

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Finally, to test the scalar property in ASD time performance in addition to the statistical examination of Weber Ratio values, we tested the superimposition of the psychophysical functions for the different duration ranges. The proportion of “long” responses for the two duration ranges was therefore plotted against a relative duration scale by dividing each stimulus duration by the corresponding BP for the duration range used [50]. Figure 2 shows the psychophysical functions obtained with this method, and indicates that the ASD children’s functions for the two duration ranges superimposed consistently well, consistent with the scalar properties of variance.

Long Duration Ranges (Range 3: 3.13/6.25 s – Range 4: 7.81/16.63 s)

A 2 × 7 × 2 ANOVA was conducted on the proportion of long responses. The main effect of stimulus duration was significant, F(3.47, 72.42) = 142.59, p < .001, and indicated that the proportion of long responses increased with the stimulus duration values. Neither the between-group effect, F(1, 22) = .21, p = .65, nor duration range effect, F(1, 22) = .19, p = .38, nor any interaction involving these factors were significant (all ps > .1). As Figure 3 illustrates, these results suggest that ASD and TD children performed equally well when asked to classify the different stimulus durations in a bisection task, even when long durations were used.

As for short duration ranges, analyses were conducted on the BP, DL and WR values calculated as previously described (see values in Table 3). Planned comparisons demonstrated that the performance of the ASD and TD groups did not differ significantly for the 3.13/6.25 s duration range when the BP was used (U(59) = 2.75, p = .48) nor when the DL was analysed (U(71) = 95, p = .98), and the same picture was obtained with the 7.81/16.63-s duration (BP: U(66) = 0, p = 1; and DL: U(57) = .55, p = .61). These findings confirmed that the two groups had similar temporal discrimination abilities. Moreover, relative sensitivity to time was examined in the same way as for short ranges using a 2 × 2 ANOVA run on the WR values. This revealed no significant effect of duration range, F(1, 21) = 2.77, p = .11, group, F(1, 21) = .05, p = .82, or two-way interaction, F(1, 21) = .12, p = .73. In addition, the psychophysical functions

Table 2. Mean bisection point (BP), difference limen (DL), and Weber ratio (WR) for the short (0.5/1.0-s) and the longer (1.25/2.5-s) duration ranges in children with autistic spectrum disorder (ASD) and typically developing children (TD).

| Group | Durations range 1 (0.5 to 1 s) | Durations range 2 (1.25 to 2.5 s) |
|-------|-------------------------------|---------------------------------|
|       | BP Mean | BP SD | DL Mean | DL SD | WR Mean | WR SD | BP Mean | BP SD | DL Mean | DL SD | WR Mean | WR SD |
| ASD   | 728.6   | 67.74 | 140.3   | 50.97 | .19     | .05   | 1781    | 181.5 | 378.7   | 182.1 | .21     | .09   |
| TD    | 778.5   | 113.0 | 153.9   | 50.51 | .19     | .04   | 1696    | 195.9 | 343.3   | 62.22 | .21     | .05   |

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Figure 2. Superimposition of the psychophysical functions for duration range 1 (R1) and duration range 2 (R2) in ASD participants.

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in the two duration ranges (see Figure 4) for ASD participants superimposed well, thus confirming that their time performance exhibited the scalar variability property. In sum, analyses revealed that ASD children’s time perception performance exhibits similar properties, i.e. discriminability and sensitivity, as typically developing children, even for durations longer than three seconds.

Short and Long Duration Ranges Comparison

Finally, because the same subjects took part in all sessions, we examined whether sensitivity to time was constant across the short and long duration ranges by performing an ANOVA on mean WR values for all four duration ranges. This analysis revealed neither a main effect of duration range, \( F(2.26, 43.1) = 2.46, p = .09 \), nor of group, \( F(1, 19) = 1.62, p = .22 \), nor any interaction between the two factors, \( F(3, 57) = .56, p = .64 \). These findings show that the time perception performance of
both groups of children exhibited the scalar property across both the examined duration ranges, short and long.

**Discussion**

Clinical reports have suggested that individuals with autism spectrum disorder have difficulties in conceptualizing the passage of time and in controlling the time taken to achieve an objective [7], [56], [57]. Despite this, the findings reported by experimental research have been contradictory, with some studies concluding that ASD subjects exhibit a deficit in time perception or atypical temporal behavior [19–23], [25], whereas other results have failed to indicate any time atypicalities [24], [26]. Using a bisection task, our results demonstrated that the children with autism spectrum disorder but without mental retardation had a high ability to discriminate durations and that they exhibited no more variability in their time judgements than control children for both the short (<2 s) and long (from 2 to 17 s) duration ranges. In addition, their time discrimination exhibited the fundamental scalar timing properties found in both humans and animals [58], [28]. ASD children’s sensitivity to time (WR) was constant across different duration values that cover a large range of durations (i.e. 0.5 to 16.63 s), consistent with Weber’s law. In sum, our study, which used a temporal bisection task, provided evidence indicating that the perception of time in people with autism might be intact. Our conclusion is thus entirely consistent with conclusions previously presented by Mostofsky et al. [24] and Wallace and Happé [26]. Concerning the scalar property, our findings are consistent with the work of Falter et al. [20] who found that the Weber’s Law hold for the timing in ASD participants, but contradictory to Allman et al.’s results [19]. Nevertheless, as highlighted by the former, a main difference between these two studies is that, in Allman and colleagues’ work, ASD participants were low IQ. A substantial body of research has described a link between intellectual efficiency and the ability to process time [42], [43], [59]. Consequently, the present findings suggest that it is necessary to exercise caution about the temporal performance of pathological individuals, when low IQ may be a mediating factor in performance. The use of HFA and AS scores to define a population without mental retardation who are, moreover, matched on a mental efficiency with control participants, therefore

| Group | Durations range 3 (3.12 to 6.25 s) | Durations range 4 (7.81 to 15.62 s) |
|-------|-------------------------------|----------------------------------|
|       | BP Mean SD  | DL Mean SD  | WR Mean SD  | BP Mean SD  | DL Mean SD  | WR Mean SD  |
| ASD   | 4459 562.5 | 997.3 368.1 | .22 .07     | 11300 1791 | 2724 1534  | .23 .10     |
| TD    | 4644 473.0 | 950.8 211.3 | .20 .04     | 11011 1639 | 2563 664.5 | .23 .05     |

**Figure 4. Superimposition of the psychophysical functions for duration range 3 (R3) and duration range 4 (R4) in ASD participants.**

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seems to be a viable way to study autism per se. Specifically, our study suggested that, with this population without mental retardation, autism would not be associated with deficits in the perception of durations in the range of hundreds of milliseconds or seconds.

However, the question arises of how to explain the discrepancy of results between studies examining time perception in autism, beyond the general IQ problem. It is interesting to note that the time perception can be considered as task-dependent. Indeed, the different temporal tasks used in different studies with ASD participants (i.e. bisection, reproduction, production, generalization) call upon certain cognitive processes (e.g. memory, decision) at different stages of time processing [60], [61], [46], [51]. Within this framework, previous studies examining time perception in people with autism were heterogeneous in terms of the tasks used. This may be a source of discrepancy between the results of different studies. By way of conclusion, we can propose that the temporal deficits observed in autistic individuals in previous studies did not result from a specific deficit in the mechanism involved in producing the “raw material” for the processing of time, i.e. an internal clock mechanism, but rather from other cognitive functions that interfere with the final time judgment, and that were required to a greater or less extent as a function of the procedures used. According to this account, the impairments in time processing observed in previous studies might be attributable to limitations to cognitive processes (e.g., attention, memory, motor or decision-related abilities) the involvement of which we have tried to minimize in our study.

As far as attention is concerned, although many studies of ASD have examined attentional capacities of such individuals, no clear consensus has as yet been reached. However, it is interesting to note that attention-deficit hyperactivity disorder symptoms often seem to co-occur in ASD [62], [63]. In addition, a number of recent studies have revealed that variation in the attention capacities of children, as evaluated using neuropsychological tests, explains a large part of the variability in their time sensitivity as a function of age [64], [65], [59], [66]. Moreover, a significant body of literature has linked attention difficulties in autism to the function of age [64], [65], [59], [66]. Moreover, a significant body of literature has linked attention difficulties in autism to the function of age [64], [65], [59], [66]. Moreover, a significant body of literature has linked attention difficulties in autism to the function of age [64], [65], [59], [66].

To conclude, autism spectrum disorder can be explained at different levels of information processing, which is why the investigation of the specific abilities of such individuals is so challenging, in particular considering timing abilities. Moreover, the assessment of timing abilities appears to be of particular interest when consider interaction deficit in autism, that is their problem in properly regulating social interactions, and the fundamental link between timing and both verbal and non-verbal communication [19], [20]. Within this perspective, our study therefore extends the literature by demonstrating that ASD children seem to have the raw material for the discrimination of durations. However, further work is necessary to clarify the specific contexts in which autistic children’s timing may be impaired and why.

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**Author Contributions**

Conceived and designed the experiments: SG SDV PC. Performed the experiments: MF CH. Analyzed the data: SG SDV. Contributed reagents/materials/analysis tools: SG. Wrote the paper: SG SDV.
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