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Signs of enhanced formation of gist memory in children with autism spectrum disorder – a study of memory functions of sleep

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Background: Autism spectrum disorder (ASD) is characterized by impaired cognitive and social skills, including emotional dysregulation, and symptoms have been suspected to partly arise from impaired formation of memory representations regulating these behaviours. Sleep, which is subjectively impaired in ASD, is critical for forming long-term memories and abstracted gist-based representations. We expected a generally reduced memory benefit from sleep in children with ASD, and a diminished enhancement of gist representations, in particular. **Methods:** We compared effects of sleep on memory consolidation between boys (9–12 years) with ASD ($n = 21$) and typically developing (TD, $n = 20$) boys, matched for age and IQ, in a within-subjects crossover design. We employed an emotional picture recognition task and the Deese–Roediger–McDermott (DRM) word list task for assessing gist memory formation in the emotional and nonemotional domain, respectively. Learning took place before retention intervals of nocturnal sleep and daytime wakefulness, and retrieval was tested afterwards. **Results:** Surprisingly, on the DRM task, children with ASD showed an enhanced sleep-dependent formation of gist-based memory (i.e. more recall of 'critical lure words' after sleep compared to wakefulness) than TD children, with this effect occurring on top of a diminished veridical word memory. On the picture recognition task, children with ASD also showed a stronger emotional enhancement in memory (i.e. relatively better memory for negative than neutral pictures) than TD children, with this enhancement occurring independent of sleep. Sleep polysomnography was remarkably comparable between groups. **Conclusions:** Children with ASD show well-preserved sleep-dependent memory consolidation. Enhanced gist memory formation in these children might reflect a compensatory response for impairments at earlier stages of memory processing, that is during encoding. **Keywords:** Autism spectrum disorder; gist abstraction; memory consolidation; sleep; emotional memory; Deese-Roediger-McDermott.

Introduction

Autism spectrum disorder (ASD) is a neurodevelopmental disorder hallmarked by deficits in social communication and interaction (American Psychiatric Association, 2013), which includes deficits in emotion regulation (Berkovits, Eisenhower, & Blacher, 2017; Samson, Wells, Phillips, Hardan, & Gross, 2015), as well as specific deficits in multiple cognitive domains (Brunsdon et al., 2015) – even if IQ is in the normal range (high-functioning ASD). Patients show distinctly reduced abilities to recognize people's emotions and to form memories for emotion-related stimuli (Boucher, Mayes, & Bigham, 2012). Memory impairments in ASD appear to be more focused on the social and emotional domain than the retention of neutral stimuli. In several studies, adults with ASD expressed a smaller benefit for recalling emotional compared to neutral memories than healthy controls (Deruelle, Hubert, Santos, & Wicker, 2008; Gaigg & Bowler, 2008). Yet, memory deficits in ASD might also extend to nonemotional neutral stimuli. Thus, although children with ASD in contrast to typically developing (TD) children showed intact explicit recall of words after a 24-hr retention interval, they did not appear to integrate the newly learned words into existing semantic knowledge (Henderson, Powell, Gaskell, & Norbury, 2014). Similarly, on the Deese–Roediger–McDermott (DRM) task, adult ASD patients recalled diminished proportions of gist-based memories compared to healthy controls (Beversdorf et al., 2000; Wojcik et al., 2018, but see Gaigg & Bowler, 2009; Hillier, Campbell, Keillor, Phillips, & Beversdorf, 2007). Gist-based memory in the DRM task refers to the recall of the 'critical lure word' for a list of words that has been learnt, which is strongly associated with all words of the list but is actually not in the list (Deese, 1959; Roediger & McDermott, 1995). In summary, consistent with the original 'weak central coherence' account of ASD (Happé & Frith, 2006), assuming a basic deficit in ASD in the processing of globally constituted meaning, the available evidence suggests that ASD patients are less capable of forming abstracted memories for the gist of experienced information (Plaisted, 2001). This impairment in gist

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memory formation might particularly hold for the abstraction of emotionally salient information but might pertain also to gist abstraction processes during the formation of neutral memories.

Sleep supports memory consolidation in adults and children (Ashworth, Hill, Karmiloff-Smith, & Dimitriou, 2014; Diekelmann & Born, 2010; Prehn-Kristensen et al., 2009). In addition to strengthening memory representations, sleep promotes qualitative transformations of the representations. These include the abstraction of regularities hidden in complex stimulus materials (Wagner, Gais, Haider, Verleger, & Born, 2004; Wilhelm et al., 2013), and of gist information in the DRM task (Diekelmann, Born, & Wagner, 2010; Payne et al., 2009). The role of sleep for gist abstraction processes might be even more pronounced in children than in adults (Friedrich, Wilhelm, Born, & Friederici, 2015; Friedrich, Wilhelm, Mölle, Born, & Friederici, 2017; Wilhelm et al., 2013).

Similarly, sleep has been found to promote the preferential consolidation of emotional over neutral memories in adults (Hu, Stylos-Allan, & Walker, 2006; Payne, Stickgold, Swanberg, & Kensinger, 2008) and children (Bolinger, Born, & Zinke, 2018; Prehn-Kristensen et al., 2009). The formation of abstracted memory representations during sleep is thought to be achieved by a system consolidation process, where representations temporarily stored in hippocampal networks are repeatedly reactivated during slow wave sleep (SWS) and thereby gradually become transformed and redistributed to neocortical long-term storage sites (Dudai, Karni, & Born, 2015; Lewis & Durrant, 2011).

Memories regulate behaviour, and it has been proposed that cognitive symptoms in children with ASD are partly based on impairments of consolidation processes during sleep (Femia & Hasselmo, 2002). ASD can be accompanied by subjectively reported alterations of sleep (Richdale & Schreck, 2009); using objective sleep physiology measures shorter total sleep time (TST, Buckley et al., 2010), less rapid eye movement (REM) sleep (Buckley et al., 2010; Maski et al., 2015), as well as reduced spindle density and duration (Farmer et al., 2018; Tessier et al., 2015), have been found. Yet, the findings in children with ASD are very variable. Moreover, research investigating sleep-dependent memory consolidation in children with ASD is sparse (Maski et al., 2015), particularly with a focus on gist abstraction processes during consolidation. Here, we compared sleep-dependent memory formation in high-functioning boys with ASD and TD boys. We used an emotional picture recognition task and the DRM word list task to scrutinize the effects of sleep on processes of gist abstraction during consolidation of emotional and nonemotional stimuli, respectively. Our main hypothesis was that sleep in children with ASD would be less effective in forming abstracted memories; that is, the sleep-to-wake benefit for the proportion of gist memories was expected to be generally lower in children with ASD than TD children, particularly for the emotional domain. We expected that alterations in sleep physiology in children with ASD would be related to their reduced ability to form abstracted memories.

Methods

Participants

Twenty-two boys with ASD and 21 TD boys (age range: 9–12 years, IQ within normal range) from Baden Württemberg, Germany, participated in the study. Due to the higher prevalence of ASD in males than females and to keep the groups homogenous in order to reduce variance, we opted to only include boys in the study. The resulting sample comprised 21 ASD and 20 TD boys, after data from one child with ASD and one TD child had to be excluded, due to insufficient sleep in the experimental night (> 40% awake) and napping in the Wake condition, respectively. Exclusion criteria for all participants were an IQ below 85 (Culture Fair Intelligence Test-20-R, Weiß, 2008), severe physical illness, and hearing or vision problems. Additionally, TD control participants were excluded if the administered clinical questionnaires and diagnostic interview (Kiddie-Sads-Present and Lifetime, Delmo, Weiffenbach, Gabriel, Stadler, & Poustka, 2000) indicated a psychiatric disorder. All children in the ASD group had a clinical ASD diagnosis according to the DSM-5 criteria and met the cut-off scores of the Autism Diagnostic Observation Schedule (Poustka et al., 2015) and/or the Autism Diagnostic Interview-Revised (Bölte, Rühl, Schmötzer, & Poustka, 2006). Nine children with ASD had comorbidities (Table S1). The presence of a comorbid diagnosis did not predict the outcome of any memory measures (all $R^2 < .08$, all $F(1,18) < 1.49$, all $p > .23$). Three of the 21 participants with ASD took medication (atomoxetin, $n = 1$; methylphenidat $n = 2$), but none of the children of the TD group did. As expected, children with ASD scored higher on several clinical questionnaire measures, including attention-deficit/hyperactivity symptoms, depressive symptoms, sleep and behavioural problems, and showed lower working memory performance (see Table S2 for participants' characteristics and clinical measures).

Children with ASD were recruited by the autism outpatient clinic and the ASD training programme at the Department of Child and Adolescent Psychiatry, University Hospital of Tübingen. Age-matched control participants were recruited through notifications via the University's email system and the database of the Institute of Medical Psychology and Behavioural Neurobiology. The study was approved by the ethics committee of the Faculty of Medicine of the University of Tübingen. All participants and their parents gave written informed consent after an initial interview and briefing on the study. For their voluntary participation, participants received a 30 € gift card and 70 € as monetary compensation.

Procedure

During the first pre-experimental session, participants and their parents were informed about the study procedures in detail and filled out the clinical questionnaires. Additionally, the clinical interview and IQ test were conducted. Children received a dummy-recording system with electrodes that they were asked to apply for a night (at home) prior to the experimental night in order to adapt to sleeping with electrodes. None of the parents and participants reported any problems using the dummy-recording system (and only two parents reported to have used the dummy system in an additional night).

All experimental sessions were carried out at the participants' homes. Each participant completed a Sleep and a Wake condition (at least 2 weeks apart), with the order of conditions balanced across participants. Each condition consisted of an Encoding and a Retrieval session (Figure 1A).

In the Encoding session (duration ~1 hr), children first performed the picture recognition task followed by the DRM word list task. Participants were aware that they would be retested on these tasks in the Retrieval session (in the same order). All sessions included additional control tasks that were performed before and between the memory tasks, respectively. The Wake condition started in the morning (~1 hr after awakening) with the Encoding session and continued (~11 hr later) in the evening with the Retrieval session. In the meantime, participants spent the day with their usual activities, but were asked not to nap, to avoid any physically or mentally stressful activities, and not to use a computer, television, smartphone or tablet (in order to minimize possible interference with the picture recognition task). Adherence to these instructions was assured by a final interview.

In the Sleep condition, the Encoding session took place in the evening, starting 3 hr before the child's habitual bedtime. The children were prepared for polysomnography recordings, and after completion of the tasks, they went to bed, lights were turned off, and the sleep recording started. The next morning, the Retrieval session started one hour after the children woke up.

Picture recognition task

The picture recognition task was used to assess effects of sleep on recognition memory for emotionally negative and neutral pictures in children. We adapted the task from Prehn-Kristensen et al. (2009) and Bolinger et al. (2018) who have shown the sensitivity of the task to the effects of sleep on memory consolidation in 8- to 13-year-old children. The task required the participants to rate each picture presented during Encoding based on their current feelings (arousal and valence ratings on the Self Assessment Manikin Scale, SAM, Bradley & Lang, 1994, see Figure 1B for a detailed description of the task). Average ratings of valence and arousal were calculated for negative and neutral pictures, separately.

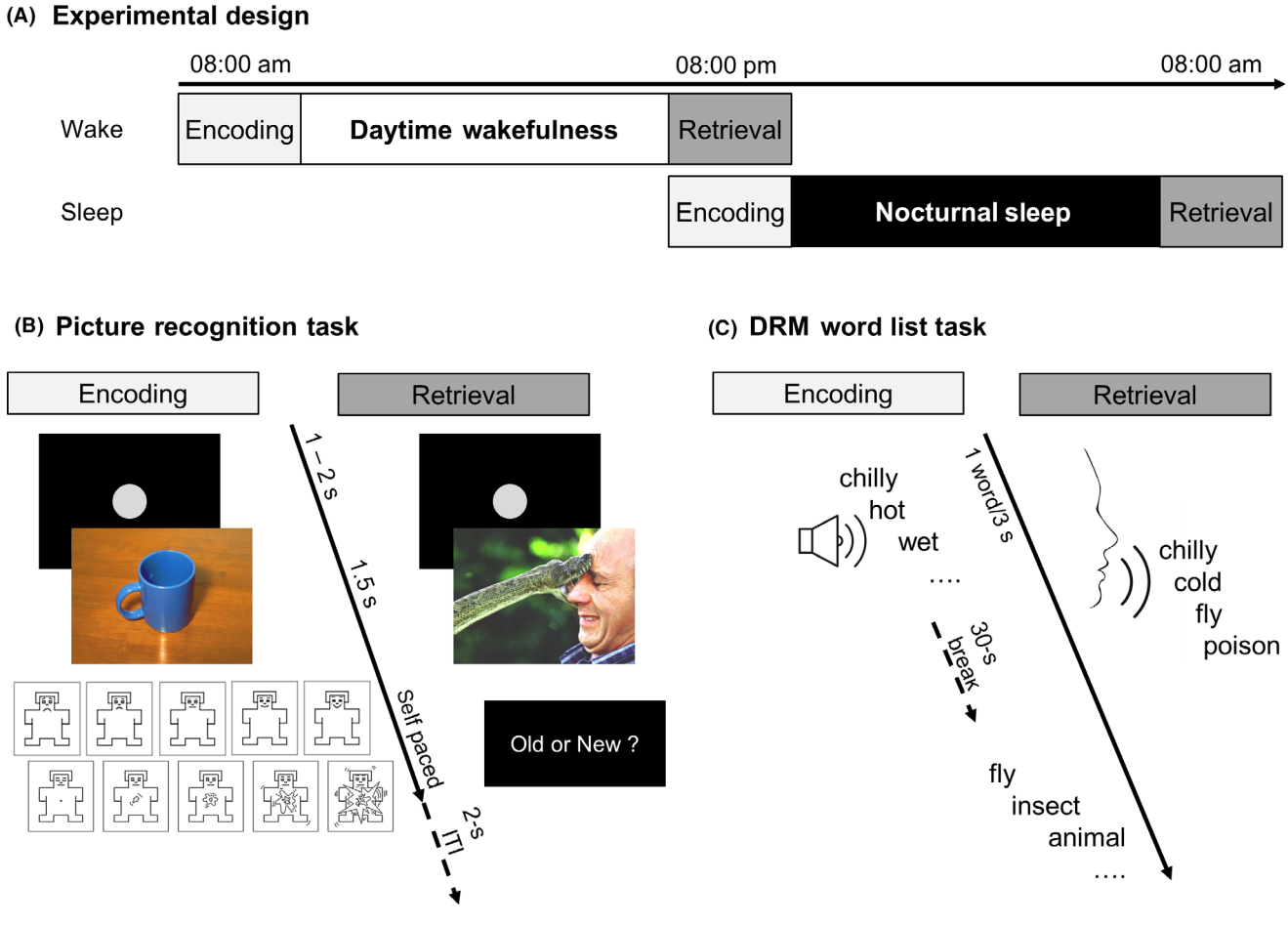

Figure 1 (A) Experimental design. Each of the ASD (n = 21) and TD children (n = 20) was tested on a Sleep and a Wake condition according to a within-subject crossover design. In the Wake condition, Encoding took place between 8:00 am and ~ 9:00 am, then a ~11-hour period of daytime wakefulness followed, and then, Retrieval was tested. In the Sleep condition, Encoding took place between 8:00 pm and 9:00 pm and then an ~11-hour period of nocturnal sleep followed. Retrieval started 1 hr after the child woke up. The Encoding and Retrieval phases comprised testing on two tasks, first a picture recognition task and then a DRM word list task, which was separated by a ~10-min interval. (B) Picture recognition task. During Encoding, children were presented with 72 neutral and 72 negative pictures, which they had to rate based on their current feeling (arousal and valence rating using the SAM). The Retrieval Session consisted of a recognition task, presenting target (all pictures from the encoding session) and distractor (36 neutral, 36 positive) pictures in random order. The children indicated for each picture whether it was old or new. (C) DRM word list task. During Encoding, the participants heard eight different word lists consisting of 12 semantically associated words each. Children were instructed to remember as many words as possible. At Retrieval, children were asked to recall as many words as possible, however, not to guess and only to name those words they were sure of to be part of one of the lists. ITI, intertrial interval [Colour figure can be viewed at wileyonlinelibrary.com]

At the Retrieval session, target and distractor pictures were presented in random order. Instead of rating the pictures, children were asked to indicate for each picture whether it was old or new. Recognition memory was calculated as the adjusted recognition of neutral and negative pictures, respectively (hits minus false alarms = old pictures correctly recognized as old minus new pictures incorrectly recognized as old). The children were not provided with any strategies on how to process the pictures at encoding or retrieval.

Deese–Roediger–McDermott (DRM) task

To assess gist-based memory in a nonemotional stimulus domain, we used the DRM task (Deese, 1959; Roediger & McDermott, 1995). A shortened version of this task has previously been shown to be sensitive to sleep-dependent improvements in the retrieval of gist-based and veridical memories in adults (Diekelmann et al., 2010; Payne et al., 2009). To the best of our knowledge, DRM tasks have so far not been used to assess effects of sleep on memory processing in children. During Encoding of the task, the children heard eight different word lists (spoken by a pre-recorded male voice at a rate of 1 word per 3 s) and were asked to remember as many words as possible. Each list consisted of 12 semantically associated words (e.g. 'night', 'dark' and 'shade'), lacking the word with the strongest common association ('critical lure word', e.g. 'black'). Each word list was separated by a 30-s pause (Figure 1C).

At Retrieval, participants were asked to name all the words they still remembered. They were asked not to guess and to name only words they were sure to be part of one of the lists. Instructions did not provide any further mnemonic strategy to be used at Retrieval (or Encoding). Gist memory was defined as the number of critical lures recalled by the child (maximum 8). Veridical word memory was measured by the correctly recalled list words (maximum 96) and intrusions (falsely recalled unrelated words). Parallel versions of the task were used for the children's Sleep and Wake condition.

Control measures

Control measures included subjective ratings of mood, motivation, tiredness and vigilance at each session. In addition, heart rate during task performance was measured. To control for possible encoding differences, children completed a number learning task and a serial reaction time task at the Encoding session. Only at Retrieval sessions they performed a word fluency task. Analyses of the control measures yielded no indication that any group or condition differences in the control measures biased the main findings (see Appendix S1 for further information on the control measures).

Sleep recordings

Sleep was continuously recorded during the night of the Sleep condition using standard polysomnography including recordings of electroencephalography (EEG; from F3, F4, C3, Cz, C4, P3, P4, referenced to linked electrodes attached to the mastoids, and an electrode at FPz serving as ground), the electrooculogram (EOG, from electrodes placed below the left and above the right canthi) and the electromyogram (EMG, from electrodes over the left and right musculus mentalis). Recordings were conducted using a portable amplifier and recording system (SOMNOscreen™ plus Neuro+, SOMNOmedics GmbH) to ensure undisturbed sleeping in the subject's home. All signals were sampled at a rate of 256 Hz and filtered between 0.3 and 35 Hz (for the EEG and EOG), and between 10 and 100 Hz (for the EMG), respectively. A 50-Hz notch filter was applied to all channels.

Sleep stages were determined offline for subsequent 30-second epochs, using standard criteria (Rechtschaffen & Kales, 1968). For each child, the TST, time spent in different sleep stages in minutes and percentage of TST, wake after sleep onset (WASO), as well as SWS and REM sleep latencies with reference to sleep onset were determined. Further spindle and power analyses were conducted with algorithms as described in Mölle, Marshall, Gais, and Born (2002) (see Appendix S2 for a detailed description of the sleep analyses).

Statistical analyses

Due to technical problems, data of one TD boy had to be excluded from the analysis of the picture recognition task and the number task, and data of another TD boy from the analysis of the SRT task. For the DRM task, two children (one in the TD and one in the ASD group) were identified as outliers (values >3 *SD* above the group mean) on the recall of correct words and were thus excluded from the respective analyses. Due to poor signal quality and equipment failure, sleep analyses could not be performed in two children with ASD.

Values are presented as means with *SEM*. The main analyses were generally based on 2 (ASD/TD) × 2 (Sleep/Wake) repeated-measures analysis of variance (ANOVA) and Student's *t*-tests. Pearson's *r* correlations were used to explore relationships between memory performance and sleep parameters known to be linked to memory consolidation (e.g. time spent in stage 2 sleep, SWS, spindle numbers and density, sigma power density, SWA). A *p*-value of $< .05$ was considered significant. For multiple *t*-tests and correlation analyses, Bonferroni corrected *p*-values are reported.

Results

Picture recognition task

All children, regardless of whether they slept or remained awake during the retention interval, correctly recognized more negative than neutral pictures (adjusted recognition scores: $M = 55.50$, $SEM = 1.04$ versus $M = 51.68$, $SEM = 1.41$; Valence main effect: $F(1,38) = 31.06$, $p < .001$, $\eta_p^2 = .45$, Figure 2). All children correctly recognized more pictures after the nocturnal sleep interval ($M = 55.67$, $SEM = 1.20$) than after daytime wakefulness ($M = 50.51$, $SEM = 1.43$; Sleep/Wake main effect: $F(1,38) = 16.72$, $p < .001$, $\eta_p^2 = .31$). Children with ASD ($M = 49.38$, $SEM = 1.60$) correctly recognized less pictures than TD children ($M = 56.80$, $SEM = 1.68$; ASD/TD main effect: $F(1,38) = 10.24$, $p = .003$, $\eta_p^2 = .21$). Notably, the emotional enhancement in memory as expressed by the difference in recognition between negative and neutral pictures was greater in children with ASD ($M_{diff} = 6.76$, $SEM_{diff} = 1.91$) than TD children ($M_{diff} = 2.87$, $SEM_{diff} = 1.25$; ASD/TD × Valence interaction: $F(1,38) = 5.08$, $p = .030$, $\eta_p^2 = .12$). This difference was independent of whether subjects had slept or remained awake ($p = .874$ for the respective ASD/TD × Valence × Sleep/Wake interaction). In fact, neither in ASD nor in TD children did sleep induce a stronger enhancement in recognition memory for negative compared to neutral pictures ($p = .713$ and $p = .920$, for respective Sleep/Wake × Valence interactions,

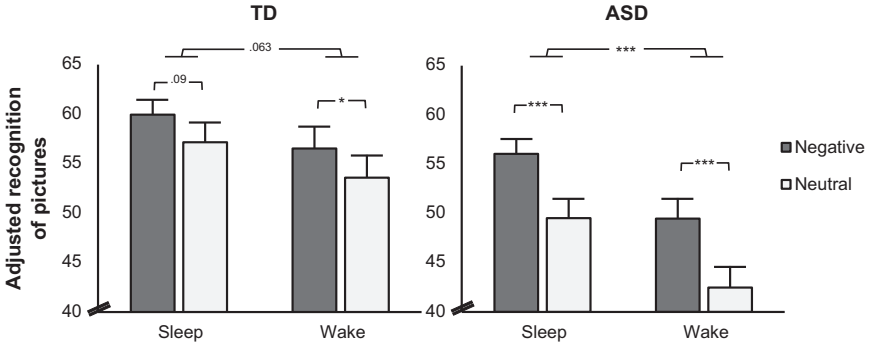

Figure 2 Mean adjusted recognition (hits minus false alarms) of negative and neutral pictures in the picture recognition task, separately for the Sleep and Wake condition, and the TD (left) and ASD (right) groups. All children recognized more negative than neutral pictures correctly and TD children performed better than children with ASD. Both groups showed a sleep over wake benefit. Error bars represent standard error of the mean. ASD, autism spectrum disorder; TD, typically developing. *$p < .05$; ***$p < .001$

for ASD and TD groups, separately). However, higher individual average recognition performance was correlated with less individual emotional memory enhancement in the sleep condition ($r = -.503$, $p = .001$) indicating that the missing sleep-dependent emotional enhancement likely reflected a ceiling effect due to generally high recognition performance after sleep.

As expected, negative pictures ($M = -1.37$, $SEM = 0.14$) were rated more negative than neutral ones ($M = 0.99$, $SEM = 0.17$) at Encoding, with the difference between neutral and negative ratings being larger in the TD ($M_{diff} = 2.79$, $SEM_{diff} = 0.28$) than in children with ASD ($M_{diff} = 1.92$, $SEM_{diff} = 0.27$, Valence main effect: $F(1,38) = 149.90$, $p < .001$, $\eta_p^2 = .80$, ASD/TD × Valence interaction: $F(1,38) = 5.16$, $p = .03$, $\eta_p^2 = .12$). No other effects were significant (all $p > .352$). There was no consistent correlation between the mean difference in valence ratings and memory performance, suggesting that the reduced differentiation in subjective valence ratings in children with ASD was unrelated to their greater emotional enhancement in memory. Arousal ratings only showed the expected overall higher rating for negative pictures ($M = 5.20$, $SEM = 0.23$) compared to neutral ones ($M = 2.44$, $SEM = 0.17$, $F(1,38) = 215.24$, $p < .001$, $\eta_p^2 = 0.85$, for Valence main effect; all other $ps > .213$).

Deese–Roediger–McDermott (DRM) task

Contrary to our hypothesis, children with ASD recalled more critical lure words in the Sleep condition ($M = 1.00$, $SEM = 0.20$) than in the Wake condition ($M = 0.50$, $SEM = 0.14$; $p = .022$), which was not the case for TD children (M_{sleep}=0.68, SEM_{sleep}=0.21, M_{wake}=0.90, SEM_{wake}=0.15; $p = .331$, ASD/TD × Sleep/Wake interaction: $F(1,37) = 5.66$, $p = .023$, $\eta_p^2 = .13$, all other effects $p > .338$, Figure 3). This enhanced abstraction of gist-based memory after sleep in children with ASD was likewise evident when the number of recalled critical lure words was expressed as proportion of total recall (of critical lures plus veridical recall; ASD/TD × Sleep/Wake interaction: $F(1,36) = 7.46$, $p = .010$, $\eta_p^2 = .17$, all other effects $p > .350$): almost 13% of the words the children with ASD recalled after sleep were critical lure words, whereas this was only true for 6% of the recalled words after daytime wakefulness.

Analyses of veridical word memory recall showed that children with ASD ($M = 6.08$, $SEM = 0.84$) performed distinctly worse than TD children ($M = 9.26$, $SEM = 0.86$; correct recall of list words, ASD/TD main effect: $F(1,37) = 7.02$, $p = .012$, $\eta_p^2 = .16$). Across all children, there was no significant benefit of sleep over wake in veridical word memory (Sleep/Wake main effect: $F(1,37) = 2.76$, $p = .105$,

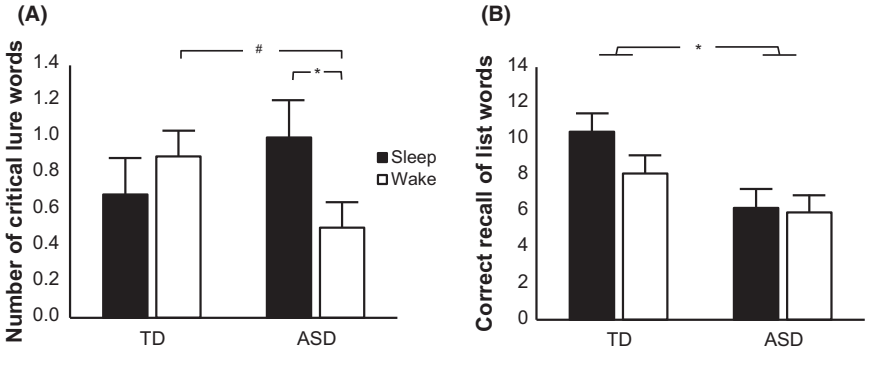

Figure 3 Mean number of recalled critical lure words (A) and correct recall of list words (B) in the Sleep and Wake condition, separately for TD and ASD children. (A) The ASD group recalled more critical lure words after a night of sleep compared to daytime wakefulness, which was not the case for TD children. (B) TD children performed better overall than children with ASD in the recall of list words. Error bars represent standard error of the mean. ASD, autism spectrum disorder; TD, typically developing. #$p < .06$; *$p < .05$

η_p^2 = .07); however, there was a trend for a sleep benefit in the TD children (p = .068 for Sleep/Wake main effect), which was not evident in the children with ASD (p = .804). Both groups named more intrusions after sleep (M = 2.05, SEM = 0.25) compared to wake (M = 1.33, SEM = 0.26, Sleep/Wake main effect: $F(1,37) = 5.03$, p = .031, η_p^2 = .12) but, importantly, groups did not differ from each other (all other effects $p > .430$).

We explored whether the generally lower memory performance in children with ASD could account for their greater sleep-induced critical lure recall. However, the ASD/TD × Sleep/Wake interaction effect in the ANOVA on critical lure recall remained significant when the veridical word recall (averaged across conditions) was introduced as a covariate ($F(1,36) = 5.43$, p = .026, η_p^2 = .13), although the covariate per se was also significant ($F(1,36) = 9.99$, p = .003, η_p^2 = .22). Surprisingly, the effect of the covariate reflected that better general memory performance was associated with higher (rather than lower) critical lure recall after sleep, especially in the children with ASD (r = .56, p = .010 vs. r = .07 p = .789 in TD children). This excludes that the generally lower memory performance in children with ASD accounts for their enhanced production of gist-based memories after sleep.

Sleep parameters

Parameters of the sleep architecture, spindles and power in sleep-stage-specific EEG frequency bands were remarkably comparable between ASD and TD children, with no significant differences (Table S4). Also, correlational analyses performed separately for the ASD and TD children did not reveal a consistent link between sleep parameters of interest and performance on the two memory tasks (none of the a priori defined correlations survived Bonferroni correction). Correlation coefficients and uncorrected p-values are reported in Table S5.

Discussion

We compared the formation of gist-based memories across periods of sleep and wakefulness between 9- and 12-year-old boys with ASD and age and IQ-matched TD boys, using a picture recognition task and a DRM task. Contrary to our hypothesis, we found that, compared to TD children, children with ASD showed a greater emotional enhancement in memory, expressing as a relatively stronger memory for negative over neutral pictures after both retention periods of sleep and wakefulness. Even more surprising and contrary to our hypothesis, children with ASD also showed an enhanced sleep-dependent formation of gist-based memories for the critical lures of the DRM task. Memory performance, in general, was worse in ASD than in TD children. However, sleep physiology was remarkably comparable between the groups. The findings contradict the view that children with ASD suffer from a basic deficit in processing globally constituted meaning, as proposed by the weak central coherence account of ASD (Happé & Frith, 2006). The signs of enhanced reliance on gist-based memory formation, as observed here in ASD, might rather reflect compensatory responses to deficits in earlier processing stages.

While picture recognition was generally worse in ASD than TD children, children with ASD showed a stronger memory benefit for emotional compared to neutral pictures. This was unexpected based on findings of reduced abilities to form memories for emotional stimuli in ASD (Boucher et al., 2012) and studies in adults with high-functioning ASD showing a smaller benefit for remembering emotional over neutral stimuli (Gaigg & Bowler, 2008). The emotional enhancement in memory typically occurs with some delay, and in the latter study, healthy controls indeed showed reduced forgetting rates for emotional compared to neutral memories after a 1-hour and a 24-hour delay, whereas the ASD group did not exhibit such a pattern. Considering that we tested retrieval about 11 hr after Encoding, this excludes that our opposite finding of a greater emotional enhancement in memory in the children with ASD is simply owed to the dynamic nature of the effect.

An alternative explanation relates to the age of the participants as most previous studies of long-term emotional memory formation were conducted in adults, whereas the present study, to our knowledge, is the only testing such memories with greater delays in children with ASD. With ageing, memories might be processed differently, in particular when these memories are already compromised at encoding. In fact, the stronger emotional enhancement in long-term memory in our children with ASD seemed to follow a weaker differentiation of negative from neutral pictures in terms of subjectively rated valence. It has been postulated that ASD is characterized by atypical associations between subjective and physiological responses to emotional stimuli (Bal et al., 2010; Gaigg & Bowler, 2007), suggesting that alterations in the formation of long-term memory are secondary to these alterations at earlier processing stages.

As expected, sleep generally enhanced picture recognition memory compared to the wake condition (Diekelmann & Born, 2010). This sleep-induced memory benefit was comparable between the ASD and TD groups, speaking for the notion that memory formation during sleep is well-preserved in children with ASD (Maski et al., 2015). Moreover, neither in ASD nor in TD children sleep produced a greater memory enhancement for negative compared to neutral pictures. As recognition memory after sleep was generally rather high, ceiling effects might have masked a preferential consolidation of emotional memories in this state, an idea, which is also supported by our exploratory correlational analyses.

However, it is also to note that a preferential strengthening of negative over neutral stimuli during sleep has not been observed very consistently in healthy populations with similar tasks (Ackermann, Hartmann, Papassotiropoulos, de Quervain, & Rasch, 2015; Prehn-Kristensen et al., 2009). The sleep-dependent emotional enhancement in memory might be more sensitively captured using an immediate recognition test prior to the sleep versus wake retention period as baseline (e.g. Schoch, Cordi, & Rasch, 2017). However, this would have required additional testing, introducing itself repetition effects on the emotional response. For scrutinizing the hypothesis of an enhanced abstraction of emotional gist during sleep in children with ASD, it seems more promising to rely, in future studies, on tasks that have more consistently demonstrated such sleep-dependent enhancement in emotional memory. For example, Payne et al. (2015) used a picture recognition paradigm with the emotional and neutral stimuli occurring on top of a picture (i.e. scene). In this task, sleep produced a robust trade-off effect by preferentially enhancing memory for negative objects but suppressing memory for the pictorial context in which these objects were presented at encoding (Payne et al., 2015).

On the DRM task, sleep strongly enhanced the proportion of gist-based memory for the critical lures in children with ASD, whereas no such effect of sleep was observed in the TD children. TD children, in contrast, showed a distinct sleep-related benefit for veridical recall of the word list (although as a trend), an effect, which was not observed in the children with ASD. This pattern suggests that children with ASD use their capacities to form long-term memory during sleep primarily for abstracting gist-based memory whereas TD children use these capacities preferentially for strengthening veridical memories. Indeed, in healthy adults, the sleep-induced strengthening of gist-based memory on the DRM task has been found to occur after some delay and may be masked by an immediate strengthening effect of sleep on veridical memory (Lutz, Diekelmann, Hinse-Stern, Born, & Rauss, 2017; Wagner, Hallschmid, Rasch, & Born, 2006). Also, in healthy subjects sleep led to more robust gist-based memory formation when memory performance was generally low (Diekelmann et al., 2010; Payne et al., 2009), suggesting that weak or compromised fresh memory traces might favour the early emergence of gist-based memory during sleep. However, exploratory analyses revealed that this mechanism is highly unlikely to explain our findings – on the contrary, in our children better general memory performance predicted more robust gist-based memory formation.

While sleep led to a distinct increase in the recall of critical lures in ASD, which was not seen in the TD children, the absolute number of recalled critical lures after sleep was comparable between groups. Likewise, absolute numbers of recalled critical lures comparable with or even higher than those in healthy controls have been shown in studies of adults with ASD (Gaigg & Bowler, 2009). However, other studies reported reduced numbers of critical lure memories in ASD patients (Beversdorf et al., 2000; Wojcik et al., 2018). Apart from testing adults rather than children, those studies generally used shorter retention intervals between encoding and recall testing and none took into account the specific role sleep plays for forming abstracted gist-based memories. In combination, these studies underline that, diverging from previous views (e.g. Happé & Frith, 2006; Plaisted, 2001), patients with ASD are able to form and use abstracted conceptual representations, even to a greater extent than healthy controls under certain conditions.

Considering findings showing that higher rates of gist-based memories arise from highly arousing situations (Corson & Verrier, 2007; Payne, Nadel, Allen, Thomas, & Jacobs, 2002), it could be argued that children with ASD produced more gist-based critical lure words in the sleep condition because they were more stressed (e.g. by higher demands for social interaction while putting on the sleep EEG). Subjective ratings of mood and motivation (which were assessed directly after the mounting of the EEG), however, did not differ between the groups, making this mechanism seem unlikely. Nevertheless, those findings illustrate how factors active already at encoding bias the process of memory consolidation, which is otherwise normal, towards increased formation of gist-based memory. Two other factors to be mentioned in this context are the encoding strength and the use of strategies, both of which might differ between ASD and TD children. Our experimental paradigm did not allow us to directly assess encoding strength (before the sleep and wake retention intervals) for the stimuli to be memorized. However, there is compelling evidence for an optimal level of encoding strength that sleep acts upon most efficiently, whereas effects of sleep are less pronounced with either too strongly encoded (Drosopoulos, Schulze, Fischer, & Born, 2007) or too weakly encoded memories (Tucker & Fishbein, 2008; Wislowska, Heib, Griessenberger, Hoedlmoser, & Schabus, 2017). Moreover, patients with ASD have been found to show alterations in using strategies to form memory representations (Bebko, Rhee, McMorris, & Ncube, 2015; Williams, Minshew, Goldstein, & Mazefsky, 2017). Such strategies, by determining the level of integration of a newly formed representation, can subsequently strongly modify sleep-dependent consolidation (Himmer, Müller, Gais, & Schönauer, 2017). Unfortunately, we did not assess whether the participants used any specific encoding strategies and, thus, cannot judge to what extent our children with ASD made use of different resources during encoding than TD children. Indeed, in light of the unexpected signs of increased gist abstraction in our ASD children, a fine-grained examination of

encoding, taking into account differences in strength and strategy, seems to be a promising approach for future studies.

In summary, the sleep-related formation of long-term memory seems to be well-preserved in children with ASD: they showed a sleep-induced memory benefit for picture recognition similar to that in TD children, and a sleep-induced abstraction of gist information on the semantic task that was even superior to that in TD children. This conclusion concurs with our sleep data revealing a surprisingly comparable sleep architecture in ASD and TD children. The finding of normal physiological sleep in children with ASD agrees with the picture from previous studies overall reporting very inconsistent sleep alterations that, if present, appear to be of marginal size (Buckley et al., 2010; Maski et al., 2015). The lack of differences in sleep parameters between our children with ASD and the TD children might also be owed to the fact that we only included children with ASD from the high-functioning spectrum (i.e. with an IQ within the normal range). In particular, sleep spindle activity seems to be positively correlated with IQ measures (Hoedlmoser et al., 2014; Reynolds, Short, & Gradisar, 2018; Ujma, Sándor, Szakadát, Gombos, & Bódizs, 2016). Consistent with these findings in typically developing children, spindle density was found to be reduced in a larger sample of children with ASD also including low-functioning ASD (Farmer et al., 2018). Lower IQ might also be associated with other sleep alterations in ASD like an overall reduced sleep duration (Taylor, Schreck, & Mulick, 2012). Thus, by restricting our sample to high-functioning ASD we successfully controlled for nonspecific, IQ-related confounding effects on sleep–dependent memory, although the findings may not be considered representative for low-functioning ASD children. Because our experimental design was tailored to minimize variance by recruiting homogeneous groups of boys only, we cannot generalize our findings to girls with ASD who may differ in memory processing from boys with ASD (Goddard, Dritschel, & Howlin, 2014). Furthermore, although analyses showed that the presence of comorbidities explained only a small amount of variance, future studies with larger samples should systematically investigate a possible contribution of comorbid diagnosis to the observed pattern. Finally, it should be noted that all of this relates to physiological sleep parameters. Yet, normal physiological sleep does not exclude subjectively reported sleep problems in children with ASD observed here as well as in other studies (Richdale & Schreck, 2009).

In conclusion, while the formation of long-term memory in children with ASD is generally impaired, they can use this process, in particular during sleep, for enhancing the formation of gist-based memories. This enhanced formation of gist-based memory might reflect a compensatory response to an altered processing of representations already at earlier stages, that is during encoding. Inasmuch as the enhancement in the formation of gist-based memory is bound to sleep, which appears to be normal in high-functioning children with ASD, ensuring optimal sleep opportunities might be considered a potential means to benefit cognitive functioning in ASD.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article:

Table S1. Comorbid diagnoses of the participants with ASD.
Table S2. Participants' characteristics and clinical measures.
Table S3. Means and standard errors of the mean of the control measures.
Table S4. Means and standard errors of the mean of the sleep parameters.
Table S5. Correlation coefficients, *r,* and uncorrected *p*-values (in parenthesis) of the correlation analyses between the sleep parameters and memory measures.
Appendix S1. Control measures.
Appendix S2. Sleep analyses.

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Key points

- Individuals with autism spectrum disorder (ASD) show social and cognitive deficits, as well as alterations in sleep.

- We investigated the role of sleep for gist abstraction in children with ASD compared to typically developing children (TD).
- Unlike TD children, children with ASD benefited from sleep in the formation of gist-based memories in the Deese–Roediger–McDermott word list task.
- Additionally, both groups exhibited a sleep benefit in the recognition of pictures.
- We conclude that sleep might have a compensating role for specific cognitive functions in children with ASD.

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