

# The impact of sleep deprivation on visual perspective taking

GAËTANE DELIENS<sup>1,2,3,\*</sup> , HENRYK BUKOWSKI<sup>4,\*</sup>, HICHEM SLAMA<sup>3</sup>, ANDREW SURTEES<sup>5,6</sup>, AXEL CLEEREMANS<sup>2</sup>, DANA SAMSON<sup>5</sup> and PHILIPPE PEIGNEUX<sup>3</sup>

<sup>1</sup>Autism in Context: Theory and Experience (ACTE), Center of Research in Linguistics (LaDisco), Université libre de Bruxelles, Brussels, Belgium; <sup>2</sup>Consciousness, Cognition and Computation at CRCN (CO3), Center for Research in Cognition and Neurosciences and UNI-ULB Neurosciences Institute, Université libre de Bruxelles, Brussels, Belgium; <sup>3</sup>Neuropsychology and Functional Neuroimaging Research Group at CRCN (UR2NF), Center for Research in Cognition and Neurosciences and UNI –ULB Neurosciences Institute, Université libre de Bruxelles, Brussels, Belgium; <sup>4</sup>Social, Cognitive and Affective Neuroscience Unit (SCAN), Department of Basic Psychological Research and Research Methods, University of Vienna, Vienna, Austria; <sup>5</sup>Psychological Sciences Research Institute, Université catholique de Louvain, Louvain-La-Neuve, Belgium; <sup>6</sup>School of Psychology, University of Birmingham, Birmingham, UK

## Keywords

cognitive empathy, executive functions, mentalizing, Visual perspective taking

## Correspondence

Gaëtane Deliens, Autism in Context: Theory and Experience (ACTE), Center of Research in Linguistics (LaDisco), Université libre de Bruxelles, Avenue F.D. Roosevelt, 50, B-1050 Brussels, Belgium.  
Tel.: +32(0)26506033;  
fax: +32(0)26502209;  
e-mail: Gaetane.Deliens@ulb.ac.be

\*These authors contributed equally to this study.

Accepted in revised form 18 July 2017; received 22 January 2017

DOI: 10.1111/jsr.12595

## SUMMARY

Total sleep deprivation (TSD) is known to alter cognitive processes. Surprisingly little attention has been paid to its impact on social cognition. Here, we investigated whether TSD alters levels-1 and -2 visual perspective-taking abilities, i.e. the capacity to infer (a) what can be seen and (b) how it is seen from another person's visual perspective, respectively. Participants completed levels-1 and -2 visual perspective-taking tasks after a night of sleep and after a night of TSD. In these tasks, participants had to take their own (self trials) or someone else's (other trials) visual perspective in trials where both perspectives were either the same (consistent trials) or different (inconsistent trials). An instruction preceding each trial indicated the perspective to take (i.e. the relevant perspective). Results show that TSD globally deteriorates social performance. In the level-1 task, TSD affects the selection of relevant over irrelevant perspectives. In the level-2 task, the effect of TSD cannot be unequivocally explained. This implies that visual perspective taking should be viewed as partially state-dependent, rather than a wholly static trait-like characteristic.

## INTRODUCTION

Sleep loss is a recognized societal issue, known to impact markedly upon a wide range of cognitive functions (Basner *et al.*, 2013). Surprisingly, however, perspective taking has received scant attention, despite the fact that we need to place ourselves regularly in another person's shoes to achieve successful social interactions. The negative effect of sleep debt on emotional empathy (i.e. emotional perspective taking) has been evidenced in some studies (e.g. Bellini *et al.*, 2002; Guadagni *et al.*, 2014), but the interplay between sleep and the cognitive side of perspective taking remains unexplored. The only study that investigated the impact of sleep loss on cognitive perspective-taking reported slower reaction time on a sarcasm detection task after a night of total sleep deprivation (TSD) than after a whole night of sleep (Deliens *et al.*, 2015a). This effect was not fully explainable by generalized cognitive slowing after TSD. However, proper completion of a sarcasm detection

task depends upon working memory integrity, to keep in mind the context in which sarcasm may be detected and a series of paralinguistic cues such as the speaker's facial expression and prosody. As TSD can affect working memory negatively (for a meta-analysis see Lim and Dinges, 2008), this adverse effect may have partially driven the observed effects on sarcasm detection.

In the present study, we assessed the impact of TSD on visual perspective taking (VPT). VPT allows inferring what can or cannot be seen by another person (i.e. a level-1 perspective), and how it is seen by that person (i.e. a level-2 perspective) (Flavell *et al.*, 1981). The ability to infer another person's visual experience is a pivotal source of information for managing social interactions. For instance, it allows inferring: (i) knowledge and beliefs of others about the nearby environment, (ii) which objects they prefer or (iii) whether they see us or pay attention to us. Congruently, VPT performance correlates with self-reported perspective-taking habits (Bukowski and Samson, 2017; Mattan *et al.*, 2016). Crucially,

compared to sarcasm, VPT does not require integrating linguistic and paralinguistic cues, thus leading to lower working memory cost than in a sarcasm detection task.

VPT requires processes to compute another person's visual experience (drawing a line of sight for both level-1 and -2 VPT and, specifically for level-2 VPT, mental body rotation; Surtees *et al.*, 2013) and executive function processes to select the goal-relevant perspective when the self- and the other person's perspectives are in conflict (Qureshi *et al.*, 2010). As TSD has been proposed to impact executive functioning (e.g. Muto *et al.*, 2012), we expected that it would affect perspective selection performance when self and other perspectives are conflicting. The influence of TSD on executive functioning could occur in two ways. According to the 'state instability' theory (Doran *et al.*, 2001), the reduction of vigilance consecutive to TSD leads to an overall slowdown in performance with indirect effects on executive functions (Lim and Dinges, 2008). A second approach states that sleep loss directly hampers executive functioning by altering the functional integrity of the prefrontal cortex (Durmer and Dinges, 2005). Given that the prefrontal cortex is part of the regions involved in visual perspective taking with the right temporo-parietal junction and the ventral precuneus (Schurz *et al.*, 2015), we should observe a negative effect of sleep loss on VPT performances.

VPT has also been shown to be impacted by the perspective-taker's emotional state. As TSD is known to affect mood (Dinges *et al.*, 1997), this may be yet a different pathway by which sleep deprivation affects perspective taking. Hence, TSD-related decrease in VPT performance might be a consequence of mood, reduced vigilance or altered executive functioning. To determine the responsible mechanism, we additionally surveyed the participants' mood state and administered vigilance and executive function tasks (i.e. inhibition, working memory and flexibility).

## METHOD

### Participants

Twenty-four participants students gave written informed consent to participate in this study, which was approved by the local ethics committee. Participants were instructed to keep a regular sleep pattern for the 3 days preceding each testing session (sleep duration > 6 h/night, no nap, bedtime before 01:00 hours and wake before 10:00 hours) and to refrain from alcohol and stimulant drinks before and during testing sessions. Sleep-wake regularity was monitored using actigraphic recording (wGT3X-BT; ActiGraph, Pensacola, FL, USA) and daily completion of the St Mary's Hospital sleep questionnaire (Ellis *et al.*, 1981). Four participants were excluded from statistical analyses due to irregular sleep pattern (sleep duration < 6 h). The 20 remaining participants (five males,  $24.2 \pm 2.7$  years) were French-speaking with intermediate or neutral chronotype (Morningness-Eveningness Questionnaire: range 39–66; Horne and Ostberg, 1976)

and no sleep disturbances (Pittsburgh Sleep Quality Index  $\leq 5$ ;  $3.7 \pm 1.3$ ; Buysse *et al.*, 1989). Participants received monetary compensation upon completion of the study.

## METHODS

### Vigilance and sleepiness measures

Vigilance was measured using the 5-min version of the Psychomotor Vigilance Task (PVT; Dinges and Powell, 1985). Participants had to press a key as quickly as possible to stop a counter that started at randomly selected intervals (from 2 to 10 s). Subjective sleepiness was self-rated on the Karolinska Sleepiness Scale (KSS; Akerstedt and Gillberg, 1990).

### Mood state

Because happiness, anxiety, shame and guilt can modulate perspective-taking abilities (Bukowski and Samson, 2016; Converse *et al.*, 2008; Todd *et al.*, 2015), they were self-rated at the start of each testing session on a seven-point Likert scale, as in the Converse and Todd studies. Personality questionnaires were also administered (see Supporting information, section 1 for detailed material).

### Flexibility task

The flexibility subtest of the Test for Attentional Performance (Zimmermann and Fimm, 2002) assesses the ability to shift the focus of attention by alternating between two sets of targets. A digit and a letter are presented simultaneously, one on the left and one on the right side of the screen. Participants must indicate the position in which the target stimulus appears by pressing the corresponding left- or right-hand key. Target stimuli were digits in the first block and letters in the second block (no-switch trials = constant target stimuli within a block). In the last block, participants had to press the keys alternately corresponding to the position of either the number or the letter (switch trials = alternating target stimuli). Switch-cost was computed as the difference between performance in switch and in no-switch trials. Each block consisted of 50 trials. This computerized task provides a precise measure of RTs (in the ms range) without requiring the retrieval of an arbitrary stimulus-response mapping (e.g. left button for red colour or circle shape), which can be affected after TSD.

### Working memory task

To assess working memory, we used the N-Back task (Owen *et al.*, 2005), a classic updating task. A series of numbers are displayed sequentially on a screen. In the control condition, participants are instructed to press a button whenever the number '2' is displayed (0-back). In the working memory updating condition, they are required to press the button

when the displayed number is the same as that presented two trials previously (2-back). To achieve the 2-back condition, participants had to maintain and update the series of numbers in working memory. Each of the four blocks (two 0-back and two 2-back blocks) consists of 30 stimuli displayed at a rate of 1/s, with 10 target trials.

### Inhibition task

In the bimodal Stroop task (Henry *et al.*, 2012), participants have to decide if the colour word heard in the headphones is identical or not to the colour of the ink of a written word displayed on the screen. The congruent condition consists of a colour word inked in its own colour (e.g. colour word RED displayed in red), the incongruent condition consists of a colour word inked in any of the four colours, other than the one to which it refers (e.g. colour word RED inked in green) and the neutral condition consists of a neutral word. Stimuli were displayed until response (see Deliens *et al.*, 2015a for further details). This task provides a precise measure of RTs without requiring arbitrary stimulus–response mapping and allows to distinguish both the inhibition effect, computed as the difference between performance in the incongruent and neutral conditions, and the congruency effect, computed as the difference between performance in the incongruent and congruent conditions.

### Level-1 VPT

In the level-1 VPT task (adapted from Surtees *et al.*, 2016; Fig. 1), participants have to decide whether a number of red dots is visible from their own or from an avatar's perspective (i.e. 'self' versus 'other' trials). Participants are first presented with a written perspective prompt ('HE/SHE' or 'YOU') indicating the perspective to take in the decision ('Does he see...?' or 'Do you see...?') followed by a written number (from 0 to 3) prompt indicating the number of red dots to verify ('Does he see 2 red dots?'). Following the presentation of the perspective and number prompts on the screen, a cartoon picture is presented depicting an avatar standing next to a table. Participants are asked to decide as fast and as accurately as possible whether the written prompts depict the picture by correctly pressing the corresponding key ('yes' or 'no' buttons). In this task, the dots are either all visible by both the avatar and the participant (consistent trials) or some are unseen by the avatar (inconsistent trials).

### Level-2 VPT

The level-2 VPT task (adapted from Surtees *et al.*, 2016; Fig. 1) is similar to the level-1 VPT, except that participants are asked to decide which number they see from their own or from the avatar's perspective (i.e. 'self' versus 'other' trials). The number prompts are 6 or 9 and refer to the number itself, visible from either the self-perspective or the other person's perspective ('Does he see a 6?'). Participants are asked to

decide as fast and as accurately as possible whether the written prompts depict the picture correctly by pressing the corresponding key. In the level-2 task, the number 6 or 9 is always visible to the participant and the avatar, but it is either presented vertically so that the number looks like the same number from both perspectives (consistent trials), or horizontally on the table, so that 6 or 9 appears different—like a 9 or 6, respectively—to the participant and the avatar (inconsistent trials).

For both levels-1 and -2 VPT, reaction times (RTs) and accuracy were collected across conditions [2 (perspective: self versus other)  $\times$  2 (consistency: consistent versus inconsistent)]. As in the original paradigm (Samson *et al.*, 2010), only matching trials ('yes' response) were analysed because mismatching trials ('no' response) are unbalanced artificially (number prompts in consistent mismatching trials can never match the self or other perspective and are thus particularly easy to respond to). Overall, for each VPT task (level-1 and -2), there were 24 trials in each condition (matching  $\times$  perspective  $\times$  consistency) plus an eight-trial practice session. In both tasks, participants were told that they had less than 2 s to provide a response, which would otherwise be considered as an error.

### PROCEDURE

The experiment had a randomized cross-over design with two conditions, total sleep deprivation (TSD) and regular sleep (RS) condition, held 1 week apart (Fig. 2).

Before the experimental night, participants followed a 3-day regular sleep schedule as verified by sleep diaries and confirmed by wrist actigraphy. In the TSD condition, participants stayed in the laboratory from 19:00 to 10:00 hours and were monitored constantly by two experimenters. Throughout the course of the TSD night, participants were instructed to remain seated and to engage in non-strenuous activities (e.g. reading, surfing the internet or watching movies). Free water and hourly isocaloric meals were available. Every hour throughout the TSD night, participants performed the PVT and completed the KSS to estimate the evolution of objective and subjective vigilance levels, respectively. In the RS condition, participants arrived at the laboratory in the morning for the testing session after a night of sleep at home. At 09:00 AM, all participants performed a battery of tasks ( $\pm$  45 min) always carried out in the following order: KSS, PVT, mood scales, flexibility, VPT level-1, VPT level-2, visual rotation (not analysed here), N-Back and Stroop.

### Statistical analyses

Statistical analyses were performed using IBM SPSS Statistics version 21.0 (IBM Corp., Armonk, NY, USA). Data expressed as mean  $\pm$  standard deviation are reported Table 1. Significance level was set at  $P < 0.05$  (two-tailed). *Post-hoc* tests in analyses of variance (ANOVAS) were

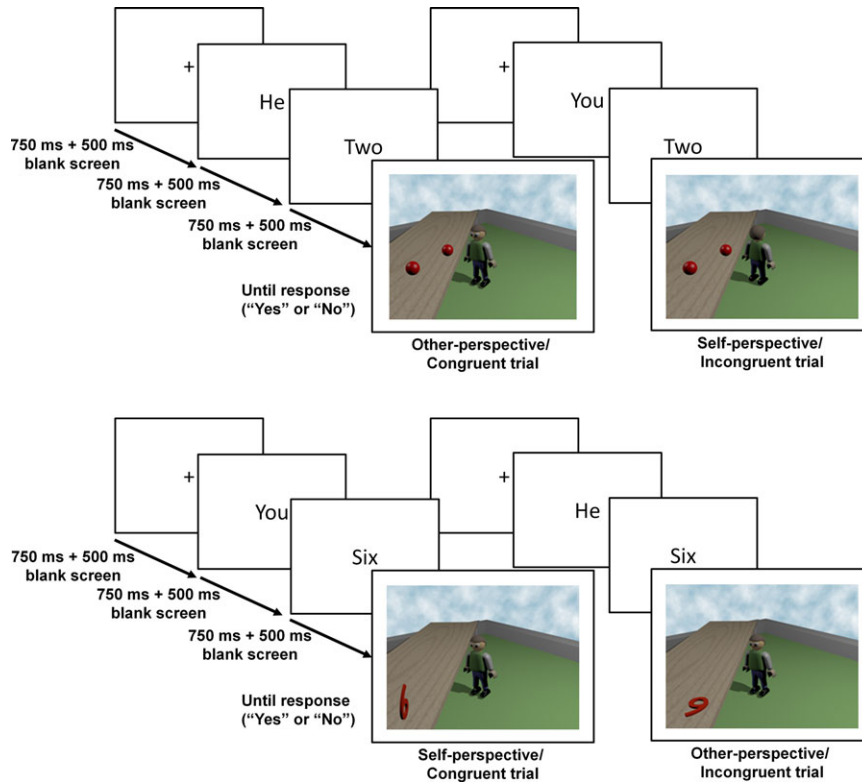


Figure 1. Time-course of a trial in the levels-1 and -2 visual perspective-taking tasks.

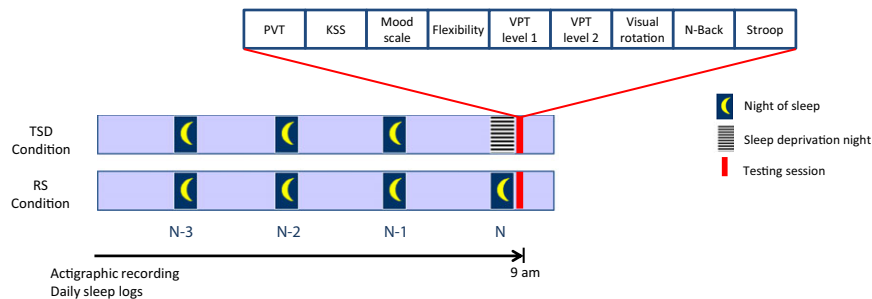


Figure 2. Experimental design. Regular sleep condition (RS), total sleep deprivation condition (TSD), Karolinska Sleepiness Scale (KSS), Psychomotor Vigilance Task (PVT) and visual perspective-taking task (VPT).

performed using paired Student’s *t*-tests; Bonferroni-corrected significance levels are added when relevant, but did not modify statistical interpretations.

In the PVT, vigilance was computed using the reciprocal response time ( $RRT = \text{mean } 1/RTs$ ; Basner and Dinges, 2011). Lower RRT reflects poorer performance.

In the other tasks, RTs for correct responses and error rates (ER) were merged to compute inverse efficiency scores [ $IES = RT/(1-ER)$ ]. The IES allows comparing different groups with a single measure. IES results were in line with RT and ER results (see Supporting information, section 2). Outliers [ $>2$  standard deviations (SD) outside the mean of the group in the TSD or RS condition] were computed for each task separately. Participants excluded in the different analyses are thus different individuals.

## RESULTS

### Sleepiness and vigilance

Participants showed higher mean sleepiness scores (KSS) for the first 5 h of the TSD night (19:00–23:00,  $3.410 \pm 1.298$ ) than for the last 5 h (05:00–09:00,  $7.880 \pm 1.100$ ;  $t_{19} = -13.705$ ;  $P < 0.001$ ) and higher vigilance level (higher RRT) for the first 5 h of the TSD night (19:00–23:00,  $3.126 \pm 0.328$ ) than for the last 5 h (05:00–09:00,  $2.732 \pm 0.480$ ;  $t_{19} = 7.394$ ;  $P < 0.001$ ). At 09:00 AM, before the testing session, participants in the TSD condition reported significantly higher sleepiness ( $t_{19} = 10.971$ ,  $P < 0.001$ ) and showed less vigilance ( $t_{19} = 5.658$ ,  $P < 0.001$ ) than in the RS condition. For more information

**Table 1** Significant effects of sleep through within-subject comparison total sleep deprivation versus rested sleep

Measure	Effects of sleep	Total sleep deprivation Mean $\pm$ SD	Rested sleep Mean $\pm$ SD
PVT RTT (msec <sup>-1</sup> )	Main effect	2.853 $\pm$ 0.441	3.153 $\pm$ 0.342
KSS	Main effect	7.750 $\pm$ 1.585	3.150 $\pm$ 1.226
Mood	No effect		
Flexibility (IES)	Main effect	905.785 $\pm$ 151.227	818.877 $\pm$ 169.902
	Sleep $\times$ switch	Repeated: 623.162 $\pm$ 93.282 Switch: 1188.408 $\pm$ 279.603	Repeated: 586.699 $\pm$ 91.851 Switch: 1051.055 $\pm$ 271.684
N-Back (IES)	Main effect	531.959 $\pm$ 98.383	499.503 $\pm$ 93.060
Stroop (IES)	No main effect		
	Sleep $\times$ congruency	Con: 661.092 $\pm$ 129.516 Neut: 729.843 $\pm$ 83.751 Incon: 995.803 $\pm$ 222.552	Con: 713.394 $\pm$ 90.938 Neut: 806.856 $\pm$ 181.812 Incon: 766.845 $\pm$ 158.547
		VPT level 1 (IES)	Main effect Sleep $\times$ congruency
VPT level 2 (IES)	Main effect	1367.979 $\pm$ 525.226	1059.058 $\pm$ 343.254

PVT RTT: reciprocal reaction time in the Psychomotor Vigilance Task; KSS: Karolinska Sleepiness Scale; IES: Inverse Efficiency Scores (IES = reaction time (RT)/1-error rate (ER)); VPT: Visual Perspective-taking Task; Con: congruent trials; Neut: neutral trials; Incon: incongruent trials; SD: standard deviation.

about sleep variables the days before the testing sessions and during the TSD night, see Supporting information, section 3.

#### Mood state

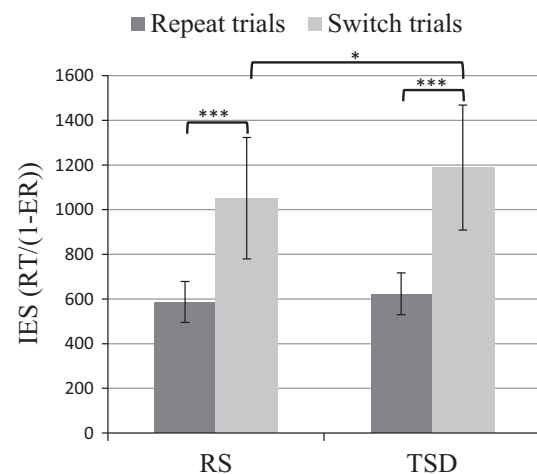
Paired *t*-tests on self-reported feelings before the testing session did not reveal any differences between the RS and TSD conditions (all *P*s > 0.119).

#### Flexibility task

A repeated ANOVA was computed on the mean IES with Sleep (RS versus TSD) and switching (repeat versus switch trials) as within-subject variables. Results showed a significant effect of sleep ( $F_{1,19} = 6.007$ ,  $P = 0.024$ ), with better performance in the RS condition, a main effect of switching ( $F_{1,19} = 94.786$ ,  $P < 0.001$ ), with better performance in repeat trials, and a sleep  $\times$  switching interaction ( $F_{1,19} = 5.228$ ,  $P = 0.034$ ). Analysis of the sleep  $\times$  switching interaction disclosed a higher switching cost (switch minus repeated trials) after TSD than after a whole night of sleep ( $t_{19} = 2.286$ ,  $P = 0.034$ ) (Fig. 3).

#### Working memory task

A repeated 2 (sleep: TSD versus RS)  $\times$  2 (load: 0- versus 2-back) ANOVA was conducted on the mean IES. Three participants were not included in the analyses, one for technical reasons and two for outlying performance in the TSD condition. The ANOVA revealed a main effect of sleep ( $F_{1,16} = 4.990$ ,  $P = 0.040$ ), with better performance in the RS condition, and a main effect of load ( $F_{1,16} = 43.097$ ,  $P < 0.001$ ), with better performance in the 0-back (low



**Figure 3.** Performance in the flexibility task. Task-switching performance in the flexibility task computed on the inverse efficiency scores (IES) as a function of factors sleep (RS versus TSD) and trials (repeat versus switch trials). RS: regular sleep group; TSD: total sleep deprivation group. \*\*\* $P < 0.001$ ; \* $P < 0.05$ . Error bars indicate standard deviations.

working memory load) trials, but no sleep  $\times$  load interaction ( $F_{1,19} = 1.574$ ,  $P = 0.228$ ).

#### Inhibition task

A repeated 2 (sleep: TSD versus RS)  $\times$  3 (congruency: congruent versus neutral versus incongruent) ANOVA was conducted on the mean IES. One participant was excluded due to outlying performance in the TSD and RS conditions. The ANOVA showed no main effect of sleep ( $F_{1,18} = 2.017$ ,



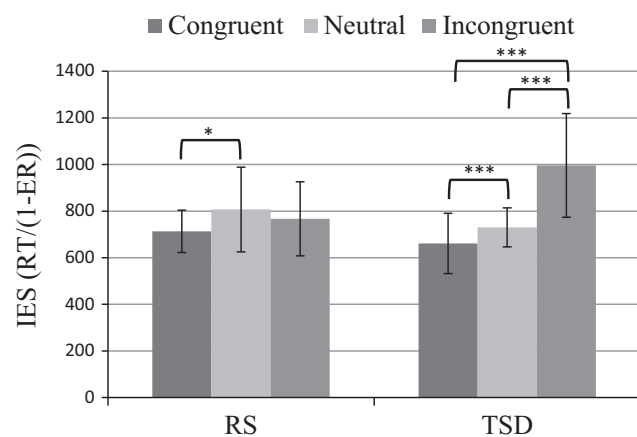
$P = 0.173$ ), but a main effect of congruency ( $F_{1,18} = 23.441$ ,  $P < 0.001$ ), and a significant sleep  $\times$  congruency interaction ( $F_{1,18} = 27.967$ ,  $P < 0.001$ ).

Analysis of the sleep  $\times$  congruency interaction showed that inhibition (incongruent–neutral trials) and congruency (incongruent–congruent trials) effects were significantly higher in the TSD condition (critical  $P_{Bonferroni} = 0.017$ ;  $t_{18} = 5.371$ ,  $P < 0.001$ ;  $t_{18} = 7.695$ ,  $P < 0.001$ , respectively) (Fig. 4). The facilitation effect (neutral–congruent trials) did not differ between conditions ( $t_{18} = 0.608$ ,  $P = 0.551$ ).

To sum up, TSD altered cognitive flexibility and inhibition but not working memory.

#### Level-1 VPT

A repeated 2 (sleep: TSD versus RS)  $\times$  2 (perspective: other-versus self-perspective)  $\times$  2 (congruency: congruent versus incongruent) ANOVA was conducted on the IES. Two participants were not included in the analyses for outlying performance (one in the TSD condition, one in the RS condition). The ANOVA showed a main effect of sleep ( $F_{1,17} = 15.647$ ,  $P = 0.001$ ) with better performance in the RS condition, a marginally significant main effect of perspective ( $F_{1,17} = 3.302$ ,  $P = 0.087$ ) with better performance on the self-perspective trials, a main effect of congruency ( $F_{1,17} = 14.157$ ,  $P = 0.002$ ) with better performance on congruent trials, a significant perspective  $\times$  congruency interaction ( $F_{1,17} = 5.295$ ,  $P = 0.034$ ) with a higher congruency effect on other-perspective trials and a **significant sleep  $\times$  congruency interaction** ( $F_{1,17} = 5.295$ ,  $P = 0.034$ ). Other interactions were non-significant ( $P_s > 0.121$ ). The congruency, perspective and congruency  $\times$  perspective effects replicated previous studies (Samson *et al.*, 2010; Surtees *et al.*, 2016).

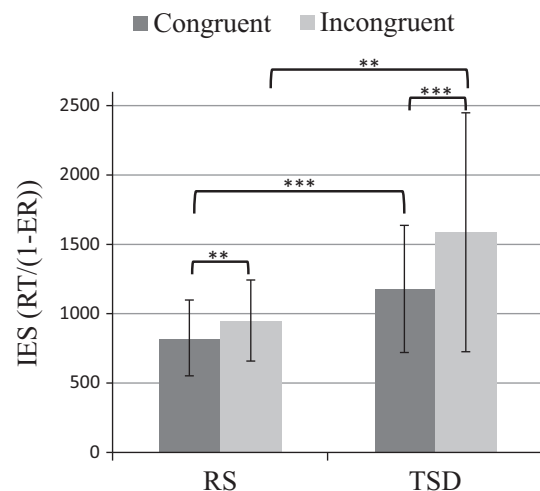


**Figure 4.** Performance in the Stroop task. Performance in the Stroop task computed on the inverse efficiency scores (IES) as a function of factors sleep (RS versus TSD) and congruency (congruent versus neutral versus incongruent). RS: regular sleep group; TSD: total sleep deprivation group. \*\*\* $P < 0.001$ ; \* $P < 0.05$ . Error bars indicate standard deviations.

Analysis of the sleep  $\times$  congruency interaction showed that the congruency effect (incongruent versus congruent trials) was significantly higher in the TSD than in the RS condition ( $t_{17} = 2.301$ ,  $P = 0.034$ ; Fig. 5). A general effect of sleep was also observed with better performance in the RS than in the TSD condition for both congruent ( $t_{17} = 4.337$ ,  $P < 0.001$ ) and incongruent ( $t_{17} = 3.545$ ,  $P = 0.002$ ) trials.

#### Contribution of executive functions and vigilance to the effect of TSD on the congruency effect

To investigate whether the impact of TSD on congruency effect is explained more clearly by changes in executive functioning or vigilance, we computed correlations between the congruency effect (incongruent minus congruent trials) in the level-1 VPT task, the executive functioning effects (switch cost in the flexibility task, inhibition and congruency effects in the Stroop task) and the level of vigilance (PVT RRT). Correlations between executive functioning effects and the congruency effect in the level-1 VPT task were not significant (all  $P_s > 0.663$ ). However, the level-1 VPT congruency effect was correlated negatively with vigilance level assessed just before the VPT task ( $r = -0.498$ ,  $P = 0.035$ ). We also conducted a within-participant mediation analysis (Montoya and Hayes, 2016) aimed at controlling whether the change in level-1 VPT congruency effects from RS to TSD conditions is mediated by the change in vigilance level. A simple mediation model was computed, with the factor sleep condition (RS versus TSD) and the level-1 VPT congruency effect as the dependent variable and the PVT RRT as the mediator variable. The indirect effect was not significant (Sobel's test



**Figure 5.** Level-1 visual perspective-taking performance. Level-1 visual perspective-taking performance computed on the inverse efficiency scores (IES) as a function of factors sleep (RS versus TSD) and congruency (congruent versus incongruent trials). RS: regular sleep group; TSD: total sleep deprivation group. \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$ . Error bars indicate standard deviations.

$P = 0.124$ ), suggesting that the change in congruency effect between RS and TSD is not mediated significantly by the change of vigilance (for more information about the correlational and mediation analyses, see Supporting information, section 4).

#### Level-2 VPT

A repeated 2 (sleep: TSD versus RS)  $\times$  2 (perspective: other- versus self-perspective)  $\times$  2 (congruency: congruent versus incongruent) ANOVA was conducted on the IES. Two participants were excluded from the analysis (one due to missing data, one with outlying performance in the TSD condition). The ANOVA showed a main effect of sleep ( $F_{1,17} = 17.929$ ,  $P = 0.001$ ), with better performance in the RS condition, a non-significant main effect of perspective ( $F_{1,17} = 0.510$ ,  $P = 0.824$ ) and a main effect of congruency ( $F_{1,17} = 23.019$ ,  $P < 0.001$ ) with better performance on congruent trials. All interactions were non-significant ( $P_s > 0.213$ ). Thus, unlike in the level-1 VPT task, no interaction was found between sleep and congruency. To quantify evidence in favour of the null hypothesis (i.e. no interaction) compared to the alternative hypothesis (i.e. interaction), complementary Bayesian analyses were performed and suggest that the lack of interaction was 3.597 times more likely than the alternative hypothesis and that this was not driven by a smaller congruency effect (see Supporting information, section 5).

## DISCUSSION

This study examined the impact of one night of TSD on levels-1 and -2 visual perspective taking, which are pivotal skills for successful social interactions. Results revealed poorer global performance in the levels-1 and -2 VPT tasks after a TSD night. In addition, TSD was found to impact perspective-taking performance specifically when self- and other-centered visual perspectives conflict with each other in the level-1 VPT task. This increased congruency effect reflects a higher difficulty in handling the conflict between perspectives after TSD and thus go against the 'state instability' theory, which claims that vigilance drop leads to an overall decrease in performance with indirect effects on executive functions. These results are in line with a previous study showing a similar increase in the consistency effect for level-1 visual perspectives when participants completed simultaneously a task taxing executive function (Qureshi *et al.*, 2010). The authors concluded that executive functions are needed to handle perspectives conflicts, but not to compute the perspectives *per se*. In the current study, results from our executive tasks indicated that TSD also alters cognitive flexibility and inhibition. Our results might thus give some credence to the idea that sleep loss directly hampers executive functioning. Importantly, however, we did not find any linear association between the reduction of performance at handling conflicting level-1 visual perspectives following

TSD and reductions of performance across the executive tasks. Hence, we cannot conclude that the increased difficulty at conflict handling after TSD (versus a night of sleep) is linked directly or solely to impaired executive functioning.

Another potential explanation is that the increased difficulties in handling perspectives conflict after TSD result from a decline of vigilance. Congruently, performance at conflict handling difficulties was correlated negatively with vigilance level. However, the reduction of performance for conflict handling was not mediated significantly by the drop in vigilance.

The reduction of conflict handling was observed in the level-1 VPT task but not in the level-2 task. This is further evidence that these two abilities are distinct and separable (as proposed by Flavell *et al.*, 1981). One key difference between the two forms of perspective taking is that inferring someone's level-1 visual perspective is effortless (Qureshi *et al.*, 2010), whereas it is effortful to infer a level-2 perspective (Surtees *et al.*, 2012, 2016). Hence, the absence of an effect of TSD specifically affecting conflict handling in the level-2 VPT task raises the possibility that performance on congruent and incongruent perspectives trials was impacted similarly by TSD. This would result in a general reduction of performance on the level-2 VPT task, which is what we observed.

An alternative explanation stems from the higher difficulty of the level-2 VPT task compared to the level-1 task (indicated by higher IES, longer RT and higher consistency effect; see also Supporting information, sections 2 and 5). Indeed, performance in complex working memory tasks often seems less affected by TSD than performance in simpler tasks (Terán-Pérez *et al.*, 2012). This finding is explained by the fact that performing a challenging task temporarily increases arousal, thus minimizing the TSD-related decline in performance (Wilkinson, 1965). Congruently, in the TSD condition, vigilance level and conflict handling performance were correlated in the level-1 but not the level-2 VPT task. However, as mentioned previously, mediation analyses showed that the difference between the congruency effect in the sleep and TSD conditions is not fully explained by vigilance.

The only study that investigated the impact of sleep loss on cognitive perspective taking showed slower reaction time on a sarcasm detection task after TSD, but no difference in the congruency effect (Deliens *et al.*, 2015a). However, the sarcasm detection task only included other's perspective trials. Not having to switch from one perspective to another throughout trials may release cognitive resources and make handling the conflict between perspectives less effortful.

To conclude, we show with this study that TSD modulates VPT ability, which supports further the view that perspective taking is not a wholly static trait-like characteristic (Bukowski and Samson, 2017). Besides a general decline of performance on both levels-1 and -2 VPT, level-1 was particularly affected in situations where one's own and another person's

perspectives were conflicting. Sleep problems are a frequent complaint in people presenting social–emotional difficulties (e.g. autism spectrum disorder: Deliens *et al.*, 2015b; schizophrenia: Monti *et al.*, 2013). Our findings suggest that sleep loss often resulting from sleep disorders might mediate part of their social–emotional difficulties, a hypothesis to be investigated in future studies.

## ACKNOWLEDGEMENTS

The authors thank Alice Rinquet for help in data acquisition. GD was supported by a Greentic grant from the Département du développement technologique (DGO6), Région Wallonne (Belgium). This study was supported by FRS-FNRS postdoctoral (1.5.184.10.F) and project (3.4.594.08.F/T.0109.13) grants.

## AUTHOR CONTRIBUTIONS

Study design: GD and HB; data collection: GD; analyses: GD, HB and HS; interpretation and manuscript preparation: all authors.

## CONFLICT OF INTEREST

None.

## REFERENCES

- Akerstedt, T. and Gillberg, M. Subjective and objective sleepiness in the active individual. *Int. J. Neurosci.*, 1990, 52: 29–37.
- Basner, M. and Dinges, D. F. Maximizing sensitivity of the psychomotor vigilance test (PVT) to sleep loss. *Sleep*, 2011, 34: 581–591.
- Basner, M., Rao, H., Goel, N. and Dinges, D. F. Sleep deprivation and neurobehavioral dynamics. *Curr. Opin. Neurobiol.*, 2013, 23: 854–863.
- Bellini, L. M., Baime, M. and Shea, J. A. Variation of mood and empathy during internship. *JAMA*, 2002, 287: 3143–3146.
- Bukowski, H. and Samson, D. Can emotions influence level-1 visual perspective taking? *Cogn. Neurosci.*, 2016, 7: 182–191.
- Bukowski, H. and Samson, D. New insights into the inter-individual variability in perspective taking. *Vision*, 2017, 1: 8.
- Buysse, D. J., Reynolds, C. F. R., Monk, T. H., Berman, S. R. and Kupfer, D. J. The Pittsburgh Sleep Quality Index: a new instrument for psychiatric practice and research. *Psychiatry Res.*, 1989, 28: 193–213.
- Converse, B. A., Lin, S., Keysar, B. and Epley, N. In the mood to get over yourself: mood affects theory-of-mind use. *Emotion*, 2008, 8: 725–730.
- Deliens, G., Stercq, F., Mary, A. *et al.* Impact of acute sleep deprivation on sarcasm detection. *PLoS ONE*, 2015a, 10: e0140527.
- Deliens, G., Leproult, R., Schmitz, R., Destrebecqz, A. and Peigneux, P. Sleep disturbances in autism spectrum disorders. *Rev. J. Autism Devel. Disord.*, 2015b, 2: 343–356.
- Dinges, D. I. and Powell, J. W. Microcomputer analysis of performance on a portable, simple visual RT task sustained operations. *Behav. Res. Methods Instr. Comput.*, 1985, 17: 652–655.
- Dinges, D. F., Pack, F. and Williams, K. Cumulative sleepiness, mood disturbance, and psychomotor vigilance performance decrements during a week of sleep restricted to 4–5 hours per night. *Sleep*, 1997, 20: 267.
- Doran, S. M., Van Dongen, H. P. and Dinges, D. F. Sustained attention performance during sleep deprivation: evidence of state instability. *Arch. Ital. Biol.*, 2001, 139: 253–267.
- Durmer, J. S. and Dinges, D. F. Neurocognitive consequences of sleep deprivation. *Semin. Neurol.*, 2005, 25: 117–129.
- Ellis, B. W., Johns, M. W., Lancaster, R., Raptopoulos, P., Angelopoulos, N. and Priest, R. G. The St. Mary's Hospital sleep questionnaire: a study of reliability. *Sleep*, 1981, 4: 93–97.
- Flavell, J. H., Everett, B. A., Croft, K. and Flavell, E. R. Young children's knowledge about visual perception: further evidence for the Level 1–Level 2 distinction. *Dev. Psychol.*, 1981, 17: 99.
- Guadagni, V., Burles, F., Ferrara, M. and Laria, G. The effects of sleep deprivation on emotional empathy. *J. Sleep Res.*, 2014, 23: 657–663.
- Henry, M., Joyal, C. C. and Nolin, P. Development and initial assessment of a new paradigm for assessing cognitive and motor inhibition: the bimodal virtual-reality Stroop. *J. Neurosci. Methods*, 2012, 210: 125–131.
- Horne, J. A. and Ostberg, O. A self-assessment questionnaire to determine morningness-eveningness in human circadian rhythms. *Int. J. Chronobiol.*, 1976, 4: 97–110.
- Lim, J. and Dinges, D. F. Sleep deprivation and vigilant attention. *Ann. NY Acad. Sci.*, 2008, 1129: 305–322.
- Mattan, B. D., Rotshtein, P. and Quinn, K. A. Empathy and visual perspective-taking performance. *Cogn. Neurosci.*, 2016, 7: 170–181.
- Monti, J. M., BaHammam, A. S., Pandi-Perumal, S. R. *et al.* Sleep and circadian rhythm dysregulation in schizophrenia. *Prog. Neuropsychopharmacol. Biol. Psychiatry*, 2013, 43: 209–216.
- Montoya, A. K. and Hayes, A. F. Two condition within-participant statistical mediation analysis: a path-analytic framework. *Psychol. Methods*, 2016, 22: 6.
- Muto, V., Shaffii-le Bourdieu, A., Matarazzo, L. *et al.* Influence of acute sleep loss on the neural correlates of alerting, orientating and executive attention components. *J. Sleep Res.*, 2012, 21: 648–658.
- Owen, A. M., McMillan, K. M., Laird, A. R. and Bullmore, E. N-Back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. *Hum. Brain Mapp.*, 2005, 25: 46–59.
- Qureshi, A. W., Apperly, I. A. and Samson, D. Executive function is necessary for perspective selection, not Level-1 visual perspective calculation: evidence from a dual-task study of adults. *Cognition*, 2010, 117: 230–236.
- Samson, D., Apperly, I. A., Braithwaite, J. J., Andrews, B. J. and Bodley Scott, S. E. Seeing it their way: evidence for rapid and involuntary computation of what other people see. *J. Exp. Psychol. Hum. Percept. Perform.*, 2010, 36: 1255–1266.
- Schurz, M., Kronbichler, M., Weissengruber, S., Surtees, A., Samson, D. and Perner, J. Clarifying the role of theory of mind areas during visual perspective taking: issues of spontaneity and domain-specificity. *NeuroImage*, 2015, 117: 386–396.
- Surtees, A. D., Butterfill, S. A. and Apperly, I. A. Direct and indirect measures of Level-2 perspective-taking in children and adults. *Br. J. Dev. Psychol.*, 2012, 30: 75–86.
- Surtees, A., Apperly, I. and Samson, D. Similarities and differences in visual and spatial perspective-taking processes. *Cognition*, 2013, 129: 426–438.
- Surtees, A., Samson, D. and Apperly, I. Unintentional perspective-taking calculates whether something is seen, but not how it is seen. *Cognition*, 2016, 148: 97–105.
- Terán-Pérez, G. J., Ruiz-Contreras, A. E., González-Robles, R. O. *et al.* Sleep deprivation affects working memory in low but not in high complexity for the N-Back test. *Neurosci. Med.*, 2012, 3: 380–386.



- Todd, A. R., Forstmann, M., Burgmer, P., Brooks, A. W. and Galinsky, A. D. Anxious and egocentric: how specific emotions influence perspective taking. *J. Exp. Psychol. Gen.*, 2015, 144: 374–391.
- Wilkinson, R. T. Sleep deprivation. In: R. Edholm and A. Bacharach (Eds.) *Physiology of Human Survival*. Academic Press, London, 1965: 399–430.
- Zimmermann, P. and Fimm, B. A test battery for attentional performance. In M. Leclercq and P. Zimmerman (Eds) *Applied Neuropsychology of Attention. Theory, Diagnosis and Rehabilitation*. Psychology Press, London, 2002: 110–151.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

- Data S1.** Mood and personality questionnaires
- Data S2.** Supplementary results: reaction times and error rates results

**Data S3.** Sleep variables the days before the testing sessions and during the total sleep deprivation (TSD) night

**Data S4.** Contribution of executive functions and vigilance to the effect of total sleep deprivation (TSD) on the congruency effect

**Data S5.** Bayesian analyses

**Table S1.** Personality traits

**Table S2.** Report of statistically significant effects of sleep through within-subject comparison (sleep deprivation versus regular sleep) on reaction times (RT) and error rates (ER)

**Table S4.** Correlations between the congruency effect in the level-1 visual perspective-taking (VPT) task, executive functions and vigilance level

**Figure S4.** (a) Relation of level-1 visual perspective-taking (VPT) task and vigilance in the total sleep deprivation (TSD) condition. (b) Diagram of the mediation model.