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Experience-dependent induction of hypnagogic images during daytime naps: a combined behavioural and EEG study

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SUMMARY This study characterizes hypnagogic hallucinations reported during a polygraphically recorded 90-min daytime nap following or preceding practice of the computer game Tetris. In the experimental group ($N = 16$), participants played Tetris in the morning for 2 h during three consecutive days, while in a first control group ($N = 13$, controlling the effect of experience) participants did not play any game, and in a second control group ($N = 14$, controlling the effect of anticipation) participants played Tetris after the nap. During afternoon naps, participants were repetitively awakened 15, 45, 75, 120 or 180 s after the onset of S1, and were asked to report their mental content. Reports content was scored by three judges (inter-rater reliability 85%). In the experimental group, 48 out of 485 (10%) sleep-onset reports were Tetris-related. They mostly consisted of images and sounds with very little emotional content. They exactly reproduced Tetris elements or mixed them with other mnemonic components. By contrast, in the first control group, only one report out of 107 was scored as Tetris-related (1%), and in the second control group only three reports out of 112 were scored as Tetris-related (3%; between-groups comparison; $P = 0.006$). Hypnagogic hallucinations were more consistently induced by experience than by anticipation ($P = 0.039$), and they were predominantly observed during the transition of wakefulness to sleep. The observed attributes of experience-related hypnagogic hallucinations are consistent with the particular organization of regional brain activity at sleep onset, characterized by high activity in sensory cortices and in the default-mode network.

KEYWORDS electroencephalography, hypnagogic hallucinations, memory, sleep onset

INTRODUCTION

Hypnagogic hallucinations are conscious mental representations that emerge spontaneously at sleep onset. They typically consist of florid and vivid perceptions of various modalities, with a predominance of visual, auditory or kinaesthetic perceptions over olfactory or gustatory hallucinations (Foulkes and Vogel, 1965; Mavromatis, 1987). They commonly incorporate thoughts (Mavromatis, 1987), but relatively little emotion (Foulkes and Vogel, 1965). Early on, some of them were recognized as 'recurrent sensations' or 'perseverative images', namely representations inspired by recently seen objects (Mavromatis, 1987; Schacter, 1976). Recent studies experimentally confirmed that incorporation of stereotypical images into night-time sleep-onset mentation can be induced by prior practice of video games, such as Tetris (Rowley *et al.*, 1998; Stickgold *et al.*, 2000) or Alpine Racer, a downhill skiing game (Wamsley *et al.*, 2010). Several features of this intriguing phenomenon are still incompletely characterized. First, experience-related hypnagogic hallucinations were exclusively reported during night-time sleep onset (Stickgold *et al.*, 2000; Wamsley *et al.*, 2010). Although it is known that other sleep-related spontaneous mental experiences, such as dreams, follow a circadian modulation (Chellappa *et al.*, 2009), the

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occurrence of hypnagogic hallucinations during daytime sleep, beyond individual experience and some anecdotal evidence (Stickgold *et al*., 2000), has not yet been experimentally assessed. Second, the vigilance state in which experience-related hypnagogic hallucinations can be induced is still to be firmly characterized. As a rule, hypnagogic hallucinations occur in a specific state of vigilance at the transition of wakefulness to sleep, which was shown to correspond to sleep stage 1 (S1; Foulkes and Vogel, 1965; Hori *et al*., 1994; Rowley *et al*., 1998). At odds with these findings, it was recently suggested that experience-related hypnagogic hallucinations might also occur during waking and sleep stage 2 (S2; Stickgold *et al*., 2000; Wamsley *et al*., 2010). However, these conclusions were not derived from standard polygraphic recordings, and the vigilance state associated with experience-dependent hypnagogic hallucinations remains to be firmly established. Third, the nature of these experience-related hallucinations has not yet been thoroughly investigated. After Tetris practice, they were categorized in images and thoughts about the game (Stickgold *et al*., 2000). After Alpine Racer training, they consisted of thoughts or visual and kinaesthetic perceptions, directly or indirectly related to the task (Wamsley *et al*., 2010). A more detailed characterization of the hallucinatory material is important because it might shed some light on the underlying organization of brain function (Schwartz and Maquet, 2002). Fourth and finally, the origin of hypnagogic hallucinations has to be experimentally confirmed in different groups of volunteers: does anticipation on task practice, as reported by Wamsley *et al*. (2010), have a similar effect to genuine task experience on the mental content at sleep onset? Moreover, it remains uncertain whether experience-related hypnagogic hallucinations reflect active memory processes or simply indicate the increased readiness to fire of neural populations whose synaptic connections were recently strengthened. In support of the former assumption, the probability of induction of hallucinations after playing Tetris tended to be negatively correlated with initial performance, suggesting that individuals who reported most hallucinations at sleep onset were those with the largest potential learning range (Stickgold *et al*., 2000).

Here we address these different issues and characterize hypnagogic hallucinations in three groups of volunteers who practiced Tetris (experimental and anticipation groups) or not (control group) using iterative awakenings during polygraphically monitored daytime naps.

MATERIALS AND METHODS

Population

Participants gave their written informed consent to this study, which was approved by the Ethics Committee of the Faculty of Medicine of the University of Liège. Participants were young (age: 18–33 years), healthy volunteers. The absence of medical, traumatic, psychiatric or sleep disorders was established in a semi-structured interview. None complained of excessive daytime sleepiness as assessed by the Epworth Sleepiness Scale (Johns, 1991; scores ≤ 10), or of sleep disturbances as determined by the Pittsburgh Sleep Quality Index Questionnaire (Buysse *et al*., 1989; score ≤ 6). All participants had normal scores on the Beck Anxiety Inventory (Beck *et al*., 1988; score ≤ 7) and the Beck Depression Inventory II (Steer *et al*., 1997; scores ≤ 13). They were right-handed as indicated by the Edinburgh Inventory (Oldfield, 1971). Extreme chronotypes according to the Horne and Ostberg morningness–eveningness questionnaire were excluded (Horne and Ostberg, 1976; scores < 30 and > 70). They were moderate caffeine and alcohol consumers, and none was on medication (except oral contraceptives for women). None had worked on night shifts during the year preceding the experiment, or travelled across more than one time zone during the last 2 months. Participants did not have extensive prior experience in the computer game Tetris.

Experimental design

During the 7 days preceding the experiment, volunteers were instructed to follow a regular sleep schedule, verified by wrist actigraphy and sleep diaries. Three groups were examined (Fig. 1).

1 Tetris group (Fig. 1, top). The experiment was run on three consecutive days. In the morning of each experimental day, they were asked to play Tetris. The aim of this computer game is to complete horizontal lines of blocks without gaps, by manipulating colourful tetrominoes while they are falling down the playing field. The version of Tetris used in this study is adapted from a freely available Matlab code from which performance scores can be derived (Pascal Getreuer's mtetris.m, http://www.mathworks.com). The melody of the original Tetris theme A, which is based on the Russian folk song Korobeiniki, was played repetitively during the practice sessions. Volunteers played Tetris during 2-h practice sessions that began 6 h after sleep midpoint and consisted of eight 15-min blocks. This schedule resulted in a total of 6 h of practice over three consecutive days. In order to discard Tetris experts, the score achieved at the end of the first training session could not exceed a fixed maximum (namely, 9500).

After training, the volunteers received a light meal and were prepared for polygraphic recordings, which included electroencephalogram (EEG; Fz, Cz, Pz, Oz, referenced to the mean of A1 and A2), vertical and horizontal electrooculograms (EOG) and chin electromyogram (EMG). Electrode impedances were kept below 5 kOhm. Data were amplified and digitized using a V-Amp 16 (Brain Products GmbH, Gilching, Germany) using a 250-Hz sampling frequency and a bandpass from DC to Nyquist frequency. Ten hours after individual sleep midpoint, volunteers were asked to sleep in a quiet room at the laboratory under constant polygraphic monitoring. They could interact with the experimenter through an intercom and wore a headset. During the nap, volunteers were

Group	SMP + 6.00h	Lunch	SMP + 10.00h	SMP + 11.30h
Tetris	KSS Tetris: 8x15′ KSS PVT PVT	Calibrated snack KSS Electrodes PSG PVT	Recording during nap + awakenings after 15″ 45″ 75″ 120″ 180″ KSS KSS KSS KSS KSS	KSS / PVT
Control	KSS / KSS PVT PVT	Calibrated snack KSS Electrodes PSG PVT	Recording during nap + awakenings after 15″ 45″ 75″ 120″ 180″ KSS KSS KSS KSS KSS	KSS / PVT
Anticipation	KSS / KSS PVT PVT	Calibrated snack KSS Electrodes PSG PVT	Recording during nap + awakenings after 15″ 45″ 75″ 120″ 180″ KSS KSS KSS KSS KSS	KSS Tetris: 8x15′ PVT

Figure 1. Time schedule of the study design for one experimental day. The same protocol was followed across 3 days in the experimental Tetris group, namely Tetris practice before the nap. The control group followed the same protocol on a single day, except for the Tetris session. The anticipation group followed the same protocol on 1 day as well, while they had Tetris practice after the nap. Karolinska Sleepiness Scale (KSS) and psychomotor vigilance tasks (PVT) were requested four times throughout the day: before and after the morning Tetris training, and before and after the afternoon nap. Tetris practice was organized in eight blocks of 15 min. Subjects were allowed to sleep for 90 min while monitored online using polysomnography (PSG). They were prompted several times to report their KSS score and mental content. SMP, sleep midpoint.

repetitively woken up by an auditory stimulus delivered 15, 45, 75, 120 or 180 s after the onset of S1, in a pseudorandom order. According to the sleep stage at the moment of the report, several conditions were possible. (1) If S1-latency exceeded 10 min, a wake report was requested 10 min after the last report. (2) If subjects woke up spontaneously within the last seconds of the foreseen interval, a wake report was requested. (3) If they descended to S2 within the foreseen interval, they received the auditory wake-up stimulus at the planned interval. If they woke up and reported, the experiment was continued. However, if they did not wake up to report their mental content within 30 s, a new auditory stimulus was sent immediately. If this new auditory stimulus was still insufficient, the experimenter went into the room to wake up the participant. On each awaking, volunteers were asked to report their level of sleepiness according to the Karolinska Sleepiness Scale (KSS; Akerstedt and Gillberg, 1990), and any 'thoughts, images, feelings, sensations or anything else going through their mind'. All verbal reports were recorded with a digital recorder.

2 Control group (Fig. 1, middle). A separate control group of volunteers followed exactly the same protocol as the Tetris group, except that the experiment was run on a single day and volunteers did not practice Tetris in the morning. They stayed in the laboratory and were allowed to read, but not play card or computer games.

3 Anticipation group (Fig. 1, bottom). A third group of volunteers was examined during one single day, and again followed exactly the same protocol as the Tetris group, except that the Tetris practice session was scheduled after the afternoon nap. All volunteers of all groups were fully informed about the schedule during recruitment. This information was repeated at arrival at the lab. It should be noted that a between-subjects design was preferred to a within-subjects protocol in order to avoid Tetris incorporation into hypnagogic mental activity due to anticipation inherent to the latter (Wamsley *et al*., 2010).

In all groups, subjective sleepiness was assessed by the KSS, and vigilance was measured objectively using a computer version of the psychomotor vigilance task (PVT; Dinges and Powell, 1985), four times throughout the experimental day (before and after task practice in the morning, before and after the afternoon nap).

Data analysis

Sleep-onset reports consisted of the level of sleepiness according to the KSS and the mental content at that particular moment. The content of all reports was classified according to whether it was related or not to Tetris. If related to Tetris, it was further categorized according to the nature of hypnagogic hallucinations (visual, auditory, kinaesthetic imagery of Tetris, thoughts of Tetris, emotions related to Tetris, other games related to Tetris). Reports containing multiple themes could be assigned to multiple categories. The following categories were considered as 'directly' related to Tetris.

Visual imagery of Tetris – these include all reports in which the subject explicitly mentioned seeing elements of the Tetris game. The reports could be exclusively visual (unimodal) or mix elements of various modalities (multimodal). Example: 'And I was just seeing the game in my head and I had the impression that I was really playing […] It was just a mental image in which I saw blocks falling'.

Auditory imagery of Tetris – these reports contain sounds of Tetris with or without other mental representations, and could be uni- or multimodal. Examples of both types: 'I've still been thinking about the Tetris music and uh … That's it, yes' or 'I had the music of Tetris in my mind, but at the same time I was thinking about other things with the music as background'.

Tetris-related kinaesthetic hallucinations – these include bodily feelings and kinaesthetic content related to the position and weight of the body, movements of the muscles, tendons and joints clearly related to Tetris practice.

Thoughts about Tetris – these are typically thoughts about the score achieved at Tetris. Example: 'I've been thinking about the scores I have achieved at Tetris'.

Emotions related to Tetris – these can consist of any primary emotion (anger, fear, sadness, disgust, surprise, anticipation, trust and joy), or any of their combinations (excitement, curiosity, happiness, boredom, frustration, disappointment, etc.). Example: 'That one with four blocks, that orange one

[…] always when you need that block in one direction, you get a block in the different direction. That's very irritating'.

The following categories were considered as being 'indirectly' related to Tetris practice.

Visual imagery of elements with spatial arrangements or movements characteristic of Tetris – these elements are ordered as Tetris blocks and can include any kind of object, such as boxes, bottles, cars, circles, crosses, beds, curtains, beehives with honeycombs, pieces of wood, snakes, eggs, balls, snow, etc. Example: 'I was ordering everything that is in my wardrobe. I have put everything in shoe boxes, but in my dream there were other shoe boxes. […] In my dream the shoe boxes were of different colours' or 'I was ordering the bottles with herbs and oils, in the cupboard, at home'.

Auditory imagery of melodies explicitly related to the Tetris theme – these melodies are different from that of the Tetris game, and are not heard during the practice sessions. However, the volunteer explicitly claims that they are induced by the Tetris theme. Example: 'I was hearing the music 'Nous aimons vivre au fond des bois'. […] I think it's the same music as the Tetris game in fact. But, it's instrumental music in fact'. It should be noted that both the Tetris melody and the song 'Nous aimons vivre au fond des bois' are Russian folk songs, and their melodies are indeed quite similar.

Images, sounds, thoughts or emotions of another game, with a mention to Tetris – these include reports about games with a goal similar to that of Tetris: video games (e.g. Pac-man); TV games (e.g. word games and quizzes); and party games (e.g. chess, downfall, connect four, battleship, card games, dice, etc.). Example: 'I was thinking about Tetris, and I was also thinking about a game 'Downfall', in which you have to turn and align four disks of the same colour'.

Finally, three further classes of hallucinations were 'not' considered as related to Tetris.

Images, sounds, thoughts or emotions related to the experimental settings, tasks or questionnaires, or sleep-related concerns – these include all reports about the PVT, scales, sleeping or sleep stages, beds, clocks, monitoring, actigraphy, questionnaires, the experimental room, the laboratory, the experimenter, the announcement of the experiment, signing the informed consent, etc. Although not related to the practice of Tetris, they are obviously related to the experiment. Example: 'A blurred image about someone who talks about his sleep'.

Content not related to Tetris – this category is a very broad one, which includes all reports that could not be assigned to any of the previous categories. These reports consist of images, sounds, thoughts or emotions without explicit relationship with Tetris. They also include references to games other than Tetris when the subject mentioned having played the game recently. Example: 'I was thinking of a game of chess I've been playing with a friend Tuesday evening'.

Nothing in mind, forgotten content – as hypnagogic hallucinations tend to disappear immediately when they are focused on, it was expected that subjects often would forget their mental content. For instance, sometimes they just mentioned the KSS score, said they had nothing going on in their mind, or mentioned they had forgotten their mental content. Example: 'It's really very blurred, I don't know anymore'.

Sleep-onset reports were given scores by three independent judges, blind to the experimental conditions, performance data and time of the recording. Only those reports that: (1) were assigned the same score by all three judges; (2) were obtained during the predefined sleep durations of 15, 45, 75, 120 or 180 s after onset of S1; (3) could be fully transcribed; and (4) contained at least one spoken word, were included in statistical analyses.

Thematic consistency was defined by the recurrence of similar images in several reports of the same volunteer, either across awakenings within a single experimental day or across days. For instance, one volunteer reported 'I've been thinking about Tetris, about the green blocks and uhm it's difficult to place them correctly', and 40 min later he reported 'I've been thinking about the Tetris game, how to complete a line'.

Tetris performance was assessed as game scores (five points per block; 100, 250, 400 and 700 points per single, double, triple and quadruple filled lines, respectively) and stored for all practice sessions.

Polygraphic sleep data were analysed offline using the FASST toolbox (Leclercq *et al*., 2011; http://www.montefiore.ulg.ac.be/~phillips/FASST.html). The data were filtered during display (using a fourth-order Butterworth filter) between 0.1 and 20 Hz for EEG, between 0.1 and 5 Hz for EOG, between 10 and 125 Hz for EMG, and scored following the criteria of Rechtschaffen and Kales in sequential epochs of 20 s (Rechtschaffen and Kales, 1968).

Statistical analyses were conducted with SPSS 16.0® for Windows (SPSS Inc., IBM company, Chicago, IL, USA). As a rule, non-parametric tests (Kruskal–Wallis and *post hoc* Mann–Whitney *U*-tests for between-group comparisons, Friedman and *post hoc* Wilcoxon Matched Pairs tests within the experimental group, Spearman's Bivariate Correlation tests for calculating correlations) were preferred given the small sample sizes. Otherwise, parametric tests (Repeated Measures Analysis of Variance, RM-ANOVA, and *post hoc* Least Significant Differences, LSD) were considered when applicable (Tetris performance, alertness).

RESULTS

Population

A total of 43 volunteers aged between 18 and 33 years were assigned in the Tetris (N = 16; eight female), control (N = 13; eight female) and anticipation groups (N = 14; six female). Kruskal–Wallis tests did not demonstrate any demographic difference between groups (Table 1).

Sleep-onset mentation reports

Database

Out of a grand total of 1460 reports, the scorers agreed in 1246 reports, corresponding to an inter-rater reliability of 85%.

Table 1 Demographic data

	Tetris group			*Control group*			*Anticipation group*			*Kruskal–Wallis*		
	Med	*Min*	*Max*	*Med*	*Min*	*Max*	*Med*	*Min*	*Max*	χ^2	*df*	P
Sex										0.933	2	0.627
SMP	3 : 37	3 : 00	4 : 30	3 : 15	2 : 45	7 : 00	3 : 30	1 : 30	7 : 00	0.210	2	0.900
Age	22	18	28	23	18	26	25	19	33	5.882	2	0.053
Epworth	5	0	9	3	0	12	5	1	11	2.368	2	0.306
Chronotype	54	43	62	55	40	61	51.5	39	66	1.185	2	0.553
PSQI	3	1	5	3	1	6	4	1	6	4.470	2	0.107
Anxiety	2.5	0	6	3	0	8	2	0	14	0.899	2	0.638
Depression	2	0	7	2	0	10	2.5	0	9	1.527	2	0.466
LSDQ2	93.5	72	104	87	68	141	86	6	141	2.745	2	0.253

Median and range (minimum and maximum) is shown for each group. Kruskal–Wallis tests did not show any difference between the experimental groups ($P > 0.05$ for all parameters).
med, median; min, minimum; max, maximum. LSDQ2, London Sleep and Dreaminess Questionnaire 2 (not yet validated); PSQI, Pittsburgh Sleep Quality Index; SMP, sleep midpoint.

Out of these 1246 included reports, 949 were collected during the predefined intervals of 15, 45, 75, 120 or 180 s after the onset of S1. Among the 949 reports, 704 usable reports that could be fully transcribed and contained at least one spoken word were included in statistical analyses (Tables 2 and 3).

Group differences

Sleep-onset mentation during the first day of the experiment was compared between groups. They did not significantly differ in the overall capacity to recall mental content at sleep onset (145 usable reports in the Tetris group out of 195 recorded on the first day; 107 out of 151 in the control group; 112 out of 151 in the anticipation group; Kruskal–Wallis $\chi^2 = 0.626$, df = 2; $P = 0.731$). By contrast, the number of Tetris-related reports differed significantly between groups (Kruskal–Wallis $\chi^2 = 10.332$, df = 2; $P = 0.006$). In the experimental group, 13 out of 145 reports were related to Tetris. On the other hand, in the control group, one usable report out of 107 was scored as Tetris-related, while in the anticipation group there were three Tetris-related reports out of 112 usable reports. *Post hoc* Mann–Whitney tests revealed that Tetris-related reports were significantly more frequent in the Tetris group than in the control ($U = 7134.5$; $P = 0.006$) and anticipation groups ($U = 7609.5$; $P = 0.039$). No significant difference could be found between the control and anticipation group ($U = 5887.5$; $P = 0.336$).

Effect of repeated training, interval and vigilance state

Within the Tetris group, Tetris-related hypnagogic hallucinations were reported by 13 of the 16 experimental subjects (Fig. 2a; Table 3). Out of 485 usable reports across the three experimental days, 48 reports contained Tetris-related content, corresponding to a proportion of 10% of Tetris-related hypnagogic hallucinations after Tetris practice. Out of these 13 volunteers, two subjects reported 1 Tetris-related hallucination, four had 2 reports, and two had 3 reports. Five further volunteers reported 4, 5, 6, 8 and 9 Tetris-related hallucinations, respectively (Fig. 2a; Table 3).

The propensity to recall mental content at sleep onset did not significantly differ across days in the Tetris group (Friedman $\chi^2 = 4.246$, df = 2; $P = 0.120$). The rate of Tetris-related reports did neither significantly differ across days ($\chi^2 = 1.542$, df = 2; $P = 0.463$; Fig. 2b) nor across intervals ($\chi^2 = 6.912$, df = 4; $P = 0.141$; Fig. 2c). Out of the 48 task-related reports, 13 were obtained during the first day (13/48 = 27%), 19 during the second day (19/48 = 40%) and 16 during the third day (16/48 = 33%). A total of 10 reports were obtained after the interval of 15 s (10/48 = 21%), 3 after 45 s (3/48 = 6%), 10 after 75 s (10/48 = 21%), 11 after 120 s (11/48 = 23%) and 14 after 180 s after the onset of S1 (14/48 = 29%).

By contrast, the rate of Tetris-related reports significantly varied with respect to vigilance stage (Friedman $\chi^2 = 25.727$, df = 3; $P < 0.001$, Fig. 2d). There were significantly more reports after awakening from S1 (40/356 = 11%) than S3 sleep (0/1 = 0%; *post hoc* Wilcoxon Signed Ranks $P = 0.001$), and from S2 (8/124 = 6%) than S3 ($P = 0.018$). Whenever present, S3 was almost never associated with hypnagogic hallucinations (0/1). There were also more reports obtained following awakenings from S1 ($P = 0.001$) and S2 ($P = 0.018$) than in the wake state (0/4 = 0%). No significant difference between S1 and S2 could be found in this study ($P = 0.650$).

The state of vigilance also significantly influenced the proportion of both indirect (33 out of 48 Tetris-related reports across all stages; Friedman $\chi^2 = 27.690$, df = 3; $P < 0.001$; Fig. 2d, grey) and direct incorporations (16 out of 48; $\chi^2 = 12.000$, df = 3; $P = 0.007$; Fig. 2d, black). *Post hoc* Wilcoxon tests confirmed significantly less indirect reports during wake (0/0) compared with S1 (25/41 = 61%; $P = 0.001$) and S2 (8/8 = 100%; $P = 0.008$), and less during S3 (0/0) than during S1 ($P = 0.001$) and S2 ($P = 0.008$).

Table 2 Content of sleep-onset mentation reports of Day 1, in Tetris ($N = 16$), control ($N = 13$) and anticipation ($N = 14$) groups

		Tetris group						*Control group*						*Anticipation group*					
		Total		*Usable*		*Tetris*		*Total*		*Usable*		*Tetris*		*Total*		*Usable*		*Tetris*	
Day 1		*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*
Day	1	195	16	145	16	13	7	151	13	107	13	1	1	151	14	112	14	3	3
Interval (s)	15	45	16	34	15	2	2	29	13	24	13	0	0	28	13	23	12	0	0
	45	35	15	27	14	0	0	31	13	18	12	0	0	31	12	25	12	0	0
	75	40	16	30	15	2	2	34	13	25	13	0	0	31	14	21	11	0	0
	120	39	14	31	14	7	5	28	13	21	10	1	1	31	13	22	12	1	1
	180	36	14	23	13	2	2	29	12	19	11	0	0	30	13	21	11	2	2
Stage	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	3	1	0	0
	1	141	16	109	16	10	6	113	13	83	13	1	1	115	14	88	14	1	1
	2	53	11	35	15	3	3	36	10	23	9	0	0	31	8	21	7	2	2
	3	1	1	1	1	0	0	2	2	1	1	0	0	2	2	0	0	0	0
Class	Image	48	12	28	12	12	7	37	11	19	8	1	1	56	11	38	9	2	2
	Sound	15	9	9	6	2	1	6	6	1	1	0	0	12	7	6	5	0	0
	Thought	21	9	11	6	0	0	21	10	17	8	0	0	30	11	16	8	1	1
	Emotion	1	1	0	0	0	0	3	2	2	1	0	0	12	5	10	5	0	0
	kinaesthetic	1	1	1	1	0	0	3	3	1	1	0	0	14	7	8	5	1	1

The total number of included reports is shown for each category (i.e. attributed the same score by the three judges and recorded during the defined intervals), the number of usable reports (i.e. containing at least one spoken word and which could be fully transcribed) and the number of usable reports related to Tetris. Also, the number of volunteers contributing to these totals is shown. Interval length since the onset of S1 is a mutually exclusive category, as well as classification into vigilance stages. However, reports could be assigned in multiple sensory classes.

Table 3 Content of sleep-onset mentation reports across days within the experimental Tetris group

		Day 1						*Day 2*						*Day 3*					
		Total		*Usable*		*Tetris*		*Total*		*Usable*		*Tetris*		*Total*		*Usable*		*Tetris*	
Tetris group		*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*	*Reports*	*Subjects*
Day		195	16	145	16	13	7	214	16	166	16	19	10	238	16	174	16	16	9
Interval (s)	15	45	16	34	15	2	2	41	15	36	13	2	2	55	16	39	15	6	5
	45	35	15	27	14	0	0	43	15	30	14	1	1	46	16	34	16	2	1
	75	40	16	30	15	2	2	39	16	28	13	6	5	43	16	35	15	2	2
	120	39	14	31	14	7	5	45	16	38	16	3	3	43	15	29	15	1	1
	180	36	14	23	13	2	2	46	16	34	16	7	6	51	16	37	13	5	4
Stage	0	0	0	0	0	0	0	3	3	2	2	0	0	2	2	2	2	0	0
	1	141	16	109	16	10	6	147	16	122	16	16	9	159	16	125	16	14	8
	2	53	11	35	11	3	3	64	14	42	13	3	3	77	15	47	15	2	2
	3	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Class	Image	48	12	28	12	12	7	59	16	39	16	17	10	64	14	38	14	14	8
	Sound	15	9	9	6	2	1	18	9	8	6	2	2	18	9	4	3	0	0
	Thought	21	9	11	6	0	0	20	8	18	8	1	1	18	10	12	7	2	2
	Emotion	1	1	0	0	0	0	1	1	1	1	0	0	3	2	1	1	1	1
	kinaesthetic	1	1	1	1	0	0	1	1	0	0	0	0	1	1	0	0	0	0

The total number of included reports is shown for each category (i.e. attributed the same score by the three judges and recorded during the defined intervals), the number of usable reports (i.e. containing at least one spoken word and which could be fully transcribed) and the number of usable reports related to Tetris. Also, the number of volunteers contributing to these totals is shown. Interval length since the onset of S1 is a mutually exclusive category, as well as classification into vigilance stages. However, reports could be assigned in multiple sensory classes.

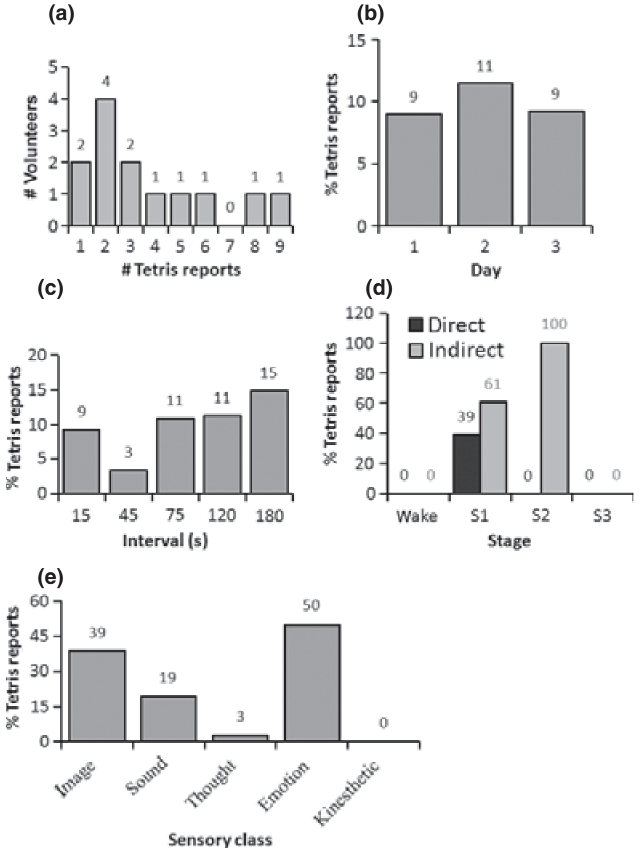

Figure 2. Content of Tetris-related sleep-onset reports in the Tetris group. (a) Contribution of individual subjects to the group total of Tetris-related sleep-onset mentation reports. (b–e) Percentage of Tetris-related sleep-onset reports relative to the number of usable reports of each category: (b) across days; (c) across interval since onset of S1; (d) according to sleep stage, separately for direct or indirect incorporations; and (e) according to sensory modality.

Again, no significant difference was found between S1 and S2 ($P = 0.112$). Despite the significant overall effect of vigilance state on direct reports, none of the *post hoc* pairwise comparisons was significant.

Characterization of mental reports

The rate of Tetris-related reports varied significantly across sensory classes (Friedman $\chi^2 = 31.141$, df = 4; $P < 0.001$; Fig. 2e). Relative to the number of usable reports in each sensory class, visual hallucinations (39/101 = 39%) occurred more frequently than auditory (4/21 = 19%; *post hoc* Wilcoxon $P = 0.009$), thoughts (1/39 = 3%; $P = 0.019$), emotions (1/2 = 50%; $P = 0.003$) and kinaesthetic reports (0/1 = 0%; $P = 0.001$). Interestingly, indirect visual Tetris imagery ($N = 14$) appeared as frequent as direct visual hallucinations of the original Tetris tetrominoes ($N = 13$). Very few reports actually consisted of Tetris-related thoughts ($N = 3$) or included an explicit emotional reference ($N = 1$).

Thematic consistency in Tetris-related reports was infrequently reported, either over days (Fig. 3a) or over successive awakenings during 1 day (Fig. 3b). Over days, thematic consistency was observed in six volunteers out of 16 in the experimental group (subjects a–f, Fig. 3a): four volunteers reported thematically consistent Tetris-related hallucinations on all three days (a–d), while two reported only the second and third day (e and f). Over repeated awakenings on a given day, four volunteers reported related Tetris content (subjects a, b, c, g, Fig. 3b). Namely, on Day 1, the 13 Tetris reports were provided by seven different subjects without any thematic persistency. On Day 2, the 19 Tetris hallucinations were reported by ten different subjects, of whom three subjects each had 2 related reports (a, c, g). On Day 3, 16 Tetris hallucinations were provided by nine different volunteers, two reporting each 2 consistent Tetris themes (b and c) and one reporting 3 consistent Tetris hallucinations (a). These reports were never consecutive: 3–11 unrelated reports (i.e. 6–26 min) were interleaved between the reports having a consistent theme.

Sleep-onset reports and Tetris performance

We examined whether sleep-onset Tetris-related reports were related to gaming performance. A RM-ANOVA showed no significant difference between the Tetris and anticipation group ($F_1 = 0.435$; $P = 0.515$) according to Tetris performance across training blocks. The learning curve was comparable in the two groups (no interaction group*block $F_7 = 1.826$; $P = 0.085$). Within the experimental group, a RM-ANOVA showed that Tetris performance changed across training blocks ($F_7 = 2.417$; $P = 0.025$) and across training days ($F_{1.178} = 9.945$; Greenhouse–Geisser $\epsilon = 0.589$; $P = 0.004$), although there was no interaction between days and blocks ($F_{14} = 1.024$; $P = 0.431$). Performance increased across training days (Fig. 4a), as indicated by *post hoc* LSD tests showing a significant progression in performance between Day 1 and 2 ($P = 0.042$), between Day 1 and 3 ($P = 0.001$), and between Day 2 and 3 ($P = 0.002$).

We did not find any significant correlation between the gain in performance across days and the rate of Tetris-related hypnagogic reports during post-training naps ($r = 0.074$; $P = 0.784$). This result was expected because, by design, 'naps' actually consisted of iterative awakening from light sleep, which interrupted and perturbed the ongoing mental processes. Moreover, in contrast to Wamsley *et al.* (2010), we only observed a trend between initial Tetris score and the rate of Tetris-related mental report density at sleep onset (Spearman's Bivariate Correlation Coefficient $r = 0.488$; two-tailed significance $P = 0.065$). However, we found that the maximum individual Tetris scores are significantly related to the absolute number of Tetris-related sleep-onset reports ($r = 0.535$; $P = 0.033$; Fig. 4b).

Alertness

The difference in content of sleep-onset reports between groups could not be attributed to difference in alertness. A RM-ANOVA

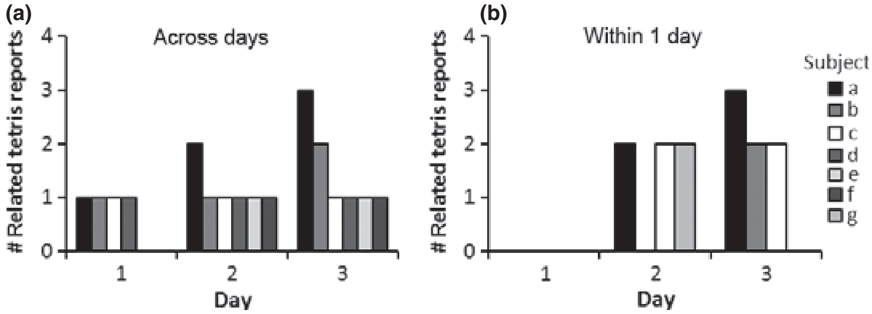

Figure 3. Thematic consistency of Tetris-related reports in the experimental group. (a) Across days; (b) over repeated awakenings during one particular day. The absolute number of Tetris-related reports with a consistent theme is shown for individual subjects.

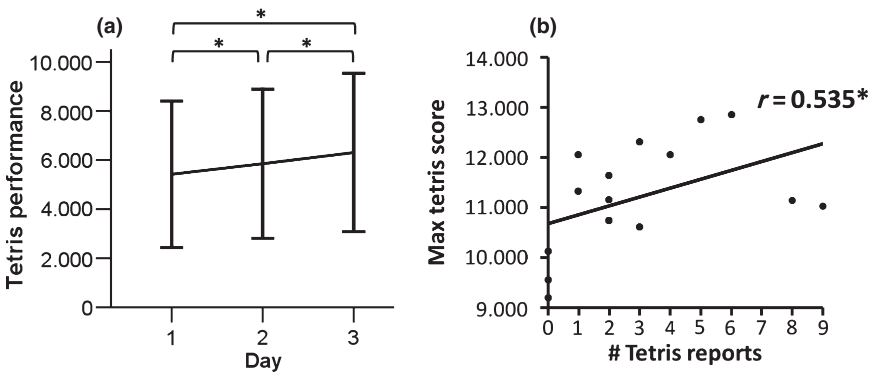

Figure 4. (a) Tetris performance scores (mean ± SD) across 3 days. Performance improved significantly across 3 days of practice. (b) Absolute number of Tetris-related sleep-onset reports in relation to Tetris performance. Each dot represents a participant. The number of reports was obtained by pooling all data of one subject across days, intervals and sleep stages. Tetris performance was measured as the maximal score obtained across 3 days of practice. The interpolation line shows a significant correlation ($P = 0.033$).

showed that there was no difference between groups either according to average reaction times during PVT ($F_2 = 2.592$; $P = 0.088$) or KSS scores ($F_2 = 0.351$; $P = 0.706$). Likewise, the RM-ANOVA across the three training days of the experimental group showed no significant effect of day on the PVT reaction times ($F_{1.356} = 0.068$; Greenhouse-Geisser $\epsilon = 0.678$; $P = 0.867$). Similarly, there was no significant difference in any sleep parameter that might account for the difference in content of sleep-onset reports between groups (Kruskal–Wallis tests; $P > 0.05$ for most parameters; Table S1) or across days in the Tetris group (Friedman tests; $P > 0.05$ for most parameters; Table S2). These negative results were expected as the experimental design essentially relied on awakenings from S1.

DISCUSSION

The data show that it is possible to reliably induce stereotypical hypnagogic hallucinations of Tetris during daytime naps in participants who have been playing the game during the preceding hours. The induced hypnagogic hallucinations, mainly visual and auditory, are stable over training days. They preferentially occur during S1 and S2, and much less frequently during full-blown wakefulness or deep non-rapid eye movement (NREM) sleep. Finally, their rate of occurrence is related to the best behavioural performance achieved over 3 days of practice. The content of hallucinations and their association to sleep onset allows some testable predictions about the organization of brain activity that they are associated with.

Hypnagogic hallucinations can be induced during a nap following training

Despite the strict rating by three independent judges, we recorded 48 Tetris-related reports at sleep onset out of 485 usable awakenings, i.e. a 10% rate of incorporation in the experimental group across 3 days. This contrasts with the 1% probability of reporting a Tetris-related hallucination in an independent group of volunteers who followed exactly the same procedures except for the practice of Tetris (one report out of 107 during one experimental day) and the 3% probability when subjects anticipated on Tetris practice (three reports out of 112 during 1 day). These data are strikingly similar to those reported following awakenings from nighttime sleep after Tetris practice (Stickgold *et al.*, 2000): 12% of all reports were task-related in the experimental groups (novices 17%, experts 10%), and 1% in the control group.

Variety of experience-induced hypnagogic hallucinations

Among all Tetris-related reports, 33% of the hallucinations corresponded to actual Tetris stimuli (16 out of 48). In keeping with their classical description (Foulkes and Vogel, 1965; Mavromatis, 1987; Schacter, 1976), these hallucinations were mostly visual and auditory. This was expected, given the visual and auditory nature of Tetris. The conspicuous absence of kinaesthetic hallucinations contrasts with their high frequency after training to Alpine Racer (37% of imagery reports; Wamsley *et al*., 2010). Again, this difference speaks for the tuning of hallucinatory content to the preceding waking experience.

Anticipation and experimental demand are not likely to explain the results. Indeed, significantly less Tetris-related reports were recorded in volunteers who knew they would practice Tetris 'after' the nap, in contrast to Wamsley *et al*. (2010) who reported an increased number of task-related reports on the baseline night. In addition, in the group who practiced Tetris 'before' the nap, a large proportion of hallucinations could hardly be explained by experimental demand because they were not identified as Tetris elements by the volunteers themselves. Far from being mere reproductions of Tetris stimuli, these representations included associations with mnemonic components and transformations of actual Tetris elements into novel elements. Finally, similar proportions of Tetris-related reports were previously observed in amnesic patients (8%; Stickgold *et al*., 2000).

It might be argued that repeated awakenings could produce an artificially high rate of Tetris-related hallucination. This is not consistent with the data: thematic consistency in Tetris-related reports (either across days or over repeated awakenings within 1 day) appeared in a minority of reports only. They never occurred consecutively and were always interspersed among thematically unrelated reports. Therefore, although it remains possible that multiple awakenings affect the incorporation of Tetris elements, mental content did not seem to be systematically biased by prior Tetris-related reports.

A substantial proportion of Tetris-related reports included mnemonic components: similar musical pieces heard in a different context, other board games, familiar objects spatially arranged as in Tetris. This finding suggests that Tetris-related memory traces interact with older memories and induce their spontaneous retrieval at sleep onset. Being preserved in amnesic patients (Stickgold *et al*., 2000), these representations potentially emerge from neocortical areas, mainly unimodal associative areas of the ventral (object identification) and dorsal visual streams (spatial arrangement, movements), unimodal auditory cortices or multimodal sensory cortices (Horovitz *et al*., 2008; Kjaer *et al*., 2002; Larson-Prior *et al*., 2009; Olbrich *et al*., 2009). The absence of affective content in Tetris-related hypnagogic hallucinations speaks for the lack of recruitment of emotion-processing structures, such as the amygdala and the reward system.

Experience-induced hypnagogic hallucinations are associated with S1 and S2

Based on polygraphic recordings, our data indisputably show that experience-dependent hypnagogic hallucinations are closely related to S1 and early S2 sleep, as is classically reported for hypnagogic hallucinations in general (Hori *et al*., 1994). This result is important because this transitory and unstable state of vigilance is associated with consistent changes in the regional organization of brain activity. During sleep onset, coherent spontaneous fluctuations in activity persist in the default-mode network (Horovitz *et al*., 2008). This network consists of a set of densely connected brain areas (medial frontal, posterior cingulate, precuneus, inferior parietal lobule; Damoiseaux *et al*., 2006; Fox and Raichle, 2007) in which the activity increases when subjects are asked to rest (Gusnard and Raichle, 2001), a condition promoting self-referential thoughts (D'Argembeau *et al*., 2008), mind wandering (Mason *et al*., 2007) and the unfocused monitoring of the environment (Gilbert *et al*., 2007), akin to sleep-onset mentation. Accordingly, activity in the medial prefrontal cortex and precuneus increases at sleep onset, relative to full blown wakefulness (Olbrich *et al*., 2009). Beyond the recruitment of this anatomo-functional backbone, sleep onset is mainly characterized by increased activity in sensory cortices (visual, auditory, somatomotor; Horovitz *et al*., 2008; Kjaer *et al*., 2002; Larson-Prior *et al*., 2009; Olbrich *et al*., 2009), which potentially underlies hallucinatory sensory experience at sleep onset.

Experience-induced hypnagogic hallucinations and learning

Although obviously related to recent experience, the present data do not provide strong evidence that experience-dependent sleep-onset hallucinations are quantitatively associated with critical steps in memory processing. We do not confirm the correlation between initial performance and sleep-onset task-related imagery reported by others (Stickgold *et al*., 2000; Wamsley *et al*., 2010). By contrast, we found that the maximal individual Tetris performance correlates with the rate of sleep-onset reports. However, the former parameter does not selectively probe memory processes as it also heavily depends on other cognitive functions, such as alertness, focused attention and motivation, during practice.

CONCLUSION

Hypnagogic hallucinations induced during daytime naps by prior practice of Tetris occur predominantly at the transition between wakefulness and sleep, especially in S1 and early S2 sleep. They mainly consist of visual and auditory hallucinations that often incorporate mnemonic components. These features predict that hypnagogic hallucinations may be associated with the state-dependent recruitment of mesial frontal and parietal areas and other components of the default-mode network, as well as with a persistent activity in neocortical unimodal or multimodal sensory areas previously recruited during prior wakefulness and in which recent experience can interact with previously encoded memories.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Comparison of the sleep parameters for Day 1 between experimental groups.

Table S2. Comparison of the sleep parameters within the Tetris group across the 3 days.

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