

temperature of 51°C, and 40 cycles on a PTC-200 thermocycler (MJ Research). A positive control was then performed under the same PCR condition with genomic DNA as template. All primer pairs generated the expected amplicons. RT-PCR were then performed on the RNA extract with a different thermocycler. All primer pairs generated amplicons of the expected sizes and sequences.

18. For the location and the designation of selected primers, see Web fig. 4 (11).
19. Primer sequences are as follows: Rc_gltX1, 5'-TCTT-TGGAATCTTGGCTGTAG-3'; Rc_gltX2, 5'-GATTAG-TGAGCAGGAAATA-3'; Rc_gltX3, 5'-GGATTGACGT-ACAAATTAC-3'; Rc_gltX4, 5'-CAAAGACTGTAGAG-ATATTGG-3'; Rc_hemC1, 5'-TACAGATAGCTTCCAA-CATC-3'; Rc_hemC2, 5'-CAAACCAATTTATGCTC-GG-3'; Rc_hemC3, 5'-CGGATTGACGTACAAATTAC-3'; Rc_hemC4, 5'-GTATCTAGATGCTAATTGCC-3';

Rc_ubiG1, 5'-CTTGCTACTGTCTAATTCTTC-3'; Rc_ubiG2, 5'-AAATATTAGACGTCGGTTGC-3'; Rc_ubiG3, 5'-CAGATTGACGCACAAATTAC-3'; and Rc_ubiG4, 5'-AATAAACCTATTGCCTTG-3'.

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region of the DnaE gene in *R. felis* (9). There is no significant similarity between this RS3-like sequence and our newly described RPE sequence.

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Replaying the Game: Hypnagogic Images in Normals and Amnesics

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Participants playing the computer game Tetris reported intrusive, stereotypical, visual images of the game at sleep onset. Three amnesic patients with extensive bilateral medial temporal lobe damage produced similar hypnagogic reports despite being unable to recall playing the game, suggesting that such imagery may arise without important contribution from the declarative memory system. In addition, control participants reported images from previously played versions of the game, demonstrating that remote memories can influence the images from recent waking experience.

People who engage in novel physical or mental activities for extended periods of time often experience a hallucinatory replay of the activities as they fall asleep, a phenomenon noted in both literary and scientific sources (1–3). Although the origin of these images in waking experience appears clear, the source within the brain and the function of such imagery are uncertain. If these images are mediated by declarative memory systems, amnesic patients with bilateral hippocampal lesions should not experience them. Because amnesics are capable of reporting dream experiences (4, 5), the question can be meaningfully addressed.

Most studies of dreaming involve reports of mental activity after forced awakenings from rapid eye movement (REM) sleep (6, 7) or after spontaneous awakenings in the middle of the night or morning (8). Hypnagogic mentation represents another source of sleep-state mental imagery

(9–12). Studies of the role of sleep in learning and memory have generally ignored the hypnagogic period, focusing instead on possible roles of REM sleep and deep, slow wave sleep (13–16).

We asked 27 participants to play 7 hours of the computer game Tetris (17) over 3 days, 2 hours at the first exposure and 1 hour each subsequent morning and evening (18). Three groups of participants were studied: 12 novices with no prior Tetris experience, 10 experts with considerable Tetris experience, and 5 amnesics with extensive, bilateral medial temporal lobe damage (19). Participants were repetitively prompted for mentation reports during the first hour of attempted sleep (20).

Even though the five amnesic patients were of average intelligence, they were unable to learn and retain new episodic information regardless of modality of presentation or the nature of the material. The performance of the amnesic patients showed only minimal, albeit significant, improvement over 7 hours of play (Fig. 1). The mean score increased from 537 points on participants' first game to a first session average of 651. Over the next five sessions, the scores increased by 36% to 884 points per game (21). Although game playing is often seen

as based on procedural learning (which is preserved in amnesia), the amnesic group demonstrated impoverished learning in comparison with normal novices, suggesting that Tetris proficiency may also depend on declarative memory systems. This interpretation is supported by the finding that left and right hippocampal glucose utilization during Tetris play decreases during training in proportion to improvement in performance, suggesting a shift away from hippocampal dependence as learning plateaus (22).

Three of the five patients produced a total of eight reports of Tetris imagery across three nights. These reports accounted for 7.4% of all hypnagogic reports collected, similar to that seen in normal participants (7.2%; Fig. 2A) (23). In contrast, there was only a single report of a thought about Tetris without clearly associated imagery (<1%; Fig. 2B). As with the normal participants, the visual imagery reported was highly stereotyped (24).

Normal controls without prior experience playing Tetris had first game scores averaging 786, significantly higher than that of the amnesics (25). They showed considerable improvement in performance over the 3 days and six sessions (Fig. 1) (26). The appearance of hypnagogic Tetris images in novices was very similar to that seen with amnesics. Nine of 12 Tetris novices produced a total of 19 reports of Tetris imagery over two nights of recording, a report rate very similar to that of the amnesics (Fig. 2A). The imagery described showed the same highly stereotyped content as seen with the amnesics (27). Novices produced 12 reports of thoughts of Tetris without imagery (Fig. 2B). Such reports, clearly linked to declarative memories, were virtually absent in the amnesics.

Ninety percent of the reports with images from these novices (17 out of 19) were obtained on the second night. In contrast, two-thirds of the reports of thoughts alone (8 out of 12) occurred on the first night (Fig. 2). Although this difference in distributions is

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REPORTS

highly significant (28), further studies will be needed to confirm the finding. Nevertheless, the distribution of images is not what would be expected if the images were the product of either demand characteristics or a simple and automatic replay of recent, repetitive, sensory stimuli.

Normal participants with extensive experience playing Tetris, but who in general had no recent practice (29), produced high scores from the start and showed no significant improvement over the six sessions (Fig. 1) (30). Nevertheless, they also produced hypnagogic Tetris imagery. Over the three nights, 5 of the 10 experts produced 11 reports of hypnagogic Tetris imagery (4.7% of 235 reports), as well as 13 reports of thoughts without images (5.5% of 235 reports). As with the other groups, the imagery reported was stereotyped (31). In addition to these stereotyped images, two of the five experts who reported Tetris imagery described images from earlier versions of the game, which they had not played in the last 1 or 5 years, respectively (32). In these cases, the image construction process followed associative links and incorporated older memories in preference to images from recent play.

Normal participants (novices and experts combined) showed significantly different patterns for reports of images and thoughts across the sleep onset period (Fig. 3). After an initial 2.5-fold increase from presleep to 15 s into sleep (4.5% compared with 11.3%), the frequency of Tetris images then dropped in half (to 5.7%) after just 2 min. In contrast, thoughts about Tetris dropped in half between the presleep period and 15 s into sleep (7.8 to 3.9%) and then remained constant across the next 3 min (4.2% at 3 min).

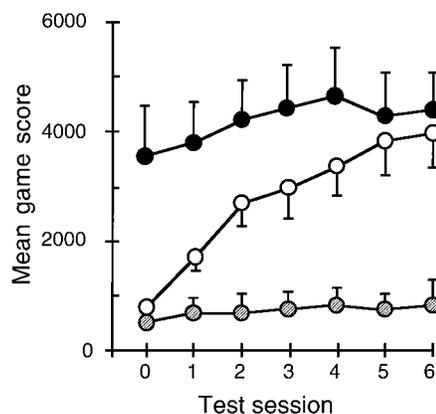


Fig. 1. Game performance. Mean scores, averaged across participants, for each play session. Participants receive about 20 points for each piece put into play. Session "0" is first game score of first session. Solid circles, experts; open circles, novices; hatched circles, amnesics. Error bars = SEM.

Identifying the sources of memories used in dream construction is normally contingent on the investigator's subjective interpretation of obscure symbolic transformations of the original memory or on the dreamer's own subjective evaluation. In the case of hypnagogic reports of Tetris images, no such subjective interpretations are needed. Only reports that explicitly described images or thoughts related to Tetris were counted. Indeed, what was most striking about the data was the strong similarity in reports from different individuals. In all cases, reported images included seeing Tetris pieces, usually falling in front of one's eyes and sometimes rotating or fitting into empty spaces at the bottom of the screen. On rare occasions, participants also reported seeing completed lines disappearing. Among the 38 reports of imagery, there were no reports of seeing the picture surrounding the play window, the scoreboard, or the keyboard or of typing on the keyboard, and there were only two reports of seeing the computer itself. In none of these reports did the imagery appear bizarre. None appeared in inappropriate settings or associated with inappropriate thoughts.

In addition to collecting hypnagogic reports at sleep onset, participants were also instructed to report any thoughts, images, or feelings about Tetris that occurred at other times. Seven of 12 novices and 4 of 10 experts reported a total of 44 images of Tetris during waking. As with hypnagogic images, the vast majority of daytime images occurred only after a 24-hour delay, with only four reports (9%) occurring on the first day of play (33). Thus, the production of this imagery is not limited to the sleep state but can occur in waking as well. Two spontaneous reports of hypnagogic Tetris imagery were reported by novices at sleep onsets other than when computer-initiated awakenings were performed. These included one report of sleep onset imagery from an afternoon nap on the first day of the protocol and one of sleep onset after a spontaneous 2:30 a.m. awakening on the

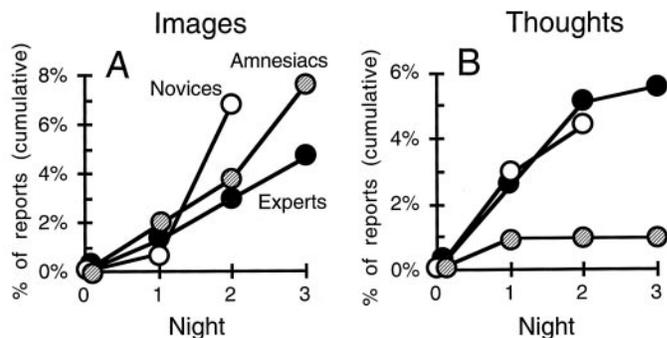
third night. These images, both conceivably sleep onset REM reports, were more complex and bizarre than the others in our sample (34).

The questions of how material is selected for and then incorporated into dreams and what function this entire process serves remain largely unresolved. But the data presented here, looking at sleep onset hypnagogic imagery, provide some insight into these issues.

Out of 27 participants, 17 (63%) reported stereotypical hypnagogic images of Tetris during the first nights of play, imagery clearly induced by the earlier Tetris play. Unlike the images of REM sleep dreams, these images were relatively accurate representations of the actual visual imagery perceived during play of the game, albeit abstracted, with removal of nonessential game elements. This highly consistent imagery across participants and groups suggests that image construction in all groups extracted and abstracted the most salient aspects of the experience by a similar process. This, along with the report rate from amnesic participants, argues strongly against demand characteristics playing a major role in the production of reports of Tetris imagery (35).

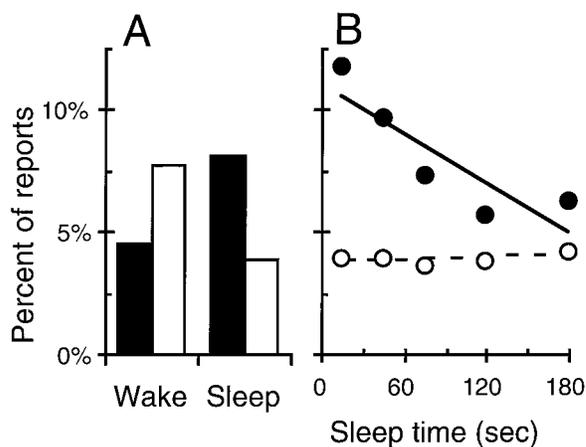
The apparent 24-hour delay between the start of play and the subsequent appearance of game images in the reports of novices suggests that the rules for selection of images for incorporation at sleep onset involves a complex algorithm. Similar lags have also been reported between waking experiences and their apparent incorporation into REM dreams (36–38). The time course of appearance of Tetris images across the sleep onset period is also striking. The rapid decay in frequency of Tetris images across the first 2 to 3 min of sleep occurred in the face of a steady or even rising rate of report of images in general over this time interval (9, 10). Thus, the occurrence of specific Tetris images seems uniquely linked to sleep onset itself.

Fig. 2. Report frequencies. For each participant group, the cumulative number of reports containing (A) visual images of Tetris or (B) thoughts of Tetris without images is given, normalized to the total number of reports collected across three nights. Reports from novices were collected on only the first two nights, and graph points are normalized for three nights. The upward curvature of the curves in (A) indicates that reported frequency of images increased across the nights, whereas the downward curvature in (B) indicates that the frequency of thoughts alone decreased across nights (53).



REPORTS

Fig. 3. Images and thoughts of Tetris across the sleep onset period. **(A)** Percentage of reports collected before sleep onset (wake) and after sleep onset (sleep) that contained either images of Tetris (solid bars) or thought of Tetris without images (open bars). Although thoughts were most common in the presleep period, images were most common after sleep onset; the difference was significant (chi-square test: $\chi^2 = 4.6$, $df = 1$, $P = 0.033$). **(B)** Percentage of reports collected after sleep onset that contained either images of Tetris (solid circles) or thoughts of Tetris without images (open circles). Although the frequency of thoughts remained constant over the 3 min of sleep onset ($P > 0.4$), the frequency of images decreased with increasing periods of sleep from 11.3% at 15 s to 5.7% at 2 min ($r = 0.86$, $df = 3$, $P = 0.06$).



Because reported images originated from recent experiences, one might assume that hypnagogic image construction is mediated by the hippocampal declarative memory system. Our data argue against this assumption. If image construction simply reflected reactivation of recent memories, the images should have been most common on the first night. Instead, only 10% of the images reported by novices occurred on the first night, whereas 90% occurred on the second night. Two of five experts reported imagery incorporating abstracted details from Tetris experiences that took place 1 to 5 years earlier. These reports underscore the influence of remote memories (that may be less dependent on hippocampal systems) on image construction. Most telling is the presence of these same images in the hypnagogic reports from amnesics. All of the patients were densely amnesic and could not produce declarative memories of recent events. Indeed, none of them remembered the Tetris game or the experimenter from one session to the next (39). These participants produced hypnagogic images of recent events even though they did not have declarative knowledge of them. The idea that the declarative memory system is not active at sleep onset is further supported by the results of Wyatt *et al.* (40, 41), who demonstrated that explicit recall of words and word pairs was impaired when words were presented within 3 min of sleep onset.

The relative preservation of hypnagogic images in amnesia suggests that they do not depend on medial temporal structures involved in declarative memory (42). Instead, it is likely that these perceptual representations are mediated by implicit memory processes, as seen in other studies with amnesic patients (43–45). It should be noted that the amnesics were substantially older than the normal novices and that the contribution of age remains an alternative explanation

that will require further investigation.

This lack of hippocampal involvement in image construction could explain many of the formal properties of dreams (46). Without the anchor of temporal and spatial associations found in hippocampal declarative memories, much of the bizarreness of dreams, including their discontinuities, incongruities, and uncertainties (47), would appear almost inevitable. This would be especially true during REM sleep, when there is evidence not only that hippocampal output is blocked (48), but also that weak associations in cortical memory systems are preferentially accessed (49), thus the hypnagogic report from an afternoon nap of Tetris pieces falling onto a garden path (34).

We have very little information concerning the function of these images or of the physiological processes underlying them. The probability of having Tetris images for both the novice and expert groups was inversely related to initial performance, suggesting a relation to the learning process itself (50). Experts incorporated related memories from earlier play, memories that were presumably activated by the recent Tetris play. One possible function for the activation of these memories would be to alter their strengths, structures, or associations in ways that are adaptive for the organism. With such predictable associations being made and presumably strengthened at sleep onset, one can only surmise that during REM sleep more unpredictable, potentially valuable, but frequently useless, associations are tested and, when appropriate, similarly strengthened.

References and Notes

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Upon my way to sleep . . .
And I could tell
What form my dreaming was about to take.
Magnified apples appear and disappear,
Stem end and blossom end,
And every fleck of russet showing dear.
My instep arch not only keeps the ache,
It feels the pressure of a ladder-round.
I feel the ladder sway as the boughs bend."

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17. The Macintosh version of Tetris (copyright 1988, Sphere, Inc.) was obtained from Spectrum HoloByte (Alameda, CA). For a more complete description of the game, see *Science Online* (51).
18. Sessions began between 7 and 11 a.m. and between 7 and 11 p.m.
19. Novices were 18 to 25 years old, had less than 10 hours of lifetime video game experience, and had no prior experience with Tetris. Experts were also 18 to 25 years old. They averaged over 200 hours of lifetime experience with Tetris (50 to 500 hours), but only one participant reported having played in the 3 weeks before testing. Amnesic patients were 21 to 62 years old [42.8 ± 14.9 (SD)] and were all apparently novices. All had extensive medial temporal lobe damage, including the hippocampal formation. Three suffered lesions secondary to anoxia, one to Herpes simplex encephalitis, and one to a cerebrovascular accident. Patients had 12 to 20 years of education (15.2 ± 3.6 years). They had normal IQs (Wechsler Adult Intelligence Scale III, FSIQ = 94 ± 11) but severely impaired memory functions (Wechsler Memory Scale III—General Memory Index: 48.6 ± 3.2). Additional neuropsychological test results can be found on *Science Online* (51). All participants provided internal review board–approved informed consent before participation in the study. Participants in the three groups provided similar numbers of hypnagogic reports. Novices averaged 7.6 reports per night, experts 7.8 per night, and amnesics 7.2 per night. In addition, nonamnesic participants were instructed to carry the recorder with them during the day and report any occurrences of "thoughts, images, or feelings" related to Tetris that they experienced while awake. Reports from nonamnesics were dictated into Pearlrecorder S950 hand-held microcassette recorders that automatically stamped the time and date onto the recording. Those from amnesics were recorded by the experimenter, who in all cases prompted the patient for the report, often as a supplement to the computer-generated prompt. Novices were probed during the first two nights of play, as were 3 of the 10 experts. On the basis of the data from these participants, the final seven experts and all amnesics were probed for three nights.
20. Experimental awakening was done with the Nightcap sleep monitoring system as described by Rowley *et al.* (10). Reports were collected from the

REPORTS

- presleep period, when participants were attempting to fall asleep, as well as after intervals of 15 to 180 s of objective sleep, during the first hour after participants retired for the night. Multiple forced awakenings were made each night, in pseudorandom order, balanced across participants and nights, after 15, 45, 75, 120, and 180 s of eyelid quiescence (10), and additional reports were requested after 3, 6, and 9 min of wake before the initial sleep onset and after 3 min of wake after any forced awakenings, when such wake periods occurred. There were a maximum of 10 report requests per night and no more than 5 from periods of wake. The five periods of sleep (15 to 180 s) produced between 48 and 55 reports each; there were 154 wake state reports. Frequencies of requests and reports of Tetris imagery or thoughts did not differ significantly between novices and experts. Participants were instructed to dictate reports of any "thoughts, images, or feelings" that they were experiencing before being prompted to report or, if appropriate, to state that there were none. Participants were normally awakened by digitized voice recordings when the computer identified an appropriate wake or sleep interval and instructed to dictate their reports into microcassette recorders. In some cases, amnesic participants were awakened by the experimenter.
21. Because of missed sessions, individual patients played four to six sessions. Repeated measures analysis of variance (ANOVA) showed significant improvement over four sessions ($n = 5$, $F = 6.65$, $P = 0.007$). All patients completed at least 18 games during the first session and showed no significant improvement across these 18 games (individuals: $r < 0.11$, $P > 0.3$ for each; group: $r = 0.01$, $P = 0.98$). By contrast, age-matched normal novices (51 ± 8.7 years) all showed significant improvement (individuals: $r > 0.5$, $P \leq 0.03$ for each; group: $r = 0.73$, $P = 0.0006$) and improved an average of 107% across the one session. The 36% increase across six sessions seen in patients is comparable to the 29% increase seen over six sessions in a single amnesic patient by Winter (52).
 22. R. J. Haier et al., *Brain Res.* **570**, 134 (1992).
 23. Normals, consisting of 12 novices and 10 experts, produced a total of 30 reports of Tetris imagery in 418 reports (see text).
 24. In all cases, reported images included Tetris-like shapes, usually falling in front of the participants' eyes and sometimes rotating or fitting together. In no case did the participant report seeing or touching the keyboard or actually playing the game and in no case was the imagery seen in inappropriate contexts. Thus, one amnesic reported, "I was just trying to figure out those shapes and how to get them aligned" (JM: day 2), whereas another reported "thinking about little squares coming down on a screen and trying to put them in place" (PLS: day 3). The third amnesic reported seeing "images that are turned on their side. I don't know what they are from, I wish I could remember, but they are like blocks" (DF: day 1). Despite references to "those shapes" and "a screen," participants gave no indication of recalling the origin of these images. Rather they appear to be images of events for which they had no conscious recollection.
 25. Two-tailed t test, $df = 14$, $t = 3.1$, $P = 0.008$. For this and all other analyses of novice scores, one participant, whose initial game score was 24 SD above the mean of the other 11 novices, was excluded.
 26. Repeated measures ANOVA across the first game and six sessions: $df = 6$, $F = 17.1$, $P < 0.0001$. Post-hoc contrasts showed significant improvements after the first game ($P < 0.0001$) and first ($P < 0.0001$), second ($P = 0.005$), and third ($P = 0.01$) sessions. There was a trend toward additional improvement after the fourth session as well ($P = 0.11$).
 27. Thus, one participant reported, "I'm just watching tiles fall down" (DW: day 2), whereas another reported, "I'm rotating it and I'm fitting the blocks in like I'm supposed to" (AM: day 2). A third reported "just seeing Tetris shapes floating around in my head like they would in the game, falling down, sort of putting them together in my mind" (JEG: day 2). It should be emphasized that none of these reports described episodic memories. For example, no one reported being in their room, sitting at their desk, or using their computer. As with the amnesics, the images occurred without reference to time or place and appeared, rather, to be extracted and abstracted from the actual experience.
 28. Chi-square test: $\chi^2 = 10.6$, $df = 1$, $P = 0.001$ for reports; $\chi^2 = 8.2$, $df = 1$, $P = 0.004$ for participants.
 29. Of the 10 participants, only one had played within the last 3 weeks, and two had not played in the previous year.
 30. Repeated measures ANOVA across the first game and six sessions: $df = 6$, $F = 1.24$, $P = 0.30$.
 31. Reported imagery included "a Tetris screen and the pieces fitting together in various ways" (ANJ: day 2), and "[I'm] seeing in my mind how the game pieces kind of float down and fit into the other pieces, and am also rotating them" (TPR: day 2).
 32. One expert reported, "It's weird ... because I don't see it the way we play it on this computer. I see it like I used to play it at home where its in different colors and stuff like that and the boxes look a little different." She also reported hearing the music that accompanied the game on her original Nintendo version, whereas the version used in the experiment was silent.
 33. Binomial distribution analysis, $P < 0.0001$.
 34. In one instance, the participant reported dozing off in the afternoon while "thinking about a project I have for work that involves designing a garden space indoors and as I was thinking about it in my mind little Tetris pieces kept falling down into the garden spaces, which they wouldn't really [do] because [they are] geometrical and garden spaces are nice and flowing."
 35. One concern in this study was whether demand characteristics would bias participants to report Tetris images when they did not, in fact, occur. Several aspects of the actual reports argue against this. The reports from amnesics obviously were not fabricated to please us, because participants could not even remember that they had played Tetris. Second, the extreme similarity between reports would not be expected. Thus, we received no reports of participants "playing" Tetris, which we would have expected from invented reports. In addition, the preponderance of images from novices on the second night and the higher rate of images reported after sleep onset compared with the presleep period are counterintuitive to the expectations of demand characteristics. A more subtle concern is that more general geometric images were being interpreted as Tetris images. To look for nonspecific effects, we searched the text of 796 hypnagogic reports from an earlier study (10) for the words square[s], rectangle[s], star[s], diamond[s], block[s], geomet[r]y,ic, sparkl[e,ing], kaleidoscop[e,ic], shape[s], pattern[s], tile[s], fall[ing], rotat[e,ed,ing], turn[ed], mov[e,ing], fit[ting,ted], Tetris, game[s], screen[s], and video[s]. Only four reports (0.5%) contained these words in relevant forms (e.g., references to Harvard "Square", "Star" Trek, "falling" asleep, and being out of "shape," were excluded). The words rectangle, diamond, sparkling, kaleidoscope, tile, geometric, rotate, and Tetris did not appear in any context. Taken together, these findings suggest that there is no important contamination of our data from responses to demand characteristics, although the possibility of some minimal contribution cannot be eliminated.
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 39. On one occasion, after playing her evening session of Tetris, participant PLS showered and put on her pajamas in preparation for bed. Upon returning to her bedroom, she was clearly surprised to find the experimenter sitting by her bed, and asked him, "Who are you, and what are you doing in my bedroom?" Nevertheless, she subsequently produced hypnagogic Tetris imagery. The complete dissociation of explicit memory from hypnagogic imagery was seen most clearly in the case of DF, who explicitly reported being unaware of the source of these images.
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 51. Supplementary material is available at www.sciencemag.org/feature/data/1050057.shl.
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 53. Total numbers of hypnagogic reports and of participants reporting images and thoughts were as follows: novices (open circles): 183 reports from 12 participants, 9 of whom (75%) provided 19 reports of images and 6 of whom (50%) gave 12 reports of thoughts without images; experts (filled circles): 235 reports from 10 participants, 5 of whom (50%) gave 11 reports of images and 5 of whom (50%) gave 13 reports of thoughts without images; and amnesics (hatched circles): 108 reports from 5 participants, 3 of whom (60%) provide 8 reports of images and 1 of whom (20%) reported a single thought without images.
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