adaptation in bats in the present study suggest the opposite conclusion: that the visual system of *Glossophaga* is monochromatic and does not include a separate ultraviolet light receptor. Because the absorption range of opsin-based pigments extends into the ultraviolet region[16], ultraviolet vision does not necessarily require the presence of a specific receptor. However, because ocular media act as ultraviolet light filters[17], use of this β-band sensitivity was not expected in mammals. Nevertheless, ultraviolet light perception of *Glossophaga* in all likelihood is accomplished by stimulation of the β-band of the photoreceptor. This is a mechanism of ultraviolet vision that has not previously been shown in intact eyes of mammals. Exceptions are aphakic humans (people who have had lenses surgically removed). Their rod-based spectral sensitivity closely resembles the spectral sensitivity obtained here[18] (Fig. 1, open squares). Thus, ultraviolet light absorbance by intact ocular media of the small eye of *G. soricina* is equal to ultraviolet absorbance by the cornea and by aqueous and vitreous humour in the absence of lenses in the larger human eye. The close correspondence of scotopic spectral sensitivities between bat and aphakic humans corroborates our inference of a single photo-receptor mechanism underlying ultraviolet and scotopic visual sensitivity in *Glossophaga* bats. □

Methods

Bats orient by echolocation, and therefore experiments were conducted in darkness without ambient adaptation light. Animals were adapted to scotopic conditions for at least 1 h before measurements were taken. Choice of the non-illuminated stimulus was always rewarded in experiments I and III from an artificial flower underneath the respective test panel.

Experiment I

Spectral sensitivities were determined on the basis of 67 threshold measurements encompassing more than 75,000 behavioural decisions by three bats (females F1 and F3, and male M4). The pigment template in Fig. 1 was calculated from equations 1 and 4, and Fig. 7 from ref. 19, and the data from the two females. The best fit was determined by a least-squares method. The degree of fit between measurements and template was compared by three-way ANOVA with individual, sex and wavelength as independent variables, and log difference between measurement and template as the dependent variable. In the spectral range from 310 nm to 485 nm, light stimuli were produced with a xenon high-pressure lamp (150 W, XBO150, Osram; VX 150/1 kf-2, Siemens AG) and guided through quartz light conductors (active diameter 5 mm) to the test panels (triangles in Fig. 1). The intensity was adjusted by quartz glass filters. For the spectral range from 382 nm to 688 nm, we used 5-mm light-emitting diodes (Kingbright Electronics; Marl International Ltd) inserted directly into the test panels (circles in Fig. 1). The spectral composition of the light stimuli was produced or modified using interference filters (Schott). The stimulus intensity was determined by using a calibrated photomultiplier with a gallium arsenide photoelectric cell (type PM270C, detector PM-270-OD, International Light). The measured values of stimulus intensity in $W\,cm^{-2}$ were corrected with the spectral-sensitivity curve of the photomultiplier and converted to number of quanta $cm^{-2}\,s^{-1}$. This value is given by the energy of a stimulus divided by the energy of a light quantum (Q) (with $Q = hn$; $h = 6.626176 \times 10^{-34}\,J\,s^{-1}$ (Planck quantum of action); $n = c/l$; $c = 3 \times 10^{8}\,m\,s^{-1}$ (speed of light); l = wavelength). The spectral emission curves of all stimuli and adaptation lights (see experiment III) were determined using a photometer (Spex 1700-III) with photomultiplier (S-20 R562, Hamamatsu).

Experiment III

The adaptation light used was a 10×10 cm illuminated panel (light box). The stimulus light (382 nm or 522 nm) was positioned within a 5-mm hole in the centre of this light box and was thus surrounded by adaptation light. Adaptation lights were generated in the ultraviolet light range ($\lambda_{max} = 392$ nm) by UG-1 glass filters (Schott) as panels in front of four fluorescent lamps (Linux-9W/78, Radium Wipperfürth), and within the red range ($\lambda_{max} = 590$ nm) by RG glass filter panels (Schott) in front of incandescent lamps. Data based on 16 threshold measurements (three each for *a*, *b*, *c* and *d*, and four controls at 382 nm and 522 nm; see Fig. 3) were obtained from individual F1.

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Consolidation during sleep of perceptual learning of spoken language

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Memory consolidation resulting from sleep has been seen broadly: in verbal list learning[1], spatial learning[2,3], and skill acquisition in visual[4–8] and motor[9–11] tasks. These tasks do not generalize across spatial locations or motor sequences, or to different stimuli in the same location[5,11,12]. Although episodic rote learning constitutes a large part of any organism's learning, generalization is a hallmark of adaptive behaviour[13]. In speech, the same phoneme often has different acoustic patterns depend-ing on context. Training on a small set of words improves performance on novel words using the same phonemes but with different acoustic patterns, demonstrating perceptual generalization[14]. Here we show a role of sleep in the consolidation of a naturalistic spoken-language learning task that produces generalization of phonological categories across different acous-tic patterns. Recognition performance immediately after training showed a significant improvement that subsequently degraded over the span of a day's retention interval, but completely recovered following sleep. Thus, sleep facilitates the recovery and subsequent retention of material learned opportunistically at any time throughout the day. Performance recovery indicates that representations and mappings associated with generaliza-tion are refined and stabilized during sleep.

In perceptual learning of synthetic speech, listeners are presented with speech produced by a computer-controlled text-to-speech synthesizer. Synthetic speech is difficult to understand and naive listeners make a greater number of perceptual errors than they do in recognizing natural speech, but show significant learning, improving by an average of 45 percentage points after eight 1-h daily training sessions. Once acquired, performance improvement lasts for at least six months[14]. This magnitude of learning is all the more remarkable in that listeners never hear the same word twice—all learning is generalization[14,15]. This paradigm allowed us to investigate the role of sleep in a naturalistic learning task that produces generalization. Two groups were given a pretest, trained, and then retested after a 12-h retention period. For one group, pretest and training started at 9 a.m., and the post-test was given after 12 h of waking, at 9 p.m.; for the second group, pretest and training were at 9 p.m., and the post-test was given at 9 a.m. the following morning, after 12 h that included sleep. A third, control group received pretest, training and post-test within a single session with no retention interval.

Training had a strong, reliable and immediate effect on the perception of synthetic speech. Control-group identification accuracy ($n = 24$ participants) increased by an average of 21.4 ± 1.6 (mean $\pm$ s.e.m.) percentage points from pretest (32.9 ± 1.9) to post-test (54.3 ± 2.5). The improved performance represents generalization, because the pretest, post-test and training words were all different. By comparison, after a 12-h waking period, performance accuracy improved by only 10.1 ± 2.0 percentage points between pretest (37.2 ± 2.4) and post-test (47.3 ± 3.3) ($n = 12$), a significant reduction compared with the full control group (Fisher's $P < 0.01$) and by comparison with the matched morning control subgroup ($t_{22} = 2.6$, $P < 0.02$), showing that the two groups, trained at the same time, differ significantly after a 12-h waking retention period. After a regular sleep period, however, performance improved by an average of 18.7 ± 1.6 points ($n = 12$). Learning displayed by the 12-h sleep group did not differ from that of the control group ($P = 0.28$), but both groups performed significantly better than the 12-h waking retention group (Fisher's $P < 0.01$ for both) (Fig. 1). We also confirmed these results within a single group ($n = 12$), given a pretest and training in the morning, a post-test after a 12-h waking period, and a second post-test after a 12-h sleep period. Performance improved by 10.5 ± 2.6 percentage points from morning pretest (28.3 ± 1.9) to evening post-test (38.9 ± 3.2), and significantly more (19.1 ± 2.0 percentage points, $P < 0.01$) from pretest to the following morning's post-test (47.6 ± 2.4).

The performance difference after 12 h awake and 12 h including regular sleep might be due to diurnal effects on testing or training. However, a comparison of morning pretest performance (32.8 ± 1.3) with evening pretest performance (32.7 ± 1.7) for all groups revealed no reliable diurnal difference ($F_{1,82} = 0.005$, $P = 0.94$). Furthermore, half of the control group was tested and trained in the morning, and the other half in the evening. The evening group ($n = 12$) improved by an average of 24.3 ± 1.5 points, whereas the morning group improved by an average of 18.5 ± 2.6 points, a marginally significant effect ($P = 0.06$). Indeed, young adults are at the acrophase of their circadian cycle in the evening, and perform better at short-term memory and other cognitive tasks than in the morning[16], a circadian effect both opposite in direction and much smaller in magnitude than the performance deficit we observed. Thus, simple circadian effects on pre- or post-test performance cannot explain the current findings.

Learning (in contrast to test performance) may also exhibit circadian effects. To examine this possibility, two further groups were tested, receiving pretest and training either in the morning ($n = 12$) or in the evening ($n = 12$). The post-test was given after a 24-h retention period, controlling for circadian effects on test performance. If sleep stabilizes learning associated only with the performance level achieved immediately before sleep, performance for the 24-h retention groups should be predicted by performance levels at the time of sleep (high for the evening-trained and low for the morning-trained groups). Instead, participants showed learning of 18.4 ± 2.1 and 18.9 ± 1.6 percentage points for morning and evening testing, respectively. These groups did not differ significantly from each other ($P = 0.86$) or from the 12-h sleep group ($P = 0.93$ for both), but both differed significantly from the 12-h awake group ($P < 0.01$ for both comparisons). Clearly, performance levels were independent of when the training took place during the first day. Moreover, sleep stabilized learning so that subsequent waking did not adversely affect retention of learning by the following evening.
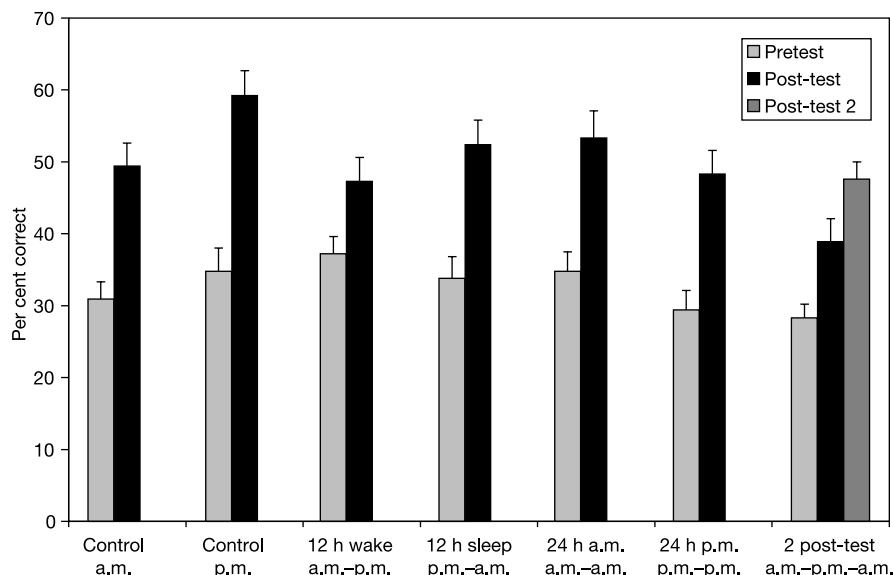
Figure 1 Sleep effect on retention of learning for word identification. Pairs of bars indicate pretest (light grey) and post-test (black) scores for each condition ($\pm$s.e.m.). Starting with the leftmost pair of bars: 9 a.m. control group, 9 p.m. control group, 12-h waking group, 12-h sleep-phase group, 24-h group with 9 a.m. sessions, 24-h group with 9 p.m. sessions, 24-h group with 9 p.m. and 9 a.m. post-tests (dark grey bar is post-test 2 at 9 a.m.).

We have demonstrated consolidation during sleep for complex, generalized skill acquisition. Previous research has shown that sleep affects perceptual[4,7,8] and motor learning[10], in tasks limited to specific patterns or spatial locations. In the present study, participants learned a new mapping from complex acoustical patterns to pre-existing linguistic categories, which generalized to new stimuli[14,15]. This behaviour involves distinct processes[17], the formation of specific memories associated with the learned words (episodic, declarative representations), and the establishment of a mapping defined over the set of learned words that supports generalization to new utterances (procedural learning). When participants are given equal amounts of training across days with a small set of repeated words or with entirely novel words, different patterns of learning are seen. Training on a set of repeated words produces near-perfect performance on those words, but very poor generalization to novel test items. Training on all novel items produces a much larger generalization effect on the post-test[15]. The generalization effect cannot be accounted for by memorizing acoustic patterns of phonemes, because different acoustic patterns may represent the same phoneme and the same pattern may represent different phonemes[18], depending on context. These context-conditioned effects even span syllable boundaries[19] and are used in perception[20]. The acoustic patterns of phonemes in different phonetic contexts cannot be statistically inferred from the distribution of a sample of those utterances[21], and rote memorization and linear interpolation across a small set of acoustic patterns for each consonant and vowel cannot explain human speech recognition[22]. To recognize new words, listeners must learn to generalize, predicting the acoustic consequences of different phonetic contexts.

Sleep has at least two separate effects on learning. Sleep consolidates memories, protecting them against subsequent interference or decay. Sleep also appears to 'recover' or restore memories. In the perceptual learning task we used, memories are sufficiently robust to last for up to six months[14] or, in a comparable reading-acquisition task, even a year[23]. Such robust memory represents a significant selective advantage that an organism might accrue from sleep-mediated processes. Learning can take place at any time during a waking period and any loss due to decay or interference will be restored by sleep. This also implies that a selective advantage of sleep is to enable organisms to learn opportunistically any time during the day without penalty as to robustness of learning.

We do not know if the reduction in performance observed after periods of wakefulness is due to decay of learned material, or to interference from listening to speech or other cognitive processing during the day. If performance is reduced by interference, sleep might strengthen relevant associations and/or weaken irrelevant associations, improving access to relevant memories. If performance is reduced by decay, sleep might actively recover what has been lost, presumably by an interaction between partially retained memories (words) and partially retained mappings that resulted from learning the word set. □

Methods

Participants listened to computer-generated monosyllabic consonant–vowel–consonant (CVC) words taken from a phonetically balanced (PB) list (approximating the distribution of phonemes in English)[24], and responded by typing the word. During training, a series of synthetic speech words were presented over headphones paired with the printed form of the word as feedback. After each training block, participants identified the trained words. A pretest and post-test were given before and after training, during which participants identified different sets of words without feedback. The pretest and post-test each consisted of 100 PB words, and the two training sessions each consisted of 150 PB words. The training sessions were structured into three blocks of 50 words. Participants rested between blocks. Word lists for testing and training were counterbalanced across participants. The 84 participants (all groups) were 20.3 ± 2.3 (mean ± s.d.) years old; each participated in one group only. Stimuli were delivered through Sennheiser HD 570 headphones with an r.m.s. sound pressure level of 66.5 dB.

One group had two post-training periods of testing. In the second post-test, participants were tested with a further set of 100 PB words that no other group was trained or tested on. The consistency of the result for the second post-test argues against any materials effect and further emphasizes the robustness of the findings.

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Dissociable stages of human memory consolidation and reconsolidation

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Historically, the term 'memory consolidation' refers to a process whereby a memory becomes increasingly resistant to interference from competing or disrupting factors with the continued passage of time[1]. Recent findings regarding the learning of skilled sensory and motor tasks ('procedural learning') have refined this definition, suggesting that consolidation can be more strictly