

The benefit of offline sleep and wake for novel object recognition

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Abstract How do we segment and recognize novel objects? When explicit cues from motion and color are available, object boundary detection is relatively easy. However, under conditions of deep camouflage, in which objects share the same image cues as their background, the visual system must reassign new functional roles to existing image statistics in order to group continuities for detection and segmentation of object boundaries. This bootstrapped learning process is stimulus dependent and requires extensive task-specific training. Using a between-subject design, we tested participants on their ability to segment and recognize novel objects after a consolidation period of sleep or wake. We found a specific role for rapid eye movement (REM, $n = 43$) sleep in context-invariant novel object learning, and that REM sleep as well as a period of active wake (AW, $n = 35$) increased segmentation of context-specific object learning compared to a period of quiet wake (QW, $n = 38$; $p = .007$ and $p = .017$, respectively). Performance in the non-REM nap group ($n = 32$) was not different from the other groups. The REM sleep enhancement effect was especially robust for the top performing quartile of subjects, or “super learners” ($p = .037$). Together, these

results suggest that the construction and generalization of novel representations through bootstrapped learning may benefit from REM sleep, and more specific object learning may also benefit from AW. We discuss these results in the context of shared electrophysiological and neurochemical features of AW and REM sleep, which are distinct from QW and non-REM sleep.

Keywords Object recognition · Perceptual learning · REM sleep · Napping · Memory consolidation

Introduction

A central question in vision science involves understanding how we segment and recognize novel objects, especially when camouflaged by a similar looking background. This ability is essential for infants learning about their new world, for animals searching for food, and predators seeking their prey. When explicit cues from motion and color are available, the calculation of an object boundary becomes relatively easy (Gegenfurtner and Rieger 2000; Theriault et al. 2009). Using these explicit cues or other regularities that define shape contours and border ownership, the visual system quickly and opportunistically assembles features into an object percept (Brady and Kersten 2003). Alternatively, bootstrapped learning occurs under conditions of deep camouflage in which objects share the same image cues as their background, and the visual system must reassign new functional roles to existing image statistics in order to group continuities for detection and segmentation of object boundaries. This bootstrapped learning process is stimulus dependent and requires extensive task-specific training (Brady and Kersten 2003).

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Opportunistic and bootstrapped learning mechanisms differ in several ways, including distinct patterns of brain activity and time courses of learning (Zhang and Kourtzi 2010). Opportunistic learning can occur during a single, 1-h training session, whereas bootstrapped learning requires days of training. Brady and Kersten (2003) examined the time course of these learning models by generating a set of objects that shared the same image cues (Fig. 1a). When one object was placed in the foreground of a scene composed of other, similar objects, it became entirely camouflaged. When the target object contained color or motion cues, recognition was immediate. However, when all the objects were grayscale and static, recognition and segmentation emerged slowly over days of exposure. Similar time courses of learning have been shown on other bootstrapped learning tasks (Zhang and Kourtzi 2010). Although the mechanism underlying bootstrapped learning is unknown, it is possible that this slow process, which emerges over days of training, may require sleep to successfully reassign new functional roles to image statistics.

Sleep plays an important role in consolidation of perceptual learning, which is the long-term improvement of performance on a task that is specific to the physical

features of the trained stimulus. For example, post-training improvement on a texture discrimination task is (1) specific to the retinotopic location and orientation of the texture; (2) develops after at least 6 h of nocturnal sleep; and (3) depends on the combination of slow wave sleep (SWS) and rapid eye movement (REM) sleep (Aeschbach et al. 2008; Gais et al. 2000; Karni and Sagi 1991; Karni et al. 1994; Stickgold et al. 2000). Importantly, perceptual learning improvements following a nap are equivalent to those following a full night of sleep. However, naps with SWS alone are not sufficient to facilitate perceptual learning; rather, naps that contain both SWS and REM are necessary for perceptual learning to occur (Mednick et al. 2003). Taken together, previous studies suggest a functional significance for sleep, particularly REM sleep, during consolidation of perceptual learning.

The present study investigates the role of REM sleep in bootstrapped learning of novel objects using a nap paradigm. Nap studies (1) eliminate circadian confounds; (2) provide a high level of experimental control [comparisons with active wake (AW) or quiet wake (QW)]; (3) allow titration of sleep stages by modulating the duration and time of day of the nap; and (4) show the same sleep-dependent learning benefits as nocturnal sleep (Mednick et al. 2003). We tested four experimental groups: naps with REM sleep (REM), naps with non-REM sleep only (NREM), QW, and AW. The two non-sleep groups allowed for two levels of control of interference. QW was a low-interference condition in which subjects remained awake while quietly resting in a dark room with their eyes closed with electroencephalographic (EEG) monitoring to confirm wakefulness, whereas the AW group went about their daily routine with no control for daytime interference. Based on the previous literature suggesting REM-dependent perceptual learning, we hypothesized that REM sleep would facilitate segmentation and recognition on the object learning task compared to NREM sleep and wake.

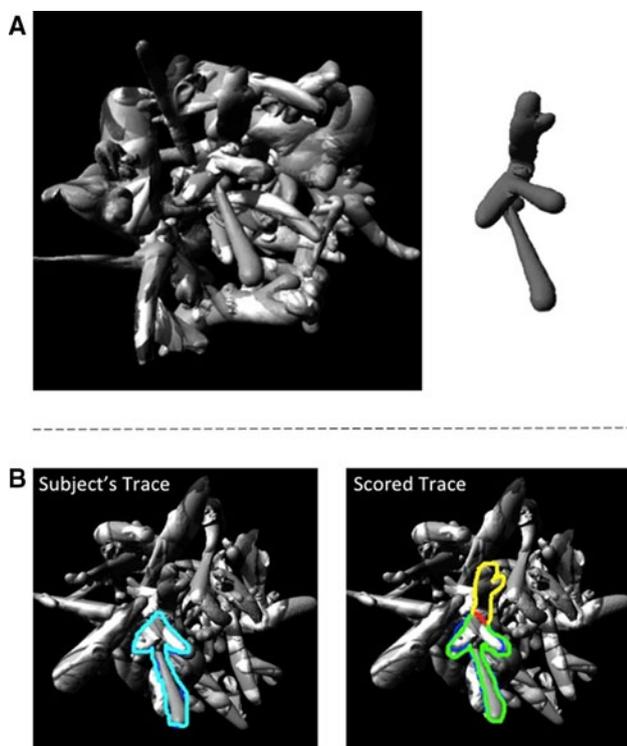


Fig. 1 **a** A digital embryo with and without background. Digital embryo scenes mimic aspects of nature's extreme forms of camouflage. **b** Segmentation task tracing example. The subject traced a segment in light blue. The tracing was color coded by the experimenter. Correct segments were coded green, extraneous were coded red, and yellow were missing in the subject's original trace

Methods

Subjects

A total of 148 (107F) native English speakers between the ages of 18–35 with no personal history of neurological, psychological, or other chronic illness gave informed consent to participate in the experiment, which was approved by the Institutional Review Board at the University of California, San Diego. Subjects were asked to maintain their usual sleep–wake schedule during the week prior to the experiment and to refrain from consumption of caffeine, alcohol, and all stimulants for 24 h prior to the beginning of the experiment as well as throughout the study

day. Heavy caffeine users were not enrolled to exclude the possibility of significant withdrawal symptoms during the experiment. Subjects completed sleep diaries for 5–7 days before the experiment and wore actigraph wrist-watches (Actiwatch-64, Respironics) the night before the experiment to provide subjective and objective measures of sleep–wake activity, respectively. We also assessed trait daytime sleepiness with the Epworth Sleepiness Scale (Johns 1991) and evaluated circadian phase preference for morningness or eveningness with the Horne–Östberg Morningness–Eveningness Questionnaire (Horne and Ostberg 1976).

Stimuli

Stimuli, adapted from Brady and Kersten (2003), were 3D shapes derived from “digital embryos” rendered using computer graphics (Fig. 1a). These objects appear to be organic forms but do not resemble a familiar class of organism. When grouped together, they create a strong camouflage. Stimuli for the segmentation task were presented using Adobe Photoshop Elements 7, and the recognition task was presented using E-Prime software (Psychology Software Tools Inc.).

Segmentation task

During Session 1, subjects were shown a scene of objects in which a target object was situated in the foreground. Subjects were given no hints or guidance, but simply instructed to find an object located in the foreground. Although there was always a specific target object present, subjects were naïve to the task and could choose anything they considered an object. Subjects used the mouse to trace a line around the boundaries of what they thought might be a possible object. They performed this task for three separate scenes each containing a different object (objects A, B, and C). In Session 2, subjects were presented the same three objects in the same scenes and again asked to trace the foreground object. The same exact instructions were given in Session 2 (e.g., no guidance except to find an object located in the foreground).

Object training

Following the segmentation task, and immediately prior to object training, subjects were oriented to the type of objects they would be asked to identify. Subjects were shown three highlighted examples of objects embedded in a scene of other similar objects. These examples were never used in the actual experiment.

During Session 1, subjects were trained on target objects A, B, and C. Training consisted of sequentially showing objects A, B, and C for 10 s each and then repeating A, B, and C until each object appeared 10 times for a total of 30 trials.

In each trial, the background objects and the target object location were changed. Sounds that mimicked three distinct birdcalls were systematically played with each object’s appearance, so as to imitate a natural object learning scenario where an object may emit a sound which helps to identify it.

Recognition task

Subjects were tested on their ability to recognize the trained objects in camouflaged scenes during Session 2. Test stimuli consisted of a target or novel object embedded in a background of other objects. Each trial was a four alternative forced choice response, where the choices were A, B, C, or novel. No sounds or segmentation clues were provided, and the background objects and the target object location changed with each trial. There were 30 trials in total, with 5 trials per target object and 15 novel trials.

Experimental timeline

The experimental timeline is shown in Fig. 2. On the experimental day, subjects reported to the Laboratory for Sleep and Behavioral Neuroscience at the San Diego Veterans Affairs Medical Center. At 9:00 a.m., subjects completed the segmentation task, followed by object training. Subjects were then randomly assigned to one of four groups: 60-min nap, 90-min nap, QW, or AW. Subjects assigned to the nap conditions took a nap recorded with polysomnography (PSG) at 1:30 p.m. Given that shorter naps have less REM sleep than longer naps, the use of two nap durations increased the likelihood of having a significant number of subjects in both the REM and NREM groups. After the completion of the experiment, sleep stage scoring was used to assign subjects to either the REM ($n = 43/30F$, naps containing one or more minutes of REM sleep) or NREM ($n = 32/25F$) groups. Of the 35 subjects originally assigned to the 90-min nap group, 25 obtained REM sleep. Eighteen subjects originally assigned to the 60-min nap group also obtained REM sleep and were included in the REM group for all future analyses. All other nap subjects comprised the NREM group; six of these subjects did not display SWS. Subjects in the QW condition sat in a recliner listening to classical music with PSG monitoring ($n = 38/25F$) to ensure wakefulness, whereas the AW group ($n = 35/27F$) carried out their normal daily activities but were instructed to abstain from caffeine, alcohol, and napping. Wakefulness in the AW group was monitored using actigraphy. At 4:00 p.m., subjects completed the segmentation and recognition tasks. Immediately prior to each testing session, subjects’ momentary state of alertness/sleepiness was measured with the Karolinska Sleepiness Scale (KSS) at 9:00 a.m. and 4:00 p.m. (Åkerstedt and Gillberg 1990).

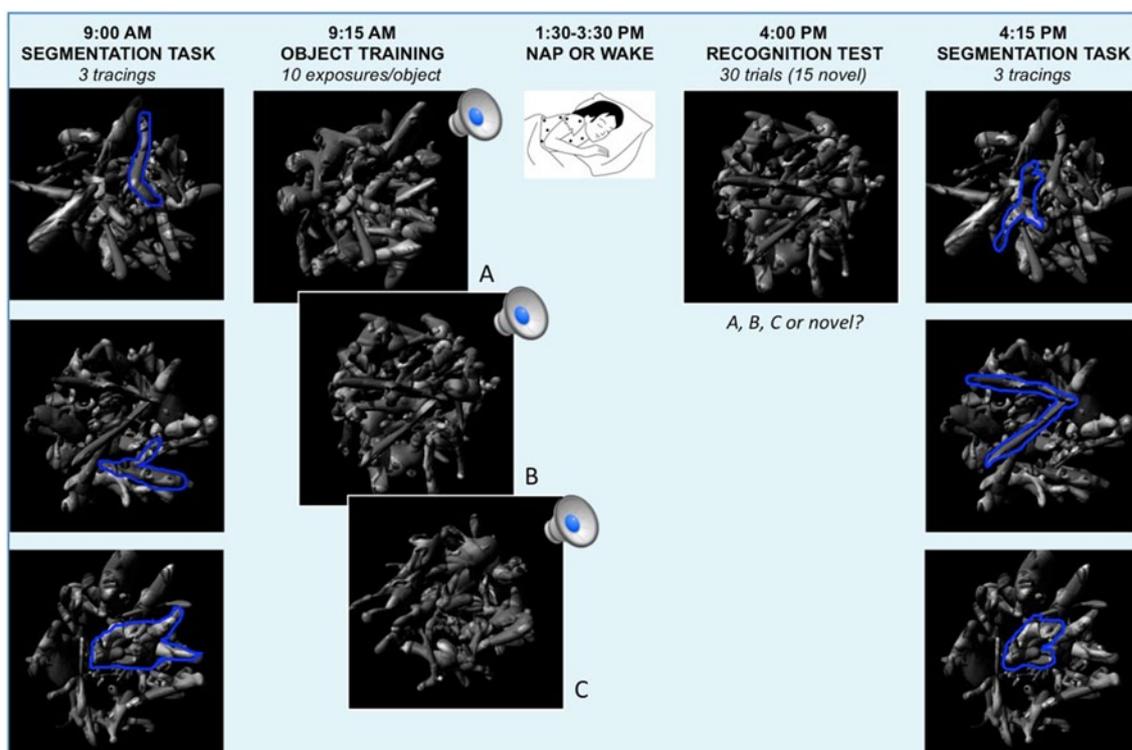


Fig. 2 Experimental timeline. At 9:00 a.m., subjects were shown three separate scenes and asked to trace a line around the boundaries of what they thought might be a possible foreground object (segmentation task). Immediately following, subjects completed object training of target objects A, B, and C. Training consisted of sequentially showing objects A, B, and C for 10 s each and then repeating A, B, and C until each object appeared 10 times for a total of 30 trials. Three distinct birdcall sounds were systematically played with each

object's appearance. Subjects either napped or remained awake from 1:30 to 3:30 p.m. At 4:00 p.m., subjects were tested on their ability to recognize the trained objects on a four alternative forced choice task (A, B, C, or novel?). The recognition test was 30 trials in total—15 novel trials and 5 trials per target object. Subjects were again shown three scenes and asked to trace a line around the boundaries of the foreground object (segmentation task)

Polysomnography

At 12:30 p.m., electrodes were attached for standard PSG recording. Subjects were in bed by 1:30 p.m. Depending on their random group assignment, subjects were allowed to nap for a maximum of either 60 or 90 min, but given no more than 120 min in bed. All subjects napped at the same time of day to control for circadian effects on sleep architecture.

All PSG data were collected using Astro-Med Grass Heritage Model 15 amplifiers and Grass Gamma software. Scalp EEG and EOG electrodes were referenced to unlinked opposite mastoids (C3/A2, O1/A2, C4/A1, O2/A1, LOC/A2, and ROC/A1), and muscle tone EMG electrodes were attached under the chin. PSG data were digitized at a sampling rate of 256 Hz and visually scored in 30-s epochs according to the sleep staging criteria of Rechtschaffen and Kales (1968). The variables examined from these PSG data were sleep latency (SL), wake after sleep onset (WASO), minutes and percentage of Stage 1, Stage 2, SWS, REM, total sleep time (TST), and sleep efficiency.

Statistical analyses

Experimental nap sleep variables were compared between NREM and REM nap groups with independent-samples *t* tests. The relationship between specific sleep variables and behavioral performance was examined by computing bivariate Pearson correlations. KSS (state subjective sleepiness) scores were analyzed using a repeated-measures analysis of variance (ANOVA) with time (9:00 a.m./4:00 p.m.) as the within variable and condition (AW/QW/NREM/REM) as the between variable.

We calculated two performance measures for the recognition task—proportion correct [as reported in Brady and Kersten (2003)] and a *d* prime (*d'*) discrimination sensitivity index.

Proportion Correct

$$= \frac{\{(\text{Correct 'target object' identification}) + (\text{Correct 'novel object' identification})\}}{\text{Total number of trials}}$$

Each trial of the recognition task had a four alternative forced choice response. Chance performance on this task is .25 for an observer who guesses at all choices with equal probability, or .5 for an observer who always guesses “other,” which is the upper bound of any guessing strategy. We first assessed overall novel object learning in each group using one-sample *t* tests, comparing proportion correct to the .5 chance level criterion.

$$d' = Z_{\text{hit rate}} - Z_{\text{false alarm rate}}$$

Hits and false alarms were calculated for each of the three target objects separately. For each object, there was a maximum of five hits (e.g., respond A to object A) and a maximum of 15 false alarms (e.g., respond A to a novel object). We averaged the hit rate and false alarm rate for all three objects and then calculated an overall *d'*.

Tracing errors on the segmentation task were of two types, missed contour segments and extraneous tracing (see Fig. 1b). Tracings were scored by combining tracing path lengths as follows:

$$\text{Trace Score} = (\text{Trace Correct}) / \{(\text{Trace Correct}) + (\text{Trace Missing}) + (\text{Trace Extraneous})\}$$

At trace score = .5, the amount of correct tracing equals the amount of tracing error. A difference score was calculated to measure improvement on the tracing segmentation task from Session 1 to Session 2.

Group differences on both tasks were examined using one-way ANOVA with four levels of the between-subject variable condition (AW/QW/NREM/REM). Post hoc *t* tests further specified differences between groups. For the recognition task, “super learners” (75th percentile and above; AW: *n* = 16/12F, QW: *n* = 6/4F, NREM: *n* = 10/9F, REM: *n* = 16/8F) and “weak learners” (25th percentile and below; AW: *n* = 8/7F, QW: *n* = 17/8F, NREM: *n* = 12/8F, REM: *n* = 14/11F) were identified by splitting participants into quartiles based on recognition proportion correct performance (as previously done in Brady and Kersten 2003). One-way ANOVA and post hoc *t* tests were repeated to examine the effect of sleep/wake conditions within each of these groups.

Results

Experimental nap variables and other sleep characteristics

We found no group differences on any non-experimental sleep variable examined in this study: (1) prior nocturnal sleep (*p* = .596); (2) trait subjective sleepiness (*p* = .372); (3) morningness versus eveningness preference (*p* = .723); or 4) nap habits (*p* = .737). These results confirm that nap assignment was not confounded by any of the above sleep characteristics.

Table 1 Experimental nap sleep variables as measured with polysomnography

	NREM <i>M</i> (<i>SD</i>)	REM <i>M</i> (<i>SD</i>)
Total sleep time (min)**	51.2 (17.4)	76.0 (16.4)
Sleep latency (min)**	9.6 (5.0)	4.8 (2.5)
Wake after sleep onset (min)*	17.2 (15.6)	9.8 (10.9)
Sleep efficiency (%)**	66.4 (20.1)	83.9 (10.8)
Minutes		
Stage 1	7.3 (5.1)	8.5 (6.0)
Stage 2**	28.8 (11.3)	39.7 (11.8)
SWS	15.1 (14.1)	13.6 (13.8)
REM	0	14.1 (9.8)
Percent (% TST)		
Stage 1	16.3 (13.5)	12.2 (10.4)
Stage 2	57.9 (16.3)	52.4 (11.7)
SWS	26.0 (21.6)	17.4 (16.8)
REM	0	18.1 (11.0)

Asterisks represent a statistically significant difference between NREM and REM nap groups

* *p* < .05

** *p* < .01

Table 1 contains a summary of the experimental nap sleep variables. By design, TST differed between the NREM and REM groups (*t*(73) = 6.30, *p* < .001). Minutes to sleep onset (SL) and minutes of WASO were both increased for NREM compared to REM naps [SL: *t*(73) = 5.47, *p* < .001; WASO: *t*(73) = 2.43, *p* = .017]. Accordingly, REM naps had greater sleep efficiency compared to NREM naps [*t*(73) = 4.86, *p* < .001]. There were no detectable differences in minutes or percent of Stage 1 or SWS. REM naps had more minutes of Stage 2 [*t*(73) = 4.04, *p* < .001], but there was no difference in Stage 2 percent. Within the NREM group, six of the naps did not contain SWS.

Object recognition task

All four groups showed significant novel object learning with proportion correct significantly greater than the .5 chance level criterion [AW: *t*(34) = 5.04, *p* < .001; QW: *t*(37) = 2.41, *p* = .021; NREM: *t*(31) = 3.70, *p* = .001; REM: *t*(42) = 5.42, *p* < .001].

There was an effect of condition on recognition task proportion correct [*F*(3,144) = 3.13, *p* = .028]. Post hoc *t* tests demonstrated significantly greater recognition performance in the AW [*t*(71) = 2.45, *p* = .017] and REM [*t*(79) = 2.79, *p* = .007] groups compared to the QW group (Fig. 3a). We repeated the same analysis for *d'* and also found a significant effect of condition [*F*(3,144) = 2.78, *p* = .043]. Post

Fig. 3 Recognition task performance as measured by proportion correct. The *dotted line* indicates chance performance for an observer who always guesses “novel,” which is the upper bound of any guessing strategy. **a** All four groups performed significantly better than chance. Recognition performance was greater for active wake (AW) and REM nap groups compared to quiet wake (QW). **b** For super learners (75th percentile and above), recognition performance was significantly greater following REM naps than AW, QW, or non-REM (NREM) naps. **c** Weak learners (25th percentile and below) performed below chance level and did not show any group differences in recognition performance. * $p < .05$, and ** $p < .01$

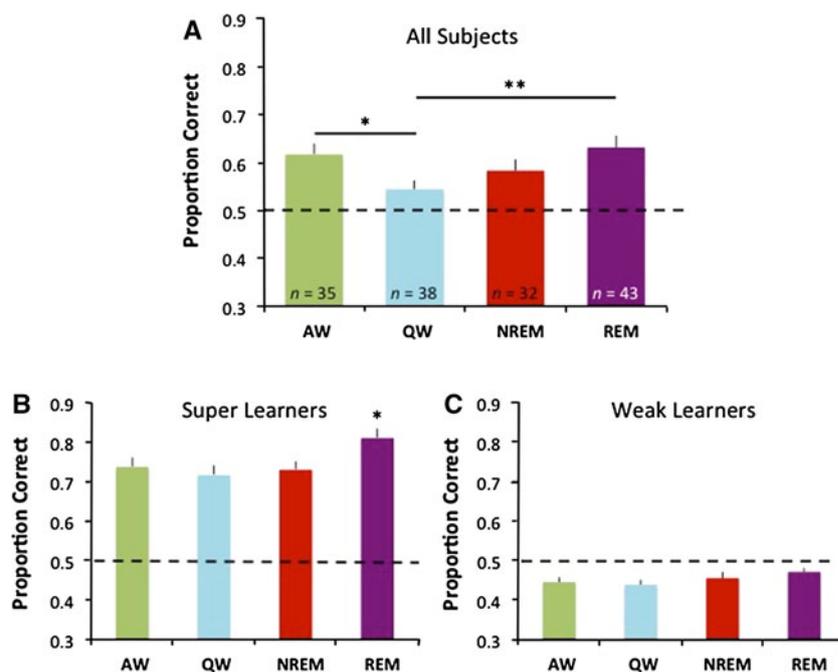
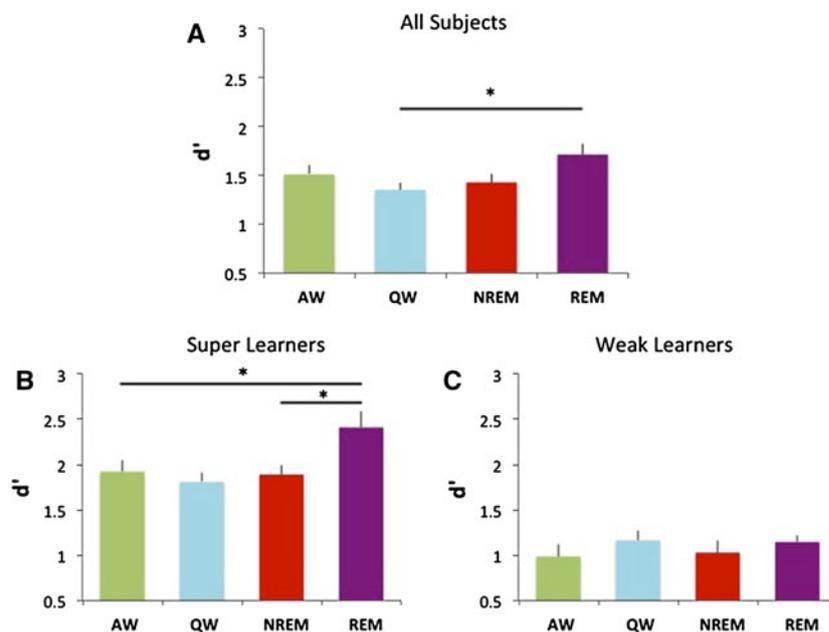


Fig. 4 Recognition task performance as measured by d' prime (d'). **a** Recognition performance was greater for the REM nap group compared to quiet wake (QW). **b** For super learners (75th percentile and above), recognition performance was significantly greater following REM naps than AW or non-REM (NREM) naps. **c** Weak learners (25th percentile and below) did not show any group differences in recognition performance. * $p < .05$



hoc t tests demonstrated significantly greater d' in the REM [$t(79) = 2.60, p = .011$] group compared to the QW group (Fig. 4a).

However, not all observers can learn to recognize and segment objects following limited training (Brady and Kersten 2003). We next examined recognition performance within the top and bottom quartiles of performers based on proportion correct (Fig. 3b, c). Super learners

had a mean recognition score of $.76 \pm .09$ ($M \pm SD$), whereas weak learners performed significantly worse ($p < .001$) with a mean recognition score of $.45 \pm .05$, which is right below the .5 chance criterion level. Interestingly, super learners benefited most from REM sleep [$F(3,44) = 3.09, p = .037$]. Within the super learners, the REM group learned better than AW [$t(30) = 2.20, p = .036$], QW [$t(20) = 2.23, p = .037$], and NREM

$[t(24) = 2.29, p = .031]$ groups. There were no group differences for the weak learners [$F(3,47) = 1.32, p = .280$]. Similarly for d' , there were differences within the super learners [$F(3,44) = 3.35, p = .027$] and no differences in weak learners [$F(3,47) = .531, p = .663$] (Fig. 4b, c). Super learners in the REM group had greater d' compared to the AW [$t(30) = 2.22, p = .034$], QW [$t(20) = 2.00, p = .059$, marginal], and NREM [$t(24) = 2.17, p = .04$] groups.

Given the difference in recognition performance between the two nap groups, sleep variables were correlated with performance for each group separately. Recognition task performance, neither proportion correct nor d' , was not correlated with any experimental nap sleep variable, including TST in either NREM ($r = .114, p = .533$) or REM ($r = -.068, p = .665$) nap groups. Therefore, it is unlikely that the REM sleep benefit was due to increased TST in the REM group.

Segmentation task

There were no Session 1 baseline differences between groups on the segmentation task [$F(3,143) = 1.17, p = .324$]. We found a between-group difference in the trace difference score [$F(3,139) = 2.93, p = .036$], which quantified improvement on the segmentation task from Session 1 to Session 2. The AW [$t(70) = 2.71, p = .009$] and REM [$t(76) = 2.07, p = .042$] groups showed greater performance improvement compared to QW (Fig. 5). Segmentation task performance was not correlated with any experimental nap sleep variable in either group, including TST (NREM: $r = .057, p = .765$; REM: $r = .134, p = .405$).

State subjective sleepiness (KSS)

We examined subjects' momentary state of sleepiness/alertness immediately prior to each testing session and found a time \times condition interaction [$F(3,143) = 6.33, p < .001$], but no main effects of time or condition (Fig. 6). Though there were no differences in sleepiness at 9:00 a.m. ($p = .786$), significant differences emerged in the afternoon (4:00 p.m.) after the nap [$F(3,143) = 6.497, p < .001$]. Specifically, the AW group was sleepier than the NREM [$t(65) = 3.13, p = .003$] and REM [$t(76) = 4.10, p < .001$] groups.

To determine whether performance could have been driven by differences in subjective sleepiness, we correlated the 4:00 p.m. KSS scores with behavioral task performance. Despite group differences, there were no significant correlations between subjective sleepiness and performance on either segmentation ($r = -.120, p = .156$) or recognition performance ($r = -.010, p = .903$).

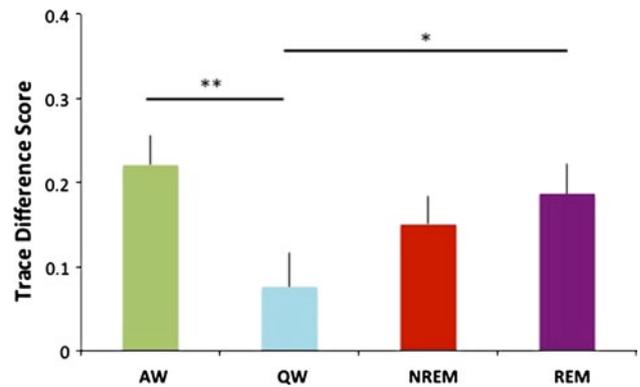


Fig. 5 Segmentation task performance. The trace difference score quantified improvement on the segmentation task from Session 1 to Session 2. Naps with REM sleep and active wake (AW) produced greater tracing performance improvements compared to quiet wake (QW). * $p < .05$, and ** $p < .01$

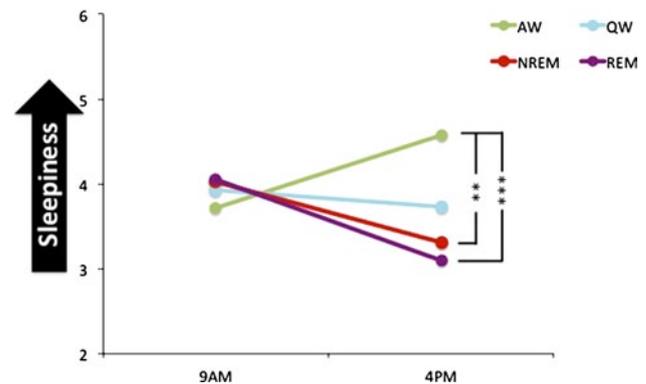


Fig. 6 Subjective sleepiness rating interaction. There was no difference in sleepiness ratings between groups at 9:00 a.m. However, following the nap at 4:00 p.m., the active wake (AW) group was sleepier than the non-REM (NREM) and REM nap groups. ** $p < .01$, and *** $p < .001$

Discussion

In the present study, we demonstrate that the process of learning to segment and recognize novel objects is enhanced during offline consolidation periods containing both wake and sleep. However, not all states of wake and sleep lead to improved performance. As predicted, we found that naps with REM sleep were beneficial for bootstrapped learning as observed in both the recognition and segmentation tasks. Surprisingly, AW also facilitated object learning in the segmentation task, compared to QW. Further, REM sleep, more so than AW, QW, and NREM, gave some subjects an even greater advantage, as measured in super learners who performed in the top quartile. Similarly, Brady and Kersten (2003) showed that super learners benefitted from training on this task across multiple days, whereas weak learners did not improve across days.

The present findings suggest that super learners, compared with weak learners, are better able to utilize the REM sleep benefits during consolidation to speed up the time course of bootstrapped learning. Thus, we found that an optimal offline state for consolidation of bootstrapped object learning is REM sleep and that some learning can also occur during AW, whereas QW and NREM states are not conducive to learning.

Differences between the segmentation and the recognition task may provide insight into why AW facilitated learning in one versus the other. First, the segmentation task presented subjects with the identical scene (same background objects and same target object location) in Sessions 1 and 2, whereas target objects were presented in a different location in front of different background objects in each training and test trial of the recognition task. Thus, the segmentation task required learning of specific contexts, which may be facilitated by both AW and REM sleep, whereas the recognition task required context-invariant generalization to novel scenarios. Generalization of learning has been associated with REM sleep in other studies (Cai et al. 2009; McDevitt et al. 2013; Smith and Smith 2003; Stickgold et al. 1999). In the present case, we have shown that REM sleep appears to benefit generalization by increasing invariance in object recognition.

What are some possible sources of similarity between AW and REM, and do QW and NREM also share similar features? Answers to these questions may come from studies examining functional changes associated with differing mental states. AW is an exploratory state during which task-dependent increases in cerebral blood flow are found in brain areas associated with the maintenance of arousal, stimulus processing, motivation, and decision-making. Similarly, during REM sleep, cerebral blood flow and metabolism are also increased in areas relevant to arousal, as well as areas associated with visual processing, emotions, and rational cognitive functions (Braun et al. 1997, 1998; Maquet et al. 2000; Koike et al. 2011; Larson-Prior et al. 2009). REM sleep is also characterized by increased low voltage, fast activity EEG patterns, and high arousal levels that are similar to active waking (Tononi et al. 1998). In addition, levels of intrahemispheric temporal coupling of fast EEG activity in perceptual regions (i.e., occipital, parietal, and temporal sites) observed during wakefulness are maintained during REM sleep (Corsi-Cabrera et al. 2003; Pérez-Garci et al. 2001).

A different network of brain areas becomes active once the subject is no longer engaged in a particular task (e.g., QW), referred to as the default mode network (Buckner et al. 2008). During the default mode state, the mind is occupied by task-independent introspection or self-referential thought (Andrews-Hanna 2012), and brain metabolism exhibits a circuit of correlated activity patterns in areas

relevant to information integration (Koike et al. 2011), mind-wandering and unconstrained thought (Mason et al. 2007), internal mentation, and autobiographical memory (Svoboda et al. 2006; Buckner et al. 2008). Interestingly, a common network of brain areas appears to be active during the default mode and NREM sleep, although these two states of consciousness are not equivalent and are distinct in many other ways. A study using simultaneous high-density EEG and functional magnetic resonance imaging demonstrated no measurable change in functional connectivity as subjects moved from QW to NREM sleep (Larson-Prior et al. 2009).

REM and AW also share neuromodulatory features associated with synaptic plasticity that are distinct from QW and NREM. For example, acetylcholine (ACh) is a neurotransmitter important for plasticity and memory that shows significant fluctuations across AW, QW, NREM, and REM sleep. Microdialysis studies report that ACh levels are higher when the animal is exploring during AW than during QW, when the animal is immobile, eating, or grooming. ACh levels fall to 1/3 of waking levels during NREM sleep, but rise to levels above AW during REM sleep (Jasper and Tessier 1971; Kametani and Kawamura 1990; Marrosu et al. 1995; Hasselmo and McGaughy 2004).

High levels of cholinergic transmission during AW and REM set the neural dynamics for increased synaptic plasticity. Much evidence shows that the cholinergic system can regulate the induction of long-term potentiation (LTP), the leading model of synaptic plasticity (Luo et al. 2008; Segal and Auerbach 1997; Blitzer et al. 1990; Patil et al. 1998). Thus, LTP is easily initiated during AW and REM sleep (Buzsáki 1989; Hasselmo 1999; Hasselmo and Bower 1993; Matsukawa et al. 1997), whereas LTP may be reduced during NREM sleep (Jones Leonard et al. 1987, however see Chauvette et al. 2012). QW is also a state of low synaptic plasticity as it is by definition a period of reduced encoding and low sensory input (Mednick et al. 2011).

Importantly, LTP is a likely mechanism of synaptic plasticity in perceptual learning (Sale et al. 2011). Perceptual learning was reduced by blockade of either NMDA or AMPA glutamatergic receptors during a sleep period, following training on the texture discrimination task (Gais et al. 2008). Additionally, many studies have shown perceptual learning increases following a consolidation period with ACh-rich REM sleep (Karni et al. 1994; Mednick et al. 2003). Also consistent with this, pharmacologically enhanced ACh increased the magnitude and specificity of perceptual learning for both motion and texture discrimination tasks (Rokem and Silver 2010, 2013; Beer et al. 2013). Taken together, these studies indicate that both AW and REM sleep are periods of ACh-associated plasticity, whereas QW and NREM sleep are periods of decreased

plasticity, with correspondingly low levels of ACh. Thus, although the brain is asleep during REM, it appears more similar to AW functionally, electrophysiologically, and neurochemically than either QW or NREM.

Returning to the present behavioral results, we found that AW and REM sleep facilitated object learning more so than QW and NREM sleep. Considering the task, subjects learned to integrate discontinuities into coherent contours for segmentation and recognition of non-traditional object boundaries. Sleep periods containing both NREM and REM sleep stages have been shown to facilitate abstraction and integration of learning on other tasks as well, such as statistical learning (Durrant et al. 2011), the integration of new information into existing associative networks (Cai et al. 2009), generalization of motion direction discrimination learning (McDevitt et al. 2013), and language learning in infants (however, sleep was not measured in this study) (Gómez et al. 2006). Interestingly, AW also appears to facilitate this integration process.

Although AW and REM are similar states in terms of plasticity, they are differentiated by the fact that REM sleep is a period of low interference from the environment. Similarly, NREM and REM groups are similar in regard to reduced external interference, but are differentiated by different levels of plasticity. Our findings suggest that the unique combination of high plasticity (possibly due to heightened ACh) and limited external interference (due to sleep) found during REM sleep is the optimal state for the construction of novel object representations through bootstrapped learning. REM sleep especially boosted performance in super learners, who demonstrated increased magnitude of learning. Although NREM sleep, specifically SWS, most likely plays a beneficial role for object recognition and perceptual learning, SWS alone is not enough to produce this benefit. Rather, these data add to a growing body of literature, suggesting that the combination of SWS and REM sleep is critical for learning and memory improvements.

Importantly, these performance differences were not related to differences in sleepiness across the four groups. Although the AW group showed the greatest levels of sleepiness in the afternoon, they could identify more objects than the other groups who showed less sleepiness. Furthermore, although naps with REM sleep were longer than NREM naps, TST was not correlated with performance. Thus, we do not think that the data can be explained by either of these factors.

Future studies directly measuring functional activity and ACh levels and/or manipulating ACh via drug intervention may help to define a more robust relationship between AW and REM sleep. Also, considering AW proved beneficial for segmentation of novel objects specifically, a more controlled AW period would allow for

a clearer picture of what specific waking activities may facilitate this type of object learning. Additionally, our interpretation of recognition performance changes was limited because we did not have a baseline measurement for the recognition task. Future studies should include an immediate recognition test following training, in order to specifically measure memory gains or losses across offline consolidation periods.

While the present findings advance our understanding of bootstrapped learning, many questions remain. First, what is the mechanism by which we utilize periods of increased plasticity for object identification and recognition? Second, do REM and AW enhance learning by similar or distinct mechanisms (i.e., context invariant vs. context specific)? Third, what is the pattern of brain activity underlying these benefits? Fourth, what is the role of REM sleep in infant object learning? While much remains to be learned, this study identifies two distinct states of consciousness (REM and AW) that can elicit similar memory benefits despite (and possibly due to) increased plasticity during offline consolidation.

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