# Cerebral asymmetries in sleep-dependent processes of memory consolidation

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## Abstract

**Preference for previously seen, unfamiliar objects reflects a memory bias on affective judgement, known as the 'mere exposure effect' (MEE). Here, we investigated the effect of time, post-exposure sleep and the brain hemisphere solicited on preference generalisation towards objects viewed in different perspectives. When presented in the right visual field (RVF), which promotes preferential processing in the left hemisphere, same and mirrored exemplars were preferred immediately after exposure. MEE generalised to much dissimilar views after three nights of sleep. Conversely, object presentation in the left visual field (LVF), promoting right hemisphere processing, elicited a MEE for same views immediately after exposure, then for mirror views after sleep. Most importantly, sleep deprivation during the first post-exposure night, although followed by two recovery nights, extinguished MEE for all views in the LVF but not in the RVF. Besides demonstrating that post-exposure time and sleep facilitate the generalisation process by which we integrate various representations of an object, our results suggest that mostly in the right hemisphere is sleep mandatory to consolidate the memory bias underlying affective preference. These inter-hemispheric differences call for a reappraisal of the role of cerebral asymmetries in wake- and sleep-dependent processes of memory consolidation.**

A MEE is obtained when prior exposure to initially novel, unfamiliar stimuli (Bornstein 1989; Butler and Berry 2004) increases the likelihood that they will be preferred to never-seen stimuli. A potent explanation for the MEE is that prior encounter with a stimulus enhances its subsequent processing fluency, which is one of the determinants of affective preference (Reber et al 2004). By this account, the MEE broadly falls into the same class of memory effects than priming, that is, the facilitation or bias in the processing of a stimulus as a function of a recent encounter with that stimulus (Butler and Berry 2004). Like priming (Biederman and Gerhardstein 1993), affective preference (Lawson 2004; Seamon and Delgado 1999) may generalise to stimulus transformations including depth-rotated views of pre-exposed objects. This suggests that the representation underlying enhanced fluency is abstract and view-point invariant, but this assumption is partially contradicted by the observation that both priming (Srinivas 1995) and mere exposure (Lawson 2004) effects may decrease or even vanish for certain rotations. Evidence gathered from priming experiments partially resolved these inconstancies in suggesting that generalisation effects are subtended by hemispheric specialisation in the cerebral cortex (Burgund and Marsolek 2000; Marsolek 2004). Indeed, when structural modifications are made to previously exposed stimuli, for instance objects' rotations (Burgund and Marsolek 2000), unseen prototypes of learned forms (Marsolek 1995) or different letter cases (Marsolek and Hudson 1999), performance was consistently higher for items displayed in the right visual field [RVF], which predominantly projects towards the left cerebral hemisphere [LH], than for items displayed in the left visual field [LVF], projecting towards the right hemisphere [RH]. These studies have suggested that the RH is specialized for the processing of view-point dependent, exemplar-based information, whereas the LH is better suited to process view-point independent, abstract information. Accordingly, it has been shown that task and stimulus demands affect which brain hemisphere most efficiently supports priming (Burgund and Marsolek 2000) and

MEE (Compton et al 2002).

From another perspective, there is now ample evidence that post-training sleep participates in the offline processing and consolidation of recent memory traces (for reviews see Maquet et al 2003; Rauchs et al 2006; Walker and Stickgold 2006). Still, the few studies having investigated a role for sleep in consolidating the memory representations subtending priming effects have yielded discrepant results (Plihal and Born 1999; Rauchs et al 2006; Wagner et al 2002). It should be noticed, however, that none of these studies has tested the effect of hemispheric specialisation on the development of these memory representations. Furthermore, although it is known that priming effects can be extremely robust over extended periods of time for same exemplars (Cave 1997), it remains unknown whether post-exposure sleep plays a significant role for the *generalisation* of priming effects towards novel instances of the exposed stimuli. Indeed, generalisation effects have always been tested immediately after exposure in published studies, which did not allow assessing the influence of time-dependent processes (McGaugh, 1966) nor a beneficial role of post-training sleep (Maquet et al 2003; Rauchs et al 2006; Walker and Stickgold 2006) for the consolidation of the memory traces underlying priming or mere exposure effects.

To address these issues, we have tested whether longer time intervals including nights of sleep may contribute to the development of affective preference towards different instances of a previously exposed stimulus. At the exposure phase, participants were presented with pictures of unfamiliar three-dimensional objects (Seamon and Delgado 1999; Srinivas 1995), and merely asked to decide whether the object was left- or right-oriented. Afterwards, they were introduced to a liking judgement phase either immediately (IMM; $n = 16$), 72 hours later after three nights of regular sleep (TRS; $n = 16$), or 72 hours later with total sleep deprivation on the first post-exposure night, followed by two recovery nights of regular sleep (TSD; $n = 29$). Test trials (Fig.

1) were composed of previously seen objects either displayed in the same orientation (SAME) than during exposure, depth-rotated at 80° in a nearly-mirror manner (MIRROR), or depth-rotated at 110° in such a way that some salient parts of the original object were masked (MASK), as well as of never seen objects (distracters). Participants were instructed to decide as fast as possible whether or not they liked the presented object. Additionally, half of the items were presented in each visual hemifield during the liking judgment phase, in order to promote preferential processing of visual memories by the contralateral left [LH] or right [RH] hemisphere (Gratton et al 1997).

## Results

To evidence a mere exposure effect, preference scores were computed as the proportion of "like" judgments for target categories minus the proportion of "like" judgments for the never seen distracters. Mean, standard deviation of the mean, and effect size (Cohen 1988) of preference for each stimulus type (SAME, MIRROR and MASK) in each experimental condition (IMM, TRS and TSD) are reported Table 1.

INSERT TABLE 1 ABOUT HERE

A three-way analysis of variance (ANOVA) was conducted on preference scores with group (IMM vs. TRS vs. TSD), visual field presentation (LVF vs. RVF) and object orientation (SAME vs. MIRROR vs. MASK) factors. This analysis disclosed a main effect of visual field presentation $F(1, 57) = 7.7$, $P < .05$, indicating that as a whole, pre-exposed stimuli were preferred to the distracters more often in the RVF (mean preference +21 ± standard deviation of the mean 4%) than in the LVF (+7 ± 4%). There was also a main effect of object orientation, $F(2, 114) = 16.7$, $P < .005$. Post hoc analyses (Duncan's test) showed that on average, pre-exposed stimuli were preferred to the distracters less often in the MASK (+2 ± 4%) than in either the

SAME (+22 ± 3%) or MIRROR (+18 ± 4%) orientations, *Ps* < .005. The difference between SAME and MIRROR orientations was non-significant (*P* >.33). Most importantly, we found a significant triple interaction effect, *F*(4, 114) = 4.40, *P* < .005, suggesting that the MEE was contingent upon a combination of stimulus orientation, visual field/brain hemisphere solicited, and time elapsed between exposure and testing, sleep being allowed or not on the first post-exposure night (Figure 2). Within-group Duncan's post hoc tests are as follows. In the IMM group, preference scores were higher in the SAME (+30 ± 6%) and MIRROR (+16 ± 7%) orientations than in the MASK orientation (–7 ± 7%), *Ps* < .005. Preference for SAME was higher than for MIRROR objects (*P* < .05). Single t-tests against the null reference mean were significant in the SAME (*Ps* < .001) and MIRROR (trend; *P* = .09) orientations, but not in the MASK orientation (*P* > .44). In the TRS group, preference scores were higher in the SAME (preference +25 ± 6%) and MIRROR (+25 ± 7%) orientations than in the MASK orientation (+7 ± 7%), *Ps* < .05. Preference for SAME was not higher than for MIRROR (*P* = 1.0) objects. Single t-tests against the null reference mean were significant in the SAME and MIRROR orientations (*Ps* < .005), but not in the MASK orientation (*P* > .16). In the TSD group, preference scores did not differ between the SAME (+9 ± 5%), MIRROR (+10 ± 5%) and MASK (+5 ± 5%) orientations, *Ps* > .58. Single t-tests against the null reference mean were significant in the MIRROR (*Ps* < .05) and SAME (trend; *P* = .06) orientation, but not in the MASK orientation (*P* > .31). It is worth noting here that the results obtained in this two-way [group X stimulus] ANOVA conducted on preference scores emphasise the importance of separately assessing the contribution of the two brain hemispheres in the MEE. When both hemispheres are merged, the ANOVA actually fails to reveal a significant role for post-training sleep in the development of affective preference towards previously exposed novel objects. Indeed, SAME and MIRROR orientations are preferred above chance by both the TRS and TSD groups, an effect actually supported by the left hemisphere only in the TSD group, as shown in the main text and here above.

A similar 3-way ANOVA conducted on response decision times yielded only a main effect of group, *F*(2.57) = 7.22, *Ps* <.005. Duncan post-hoc tests indicated that response times were on average slower in the TSD (1016±50 ms) than in the TRS (730±66 ms) or IMM (785±67 ms) groups (*Ps* < .05). This effect was not attributable to attentional alterations in the TSD group at day 4 since RTs in a psychomotor vigilance task conducted at the same moments were similar from exposure to test time both in TSD and TRS groups (group by time interaction term *F*(1, 42) = .39, *p* > .53).

The addition of a gender (Male vs. Female) factor in the ANOVAs did not yield any supplementary effect (*Ps* > .12), in line with a prior report (Compton et al 2002). In the remaining of this report, we will further detail the hemisphere by orientation effects on preference judgment scores within each group.

**Hemispheric asymmetries in immediate MEE.** In the IMM group, tested immediately after exposure, preference for pre-exposed objects was significant in the SAME orientation in both visual fields, and in the MIRROR orientation in the RVF only (t-tests against the null reference mean, *Ps* < .05; all other t-tests *Ps* > .41; Table 1). In the RVF, pre-exposed objects were preferred to the distracters more often in the SAME (+36%) and MIRROR (+30%) orientations than in the MASK (–5%) orientation (Duncan's post-hoc tests, *Ps* < .005). In the LVF, MEE was greater in the SAME (+25%) orientation than in the MIRROR (+3%) or MASK (–9%) orientations (*Ps* < .05; Figure 2, left part). These data evidence a MEE in both cerebral hemispheres for objects displayed in the same study-test orientation, along with sensitivity of the LH, but not of the RH, for nearly mirror rotations which preserved complete objects' visibility.

**MEE generalization with post-exposure time.** In the TRS group, tested 72 hours after exposure with a regular sleep schedule, MEE was significant in the SAME and MIRROR orientations in both visual fields, and in the MASK orientation in the RVF only (*Ps* < .05; no preference for MASK orientation in the LVF, *P* > .3; Table 1). In the RVF, pre-exposed objects were equally preferred in the SAME (+27 %), MIRROR (+31 %) and MASK (+23%) orientations (*Ps* > .34). In the LVF, objects were preferred more in the SAME (+23 %) and MIRROR (+19 %) than in the MASK (-8 %) orientation (*ps* < .005; Figure 2, middle part). These results indicate that the MEE generalises with post-exposure time, and possibly sleep, in the RVF (LH) to different kinds of depth-rotation transformations, including those that put out of sight salient parts of the pre-exposed objects. In the LVF (RH), it generalises only to rotations that preserve the entire visibility of the object.

**Sleep, MEE generalisation and cerebral asymmetries.** Finally, we aimed specifically to probe the role of post-exposure sleep in the formation and generalisation of affective preference towards pre-exposed objects. In the TSD group, sleep-deprived on the first post-exposure night then tested after two recovery nights of sleep, there was a preference in the RVF for previously displayed objects in the SAME and MIRROR (*Ps* < .05) orientations, but no more preference in the MASK orientation (P > .42), whereas preference was abolished in the LVF for all kinds of stimuli (*Ps* > .45; Table 1). Preference for objects presented to the RVF was higher in the SAME (+21%) than in the MASK (+5%) orientation (P < .05). Preference in the MIRROR (+ 16%) condition was not significantly different than in the two other conditions (*Ps* > .14). In the LVF, no difference was found between SAME (-3%), MIRROR (+4%) and MASK (+5%) orientations (*Ps* > .32; Figure 2, right part). In the TSD condition however, the baseline rate of “like” responses for the distracters was higher in the LVF (52±5%) than in the RVF (38±5%; *P* < .05), which was not the case in the IMM or TRS conditions (*Ps* > .7; Table 1). Actually, this lateralized pattern of preference for distracters replicated the effects observed in a fourth group (*n*

= 12), tested in a supplementary "no-exposure" condition, i.e. in volunteers who had to perform the judgment task without any prior exposure to the material. In this group, a 2-way ANOVA conducted on hemisphere (LH vs RH) and stimulus type (SAME vs MIRROR vs MASK vs distractor; arbitrarily defined here since the absence of a learning condition) on "like" scores failed to disclose an interaction effect ($F(3,33) = 1.14$, $P > .34$) nor a main effect of stimulus type ($P > .54$). Only the main effect of hemisphere presentation was significant ($F(1,11) = 6.84$, $P < .05$), actually indicating a natural propensity to produce more "like" response for items presented in the RH (57±5%) than in the LH (45±4%). Taken together, these results indicate that in subjects deprived of sleep on the first post-training night, generalisation effects are suppressed in the LH, whereas the RH behaves as if it had never gone through the original exposure session. Indeed, there was no more difference in preference judgments between any kind of exposed stimulus and the distracters in the RH.

## Discussion

To the best of our knowledge, the present study provides the first evidence for both sleep- and laterality-dependent processes of generalisation of the memory bias subtending preference judgments towards novel perspectives of previously exposed objects.

In the present study, laterality effects in preference judgments were already present at the immediate post-exposure phase, in line with the long-standing idea that cerebral asymmetries modulate cognitive specialization in the brain [e.g., Marc Dax 1836 in Springer and Deutsch 1998; Toga and Thompson 2003). Here, results for preference judgments conducted immediately after exposure disclosed a LH specialisation for the generalisation of the MEE. When objects were presented in the RVF, connected to the LH, affective preference was present for same and mirrored three-dimensional objects. In the LVF, connected to the right hemisphere (RH), only objects displayed in the same orientation as in the study phase were preferred. This profile of hemispheric specialisation is congruent with reports of lateralized priming effects having led to the dissociable neural subsystems theory (Burgund and Marsolek 2000; Marsolek 1999), which proposes that objects are stored in the LH in a way that produces more viewpoint-invariant effects, whereas objects are preferentially stored in the RH in a viewpoint-dependent manner (but see Curby et al 2004). Additionally, competition between hemispheric-lateralized subsystems may provide an explanation for discrepant findings of view-point invariant (Seamon and Delgado 1999) *versus* view-point dependent (Lawson 2004) patterns of MEE, reported in prior studies where stimuli were displayed centrally, i.e. exposed at once to the whole visual field.

Above immediate post-exposure effects, a prominent contribution of the present study is the demonstration that MEE generalizes with post-exposure time. In the LH, it generalizes to all types of structural transformations of unfamiliar objects, whereas in the RH it generalizes only to structural transformations where visibility on all salient parts of the object was preserved. Prior studies already showed the persistence of mere exposure (Seamon et al 1983) or priming (Cave 1997) effects for identical (i.e., SAME) stimuli over several days or weeks. Here, we additionally demonstrate that the MEE generalises over time towards novel transformations of the exposed objects, suggesting that the memory traces underlying fluency-based mechanisms of MEE are actively remodelled over extended periods of time up to several days. In the RH, where MEE effects were absent for mirror-rotated objects at immediate testing, an alternative interpretation would be that performance during the judgment phase was partially supported by inter-hemispheric transfer of abstract information consolidated in the LH (Marsolek et al 2002). Further studies should investigate whether generalization to all types of rotations can take place in the RH across more extended periods of time. Also, it remains to be ascertained whether time-dependent generalisation effects would be observed in the context of perceptual priming, where performance is thought to be subtended by the same memory-based processing fluency bias (Reber et al 2004).

Considering the role of post-exposure sleep within long-term, offline processes of memory consolidation, we have found that sleep deprivation on the first night after exposure, albeit followed by two recovery nights, extinguishes affective preference for all forms of previously exposed objects in the RH. Moreover, sleep-deprived subjects exhibited a propensity to produce more "like" response for novel objects presented in the RH than in the LH, a peculiar behaviour also found in subjects tested in a no-exposure condition. Combined with the abolition of preference effects, these data indicate that in the RH, subjects deprived of sleep on the first post-training night behave as if they had never gone through the original exposure session. Although far less pronounced in the LH, the effect of sleep deprivation on the post-exposure night was also significant since the pattern of performance fell back to the effects observed for preference judgments performed immediately after exposure. Altogether, these results suggest that sleep deprivation on the night after exposure disrupts to some extent the fluency-based mechanisms of affective preference (Bornstein and D'Agostino 1992; Jacoby and Kelley 1987; Reber et al 2004) for previously exposed objects. This would be consistent with earlier studies having shown that intervening deprivation of sleep, and especially rapid-eye-movement (REM) sleep, may alter priming effects (Plihal and Born 1999; Smith 1995; Wagner et al 2002). However, another study failed to disclose sleep-dependent effects using tachistoscopic identification of drawings (Rauchs et al 2006). Along with our own data, the discrepancy between these results emphasizes the importance to assess separately the respective contributions of the left and right cerebral hemispheres in studies targeting time- and sleep-dependent processes of memory consolidation. In our present study indeed, the group by stimulus partial ANOVA conducted on preference scores irrespective of laterality presentation actually failed to reveal a significant role for post-training sleep in the development of affective preference towards previously exposed novel objects. Results indicate that when data from both hemispheres are merged, SAME and MIRROR orientations are preferred above chance levels by both the TRS and TSD groups, an effect actually supported by the left hemisphere only in the TSD group, as shown in the results reported above. Therefore, it cannot be excluded that discrepancies between results of published studies stem from differences in the hemispheric requirements of the material and/or the experimental procedure used.

Although detrimental in both hemispheres, sleep deprivation did not affect performance to the same extent, suggesting inter-hemispheric differences in sleep-dependent processes of memory consolidation. Preference for SAME orientation, although present immediately after exposure, was lost in the RH following sleep deprivation, whereas that preference was preserved in the LH for SAME and MIRROR objects. This suggests that sleep on the night after exposure is more beneficial to the consolidation of fluency-based effects in the RH than in the LH. To the best of our knowledge, a generalisation over time of affective preference or priming effects towards different instances of pre-exposed stimuli has not previously been reported. Furthermore, we reveal here that sleep-dependent effects on the consolidation of memory-based affective preference are actually prominent in the right hemisphere. From this perspective, hemispheric differences in the development of the MEE call for a reappraisal of the role of cerebral asymmetries in wake- and sleep-dependent processes of memory consolidation in humans. Nowadays, the mechanisms underlying these inter-hemispheric differences remain unknown. A putative candidate could be an indirect, modulatory influence of the noradrenergic systems during sleep. Indeed, noradrenergic pathways that mediate not only vigilance but also selective attention towards behaviourally relevant stimuli are more strongly lateralised in the RH (Corbetta and Shulman 2002; Posner and Petersen 1990), and it has been shown that sleep deprivation affects arousal and performance more in the RH than in the LH (Johnsen et al 2002; Kim et al 2001; Pallesen et al 2004). Future studies are needed to elucidate the neural mediators underpinning laterality-based memory consolidation effects.

Finally, it remains debatable whether MEE patterns could reflect a combination of effects of sleep on both explicit and implicit memory. On the one hand, the mere exposure effect (MEE) met the very conservative chance recognition criteria proposed by Reingold and Merikle (Reingold and Merikle 1990), which requires that the effect of a variable has to be shown to be greater on an implicit than on an explicit memory task. Accordingly, subliminal presentation influences more the preference judgment task than an explicit recognition memory task (e.g. Bornstein 1989; Kunst-Wilson and Zajonc 1980; Seamon et al 1998). On the other hand, it is accepted nowadays that the processes subtending the MEE are to some extent similar to some of the processes subtending explicit recognition (e.g. familiarity/fluency based recognition; (Bornstein and D'Agostino 1994; Whittlesea and Price 2001). Nonetheless, although we have not specifically tested explicit recognition in the present study, it has been previously shown that the MEE is independent of (explicit) recollection-based recognition (Bornstein 1989; Bornstein and D'Agostino 1992). Further studies should investigate whether these hemispheric effects are solely relevant to the memory traces underlying processing fluency and affective preference, especially in terms of potential implicit and explicit contributions to a sleep-dependent memory effect (Born and Wagner 2004; Drosopoulos et al 2005; Robertson et al 2004).

## Materials and Methods

### Participants

Seventy-three healthy right-handed volunteers (38 males, 35 females; mean age, 22 years; range, 18-30 years) gave their informed, written consent to participate in this experiment, which was approved by the Ethics Committee of the University of Liège. Subjects were explicitly instructed not to consume psycho-stimulants, drugs or alcohol for 72 hours prior to and throughout the experiment period. In the regular sleep (TRS) group (6 males, 10 females), subjects were exposed to the stimuli then allowed to sleep at home as usual for the three post-training nights. In the TSD group (16 males, 13 females), subjects were exposed to the stimuli then stayed awake in the laboratory on the first post-training night until 7:00 a.m. During this night, participants' physical activity was maintained at as low a level as possible and subjects remained under constant supervision by the experimenters. In particular, they were instructed to remain seated throughout the experimental night and the consumption of psychoactive stimulants was prohibited. They had to engage in their usual daytime activities and slept normally at home during the next two post-training nights. Data from one subject in the sleep deprivation (TSD) group were excluded from the analyses due to alcohol consumption before the sleep deprivation night. In the TSD and TRS groups, exposure and test phases occurred at the same time of day, between 9:00 a.m. and 7:00 p.m., in order to avoid circadian confounds. In the IMM group (10 males, 6 females), subjects were exposed to the stimuli and then tested immediately afterwards, between 10:00 a.m. and 5:00 p.m. In the no-learning condition (6 males, 6 females), subjects were tested without any prior exposure to the stimulus, between 10:00 a.m. and 6:00 p.m.

### Sleep, Vigilance and Circadian parameters (TSD vs. TRS)

Sleep parameters. Sleep duration and quality [from *very poor* (1) to *very good* (6)] were subjectively assessed using the St. Mary's Hospital sleep questionnaire (Ellis et al 1981) for the one night preceding and the three nights during the study period in the TSD and TRS groups (Table 2). Mean sleep duration was no different for the TSD and TRS groups on night 1 ($t(29) = -0.41$, $P > .68$) and night 4 ($t(29) = -1.65$, $P > .1$), which preceded day 1 (exposure to the stimuli) and day 4 (test session), respectively. Likewise, median subjective sleep quality was equivalent for the TSD and TRS groups for night 1 (Mann-Whitney $U = 90.5$, $P > .24$) and night 4 ($U = 94$, $P > .3$). These results suggest that all participants were tested in similar states of alertness on both day 1 and day 4. While some subjects were sleep-deprived on night 2, the other participants slept normally at home. Finally, mean sleep duration was longer for the TSD group than for the TRS group on the night following the post-training night ($t(29) = –3.49$, $P < .005$), as well as subjective sleep quality (Mann-Whitney $U = 64$, $P < .05$), showing the expected sleep rebound after deprivation.

INSERT TABLE 2 ABOUT HERE

Vigilance. To assess psychomotor vigilance at the time of exposure and at the judgement phase in the TRS and TSD groups, subjects performed a simple reaction time task. In this vigilance task, a white cross was repeatedly displayed in the centre of a black screen after a variable time interval, randomly ranging from 2,000 to 5,000 ms. Subjects were instructed to press the space bar of the keyboard as fast as possible when the cross was displayed on the screen. Eighty trials were presented during one session, for an approximate duration of 6 minutes. The dependent measure of vigilance was response time (RT). A two-way ANOVA conducted on RT with group [TSD vs. TRS] as between-subjects factor and time [Exposure vs. Judgement phase] as a repeated measure showed that performance was similar from exposure to test time both in subjects allowed to sleep (357 ±11 versus 347 ±8 ms) and in subjects who were sleep deprived on the first post-exposure night (302 ±11 versus 296 ±8 ms; group by time interaction term $F(1, 29) = .03$, $p > 85$).

Circadian rhythms. A self-assessment questionnaire (Horne and Ostberg 1976) did not reveal 'morningness-eveningness' differences in circadian rhythms between the TRS and TSD groups [respectively, median scores = 48 and 50; ranges = 29–74 and 34–68; Mann-Whitney U-test adjusted $Z = -0.98$, $P > .32$].

**MEE task: Material, Apparatus and Procedure.**

Stimuli were 32 pictures of solid symmetrical objects (Seamon and Delgado 1999; Srinivas 1995). For each object, pictures were obtained in an arbitrary 0° visual angle orientation (SAME), after a nearly-mirror 80° depth-rotated orientation that preserved visibility of all parts of the object in its arbitrary position (MIRROR), and after an 110° depth-rotated orientation hiding some salient parts of the object in its arbitrary position (MASK; see Fig. 1). Illumination and black background conditions were kept constant in all orientations. Images were presented using E-Prime software (Psychology Software Tools) on a 17-inch computer screen (refresh rate 60 Hz). Responses and decision times were recorded.

During the exposure (encoding) phase, 24 pictures of objects were presented twice each in randomised order. Half of the objects faced left and half faced right. Left–right view was randomised across study trials. Each object was presented in its arbitrary position in the centre of the screen for 2,500 ms, followed by a blank screen for 3,500 ms. Participants were instructed to press a key (one of two) on the computer keyboard to decide whether the object was left- or right-oriented.

During the subsequent preference judgement (test) phase, the participants were presented with test views for each of the 24 objects and 8 previously unseen distracters, in a randomised order. Of the 24 pre-exposed objects, 8 objects were presented in the arbitrary orientation used at encoding (SAME). Eight other objects were presented rotated at 110° from the arbitrary position used at encoding, such that the visibility of all salient parts was preserved (MIRROR). The 8 remaining objects were presented rotated at 110° from the arbitrary position used at encoding, in such a way that at least one salient part was masked by comparison with the arbitrary encoding view (MASK). Within each category, half of the objects were presented in the left visual field (LVF) and the other half were presented in the right visual field (RVF). With reference to the fixation point located at the centre of the screen, the centre of each object was positioned 7.4° to the side and its inner edge was never closer than 4.2°. Each test trial began with the presentation of the fixation point for 750 ms. Participants were instructed to focus their attention on the fixation point and not to try to anticipate on which side of the fixation point the next object would appear. Immediately after the fixation point disappeared from view, the object was displayed on the left or right side of the screen until a response was given. Participants were asked to continue to focus their attention on the centre of the screen and to decide as fast as possible whether the object was pleasant (yes or no) by pressing a key (one of two) on the computer keyboard. A blank screen was displayed for 500 ms after the subject's response, followed by the next trial. A different, counterbalanced combination of objects was assigned to pre-exposed and distracter categories for each participant. More precisely, inter-individuals counterbalancing was randomly done as well for hemispheric field presentation than between distracters, SAME, MIRROR and MASK stimuli.

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**Table 1. Affective Preference Judgement**

| Group | Hemisphere | Distracter | SAME | | MIRROR | | MASK | |
|---|---|---|---|---|---|---|---|---|
| | | μ (SEM) | μ (SEM) | *d* | μ (SEM) | *d* | μ (SEM) | *d* |
| **IMM** | **LH** | 33 (±7) | +36 (±8) | *1.86 *** | +30 (±11) | *1.08 ** | –5 (±9) | *-0.18* |
| | **RH** | 36 (±7) | +25 (±9) | *0.79 ** | +3 (±10) | *0.13* | –9 (±11) | *-0.40* |
| **TRS** | **LH** | 34 (±4) | +27 (±9) | *0.78 ** | +31 (±9) | *1.04 *** | +23 (±7) | *1.07 ** |
| | **RH** | 33 (±4) | +23 (±8) | *0.94 ** | +19 (±7) | *0.88 ** | –8 (±7) | *-0.30* |
| **TSD** | **LH** | 38 (±6) | +21 (±7) | *0.72 ** | +16 (±6) | *0.54 ** | +5 (±7) | *0.18* |
| | **RH** | 52 (±6) | +3 (±6) | *-0.09* | +4 (±6) | *-0.10* | +5 (±7) | *-0.20* |

Notes. Values in the ‘distracter’ column are mean (μ) percentages of ‘like’ responses for the distracters presented. Values in the ‘SAME’, ‘MIRROR’ and ‘MASK’ columns are mean (μ) preference scores, i.e. the percentage increase (or decrease) in ‘like’ responses as compared to the distracters. All values are given with the standard error of the mean (SEM). Effect sizes ($d$) of single t-tests against the null computed on preference scores are provided with reference to the classification of effect sizes proposed by Cohen (1988*) Statistical power for the behavioral sciences*, 2nd edition, New-York, Academic Press; i.e. small $d = 0.20$, medium $d = .50$ and large $d = 0.80$). Statistically significant tests are mentioned * $P < .05$ ** $P < .005$.

**Table 2. Sleep parameters.**

| | | Night 1 | Night 2 | Night 3 | Night 4 |
|---|---|---|---|---|---|
| **Sleep duration** [hours: mean (± SD)] | | | | | |
| | **TRS** | 8.4 (±1.2) | 8.3 (±1.3) | 8.1 (±1.2) | 8.1 (±1.2) |
| | **TSD** | 8.3 (±1.4) | ------------ | 10.1 (±1.7) | 8.4 (±1.4) |
| **Subjective sleep quality** [rating: median (IQI)] | | | | | |
| | **TRS** | 5 (1) | 4 (1) | 4 (1.5) | 4((1) |
| | **TSD** | 4 (1.5) | ------------ | 5 (2) | 4 (1) |

Notes. (SD) = standard deviation of the mean; (IQI) = inter-quartile interval; TRS: subjects tested 72 hours after exposure including three nights of regular sleep; TSD: subjects tested 72 hours after exposure with sleep deprivation on the first night after exposure, followed by two recovery nights of regular sleep.

## FIGURE LEGENDS

**Figure 1**. Sample of three-dimensional unfamiliar objects. Each row shows an object presented in its original position (ARBITRARY) during the left-right orientation decision at the exposure phase. During the liking judgement phase, objects are displayed either in the same arbitrary position (SAME), after a nearly-mirror rotation (MIRROR), or after a rotation masking at least one salient part of the original object (MASK), along with non–previously seen objects (DISTRACTERS).

**Figure 2.** Preference scores for stimuli displayed in the left (LH) and right (RH) hemispheres in SAME, MIRROR and MASK orientations, in subjects tested immediately (IMM), 72 hours later including three nights of regular sleep (TRS), or 72 hours later with sleep deprivation on the first night after exposure (TSD). Bars represent the difference between the percentages of 'like' responses for a given category of pre-exposed objects versus the distracters category (thus, a zero value means no preference). Asterisks indicate a significant preference score (t-test against the null reference mean): * $P < .05$ ** $P < .005$. Error bars are standard errors of the mean.

**Figure 1**

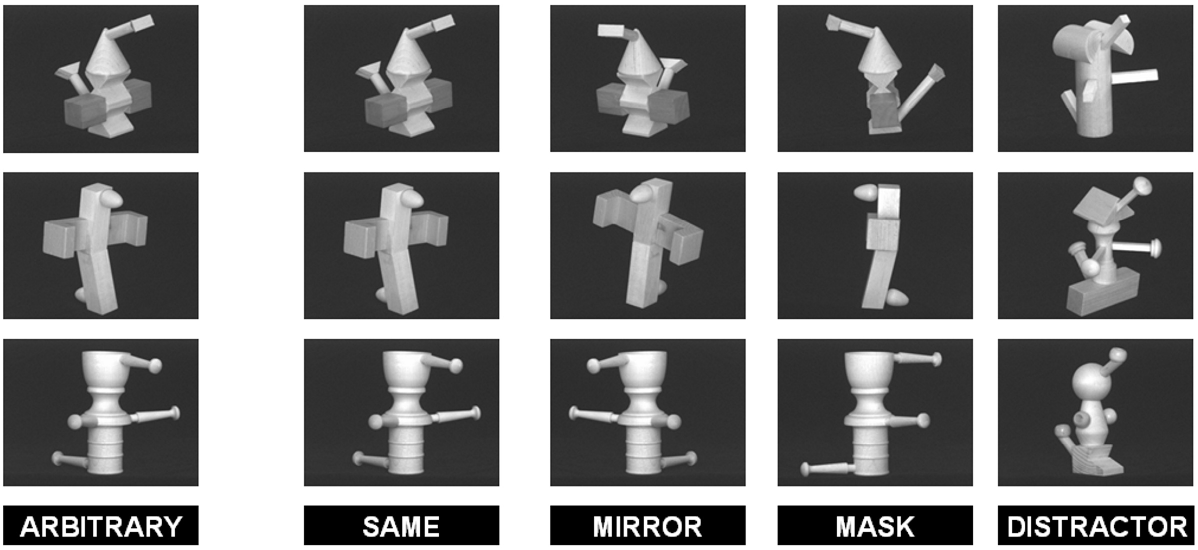
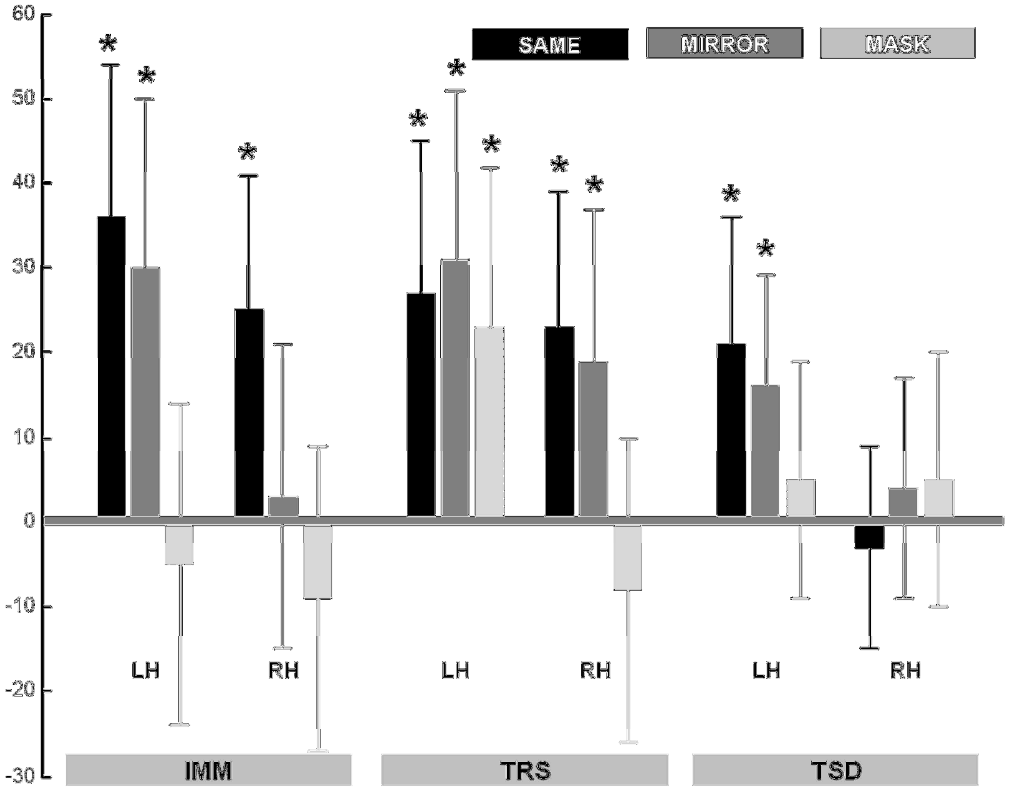


**Figure 2**


60
50
40
30
20
10
0
-10
-20
-30
SAME
MIRROR
MASK
*
LH
RH
LH
RH
LH
RH
IMM
TRS
TSD