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Meta-analysis

Sleep-dependent motor memory consolidation in healthy adults: A meta-analysis

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ABSTRACT

It is widely accepted that sleep better facilitates the consolidation of motor memories than does a corresponding wake interval (King et al., 2017). However, no in-depth analysis of the various motor tasks and their relative sleep gain has been conducted so far. Therefore, the present meta-analysis considered 48 studies with a total of 53 sleep ($n = 829$) and 53 wake ($n = 825$) groups. An overall comparison between all sleep and wake groups resulted in a small effect for the relative sleep gain in motor memory consolidation ($g = 0.43$). While no sub-group differences were identified for differing designs, a small effect for the finger tapping task ($g = 0.47$) and a medium effect for the mirror tracing task ($g = 0.62$) were found. In summary, the meta-analysis substantiates that sleep generally benefits the consolidation of motor memories. However, to further our understanding of the mechanisms underlying this effect, examining certain task dimensions and their relative sleep gain would be a promising direction for future research.

1. Introduction

The increased strength of memories after a single night of sleep was already observed by the early Roman scholar Quintilian (Baddeley et al., 2015). Roughly 2000 years later, Jenkins and Dallenbach (1924) provided experimental evidence that sleep in fact consolidates the learning of non-sense syllables, which was shown by superior recall performance after sleep than after a wake interval. Subsequently, the idea of different memory systems gained impact; particularly regarding their functional or anatomical systems, their dependence on sleep, and their reign over the newly distinguished concepts of declarative and procedural knowledge (Plihal and Born, 1997; Smith, 1995). Declarative knowledge was defined as the conscious recollection of facts and events, whereas procedural knowledge was regarded as a collection of abilities, such as skill learning, that does not involve direct recall of previous episodes (Squire and Zola, 1996). Based on this framework, the foundational study of Smith and Macneill (1994) assessed the influence of systematic variation of sleep on procedural learning for the first time. Here, a pursuit rotor task was used in which participants were asked to track a constantly moving light area with a hand-held stylus. The groups with total sleep deprivation and REM-deprivation showed worse performance than the control group, whose sleep had not been interrupted. Thus, it was inferred that the consolidation of procedural memory contents is sleep-dependent. However, over the following 25 years of research on the effect of sleep on motor memory consolidation, the notion that sleep benefits motor learning has been repeatedly challenged, leading to a rather ambiguous view on the topic (cf. King et al., 2017). In response, Pan and Rickard (2015) conducted a comprehensive meta-analysis on motor sequence learning. On the basis of 34 articles, they concluded that the existing literature speaks against the hypotheses that sleep improves motor performance and rather conclude that sleep seems to stabilize performance whereas wakefulness leads to deterioration. This meta-analysis triggered a commentary by Adi-Japha and Karni (2016) that criticized overlooked developmental differences in some of the included groups and disregarded tasks demands. However, in response, Rickard and Pan (2016) were able to refute this critique by presenting a reanalysis of the original data that upheld the initial conclusions. Subsequently, King et al. (2017) broadened the scope by reviewing empirical work on a larger variety of motor tasks. The conclusion from King et al. (2017), albeit without quantitative analyses, was that sleep benefits the broad class of motor sequence learning tasks while the influence on other tasks categories remains unclear. Thus, the influence of sleep on motor learning on a task level is still a matter of ongoing controversial discussions.

In the current debate on the function of sleep for motor memory consolidation, it becomes apparent that three aspects need to be considered when explaining either observed or not observed empirical effects. First, the age (Gui et al., 2017) and clinical status (Cellini et al.,

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2014; Djonlagic et al., 2012) of the examined population influence procedural memory consolidation as a function of sleep. Second, the detection of sleep-related effects depends on the way these effects are calculated, which implies that more recently introduced measures should be preferred (Pan and Rickard, 2015). And third, performance change after sleep and wake at least partly depends on the chosen experimental design (Pan and Rickard, 2015). Hence, these three aspects deserve closer inspection.

(1) Regarding the demographics of the examined populations, a recent meta-analysis conducted by Gui et al. (2017) focused on the specific aspects of age and its influence on memory consolidation in 22 studies on both declarative and procedural memory tasks (12 thereof on motor learning). Although no in-depth analysis on the different motor tasks was included due to the broad range of tasks used, it is worthwhile to note that an overall strong significant effect for sleep-dependent consolidation was found for young participants (ca. 18–35 years) and a smaller non-significant effect for older participants (ca. 60–85 years). Studies that focused on children (ca. 9–12 years) also revealed differences in the strengthening of motor memories over different offline intervals (Dorfberger et al., 2007; Wilhelm et al., 2008). Furthermore, it has been shown that clinical populations differ in the consolidation of motor skills in comparison with healthy controls (Cellini et al., 2014; Djonlagic et al., 2012). Taken together, these results imply that one should refrain from analyzing motor memory consolidation without considering the age and health status of the study population.
(2) On the basis of current methodological discussions, it is inadequate to attribute a significant improvement of a sleep group and a non-significant improvement in the wake group to sleep-dependent motor memory processes without reporting the group × time interaction resulting from the pre- and posttest measures (King et al., 2017; Nieuwenhuis et al., 2011). Following this argument, the relative sleep gain (RSG) has been introduced as a well-grounded operationalization for the effect of sleep on motor memory consolidation (Pan and Rickard, 2015). To calculate this variable, the performance change *post-wake* (i.e., the performance after the wake interval minus the performance before the wake interval) and the performance change *post-sleep* (i.e., the performance after the sleep interval minus the performance before the sleep interval) are computed. These performance changes are then transformed into effect sizes that are standardized to ensure comparability between different motor tasks (Pan and Rickard, 2015). Specifically, this standardization notably controls for the fact that detected sleep effects can correspond to either positive or negative statistical effects depending on the task and its dependent variable (e.g., a finger tapping task regards a higher number of correct sequences as better performance in comparison with a mirror tracing task in which a shorter processing time indicates better performance). Consequently, the raw effect sizes are transformed so that a positive effect always indicates better performance after the offline interval. Finally, the effect post-wake is subtracted from the effect post-sleep to obtain the RSG. A positive RSG can be interpreted as the standardized behavioral manifestation of sleep-dependent consolidation. Such a manifestation would be found in two cases. In the first case, the performance gain from knowledge acquisition to retrieval is positive in the sleep group and none or negative in the wake group, indicating that sleep had a performance-enhancing effect. In the second case, the sleep group shows the same or deteriorated performance from acquisition to retrieval and the wake group even more deterioration over the same interval, indicating that sleep had a stabilizing effect on performance.
(3) A final important factor to consider when investigating the effect of sleep on motor memory consolidation regards the specifics of the chosen experimental design (Pan and Rickard, 2015), especially with respect to circadian (e.g., Facer-Childs et al., 2018) and homeostatic (sleep pressure, e.g., Facer-Childs and Brandstaetter, 2015) factors. In the *varied time design*, both groups have a time interval of the same length (e.g., 12 h) between knowledge acquisition and retrieval that contains nocturnal sleep for the sleep group and daytime wakefulness for the wake group. Hence, performance is measured at different times of day. As this design does not control for time of training or testing, it is vulnerable to circadian and homeostatic confounders (Keisler et al., 2007; Pan and Rickard, 2015). A similar design is the *varied delay design* that also compares nocturnal sleep and daytime wakefulness, but controls for circadian and homeostatic factors by implementing a different time delay between acquisition and retrieval for the two experimental groups. Despite controlling for such factors, it could be argued that the unequal time interval could potentially favor the sleep group because more sleep-independent consolidation processes could take place over the longer retention interval. A more often used design in the recent years is the *nap design*, in which the sleep group has an interval of diurnal sleep in the afternoon (e.g., 2 h) and the wake group stays awake for the same time interval. Although the potential release of homeostatic sleep pressure can be seen as a disadvantage of this design, the nap design controls for circadian effects. In the *deprivation design*, participants in the wake group stay awake the whole night while participants in the sleep group have a full night of uninterrupted sleep. Retrieval is then tested directly after the sleep interval for the sleep group and after 1–2 nights of recovery sleep in the sleep deprived group. Furthermore, additional tests are administered to control for extraneous confounding factors – like motor slowing or reduced vigilance at retrieval (Kurniawan et al., 2016). A potential downside to this design is the unequal duration between training and retrieval for the two groups, which could be seen as either advantageous by providing more time to consolidate or disadvantageous by introducing a prolonged time interval for one to forget.

Finally, and branching from the designs sketched so far, a recently introduced approach is to dissociate different task dimensions at retrieval. The underlying rationale for this design is that procedural memory contains a heterogenous set of tasks that can thus be subdivided; a finding supported by both behavioral (e.g., Van den Berg et al., 2019; Verwey and Wright, 2004) and neurological (e.g., Hikosaka et al., 2002) evidence. This means that, after the consolidation phase (containing either sleep or wakefulness), the experimental groups are tested in different dimensions of the same task, for example, the goal or movement dimension (Cohen et al., 2005). Hence, this design is called a *dimension transfer design*. Evidently, the reported advantages and disadvantages of the different sleep-research designs might lead to varying results when investigating the function of sleep in motor memory consolidation.

Consequently, the aim of the present meta-analysis is to provide an overview on the current state of the art on the effect of sleep on motor memory consolidation; extending existing analyses beyond the field of motor sequence learning and accounting for the above highlighted issues of (1) age and clinical populations, (2) effect operationalization, and (3) experimental design. More precisely, the first issue will be addressed by only including studies on healthy adults, the second by consistently using the RSG variable to operationalize sleep-related effects, and the third by including the experimental design as a potential explanatory factor.

2. Methods

2.1. Literature search

The present meta-analysis followed the guidelines of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA; Moher et al., 2009). A literature search was conducted in December of

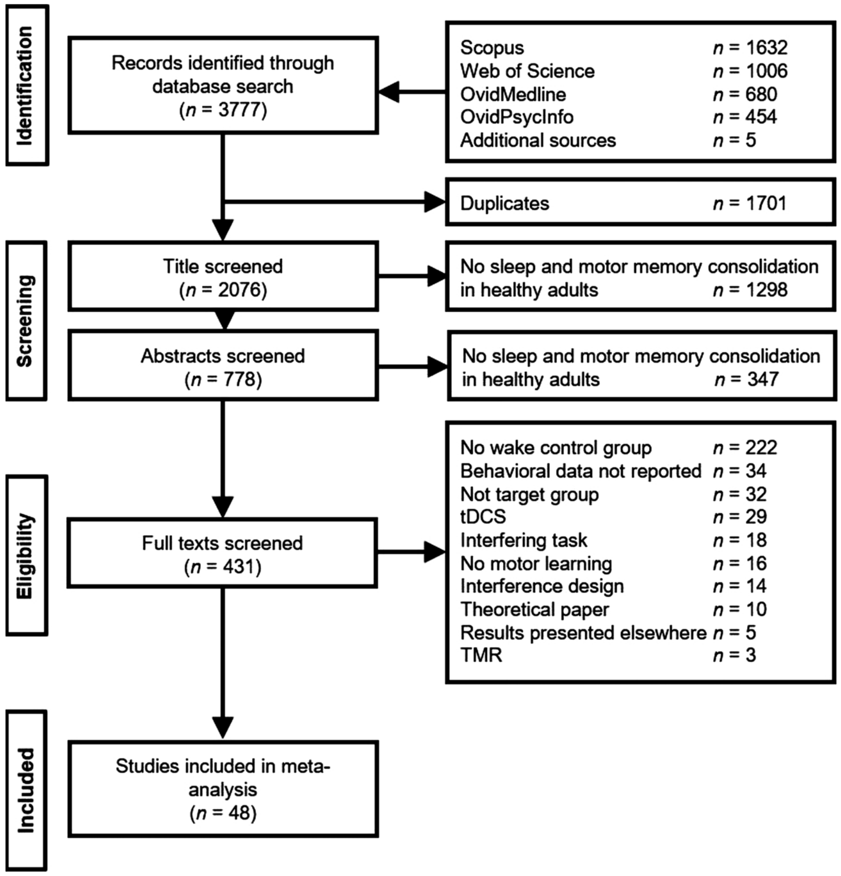

Fig. 1. PRISMA flowchart for the literature search and selection process.

2018 in the following academic databases: Ovid Medline, Ovid PsycInfo, Scopus, and Web of Knowledge. To obtain a comprehensive list of literature on sleep and motor learning, the following keywords were combined with Boolean operators: [sleep OR nap*] AND [procedural learning OR motor learning OR movement learning OR skill learning OR motor control OR skill development OR skill acquisition]. In all databases, filters were applied to search the title, abstracts, and keywords of peer-reviewed articles published in English language.

The results of each database were imported into EndNote X8.2. Following, an ancestral search was performed by checking the reference lists of the full texts. After removing duplicates, the articles were screened on three levels. First, articles were included if the title seemed relevant to sleep and motor memory consolidation in healthy adult people. If the title was ambiguous, the article was not excluded. Second, articles were reviewed on the abstract level and excluded if the focus of the study was on other memory systems than procedural memory, if the study examined the effects of substances administered to participants, or if clinical populations, too young (< 18 years) or too old (> 50 years) people, or animals were investigated. If one of the aforementioned criteria was ambiguously met, the article was not excluded. Third, the full texts of the remaining articles were screened. At this stage, articles were excluded if participants did not meet the inclusion criteria (healthy, adult, human subjects), if the study did not actually focus on motor learning, if the experiment did not include a corresponding wake group, or if the time interval between acquisition and retrieval was not the same for both groups. Moreover, studies were excluded if the method could potentially influence motor memory consolidation; specifically by employing transcranial direct current stimulation (tDCS) methods, targeted memory reactivation (TMR), an interference design (e.g., different motor sequences in succession) or interfering tasks (e.g., learning of other declarative material) between acquisition and retrieval phases. Finally, articles that had a theoretical rather than an empirical focus, reanalyzed previously published data, or reported no behavioral data were excluded. The remaining articles were then used for quantitative analyses.

2.2. Effect size calculation and random-effects model

The RSG, an operationalization for the effect of sleep on motor memory consolidation based on group differences, was taken as the measure of interest for the present meta-analysis. Therefore, for each sleep and wake group, Cohen's d (d) was calculated according to the equation below for pre-post scores (Borenstein et al., 2009).

$$d = \frac{\overline{Y}_{diff}}{S_{within}} = \frac{\overline{Y}_{post} - \overline{Y}_{pre}}{S_{within}}$$

In cases in which the standard deviation of the pre/posttest difference were provided by the authors, the standard deviation within groups (S_{within}) was calculated with the following equation (with r = 0.5 as a conservative estimate for the pretest-posttest correlation).

$$S_{within} = \frac{S_{diff}}{\sqrt{2(1-r)}}$$

If the standard deviation of the difference was not reported, the required d-value was computed with the standard deviation of the pretest (Hunter and Schmidt, 2004, pp. 350–351).

$$d = \frac{\overline{Y}_{post} - \overline{Y}_{pre}}{S_{pre}}$$

In some cases, the necessary statistics were only derivable through bar graphs. In these cases, values were manually determined from the height of the bar on the y-axis and its error measure before applying the formulas above. Due to the overestimation of the population effect size

Table 1
Descriptive overview of all studies included in the meta-analysis, including the sample sizes of the sleep and wake groups, the motor task, the experimental design, as well as the relative sleep gain (RSG) effect as Hedges *g* with its corresponding 95 % CI interval and weight in the overall random-effects model.

Reference	Sample size S	W	Task	Design	RSG	95 % CI	W (%)
Albouy et al. (2013)	13	11	FTT[a,i]	Dtd	0.65	[0.08; 1.22]	2.0
Al-Sharman and Siengsukon (2013)	12	12	Novel walking task	VT	0.50	[-0.07; 1.08]	2.0
Backhaus and Junghanns (2006)	17	17	MTT[j]	Nap	1.14	[0.43; 1.84]	1.6
Blischke et al. (2008)	12	12	FTT[a,e]	Vt	0.43	[-0.17; 1.03]	1.9
Blischke et al. (2008)	11	12	FTT[a,f]	Vt	−0.01	[-0.65; 0.64]	1.7
Blischke et al. (2008)	10	10	Diamond tapping task	Vt	0.20	[-0.42; 0.83]	1.8
Blischke et al. (2008)	11	12	Countermovement jump	Vt	0.68	[0.03; 1.32]	1.7
Blischke et al. (2008)	16	16	Pursuit tracking task	Vt	0.24	[-0.26; 0.74]	2.2
Bottary et al. (2016)	20	14	FTT[b]	Vt	0.48	[-0.02; 0.98]	2.2
Brawn et al. (2008)	20	29	First-person shooter	Vt	0.49	[0.05; 0.93]	2.5
Brawn et al. (2010)	14	20	FTT[a]	Vt	0.81	[0.31; 1.31]	2.2
Cohen et al. (2005)	10	10	SRTT[d,i]	Dtd	1.11	[0.41; 1.81]	1.6
Fogel et al. (2014)	13	15	FTT[a]	Nap	0.57	[-0.03; 1.16]	1.9
Genzel et al. (2012a, 2012b) - men	10	10	FTT[a]	Nap	0.39	[-0.27; 1.05]	1.7
Genzel et al. (2012a, 2012b) - women	10	10	FTT[a]	Nap	0.00	[-0.62; 0.62]	1.8
Genzel et al. (2012a, 2012b)	18	18	Video game dance stage	Vt	0.71	[0.12; 1.29]	1.9
Gregory et al. (2014)	11	9	FTT[a]	Vt	1.38	[0.60; 2.15]	1.4
Hoedlmoser et al. (2015)	10	10	Inverse steering bicycle	Nap	−0.53	[-1.21; 0.15]	1.6
Huber et al. (2004)	10	10	Rotation adaptation	Vt	1.29	[0.58; 1.99]	1.6
Johnson et al. (2018)	5	5	Ball throwing	Vt	−0.06	[-1.19; 1.06]	0.8
Kempler and Richmond (2012)	35	35	Coordinated arm reaching	Vt	0.26	[-0.07; 0.60]	3.0
Korman et al. (2007)	8	8	Finger-to-thumb opposition task[a]	Nap	0.94	[0.10; 1.78]	1.2
Landry et al. (2016)	22	22	FTT[V]	Nap	0.56	[0.13; 0.98]	2.5
Lugassy et al. (2018)	15	16	Complex fine motor movements	Vt	0.16	[-0.34; 0.66]	2.2
Maier et al. (2017)	36	36	FTT[a]	Nap	0.51	[0.13; 0.88]	2.8
Malangré et al. (2014)	12	12	Pegboard	Vt	−0.11	[-0.83; 0.61]	1.5
Morita et al. (2012)	8	8	Juggling	Nap	1.61	[0.55; 2.68]	0.9
Morita et al. (2016)	9	9	Juggling	Nap	−0.53	[-1.40; 0.35]	1.2
Nissen et al. (2011)	36	17	MTT[j]	Vt	1.10	[0.52; 1.69]	1.9
Pace-Schott and Spencer (2013)	13	17	SRTT[d,i]	Dtd	0.60	[0.08; 1.13]	2.1
Pereira et al. (2015)	15	15	FTT[a]	Nap	0.35	[-0.19; 0.88]	2.1
Rångtell et al. (2017)	60	54	FTT[a]	Vt	0.35	[0.07; 0.62]	3.3
Rickard et al. (2008) - Experiment 1, conservative formula	16	16	FTT[a]	Vt	0.75	[0.23; 1.26]	2.2
Robertson et al. (2004)	10	10	SRTT[d,g]	Vt	0.65	[-0.02; 1.31]	1.7
Robertson et al. (2004)	10	10	SRTT[d,h]	Vt	0.21	[-0.47; 0.89]	1.6
Schichl et al. (2011)	17	15	MTT[k]	Nap	0.77	[-0.01; 1.54]	1.4
Schönauer et al. (2014) Experiment 2	16	18	FTT[d]	D	−0.11	[-0.66; 0.43]	2.1
Schönauer et al. (2014) - Experiment 3	31	31	FTT[d]	Vt	0.22	[-0.21; 0.64]	2.6
Schönauer et al. (2015) - Experiment 2	12	12	FTT[a]	Vt	0.07	[-0.59; 0.73]	1.7
Seeck-Hirschner et al. (2010)	11	11	MTT[k]	Nap	0.74	[-0.19; 1.66]	1.1
Siengsukon and Al-Sharman (2011) - Experiment 1	14	14	SRTT[c,g]	Vt	0.52	[-0.04; 1.09]	1.6
Siengsukon and Al-Sharman (2011) - Experiment 2	11	11	Continuous tracking	Vt	−0.41	[-1.08; 0.26]	2.0
Simmons and Duke (2006) - AM-PM/PM-AM group	24	21	Playing the piano	Vt	−0.03	[-0.44; 0.38]	2.6
Simmons and Duke (2006) - AM-PM-AM/PM-AM-PM group	10	10	Playing the piano	Vt	−0.24	[-0.86; 0.39]	1.8
Tamaki et al. (2007) – non-rotated image	9	10	MTT[l]	Vt	1.13	[0.41; 1.85]	1.5
Tucker et al. (2006)	12	17	MTT[k]	Nap	−0.45	[-1.11; 0.22]	1.7
Tucker et al. (2016)	9	11	FTT[a]	Vt	0.69	[0.00; 1.39]	1.6
Van Schalkwijk et al. (2017)	17	19	MTT[m]	Nap	0.05	[-0.42; 0.52]	2.4
Verweij et al. (2016)	21	21	SISL	Nap	0.63	[0.14; 1.12]	2.3
Walker et al. (2002)	15	15	FTT[a]	Vt	0.85	[0.28; 1.41]	2.0
Walker et al. (2003)	15	15	FTT[a]	Vt	0.90	[0.33; 1.47]	2.0
Wilhelm et al. (2008)	15	15	FTT[a]	Vt	0.66	[0.06; 1.27]	1.9
Witt et al. (2010)	12	12	FTT[a,i]	Dt	0.03	[-0.53; 0.60]	2.0

Note. FTT = Finger tapping task, MTT = Mirror tracing task, SRTT = Serial reaction time task, SISL = Serial interception sequence learning, Vt = Varied time design, Dt = Dimension transfer design, D = Deprivation design. RSG = relative sleep gain (Hedges *g* sleep group – Hedges *g* wake group); W (%) = Weight of each effect size in the overall random-effect model.

[a] Five-item sequence.
[b] Seven-item sequence.
[c] Ten-item sequence.
[d] Twelve-item sequence.
[e] Guided.
[f] Unguided.
[g] Explicit.
[h] Implicit.
[i] Only the goal dimension is shown.
[j] Six different figures.
[k] Star.
[l] One of six irregular figures or a star.
[m] Twelve figures.

of Cohen's d, especially for small sample sizes, the effect sizes were then transformed into a bias-corrected standardized mean difference effect size, called Hedges g (g) (Borenstein et al., 2009). Here, the sign of the g-values was adjusted to correspond to respective task improvements, such that a higher number always indicates better performance. Finally, the effect sizes of the RSG was ultimately calculated by subtracting the transformed and standardized effect size of the wake group (g_{wake}) from that of the sleep group (g_{sleep}). Hence, a positive Hedges g indicates a better performance after a sleep interval than after a wake interval – independent of the task and the dependent variable.

$$g_{RSG} = g_{sleep} - g_{wake}$$

The sizes of the effects were interpreted according to Cohen (1988) as small (≥ 0.2), medium (≥ 0.5) or large (≥ 0.8).

The resulting RSG effect sizes were used to perform a random-effects meta-analysis with the metaphor package for R (Viechtbauer, 2010). An overall random-effects model with all tasks was calculated to infer the relative sleep enhancement of motor tasks. Additionally, separate random-effects models were calculated for the finger tapping task (FTT) and the mirror tracing task (MTT) due to the frequent use of these tasks in sleep research. Subgroup analyses were additionally performed for the varying experimental designs. A Hartung-Knapp adjustment for the random-effects model and an inverse variance method were applied. With the latter, each study was weighted based on the number of participants in the study, assigning more weight to studies with a larger number of participants than to those with a smaller number of participants. To assess the variability between studies, Q was taken as a measure of heterogeneity (Cumming, 2013, pp. 214–230). In addition to Q, the more intuitive I^2 metric was calculated, which is the percentage of total variation across studies that is due to heterogeneity rather than chance (Higgins et al., 2003). To assess publication-bias, Egger's test of the intercept (Egger et al., 1997) and Funnel plots were further examined.

Since some tasks allow for the measurement of more than one dependent variable (e.g., FTT: number of correct sequences as well as number of errors), the main variable of each study was always selected. This variable was identified as either that explicitly stated by the authors or that most commonly used for the respective experimental task (e.g., FTT: number of correct sequences in 30 s).

3. Results

3.1. Search results and study selection

The PRISMA flow chart is shown in Fig. 1. The initial search yielded 3777 results. After removing of duplicates, 2076 articles were screened on the title level. In 1298 cases, the title indicated that the paper was not relevant to sleep and motor memory consolidation in healthy adult people and the respective articles were excluded. The same procedure was applied to screen articles on the abstract level, which led to the exclusion of 347 further articles. Next, the articles were screened in depth on the full-text level. At this stage, articles were excluded in which: the experiment did not include a corresponding wake group (n = 222), the participants were not healthy adult people (n = 32), an interfering task was introduced during the acquisition phase or the retrieval phase (n = 18), the main task did not regard motor learning (n = 16), the paper had a theoretical rather than empirical focus (n = 10), the results were already published elsewhere (n = 5) or behavioral data was not reported (n = 34), or the study employed a tDCS method (n = 29), an interference design (n = 14) or a TMR paradigm (n = 3). After this exclusion step, 48 articles remained for the quantitative meta-analysis. In total, these studies comprised of 106 groups, of which 53 were sleep and 53 were wake groups with 829 and 825 participants, respectively.

A comprehensive overview of the included papers is provided in Table 1, in which all studies are presented in alphabetical order. Furthermore, the sample sizes of the sleep and wake groups used to calculate the RSG and the corresponding task for each study are reported. More information on the specifics of each task is provided in the footnotes (e.g., length of the sequence in the FTT or which figures were used in the MTT). The designs of the studies are additionally indicated. A design was classified as a varied time design when the acquisition phase of the sleep group was in the evening and the retrieval test was roughly 12 h later the next morning, with an average of eight hours of sleep in between. The corresponding wake group then had their acquisition phase in the morning and the retrieval test 12 h later in the evening without a sleep interval in between. A nap design was characterized by an acquisition and retrieval phase separated by some hours (e.g., less than 6 h), in which the sleep group had a short sleep interval (> 15 min and < 120 min) and the wake group did not sleep. A deprivation design required that both groups had their acquisition phases in the morning and their retrieval phases the next morning, with one group having slept and the other group staying awake the whole night. The dimension transfer design refers to a design in which both groups learned the same motor task during the acquisition phase but were tested in transfer tasks during the retrieval test. The last three columns of Table 1 show the relative sleep gain, the 95 %-CI, and the weight of each study in the overall random-effects model.

3.2. RSG in motor learning tasks

An overall comparison of the sleep and wake groups of all included studies is depicted in Fig. 2. The analysis resulted in a significant, but small effect size for the RSG in all motor learning tasks (g = 0.43, 95 % CI = [0.31, 0.55], t = 7.11, p < .0001). Heterogeneity between studies was confirmed with a Q test (Q = 103.62; p < .0001). Between study variability was shown to be moderate (I^2 = 50.40 %). Subgroup analysis for experimental designs – independent of the task used – revealed small effects for the varied time design (g = 0.45, 95 % CI = [0.31, 0.60]) and the nap design (g = 0.39, 95 % CI = [0.10, 0.68]) as well as a medium effect for the dimension transfer design (g = 0.57, 95 % CI = [-0.11, 1.25]). No positive effect of sleep in the deprivation design was found (g = -0.11, 95 % CI = [-0.66, 0.43]). However, despite these individual effects, the overall subgroup analysis for experimental designs resulted in no significant group difference (p = .24).

3.3. RSG in FTT performance

As shown in the forest plot of Fig. 3, a random-effects model was calculated for the studies in which the FTT was used as the motor learning task. In these experiments, the RSG was significant with a small effect (g = 0.47, 95 % CI = [0.33, 0.60], t = 7.17, p < .0001). No significant heterogeneity between studies (Q = 28.44, p = .16) was found and between-study variability was low (I^2 = 19.4 %). A subgroup analysis for experimental designs resulted in a medium effect size for the varied time design (g = 0.54, 95 % CI = [0.34, 0.75]), small effect sizes for the nap design (g = 0.43, 95 % CI = [0.24, 0.63]), a negative effect for the deprivation design (g = -0.11, 95 % CI = [-0.66, 0.43]) and a small effect size for the dimension transfer design (g = 0.44, 95 % CI = [-0.40, 1.27]). Although differences in the effect size differences of the four designs showed a tendency towards group differences, they did not reach statistical significance (p = .162).

3.4. RSG in MTT performance

Fig. 4 depicts the forest plot of all studies in which an MTT was used. A random-effects model calculation revealed a significant and medium-sized effect of a sleep interval in comparison with a corresponding wake interval (g = 0.62, 95 % CI = [0.04; 1.20], t = 2.62, p = .040). Significant heterogeneity between studies (Q = 22.10, p = .0012) and high between-study variability was found (I^2 = 63.50 %). A subgroup analysis for experimental design resulted in a large effect for

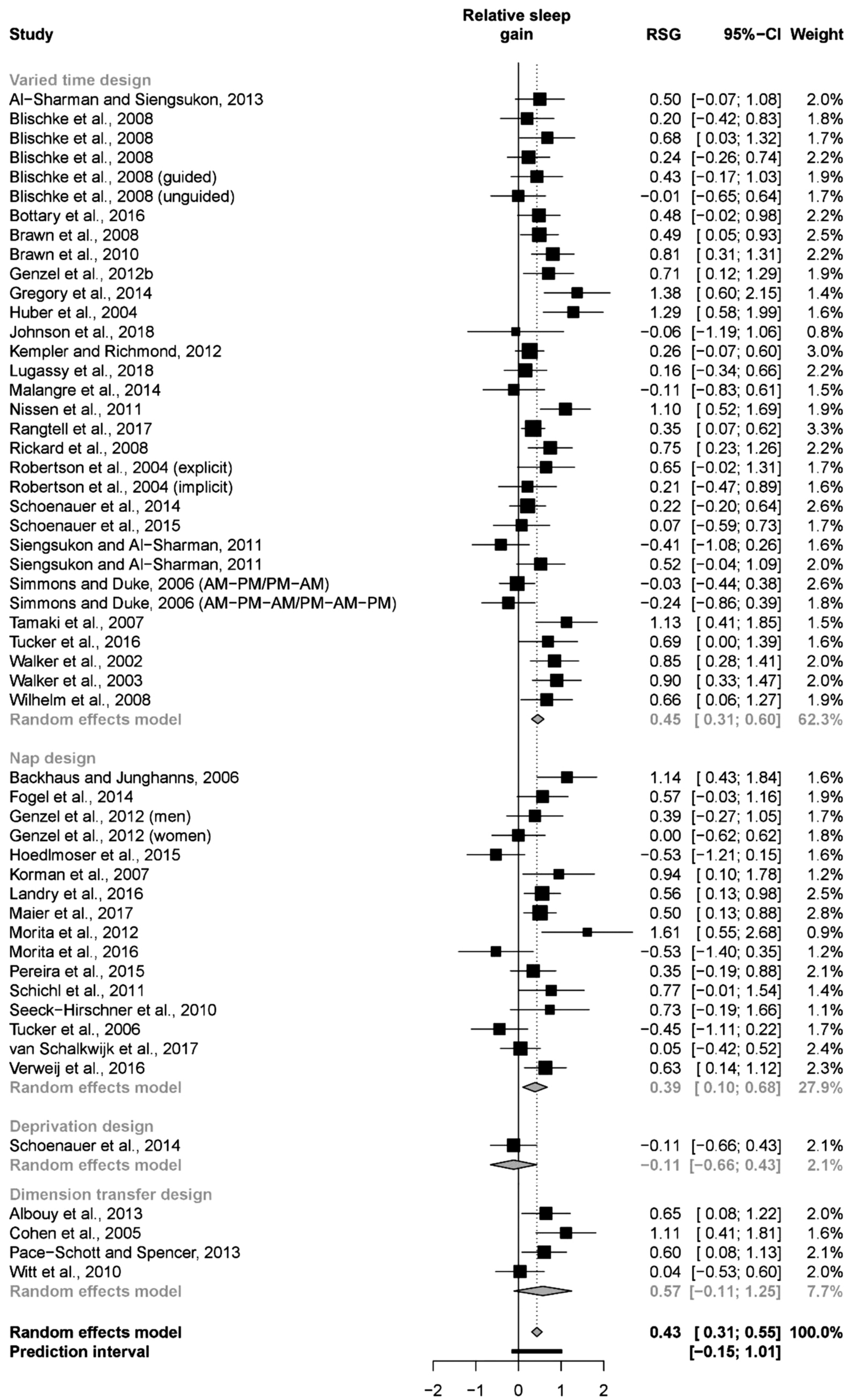

Fig. 2. The relative sleep gain (RSG) of all studies included in the meta-analysis. The size of the black squares represents the weight of each study in the random-effects model and the bars the 95 % CI of the corresponding effect size. Studies are ordered in terms of the experimental design used, with the results of the random-effect models displayed below each grouping and at the end of the list for the overall model.

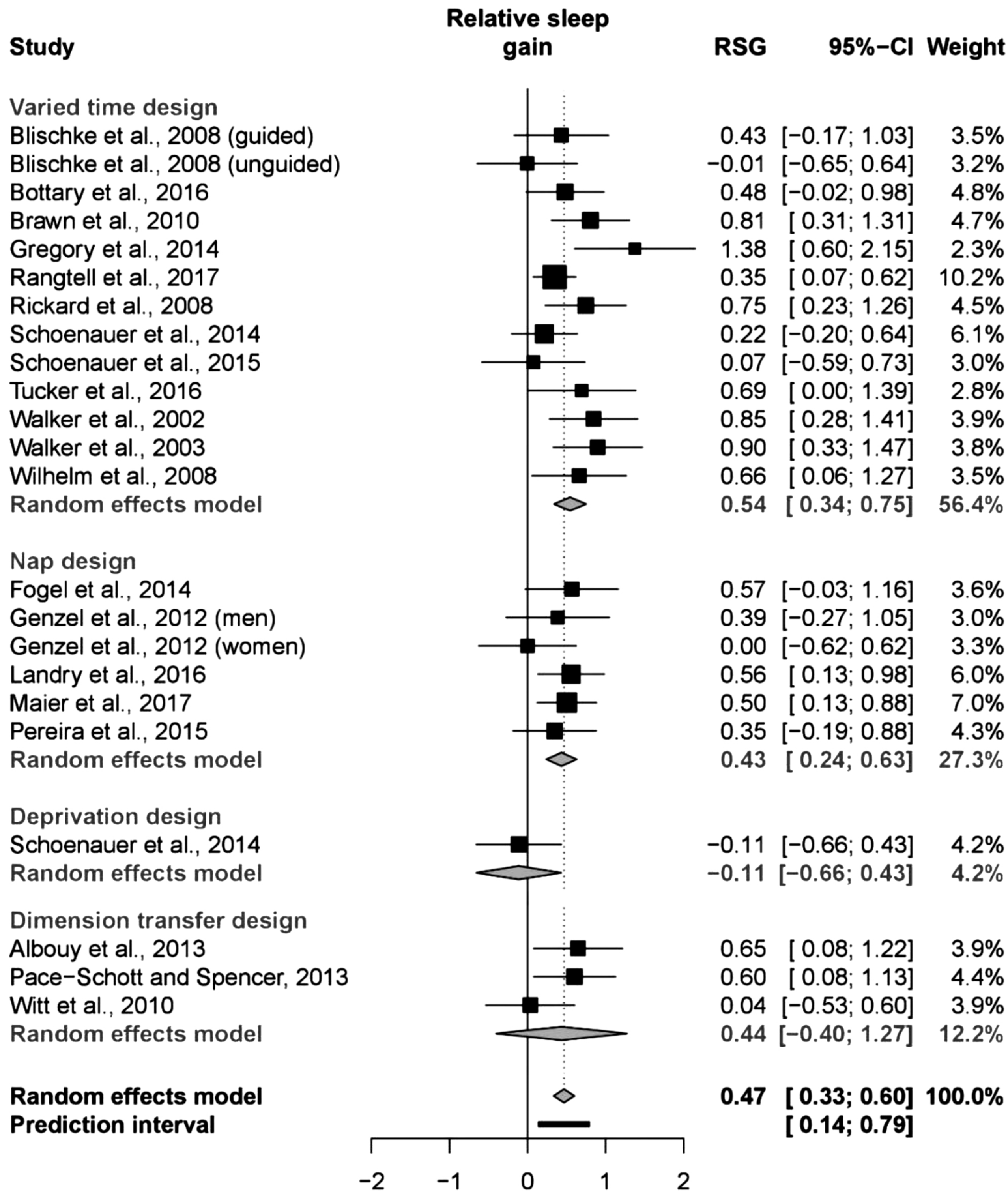

Fig. 3. The relative sleep gain (RSG) of all studies that used a finger tapping paradigm. The size of the black squares represents the weight of each study in the random-effects model and the bars the 95 % CI of the corresponding effect size. Studies are ordered in terms of the experimental design used, with the results of the random-effects models displayed below each grouping and at the end of the list for the overall model.

the varied time design (g = 1.11, 95 % CI = [0.95; 1.27]) and a medium effect size for the nap design (g = 0.41, 95 % CI = [-0.39; 1.21]) with a significant subgroup difference (p = .015).

3.5. RSG in other task performance

As illustrated in Fig. 5, a random-effects model was also calculated for the tasks used in the studies remaining after the FTT and MTT subgroup analyses. The analysis resulted in a significant effect for the RSG, though with a small effect size (g = 0.34, 95 % CI = [0.13, 0.56], t = 3.26, p = 0.004). The heterogeneity of these studies was significant (Q = 49.34, p = .001) with moderate variability (I^2 = 54.40 %). Subgroup analysis for experimental design resulted in medium effect sizes for the varied time design (g = 0.30, 95 % CI = [0.10; 0.50]) and

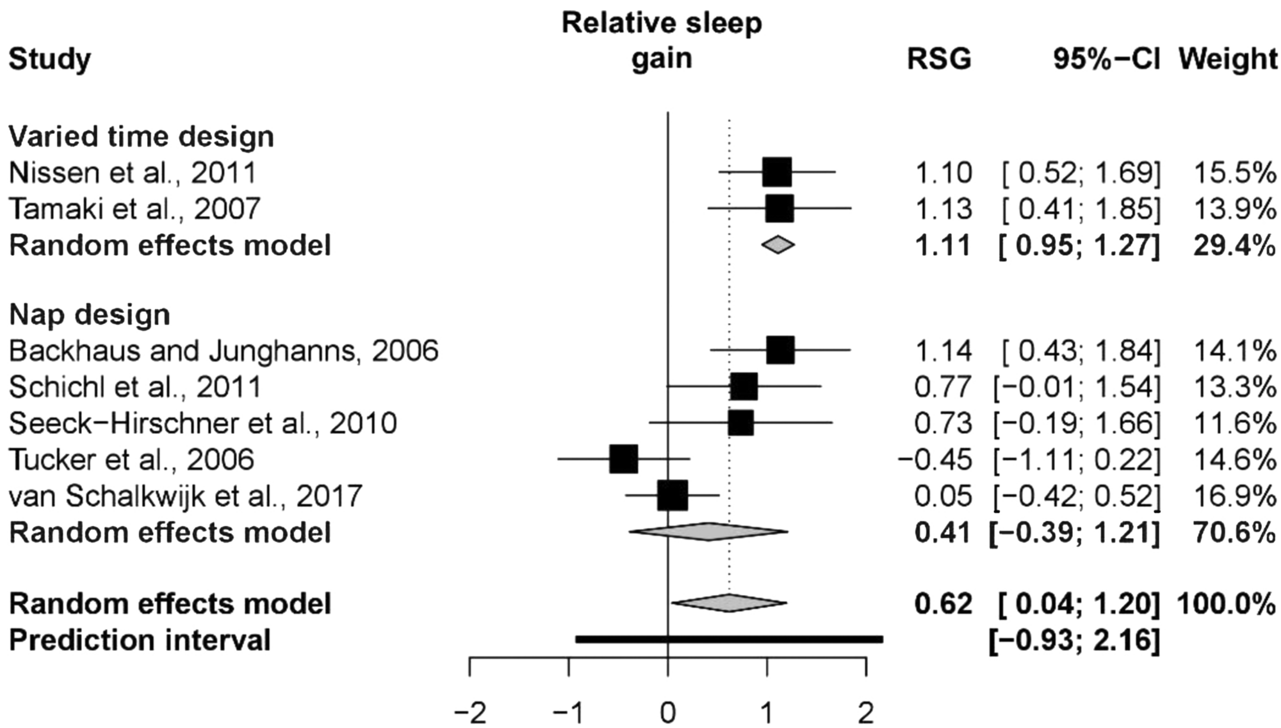

Fig. 4. The relative sleep gain (RSG) of all studies that used a mirror tracing paradigm. The size of the black squares represents the weight of each study in the random-effects model and the bars the 95 % CI of the corresponding effect size. Studies are ordered in terms of the experimental design used, with the results of the random-effects models displayed below each grouping and at the end of the list for the overall model.

the nap design (g = 0.39, 95 % CI = [-0.74; 1.52]), with no significant difference between groups (p = .088).

3.6. Publication bias

Publication bias was assessed by the funnel plot depicted in Fig. 6, indicating no publication bias. This result was confirmed by Egger's test of the intercept, which was not significant (p = .26).

4. Discussion

The present meta-analysis aimed to quantify RSG differences as a function of different motor tasks and experimental designs. The literature search yielded 48 studies that were quantitatively analyzed. A comparison of all tasks and designs resulted in a small effect for the RSG (g = 0.43). This shows that, generally speaking, sleep benefits motor memory consolidation when compared with a corresponding wake interval. No overarching differences could be revealed for different experimental designs. An in-depth analysis was performed on the two extensively studied tasks, the FTT and the MTT, which resulted in a small and medium effect for the RSG, respectively. Differences in experimental designs could only be identified with the MTT; however, as the number of respective studies was rather small, it is questionable whether the subgroup difference actually reflects a relevant distinction between the varied time and the nap design.

The conducted meta-analysis has three main limitations. First, the aim of the meta-analysis was to compare studies with a sleep and a corresponding wake interval of the same duration between acquisition and retrieval. Due to this criterion, a number of studies were excluded; in particular, studies that used the varied delay design (i.e., different time delays between acquisition and retrieval for the sleep and wake groups). However, from our point of view, this limitation is compensated by the heightened comparability between the included studies, as the presented effects are free from sleep-independent confounds such as time-dependent memory processes. Second, as polysomnographic data was not considered in our meta-analysis, a dichotomous distinction was made between long sleep periods (e.g., 8 h) and short sleep periods (e.g., 2 h). It should be noted that this rough distinction does not allow for inferences to be drawn on the importance of different electrophysiological states or events (e.g., sleep stages or sleep spindles). Third, most of the studies included are based on a relatively small number of participants, which might result in an improper estimation of the respective effect sizes in these studies. Therefore, despite the fact that sleep studies – especially those with polysomnography – are difficult to conduct, future studies should aim for larger sample sizes based on the estimated effect sizes reported in this meta-analysis.

However, even when taking these limitations into account, our results still claim relevance on a behavioral level regarding the main research question on sleep-dependent effects on motor memory consolidation. In particular, the presented findings further strengthen previous research on motor sequence learning, as the revealed effects are of similar magnitude (Pan and Rickard, 2015) and hold even when controlling for participant age (Adi-Japha and Karni, 2016; Rickard and Pan, 2017). Moreover, the present meta-analysis expands the current sleep and motor memory research, building on existing literature (King et al., 2017) by quantifying the effects of sleep on motor sequence learning, motor adaptation and an even larger variety of tasks. With respect to the experimental designs considered in our meta-analysis, the nap design seems to offer a promising direction for future research on sleep and the consolidation of procedural memory. Beyond the economic advantages and the (partial) control of circadian factors, it has already been shown that motor memory consolidation can be studied with rather short sleep durations (Tucker and Fishbein, 2009). The present meta-analysis perfectly supports these previous findings, as only slightly smaller effect sizes for short than long sleep durations were found. This evidence can be taken as a call for a shift in sleep research from whole-night studies to designs with shorter daytime sleep periods. Moreover, from an applied perspective, studies based on rather short daytime naps generally seem to be more appealing to a variety of practitioners (e.g., in the fields of rehabilitation or sports practice).

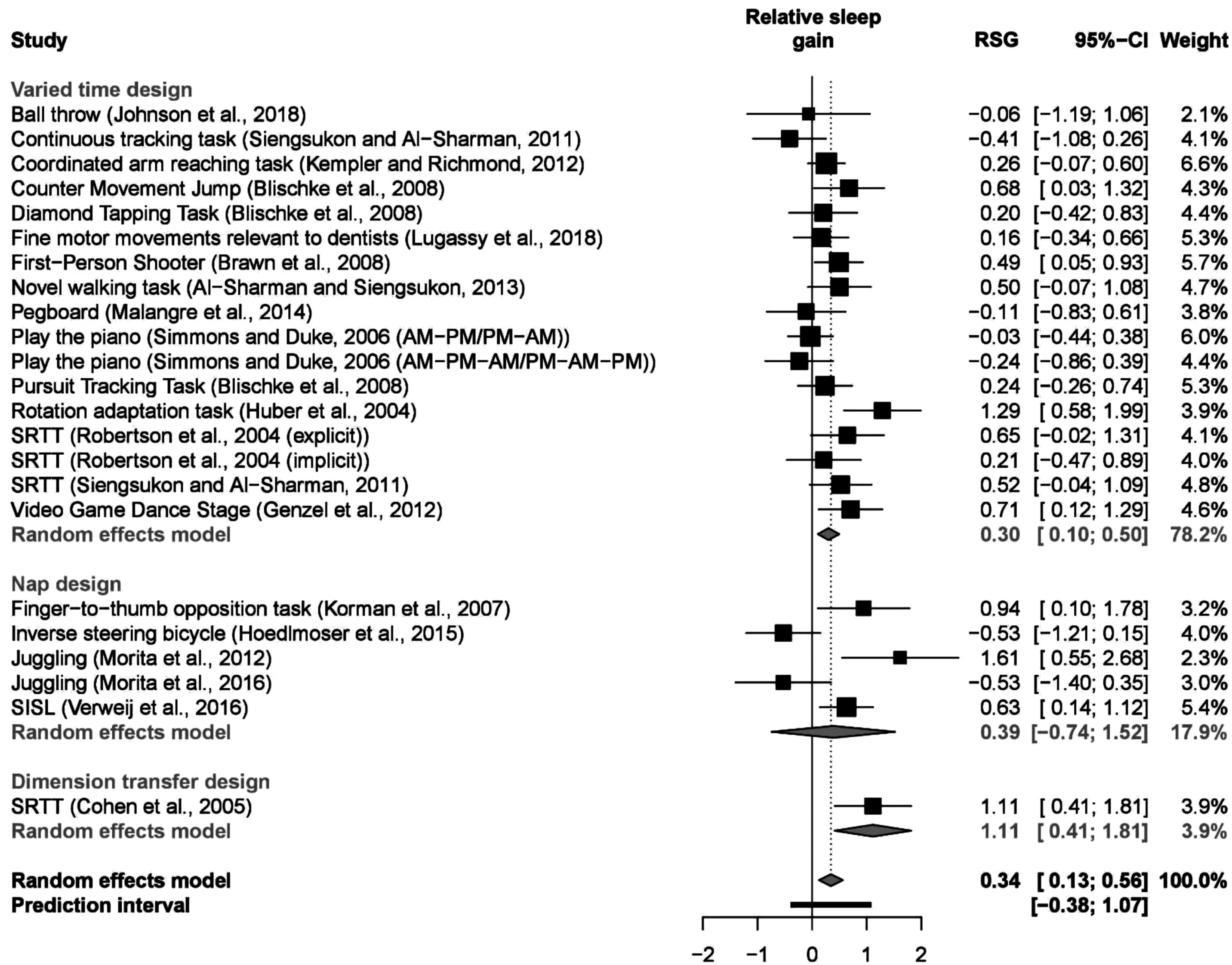

Fig. 5. The relative sleep gain (RSG) of all studies that used a miscellaneous task. The size of the black squares represents the weight of each study in the random-effects model and the bars the 95 % CI of the corresponding effect size. Studies are ordered in terms of the experimental design used, with the results of the random-effects models displayed below each grouping and at the end of the list for the overall model.

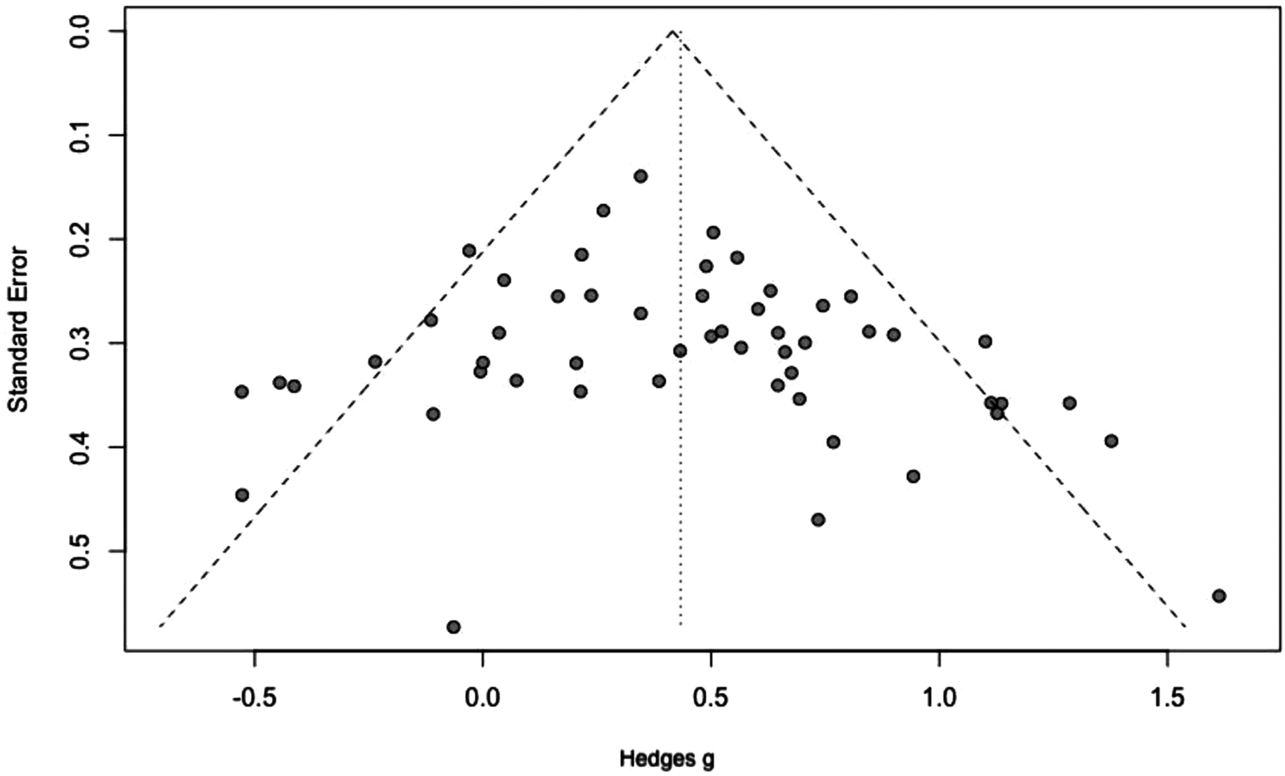

Fig. 6. Funnel plot for the studies included in the meta-analysis. The horizontal axis represents the effect size of each study and the vertical axis represents the standard error.

Regarding the examined tasks, the present meta-analysis confirms the conclusion already drawn in the early review of Blischke and Erlacher (2007) on how sleep enhances motor memory consolidation; namely, that most research is conducted with the FTT and the MTT. With a closer look at the presently included studies, both whole night and short diurnal sleep have been shown to yield positive effects on the FTT and MTT in a majority of studies (e.g., Brawn et al., 2010; Landry et al., 2016), but not in all studies (e.g., Blischke et al., 2008; Fogel et al., 2014). Only a comparably small set of studies used other experimental tasks, regarding the learning of gross motor tasks (Hoedlmoser et al., 2015; Kempler and Richmond, 2012), functional motor tasks (Al-Sharman and Siengsukon, 2013), clinically-relevant fine motor tasks (Lugassy et al., 2018), multimodal sensorimotor tasks (Brawn et al., 2008), musical tasks (Simmons and Duke, 2006) or sport skills (Blischke et al., 2008; Genzel et al., 2012b; Morita et al., 2012, 2016). Notably, no clear-cut task dependency could be inferred from the present meta-analysis. On the contrary, the analysis rather supports the findings of previous research that there exists a general positive but small effect of sleep on motor memory consolidation with no notable differences between the FTT, the MTT and other various motor tasks.

The apparently task-independent effect of sleep may serve as an explanation for earlier failed attempts to categorize motor tasks with respect to consolidation, given the respective motor control features and memory requirements (e.g., Blischke et al., 2008). From this perspective, motor tasks were characterized according to type (e.g., discrete-repetitive vs. continuous), range of movement (e.g., fine vs. gross motor movements), performance criterion (e.g., sequence, force impulse, coordination strategy, space-time pattern), memory demands (ranging from declarative to non-declarative) and learning conditions (e.g., explicit vs. implicit). Although earlier (Robertson, 2004) and more recent (Van den Berg et al., 2019) evidence support the claim that implicit motor skills preferentially benefit from sleep, this pattern could not be identified in the current analysis. Furthermore, it is worth mentioning that other authors have tried to link the level of mastery and its consolidation with particular sleep stages (Smith et al., 2004), such as associating an early stage of learning (e.g., first time practice on a MTT) with REM sleep and refining an already known movement (e.g., pursuit rotor task) with Stage 2 sleep. However, the proposed framework is unable to integrate all the findings at this level of specification. Thus, as these categorization systems did not help to reliably predict whether a certain task would show a positive RSG or not, the present meta-analysis supports the conclusion that, at this level of analysis, no relevant differences exist between tasks.

When recognizing that it is impossible to disentangle the effects of sleep on a task-specific level of analysis, another promising approach should be highlighted: the utility of the dimension transfer design. Studies in the present meta-analysis employed this design by double dissociating the goal or movement dimension of sequencing tasks (Albouy et al., 2013; Cohen et al., 2005; Pace-Schott and Spencer, 2013; Witt et al., 2010). Concerning the central mechanism in this learning context, it is proposed that performance in the spatial and effector-unspecific dimension can be optimized separately from performance in the motor and effector-specific dimension (Hikosaka et al., 2002). Pursuing this line of thought, additional promising task-relevant dimensions could be inferred from the present meta-analysis; in particular, dimensions regarding the potentially sleep-dependent consolidation of a cognitive strategy in contrast to that of general motor skills (cf., Van den Berg et al., 2019). On the basis of motor-control theory, higher-order performance changes could be explained by the more efficient task-space differentiation of task-relevant dimensions during sleep (Hossner et al., 2020). Thus, taken together, pursuing research that employs a dimension transfer design, adopts a fine-grained task analysis, and aims towards identifying the sleep-dependent and sleep-independent task dimensions inherent to different tasks would be a promising avenue for further investigation of sleep and its role in motor memory consolidation.

5. Conclusion

It is widely accepted that sleep plays a major role in the consolidation of motor memories. In the present meta-analysis, the RSG of different motor tasks revealed a small to medium effect size. Moreover, a short daytime sleep period was found to yield nearly the same effect as a whole night of sleep. As no relevant differences were identified on the task level, it could be opportune for future research on motor memory consolidation to shift the focus from attempting to delineate various tasks per se to identifying different task dimensions and their sleep dependence.

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Data availability statement

All relevant data are within the paper.

Declaration of Competing Interest

The authors have declared that no competing interests exist.

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