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REVIEW

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The diving response and cardiac vagal activity: A systematic review and meta-analysis

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Abstract

This article aimed to synthesize the various triggers of the diving response and to perform a meta-analysis assessing their effects on cardiac vagal activity. The protocol was preregistered on PROSPERO (CRD42021231419; 01.07.2021). A systematic and meta-analytic review of cardiac vagal activity was conducted, indexed with the root mean square of successive differences (RMSSD) in the context of the diving response. The search on MEDLINE (via PubMed), Web of Science, ProQuest and PsycNet was finalized on November 6th, 2021. Studies with human participants were considered, measuring RMSSD pre- and during and/or post-exposure to at least one trigger of the diving response. Seventeen papers (n = 311) met inclusion criteria. Triggers examined include face immersion or cooling, SCUBA diving, and total body immersion into water. Compared to resting conditions, a significant moderate to large positive effect was found for RMSSD during exposure (Hedges' g = 0.59, 95% CI 0.36 to 0.82, p < .001), but not post-exposure (g = 0.11, 95% CI -0.14 to 0.36, p = .34). Among the considered moderators, total body immersion had a significantly larger effect than forehead cooling ($Q_M = 23.46$, df = 1, p < .001). No further differences were detected. Limitations were the small number of studies included, heterogenous triggers, few participants and low quality of evidence. Further research is needed to investigate the role of cardiac sympathetic activity and of the moderators.

KEYWORDS

cardiac vagal activity, diving reflex, diving response, heart rate variability, meta-regression, physiology

1 **INTRODUCTION**

In recent years, the diving response has received remarkable attention regarding improving mental health and well-being (Pubmed search "diving response" from 0 to 2010 = 125 articles, from 2011 to 2022 = 372 articles). This line of research has shown promising results, including reducing symptoms of depression, followed by a gradual reduction and eventually cessation of medication (van Tulleken et al., 2018), increases in well-being and positive

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mood (Massey et al., 2020), reduction in both panic symptoms (Kyriakoulis et al., 2021) and acute psychosocial stress responses (Richer et al., 2022). One possible explanation of these findings might be a connection of the diving response to the neurovisceral integration model (Smith et al., 2017; Thayer et al., 2009; Thayer & Lane, 2000). This article aims to synthesize the various triggers of the diving response and their effects on cardiac vagal activity, to provide further insight into the underlying psychophysiological mechanisms, and to lay the foundation for more effective interventions.

The diving response was first described by Paul Bert in 1870 and is a very important oxygen conserving mechanism (Bert, 1870; Gooden, 1993; Shattock & Tipton, 2012) that occurs in all air-breathing animals so far tested, including human beings (Elsner & Gooden, 1983; Elsner et al., 1971; Gooden, 1993; Lindholm & Lundgren, 2009). It is triggered by breath-hold diving and involves a characteristic pattern of respiratory, cardiac and vascular responses (Elsner & Gooden, 1983). To be specific, the diving response may be defined as a combination of (a) increased sympathetic outflow to the periphery (Leuenberger et al., 2001) with consequent peripheral vasoconstriction and reduced blood flow to peripheral capillary beds (Elsner et al., 1971), rising mean arterial blood pressure (Gooden, 1993), and (b) parasympathetic activation marked by bradycardia, that is, a reduction in heart rate (Elia et al., 2021; Elsner & Gooden, 1983; Foster & Sheel, 2005; Lindholm & Lundgren, 2009; Shattock & Tipton, 2012). In particular, via the nucleus tractus solitarii, the diving response is expected to have substantial effects on cardiac vagal activity, the activity of the vagus nerve regulating cardiac functioning (Foster & Sheel, 2005; Gooden, 1993; Lindholm & Lundgren, 2009; Shattock & Tipton, 2012).

While these effects on cardiac vagal activity have been investigated on various occasions, to date, there is no comprehensive overview of the effects of the various diving response triggers on cardiac vagal activity in humans. Previous reviews, while contributing greatly to our knowledge, focused on specific and different research questions. This focus includes animals (Panneton & Gan, 2020; Ponganis et al., 2017), different physiological aspects, such as those involved in increased apnea duration (Caspers et al., 2011; Elia et al., 2021; Patrician et al., 2021; Pendergast et al., 2015), or on autonomic conflict (i.e., the activation of two antagonistic autonomic responses to cold water submersion, one being the cold shock response triggering a sympathetically driven tachycardia, and the other being the diving response triggering a parasympathetically mediated bradycardia) (Shattock & Tipton, 2012). While the models presented in these articles attribute the bradycardia to increased cardiac vagal activity without further explanation, some further details about the mechanisms at stake may be found in Shattock and Tipton (2012) and Foster and Sheel (2005). However, to date, no meta-analysis investigating the effects of different diving response triggers on cardiac vagal activity has ever been performed, a gap sought to be addressed in the current article.

Discovering optimal triggers of the diving response, that is, effective, cheap and easy to implement, is relevant for both research and applied purposes. In the psychotherapeutic treatment of panic disorder, for example, one major challenge when fear is elicited is the patient's dysregulated autonomic nervous system. Cold water face immersion has been found to decrease anxiety and panic symptoms (Kyriakoulis et al., 2021). Facial cooling using ice packs, on the other hand, reduces stress responses in healthy participants (Richer et al., 2022). In both these examples it remains unclear why exactly these results occur, and which intervention should be preferred by a practitioner. Furthermore, these interventions suggest that the diving response can be triggered independently of breathholding, which is in accordance with the model by Foster and Sheel (2005). Thus, the diving response holds very promising potential as an intervention in psychotherapy (Kyriakoulis et al., 2021; Massey et al., 2020; van Tulleken et al., 2018), the work place (Richer et al., 2022), and as a recovery strategy for athletes (Al Haddad et al., 2010). Yet, to fully develop this potential, it is mandatory to understand the mechanisms behind the diving response and its effects on health, well-being, and performance. Due to its suggested effects on cardiac vagal activity, one possible explanation could be found in the neurovisceral integration model (Smith et al., 2017; Thayer et al., 2009; Thayer & Lane, 2000).

The neurovisceral integration model proposes that a central autonomic network plays an important role in both emotional well-being and cognitive performance, with its functioning reflected in cardiac vagal activity; that is the activity of the vagus nerve regulating cardiac functioning (Smith et al., 2017; Thayer et al., 2009; Thayer & Lane, 2000). Cardiac vagal activity can be indexed non-invasively using heart rate variability (HRV) (Berntson et al., 1997). HRV represents the variation in the time intervals between successive heartbeats. In order to evaluate cardiac vagal activity, the HRV parameters assess the root mean square of successive differences (RMSSD) (Berntson et al., 1997; Malik et al., 1996) and a breathing frequency of 9 to 24 cycles per minute, the high frequency (HF) (Berntson et al., 1997; Kromenacker et al., 2018). In the current analysis, we want to compare the diving response in different breathing conditions (e.g., breath-hold, breathing through a snorkel,

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or SCUBA diving), potentially affecting breathing frequency. Consequently, because RMSSD is less affected by breathing influences (Penttilä et al., 2001), only RMSSD was considered for the present meta-analysis, allowing comparison between various breathing conditions.

There are several ways to trigger the diving response, such as facial immersion in water (Al Haddad et al., 2010; Kinoshita et al., 2006), and total body submersion. In both cases, variations may include breathhold (Costalat et al., 2015; Schipke & Pelzer, 2001), breathing through a snorkel (Al Haddad et al., 2010; Schipke & Pelzer, 2001), or, for total body submersion only, case self-contained underwater breathing apparatus (SCUBA) diving (Chouchou et al., 2009; Lundell et al., 2019; Lundell et al., 2021; Noh et al., 2018; Schipke & Pelzer, 2001; Weist et al., 2012). A third potential trigger is cooling of the face (e.g., using an ice pack) (Allen et al., 1992; Louis et al., 2015; Ruschil et al., 2021; Schlader et al., 2016). However, it is yet unclear to which extent these triggers affect cardiac vagal activity. Thus, the current article aims to systematically synthesize this information and conduct two meta-analyses of the existing literature about RMSSD pre-exposure compared to exposure and pre- compared to post-exposure.

Given the multitude of triggers of the diving response, several potential moderators were also considered. According to the model of the diving response by Foster and Sheel (2005), apnea is essential to experiencing the full diving response, and cold water (<15°C) leads to larger effects than warm water (>15°C) (Asmussen & Kristiansson, 1968; Daly, 1997; Mukhtar & Patrick, 1986). Thus, water temperature and apnea (versus breathing, for instance via snorkel or SCUBA diving) were investigated as moderators. Further, we differentiated between face and total body immersion. Cooling of the body up to the breastbone is associated with increased cardiac vagal activity (Kovacs & Baker, 2014); hence, different types of immersion might have different effects on cardiac vagal activity. Movement (versus remaining still during exposure to the trigger) was investigated as a moderator, because cardiac vagal activity decreases during movement (Stanley et al., 2013).

2 | METHOD

The Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al., 2009; Page, McKenzie, et al., 2021; Page, Moher, et al., 2021; Shamseer et al., 2015) were adopted for the literature search and writing process. The PRISMA checklist is provided as a supplementary file. The protocol was registered on PROSPERO (CRD42021231419) before the analysis (last edited version: 01.07.2021).

2.1 | Information sources

The literature search was conducted using MEDLINE (via PubMed), Web of Science, ProQuest, and PsycNet from inception until November 6th, 2021. The following search string was used for all libraries: (("diving reflex"[MeSH] OR "diving response" OR "water immersion" OR "water submersion" OR "dive reflex" OR "facial immersion" OR "facial submersion" OR "SCUBA" OR "snorkel" OR "diving" [MeSH] OR "facial cooling") AND ("HRV" OR "heart rate variability" OR "parasympathetic" OR "vagal" OR "vagus" OR "RMSSD")). One researcher extracted eligible articles (LP, see acknowledgements) that were then independently checked by another reviewer (MRe). Discussion with a third researcher (SA) resolved any disagreements between the two reviewers.

2.2 | Eligibility criteria

Eligible studies were selected using the following PICOS criteria.

2.2.1 | Population

The scope of this review is restricted to human beings, and therefore any studies conducted on animals were excluded. No inclusion or exclusion criteria were set for participants' health conditions, age ranges, or gender.

2.2.2 | Intervention

This systematic review and meta-analysis targeted all empirical studies examining the acute effects of the diving response induced by the various triggers (face immersion, total body submersion, and cooling of the entire face) on RMSSD. Studies involving cognitive or emotional tasks while underwater were excluded.

2.2.3 | Comparison

Studies measuring RMSSD before and during, and/or before and after triggering the diving response were included in this analysis. The pre-exposure condition was used as the control condition.

2.2.4 | Outcomes

The study had to be empirical and assessed the diving response's influence on RMSSD.

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2.2.5 | Study design

Controlled mixed and within-subject-designs were considered. Non-peer-reviewed works without a complete methods section (such as published abstracts), as well as single-case studies, were excluded.

In addition, only studies in English and German that were published or pre-registered for publication in peerreviewed scientific journals were considered. If necessary, authors were contacted and asked to provide missing data. Yet, despite contacting the authors, three articles (Berry et al., 2017; Louis et al., 2015; Schirato et al., 2018) had unclear RMSSD data with missing information on moderators or the included participants. Thus, these articles were excluded from the meta-analysis but still considered in the systematic review. No restrictions were made regarding the year of publication.

2.3 | Risk of bias

Two researchers independently (SV & DS) assessed the risk of bias for each included study using the Cochrane risk-of-bias tool (Sterne et al., 2019). Each study was classified into one of the following categories: low risk, some concerns, or high risk of bias. The Cochrane risk-of-bias tool utilizes the "intent-to-treat principle" that focuses on the intervention assignment. As such, the fixed set of items used in the risk of bias appraisal is "bias arising from the randomisation process"; "bias due to deviations from intended interventions"; "bias due to missing outcome data"; "bias in measurement of the outcome"; and "bias in the selection of reported results" as well as the overall risk of bias assessment for each study. The overall risk of bias was determined based on the highest classification among the five risk categories. The inter-rater agreement coefficient was calculated by comparing each of the item's risk of bias appraisal as well as the overall risk of bias judgment between both researchers. Disagreements between the two researchers regarding the risk of bias were discussed between the two assessors (SV & DS) in every case.

The initial inter-rater agreement coefficient was calculated for each domain category as a sum of the agreement scores divided by the number of graded items. The initial disagreements between authors (SV & DS) were resolved via discussion of the signaling questions and everyone's impression of the category, with the final resolution being in favor of the stricter ranking. This way of resolving initial disagreements led to a 100% inter-rater agreement coefficient.

2.4 | Synthesis of results

The following data were extracted from each study: participants' demographic data, RMSSD values (mean and standard deviation [SD]) of the various conditions, the method for inducing the diving response, and information about the moderators listed above.

RMSSD means and SD were pooled following the guidelines in the Cochrane Handbook (see formulae in chapter 6.5.2.10 Combining groups, Table 6.5.a) (Higgins et al., 2019). The tables used are accessible via Open Science Framework (DOI 10.17605/OSF.IO/9W2QY or https://osf.io/9w2qy/?view_only=6146276c0a1343469a6d d5d65b7bfd6c).

In the within-subjects-designs, data were pooled into one mean and SD for each pre- and during and/or postexposure. Differences between the total studies' sample size and the sample size used in this analysis are due to additional conditions which were not relevant for this meta-analysis (e.g., comparison of different breathing gases), and missing data in individual cases (e.g., because of technical issues during the measurement).

2.5 | Statistics

Statistical analyses were conducted using R (version 4.1.0). The script can be accessed via Open Science Framework (see 2.4).

All outcome measures were standardized using Hedges' g for changes from pre- to exposure, and pre- to post-exposure conditions. The Hedges' g (SMD = MD/ SD_{pooled}) and its standard error were computed according to the formula for crossover trials from the Cochrane Handbook (chapter 23, section 23.2.7.2). The standard error computation required the imputation of a correlation coefficient between the pre- and during exposure, and between the pre- and post-exposure RMSSD values. To do so, correlation coefficients were computed from the available (or provided by the authors) raw values in the included studies. Then, these coefficients were averaged per condition ((0.39 + 0.29 + 0.35)/3 = 0.34 for pre-during and (0.73 + 0.59)/2 = 0.69 for the pre-post). To assess the reliability of the emitted coefficients, sensitivity analyses were run up to the averaged coefficients of correlation ± 0.10 per 0.05 interval (0.24, 0.29, 0.39, 0.44 for pre-during and 0.59, 0.64, 0.74, 0.79 for the pre-post; emitted data files available on OSF). Only minor differences in the relationships between effects sizes, significance tests, and moderator analyses were detected. Thus the conclusions remained unaltered, underlining the reliability of our results. A positive g denotes an increase in RMSSD during the exposure or the post-exposure condition. Hedges' g of 0.2, 0.5, and 0.8 are, respectively, considered small, moderate, and large (Cohen, 1977; Hedges & Olkin, 1985).

Outcomes across studies were pooled using a randomeffects model (Higgins et al., 2019). Between-study heterogeneity was quantified using tau² (variance of true effects, using Hedges' estimator [Hedges & Olkin, 1985]), and further assessed using I², which provides the percentage of the observed variance reflecting the variance of the true effects rather than sampling error (Higgins et al., 2003). The prediction interval was computed to consider the potential effect of the diving response on cardiac vagal activity when reported in an individual study setting, as this may be different from the average effect (Riley et al., 2011). The Hartung and Knapp method was used to adjust confidence intervals and test statistics (Hartung & Knapp, 2001a, 2001b; IntHout et al., 2014).

Cook's distance with a cutoff of 0.45 was used to detect potential outliers (Das & Gogoi, 2015). If outliers were found, the analyses were to be performed both with and without the outliers and the differences, potential reasons for the outliers as well as implications were discussed. Potential asymmetry was assessed by visually inspecting the funnel plots. Furthermore, when at least ten studies were available, the asymmetry was assessed using Egger's test. If evidence for asymmetry was found (p < .1 on the Egger's test), the Duval and Tweedie trim and fill method was used to quantify the magnitude of the small study effect (Duval & Tweedie, 2000).

To detect moderator effects, subgroup analyses were applied to the categorical variables of interest (i.e., type of immersion, movement and breathing). Q-tests were performed to evaluate differences between subgroups (Higgins et al., 2019). A meta-regression was used to analyze the moderating effect of the continuous variable temperature (Borenstein & Higgins, 2013). The predictive value of this continuous moderator was evaluated by the goodness of fit (\mathbb{R}^2) and significance at the p = .05 level.

2.6 Certainty of evidence (grading of recommendations, assessment, development, and evaluation [GRADE] approach)

After the analysis, SA and SB assessed the quality of evidence independently using the GRADE approach (Ryan & Hill, 2018). The evidence was graded based on the risk of bias assessments, inconsistency, indirectness, imprecision, and publication bias. The quality of evidence can be high, moderate, low, or very low. An overall judgment about the certainty of evidence was assigned for both the pre- during-, and the pre- post-exposure comparisons.

3 | RESULTS

Figure 1 describes the selection process. After removing duplicates, the first step was to screen all identified articles based on their title and abstract. Step two was to scan the full-text versions, leaving 29 articles in the selection process. The authors were then contacted and asked to provide missing data (e.g., RMSSD means and SD that were not reported or unclear). Due to unclear RMSSD data (Berry et al., 2017; Louis et al., 2015; Schirato et al., 2018), three articles were removed from the metaanalyses and retained only for the systematic review. Ten articles that reported heart rate (Ferrigno et al., 1991; Hayashi et al., 1997; Hurwitz & Furedy, 1986; Khurana & Wu, 2006; Marabotti et al., 2013; Simmons et al., 2017) or HRV parameters other than RMSSD (Costalat et al., 2021; Kinoshita et al., 2006; Kiviniemi et al., 2012; Wieske et al., 2013) had to be excluded because no RMSSD data were provided. One article did not provide pre- exposure RMSSD values (Lemaître et al., 2008). A total of 17 articles were eligible for the systematic review, among which 13 were included in the meta-analysis (k = 14) investigating the effect on RMSSD pre- compared to during exposure. Six were included in the meta-analysis (k = 7) investigating the effect on RMSSD pre- compared to post-exposure. One article reported two independent effect sizes for each condition (Schlader et al., 2016).

3.1 | Participant characteristics

As shown in Table 1, the total number of participants in the 17 included studies was 311 (80.1% male), with a mean age of 34.6 \pm 6.6 years. The included studies only investigated healthy participants, with an overall mean height of 177.3 \pm 5.7 cm, mean weight of 77.7 \pm 10.0 kg, and mean body mass index of 24.7 \pm 1.8 kg/m².

3.2 | Risk of bias

For the overall risk of bias assessment, according to the Cochrane Risk of Bias tool, all studies were ranked as having "some concerns" (Figure 2).

Figure 2 shows the breakdown of each study's domain rankings.

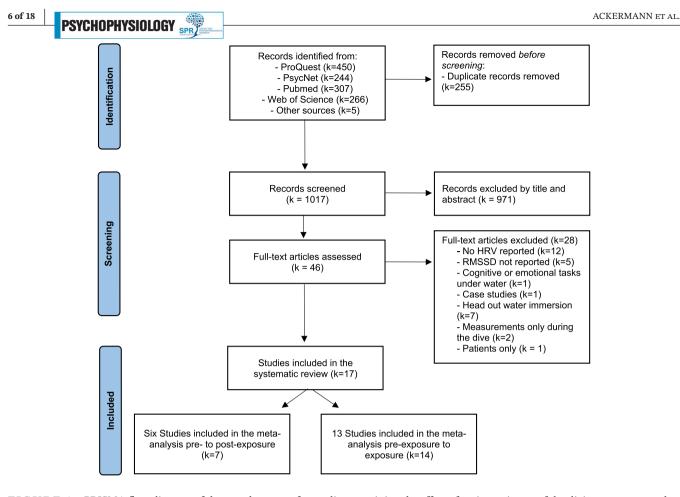


FIGURE 1 PRISMA flow diagram of the search process for studies examining the effect of various triggers of the diving response on the HRV parameter RMSSD. HRV, heart rate variability; PRISMA, preferred reporting items for systematic reviews and meta-analysis; RMSSD, root mean square of successive differences.

3.3 Diving response inducing interventions

As shown in Table 1, the diving response triggers differ substantially among studies. One of the included trials tested the effect of facial immersion (Al Haddad et al., 2010) of facial cooling (Schlader et al., 2016), two of forehead cooling (Jarczok et al. unpublished, DRKS00016597) (Ruschil et al., 2021) and 12 of total body immersion (Berry et al., 2017; Chouchou et al., 2009; Costalat et al., 2015; Lundell et al., 2019; Lundell et al., 2021; Noh et al., 2018; Schaller et al., 2021; Schipke & Pelzer, 2001; Schirato et al., 2018; Solana-Tramunt et al., 2019; Vicente-Rodríguez et al., 2020; Weist et al., 2012). Two trials tested immersion combined with apnea (Costalat et al., 2015; Vicente-Rodríguez et al., 2020), two with snorkel breathing (Al Haddad et al., 2010; Schipke & Pelzer, 2001), and nine trials tested the effect of SCUBA diving (Berry et al., 2017; Lundell et al., 2019; Lundell et al., 2021; Noh et al., 2018; Schaller et al., 2021; Schipke & Pelzer, 2001; Schirato et al., 2018; Weist et al., 2012). Another five studies did not use any breathing device or aid (Jarczok et al. unpublished, DRKS00016597) (Louis et al., 2015; Ruschil et al., 2021; Schlader et al., 2016; Solana-Tramunt et al., 2019).

Nine studies used cold water, ice bags or in one case cryostimulation to induce the diving reflex (Jarczok et al. unpublished, DRKS00016597) (Al Haddad et al., 2010; Louis et al., 2015; Lundell et al., 2019; Lundell et al., 2021; Noh et al., 2018; Ruschil et al., 2021; Schaller et al., 2021; Schlader et al., 2016), whereas the other seven used water above 15°C (Berry et al., 2017; Chouchou et al., 2009; Costalat et al., 2015; Schipke & Pelzer, 2001; Solana-Tramunt et al., 2019; Vicente-Rodríguez et al., 2020; Weist et al., 2012). In three studies, the exposure condition was dynamic (Chouchou et al., 2009; Solana-Tramunt et al., 2019; Vicente-Rodríguez et al., 2020). In one study, movement status was not reported (Lundell et al., 2021) and in every other case, the participants remained static during exposure.

3.4 | Primary analysis

3.4.1 | Pre-exposure compared to during exposure

The relation between RMSSD pre-exposure and during exposure (k = 14) had an average effect size of 0.59 (95%)

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		Dynamic vs static	Static	Static	Dynamic	Static	Static	Static	Static	n/a	Static	Static	Dynamic	n/a	Static Static	Static	Dynamic	Dynamic	Static (Continues)	
		Immersion	Face	Total body	Total body	Total body	Forehead cooling	Total body	Total body	Total body	Total body	Forehead Cooling ^h	Total Body	Total body	Face cooling ^d No Face cooling ^d	Total body	Total body	Total body	Total body	
		Water temperature [°C]	11	32–33	16	27	$2,96 \pm 1,83$	CTL: 24 WBC: –60	0	œ	14	3 (cold pack)	median surface water temperature: 23.0 (IQR 20– 25.0) median minimum water temperature: 6 (IQR 5.3–1.3) ^g	n/a	0 34	27	26	26	28	
		Height [cm] (mean±SD)	180.0 ± 6.0	178.8 ± 6.1	178.9 ± 5.3	175.7 ± 4.2		CTL: 177.0 ±0.1 WBC: 174±0.1	178.0 (range: 178–181)	179.0 (range: 163–189) ^a	n/a	n/a	181 (IQR 170.5–181.8) ^g	n/a	174.0 ± 10.0 172.0 ± 13.0	n/a	170.1 ± 5.8	174.2 ± 7.4	182.0 ± 2.0 ^b	
		Weight [kg] (mean±SD)	76.1 ± 13.0	84.6 ± 6.6	73.7 ± 15.7	71.2 ± 8.9		CTL: 74.4 ±11.8 WBC:69.9 ±12.3	83.2 (range: 79.2–86.8)	88.4 (range: 65.4–140.5) ^a	83.4 ± 2.9	n/a	90 (IQR 80-98) ^g	n/a	73.0 ±12.9 72.2 ±17.6	73.0 ± 10.0	56.3 ±5.7	76.4 ±12.0	86.7 ±2.8 ^b	
		Age [years] (mean±SD)	21.0 ± 1.3	34 ± 10	27.3 ± 9.7	36.0 ± 9.6	$59,8 \pm 5,35$	CTL: 33.9 ± 12.3 WBC: 34.8 ± 9.1	39.0 (range: 25–43)	44.0 (range: 28–57) ^a	41.8 ± 2.1	30.3 ± 9.4	51.5 (IQR 46−55) ^β	n/a	22.0 ± 2.0 25.0 ± 4.0	33.0 ± 10.0	21.5 ± 3.5	39.1 ± 9.0	31.6 ± 1.2^{b}	
		N (men %)	13(100%)	10(100%)	10(90%)	11 (91%)	61	$30^{e} (100\%)$	4(100%)	25 ^L (88%) ^c	11 (n/a)	16~(69%)	16 (92%)	10 (n/a)	FCT: 10 (70%) FWT: 10 (40%)	25 (80%)	12 (0%)	36 (72%)	8 (100%)	
•	(A)	Studies	Al Haddad et al. (2010)	Berry et al. (2017)	Chouchou et al. (2009)	Costalat et al. (2015)	Jarczok et al., ^j	Louis et al. (2015)	Lundell et al. (2019)	Lundell et al. (2021)	Noh et al. (2018)	Ruschil et al. (2021) ⁱ	Schaller et al. (2021)	Schirato et al. (2018)	Schlader et al. (2016)	Schipke and Pelzer (2001)	Solana-Tramunt et al. (2019)	Vicente-Rodríguez et al. (2020)	Weist et al. (2012)	

TABLE 1 Participant characteristics of studies included in the systematic review

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(B)						
-	Diving experience	Personal static breath-hold	Breathing gas		Duration of	PS
Studies	[years]	pertormance [s] (mean±SD)	composition	Apnea vs breathing	exposure	YCł
Al Haddad et al. (2010)	n/a	n/a	Normal air	Breathing: Snorkel	5 min	HOP
Berry et al. (2017)	experienced military divers (U.S. Navy)	n/a	Normal air	Breathing: MK 20 breathing apparatus	6 h (10 min break after 3 h)	HYSIO
Chouchou et al. (2009)	"experienced SCUBA divers (227.7 ± 590 dives)" (p. 346)	n/a	n/a	Breathing: SCUBA	About 30 ±10.6 min	
Costalat et al. (2015)	"healthy active BHDs" (p. 1476)	316土40	n/a	Apnea	268.0 ±40.2 s	OCETY FOR INCREMENTALIDATION
Jarczok et al., ^j	None	n/a	Normal air	Normal breathing	5 min	
Louis et al. (2015)	n/a	n/a	Normal air	Normal breathing	3 min per day for 5 days	
Lundell et al. (2019)	"Navy divers" (p. 2)	n/a	Air	Breathing: SCUBA	50 min; decom- pression profile "Suunto Fused RGBM 2"	
Lundell et al. (2021)	13.9 (6.1–30)	n/a	Standardized diluent trimix 20/40	Breathing: SCUBA	55 min	
Noh et al. (2018)	"experienced SCUBA & rebreather divers" (p. 3)	n/a	Air ^f	Breathing: SCUBA	30 min bottom time duration	
Ruschil et al. (2021)	n/a	n/a	Normal air	Normal breathing	5 min	
Schaller et al. (2021)	experienced divers	n/a	Compressed Air; 32% nitrox mixture (only one diver)	Breathing: SCUBA	35 min (1QR 31–39) ^h	
Schirato et al. (2018)	"trained scuba divers" (p. 174)	n/a	21% O ₂ /35% He/44% N ₂ ; 50% O ₂ /50% N ₂ ; 32% O ₂ /68% N ₂ ; 100% O ₂	Breathing: SCUBA	30 min bottom time; decompression rate of 9 msw/ min ^g	
Schlader et al. (2016)	FCT: n/a CTL: n/a	n/a n/a	Normal air Normal air	Normal breathing Normal breathing	15 min 15 min	AC
Schipke and Pelzer (2001)	"experienced scuba divers" (p.174)	n/a	n/a	Breathing: snorkel and SCUBA	Submersion: 10 min SCUBA dive: 10 min	CKERMA
Solana-Tramunt et al. (2019)	n/a	n/a	Normal air	Normal Breathing	4 h	NN ET A

TABLE 1 (Continued)

1469986, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/pyp.14183 by Test. Wiley Online Library on [20/10/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Studies [ye	Diving experience [years]	Personal static breath-hold performance [s] (mean±SD)	Breathing gas composition	Apnea vs breathing	Duration of exposure
Vicente-Rodríguez et al. (2020) n/a	æ	n/a		Participants rehearsed apnea training underwater using a portable oxygen cylinder	30 min
Weimer et al., ^k No	None	n/a	Normal air	Normal breathing	5 min
Weist et al. (2012) ≥3	≥30h of diving & ≥30 dives	n/a	Air ^f	Breathing: SCUBA	15 min bottom time; Decompression at 15 and 18 m

covered forehead, eyes and cheeks; n/a, not available; $^{o}n = 10$ per group, however, only the control and the whole body group were relevant for this systematic review; ^fOther breathing gases were used in this study, but are not included in this meta-analysis, ^g median and interquartile range (IQR), minimum water temperature ranged from 5 to 20° C depending on immersion depth; ^h a cold pack ($T \approx 4^{\circ}$ C) was placed on the participants Note for (A) BMI, body mass index; BHD, breath-hold divers; CTL, less trained control divers who were exposed to the same condition; WBC, whole-body cryostimulation; FCT, Face cooling trial; FWI, Face warming Note for (B) BMI, body mass index; BHD, breath-hold divers; CTL, less trained control divers who were exposed to the same condition; WBC, whole-body cryostimulation; FCT, Face cooling trial; FWT, Face warming forchead for 5 min to induce an automatic activation of the parasympathetic nervous system; ⁱHealthy controls (n = 15), Neurological Patients with medically unexplained sensory symptoms (n = 15), ^j(unpublished; trial; ${}^{a}n = 26$ reported in the article, but e.g., due to incomplete data only the sample mentioned in the table was considered for the meta-analysis (dto. For b-d); ${}^{b}n = 15$; ${}^{c}n = 26$; d using a flexible bag of ice water that DRKS00016597), bereaved; ^k(unpublished; DRKS00016412), psychosomatic patients (pre therapy), ¹pre-during: n = 25; pre-post: n = 23.

trial; ^an = 26; ^bn = 15; ^cn = 26; ^d using a flexible bag of ice water; n/a, not available; ^en = 10 per group, however, only the control and the whole body group were relevant for this systematic review; ^fOther breathing gases were used in this study, but are not included in this meta-analysis; ^gmeters of salt water per minute; ^hmedian and interquartile range (IQR). 9 of 18



	D1	D2	D3	D4	D5	0
Chouchou et al. (2009)	(+/-)	(-)	(+)	(+)	(-)	(-)
Noh et al. (2018)	(+/-)	(-)	(+)	(+)	(-)	(-)
Schipke et al. (2001)	(+/-)	(-)	(+)	(+)	(-)	(-)
Schlader et al. (2016)	(+/-)	(-)	(+)	(+/-)	(-)	(-)
Weist et al. (2012)	(-)	(+/-)	(+)	(+)	(-)	(-)
Al Haddad et al. (2009)	(+)	(-)	(+)	(+)	(+/-)	(-)
Lundell et al.(2019)	(+)	(-)	(+)	(+)	(+/-)	(-)
Lundell et al.(2021)	(+)	(-)	(+)	(+)	(+/-)	(-)
Rodriguez et al. (2020)	(+)	(-)	(+)	(+)	(+/-)	(-)
Solana et al. (2019)	(+)	(-)	(+)	(-)	(+/-)	(-)
Costalat et al. (2015)	(-)	(-)	(+)	(+)	(-)	(-)
Schirato et al. (2018)	(-)	(-)	(+)	(+)	(-)	(-)
Schaller et al. (2021)	(-)	(-)	(+)	(-)	(-)	(-)
Berry et al. (2017)	(-)	(-)	(+)	(-)	(-)	(-)
Ruschil et al. (2021)	(-)	(-)	(+)	(+)	(+)	(-)
Jarczok et al. (unpublished) DRKS00016597	(-)	(-)	(+)	(+)	(+)	(-)
Weimer et al. (unpublished) DRKS00016412	(-)	(-)	(+)	(+)	(+)	(-)

Low Risk (+) Low Risk/Some Concerns (+/-) Some Concerns (-)

FIGURE 2 Risk of bias analysis. (+), low risk; (+/-) low risk/some concerns; (-) some concerns.

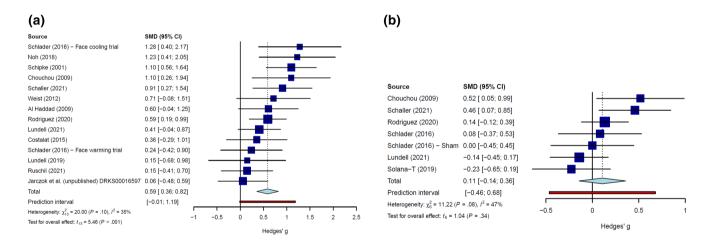


FIGURE 3 Forest plots of the comparison pre-exposure to exposure (a) and of the comparison pre- to post-exposure conditions (b). SMD, standardized mean difference; CI, confidence interval.

CI 0.36 to 0.82, p < .001), indicating a moderate positive effect (Figure 3). The heterogeneity was large (prediction interval [-0.01 to 1.19]) with a small to moderate part representing the variance of the true effect ($I^2 = 35\%$; Tau² = 0.06; Figure 3) and the rest being due to sampling error. The prediction interval (g = -0.01 to 1.19) also indicates that future studies are likely to have null or large positive effects. No outlier was detected. No asymmetry was detected, neither visually nor by Egger's test (intercept = 0.075, p = .252). Finally, the quality of evidence was rated as low (Table 2).

3.4.2 | Pre-exposure compared to postexposure

The relation between RMSSD pre-exposure and postexposure (k = 7) had an average effect size of 0.11 (95% CI –0.14 to 0.36, p = .34, Figure 3). The heterogeneity was large (prediction interval [-0.46 to 0.68]) with a small to moderate part representing the variance of the true effect ($I^2 = 46.5\%$; Tau² = 0.04; Figure 3) and the rest being due to sampling error. The prediction interval (g = -0.46 to 0.68) indicates that future studies are likely to have between

Comparison	Hedges'g (95% confidence interval)	Risk of bias	Inconsistency ^a	Indirectness ^b	Imprecision	Publication bias ^c	Quality of evidence
Pre-exposure to exposure	0.59 (0.36 to 0.82)	No	No	No Serious Indirectness	No	Undetected	Low
Pre- to post-exposure	0.11 (-0.14 to 0.36)	No	NA	No Serious Indirectness	Serious	?	Very Low
Abbreviations: GRADE, Gra	Abbreviations: GRADE, Grading of Recommendations Assessment, Development, and Evaluation; NA, Not applicable.	nt, Development,	ınd Evaluation; NA, Not apl	plicable.			
^a Only one comparison was s	'Only one comparison was studied in multiple trials. In this case, estimates and confidence intervals showed substantial overlap.	estimates and cor	fidence intervals showed su	bstantial overlap.			
^b Populations, treatments, an	d outcome measures followed those	relevant to the fiel	d, hence there was no indic	^b Populations, treatments, and outcome measures followed those relevant to the field, hence there was no indication of indirectness in the evidence.			
^c Publication bias could only	^c Publication bias could only partially be assessed as there were < 10 trials available for one of the comparisons.	10 trials available	or one of the comparisons.				

Certainty of the evidence (GRADE approach)

TABLE 2

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moderate negative and moderate to large positive effects. While the use of this information is very limited, it illustrates the heterogeneity in the results and the small sample of studies captured, leading to the large heterogeneity in the prediction interval. No outlier was detected. Visual inspection indicated no asymmetry. Due to the small number of studies, neither the Egger's test nor the trim and fill analysis were performed. The quality of evidence was rated as very low (Table 2).

These results indicate that the diving response was associated with increased cardiac vagal activity during but not after exposure. One can note that the results described in the article only included in the systematic review (Schirato et al., 2018) were going in the same direction as the meta-analysis's average effect comparing pre- to postexposure conditions.

3.5 | Moderator analyses

Because too few of the included studies presented results comparing a pre-exposure to a post-exposure condition (k = 7), it was only possible to run a moderator analysis for the comparison between the pre-exposure and exposure conditions. However, all the moderators were asymmetrically distributed, with some categories largely underrepresented (k = 1 or 2), leading to averaged effects per category being primary individual-study-dependent and not fully assessing the moderators' effect. Thus, all results presented in these moderator analyses should not be considered as conclusive pieces of evidence but only as indicators of the current state of research depicted in the current meta-analysis.

3.5.1 | Cooling/immersion

Face cooling or immersion (k = 3, g = 0.65, 95% CI –0.59 to 1.90), total body immersion (k = 9, g = 0.69, 95% CI 0.43 to 0.96) and forehead cooling (k = 2, g = 0.10, 95% CI –0.46 to 0.66) effects on RMSSD were significantly different ($Q_M = 26.10$, df = 2, p < .001). Post-hoc head-to-head tests showed that total body immersion had a significantly larger effect than forehead cooling ($Q_M = 23.46$, df = 1, p < .001); however, face cooling or immersion did not ($Q_M = 3.55$, df = 1, p = .060). No further differences were detected.

3.5.2 | Movement

One of the studies (Lundell et al., 2021) had to be excluded from this moderator analysis because whether the

participants moved or remained still during the dive was not made clear. Movement (k = 2, g = 0.70, 95% CI -1.95 to 3.35) and remaining still (k = 11, g = 0.58, 95% CI 0.28 to 0.88) effects on RMSSD were not significantly different ($Q_M = 0.24$, df = 1, p = .630).

3.5.3 | Breathing

Only one study was in the category breath-holding, thus no group difference was run. Yet, one can mention that the average effect in the breathing category was g = 0.61, 95% CI 0.36 to 0.86 (k = 13) and g = 0.36, 95% CI -0.29 to 1.01 in the breath-holding category (k = 1).

3.5.4 | Water temperature

A meta-regression was used to investigate temperature as a continuous moderator and revealed that temperature accounted for none of the heterogeneity in the results ($R^2 = 0\%$, df = 12, p = .372).

4 | DISCUSSION

This article is the first systematic review and metaanalysis assessing the effects of the diving response on cardiac vagal activity pre- compared to during- and precompared to post-exposure. Out of 17 articles included in the systematic review, 13 (reporting k = 14 independent effect sizes) were relevant for the meta-analysis pre- compared to during-, and six (reporting k = 7 independent effect sizes) for the meta-analysis pre- to postexposure. The principal findings were a positive average effect for RMSSD during exposure (k = 14g = 0.59; 95% CI 0.36 to 0.82), but not post-exposure (k = 7; g = 0.11; 95% CI -0.14 to 0.36). In both meta-analyses, the heterogeneity was large, but the variance of the true effect was only small to moderate.

Three studies were part of the systematic review, reflecting to some extent our main findings, but had to be excluded from the meta-analysis (Berry et al., 2017; Louis et al., 2015; Schirato et al., 2018). In (Schirato et al., 2018), the authors found no difference between the resting and the recovery condition for the intervention group, but a significant increase in RMSSD for the second half of the recovery condition in the control group compared to the resting condition pre-submersion (Schirato et al., 2018). The second study also found a significant increase in RMSSD during a six-hour dive (Berry et al., 2017). Finally, the third study compared RMSSD before and after either a 24°C control condition or a-60°C whole-body cryostimulation in a between-subjects design (Louis et al., 2015). Each group participated in five identical trials over five consecutive days. The results of this study showed that RMSSD (in %) changed moderately to largely on each of the five days in the intervention group and differed significantly from the control group on three days (Louis et al., 2015). The overall lack of a reliable effect on post-exposure might be interpreted as a sign of the ability of the parasympathetic nervous system to adapt to the new environment quickly. However, given the low quality of evidence of the pre-during comparison, as assessed by GRADE, and the very low quality of evidence of the prepost comparison, these results require further, systematic investigation.

As mentioned in the results section, the moderator analysis was only possible for the condition pre- to during exposure. For the water temperature, it showed no effect ($R^2 = 0\%$, df = 12, p = .372). These results appear surprising at first because cold receptors of the face play an important role in the diving response, and thus, cold water has been found to cause a stronger reduction in heart rate than water above 15°C (Foster & Sheel, 2005). However, this might be explained by the breathing frequency, which tends to be lower during diving (Hesser et al., 1990; Mummery et al., 2003; Salzano et al., 1984). Slow-paced breathing has been found to have a strong effect on cardiac vagal activity (Laborde et al., 2017; Laborde et al., 2021; Laborde et al., 2022; Sevoz-Couche & Laborde, 2022; Wells et al., 2012), and apnea is discussed to be a stronger trigger of the diving response than temperature (Foster & Sheel, 2005). The effect of breathing frequency might, therefore, have overshadowed the effect of water temperature.

Because of the necessary activation of the body, movement is usually associated with a decrease in RMSSD (Laborde et al., 2018; Stanley et al., 2013). Here, however, it did not influence RMSSD during exposure compared to individuals being still ($Q_M = 0.24$, df = 1, p = .630). However, as only two (Chouchou et al., 2009; Vicente-Rodríguez et al., 2020) of the included studies measured RMSSD in moving participants, these results require further investigation.

The effects of breath-holding have been discussed as essential to experiencing the full diving response (Foster & Sheel, 2005). In the current review, the only study included in the breath-holding category had a small to moderate effect (g = 0.36), and thus, does not seem to align with this point. Yet, it is important to consider that the RMSSD response to breath-holding is made of two distinct phases (Costalat et al., 2015; Lemaître et al., 2008). Over the first half of the apnea (normoxic condition), the RMSDD is relatively stable (Costalat et al., 2015; Lemaître et al., 2008). But, over the second phase of the apnea

(hypoxic condition), the RMSSD drastically increases (Costalat et al., 2015; Lemaître et al., 2008). In the current analysis, the RMSSD was averaged over the entire apnea, and thus it is very likely that the effects of the normoxic and hypoxic conditions were canceled out. More research on breath-holding and RMSSD as well as the influence of various breathing frequencies during water immersion on RMSSD is warranted. Future studies should consider observing participants' breathing patterns during the resting measurements before, after, and, in cases other than breath-hold diving, during immersion. This might shed light on the mechanisms influencing the diving response and explain the findings of the current moderator analysis (Grossman et al., 2004; Grossman & Kollai, 1993; Ritz & Dahme, 2006).

Regarding the immersion type, no difference was found between face immersion and total body immersion. This suggests that face immersion might be as effective as total body immersion in increasing RMSSD; however, more studies using face immersion are required to consider the effect of this moderator properly. Finally, a significantly larger effect size was found for both total body immersion (k = 9, g = 0.69, 95% CI 0.43 to 0.96) compared to forehead cooling (k = 2, g = 0.10, 95% CI –0.46 to 0.66). These results suggest that forehead cooling is a less efficient trigger of the diving response from a cardiac vagal activity perspective. Nevertheless, due to the small number of studies, further investigation is required to confirm that face immersion is a more effective trigger than forehead cooling.

4.1 | Limitations

Despite the findings of the present systematic review and meta-analysis about the effects of the diving response on RMSSD, several important limitations exist. First, the numbers of studies and of independent effect sizes were relatively low (pre- vs. during exposure meta-analysis: k = 14; pre- vs. post-exposure meta-analysis: k = 7). Second, the included studies varied substantially regarding triggers used, duration of exposure to the trigger, participant's diving experience, and depth of the dive. Third, sample sizes were rather small throughout most of the included studies (n < 30). Thus, the statistical power and the implications of the results in general and the moderator analysis specifically are limited (e.g., only two of the included studies investigated the diving response by face immersion). Fourth, multiple moderator categories' distributions were asymmetrical, with several being largely underrepresented, limiting our results' extent.

Additional limitations might arise from the fact that the Cochrane Risk-of-Bias tool is not specialized in HRV measurements. Different measurement tools and frequencies, as well as different measurement periods were used in the various studies, which might affect the quality of the included studies.

4.2 | Research perspectives

The research about the effect of the diving response on cardiac vagal activity in humans appears to still be in its early stages in general. While the theoretical model of Foster and Sheel (2005) explaining the cardiorespiratory mechanisms of the diving response provides a solid foundation regarding the mechanisms of the diving response, several inconsistencies need to be addressed in future research. Firstly, the assumption that the bradycardia observed in the diving response solely results from an increased cardiac vagal activity is challenged by the results of one of the study included in this systematic review (Costalat et al., 2015), as well as by the results of other studies not included (Gallo Jr. et al., 1988; Kiviniemi et al., 2012; Lemaître et al., 2008). In these studies, cardiac vagal activity remained constant for the first half of the maximal breath-hold dive and increased exponentially during the second half, while the heart rate decreased immediately, and showed an additional reduction during the second half. Thus, increased parasympathetic activity might only cause further bradycardia in the second half of a breath-hold dive, while the main reason for the strong bradycardia observed during the first half of the breathhold dive might be decreased cardiac sympathetic activity, or another mechanism. For example, mechanical influences on heart rate as part of the diving response have also been suggested (Shattock & Tipton, 2012); however, the precise nature of these influences, under which conditions they occur, and their particular effects have yet to be investigated.

Understanding these mechanisms is important both from an applied, as well as from a theoretical perspective (Foster & Sheel, 2005; Shattock & Tipton, 2012). According to the neurovisceral integration model, cardiac vagal activity is related to emotion regulation and cognitive performance (Smith et al., 2017; Thayer et al., 2009; Thayer & Lane, 2000). Therefore, if an increased cardiac vagal activity is the causal link between (breath-hold) face immersion and the observed bradycardia, a bowl of cold water might be an effective intervention, e.g., before job interviews and certain athletic tasks (penalty, free throw, playing darts, etc.). On the other hand, if a reduced cardiac sympathetic activity is responsible for the bradycardia, or perhaps a different explanation altogether, the possible applications might be different. As face immersion is already being investigated as a recovery strategy (Al Haddad et al., 2010) and in psychotherapy (Kyriakoulis

et al., 2021), understanding exactly how it works and which triggers offer the best compromise (strong, significant effects, and cheap, easy to implement), is important to improve such interventions.

Therefore, future research should combine cardiac vagal activity measurements with other markers, such as the pre-ejection period measured with impedance cardiog-raphy to index cardiac sympathetic activity (Forouzanfar et al., 2018; Sherwood et al., 1990). Furthermore, when investigating the diving response in a systematic and controlled manner, example, for 30 s per condition (Kinoshita et al., 2006), measuring the maximal breath-hold time is essential to put the fixed conditions in perspective. While RMSSD might be increased in someone who can breath-hold dive for 35 s, there might be no significant changes in someone who can breath-hold dive for several minutes. Without considering the maximal breath-hold time, the misleading conclusion might be that a certain trigger is ineffective when the exposure was too short.

Secondly, according to the theoretical model of (Foster & Sheel, 2005), breath-holding is essential to experience the full effect of the diving response, and cold water causes a stronger response than warm (>15°C) water. Potentially due to the few studies included here and the large heterogeneity between diving response conditions, the results of the current moderator analyses do not support this claim. Further investigation is needed to verify these results. Yet, one possible explanation for these findings is the strong effect of slow-paced breathing on cardiac vagal activity (Laborde et al., 2022; Sevoz-Couche & Laborde, 2022) that might have overshadowed any other effects of water temperature, movement, or type of immersion. Future research should observe breathing alongside cardiac vagal and sympathetic activity to investigate the role of breathing frequency and breath-holding.

We encourage future research to focus on face immersion, given that we found the effects to be comparable to full-body immersion. This is in line with studies that found no changes in heart rate due to head-out water immersion (Christie et al., 1990; Park et al., 1999). Moreover, its implementation appears particularly adequate in a large range of practical applications, such as sport (Al Haddad et al., 2010; Mosley & Laborde, 2022; Schnell et al., 2018), psychotherapy (Kyriakoulis et al., 2021), and medicine (Takahashi et al., 2020; Winter et al., 2018), in comparison to full-body immersion. Regarding the effectiveness of such interventions for a given individual, it is important to note that the effects of the diving response on heart rate (and thus, potentially, cardiac vagal activity) vary among humans (Caspers et al., 2011; Lindholm & Lundgren, 2009). Conceivable causes for this variation might be found in the potential influences of inter-individual differences in sensitivity of chemoreceptor and baroreceptor reflexes (Berntson et al., 1997; Houtveen et al., 2002), as well as in respiratory behavior (Grossman et al., 2004; Grossman & Kollai, 1993; Ritz & Dahme, 2006).

Additionally, the effects of repeated face immersion on cardiac vagal activity should be investigated, given an increase in the maximal apneic duration of 54% over five maximal apneas with face immersion have been found in healthy individuals (Schagatay et al., 2001). Simultaneous investigation of both cardiac parasympathetic and sympathetic activity, as well as other factors such as blood pressure might result in greater insight into the responsible mechanisms. Finally, it has never been tested whether a long-term intervention, example, 30 days, might lead to effects on RMSSD that outlast the exposure.

5 | CONCLUSION

To summarize, the diving response has been found to be moderately effective in increasing RMSSD during exposure. However, no effect has been found when comparing pre- to post-exposure conditions. Immersion was found to be the only significant moderator of the results. Yet, some moderator categories were largely underrepresented and should be further investigated before making definitive conclusions.

To conclude, research about the diving response holds many promises for both the research and applied psychophysiology fields. The current systematic meta-analysis may raise more questions than it answered, but we hope to stimulate the interest of researchers and practitioners toward a better understanding of this simple yet potentially effective technique to voluntarily influence the autonomic nervous system.

AUTHOR CONTRIBUTIONS

Stefan Peter Ackermann: Conceptualization; data curation; formal analysis; investigation; methodology; writing – original draft; writing – review and editing. Markus Raab: Supervision; writing – review and editing. Serena Backschat: Conceptualization; writing – original draft. David John Charles Smith: Data curation; formal analysis; writing – review and editing. Florian Javelle: Formal analysis; methodology; writing – review and editing. Sylvain Laborde: Conceptualization; methodology; project administration; supervision; writing – review and editing.

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CONFLICT OF INTEREST

None of the authors reports any kind of competing interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in OSF at DOI 10.17605/OSF.IO/9W2QY or https://osf.io/9w2qy/?view_only=6146276c0a1343469a6d d5d65b7bfd6c.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1

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